1. Summary

Biological invasions by alien species are dynamic processes consisting of several steps: introduction, establishment, population growth and spread. This paper deals specifically with establishment and spread. The probability of establishment of an alien species varies highly and depends generally on three factors: the characteristics of the species, the characteristics of the recipient environment to invasion by a new species, and a set of conditions, especially propagule pressure. Once establishment is achieved, a population can build up, providing new propagules for the colonization of new areas. As more and more populations are formed, the species spreads and expands its range in the new area. Rates of spread of invasive plants can be very high, e.g. several hundred square kilometres per year. In many
instances, there is a lag-phase between the time of introduction and the time of rapid range expansion and the reasons for this are not always obvious. Some implications for management are discussed.

2. Background

The impacts of invasive plant species are among the most significant threats for the conservation of biological diversity (Williamson, 1999). Plant invasions are both dynamic and spatial processes, as populations grow and occupy larger areas and the range increases over time. The process of invasions by alien species consists of the following stages: introduction, establishment and spread (e.g. Heger and Trepl, 2003). Introduction refers to the translocation of plants or propagules by people from a source region to a new region, either accidentally or deliberately. In the Guiding Principles on invasive alien species of the Convention on Biological Diversity (CBD, 2002) establishment is defined as "the process of an alien species in a new habitat successfully producing viable offspring with the likelihood of continued survival"; in ISPM No. 5 of the International Plant Protection Convention (IPPC, 2002) it is the "perpetuation, for the foreseeable future, of a pest within an area after entry". Once it forms self-sustaining populations beyond the site of initial introduction ('escape') in natural or semi-natural vegetation, the stage is called naturalization (Cronk and Fuller, 1995).

Spread occurs if the number of populations increases and covers larger and larger areas, ultimately leading to range expansion. Before a population of an invasive plant species can expand, the species must establish, e.g. propagules must find suitable sites for germination and growth. If the site conditions are favourable, a founder population may build up and reproduction occurs. Once this step is achieved, dispersal leads to the colonization of other suitable habitats, and the number of populations may increase. Finally, the expansion of populations and the formation of new populations lead to an expansion of the species' range. In this article, some of the factors influencing establishment and spread are illustrated.

3. Establishment

In most cases, alien species will have environmental impacts only if they are able to establish and spread in a novel environment. Establishment may be regarded as the most crucial and also the most vulnerable step of a plant invasion. Most of the arriving alien plant species fail to establish (Williamson, 1996) because of a lack of suitable environmental conditions, poor adaptation of the species, or an insufficient number of individuals being introduced. The probability of establishment of an alien species is highly variable and depends generally on three factors: the characteristics of the species, the characteristics (including ecological processes) and susceptibility of the environment to invasion by a new species (Table 1), and a set of conditions, especially the number of propagules entering the new environment ('propagule pressure'; e.g. Lonsdale, 1999; Williamson, 1999). In many cases of successful establishment, repeated introductions had been necessary. There are numerous obstacles an alien plant has to face when entering and establishing in a novel environment, but the many examples of economic and environmental impacts of
alien species demonstrate, that certain plants can cope with these obstacles very effectively.

Table 1. Factors facilitating establishment of invasive plant species.

<table>
<thead>
<tr>
<th>Plant traits</th>
<th>Environmental traits</th>
</tr>
</thead>
<tbody>
<tr>
<td>High genetic variation</td>
<td>Suitable climate and soil conditions</td>
</tr>
<tr>
<td>Frequent planting by man</td>
<td>Presence of efficient pollinators and seed dispersers</td>
</tr>
<tr>
<td>Lack of pests and diseases</td>
<td>Safe sites for germination</td>
</tr>
<tr>
<td>High reproductive output</td>
<td>Disturbances</td>
</tr>
<tr>
<td>Fast growth</td>
<td></td>
</tr>
<tr>
<td>High competitive ability</td>
<td></td>
</tr>
</tbody>
</table>

3.1 Characteristics of the species

To establish in a new environment, an individual plant or population requires characteristics that are favourable for coping with this new situation, and the ability to maintain relatively constant fitness (‘fitness homeostasis’; Hoffman and Parsons, 1991). The plant needs to be capable of reproduction without human support, e.g. the seeds need to be resistant to predation and pre-adapted to the local climate, to be able to germinate and to grow to maturity. Mechanical or chemical defence mechanisms against predators can reduce threats by seed predators or herbivores.

Many invasive plant species reproduce asexually by apomixis or vegetative reproduction (Baker, 1995; Calzada et al., 1996). In both cases, there will not be any inbreeding depression as the progeny is genetically identical to the parental plants. In addition, many invasive plant species are polyploid and can reproduce by selfing, maintaining this by genetic variation (Brown and Marshall, 1981). For successful establishment, vegetative reproduction is advantageous, as the plant does not depend on pollination. Often, the founder population is quite small (Mack, 1995). For example, invasion of *Hydrocotyle ranunculoides* in the UK is assumed to have originated from a single clone which was sold by aquatic garden centres and nurseries (Newman and Dawson, 1999). Another benefit of the production of vegetative propagules is that these are, in general, less often attacked by predators (Pyšek, 1997). Dormancy can be helpful for establishment, because adverse conditions (e.g. low temperatures) can be endured, as long as the species does not need an environmental trigger to initiate germination that does not occur in the new environment.

Competitive strength, e.g. the ability to grow well even when partially shaded, and to produce seed and infest an area while growing under a dense canopy, is a very useful characteristic for establishment. Some invasives tend to form monospecific stands while the population of dominant native species decreases rapidly, which suggests a strong competitive effect on native species (Bakker and Wilson, 2001). Some species may be intrinsically better competitors because they evolved in a more competitive environment (Callaway and Aschehoug, 2000). Other favourable
characteristics to facilitate establishment are adaptability to novel biotic or abiotic conditions or a broad ecological amplitude, defence mechanisms against predators, and the ability to tolerate loss of tissue (e.g. due to herbivory).

3.2 Characteristics of the recipient environment

It is essential for successful establishment, that habitats suitable for germination and growth to maturity, and with enough space for reproduction, are available. Invasibility of a certain habitat is the outcome of several factors including the region's climate, microhabitat conditions, the environment's disturbance regime, and the competitive abilities of the resident species (Lonsdale, 1999). For successful germination and growth, a suitable temperature, humidity, redox-potential and oxygen are necessary. The probability that habitat conditions do not hinder establishment is higher, the greater the similarities of the new environment to that of the native range. However, secondary ranges are often different from primary ranges (Rejmánek, 2000). On an individual level, the plant needs access to sufficient light, nutrients and water. An intentionally imported plant intended for planting will usually be planted in a habitat suitable for its successful establishment, as was the case for Prunus serotina in central Europe (Starfinger, 1997). The situation is different for unintentional introductions, for example, the establishment of Ambrosia artemisiifolia in Europe can, in many cases, be correlated with bird seed that was contaminated with Ambrosia seeds and placed only by mere chance in an area close to a suitable habitat (Zwander, 2001).

A species needs access to available resources, e.g. light, nutrients and water. According to the theory of fluctuating resource availability by Davis et al. (2000), a plant community becomes more susceptible to invasion whenever there is an increase in the amount of unused resources and the species does not encounter intense competition for these resources from resident species (Davis et al., 1998). Fluctuations in the abiotic conditions of the site during the growth of the plant can favour or hinder establishment. Demands for light, water and nutrients generally increase as the plant grows, whereas the site may not be able to meet these increasing demands. Any factors that increase the availability of limiting resources will increase the vulnerability of a community to invasion. Maron and Connors (1996) found that invasions by alien species in a coastal prairie in California, USA were facilitated by a native nitrogen-fixing shrub. Burke and Grime (1996) conducted an experiment on plant invasions in limestone grassland in the UK and found that invasion was highest in nutrient-enriched sites, and particularly rapid when this enrichment was accompanied by disturbance. Other studies (e.g. Burgess et al., 1991; Harrington, 1991) have shown that in dry regions, an increase in water availability increases the establishment of alien plants. However, if there is a severe drought that causes mortality and creates gaps in formerly closed vegetation, the chance of alien plant establishment can also be increased, during the drought or after it. If an environment experiences a pulse of resource supply or a decline in resource uptake, an invading species may be able to exploit the unused resources even though its ecology is not fundamentally different from that of the resident species. Invading species are particularly successful in disturbed habitats, especially in those which are altered by human activities (see Case Study 'Forest Gaps in West Africa: A New Frontier for an Invasive Pioneer'). Disturbance, which results in reduced competition and an increase in resources at the individual plant
level, often appears to be necessary for many alien plants to establish (Hobbs and Huenneke, 1992).

3.3 Biotic characteristics of the recipient environment

In novel environments, alien plants are released from many biotic interactions they have to cope with in their native range, potentially giving the alien plant an advantage over native species (Cox and Elmqvist, 2000). This is especially the case if there are no congeners in the novel environment (Orians, 1986). Biotic interactions with the receptive community include release from enemies (herbivores and/or pathogens) and mutualisms.

Invasive success can be affected by the presence or absence of herbivores and pathogens (D’Antonio, 1993; Lonsdale, 1999). Leaving behind the adapted antagonists present in the native range is an important factor for successful establishment (e.g. Keane and Crawley, 2002). On the other hand, a new competitor growing faster than the plant in question can hamper establishment. A foreign predator arriving or already prevalent at the site may threaten the newly arrived species. This is especially probable if increased multiplication of the individuals leads to the availability of many similar seeds, seedlings and adults, as this increases the attractiveness for predators. Also, the prolonged period of presence in the new area may cause a shift of generalist or even specialist predators to the new host, though the probability of such a shift is smaller if there are no congeners in the new area.

Plant species not depending on mutualism or depending on non-specific mutualism (e.g. pollinators) are more likely to overcome many abiotic and biotic barriers in new environments (Richardson et al., 2000). If mutualists are needed, it is advantageous if the mutualist partner is cosmopolitan, already present in the area, or is dispersed together with the plant. Specifically co-evolved plant-vertebrate seed dispersal systems are extremely rare, so that vertebrate-dispersed plants are generally not limited reproductively by the lack of dispersers. Most of the mycorrhizal plants are associated with arbuscular mycorrhizal fungi, which are low in specificity and widespread, and therefore this is, in most cases, not restrictive to establishment. This is different with ectomycorrhizal plants, especially for Pinus spp. in for example New Zealand. Nitrogen-fixing associations between legumes and rhizobia and between actinorhizal plants and Frankia spp. can play an important role in promoting or hindering establishment. Some of the world’s worst invasive alien species only invaded after the introduction of symbionts (Richardson et al., 2000).

3.4 Propagule pressure and frequency of introduction

Propagule pressure has emerged as the most important factor for predicting whether or not a non-indigenous species could become invasive (Kolar and Lodge, 2001). Successful establishment increases with increasing number of propagules entering the new environment, and initial population size. Though the starting point for the establishment of a plant in a novel environment is its independent growth and the reproduction of at least one individual, for continued survival it is necessary that the number of species reaches a minimum viable population size, which is then able to
cope with demographic, environmental and genetic stochasticity (Gilpin and Soulé, 1986; Mack, 1995; Poethke et al., 1996; Minton and Mack, 2003). Often, even those alien species that have become abundant have failed to establish in earlier introductions. A combination of demographic and environmental stochasticity is one possible reason why the majority of alien species fail to establish in a new environment.

Demographic stochasticity is only a problem for populations smaller than 10-100 individuals (Poethke et al., 1996). Therefore, if the newly arriving plants already start with a founder population which is larger (e.g. because of cultivation) they are not confronted with this set of problems (Mack, 2000). The problems connected to genetic stochasticity are mainly genetic drift and inbreeding depressions (e.g. Oostermeijer et al., 1996). These genetic effects may cause a genetic impoverishment of the population and may thus (eventually also combined with environmental changes) lead to its extinction. Inbreeding depression may limit population growth and lower the probability that the population will persist. Another negative effect of reduced genetic diversity in introduced populations is a limitation in the ability to evolve in the new environments (Allendorf and Lundquist, 2003).

To encounter adverse stochasticity effects, favourable traits include: the ability for rapid population growth, facilitated by a short reproduction cycle and the production of many descendants; and high genetic variability within the population combined with a short generation time and the ability to produce many descendants. Coping with stochasticity problems can also be triggered by repetitive introductions, such as with Senecio inaequidens in Europe (Böhmer et al., 2001), not only because this increases propagule pressure, but also because different releases may have different source populations. Genetic exchange or hybridization between individuals from genetically divergent native populations may result in introduced populations with more genetic variation than native populations of the same species. Hybridization also may play an important role in introduced species becoming invasive (Ellstrand and Schierenbeck, 2000).

3.5 Dispersal of introductions in space and time

Dispersal of species over space and time can result in a failure of establishment. Population growth is possible due to aggregation of the descendants (Clements, 1928), which is facilitated by mechanisms which increase the probability for the descendants to find safe sites for establishment near to the parental plants. It is also favourable if the species is able to produce a permanent seed bank, because this may help to survive periods of adverse conditions and hence facilitate aggregation. Seasonal timing plays an important role, as the probability for a successful establishment is increased if the entry takes place within a suitable period for germination and growth. For increased propagule pressure, transportation starting at the fruiting time of the considered species increases the probability that many diaspores are available.

4. Spread

Ranges of plant species usually show fluctuations over time and are not stable as the species’ vitality depends on the environmental conditions and the ability to cope with
these. In the case of plant invasions, ranges rarely contract but mostly expand due to spread. Two typical courses of range expansion are given in Figure 1. The range expansion may be immediate or delayed, starting some time after the species occurs at low levels in the new area. Such lag-phases are common and are discussed below. Maps showing range expansions of various invaders can be found, for example, in Elton (1958) and Hengeveld (1989). The spread of invasive species can be at any speed and in any direction (Williamson, 1996), depending on the species and the environment. Spread is only possible if the species is able to produce enough descendants which may be dispersed. For plants producing seeds this is in most cases not a problem, but it may be one for clonal plants. However, there are many examples of invasive plants that spread solely by vegetative means, e.g. *Eichhornia crassipes*, *Elodea canadensis* and *Salvinia molesta*. The process of spread is probably the most studied step of an invasion, and it is a process that can be mathematically modelled and hence predicted.

**Figure 1. The spread of invasive plants.**
The lines show the increase in range (area covered, number of localities) or the abundance over time. In A, spread starts immediately after introduction. In B, the beginning of spread is delayed and a lag-phase is apparent. If spread slows down, an equilibrium is achieved.
4.1 Rates of spread

Local dispersal of a plant can be measured in the field, e.g. by determining the dispersal distance of propagules. Range expansions are expressed as a relationship between time and the number of grid squares occupied, or time and the number of known localities, mostly inferred from herbarium records. The mathematical approach to quantify and model range expansion is based on combining the population growth curve (increase in number of individuals) with a diffusion term (spatial expansion of the increasing population) [see Shigesada et al. (1995) for a discussion]. This leads to a linear relationship between time and the square root of the area occupied (Skellam, 1951). Real data, however, exhibit a rather large variation in the spread rates and types of spread, as can be seen in Table 2. The reason is that range expansion is a complex process that consists of population growth, short distance dispersal, long distance dispersal, and the interaction of the plant with the climate and environment. It is the sum of expanding populations and the distance between them that determines the range size.

Table 2. Rates of spread and spread pattern in some invasive plant species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Geographic Area</th>
<th>Spread Pattern</th>
<th>Spread Rate</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alliaria petiolata</td>
<td>North America</td>
<td>exponential</td>
<td>&gt;366 km²y⁻¹</td>
<td>Nuzzo (1993)</td>
</tr>
<tr>
<td>Impatiens glandulifera</td>
<td>UK</td>
<td>exponential</td>
<td>645 km²y⁻¹</td>
<td>Perrins et al. (1993)</td>
</tr>
<tr>
<td>Lythrum salicaria</td>
<td>North America</td>
<td>exponential</td>
<td>100 km²y⁻¹</td>
<td>Thompson (1991)</td>
</tr>
<tr>
<td>Solidago canadensis</td>
<td>Europe</td>
<td>linear</td>
<td>741 km²y⁻¹</td>
<td>Weber (1998)</td>
</tr>
<tr>
<td>Solidago gigantea</td>
<td>Europe</td>
<td>linear</td>
<td>910 km²y⁻¹</td>
<td>Weber (1998)</td>
</tr>
</tbody>
</table>

Range expansions of invasive plants can be rapid and the spread rates high. The examples given in Table 2 contrast with low natural migration rates found for example, in tree species after the ice shield retreated at the end of glacial times (range 25-2000 m per year; Hengeveld, 1989). Range expansions in invasive plants reflect both spontaneous spread of the plant (seed dispersal, population growth) and human-assisted spread. Spread of many invasive plants would be significantly slower if they had to spread only by their own means. Short-distance dispersal is mostly natural dispersal and depends on the species’ biology. Long-distance dispersal of weeds and invasive plants is very often provided by human assistance, either acting directly as a dispersal vector, or providing such vectors. These include: seed dispersal by exotic birds, seed dispersal by attaching to agricultural machines and livestock, vegetative plant parts dispersed by boats, vegetative plant parts dispersed by soil movement, deliberate planting, and provision of dispersal corridors (e.g. roads, railways). Corridors such as roads and railway embankments, artificial channels or river embankments are particularly supportive for the movement of non-native species as their edges are highly disturbed and provide habitats for weedy species to establish.
Thus, range expansion by invasive plants is best described by the hierarchical diffusion model (Hengeveld, 1989) or the scattered colony model (Shigesada et al., 1995). Both models suggest long distance dispersal by human activity (‘big jumps’) leading to satellite populations, which themselves spread by natural dispersal (‘neighbourhood diffusion’). Long-distance dispersers create new colonies, and the big jumps between a founder population and new satellite populations allow a rapid filling up of an area that is suitable for growth of the plant.

It can be shown mathematically that the rate of spread is faster if several populations exist at the beginning of the range expansion, compared to a single spreading population, even if the total size of the several populations is the same as that of the single population (Moody and Mack, 1988). This has important implications for the management of plant invasions: if small populations at the edge of an infestation are contained, the spread of the species can be slowed down or stopped. Controlling small patches is often more practical than containing large infestations.

Rates of spread can exhibit large variation even among a set of closely related species. Mihulka and Pyšek (2001) compared the spread rate of 12 species of weedy Oenothera that became naturalized in Europe. The highest spread rate exceeded the lowest one by a factor of 2.2, and the authors conclude that the spread rate is determined by a similarity between climatic conditions in the introduced and the native range. Forcella (1985) compared rates of spread of alien weeds in Australia and found a positive relationship between the current range of the weeds and their rates of spread. This implies that fast spreading plants have the potential to achieve a large range where they are introduced, a finding that can be used in the prediction of weediness.

### 4.2 Lag-phases and sleeper weeds

In many instances, a time-lag is observed between the introduction of a species and the beginning of fast spread (Figure 1). In such cases, an introduced plant initially occurs at low levels, but later, suddenly undergoes rapid population growth. The reasons for this is poorly understood (Cronk and Fuller, 1995), and there are several mechanisms that could lead to a lag-phase:

- A population is actually growing exponentially but the abundance is very low and individuals are not noticed until they appear in a sufficiently high number.
- The species was under-recorded when at low levels in botanical surveys.
- The population was unable to increase until changes in environmental conditions occurred.
- Population growth is enhanced by arrival of a suitable pollinator.

Finding suitable habitats may also take some time and lead to a lag-phase. It has also been postulated that species introduced to new areas need some time to genetically adapt to the new environmental conditions (Crooks and Soulé, 1996).

The length of lag-phases shows considerable variation. An extensive analysis provided by Kowarik (1995), listing numerous shrub and tree species introduced and naturalized around Berlin, Germany, indicated lag-phases ranging very widely, from
8 to 388 years. The presence of lag-phases suggests that among the many alien plant species growing in a region, certain species will eventually begin to spread in the future. It is a challenge to recognize such potentially invasive plant species. Species that are apparently in lag-phase are called ‘sleeper weeds’ (Grice and Ainsworth, 2003).

5. Conclusion

The establishment phase is the most crucial for the success of an invader, and it is here where most species fail to become invasive. In many cases of successful establishment, repeated introductions were necessary. Favourable species traits include a high competitive ability, fast growth, and a broad ecological tolerance. Suitable environmental traits include appropriate climatic conditions and safe sites for propagules to germinate. Disturbance is commonly believed to facilitate establishment of invasive plants. Rapid range expansions are most often achieved by human-assisted long-distance dispersal, leading to new populations far away from the original population, and by local dispersal. It can be shown that the spread rate is faster if several infestation foci exist as compared to a single focus. One management implication is that small populations at the edge of the range should be eradicated to stop the spread. Lag-phases between introduction and invasion can last up to several hundred years. Time-lags imply that among currently rare alien plant species, some might become invasive in the future. These ‘sleeper weeds’ thus pose a potential future threat and weed risk assessments should aim to recognize such potentially invasive plant species.

6. References


Back to Top

Back to Contents page