

The dispersal characteristics of the invasive plant *Mimulus guttatus* and the ecological significance of increased occurrence of high-flow events

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Summary

1 Increased occurrence of high-flow events as a result of climate change may affect the dispersal success of an invasive plant species *Mimulus guttatus* and may result in range expansion. Predicted changes in climate point to a continuation of the recent observed trends in increased precipitation and high-flow events in Northern Europe.

2 The study focused on the dispersal characteristics of *M. guttatus*, and especially the roles of vegetative fragmentation with increasing water velocities, subsequent fragment survival, regeneration and colonization, as well as the buoyancy, survival and germination success of seeds.

3 *M. guttatus* was found to fragment readily under velocities typical of high flow conditions and even small fragments had high survival, regeneration and colonization capacity.

4 Large numbers of small (< 0.02 mg) seeds are produced; however, seeds have a short buoyancy period so the timing and magnitude of high-flow events is crucial in determining potential dispersal distances. Seeds germinate readily both in water and on sand with an average 33% germination within 9 days.

5 The dual strategy of dispersal by vegetative fragments and seeds, together with the opportunity of dispersing the two types of propagules during different periods of the year, facilitates local dominance by *M. guttatus* as well as long-distance colonization. As a result, the rate of spread of *M. guttatus* into inundation communities along rivers is likely to increase with more frequent high-flow events, especially if these coincide with the growing season. Thus, predicting the response of riparian invasive species to environmental change requires not only an understanding of the role of climate in plant demography but also the impact of changes in hydrology on rates of spread.

Key-words: biological invasion, climate change, flooding, fragment, regeneration, riparian, spread

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Introduction

The spread of non-native plant species is increasingly recognized as a potential threat to the biodiversity and ecological integrity of semi-natural ecosystems (Tickner *et al.* 2001; Hulme 2003) yet historical patterns of invasion may not necessarily reflect future trends under environmental change. To date, concern as to how environmental change may impact on non-native plant invasions has

largely focused on the direct effects of climate (Walther 2000; Thuiller *et al.* 2005). By contrast, the potential effects of changes in the seasonality and volume of precipitation on non-native plant spread has received far less attention. Empirical evidence and climate change scenarios point to a recent and ongoing increase in the frequency and magnitude of high precipitation and high-flow events, particularly in the autumn and winter in the middle and high latitudes of the northern hemisphere, including the United States (Karl & Knight 1998; Milly *et al.* 2002; Groisman *et al.* 2004), the UK (Osborn & Hulme 2002; Werritty 2002; Ekstrom *et al.* 2005) and

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most extratropical land areas except China (Groisman *et al.* 1999).

Short-term high-flow events (flood pulses) are increasingly recognized to shape riverine landscape heterogeneity, productivity and nutrient status, as well as the composition and structure of riparian vegetation (Junk *et al.* 1989; Bendix & Hupp 2000; Tockner *et al.* 2000). In addition, such hydrological disturbance facilitates the establishment of non-native species and as a consequence riparian habitats appear to be particularly susceptible to plant invasions (Stromberg *et al.* 1997; Pyšek *et al.* 1998; Hood & Naiman 2000). Therefore, unpredictable flood pulses may increase the likelihood of plant invasion by altering the competitive balance between native and non-native species, redistributing nutrients, facilitating the colonization of non-native species through increased disturbance and/or enhancing the dispersal of propagules within catchments. Recent research has highlighted how changes in the hydrological regime may alter the competitive balance between native and non-native species to favour the latter (Pettit *et al.* 2001; Wei & Chow-Fraser 2006). However, in addition to changes in competitive interactions, increased frequency of flood pulses may also facilitate wider dispersal of non-native plants within catchments.

Invasive plant species often possess life-history traits that might predispose them to succeed in the face of unpredictable flood pulses, including vegetative reproduction, release of large numbers of small seeds with broad germination requirements, effective long- and short-distance dispersal mechanisms, and long flowering period (Perrins *et al.* 1992; Thompson *et al.* 1995; Williamson & Fitter 1996; Goodwin *et al.* 1999; Higgins *et al.* 2003; Pyšek & Hulme 2005).

Dispersal of seeds by water (hydrochory) is one of the major dispersal mechanisms for plants along rivers, and dispersal is normally unidirectional (Johansson *et al.* 1996). Per capita seed output has been shown to explain most of the variation in the number of seeds trapped downstream in a diaspore trap (Boedeltje *et al.* 2003) and in determining the probability of patch invasion (Levine 2000). In addition, if seed release coincides with high flows, seed buoyancy may also be significant in determining the effectiveness of hydrochorous dispersal (Johansson *et al.* 1996; Nilsson *et al.* 2002; Boedeltje *et al.* 2003, 2004).

Traditionally, vegetative propagation has been viewed as a feature facilitating the local dominance of invasive species (Williamson & Fitter 1996), yet if it facilitates vegetative fragmentation, this may represent an efficient adaptation to the unpredictability of high-flow events (Barrat-Segretain *et al.* 1998). Dispersal via vegetative fragments is frequently found in aquatic and riverine plants and can contribute significantly to long-distance dispersal along rivers (Johansson & Nilsson 1993; Barrat-Segretain *et al.* 2002; Boedeltje *et al.* 2004). Long-distance dispersal may be of particular significance in maintaining regional populations of species that are patchily distributed and exhibit local extinction and colonization events (Freckleton & Watkinson 2003). In

addition, for species management, knowledge of the likely dispersal patterns is essential to predict rates of spread (Collingham *et al.* 1997) and in the targeting of resources in control strategies (Wadsworth *et al.* 2000).

It is with this background that the riparian invasive species *Mimulus guttatus* L. (Scrophulariaceae) (hereafter *Mimulus*) is used as a model to address the likelihood that flood pulses might facilitate the spread of non-native plants and understand the relative contribution played by vegetative fragments and seeds. A series of experimental glasshouse studies was designed to determine whether vegetative fragments are able to regenerate (regrow into viable plants) and colonize (produce roots) above a minimum fragment length. Flume experiments were used to assess whether a threshold velocity existed above which plants fragment or are uprooted, and hence to predict the potential effect of high-flow events on vegetative fragment dispersal. Seed dispersal success as an important determinant of patch invasion was assessed by quantifying per capita seed output and seed buoyancy and relating this to the hydrological conditions during the seed release period.

Materials and methods

STUDY AREA

The study was conducted in the Tarland Burn, a tributary of the River Dee in north-east Scotland (57°07' N, 02°51' W). Sections of the main stem of the Tarland Burn are heavily channelized, like many rivers in north-east Scotland (Soulsby *et al.* 2001). The hydrological regime shows marked seasonal and interannual fluctuations with high flows and flooding in recent years (April 2000 and October/November 2002). On 22 October 2002, the River Dee reached the third highest level in 31 years; on 21 November it reached the highest levels since records began (gauging station 57°04' N, 02°20' W). This pattern was reflected across the major tributaries including the Tarland Burn. High summer flows have also occurred; in August 2004 at a gauged section of the Tarland Burn, flows of 5.24 m³ s⁻¹ were recorded compared with a yearly average flow of 0.83 m³ s⁻¹ (R. Fraser, personal communication). To examine how temporal variability in hydrological and hydraulic conditions might affect *Mimulus* dispersal within and between years, a velocity time-series for the Tarland catchment was constructed (Fig. 1).

STUDY SPECIES

Mimulus was introduced to the UK from western North America in c. 1812, being established in the wild by 1824. Records of *Mimulus* in the River Dee catchment date back to 1865. A perennial riparian herb, it is generally found in wet places by streams, rivers, ponds, and in marshy-ground (Preston *et al.* 2002). *Mimulus* exhibits several traits thought to characterize a successful invasive species: a competitive-ruderal life history strategy (Grime *et al.* 1988), high seed production (Vickery 1999), a short germination period (Lindsay 1964), effective

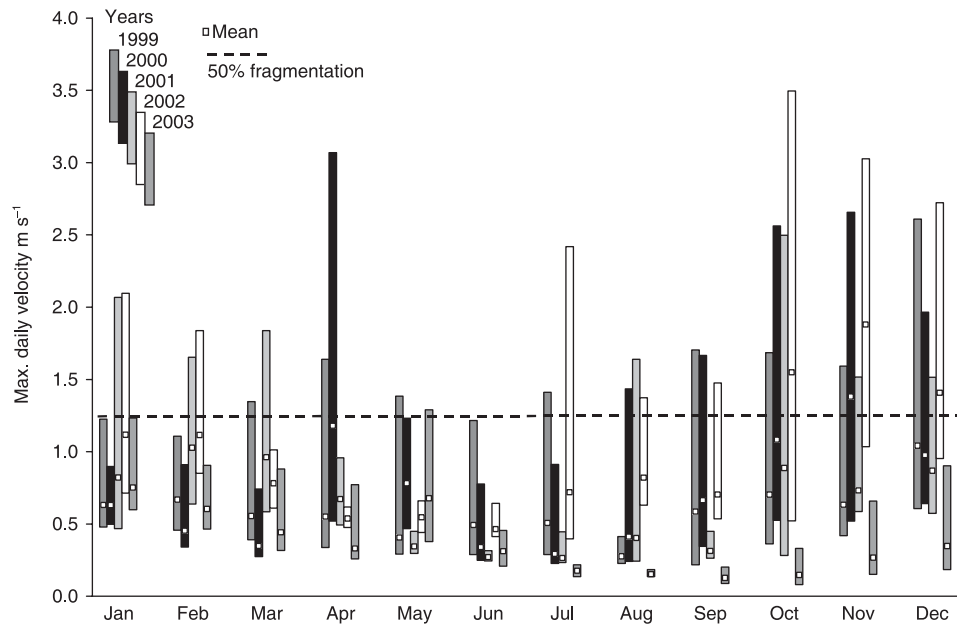


Fig. 1 Velocity time series for the Tarland catchment, 1999–2003. The extent of the bars shows the range of the maximum daily velocities throughout the month; the squares show the monthly average of the maximum daily velocities. The discharge-mean velocity relationship for a gauged section of the Tarland Burn at Aboyne ($57^{\circ}07' \text{ N}$, $02^{\circ}46' \text{ W}$) was derived (for derivation see Tetzlaff *et al.* 2005). A power function best described the relationship for mean flows ($r^2 = 0.97$) and maximum flows ($r^2 = 0.92$). Five years of discharge data collected at Coull in the Tarland catchment ($57^{\circ}06' \text{ N}$, $02^{\circ}48' \text{ W}$) were adjusted to discharges equivalent to those at Aboyne on a catchment area proportional basis and from these data the velocity time series was constructed. The dotted line represents 50% *Mimulus* fragmentation threshold as determined in the flume (see Methods).

long- and short-distance dispersal mechanisms (Vickery *et al.* 1986) and rapid growth (Vickery 1978; Waser *et al.* 1982). In north-east Scotland, *Mimulus* plants emerge in April/May, flowering commences in mid-June and seeds ripen any time from the beginning of August to the end of September (peaking in mid-August). Plants then die back in October, but rhizomes survive well over winter.

Mimulus was recorded in 744 (c. 25%) of the 10-km squares of Great Britain in the recording period 1987–99 (Preston *et al.* 2002). A survey of the Tarland Burn in 2003 revealed that *Mimulus* occurred throughout the 74-km² catchment, and that the largest populations, occurring at the top of the tributaries, may act as source populations (A.-M. Truscott *et al.* unpublished data). *Mimulus* often occurs in discrete patches along streams. Inter-annual variations in local population size reflect frequent extinction and colonization events, such that only a proportion of patches suitable for *Mimulus* appear occupied at any time. The mean distance between *Mimulus* patches along a tributary in the study catchment was c. 9 m, but some patches were separated by as much as 2 km. Therefore, both short- and long-distance dispersal events may be important.

REGENERATION AND COLONIZATION POTENTIAL OF VEGETATIVE FRAGMENTS

Ninety *Mimulus* plants were collected in July 2004 from each of four sites in Aberdeenshire separated by between 1 km and 15 km within a 20-km radius of the Tarland catchment. The plants from each site were allocated at random to 15 samples each of six types of

vegetative fragments: whole plant (including below-ground parts) and fragments of shoot (one, two, three, four or five nodes). The fragments were placed on the surface of 30 plastic trays ($54 \times 34 \times 8$ cm) filled to a depth of 1 cm with sand that was subsequently covered to a depth of 3 cm by local river water. The river water had relatively low nutrient concentrations, annual mean $\text{NO}_3\text{-N}$ content of 3.2 mg L^{-1} , pH 7.4 with soluble $\text{PO}_4\text{-P}$ always below the limit of detection (C. Soulsby, unpublished data) and the sand used was lime-free horticultural-grade sharp sand (William Sinclair Horticulture Ltd). Trays were kept in a glasshouse with ambient light conditions, maintained as closely as possible to monthly average temperatures, and river water was regularly added to maintain a constant water level. Each tray contained 12 samples, one of each type of fragment from two sites using a combination of pairs of sites. Fragment length and stem diameter were recorded at the start of the experiment. At 1, 2, 4 and 6 weeks, the number of new nodes, new shoots per node and leaves per node were recorded for each node on each fragment as a measure of regeneration success. The number of new flowers per fragment was also recorded. The number and position of nodes with root development were recorded as a measure of colonization potential.

FRAGMENTATION OF *MIMULUS* AT DIFFERENT VELOCITIES

Experiments to examine the effect of velocities on *Mimulus* fragmentation were carried out in an indoor

open channel flume at Aberdeen University. The flume was 12 m long \times 0.3 m wide \times 0.5 m deep with a variable bed slope. A pump controlled water discharge with a range of $\approx 5 \text{ L s}^{-1}$ up to 40 L s^{-1} . A weir controlled depth. Discharge was manipulated at intervals of 5 L s^{-1} with bed slope set at 0.01 m to achieve a range of velocities from 0.8 m s^{-1} to 1.5 m s^{-1} , similar to the velocities within the Tarland catchment (Fig. 1). A drift net (mesh size 1 mm^2) that filled the entire width and depth of the flume was fixed at the downstream end of the flume to capture all plant fragments and sediment. Velocity was measured using an electromagnetic flow meter (SENSARC2; Aqua data services Ltd) at $0.4 \times$ depth of the water channel. The mean velocity and standard deviation over a 30-s period was recorded. A series of four 15-min trials was conducted at each discharge rate to estimate the parameters of a linear regression relationship between discharge and velocity.

Sample cores of *Mimulus* rooted in sediment were collected from four sites in the Tarland catchment on two different tributaries, with no two sites closer than 0.5 km. Sites were selected from the uppermost reaches of tributaries (within 1.5 km of source). Plants growing in these uppermost reaches are likely to be important in the long-distance dispersal of fragments, as they formed the largest populations and dispersal is principally downstream. Hence, we regard them as the principal source populations. The cores had a surface area of approximately 700 cm^2 and had a *Mimulus* cover of more than 75%. Prior to placing in the flume, the number of erect *Mimulus* stems in each core was counted. Seven cores were collected from each site and allocated at random to seven discharge rates ranging from 5 L s^{-1} to 35 L s^{-1} . The cores were set in the upper quarter of the flume so that the presence of the drift net did not increase hydraulic resistance in the area where the cores were positioned. The cores were affixed in position using marbles to act as artificial sediment. During the trials the *Mimulus* stems were submerged in water. Each trial was operated for 15 min and fragments that broke off were counted and collected, and records made of the length, diameter, number of nodes, number of leaves and whether the break was at a node or not. Trials were also conducted in which single stems were attached in the flume using a clamp.

SEED NUMBER, BUOYANCY AND GERMINATION SUCCESS

To assess propagule pressure, the number of seed heads per upright stem was counted in September 2002 and September 2003 and the number of seeds per seed head was counted in September 2002. Seeds were collected from three sites on three different tributaries in the Tarland catchment in September 2003 and 100 ripe seeds were introduced immediately after seed collection into each of 15 replicated polythene beakers per site containing river water. The beakers were allocated at random to one of three treatments to reduce the influ-

ence of surface tension and simulate water movement, namely stirring for 5 s, exposure on a shaker for 1 min and exposure on a shaker for 5 min; experiments without stirring tend to overestimate the floating abilities of seeds (Bill *et al.* 1999). Each site/treatment combination was replicated five times. The number of floating seeds was counted after 1, 2, 4 and 8 h and then after 1, 2, 3, 4, 6 and 9 days. The proportion of propagules staying afloat provides an index of buoyancy (Danvind & Nilsson 1997; Boedeltje *et al.* 2003). Seeds germinated while in the beakers and their germination in water was recorded in half the beakers after 9, 12, 18 and 90 days.

After 2 days in the buoyancy trial, seed samples from half of the beakers were sprinkled onto the surface of seed trays lined with 2 cm of sterile sand and covered with a further thin layer ($< 1 \text{ mm}$) of sand. To compare the effect of water immersion on germination rate, 100 seeds that had no prior immersion in water were placed in each of 15 seed trays (five trays from each of three sites). The seed trays were kept in a glasshouse with ambient light conditions, mean temperatures of $17 \text{ }^\circ\text{C}$ by day, and $12 \text{ }^\circ\text{C}$ by night, daily watering and no fertilizing. For both trials in sand, germination rates were recorded after 7, 10, 17, 24 and 38 days.

DATA ANALYSIS

All analyses were carried out in SAS v.8.02 (SAS 1999). Analyses of regeneration (development of new nodes, shoots and leaves, and shoot extension) and colonization potential (development of roots) of the different fragment types were performed by fitting generalized linear mixed models (GLIMMIX macro). Tray, site and a tray by site by fragment type interaction term were included as random effects; fragment type and week plus their interaction term were fixed effects. The models included as appropriate either: (i) a Poisson error term, logarithmic link function and the logarithm of initial node number as an offset; or (ii) a binomial error term and logit link function.

Fragmentation was analysed as a function of velocity by fitting general linear models (GLM procedure). The linear regression equation for the relationship between discharge and velocity was used to calculate estimated velocity. The proportion of stems fragmenting within each core was transformed by the logit function. Velocity and site were included as fixed effects. A quadratic velocity term was included to allow for maximum fragmentation probability at intermediate velocities, but as this was non-significant it was discarded. Fragment characteristics were analysed by fitting linear mixed models (MIXED procedure). Velocity and site were included as fixed effects and core as a random effect. Response variables were log transformed to meet assumptions of homogeneity of variance.

Analyses of seed buoyancy and seed germination were performed by fitting generalized linear mixed models (GLIMMIX macro). Site and replicate were included as random effects; treatment and a treatment by log time

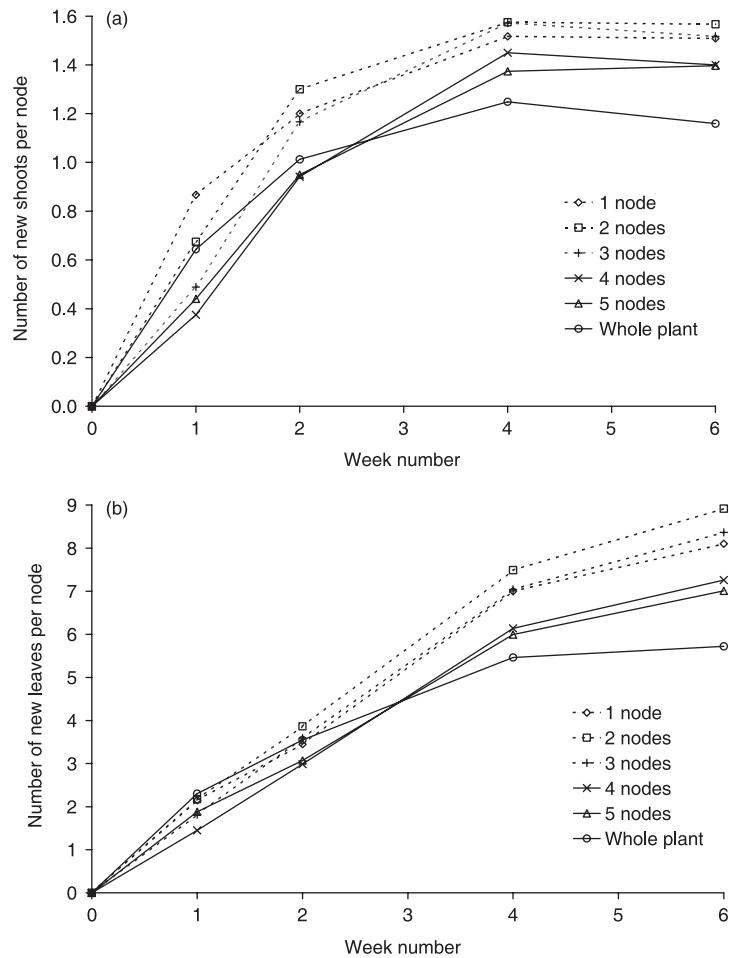


Fig. 2 Number of (a) new shoots and (b) new leaves per node developed by six fragment types of *Mimulus* over a 6-week period.

interaction were included as fixed effects for the seed buoyancy model; treatment and hour were included as fixed effects for the germination model; both models had a binomial error term and logit link function.

Results

REGENERATION AND COLONIZATION POTENTIAL OF VEGETATIVE FRAGMENTS

Regeneration potential

The vegetative regeneration of *Mimulus* fragments was high. After only 1 week, 60% of the fragments produced new shoots and 75% produced new leaves, and at 6 weeks, 96% of fragments had new shoots. There were significant differences between fragment types in the number of new shoots and the number of new leaves produced per node ($F_{5,284} = 5.1, P < 0.001$; $F_{5,264} = 5.5, P < 0.001$, respectively; Fig. 2a,b). Fragments of one and two nodes produced significantly more shoots per node than fragments of four nodes, five nodes and whole plants (Tukey HSD test $P < 0.01$). There was a highly significant effect of week for the number of new shoots and new leaves per node ($F_{3,1024} = 266, P < 0.001$; $F_{3,990} = 702, P < 0.001$, respectively), but fragment types differed

temporally in their development (interaction terms: $F_{15,1024} = 5.2, P < 0.001$; $F_{15,990} = 6.1, P < 0.001$, respectively). Fragments of one and two nodes showed significantly greater shoot development in week 1, but not thereafter, whereas whole plants had produced the fewest shoots per node by week 6 (Tukey HSD test $P < 0.05$).

Only 2% of fragments produced a new node within the first 2 weeks. However, by week 4 this had risen to over 80%. In week 4, fragments of one node were significantly less likely to produce new nodes than any other fragment types ($F_{3,324} = 6.7, P < 0.001$; Tukey HSD test $P < 0.05$). Over the 6-week period there was a mean increase of 49 mm in length for fragments of one node, equivalent to 1.2 mm day^{-1} , substantially less than the 4.5 mm day^{-1} and 6.1 mm day^{-1} for fragments of five nodes and for whole plants, respectively. After 6 weeks, 24% of fragments had produced flowers. There was a high survival rate of fragments. Less than 10% of fragments had any dying shoots even after 6 weeks and half of these were fragments of five nodes or whole plants.

Colonization potential

After 1 week, 36% of fragments formed roots at the nodes, and after 6 weeks, this figure had risen to 99%. There was a highly significant difference between weeks

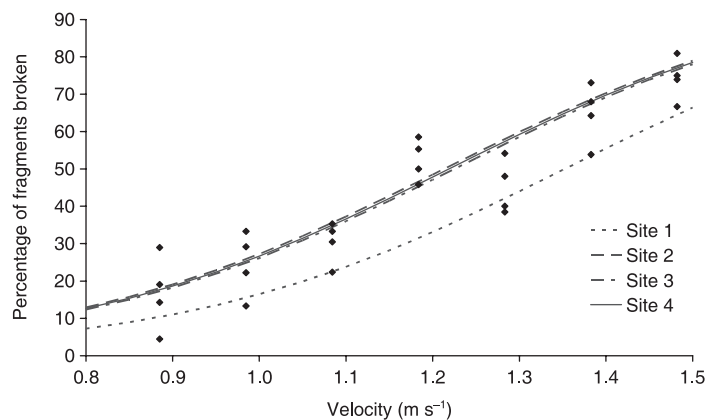


Fig. 3 Modelled probability of fragmentation as a function of flume velocity for *Mimulus* fragments collected from four sites.

($F_{3,957} = 804$, $P < 0.001$) in the probability of a node producing roots except between weeks 4 and 6, as the majority of roots had been produced by week 4. However, fragment types differed in the timing of root development (fragment type-week interaction: $F_{15,1016} = 19.6$, $P < 0.001$). Nodes on whole plants were more likely to develop roots after 1 week than on any other fragment type (Tukey HSD test $P < 0.05$), whereas from week 2, nodes on fragments of one and two nodes were significantly more likely to develop roots than other fragment types (Tukey HSD test $P < 0.001$). Roots were produced between nodes as well as at nodes, and the incidence of root production along the main stem after 6 weeks was significantly lower for whole plants compared with all other fragment types ($F_{5,325} = 17.0$, $P < 0.001$; Tukey HSD test $P < 0.001$). Roots were also observed to develop on new shoots with 71% of new shoots possessing roots by week 6.

FRAGMENTATION OF *MIMULUS* AT DIFFERENT VELOCITIES

There was a highly significant linear relationship between discharge manipulated at 5 L s⁻¹ intervals and flume velocity (velocity = $0.0199 \times \text{discharge} + 0.786$; $R^2 = 0.96$). The proportional fragmentation was significantly greater at higher velocity ($F_{1,23} = 139$, $P < 0.001$; Fig. 3); 74% of stems were broken at 1.48 m s⁻¹ compared with 17% at 0.88 m s⁻¹. Velocity accounted for 80% of the total variance and site for an additional 7%. There was a significant difference between site 1 and sites 2, 3 and 4 (Tukey HSD test $P < 0.01$).

Fragment length ($F_{1,21} = 6.1$, $P < 0.05$; Fig. 4a) stem diameter ($F_{1,26} = 11.5$, $P < 0.01$; Fig. 4b) and the number of nodes per fragment ($F_{1,23} = 7.37$, $P < 0.05$) all increased significantly with increased velocity. At the lower velocities, it was principally the most recent plant growth that fragmented, whereas at higher velocities, stem breakage also occurred further down the plant. A few fragments were broken at both ends, indicating that two separate fragmentation events had occurred. At a velocity of 1.38 m s⁻¹, the largest broken fragment was 16 nodes long and measured 64 cm. Overall, 76% of stems

fragmented at a node. However, some stems fragmented between nodes (internodal), and at higher velocities a number of stems were uprooted from the sediment. At a velocity of 1.28 m s⁻¹, 33% of fragments broke between nodes, 58% at a node and 9% were uprooted.

The number of fragments of different node number varied over the velocities applied. Single node fragments were most numerous at intermediate velocities of 1.18 m s⁻¹, whereas fragments of more than six nodes were most numerous at the higher velocities. Trials conducted in which single stems were attached in the flume revealed that single stems rarely broke, as the stem orientated itself in the direction of the flow (i.e. in the line of least resistance), whereas the chaotic nature of plant stems in a patch resulted in high rates of breakage.

SEED NUMBER, BUOYANCY AND GERMINATION SUCCESS

Individual *Mimulus* stems produced on average 15.7 seed heads in 2002 (± 0.8 SE, $n = 75$) and 15.1 seed heads in 2003 (± 0.3 SE, $n = 912$). In 2002, average seed production per head was 464 (± 18 SE, $n = 148$), with a range of 65–1248. Thus, an average *Mimulus* stem may release over 7000 seeds. *Mimulus* seeds are small (c. 0.02 mg, 0.5 mm wide \times 1.0 mm long) and have a high terminal velocity in air (1.19 ± 0.13 m s⁻¹; $n = 20$; K. Thompson, personal communication).

In the seed buoyancy trials, there was a highly significant log time by treatment interaction ($F_{3,364} = 462$, $P < 0.001$; Fig. 5) over the full experimental period of 216 h. The average rate of seed sinking differed significantly between the 5-s stirring treatment and the two shaking treatments ($F_{1,364} = 4.3$, $P < 0.05$), although the most marked differences between treatments occurred in the first 2 h. After 2 h, on average 79% of the seeds had sunk, 90% of the seeds after 4 h, and after 2 days of immersion 99% of the seeds had sunk.

Germination in the beakers occurred 4 days after the seeds were placed in water. After 9 days, 33% (± 2.5 SE) of the seeds had germinated, and after 18 days, 40% (± 2.8 SE) of the seeds had germinated on average, of

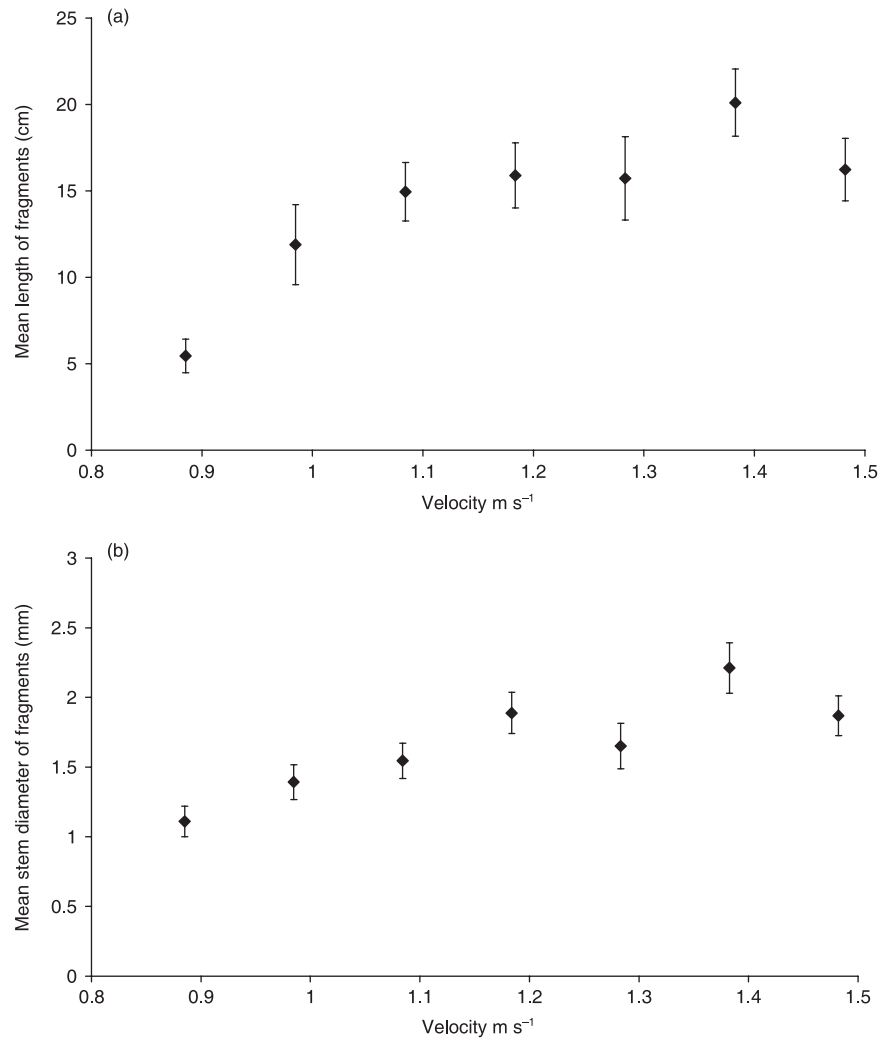


Fig. 4 (a) Mean length and (b) mean stem diameter of *Mimulus* fragments as a function of flume velocity. Error bars show ± 1 standard error.

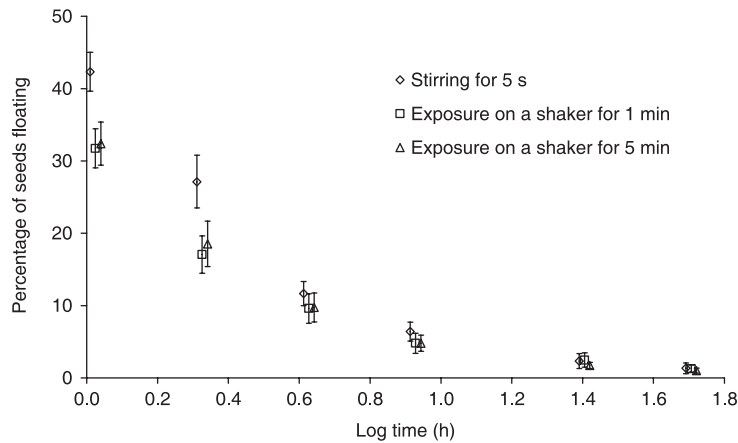


Fig. 5 Buoyancy of *Mimulus* seeds following three water movement simulation treatments. Symbols are offset on the x-axis for clarity. Error bars show ± 1 SE.

which two-thirds were floating on the surface. Seedlings that had germinated in water had a high survival rate, and after 90 days in the beakers, only 20% had died. Seeds exposed to the 5-s stirring treatment were significantly more likely to germinate than those that had

experienced the 5-min shaking treatment ($F_{2,20} = 4.3$, $P < 0.05$; Tukey HSD test $P < 0.05$; Table 1). There was also a significant effect of time ($F_{3,70} = 11.4$, $P < 0.001$; Tukey HSD test $P < 0.01$) in the percentage germination except between 12 and 18 days.

Table 1 Germination (%) of *Mimulus* seeds following three water movement simulation treatments. Standard errors are shown in parentheses

Number of days	Stirring for 5 s	Exposure on shaker for 1 min	Exposure on shaker for 5 min
9	43 (3.3)	30 (3.9)	29 (4.3)
12	47 (4.5)	33 (4.3)	36 (5.2)
18	51 (4.2)	36 (4.0)	35 (4.5)
90	42 (5.6)	28 (4.4)	30 (4.6)

Germination of seeds in sand was rapid; seedlings emerged 3 days after planting. There was no significant difference in percentage germination between seeds exposed to the initial three water movement simulation treatments or between those that had experienced a buoyancy trial and those that had not. After 7, 10 and 38 days, 23% (± 2.7 SE), 31% (± 3.6 SE) and 39% (± 4.6 SE) of seeds had germinated, respectively. Comparable levels of germination ($31 \pm 2.1\%$) of seeds in sand were recorded in 2002.

Discussion

REGENERATION AND FRAGMENTATION OF *MIMULUS* IN RELATION TO RIVER VELOCITIES

Mimulus fragments show a range of regenerative characteristics, which make the species well adapted to the uncertainty of high-flow events. Survival of fragments was high and in agreement with data from North American populations (Lindsay 1964). *Mimulus* exhibited similar, if not higher, regeneration (95% vs. 75%), growth and survival rates compared with another highly successful invasive species *Fallopia japonica* (De Waal 2001; Bimova *et al.* 2003). The invasive species *Elodea canadensis*, *E. nuttallii* (Barrat-Segretain *et al.* 2002) and *Reynoutria* spp. (Bimova *et al.* 2003) have also been shown to have high fragment survival rates. Even small *Mimulus* fragments survived and grew in nutrient-poor sediments, such as sand.

Mimulus fragments are well adapted to colonization, as fragments of any length exhibited root extension from both the nodes and along the main stem. New shoots also produced roots; hence, these could also fragment and potentially regenerate and colonize. Again, rapid root development has been found in other invasive plants, e.g. *Myriophyllum spicatum*, *E. canadensis* and *E. nuttallii* (Valley & Newman 1998; Barrat-Segretain *et al.* 2002). The conditions after high water levels, including the water saturation of the soil, may influence the regenerative potential of deposited fragments, i.e. if they do not establish roots within a short time period after high water levels they may not survive. However, after 6 weeks, only a small proportion of *Mimulus* fragments displayed leaf or stem senescence. Some fragments developed their first roots after 4 weeks, and hence had the capacity to colonize. The regenerative potential will decrease as

plants senesce, yet the 5- to 6-month growing season results in a prolonged high regenerative capacity.

Mimulus readily fragments under high flow conditions. The mean percentage fragmentation was significantly greater at higher velocities. The average fragment length, stem diameter and the number of nodes all increased with increasing velocities in the flume. At lower velocities, it was principally recent plant growth, typically the top few nodes of the stem, that fragmented. Young shoots may therefore be most prone to fragmentation, but it will be dependent on species associations, vegetation height and hence orientation of stems and drag resistance. Most of the fragmentation in the flume occurred in the first 5 min of the 15-min exposure. Although events with high (above fragmentation threshold) velocities can last for 24 h or more, the highest shear stresses during events are usually experienced on the rising line of the hydrograph. Thus, fragmentation would primarily be a stress magnitude rather than a duration issue. Alternatively, prolonged high-flow events may gradually weaken *Mimulus* stems, so the estimates of percentage fragmentation may be conservative. Flumes provide an idealized representation of a river channel and can be used for controlled measures of effects of water velocity on aquatic organisms or sediment mobilization (Gibbins *et al.* 2005). Although the experimental flume was narrow and lacked heterogeneity, many streams in north-east Scotland have been straightened and simplified as a result of past canalization (Soulsby *et al.* 2001).

The flume velocity at which half of the *Mimulus* stems fragmented was approximately 1.25 m s^{-1} , and in the Tarland catchment the maximum velocity exceeded this value on c. 10% of days between 1999 and 2003, representing 3% of days during the main growing season of *Mimulus* from May to October, and 15% of days from October to May. Over winter, perennial plants may exist as stolons or small plants and therefore the rates of fragmentation may differ from those in July. The probability of fragmentation of *Mimulus* plants would have been low in July 2003, a month with uncharacteristically low rainfall (mean and highest maximum daily velocity of 0.18 m s^{-1} and 0.22 m s^{-1} , respectively). In comparison, in July 2002, half of the 45 000 stems recorded along the main stem (9 km) of the Tarland catchment (A-M. Truscott, unpublished data) could have been prone to fragmentation as the 50% fragmentation threshold of 1.25 m s^{-1} was exceeded on 3 days (mean and highest maximum daily velocity of 0.72 m s^{-1} and 2.41 m s^{-1} , respectively). Therefore, at the 50% *Mimulus* fragmentation threshold of 1.25 m s^{-1} , fragments could be transported 4.5 km in a hour and a fragment could cover the length of a tributary in a couple of hours. However, this is unlikely, as the vegetated banks are hydraulically rough and will trap fragments. Similarly, fragments will be trapped by stones, debris, fence posts, bridge piers, etc., as has been observed following high water levels in the Tarland catchment (A-M. Truscott, unpublished data). *Mimulus* patches generally occur within 1 m of the river edge with patches closest to the

river most prone to fragmentation. Although the precise relationships between velocity and percentage fragmentation in the flume cannot be used as universal predictors for fragmentation rates in river systems, the data provide an indication of the high levels of fragmentation that can occur under high flow conditions and the associated temporal variability.

Mimulus possesses a shallow root system (1–2 cm depth), and where it colonizes fine sediment, such as silt, plants can be easily uprooted under high flow conditions. Levine (2001) found that downstream dispersal of entire tussocks containing *Mimulus* occurred during winter floods, with subsequent re-establishment downstream. High-flow events will affect different stages of *Mimulus* colonization, establishment and spread. If high-flow events occur at too high a frequency, populations may not re-establish before the next high-flow events, preventing growth and long-term survival (Johansson & Nilsson 2002). Owing to its rapid regeneration and colonization ability, however, this may not be so significant for *Mimulus*.

SEED DISPERSAL OF *MIMULUS* IN RELATION TO TEMPORAL VARIATION IN RIVER VELOCITIES

Mimulus seed numbers per seed head (mean 464) were higher than those reported from populations in the native range (mean 110; Lindsay 1964). *Mimulus* seeds do not remain buoyant, and seeds that were shaken in water to simulate turbulent water and high flows had significantly lower buoyancy in the first couple of hours than those that were stirred for 5 s. Seed buoyancy and seed release period have been shown to account for 43% of the variation in the length of the seed dispersal period (Boedeltje *et al.* 2004). Buoyancy may not be so significant in rivers that experience high flows as even seeds that have a short buoyancy time are dispersed effectively during floods (Bill *et al.* 1999; Andersson *et al.* 2000).

The timing and length of the seed release period and the prevailing flow conditions may be especially important in determining seed dispersal success. *Mimulus* seeds are released any time from the beginning of August to the end of September in north-east Scotland. The velocity data for the Tarland catchment reveal that the seed release period coincided with low velocities in August 1999 (average maximum daily velocity 0.28 m s^{-1}), whereas in August 2002 the average maximum daily velocity was 0.82 m s^{-1} with a peak at 1.37 m s^{-1} . Therefore, in August 2002, seeds that were still buoyant after an hour (c. 35%) could be transported 3 km compared with 1 km in 1999. Hence, in 2002, we would expect higher mean and maximum dispersal distances and hence potential range expansion. Seed mimics of *Mimulus* have been found 4.5 km downstream from release points following winter floods (Levine 2001). Similarly, the rapid spread of *Fraxinus ornus* along a river in southern France is thought to have been due to periodic flooding in

autumn (Thebaud & Debussche 1991). Further examples have been cited by Andersson & Nilsson (2002) and Boedeltje *et al.* (2004).

The relative significance of seed dispersal vs. vegetative dispersal is an important consideration. Although vast numbers of seeds are produced (c. 7000 per upright stem) they are only dispersed from the beginning of August to the end of September. Therefore, their importance in terms of long-distance dispersal is dependent on the flow and weather conditions during that period. By contrast, fragments have been observed throughout the summer, autumn and early winter, and high-flow events may result in fragmentation, long-distance dispersal and colonization of new patches. The largest populations of *Mimulus* were at the top of the tributaries, where velocities are generally lower and the riverbanks hydraulically rougher than downstream; hence, one would expect less fragmentation but higher trapping and establishment success than further downstream. Fragments have different deposition patterns than seeds. Fragments are more likely to be deposited among closed vegetation and debris whereas seeds may be deposited principally on bare sediment. In addition, regenerating fragments may be able to compete with established vegetation and thus have a higher probability of establishment than individual seeds.

The existence of seed banks needs to be considered if effective management of invasive species is to be carried out. A transient, over-winter seed bank exists for *Mimulus*, although it was not sizeable. For example, only six seedlings germinated from soil cores of 8 cm depth by 6 cm diameter taken from each of 20 sites in March 2003 where *Mimulus* was known to be present the previous summer (A.-M. Truscott, unpublished data). As *Mimulus* seeds may establish a short-term seed bank (Goodson *et al.* 2002), the potential exists for the seeds in seed banks to be redistributed in sediment following flood pulses, subsequently germinating and colonizing areas elsewhere. The highest maximum flows are generally observed through the winter months from October to February, and this is when sediment is most likely to be re-deposited, which will affect seedbank persistence and turnover. Other agents known potentially to disperse *Mimulus* such as deer and birds (Lindsay 1964; Vickery *et al.* 1986) should also be considered, as they may be particularly important in dispersal upstream and between tributaries and catchments. Deer frequent stream banks and graze *Mimulus* and cattle seem to graze *Mimulus* stems selectively. Wind appears unlikely to disperse *Mimulus* seeds over long distances (Waser *et al.* 1982; Vickery *et al.* 1986), despite their small size. Long-distance dispersal events play an important role in plant invasions yet are notoriously difficult to estimate. Genetic analyses could be a promising way of estimating the rates of migration and population connectivity. However, the use of genetic analysis for assessing dispersal can be complicated by a number of factors, including independent introductions, genetic drift and stochastic events (Walker *et al.* 2003).

THE IMPLICATIONS OF CLIMATE CHANGE
AND INCREASED OCCURRENCE OF HIGH-
FLOW EVENTS FOR *MIMULUS* DISPERSAL

Changes in the seasonality of extreme rainfall and high-flow events will have ecological implications for the dispersal of riverine species. The magnitude and frequency of high-flow events may be important in determining the level of fragmentation, the dispersal distance and the disturbance intensity. Changes in 'flood pulse' activity, in particular length, amplitude, frequency, timing and predictability, will affect community composition and structure (Junk *et al.* 1989; Tockner *et al.* 2000). Pettit *et al.* (2001) found that the cover of exotic shrubs and annual herbs increased with flooding, and in a review conducted by D'Antonio *et al.* (1999), nearly half of the studies examined showed that natural flood regimes promoted the growth of invasive species. Analyses of daily precipitation records in the UK over the period 1961–2000 have revealed an increase in the frequency of 5-day heavy rainfall events concentrated during the winter months (Osborn & Hulme 2002) and of 5- and 10-day duration events in the autumn and spring (Fowler & Kilsby 2003). These changes have translated into significant increases in mean river flows in Scotland, where 17 of 38 river gauging stations showed significant increases in the spring and autumn and 15 showed significant increases in mean winter flows (Werritty 2002). Since 1989, an unexpectedly high proportion of Scotland's largest catchments (8 of 16) have exceeded the flow maxima previously recorded (Black & Burns 2002). Under future climate change, Hulme *et al.* (2002) predicted increases of up to 25% in winter precipitation across parts of Scotland by the 2080s. Thirty-day rainfall events in the UK, which happened once every 20 years in the recent past, are predicted to occur every 3–5 years (Huntingford *et al.* 2003). Thus, high-flow events may occur with increasing frequency and magnitude if climate predictions are realized (Werritty & Chatterton 2004; Ekstrom *et al.* 2005). In the middle and high latitudes of the northern hemisphere and most extratropical areas similar trends and predictions are recorded (Groisman *et al.* 1999; Milly *et al.* 2002; Groisman *et al.* 2004).

Future projections under climate change are consistent with recent increases in rainfall intensity and high flows seen in Scotland. This will potentially increase the invasive potential of *Mimulus*, owing to the temporal heterogeneity and diversity of its dispersal mechanisms. Because low-order stream flood pulses are brief and unpredictable, organisms may have limited adaptations (Junk *et al.* 1989). However, the high propagule pressure and rapid germination of seeds, in conjunction with the high survival, regeneration and colonization of fragments, shows that *Mimulus* is highly adapted to dispersal by both seeds and vegetative means. High flow events that result in the creation of new sediment patches and gaps in established vegetation may provide a colonization niche for *Mimulus* and, as a fast-growing ruderal species,

give it a competitive advantage. As many invasive species reproduce by vegetative fragments, high-flow events may result in preferential input, transport, germination and establishment of invasive species.

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