THE DISTRIBUTION AND DISPERSAL OF TWO ALIEN SPECIES OF IMPATIENS, WATERWAY WEEDS IN THE BRITISH ISLES

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Summary The distributions are described and compared for Impatiens capensis Meerb. and I. glandulifera Royle., two alien waterway weeds in the British Isles. The rates of spread and habitat preference of these two species are investigated and related to possible dispersal strategies. Models are derived based on data extracted from detailed records of the movement of the species since their introduction in the 19th century. Various scales of sampling are employed in order to reflect characteristics attributable to different levels of organisation. The implications for controlling waterweed infestations are considered and the need to deal with each species as a separate entity is emphasised.

INTRODUCTION

Many of the most serious infestations of aquatic plants have arisen from the invasion of waterways and other waterbodies by alien species. Impatiens capensis Meerb. and I. glandulifera Royle are two species with a similar growth form and habitat requirements which have established themselves along the margins of water bodies and are now widely regarded to be denizen in the British Isles. I. glandulifera has become a significant pest along the margins of some waterways, for example stretches of the River Severn. The date of introduction is known for both species, 1822 and 1839 respectively, and the changes in their distributions have been noted by botanists over the decades. The attractive nature of their flowers and the curious mode of seed dispersal (explosive dehiscence of seed pods) has ensured that the occurrences of these species have been well recorded. This paper aims to compare the rates of spread and habitat preference for these two species in the British isles in order to understand more clearly the dispersal strategies used by these plants in extending their distributions. Some of the lessons learnt from this study may be applicable to the control of more serious aquatic infestations, both in the British Isles and in other parts of the world.

METHODS

The characteristic flowers and other obvious features of Impatiens species make them excellent plants in which to study changes in distribution at a national level. Records of the species were derived from herbarium

collections and botanical literature. Thirteen national herbaria were thoroughly searched for specimens of all Impatiens species: **BM, CLR, CGE, DBY, E, K, LIV, LSR, LTR, MANCH, NMW, OXF, WAR** (abbreviations according to Kent & Allen, 1984). Location of species, grid reference, collector and date of collection were noted. Similar information was retrieved from botanical journals and county floras. Care was taken to check the identification of material and cross-reference the herbarium specimens with the published records. Present day records were collected from surveys undertaken in July and August 1984. Additional larger scale county distributions were obtained for Leicestershire and Warwickshire (Cadbury, Hawkes and Readett, 1971).

A database was created through the Biological Records Centre, Monks Wood Experimental Station, Huntingdon. This was interrogated for specific information, e.g. all the records for a particular county, and also used to generate distribution maps for the British Isles based on 10 km squares.

The data were analysed to determine rates of spread (Grieg-Smith 1964) by plotting the cumulative number of 10 km square records for each species using a logarithmic transformation. A negative binomial model (Jeffers, 1978) was used to classify the distribution of the two species based upon the large scale occurrence using the location of sites where a species had been found. The model was based upon the occurrence of the species in 285 km^2 of the Midlands (Ordnance Survey 1:250,000 series sheet 13). The habitat preference of the two species was examined in relation to canals, canals and rivers/streams, and rivers/streams using a chi-square test.

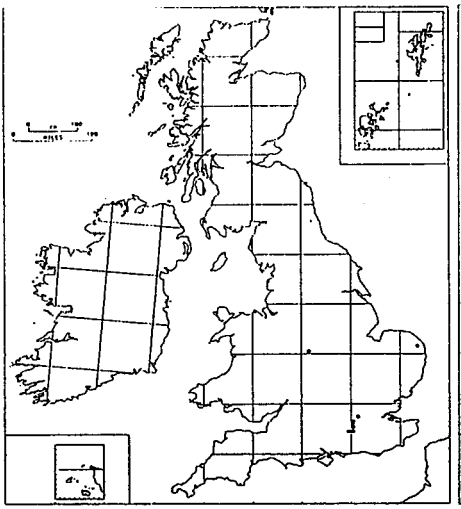
RESULTS

I. capensis spread from its original site, a tributary of the River Thames in Surrey, both in the direction of the flow down to, and along the River Thames and also in a counterflow direction up other tributaries into Middlesex. Over the period 1849-1899 the species moved considerable distances (up to 300 km) to various sites from which it again began to steadily spread locally. I. capensis is almost entirely excluded from Scotland, and most of the northern counties, and has not been recorded in Ireland nor in any other of the more distant isles (Fig. 1).

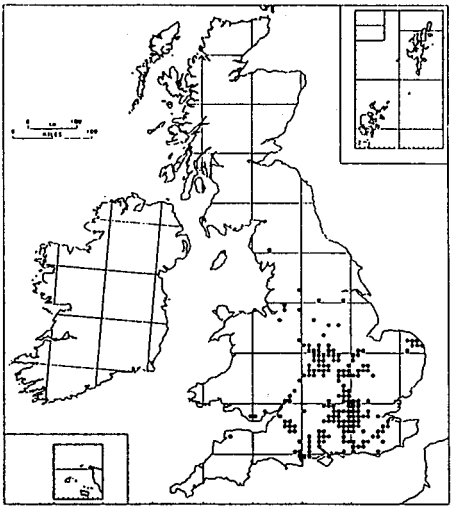
I. glandulifera has similarly "jumped" long distances whilst expanding its local range in the vicinity of centres already colonised. The species has invaded most parts of mainland Britain as well as becoming frequent in Ireland and reaching the Shetland and Scilly Isles (Fig. 1). This species has clearly found the environment of the British Isles more conducive to rapid spread than its relative having achieved a greater distribution that I. capensis despite having appeared some 40 years after I. capensis.

This observation is supported by the regression equations calculated for the number of records (log/no. 10 km^2 records) against time. For I. capensis the equation was $y = 0.634 + 0.1161 x$ ($t = 10.52$, $p < 0.001$) and for I. glandulifera, $y = 0.471 + 0.0223 x$ ($t = 11.28$, $p < 0.001$). The plots are significant for both species with I. glandulifera having a higher intrinsic rate of spread than I. capensis.

The distribution of the two species was classified using a negative binomial model (Jeffers, 1978) based upon the location of sites for a given species in the Midlands. The chi-square values and probability levels for the two species were: I. capensis = 2.79, d.f. = 6, $p > 0.50$; and I. glandulifera = 18.29, d.f. = 7, $p < 0.9$. The probability for the chi-squared value derived for I. capensis is not sufficiently small for the

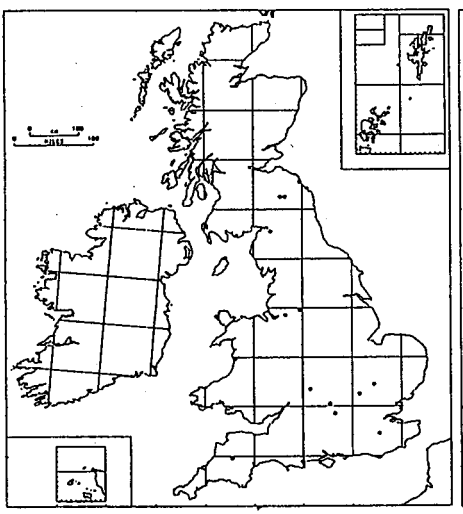


(a) up to and including 1849

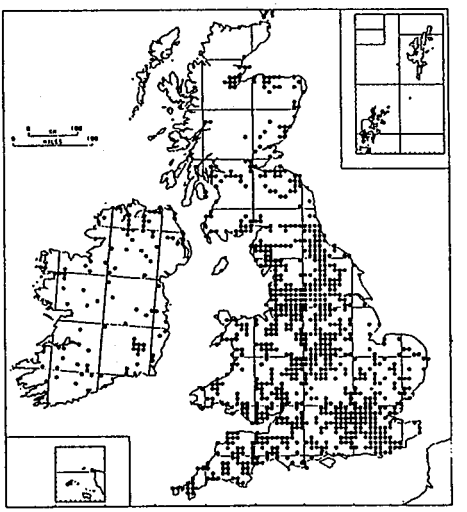


(b) up to and including 1985

Impatiens capensis Meerb



(c) up to and including 1849



(d) up to and including 1985

Impatiens glandulifera Royle.

Figure 1 (a-d). Distribution of Impatiens capensis (a and b) and I. glandulifera (c and d) in the British Isles.

hypothesis of a negative binomial distribution to be rejected, whereas with I. glandulifera the hypothesis would be rejected. One interpretation of these differences in the nature of the distribution of the two species may be the result of a restricted habitat preference operating for I. capensis, I. glandulifera being a more cosmopolitan species.

The main habitats exploited by these species are canals and/or rivers/streams and an analysis of the preference of these two species for these habitat types was undertaken for all the known sites in the counties of Leicestershire and Warwickshire (Cadbury, Hawkes & Readett, 1971) using a chi-square analysis. The analysis gave a value of 134 (d.f. = 3, $p < 0.001$) indicating a clear preference between the habitats in which the two species were found. I. capensis was most common in areas where there were canals and I. glandulifera occurred more frequently near rivers and in regions with less obvious waterways.

DISCUSSION

A rapid spread has been observed for both of these alien Impatiens species, although I. capensis is clearly the least successful in achieving a wide distribution. This species has a preference for canals and has spread rapidly through the extensive canal system of the Midlands. I. glandulifera, a species of rivers, streams and other habitats has established itself as a widely distributed species throughout the British Isles. The dispersal of these species could be dependent upon a number of factors, and, in order to explain the differences in their rate of spread and habitat preferences, these factors will be considered in turn.

The basic mechanism of seed dispersal in both species is by explosive dehiscence of the seed pods. I. glandulifera is a much taller plant (1-2 m) than I. capensis (0.2-0.6 m), but although this might increase stand size, it is unlikely to explain any differences between the local or long distance dispersal of the species. I. glandulifera seeds only travel short distances (Grime, 1979) and the species has been recorded moving by about 3 m per year using this mechanism (Fitch, 1976), while the distance of dispersal of I. capensis is reduced to "almost nothing" when the species is growing in its normally dense stands (Winsor, 1983).

A more relevant factor in the local dispersal of the species from points of colonisation is that of water transport. Examination of the distribution maps of the species show how they have spread along waterways, for example Philp (1982). Clarke (1961) observed that in one year I. capensis moved 1.6 km eastwards along a canal, a distance too far to be accounted for by explosive dehiscence. The dispersion was probably due to the seeds of I. capensis floating along the canal (Ridley, 1930). Observations on the distribution of I. capensis in a lake in Finland lend further support to the transport of propagules by water (hydrochorous dispersal) (Krogerus, 1977). In this example the species spread to many discrete sites on the shoreline and islands of the lake, covering a distance of 6km over 27 years.

I. glandulifera seeds are negatively buoyant and the plant relies on the germination of the seeds on the bottom of the waterbody, a process termed bythisolydrochory. It is not clear whether the seedlings become positively buoyant as in Scrophularia aquatica L. (Ridley, 1930) or are brought to the river margins of the waterway by currents and wave action. Bythisolydrochory was found to be responsible for the distribution of I. glandulifera in the Czech rivers, Svitava, Svaratka and Odra (Lhotska & Kopecky, 1966).

The appearance of the species in new and distant localities up to 300 km from the nearest known source and the transport of I. glandulifera to the Scilly Isles and the Shetland Isles cannot be explained by either the explosive dehiscence of the seed pods or the transport of seeds and seedlings by water. Man must have aided the spread of both species, a conclusion supported by a correspondent in the late nineteenth century who wrote: "I spent some time ... gathering the seed of the plant (I. capensis) with a view to naturalising it on the banks of the Nene" (OXF). Both species have been deliberately introduced into gardens and parklands and have escaped into natural habitats. There is no evidence to support the idea that birds might be responsible for the long distance distribution of the seeds of either of these species. Nevertheless, the possibility of birds and wildfowl in particular feeding on the seeds and acting as a means of dispersal should be investigated.

Consideration of these factors does not satisfactorily explain why I. capensis has not spread as quickly as I. glandulifera. Further investigation is needed to both explore the reference of I. capensis for canal habitat and to investigate other aspects of the autecology of these species, for example possible competition between the two species and the significance of the lack of prolonged seed dormancy in I. capensis (Winsor, 1983).

I. capensis and I. glandulifera have all the advantages of alien species: few pathogens, phytophagous insects and other herbivores, and none which are known to be specific to either species. Additionally they have all the advantages of being annual plants. It is easy to understand their success in establishing themselves in the flora of waterways. The difference between such superficially similar plants in the degree to which they have distributed themselves is both surprising and harder to account for. This observation emphasises the care which needs to be taken before coming to conclusions about the potential for a given species to reach pest status on the basis of the autecology and biology of similar closely related species.

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Résumé: Les distributions sont décrites et comparées pour Impatiens capensis Merrb. et I. glandulifera Royle., deux mauvaises herbes récemment introduites dans les canaux des iles britanniques. La vitesse de propagation et les caractéristiques d'habitat de ces deux espèces ont été analysées et correlées à des stratégies possibles de dispersion. Des modèles fondés sur des données détaillées de la migration de ces espèces dans trois régions depuis leur introduction au cours du dix-neuvième siècle sont proposés. Les implications pour contrôler les infestations de ces plantes aquatiques sont prises en consideration et la nécessité de considérer chaque entité séparément est mise en valeur.