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Ecological long-term effects of cultigens becoming feral and of naturalization of non-native species

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Abstract. Transgenic cultigens may become feral as we know of some non-transgenic cultigens. The article explains two basic ways how cultigens become feral: through hybridization with a closely related wild plant and through revert to the wild-type. A long list of examples of cultigens becoming feral in Central Europe is presented. The process of becoming feral is compared to the naturalization of non-native species ('Exotic Species Model'). Ecological long-term effects of both cultigens becoming feral and non-native species being naturalized are discussed with special regard to the predictability of such events. The ecological aspects discussed in the article are as significant for transgenic cultigens as for non-transgenic cultigens.

Key words. Cultigens; hybridization; becoming feral; non-native species; naturalization; transgenic cultigens; deliberate release; ecological long-term effects.

Introduction

Transgenic cultigens will be deliberately released into agricultural ecosystems which are characterized by a high degree of evolutionary dynamics. The same dynamics will also affect the genes added artificially. To assess – from an ecological point of view – the effects of a deliberate release of transgenic cultigens, two questions, which – however – can not be addressed in this article, are of primary importance: First, does the transgenic organism remain on the intended agricultural plots because it has no or only rudimentary dispersal abilities? Second, is it possible to erase its populations from such areas at any (given) time? Such questions assume a constancy of transgenic organisms at the level of population genetics.

This article deals with the possible ecological effects of a deliberate release on the biologically realistic assumption that the gene pool of such organisms will be subject to considerable evolutionary dynamics. We will discuss two specific aspects: First, mutation and selection, which in agricultural ecosystems are highly determined by farmers, will affect transgenic cultigens in the same way as any other organism. Therefore, the transgenic cultigen will change both genotypically and phenotypically. For instance, new characteristics that are typical of weeds may appear. The transgenic cultigen evolves into a transgenic weed race that might cause tremendous difficulties in control. Second, the cross-fertilization of transgenic cultigens with closely related taxa (other cultigens, weeds, wild plants) may facilitate the direct spread of parts of their genome. Due to the evolutionary dynamics we face a completely new dimension in assessing the risks of transgenic organisms: Even if it were possible to recall the transgenic organism, this does not hold true for some of its genes and, for precisely the same reason, it does not hold true for the artificially added genes either. Vast and virtually not foreseeable ecological effects may appear after a variable time-lag.

If we consider the enormous speed of developments in genetic engineering, it becomes obvious that we are in great need of knowledge that will help us assess the potential ecological risks of the deliberate release of transgenic cultigens. By 1988 22 cultigens, some of them with world-wide significance, had been completely regenerated as transgenic lines[17]. In this list we find among others: alfalfa, garden carrot, cultivated flax, horse-raddish, maize, potato, rape, rye, sunflower, and tomato.

In the process of becoming feral, weeds may evolve that can be found on highly disturbed sites such as farm land, gardens, roads, and fallow land. These weeds may still show quite an array of the characteristics of domestication. However, they may also invade semi-natural and more or less natural vegetation.

We now address the following three questions:

- What is the frequency or the probability of cultigens becoming feral?
- In which cases should we expect a gene flow from a population of cultigens to a population of wild plants?
- What are the ecological effects on plant communities in cultivated areas or in neighbouring sites caused by cultigens becoming feral?

Differences between collected plants, facultative cultigens and obligate cultigens

Willerding[68, 69] classifies plants used by people into three categories: collected plants (wild plants of which people collect specific parts such as leaves, rhizomes or fruits), facultative cultigens (wild plants that are grown and used by people), and obligate cultigens (plants that have acquired genetically fixed characteristics of domestication due to human breeding).

Collected plants are plants that people collect and use where they find them in the wild (e.g. hazel-nut). Facultative cultigens do not differ genetically from the original wild taxa. They may be cultivated within their natural area or be transferred by people into regions where they did not exist originally. Within their original area, they can escape from cultivation at any time and without any restriction. If a facultative cultigen manages to escape from cultivated land which lies outside its natural but within its potential area, we have the case of a naturalization of this species into a new area and not of a species becoming feral in the proper sense of the term. However, such cases of naturalization of non-native plant species may be regarded as analogous to genetically modified cultigens becoming feral, particularly since we define the result of a naturalization process and of the process of becoming feral identically.

Obligate cultigens have genetically fixed characteristics of domestication. Since, as a rule, they have lost their competitive capacity and their natural ability to spread (to various degrees, depending upon the duration and level of domestication), they depend on people who sow or plant seedlings and cultivate the plants. This applies both within the original area of their wild ancestors and for every region into which people have transported them. If the cultivation disappears, the populations of such obligate cultigens tend to die quickly. Nevertheless, we know of many examples of current and past cultigens which formed spontaneously spreading populations on fields as well as in semi-natural and even natural plant communities[22,23]. The spontaneous escape from cultivation basically happens in two different ways[67]: First, through hybridization of a cultivated plant with a closely related wild plant (often we are dealing with wild and cultivated races of one species or with two sister species) off-spring form that may successfully reproduce in a vegetative or sexual way. Second, the obligate cultigen looses some of its domestication traits through the revert to the wild-type and possibly develops qualities typically found in weeds. If we know the number of genes coding for weedy qualities, we can predict the probability of a spontaneous acquisition of these qualities.

Definition of cultigens becoming feral

Following the definition of naturalization given by Thellung (see ref. 61, p. 638) we can define the term "cultigens becoming feral" as follows: A species which is equipped with traits of domestication is considered to have gone wild if "it shows all characteristics of a wild native species such as growing and propagating by natural means of reproduction (seeds, tubers, bulbs, etc.) without requiring direct assistance of man, and if it exists more or less frequently and regularly on suitable sites, and remains there for a number of years (even in extraordinary climatic conditions)".

Hybridization and revert to the wild-type

The cross-fertilization of two taxa which are not completely isolated in terms of reproduction, but show clear differences in genotype and phenotype, is called hybridization. Almost all current cultigens and at least a third of all cormophytes evolved in the context of hybridization processes – most often as allopolyploidic taxa.

Plants that originated from hybridization of two individuals of the parental populations A and B are usually capable of crossing with other individuals of one of the two parental populations. If this procedure of back-crossing is repeated several times with plants of the parental population A, at least a small proportion of the genome of the plant of the parental population B will gradually be incorporated into the gene pool of the parental population A. This process is called introgression or introgressive hybridization. A description of the basic genetical and ecological principles of introgression is given by Anderson[2]. Further specifications on introgressive hybridization can be found in Briggs and Walters[6] and Heiser[24].

In many cases it is extremely difficult to decide whether the process of becoming feral was initiated by hybridization or whether a mutation led to a revert to the wild-type[12,24,54]. This is especially true in those cases in which we find introgressive hybridization with back-crossings over several generations and the population of hybrids differs only slightly from the infiltrated parental population.

Until now, we do not have any definite data on the frequency of hybridization processes occurring in nature. But the number of known hybrids within the flora of a certain region may serve as a very rough estimate. The great difficulty we have in defining and recognizing hybrids is responsible for this situation[28,54]. Furthermore, we have to take into consideration that the degree of floristic exploration of particular regions varies greatly. About 2000 wild vascular plants of the British flora[8] form 1439 naturally evolved interspecific and intergeneric hybrids according to the compilation by Stace[54]. 975 of these hybrids are to be found on the British Isles. 464, however, could only be certified from outside of the British Isles. Table 1 gives a synopsis of those 14 families of the British flora which show the highest number of natural hybrids. Among them we also find numerous families from which many cultivated plants and weeds have originated.

In order to get an empirically sound estimate of the probability of a successful hybridization between two

Table 1. The 14 families of the British flora which show the highest number of natural hybrids (from Stace[54]).

Family	Number of natural hybrids	Number of species	Percentage of natural hybrids
Cyperaceae	140	103	136
Asteraceae	126	153	82
Poaceae	126	156	81
Salicaceae	125	24	521
Orchidaceae	104	50	208
Scrophulariaceae	103	85	121
Rosaceae	93	120	78
Onagraceae	59	20	295
Polygonaceae	58	44	132
Liliaceae	56	32	175
Chenopodiaceae	39	30	130
Brassicaceae	39	91	43
Lamiaceae	39	65	60
Caryophyllaceae	34	80	43

taxa, we need to investigate for every single case a whole array of parameters that influence the probability of cross-pollination as well as the probability of subsequent fertilization and development of viable off-spring[12], see also Crawley[11]:

- extent of pollen production,
- degree of inter- and intraspecific pollination in both populations,
- ways and means of pollen transport,
- amount of transported pollen,
- properties of the insects transmitting the pollen (in case of entomogamy),
- spatial distance among individuals of the two populations,
- phenological differences among individuals of the two populations,
- density of individuals of the two populations,
- compatibility of the two genomes.

Only the last of the parameters listed is of genetic nature and it may be determined relatively simply through artificial pollination experiments conducted in glasshouses. All other parameters are of an ecological nature; they can be quantitatively studied only under natural conditions found in the countryside with a comparatively high expenditure. And yet, only the quantitative estimation of all of these parameters will produce a scientifically sound estimate on the order of magnitude of the probability of a successful hybridization between two plant populations. The probability of such an event must be measured in relation to specific area- and time-scales[12].

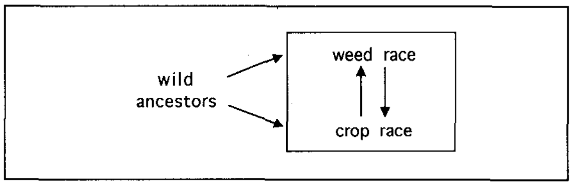
In summary, we can say that processes of natural and artificial hybridization happen relatively often between different cultigens and between cultigens and closely related wild plants[12,24]. It is of great importance to include a time-scale: for the present and the near future, the probability of a spontaneous hybridization event can be predicted to be small or even very small. If we think of the time-scale of evolution, however, we see a vast potentiality of hybridization for the majority of our current cultigens.

Crop-weed complexes

The genetic and evolutionary relations between cultigens (or less precisely: crops) and weeds are very tight and as old as the earliest forms of agriculture[23]. Cultigens as well as weeds are "the result of rather similar evolutionary processes"[20]. Almost all of today's most common cultivated plants form weed races with which they cross where there is an overlapping distribution[22]. Many cultigens evolved directly from weeds. Rye is a well-known example of such a so-called secondary cultigen[16]. Many former cultivated plants developed into weeds without or with only very slight genetic change after cultivation was abandoned. Cultigens which have been domesticated only to a low degree become feral very easily. They are perfectly suited to the conditions of cultivation and therefore turn into weeds that can scarcely be controlled[20]. These genetic and evolutionary relations are summarized by Harlan[22] in form of a model (fig.).

The model assumes that crop-weed complexes evolved from common wild ancestors and that until now a more or less extended gene-flow between crop and weed races has taken place in both directions. New crop races evolve from weed races and the other way around. If only minor genetic barriers exist (e.g. equal number of chromosomes), hybrid swarms regularly appear, and even though the swarms soon disappear, they can cause an introgression of genes in both directions. Even if the genetic barriers are higher (e.g. different numbers of chromosomes), we may still find a gene flow, although this happens much less frequently and mostly just in one direction.

Crop-weed complexes are evolutionary entities that show enormous potential to produce new plant taxa. This is particularly so if, on one hand, two populations – one of a crop race and one of a weed race – are isolated to a large extent in terms of reproduction (therefore they can develop sympatrically and retain their specific characters), and if, on the other hand, the genetic barriers occasionally open and allow the exchange of genes over a number of generations. The result of such alternations of reproductive isolation and recombination is a considerable increase of variability, heterozygosity, and heterosis in both participating populations. Crop-weed complexes form the basis of the multitude of highly productive cultigens that people use nowadays[22]. In Wet and Harlan[67]



Crop-weed complexes according to Harlan[22].

we find an extensive discussion on the parallel evolution of crop and weed races on segetal and ruderal sites, with abundant examples from America.

Pickersgill and Heiser[44] stress that from the genetic point of view the majority of our current cultigens have not moved far from their wild ancestors, even though the phenotypical differences may appear very pronounced at times.

Examples of cultigens becoming feral in Central Europe

The cases listed below are examples of a successful return to the wild of facultative and obligate cultigens in Central Europe (paragraph 1–4). As a classification principle, we use the biologically important fact of whether a potential hybridization partner is available among the Central European wild plants or not (paragraph 1–2). Because in many cases several hypotheses exist among botanists on the precise origin of the plant taxa that has become wild, it is not always possible to classify the cases in an unambiguous way. Some cultigens, which play a very important economic role in Central European agriculture, and which, until now, are only known to become feral in other places of the world, are listed separately (paragraph 3). Extensive specifications on all of the species listed in paragraph 1–3 can be found in an expertise for that we were commissioned by the Wissenschaftszentrum Berlin. The expertise is part of a trial to assess the technology risks and chances which are to be expected in case of releasing cultigens with genetically added herbicide-resistance. Further examples are presented in paragraph 4. Deviating from the chosen subdivision, the listed facultative and obligate cultigens could also be classified according to the way people use them: as agricultural crops, as fruit-trees and fruit-shrubs, as ornamental plants, and as forestry plants.

1 Cultigens becoming feral with closely related Central European wild plants as potential hybridization partners

Cultigens	Wild relatives
Beta vulgaris subsp. *rapacea* *Beta vulgaris* subsp. *vulgaris*	*Beta vulgaris* subsp. *maritima*
Brassica napus *Brassica rapa* *Brassica oleracea* *Brassica juncea*	*Brassica nigra* *Raphanus raphanistrum* *Sinapis arvensis* *Hirschfeldia incana*
Setaria italica subsp. *italica*	*Setaria italica* subsp. *viridis*
Daucus carota subsp. *sativus*	*Daucus carota* subsp. *carota*
Medicago sativa	*Medicago falcata*

2 Cultigens becoming feral without closely related Central European wild plants as potential hybridization partners

Avena sativa subsp. *sativa*
Panicum miliaceum subsp. *miliaceum*
Cannabis sativa
Malus domestica
Pyrus communis
Helianthus tuberosus
Reynoutria japonica
Galanthus nivalis
Prunus serotina

3 Cultigens of great importance in Central European agriculture which are only known to have become feral in other parts of the world

Solanum tuberosum
Hordeum vulgare subsp. *vulgare*
Zea mays

4 Further examples of culitgens becoming feral in Central Europe

Lohmeyer and Sukopp[40] present a list of species which people originally brought to Central Europe for cultivation and which later on successfully became wild. Today they appear as agriophytes outside of cultivated land and have caused changes to various degrees in more or less natural vegetation. 'Agriophytes' are defined as plants which have moved into alien regions exclusively through activities of people, but now form an integral part of the natural vegetation and no longer depend on man[27], quoted according to Zizka[72]. Some examples of this large and heterogeneous group are:

Acorus calamus
Amelanchier lamarckii
Antirrhinum majus
Armoracia rusticana
Asparagus officinalis
Aster lanceolatus
Aster salignus
Brassica nigra
Bryonia dioica
Castanea sativa
Centranthus ruber
Chaerophyllum bulbosum
Cheiranthus cheiri
Chrysanthemum vulgare
Cymbalaria muralis
Digitaria sanguinalis
Echinocystis lobata
Heracleum mantegazzianum
Hesperis matronalis
Impatiens glandulifera
Iris germanica
Iris sambucina
Isatis tinctoria
Juglans regia
Laburnum anagyroides
Lycium barbarum
Mahonia aquifolium
Populus x *canadensis*
Reseda luteola
Robinia pseudacacia
Rosa rugosa
Rudbeckia laciniata
Solidago canadensis
Solidago gigantea
Syringa vulgaris
Tulipa sylvestris
Verbena officinalis
Vinca minor
Viola odorata

Prunus avium (sweet cherry), *Prunus cerrasus* (sour cherry), and *Prunus domestica* (plum) would be further examples of fruit-tree species that can become wild. *Ribes uva-crispa* (gooseberry), *Ribes rubrum* (red currant), *Ribes nigrum* (black currant), *Rubus idaeus* (raspberry), and *Rubus fruticosus* (blackberry) are native Central European species that have been cultivated since the late Middle Ages[51]. Both intentional and unintentional breeding measures produced considerable enlargement and multiplication of the berries, and often self-fertility to a large extent. All of the named species occur nowadays as wild plants in Central Europe and can freely cross-fertilize with the cultivated forms.

Comparison to the naturalization of non-native species

Of all the models we know of, the analogy between the introduction of non-native species and the deliberate release of transgenic organisms into the environment is the most suitable model to assess the potential ecological effects of such a deliberate release: 'Exotic Species Model'[45]. The question concerning the origin of a species – be it from a gene-technology lab, be it from conventional breeding, or be it from another continent as a non-native species – is of no significance regarding the potential ecological risks. The single crucial factor from the ecological point of view is the phenotype of the organism[62].

We would like to stress that the 'Exotic Species Model' is equally valid as a model to assess the ecological risks of the release of new plants which are the result of either gene-technological or conventional breeding methods. As the analogy only applies to the phenotype, such discrimination is beyond the capacity of this model. In purely ecological terms, it is impossible to detect a special risk in the release of transgenic plants that could be assumed to be absent in the case of conventionally bred plants. If we accept the necessity of a risk assessment in the case of the deliberate release of transgenic plants, we should also assess the potentially harmful ecological effects of growing conventionally bred plants. It is interesting to note that many non-native species of the Central European flora were introduced by man originally as cultigens, then they were cultivated over long periods of time, and finally became wild (see listing above in paragraph 4). For those plants we do not need to apply the 'Exotic Species Model' because today they both have the status of 'exotic plants' and also meet the criterion of having become feral. But anyway, they are an unbeatable proof of the ecological validity of the 'Exotic Species Model'.

The inestimable value of the 'Exotic Species Model' resides in the opportunity to use the numerous empirical investigations on the (historical) behaviour of non-native species in a variety of ecosystems of many regions of the world[30,32,34,35,57]. The origin, migration, and dispersal of non-native species (adventive species, xenophytes) has been the subject of scientific investigations since Candolle[7]. In some cases, the history of naturalization of non-native species and the ecological effects have been documented for decades and centuries. Unfortunately, there is a great lack of analysis that compares precisely the ecological behaviour of a species in a region where it is native with its behaviour in a region where it is non-native, counter-examples in Kohler[29], Kowarik[33] for *Robinia pseudacacia* in Sukopp and Sukopp[60] for *Reynoutria japonica*, in Starfinger[55,56] for *Prunus serotina*, in Sachse[49] for *Acer negundo*.

The real strength of the 'Exotic Species Model' consists in the possibility of making general estimates of ecological risks that may result in the long-term from deliberate releases of numerous genetically modified cultigens. On the basis of extensive ecological data going historically far back, the 'Exotic Species Model' offers so far the only methodical approach of raising the level of purely speculative statements in ecological long-term prognosis. If, however, one would like to make statements on the short-term ecological risk of a deliberate release of a single, precisely characterized, genetically modified plant in the context of a so-called 'case by case study', it would make far more sense to compare it first of all with the ecological behaviour of the original plant conventionally bred and cultivated for a long time.

Ecological long-term effects of introduced and naturalized non-native species

Far more than 100 examples of neophytes that have spread under the influence of man have been investigated and are well documented in literature[26], (a neophyte is a plant species that migrated to a region after 1500 A.D. and is now naturalized). With regard to the potential ecological long-term effects of the deliberate release of transgenic cultigens, such investigations are the only empirical foundation available to assess the risk. Since ecological statements only make sense in the light of the evolution of organisms and biocoenoses, it is necessary to consider appropriately long periods if we are to make a prognosis. In this context it is interesting to note the statement of Wet and Harlan[67] that evolutionary processes are considerably accelerated on anthropogenic sites in comparison to natural sites.

The history of the naturalization of some species has been observed for decades and centuries. The necessity to observe such long periods becomes evident if we consider that there might be a time-lag of, in the extreme case, several centuries between the first appearance of a species and the first ecological change caused by it (and recognized by people). Simply because of the dynamics of populations, such large delays may happen before ecological effects become visible.

Table 2. Number of introduced and naturalized ferns and flowering plants in different parts of Europe

	British Isles	Germany	Netherlands
Introduced species	32,000[19]	> 12,000[58]	7,000[66]
Naturalized species	322[71]	385[58]	220[66]
Of these in natural vegetation	?	ca.200[40]	75[66]
Pests	39[71]	?	?

To answer the question of the frequency of naturalization events and their harmful effects we can look at some figures from Great Britain (table 2). Approximately 32,000 species of ferns and flowering plants have been introduced to the British Isles[19]. 322 (1.0%) of these are today naturalized[71], and 39 (0.1% of the introduced species, 12.1% of the naturalized species) have caused undesired changes[71]. According to these figures, the probability of naturalization of a foreign plant species is approximately at 1:100 and the probability of undesired changes in the existing ecosystems is approximately at 1:1000. Simberloff[53] investigated world-wide 854 cases of naturalization of predominantly animal species and discovered that in 71 cases (8.3%) this meant the extinction of a native species. Diamond[14] gives a synopsis of numerous historical examples of the extinction of birds and mammals that people caused through the introduction of non-native species. The extinction of a native species is an easily recognizable negative effect, but it is only one of many harmful consequences we can think of. As a matter of fact, it is very difficult to answer the question what exactly is an undesired effect of the naturalization of non-native species or of the uncontrolled spread of a gene that was artificially implanted in a cultigen. Agriculture and forestry traditionally decided according to exclusively economic criteria[70]. In the context of ecology and nature conservation, however, it is equally important to consider the potentially destructive effects that the dispersal of a genetically modified species becoming feral could have on existing natural and semi-natural plant and animal communities. To assess this we distinguish between a structural and a functional destruction[35,52]:

– The structure of a biocoenosis may be dissolved through the spread of new species which are highly competitive (changes of the composition of species, of the spectrum of life-forms, of the stratification). In extreme cases, native species may be driven out. As a rule, the vegetation undergoes a structural levelling out. The species diversity of the original plant community is replaced by species-poor stands with single dominating new species. Central European examples are reported for *Helianthus tuberosus*[38,39], for *Spartina anglica*[15,18], for *Reynoutria japonica*[60], and for *Prunus serotina*[55,56].

– Changes of the composition of species may impair the fundamental functions of complex ecosystems because the new species do not inevitably adopt the functions of the species driven out. This affects interdependent groups of organisms, such as consumers. In Germany we find numerous species of insects living on native trees and shrubs. On non-native trees and shrubs, however, extremely few species exist because the 'exotics' do not offer the specific food required by the insects[31].

The following reflections on the consequences of the extinction of species resulting from human activities[59] are of course also valid for the potential extinction of species caused by the deliberate release of genetically modified cultigens.

If an animal or a plant species is of economic interest, at least the people who want to make a profit of them usually recognize their ecological requirements. This has been the case in forestry and agriculture for a long time. In some areas of fishing and whaling, the economic and ecological questions connected with the danger of extinction of species are discussed thoroughly. It is here that we sometimes see a far-reaching interdisciplinary cooperation of ecology and economics, e.g. Clark[9]. On the other hand, there are only very few investigations on endangered plant and animal species that are not exploited by man[1,3,21,36,41,42,63]. Yet, these few investigations show that the extinction or preservation of wild species are also of economic importance. Economics must be understood in its original and proper sense as a science that teaches the rational use of limited and valuable resources. Of such a theory we can expect that it will be helpful in providing arguments for species conservation and that it will allow to make a better estimate on the consequences of people's different attitudes towards nature.

Predictability of cultigens becoming feral and of their dispersal

The probability that a genetically modified cultigen runs wild is directly connected with the size and the frequency of deliberate releases. The size of a deliberate release of a transgenic cultigen is a factor that in the literature on the biology of populations and invasions is discussed as the problem of the size of founding populations[4,5,25,50]. The frequency of the deliberate release of a transgenic cultigen can be seen as an analogy to the frequency of the introduction of non-native species[10,47]. To quantify the size and frequency of deliberate releases the following parameters must be known:

– On how many locations are populations of a transgenic cultigen deliberately released?

– How many individuals of the transgenic cultigen are deliberately released at each location?

- How many times a year does the deliberate release of the transgenic cultigen take place at each location?

In principle, an increase in any one of these three parameters increases the probability that the transgenic cultigen becomes feral. The history of the introduction of non-native species to Central Europe includes a number of cases which show that a sudden acceleration of the spread was actually not possible before certain species had been planted on large areas of land (*Prunus serotina*, *Castanea sativa*, *Spartina anglica*, *Robinia pseudacacia*, *Lupinus polyphyllus*).

To answer the question whether a cultigen that has become feral can establish itself on agricultural areas or in natural vegetation, the knowledge of the 'resistance' of biocoenoses to an invasion is of great importance. As very few practical investigations are available on this subject, Trepl[65] discusses the matter predominantly from an ecological-theoretical point of view. Unfavourable abiotic conditions can directly prevent such invasions. If, however, the abiotic conditions are favourable, the biotic resistance, which means the resistance of the already present species and their combinations, can impede an invasion. It is the more or less tight biocoenotic connexion which prevents the establishing of alien species or individuals. Here the old controversy of whether to define a biocoenosis in an organismic-holistic or individualistic-reductionary way becomes relevant[64]. If one gives priority to the ecological interaction among species as a factor of primary importance, then only those alien species that manage to fit themselves into an already existing but not yet closed system of ecological niches are capable of intruding a biocoenosis. If, however, one prefers the view that a biocoenosis results from the coincidental meeting of species corresponding to the abiotic conditions of a given location and that they do not ecologically interact at all (apart from their spatial neighbourhood and the competition that goes with it), then such biocoenoses are seen to be in principle open for new species, even though they may be closed at the moment for individuals of any species because the species already present use all the available resources. In closed vegetation the resource 'space' is completely in use, so that new species can only intrude if some disruptive influence has caused a gap in the system.

It is impossible to make an exact scientific prediction on the ecological behaviour of a particular transgenic organism. The same is true for the effects that a transgenic organism may have on an ecosystem. Of course, the statement (trivial and much discussed in the field of invasion biology on the basis of numerous historical cases) is correct that the effects of the introduction of a new species into an ecosystem depend on the specific properties of the introduced species and the specific structures and functions of the affected ecosystem. As we know very little of all these ecologically relevant parameters, we are not in the position of making a scientifically sound prediction for any particular case at the level of the ecosystem. It is also true that species as well as ecosystems change in the course of time. Even if we knew all the relevant parameters for a certain species and every single ecosystem at its present state, we could not make a sure prediction. In the near future, we will find for example numerous new ecosystems bearing in mind that a great number of the present ecosystems did not exist a hundred years ago, or at least not in their present composition. Empirically we can only use the documentation of historical cases of plants that have invaded ecosystems or that have become feral to set up approximate rules to decide whether a deliberate release has a higher or lower risk.

Regal[46] discusses the difficulties of making a prediction on the adaptive potential of genetically modified organisms in a similar way. Surely, the majority of transgenic cultigens, which originate from highly domesticated taxa and therefore depend upon intensive cultivation measures, will not be capable of threatening neighbouring ecosystems. However, not all organisms that are planned to be artificially modified depend upon such cultivation measures. Examples for such organisms are the many pasture grasses or forest trees, which are only slightly, if at all, domesticated, and which can sometimes hardly be distinguished from the wild forms. But also in the case of transgenic cultigens that show a pronounced syndrome of domestication it is not possible to make a clear prognosis about their ecological behaviour.

The fundamental difficulty in predicting biological dispersal processes exists for both newly introduced species and transgenic cultigens becoming feral. Williamson and Brown[71] summarize the current knowledge on this matter, based on those biological invasions of Great Britain that they examined: "Although certain habitat and biological features increase the probability of invasion and establishment, these features are neither necessary nor sufficient. The prediction of invasions is not yet possible." Seemingly promising characters such as: short life-cycle, speedy growth, high production of seeds, facultative self-fertilization, high genetic variability, and wide ecological amplitudes, do not guarantee a successful spread in every case[34]. Under certain conditions, some species with contrary features may be just as successful[13,43,48]. If predictions are attempted, mostly they are orientated towards the momentary conditions. With this set-up, the analysis is limited to considering only the currently recognizable ecological features of the specific organism and of those ecosystems that are thought to be suitable for a dispersal. Yet, the spread of organisms is a historical process that may continue for decades and centuries, for periods long enough to allow that organisms may undergo many and diverse genotypical and phenotypical changes[37,46] and furthermore it is possible that structural as well as functional changes may occur in the involved ecosystems.

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