Invaders, weeds and the risk from genetically manipulated organisms

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Abstract. Invaders, weeds and colonizers comprise different but overlapping sets of species. The probability of successful invasion is low. The 10:10 rule states that 10% of introduced species (those with feral individuals) become established, 10% of established species (those with self-sustaining populations) become pests. The rule gives an adequate fit to British plant data. The rule predicts that invaders will be rarer than natives. This is shown for British Anatidae. There is a continuous spectrum of perceived weediness. Although this spectrum is significantly related to Baker characters, neither those characters or any others can usefully predict which species will be weeds over a wide range of species. Characters tuned to sets of closely related species show more promise. A study of British *Impatiens* shows that the characters responsible for critical ecological behaviour are still obscure. Small genetic changes can cause large ecological changes. GMOs will have characters entirely new to that species' evolutionary history. While most will have little ecological effect, a few may be ecologically and economically damaging. A sensible programme of field trials and monitoring is justified to minimize the risk.
Key words. Invaders; weeds; Baker characters; *Impatiens*; GMOs.

Introduction

The work reported here derives from two activities that have occupied much of my time in the last nine years. These are the SCOPE programme on the ecology of biological invasions[6], and my work on the British committees regulating the release of genetically manipulated organisms (GMOs)[24,26]. Although I have had to be concerned with the risks from animal and microbe GMOs[9,25], in this paper I will only consider plants. The majority of releases of GMOs so far, and for some years to come have been[28] and will be of agricultural plants. It has been argued that these are not really like invaders, being merely varietal improvements. If that were so, there would not be so much attention paid to GMOs by national and international committees. In the discussion, I will return to the question of how far GMO crops are mere varieties, and how far they may be expected to produce novel risks.

The main risk from any crop plant, or any horticultural or forestry plant, is that it will become a pest, that is a weed. It may also be toxic in some situations; I will not consider that type of risk here. Many crops have given rise to pest populations[22,24,26,28], and pests are pests partly because they invade. Weeds of agricultural habitats are characteristically plants of disturbed ground of the type known as colonizers, plants that habitually establish themselves in transient habitats. Although some people restrict the term weed to agricultural pests[1,2], pest plants occur in many habitats, and I will refer to all pest plants as weeds. Invaders are plants that come from some distant ecosystem.

So invaders, weeds and colonizers are distinct types of plants. This is shown in figure 1, which gives counts of the number of species of British angiosperms in different categories. As will be shown below, different scientists differ on which plants are weeds, and similarly, they will differ on which are colonizers. Floras show that the native or invasive status of British plants is in doubt for between 5 and 10% of the flora[5,20]. So while all the numbers in figure 1 are fuzzy, the point that plants may be invaders, weeds or colonizers, or any combination of these, is indisputable. Note that 696 species, 46% of the total, were classed as none of these. In order to look at the risks from GMOs, I will look first at the properties of invaders, then the characters of weeds. The genus *Impatiens* has species in Britain that are native, that are invaders and that are pests, and a detailed study of their biology shows some of the difficulties in assessing the risks of GMOs, the topic I will finish with.

Relevant properties of invaders

There are probably no properties shared by all invaders, but there are some statistical regularities that can help to understand why some invasions succeed while most fail. For instance, climatic matching and abundance in the source ecosystem both improve the chance of an invader succeeding[12], as does a sufficient inoculum and repeated introductions[23]. But first it is necessary to have a clear idea of how frequently invaders do succeed, and how their populations compare with native species.

In 1986 I put forward the 10:10 rule[10,27] that, for Britain, over all groups that had been studied, roughly 10% of invaders establish, become fully naturalized, and again roughly 10% of those become pests. That is, only something of the order of 1% of British invaders become pests. In the same year, Groves[8] found that about 2.5%, or less, of plant species introduced into Australia

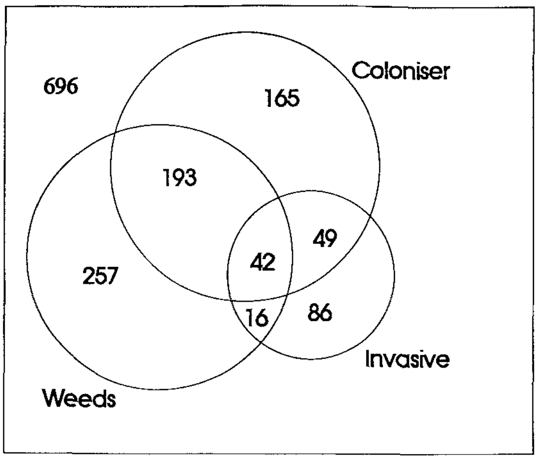

Figure 1. Numbers of British angiosperms in different categories. The figure outside the circles is 'None of these'. The counts are derived from a standard flora[15].

had become pests. These figures are very similar[22], though it is possible that the probability of becoming a pest is greater in Australia. If true, that may reflect Australia's greater biogeographic distinctness. Certainly, much modified isolated places, such as Hawaii, are more susceptible to invasion; over 50% of bird species introduced there have established[19]. There may well be real differences in the probability of invasion success between groups and between places. Before that is studied, let me clarify how well the 10:10 rule applies to British plants.

The table shows the result of discussions between Dr M. J. Crawley of Imperial College and my group. We differ mildly over the status of some species, no doubt reflecting our different experiences in the field and our different view of the status of some populations. But the most striking feature of the table is the support the figures give for the 10:10 rule as a rule of thumb, as a general approximation. There was some misunderstanding of what I had meant by introduced, established and pest in 1986. Clarifying that lead to an interesting new generalization, which I call 'the Crawley ten'.

Introduced means having feral individuals. Established means having an apparently self-sustaining population under current conditions. Pest is a subjective category, subject to different interpretations[10]. In the table 'severe pests' means widespread species subject to much control effort, while 'all pests' refers to those species described as pests in the published literature[27]. It could be thought that introduced meant brought into the country and planted, including all those grown in botanic and other gardens. Dr Crawley's count of the latter shows that, again roughly, 10% of those imported become introduced in the sense of resulting in feral individuals. This is 'the Crawley ten'.

The 10:10 rule is not exact. A variation of times two is perhaps as exact as one could expect for a standard ecological rule, making 'roughly 10%' mean 'between 5 and 20%'. As the rule uses powers of ten, a broader interpretation using root ten would also be reasonable. That would make roughly 10% mean between 3.2 and 32%. It can be seen in the table that, despite a considerable difference about how many species are established, all the ratios fall within the broad definition, all but one within the standard one.

The 10:10 rule is a useful rough guide, and places the regulation of GMOs in context. Even without trials and

Categories of non-native British angiosperms

	MJC	AHF/MHW
Pests		
Severe pests	11	14
All pests	-	39
Established, not pests (= successful invaders)		
Widely naturalized	56	-
Fully naturalized	-	196
Subtotal: established including pests	67	210
Percentage pests	16.4%	6.7%
Introduced, not established (= unsuccessful invaders)		
Locally naturalized	498	348
Garden outcasts	223	216
Casuals	898	868
Subtotal: all introductions	1686	1642
Percentage established	4.0%	12.8%
Severe pests as a % of all introduced	0.65%	0.85%
All pests as a % of all introduced	-	2.38%
Other imports	10821	
All imports	12507	
All introduced as a % of all imports	13.5%	

MJC: from lists kindly provided by Dr Crawley from his data base.
AHF/MHW: the York view of the status of plants in Dr Crawley's lists.

monitoring, only roughly 1% of introductions become pests. A regulated system should be able to be an order of magnitude better[22], so that only one in a thousand causes trouble. Conversely, a small number of innocuous trials is not evidence of over-regulation.

One prediction, from the fact that most invading species fail to establish, is that those that do will have, on average, lower population densities than native species (see fig. 2). There are little data to test this prediction. Almost the only group, in Britain, in which there are good comprehensive estimates of population size of all species is birds[13]. Even there, comparisons are difficult because of size and food chain effects. Small passerines are commoner than large predators. But within the wildfowl or Anatidae, that is ducks, swans and geese, there is much homogeneity and a surprising number of species that have invaded spontaneously since 1800, as well as several that have been introduced deliberately.

The data are shown in figure 2, on a logarithmic scale. There are ten native species, six invasive and nine have been introduced deliberately or escaped to establish feral populations. For clarity, the data have been shown as box and whisker diagrams. The line in the center of the box is the median. The two ends of the box are the quartiles, while the ends of the whiskers show the extreme values. It can readily be seen that each of the three distributions is approximately log-normal. Using t-tests there is, rather obviously, no significant difference between the invaders and the introduced. There is a significant difference between the natives and the introduced. There is a significant difference between the natives and the other two groups combined ($p = 0.015$), and very nearly, despite the small numbers, between the natives and the others separately ($p = 0.063$, $p = 0.057$). So, for these birds at least, the natives are definitely more abundant than invasive and feral species. Both the 10:10 rule and this preliminary result on population size indicate that most invaders will be benign. But it is well known that some are not. Is it possible to predict, from their characters, which invaders will become pests? One way to examine this is to see if weeds, both natives and invaders, have distinctive constellations of characters.

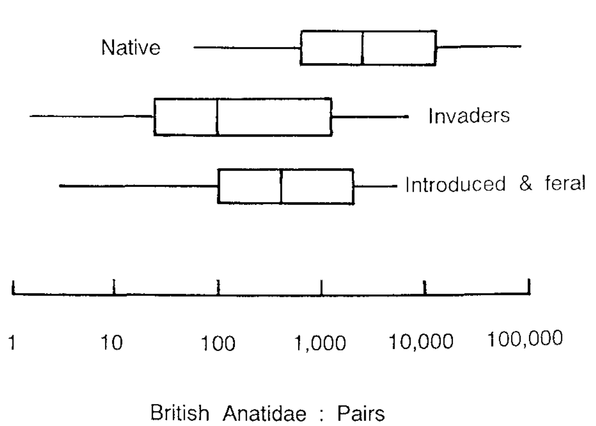

Figure 2. The abundance of British wildfowl (Anseriformes, Anatidae). The data are the number of breeding pairs, from the latest estimates[13].

What is a weed?

It might be thought that there was little disagreement about which species are weeds and which are not. There are, after all, many guides to weeds and their management; floras often describe some species as weeds. However, a plant may be benign in one place and yet a serious pest in another. Sometimes this a question of geography, sometimes of habitat. Early in this project it became apparent that there was much disagreement about what is a weed. So we circulated widely, in Britain, a list of 49 reasonably common and well-known angiosperm annuals and asked for opinions on which were weedy and which were not[17]. We also asked respondents to classify themselves. The 65 people replying consisted of 18 agriculturists, 17 conservationists, 46 ecologists, 10 gardeners and 33 taxonomists. Obviously, several put themselves in more than one category.

The results by species are shown in figure 3. There is an almost continuous variation in perceived weediness across the 49 species. We have published the species names with their scores[17,18]. A definite weed was scored as +2, a definite non-weed as −2; +1, 0 and −1 were used for the, relatively rare, less certain replies. Not a single species scored all +2s or −2s, the range being from −1.98 to +1.85.

A multivariate analysis showed that the scores in figure 3 accounted for almost half the variation in the replies. The other major variable, about a quarter of the remaining variation, was the mean score of the scientist. Agriculturists saw many species as weedy, conservationists rather few. Taxonomists were intermediate, with ecologists and gardeners tending to the agricultural view[17].

For analyses, we have either used the individual scores of the species, or classified them as shown in figure 3, saying that those with scores outside +1 or −1 are weeds or non-weeds and calling the rest intermediate. First and foremost we wanted to know if characters could be found, singly or in combination, that would predict weediness.

Baker and other characters

One set of characters that have been much quoted are those given by the distinguished weed scientist H. G. Baker as those of the 'Ideal weed'. Originally fourteen characters[1], these were condensed to twelve[2]. They were, probably deliberately, given in rather vague terms, and this leads to disputes about scoring[7]. We have attempted to find objectively scorable characters[17,18] that match the Baker characters. Two of the Baker twelve apply only to perennials, and we found no way of

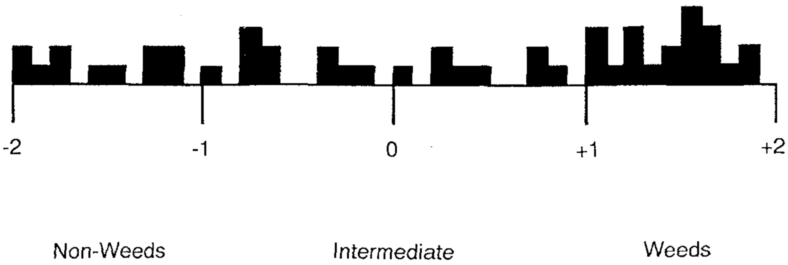

Figure 3. The average scores given to each of 49 British annual plants by 65 scientists. +2 means a weed, −2 a non-weed. Not one species was scored identically by all scientists[17].

scoring objectively one other. So, for annuals, we dealt with nine characters.

Our conclusions on Baker characters can all be derived from figure 4. There is a relationship between his characters and weediness. Given his eminence as a weed scientist, it would be surprising if there were not. But the characters have very little predictive power. Serious weeds can have rather few Baker characters, plants with many Baker characters may be scarcely weedy. The plants that are most clearly, and seriously, weedy in our set of 49 have, as can be seen in figure 3, variously only 3, 4 or 5 Baker characters out of 9. The plants with 6 and 7 Baker characters are *Rorippa palustris* (*R. islandica* of the older British floras[14,20]) and *Chenopodium rubrum* respectively. One is a non-weed, the other an intermediate species on our grouping.

Regression analyses make the points quantitatively. The linear regression of weed score against Baker characters is significant ($p = 0.013$), but has weak predictive power ($r^2 = 0.125$). On this result, adding three Baker characters increases the weed score by one. But the quadratic regression is more significant ($p = 0.004$) and a better predictor ($R^2 = 0.214$). The sum of squares divide almost equally across the (orthogonal) linear and quadratic terms. This curve line predicts that the most weedy species will have only 4.7 Baker characters, slightly more than half the possible.

Baker characters are not predictive. It is not necessary to add Baker characters to make a crop into a weed.

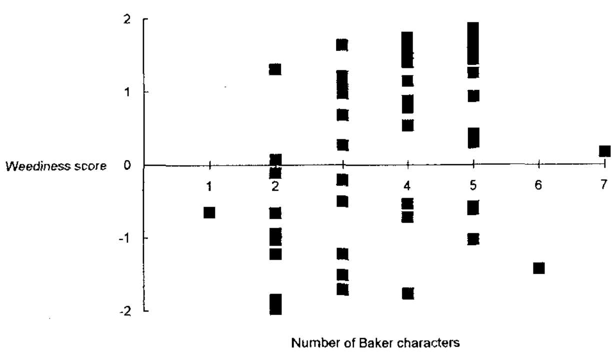

Figure 4. The relationship between weediness, as scored by 65 scientists, to the Baker characters, scored by the York criteria[17,18], for 49 species of British annual plants.

For one thing, many crops, including those commonly used to make GMOs in Britain[22,24,26], are already also weeds. Adding or subtracting Baker characters leads to no useful prediction about weediness.

Are there other characters that are more useful? We have looked at both annuals[17,18] and perennials[15]. We have examined single characters and sets, using a variety of simple and sophisticated techniques. We have used every character that we could score over a reasonable set of species, trying especially to score characters directly related to the life table, such as seed production. It is easy to find multivariate discriminant functions that separate sets of species. It is not possible to find discriminant functions that have worthwhile predictive power. To that extent, all the characters we have examined behave as Baker characters do.

It is possible to find weak relationships with single characters. Taking the three sets labelled on figure 3, normally weeds cease flowering in September to October, intermediate species in August to September, non-weeds in June to August[18]. Weeds are more likely to survive gut dispersal than non-weeds. Weeds normally germinate in the spring more than non-weeds.

In perennials[15], examining groups of species in different genera, there were relationships of weediness to distribution, altitudinal range, seed weight, root depth, chromosome number and so on. None of the characters behave consistently across genera. If weediness is to be predicted at all, it will only be done by comparing characters in closely related species. That is one reason why we looked closely at *Impatiens*.

Comparative studies on Impatiens

There are many examples of genera in which some species are pests, some are not. More generally, closely related species differ in geographical range and ecological success. Ecological success can be measured in many ways, such as habitat range, population density and so on. In Britain, species of *Impatiens* (Balsaminaceae) show a range of ecological behaviour, with relatively small morphological differences. All are annuals.

Only one species is native. *I. noli-tangere* is now a fairly rare plant in Britain, with most records around the Lake District of north-west England, though it was formerly more widespread[14]. Three species are established invaders, *I. capensis* from North America, *I. parviflora* and *I. glandulifera* from central Asia and the Himalaya. *I. balfourii*, also from the Himalaya, is a garden plant scarcely if ever found feral[16,20]. There are good historical records of the rate of spread of the invaders, the characters of all are reasonably well known, and experiments can be done both in cultivation and the wild.

Only *I. glandulifera* can be considered a pest. It grows in dense stands along rivers and canals, and also in some nature reserves and in wet woodlands. It is the tallest British annual and suppresses all other species beneath it. Compared to the other species, it germinates earlier, grows faster and produces more seed. In nature reserves it is very difficult and expensive to control[3,16].

I. glandulifera has only two Baker characters[17,18]. In our survey of annual weeds (fig. 3) it scored only −0.32, making it an intermediate species on the non-weedy side. Part of the explanation of its low score is that most people are not concerned about dense stands of an invasive species in disturbed, and sometimes distinctly unattractive, places along canals. Only those who have had to try and control it in woods regard it as a pest. That applies to many woodland owners round York. It was first recorded feral in 1855 and listed as a weed in 1898[16]. But in 1986 Usher[21] found that it was not on official lists as an unwanted alien and said 'it appears to be neutral for conservation management'. This view comes from averaging its behaviour over different habitats.

If pest status is to be predicted, the variation in population behaviour in different habitats, and the perceived value of those habitats, must be considered. But the underlying reasons for the primary cause of *I. glandulifera* being a pest where it is one, its ability to grow well when closely packed, are still not known.

Using vice-county records from England[16], it is possible to compare the rate and extent of spread of the three invasive species. All follow a logistic curve. The biology of the species, which have explosive seed capsules, predicts a spread of around 2 m a year. The records show a minimum spread of 1.4–2.6 km a year. That is a thousand times faster. The maximum rate of spread varies from 13 km for *I. capensis* to 24 km for *I. parviflora* to 38 km for *I. glandulifera*[16]. The importance of human, and possibly animal, spread is clear and clearly different between the species.

I. glandulifera and *I. parviflora* occur in almost all English vice-counties, and are predicted, by the logistic fits, to occur in all 59 of them eventually. The prediction for *I. capensis* is that it will occur in only 37, and indeed it is evidently a south-eastern species in England[14]. This is surprising, as Hulten[11] shows that *I. capensis* is an allospecies (a species that scarcely overlaps geographically) with *I. noli-tangere*. The latter is found across Eurasia from the Atlantic to the Pacific and on through Alaska and western Canada. There it overlaps slightly with the predominantly eastern North American distribution of *I. capensis*.

Although *I. noli-tangere* and *I. capensis* behave differently ecologically in England, their morphologies are very similar. The former is an uncommon, declining, now largely north-western species, the latter an invasive, quite common in places, south-eastern species. There are differences in flower colour (yellow vs orange), angle of the flower spur and strength of blotching on the flower, and small differences on the teeth of the leaf edges[5,20]. I would suggest that the genomic differences must be small. Small genetic differences can lead to important ecological differences.

Conclusion: The risks from GMOs

Both our wide surveys and our detailed studies of *Impatiens* show that pest plants differ from other closely related plants only in a small number of characters. The important differences ecologically are difficult to quantify. The important characters vary from case to case.

The implication for the regulation of the release of GMOs is that minor gene differences can have major effects. This alone justifies proper field trials and monitoring.

How much effort should be put into field trials and monitoring depends on how different the GMO is from its parent line. There is an argument that GMOs are only standard agricultural varieties and not sufficiently novel to justify the extra-expense of regulation. The validity of this argument will vary from case to case. Where GMOs are used to speed up developments that could be done by conventional methods, they may require little, if any, extra scrutiny.

But the reason why the industry is putting so much effort into GMOs, and the reason why regulators and some of the general public are interested in GMOs, is that they offer the possibility of real novelty. Novelty for agricultural processes, novelty as products and novelty as invading species.

Some have thought that anything that could have happened in evolution will have happened. This is deeply mistaken. Evolution has been limited by the availability of variability at the right time and place[4]. GMOs offer the prospect of genuinely novel life forms, whether they be plants with cubical fruit, or nitrogen-fixing cereals. Some of these novelties, and not necessarily those that appear to have novel ecological characters, will become invasive.

The proportion of these novel GMOs that will become invasive or otherwise undesirable[24] is small. But the history of invasions and other environmental disbenefits shows that the costs of those that misbehave is large. This is a familiar situation in insurance, and the same principle applies to the regulation of GMOs. A small recurrent cost is justified by the protection it gives against a large and unpredictable loss.

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