CLONALITY AND PLANT INVASIONS: CAN A TRAIT MAKE A DIFFERENCE?

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Introduction

In studies on biological invasions, attempts to identify general characteristics of a successful invader (Baker 1965) have been replaced by the agreement that it is impossible to identify simple traits providing us with some power to predict the invasion success (Crawley 1987; Roy 1990; di Castri 1990; Mack 1992; Perrins *et al.* 1992; Lodge 1993). However, if reasonably large data sets are used, some differences between alien and native (Pyšek *et al.* 1995) or between increasing and decreasing species (Thompson *et al.* 1995) can be found, provided that the performance of invading species is assessed with respect to invaded habitats (Crawley 1987; Noble 1989; Mooney and Drake 1989; Lodge 1993; Pyšek and Pyšek 1995). It appears that some plant traits have more to do with invasion success than others (Rejmánek 1995), and the capability of vigorous vegetative reproduction is often mentioned among the former (Baker 1986; Newsome and Noble 1989; Crawley 1986, 1987; Lodge 1993).

Clonal growth is very common among plants and it is estimated that clonal species constitute 70 % of the flora of temperate, deforestated zone of the earth's surface (van Groenendael and de Kroon 1990; Kelly 1995). Clonal plants are generally very plastic and many of them reduce the risk of genet extinction by placing ramets relatively far away from parents (Oborny and Cain, this volume). Storage of resources in clonal structures such as rhizomes, tubers and bulbs buffers temporal variation in resource availability, whereas the connection between ramets buffers the spatial variation in availability of resources (Jónsdóttir and Watson, this volume). Foraging ability allows the plant to perceive patchiness and 'forage' for patchy resources in their habitats (de Kroon and van Groenendael 1990; Oborny and Cain, this volume; Alpert and Stuefer, this volume). On the other hand, investments into vegetative growth are usually at the cost of sexual reproduction (Westley 1993; Cheplick 1995).

The way in which a complicated process such as biological invasion is affected by a trait as complex as clonality is unlikely to be simple and will depend on a variety of factors including timing and chance (Crawley 1989).

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Nevertheless, alternative reproductive strategies (*i.e.* allocation of resources to sexual reproduction or vegetative propagation) are known to affect the outcome of invasion (D'Antonio 1993). The present paper reviews available literature on invasions by clonal plants and attempts to determine whether plants capable of clonal growth differ from non-clonal plants in their ability to pass through the particular phases of a successful invasion process (*i.e.* introduction, establishment, and spread) and become successful invaders. The terms 'invader' and 'alien' are considered to be synonymous and defined as any spontaneously occurring plant which reached a given area as a consequence of the activities of neolithic or post-neolithic humans or of domestic animals (Webb 1985; Pyšek 1995).

Data sources and methods

Besides particular case studies on the behaviour of clonal species in areas of their adventive distribution, the following data sets were used to analyse species' invasiveness with respect to clonality:

(1) A list of both native and alien species of Central European flora based on the database of Frank and Klotz (1990), modified and completed (Klimeš *et al.*, this volume). For practical reasons, archaeophytes (*i.e.* species introduced before 1500 A.D.) were not considered as aliens (Pyšek 1995) so the number of aliens analysed (n) was 457.

(2) A catalogue of the world's most aggressive invaders into natural vegetation, compiled by Cronk and Fuller (1995, n = 207).

(3) The complete alien flora of the Auckland conurbation, New Zealand, covering 308 km^2 (Esler 1987b, n = 615).

(4) The established invaders of South African natural vegetation (Dean *et al.* 1986, n = 64).

These data sets will be used to illustrate quantitatively how clonality is related to various aspects of the invasion process. Unfortunately, reasonably large lists of alien species containing information on clonality (or information on the morphology of particular species allowing inference concerning their clonality) are very rare.

The term 'clonal' is by no means unambiguous. In the present paper, I have attempted to follow the definition adopted in van Groenendael and de Kroon (1990) according to which clonal growth is characterized by the production of new, potentially independent but genetically identical ramets.

In each data set, the species were classified according to their ability for clonal growth. Data on morphology of vegetative organs given in the original papers were used to classify the data of Esler (1987b) and Dean *et al.* (1986). Case studies on particular species and floras related to the areas of their origin served as the basis for classication of those species listed by Cronk and Fuller (1995). The classification of clonality in the Central European flora corresponds to that used by Klimeš *et al.* (this volume).

The role of clonality in plant invasions will be discussed for particular phases of the process (*e.g.* Hobbs and Mooney 1993; Cronk and Fuller 1995). Dispersal is the period up to the delivery of a propagule in a given area. Establishment is the development of a viable, self-reproducing population in a site, further independent of (though possibly encouraged by) humans. Spread (and persistence as an integral part of it) means increase in abundance and/or density in the adventive area. It should be kept in mind, however, that these three phases are closely associated.

When analysing large comparative datasets, potentially confounding effects of phylogenetic relatedness should be taken into account (Harvey and Pagel 1991; van Groenendael *et al.* 1996; Kelly and Woodward 1996; Crawley *et al.* 1996; see also Westoby *et al.* 1995; Harvey *et al.* 1995 for discussion). For that reason, evolutionary comparative methods were used on the data from Central Europe and Auckland. The 'tree' of families was constructed using phylogenies of Chase *et al.* (1993). The percentage of species possessing the trait analysed and the percentage of clonal species was calculated in families with at least 5 species. The difference in clonality and the trait analysed was then calculated in every node in the 'tree', and the relation between clonality and the trait analysed was tested using regression fitted through the origin (Harvey and Pagel 1991).

Distribution pattern: representation of clonal species in alien floras

In Central Europe, there are 69.4 % clonal and 30.6 % non-clonal species among the native flora. However, the situation is reversed in the alien flora: non-clonal species contribute 63.8 %. The aliens are thus less often clonals and this relation is highly significant (Fig. 1). Since the aliens of the area are very well recorded due to a long-term floristic tradition, and the list also covers ephemeral introductions, escapes from cultivation etc., these figures can be considered as a very good record of the regional flora assessed on an historical time scale. When evaluating these results, it should be borne in mind that the numerical preponderance of non-clonal species results from a large number of casual, annual species. If some measure of ecological impact is used, then the clonal species tend to come out as being much more important.

Unfortunately the data from Central Europe are rather exceptional in that they can be used to compare, with respect to clonality, the alien flora of a relatively large region with its native flora. Most data sets only allow one to evaluate the representation of clonal species among aliens.

Fig. 2 illustrates the geographical pattern of representation of clonal species among aliens. There are certain limitations to the data, namely the lack of quantitative figures from the tropics, the different quality of the data sets (some cover complete floras, some represent selective lists of aliens), and the variety of habitats included (ranging from urban to natural vegetation). Nevertheless, the increase of clonal species in alien floras with latitude is clear in both Northern and Southern Hemispheres (Fig. 2).

The observed pattern corresponds well to the general principles of geo-

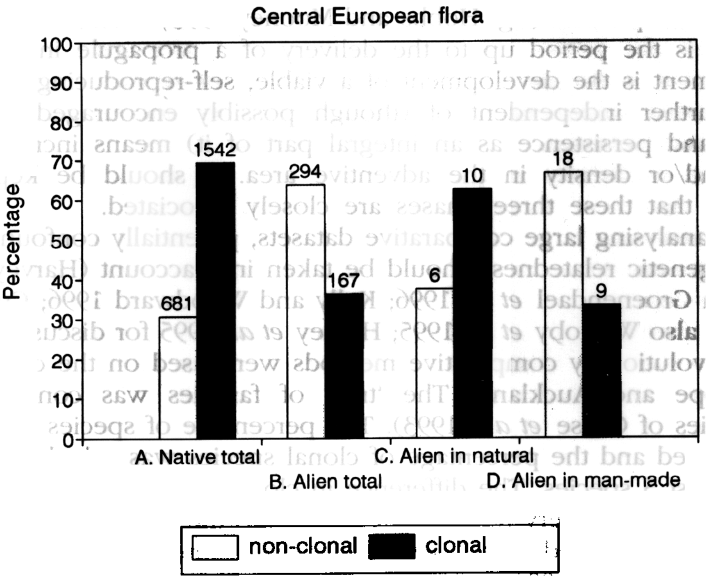

Fig. 1. Proportion of non-clonal and clonal species among native Central European flora (A), Central European aliens (B), aliens established in Czech seminatural habitats (C), and aliens established in Czech man-made habitats (D). Data on complete native and alien floras correspond to those analysed by Klimeš *et al.* (this volume), those on established aliens were taken from Pyšek *et al.* (1995) (those with score 2–3 in the original paper were taken as established aliens; see details on the classification of habitats therein). Species numbers in each group are shown on top of the bars. Phylogenetic comparisons of A and B (see text for details on statistics) revealed that aliens are less often clonals and this relation is highly significant ($p < 0.0001$). For C and D, the chi^2 test on contingency tables was used and the difference between clonals and non-clonals was marginally significant ($chi^2 = 3.46$, df 1, $P<0.06$)

graphical distribution of plants with respect to clonality (de Kroon and van Groenendael 1990). A smaller range of expansion can be expected in species which rely entirely on reproduction by seed since at the border of their distribution, they often become less fecund and may become sterile (Thompson *et al.* 1995). Moreover, species that have migrated far from the areas of their native distribution may suffer from the loss of genetic diversity and/or the absence of specialized pollinators and dispersers. At the same time, the intensity of land-use is decreasing with latitude which also favours clonal species (Thompson *et al.* 1995). Furthermore, the specific environmental features such as short growing period, low soil and air temperatures, low nutrient availability and patchiness of soil and vegetation also contribute to the increase of clonality in arctic environments (Carlsson *et al.* 1990).

Whereas Fig. 2, by taking into account the presence of clonal species, illustrates their ability to become established, Fig. 3 is based on the list of the world's most serious invaders into natural vegetation, reflecting the ability of clonal species to spread. The pattern is very similar – the regions closer to the equator (Africa, Malagassia, Malesia – see Cronk and Fuller 1995 for the

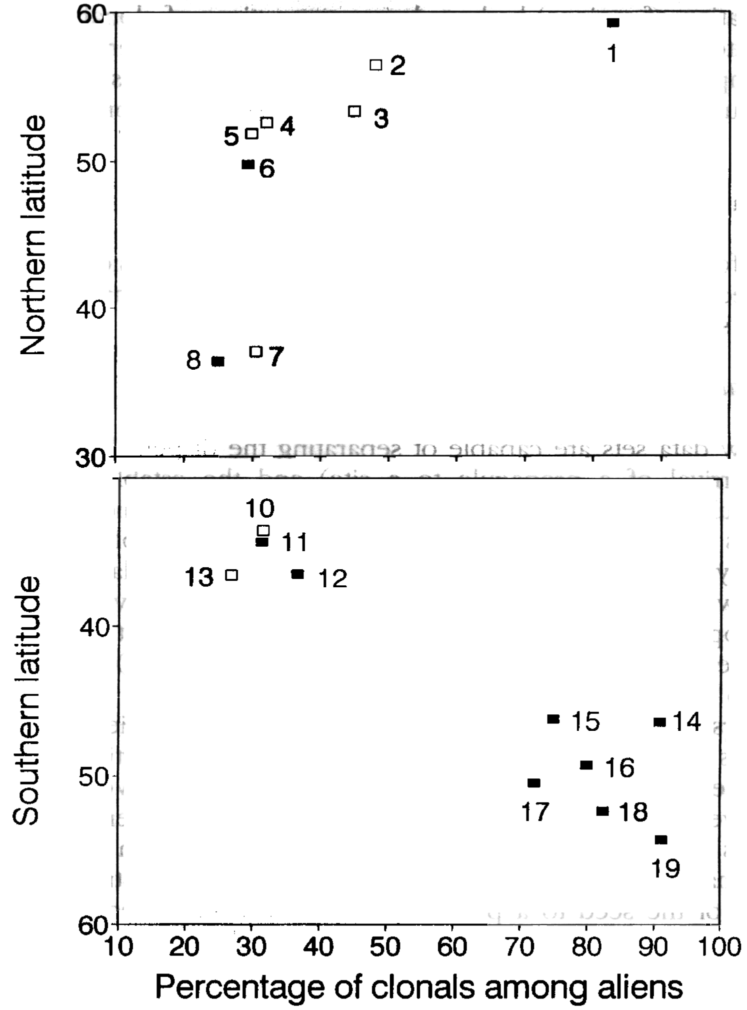

Fig. 2. Latitudinal trend in the representation of clonal species in alien floras. Data based on complete floras of the respective areas are shown by solid symbols, selective data sets are shown by open symbols, and criteria of selection are given in parentheses together with the total number of species analysed. Data sources: 1. Kärsö-Högholmen Island (Lake Malaren, 10 km W of Stockholm, Sweden), n = 29 (Holmberg 1975); 2. Scotland (n = 17), 3. Ireland (n = 7), 4. England (n = 35), 5. Netherlands (n = 30) – increasing aliens in the floras (Thompson *et al.* 1995); 6. Czech Republic, n = 457 (this study); 7. Northern Africa, naturalized aliens, n = 87 (Le Floch *et al.* 1990); 8. California, USA, Hastings Reservation, n = 143 (Knops *et al.* 1995); 9. Chile, mediterranean zone of the country, n = 132 (Montenegro *et al.* 1991); 10. South Africa, Cape of Good Hope Nature Reserve, permanently established aliens, n = 38 (Taylor 1985); 11. Argentina, Buenos Aires province, n = 404 (Söyrinki 1991); 12. New Zealand, urban flora of Auckland area, n = 615 (Esler 1987b); 13. Australia, noxious invaders of Victoria, n = 86 (Newsome and Noble 1986); 14. Crozet Island, n = 12 (Carcaillet 1993); Subantarctic islands (Walton 1975): 15. Prince Edward and Marion Island, n = 11, 16. Kerguelen, n = 10, 17. Auckland Island, n = 18, 18. Campbell Island, n = 23, 19. South Georgia, n = 23. The regression of the proportion of clonal species among aliens on the latitude was significant both for Northern (r = 0.73, $F_{1,6}$ = 7.01, $P < 0.05$) and Southern Hemispheres (r = 0.95, $F_{1,9}$ = 85.78, $P < 0.0001$).

classification of regions) harbour lower proportions of clonal species. In more temperate climates (Europe, North America, South America) clonals play a more important role among major invaders. North Asia, as presented in Fig. 3 is difficult to assess as the total number of species is only seven.

Invasion as a process: an effect of clonality

In the following section, particular phases of the invasion process will be discussed and support for theoretical considerations, summarized in Table 1, will be sought in the available data sets.

Dispersal and establishment

Very few data sets are capable of separating the dispersal phase (understood as an arrival of a propagule to a site) and the establishment phase (the successful reproduction in a new site). The species which appear on a list of aliens have passed both the 'dispersal' and the 'establishment' filters. The efficiency of the filter acting upon the dispersal remains largely unknown and we know almost nothing about the introductions that have failed at the stage of a propagule (di Castri 1990; Kowarik 1995). For that reason, both processes are discussed separately only in theory (Table 1) and no attempt is made to separate them on the basis of available data.

Dispersal of a propagule to a region where the species has not occurred before is a crucial starting point of any invasion (Martins and Jain 1979). Specialized dispersal structures (*e.g.* van der Pijl 1982; Vogt Andersen 1995) and/or vectors associated with dispersal by seed represent an advantage for seeds as compared to clonal propagules, even though the seed dispersal agents may be absent from the region of adventive distribution so that the delivery of the seed to a proper site may be endangered. Moreover, a seed is generally more resistant to desiccation, mechanical damage or frost than most vegetative propagules (*e.g.* stem or rhizome fragments). For these reasons, a less effective dispersal would be predicted in clonally reproducing species (Table 1).

Having reached the region and site to be invaded, there are number of advantages and disadvantages with respect to the chance of successful establishment for both seed and vegetative propagules (Table 1). The establishment depends on whether or not the ecological requirements of the invading species are met (Hobbs and Mooney 1993). To invade successfully, an individual has to grow to maturity and reproduce (Hobbs and Mooney 1993). Clonally propagated species, however, can make use of an immediate production of ramets and effective site preemption. Fuller and Borman (1977) found that populations of an alien species *Rhododendron ponticum* on the Norfolk coast, England, took much longer to become established, as pioneer plants only become reproductive after a period in which the population of the competing species, *Hippophaë rhamnoides,* could have produced three generations. *Rhododendron,* though capable of clonal propagation (Gritten 1988) relies heavily on spread by seed.

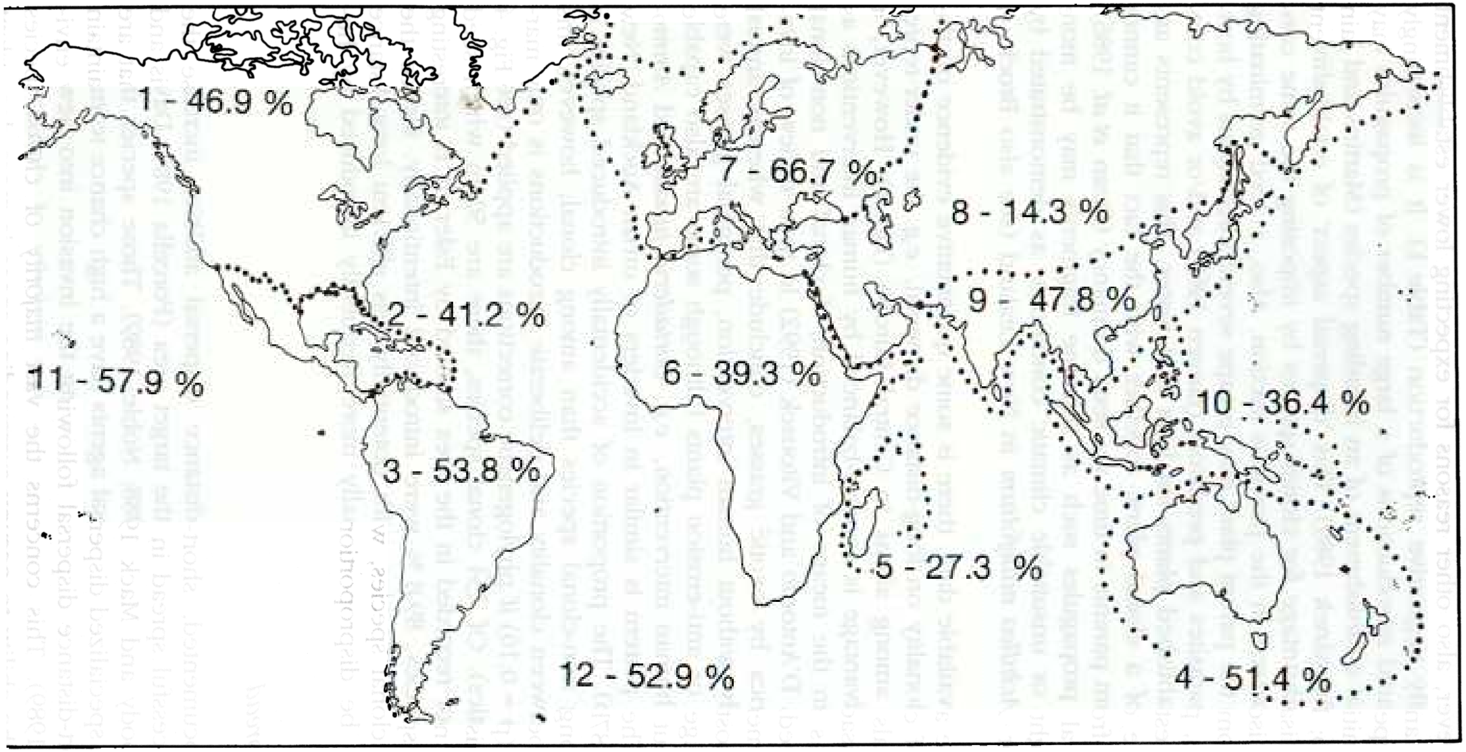

Fig. 3. Proportion of clonal species among the most aggressive aliens of natural habitats in particular geographical regions of the World. Regions used by Cronk and Fuller (1995, see for the detailed description) are indicated: 1 - North America (total number of alien species n = 36); 2 - Central America; 3 - South America (n = 13); 4 - Australasia (n = 81); 5 - Malagassia (n = 23); 6 - Africa (n = 59); 7 - Europe (n = 24); 8 - North Asia (n = 7); 9 - South Asia (n = 23); 10 – Malesia (n = 12); 11 - Pacific (= Oceania, n = 59); 12 – Oceanic Islands (including the most isolated oceanic islands in Eastern Pacific, Atlantic, Indian Ocean and Subantarctic area, n = 17). The percentage of clonal species (*i.e.* those capable of clonal propagation) is shown for each region. Aquatic species were not considered because of cosmopolitan pattern of distribution.

There are, however, also other reasons for expecting lower establishment through predominantly vegetative reproduction (Table 1). It is increasingly recognized that repeated introductions of a large number of propagules may be necessary for initial establishment of an invading species (Martins and Jain 1979; Bazzaz 1986; Rejmânek 1989). This 'dispersal aspect' of establishment represents some disadvantage for clonal species by imposing the same constraints as those discussed in the previous section. Also, a seed germinating at a site remote from the parent plant may escape severe infestations by host-specific pathogens, parasites and predators (Janzen 1969) and/or avoid competition with the established plants for light and water. This represents another disadvantage of a clonal plant, together with the fact that it cannot separate offspring from parents in time via seed dormancy (Dean *et al.* 1986). Furthermore, clonal propagules such as rhizome fragments may be more sensitive to drought or unsuitable climatic conditions, as demonstrated by Bourdot (1984) for *Achillea millefolium* in New Zealand (see also Brock *et al.* 1995).

Summarizing the available data, there is some quantitative evidence on the restrictive effect of clonality on long-distance dispersal, *e.g.* the under-representation of clonals among aliens in Central Europe (Fig. 1). However, it seems that this disadvantage is counter-balanced by human interventions as there is some bias in the means of introduction, if clonal and non-clonal plants are compared. D'Antonio and Vitousek (1992) in their review of invasion of North America by exotic grasses, conclude that whereas annual grasses arrived mostly without human intervention, perennial grasses were introduced as forage or anti-erosion plants (although some are also capable of invading without human intervention, *e.g. Cortaderia jubata* and *Ammophila arenaria*). The pattern is similar in invaders of urban Auckland, New Zealand (Esler 1987b). The proportion of accidentally introduced species is much higher among non-clonal species than among clonal; however, this negative relation between clonality and deliberate introductions is only marginally significant ($p = 0.10$) if phylogenetic corrections are applied (see Fig. 4 for details on statistics). Of 234 clonal species, there are 50 in which seed reproduction was not recorded in the area studied by Esler. It is interesting that of these 50 species, 89.8 % were introduced intentionally. Hence the data suggest that clonal species, with potentially less efficient long-distance dispersal, tend to be disproportionally more frequently introduced by humans.

Persistence and spread

As repeatedly documented, short-distance dispersal abilities increase the probability of successful spread in the target area (Forcella 1985; Davis and Mooney 1985; Moody and Mack 1988; Noble 1989). Those species that are not dependent on specialized dispersal agents have a high chance to maintain the ability of short-distance dispersal following the invasion into new environment (Noble 1989). This concerns the vast majority of clonal species because in these the ability to occupy surrounding space is more dependent

Table 1. Factors promoting (Pros) and restricting (Cons) the chance to go successfully through particular phases of the invasion process compared for non-clonal and clonal strategies. See text for details.

	Non-clonal	**Clonal**
DISPERSAL	PROS: - specialized dispersal structures and dispersers - resistant to desiccation, mechanical damage	PROS: - easy fragmentation and spread by *e.g.* water
	CONS: - dispersers may not be available	CONS: - less effective dispersal (absence of specialized structures) - sensitivity to drought, desiccation etc.
ESTABLISHMENT	PROS: - dormancy (coping with heterogeneity in time) - large number of propagules	PROS: - not-dependent on dormancy-breaking mechanisms - damage to shoot does not necessarily mean the death of a plant - immediate reproduction (no partner needed) - usually large propagules that easily compete and establish
	CONS: - seed predation - dependence on dormancy-breaking mechanisms - risk of the seedling stage (herbivory, extreme environmental conditions) - failure to set seed (climatic constraints) - if not capable of uniparental reproduction, the lack of partner for sexual reproduction	CONS: - risk of unsuitable conditions (desiccation, frost) limiting or preventing vegetative growth - usually less numerous propagules
PERSISTENCE AND SPREAD	PROS: - genetic differentiation - spread via foci (long-distance dispersal) - escape from host-specific pests and pathogens	PROS: - effective site occupation (short-distance dispersal) - independent of specialized pollinators and dispersers - immediate spread (no delay due to pre-reproductive phase)
	CONS: - time delay before the pioneer plant reaches maturity - absence of specialized pollinators and dispersers - usually less compact site-preemption	CONS: - less effective long-distance spread - lower genetic differentiation, less effective adaptation to the changing environment - sensitivity to damaging effects of herbivory

on intrinsic biological and ecological traits rather than on external factors. Generally, the process of successful invasion consists of both short-distance dispersal around the primary source and long-distance hops at the same time. Wilson and Lee (1989) suggest the term 'infiltration invasion' to describe this pattern (see also Moody and Mack 1988; Hengeveld 1989; Shigesada *et al.* 1995) which is typical for populations spread by seed, but can also be applied to species with vegetative propagules. Martins and Jain (1979) suggested that those species in which some disturbance is required to make their spread possible would spread in the form of small isolated foci whereas

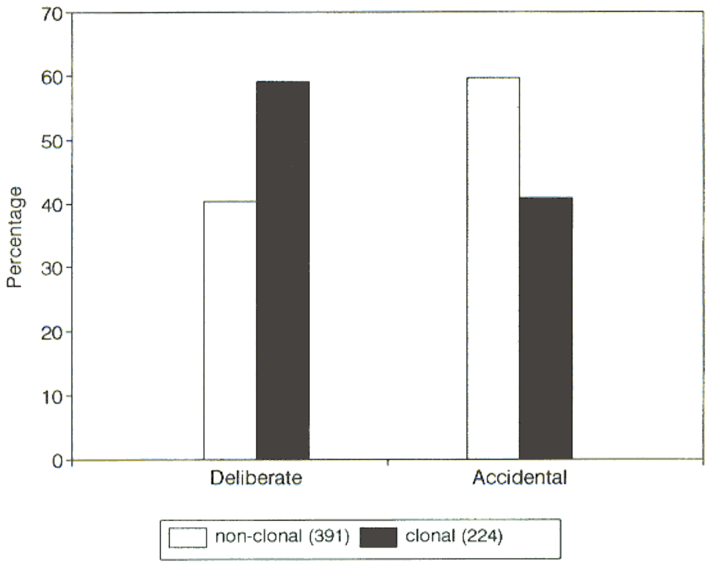

Fig. 4. Means of introduction of aliens into the urban Auckland area, New Zealand, with regard to the clonality status. Calculated from the data of Esler (1987b). Class 1 and Class 2 recognized by the original author were pooled. Pearson correlation coefficient of the relationship between the percentage of accidental introductions and the percentage of clonals in a family was R = – 0.32 (p = 0.12, n = 24). When using phylogenetic corrections, the relationship turned out to be marginally significant (p value of the regression through the origin = 0.10).

species not depending on disturbance would create an expanding front.

Populations that do not require genetic adjustment in their new habitat may be expected to initially spread more quickly than those that do (Bazzaz 1986). If the newly introduced genotype of a clonal species happens to be adapted to the new site, an immediate establishment and rapid spread may follow, rather than a long-lasting lag-phase. Moreover, species capable of uniparental reproduction (by self-fertilization, apomixis or clonal propagation) are predicted to establish more effectively because of capability to start reproduction immediately following long-distance dispersal of a single individual (Barrett and Richardson 1986). They can maintain reproduction throughout the initial phase of the invading process, during which periods of low population density are expected (Baker 1986; Roy 1990).

In contrast, lower genetic variation and less effective adaptation to environmental changes are usually considered as possible constraints to spread in clonal species (Table 1). The alien population may have originated from a single clone. Such populations may possess just a few genotypes that persist through vegetative propagation (Barrett and Richardson 1986; Mack 1992). Reduced gene flow and low genetic variation can make them extremely sensitive to unpredictable changes in environment, herbivore attack etc. (Ashton and Mitchell 1989). However, these conclusions must be taken with caution because predominantly clonal species may maintain as much genetic diversity within populations as sexually reproducing species (Ellstrand and Roose 1987; Hamrick and Godt 1989; Widén *et al.* 1994; McLellan *et al.*, this volume).

Little of the variation in the population of the invader would usually be expressed in a small founder population initiating invasion, and it is unknown whether this population bottleneck in natural selection commonly hampers an invasion (Mack 1992). Examples of aggressive invaders with little genetic variation are at least as common as those with high variability (Barrett and Richardson 1986). Successful invaders do not necessarily share high genetic variability, high ploidy, or high levels of heterozygosity, and they may have a wide variation in breeding systems (Mack 1992). The low number of available studies makes it impossible to conduct a concise comparison (information on compatibility and genetic variation is unknown for many invasive species), and the pattern is far from being unequivocal (Cronk and Fuller 1995). For species with extensive asexual recruitment, theoretical models of genetic variation predict both that (a) clonal populations will consist of a few genotypes, or (b) that they will possess as much genetic variation as sexual populations. Both groups of models have received experimental support (Novak and Mack 1995), and the effect of clonality on invasion success viewed from a genetical point is not clear (see also McLellan *et al.*, this volume).

There is a large body of evidence on the regeneration potential of clonal invaders (*e.g.* Dickens 1974; Bourdot *et al.* 1982; Bourdot and Field 1988; Saner *et al.* 1995; Brock *et al.* 1995). For example, a single plant of *Sorghum halepense* is able to produce up to 90 m of rhizomes during a month (McWhorter and Jordan 1976) and a single cladode of *Opuntia aurantiaca* produced 720 cladodes in a six month period (Whiting *et al.* 1986). *Reynoutria japonica*, an Asian invader into Europe, spreads exclusively by vegetative means in the adventive area (Bailey *et al.* 1995); not only does it exhibit 40 % regeneration from rhizome fragments with as little as 0.7 g fresh weight (Brock and Wade 1992), but is also capable of effective regeneration from stem tissues (Brock *et al.* 1995). There is also some evidence of better performance of species in the adventive area compared to that in the region of native distribution, both in terms of stature (Crawley 1987) and seed production (Weiss and Milton 1984; Pieterse and Cairns 1988). *Reynoutria japonica* represents a good example as it is remarkably taller in Central Europe than in its native Japan (Pyšek and Prach 1993).

Clonal invaders appear to be rather successful in competition with native species because of faster growth, regeneration from rhizome fragments (Partridge 1992; Gilfedder and Kirkpatrick 1993) or physiological features (Forseth and Tenamura 1987; Caldwell *et al.* 1981). The South African clonal succulent *Carpobrotus edulis* (Aizoaceae) may serve as an interesting example of the latter. In California, it restricts the amount of water available to native shrubs by forming a dense mat of fibrous roots and adding new roots at each node as the plant spreads outwards (D'Antonio and Mahall 1991). A specific pattern of site occupation was also reported as a reason for success. *Tradescantia fluminensis* from South America was introduced to the remnants of natural

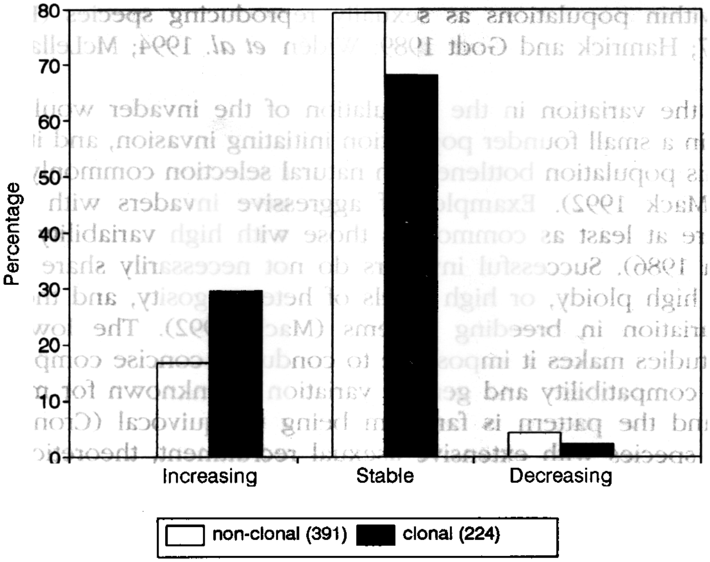

Fig. 5. Dynamics of alien species abundance in the urban Auckland area, New Zealand, during 1970-85. Calculated from the data of Esler (1987b, Class 1 and Class 2 pooled). Pearson correlation coefficient of the relationship between the percentage of increasing species and the percentage of clonals in a family was R = 0.54 (p = 0.0067, n = 24). When using phylogenetic corrections, the value of the regression fitted through the origin was p = 0.0033.

forests in New Zealand where it does not produce seed and forms a dense mat up to 60 cm in depth and prevents seedlings of native species from germinating (Maule *et al.* 1995).

Some quantitative evidence of the ability of clonal aliens to persist in a site and/or increase in abundance comes from the data of Esler (1987b) from the Auckland conurbation (Fig. 5). Species capable of vegetative propagation were doing significantly better in terms of population dynamics.

Despite the obvious success of clonal species in terms of persistence in a site, one would still expect a slower natural rate of spread on a landscape scale given their disadvantage in long-distance dispersal (Table 1). Dispersal rates of alien species are reported to be in the range of kilometres or tens of kilometres per year (Thompson 1994 and references therein; Baker 1986; Perrins *et al.* 1993). The paucity of available data does not make it possible to assess the effect of clonality in terms of real units. Analysis of the historical dynamics of major invasive aliens in the Czech flora (Pyšek and Prach 1993) provides some possibility to compare the course of invasion in those species that reproduce exclusively by clonal means in this country (*Reynoutria japonica, R. sachalinensis*) with that of prolific seed producers (*Impatiens glandulifera, Heracleum mantegazzianum*). The latter two species entered the exponential phase of spread after having established themselves in relatively few localities in the region and their subsequent rate of spread was significantly higher than that of both clonals whose invasion proceeded at a more even rate (Pyšek and Prach 1993). Another indication of the same

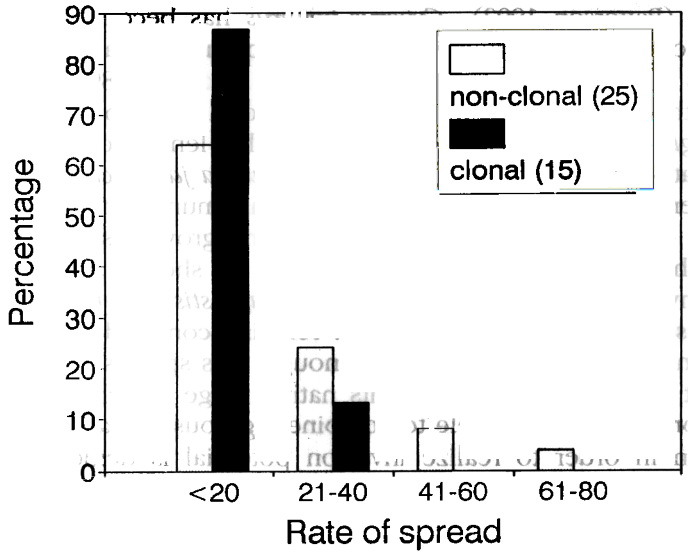

Fig. 6. Initial rate of spread compared for clonal and non-clonal species among 40 aliens of the northwestern USA. Data from Forcella (1985) include those species that have reached their final distribution in the area. The initial rate of spread was expressed as the coeficient b of the exponential equation of the form: $E(y) = n + b \,\mathrm{Ln}\,(x)$, where $E(y)$ is the estimated number of counties in which the species occurred at time x; n is a constant and b is the initial rate of spread up to the approximate midpoint of its calculated final distribution (see Forcella 1985 for details). Rate of spread of clonal species (13.68 on average) was not significantly different from that of non-clonal (18.42) in Kruskal-Wallis test (test statistics 0.08, $P>0.05$). Total species numbers are given in parentheses.

pattern is provided by the data of Forcella (1985) who calculated initial rates of spread of 40 species alien to the northwestern United States. Though the rate of invasion did not differ significantly between clonal and non-clonal species, it was on average 34.6 % higher in the latter which suggests faster spread in non-clonal species (Fig. 6). The same pattern was found when analysing the invasion dynamics of the 50 established aliens of the Czech flora (Pyšek *et al.*, unpubl.).

The different "spreading strategy" of clonal versus non-clonal species can be documented through case studies comparing alien congeners. Of Eurasian invaders of North American rangelands, non-clonal *Centaurea solstitialis* and clonal *C. repens*, the former is perceived as a more serious weed because it disperses more rapidly and exhibits greater ecological amplitude. The latter, relying on extensive rhizome/root system, however, is increasing in local distribution and density (Watson 1980; Maddox *et al.* 1985; Roché and Roché 1988; Lacey *et al.* 1992). More reports on restrictions to the long-distance spread associated with clonality are available: *Galega officinalis* is a clonal species producing seeds that are not dispersed by wind but float on water. The species remains limited to 155 square miles since its introduction to the United States a century ago because neither clonal propagation nor seed dispersal by water are efficient enough to extend the distribution range significantly (Patterson 1992). *Cyperus papyrus* has become naturalized in a number of countries but does not spread vigorously because the naturalized populations are probably sterile (Ashton and Mitchell 1989). Beerling (1993) concluded that the northern distribution limit of a non-clonal annual invader, *Impatiens glandulifera*, is limited only by the length of growing period, whereas that of rhizomatous perennial *Reynoutria japonica* also depends on minimum temperature. In the latter species, minimum temperatures influence the survival of the rhizomes since above-ground growth is susceptible to late frosts which frequently result in the death of shoots (Beerling 1993). A European invader into North America, *Calamagrostis epigejos*, usually became well established where introduced, but remains confined to relatively small areas (Aiken *et al.* 1989). Interestingly enough, this species appears to be one of the most expansive in a part of its native range (Prach and Wade 1992).

The importance of being able to combine vigorous clonal growth with seed reproduction in order to realize invasion potential is demonstrated by one aspect of the classical *Spartina* story (Gritten 1988). Although *S.* × *townsendii*, the sterile product of hybridization between North American *S. alterniflora* and European *S. maritima*, spread by clonal growth, it was not until the allopolyploid fertile form, *S. anglica*, evolved that the invasion was triggered (D'Antonio and Vitousek 1992). In New Zealand, *S. anglica* has replaced *S.* x *townsendii* so successfully that only one specimen of the latter, which originally covered more than 40 ha of the New River estuary, has been collected in New Zealand since the introduction of *S. anglica*. Obviously, the species with greater ability for natural spread is *S. anglica* as it disperses readily by seed whereas the sterile *S.* × *townsendii* is spread only by planting and outward growth of clones (Partridge 1987). It should be stressed that these two very similar species (it is even doubtful if separate species are justified, see Drok 1983, cited by Partridge 1987) differ probably in a single trait (*i.e.* capability of seed production), making it thus possible to assess the effect of such a trait on invasion success.

The review of available data suggests that, as far as spread is concerned, the lower ability of long-distance dispersal in clonal species is compensated by the advantage of effective space occupation at the local scale. This appears to be an explanation for the the fact that at regional and global scales no quantitative difference between clonal and non-clonal species in the invasion success was found. Among established invaders of the Czech Republic (data from Pyšek *et al.* 1995), clonal species did not differ from non-clonals in invasion success, neither in seminatural ($chi^2 = 0.35$, df 1, $p > 0.05$) nor in man-made habitats ($chi^2 = 0.66$, df 1, $p > 0.05$). At the global scale, clonal species included in the list of Cronk and Fuller (1995) did not differ from non-clonals in the Kruskal-Wallis test (test statistics 0.08, $p > 0.05$, aquatic species not included) with respect to the invasive category, *i.e.* the measure of their invasiveness.

Effect of habitat on the success of clonal invaders

Invading species frequently have attributes taking advantage of disturbance, such as a generalist mode of dispersal, rapid germination and growth, and relatively short maturation time (Hobbs 1991). These traits appear more applicable to annual species which are usually among those most supported by various kinds of disturbances. Hobbs and Huenneke (1992) report a decline in native perennial grasses, due to disturbances by introduced livestock following European settlement, and their replacement with non-native annual grasses in several grassland areas in North America and Australia (see also Mack 1989). Clonal species, however, seem to be less favoured by disturbance. They are more capable of invading natural and seminatural habitats (Geldenhuys *et al.* 1986; Timmins and Williams 1987, 1991; Brothers and Spingarn 1992; Beattie *et al.* 1992; Weaver *et al.* 1990)

Analysing aliens permanently established in the Czech flora (Pyšek *et al.* 1995), clonal species differ from non-clonals in the establishment rate (defined as the percentage established in the given habitat of the total number present in the Czech alien flora) in seminatural versus man-made habitats. In seminatural sites, clonal species become more easily established (6.0 %) than non-clonal species (2.0 %). In man-made habitats, the rate of establishment for non-clonal species is higher (6.1 %), and does not differ from clonals in this habitat (5.4 %).

Among the 28 permanently established Czech aliens, the non-clonal species are over-represented in man-made habitats, whereas clonals are over-represented in seminatural vegetation (Fig. 1). It is interesting, that the proportion of clonals among invaders of seminatural vegetation (62.5 %) is similar to the proportion of clonals among the native flora (69.4 %). This indicates that the recipient vegetation operates as a filter, *i.e.* it is difficult for species that are not capable of clonal propagation to become established in certain types of seminatural vegetation (Pyšek *et al.* 1995).

Two sets of data are available to illustrate the representation of clonal species among aliens in particular habitats (Dean *et al.* 1986; Esler 1987b). Though rather contrasting in terms of the level of disturbance (the urban flora of Auckland and the natural vegetation of the floristically extremely rich Cape Province) and geographical location (New Zealand and South Africa) both reveal a very similar pattern (Fig. 7) in that the clonal species are most represented in aquatic, wetland and grassland habitats. Their role is minor in ruderal and agricultural habitats, wasteland, rocky sites and shrubberies, *i.e.* in the highly disturbed habitats of the Auckland conurbation. In South Africa (Dean *et al.* 1986) they seem to be restricted to more extreme, drier environments such as desert (Wells *et al.* 1986). Clonal aliens also play a minor role in fynbos (Wells 1991); fire as a disturbance has an ambiguous effect on annuals and perennials and there is evidence of increase and retreat in both life forms (Hobbs and Huenneke 1992). It seems that sexual reproduction, often associated with serotiny and vigorous coppicing, is a more convenient strategy in an environment with periodic, predictable fire (Richardson and Cowling 1992) than vegetative regeneration. The damaging effect of fire on

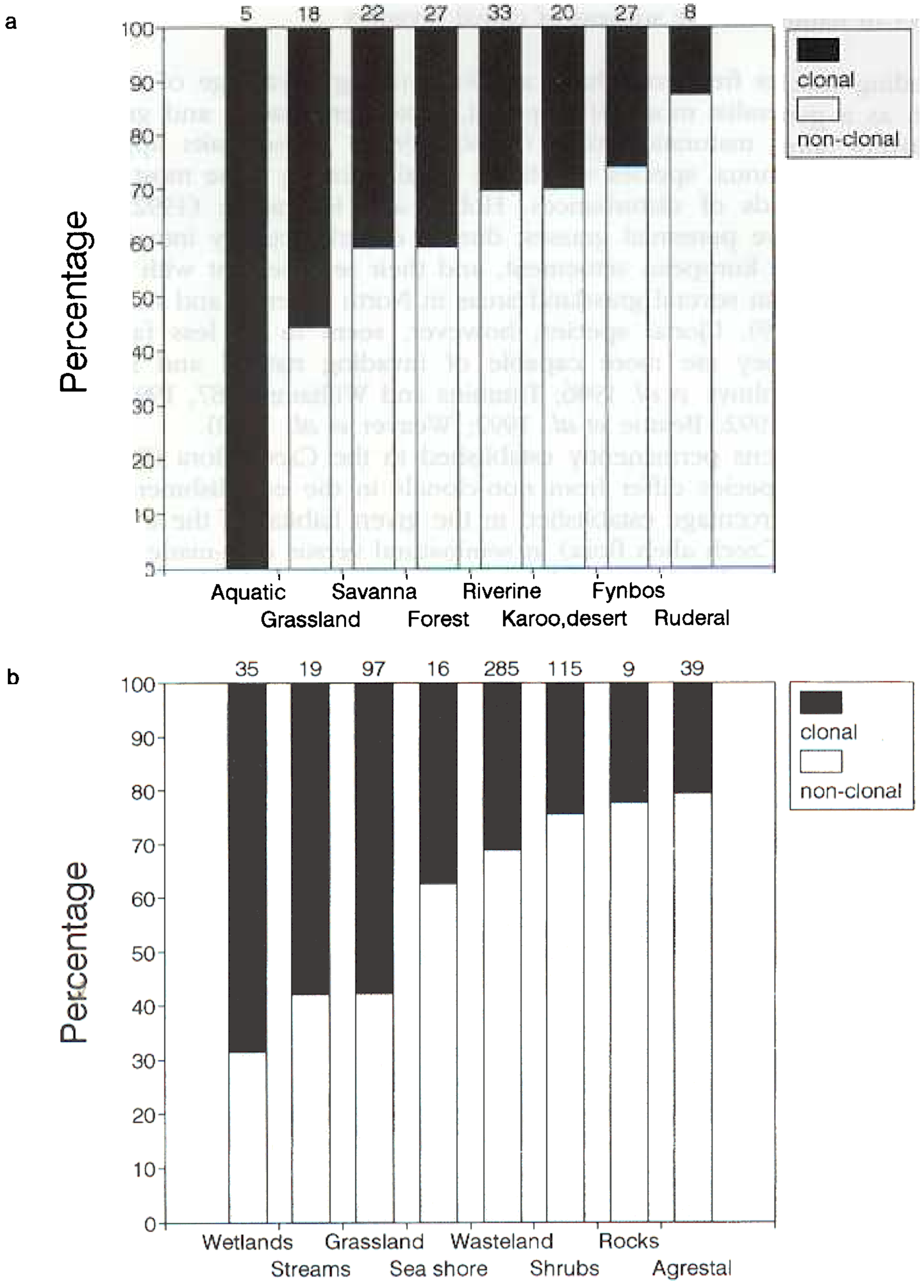

Fig. 7. Representation of alien species in particular habitats with respect to clonality. Habitats are arranged according to the decreasing proportion of clonal species. The number of species in a particular habitat is given on the top of each bar. (a) South African natural vegetation (calculated from the data of Dean *et al.* 1986). (b) Urban Auckland area, New Zealand (calculated from the data of Esler 1987b, Class 1 and Class 2 recognized by the original author were pooled).

the organs of vegetative growth would be more serious than on seed.

Dean *et al.* (1986) classified the principal invaders in South African natural habitats according to the character of the seed. Species capable of vegetative regeneration, either by shedding of cladodes or resprouting, were most represented among plants with soil-stored seed embedded in soft fruits (71.4 % species in this group were clonal). This group of long-lived species are mostly restricted to fertile soils and occur in environments where fire is rare. Seeds in the fruit tend to be short-lived. They are important invaders of riverine, forest, forest margin, plantation, savanna and bushveld habitats.

Careful reviews of aliens throughout the world demonstrate that no particular life history predominates in aggressive invaders (D'Antonio 1993). Some species combining capability of both long-distance dispersal and effective short-distance spread are among the most sucessful invaders (Turkington and Burdon 1983; Groves 1986; Kornas 1990; Mal *et al.* 1992). These species can use different strategies in contrasting habitats. For example, the invasion of coastal plant communities in California by *Carpobrotus edulis* is a habitat-specific process depending on soil disturbance, herbivory and identity of competitors (D'Antonio 1993).

Summary and prospects

The role of clonality in plant invasions is context-dependent. Clonal invaders are more represented than non-clonal in wetter and colder than in drier and warmer climatic areas, and in natural, less disturbed rather than man-made habitats.

Compared to non-clonals, clonal invaders appear to be at an disadvantage in the dispersal phase of invasion. On a historical time scale, this handicap was compensated for by humans, introducing clonals at a higher rate than non-clonals. Once established, clonal plants seem to be more persistent and competitive which leads to an effective occupation of the available space. On the other hand, their further dispersal in the adventive area tends to be slower (due to the dispersal limitations) than that of non-clonal plants. Consequently, due to this balance, both groups are similarly successful invaders in terms of achieving dominance and become noxious.

The available data are generally very poor. The lack of information on clonality in local floras makes it difficult to carry out a more detailed comparative analyses. Analyses of large data sets are always a compromise between quantity of species included and the quality of information available. The inspection of traits listed in Table 1 and their comparison with evidence available in the literature indicates that most of them remain fairly speculative. The following subjects can be suggested for future research:

(a) It would be very useful to obtain some measure of 'degree of clonality' (*e.g.* the rate of vegetative spread or final genet size) for a reasonable number of species. Also the capacity of vegetative fragments to establish, not necessarily correlated with clonality, may be expected to affect the outcome of invasion. Knowledge of that kind would increase the quality of comparative analyses, and would allow to analyse the success of different forms of clonality.

(b) Concerning the phases of the invasion process, dispersal (particularly long-distance) is the one which is most deficient in terms of good quantitative data. Experimental studies on the effectiveness of dispersal mechanisms and the fate of propagules of both non-clonal and clonal aliens following the introduction into a target area would be most useful.

(c) Comparison of congeners (clonal versus non-clonal alien, clonal alien versus non-clonal native, clonal alien versus clonal native) appears to be a promising approach to assess the role of not only clonality, but of any particular plant trait, in the invasion process.

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