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Does temperature limit the invasion of *Impatiens glandulifera* and *Heracleum mantegazzianum* in the UK?

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Summary

1. *Impatiens glandulifera* Royle and *Heracleum mantegazzianum* Sommier et Levier are widespread, non-indigenous plant species in the UK. A variety of correlational analyses suggest that their spatial extent is limited by climate, although no experimental studies have tested this hypothesis. This paper reports the first detailed experimental examination of the impact of climate on the performance of the two species.

2. Seeds of each species were sown, in each of 2 years, in replicated plots along an elevational gradient (10–600 m a.s.l.) in north-east England. Both species germinated readily at all elevations, even in areas well above their current limits within the study area. The plants were, however, smaller at higher altitudes. *Impatiens glandulifera* also produced fewer seeds with increasing elevation.

3. Plant performance was assessed in relation to actual and interpolated climate data along the elevational transect. For *H. mantegazzianum*, the timing of germination was correlated most strongly with the pre-emergence heat sum; for *I. glandulifera* this relationship was significant in one year only. Maximum height of both species was correlated with increasing post-emergence heat sum, as was pod production by *I. glandulifera*. The biomass of second-year *H. mantegazzianum* plants varied non-linearly with post-emergence heat sum. For both species, overwinter survival of seeds was not related to winter temperature or frost days. Overwinter survival of first-year *H. mantegazzianum* plants declined with increasing frost incidence.

4. The results suggest that, of the two species, only *I. glandulifera* is currently most limited by temperature, although this is not the only factor determining the distribution of the species.

Key-words: Biological invasions, climate change, non-indigenous species, seedling regeneration, survivorship

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Introduction

Biological invasions by non-indigenous (NI) plant species are a significant component of global environmental change (Mack *et al*. 2000). Over 900 NI plant taxa are established in the UK, of which at least 200 are widespread (Clement & Foster 1994; Stace 1997). Invasive, non-indigenous plant species have the potential to threaten human health, the economy, and/or native biological diversity (Chittka & Schürkens 2001; Manchester & Bullock 2000; Mooney & Hobbs 2000; Pimentel *et al*. 2001; Usher 1986). An important factor in assessing the potential threat of introduced species is the likelihood that they will become more widespread in the future, exacerbating any problems currently associated with their occurrence. However, despite the problems associated with invasive species and the considerable resources spent on their control (e.g. Gritten 1995; Prus 1997; Sampson 1994), relatively little is known of the factors that limit their geographic spread.

The fundamental role played by climate on plant species distribution is widely recognized (e.g. Franklin 1995; Woodward 1987), and correlative models suggest that a major constraint on the distribution of NI species is temperature (Beerling 1993; Collingham *et al*. 2000). However, the ecological and physiological processes that operate to limit them remain largely unknown. The ranges of many non-indigenous species have yet to reach equilibrium, and this hinders the identification of environmental constraints, demographic limits, and hence future spread (Beerling 1993; Collingham *et al*. 2000; Mihulka & Pysek 2001; Pysek

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et al. 1998; Sindel & Michael 1992; Weber 2001). A partial solution is to study the species in controlled-temperature environments (Beerling 1993), or to model the distribution in its native environment (Beerling 1994; Beerling, Huntley & Bailey 1995; Weber 2001). Research that focuses on the ecological mechanisms operating to limit species distributions is essential to assess the reliability of bioclimatic predictions (Beerling 1993; Panetta & Mitchell 1991; Pysek *et al*. 1998).

This study aimed to examine the extent to which climate, as experienced along an elevational gradient, might limit the geographic distribution of two invasive, non-indigenous plant species: *Impatiens glandulifera* and *Heracleum mantegazzianum*. Specifically, the objectives were to: (i) establish which life-history parameters were most sensitive to changes in elevation; (ii) examine the extent to which specific climate variables were associated with plant performance; (iii) estimate the species' abilities to establish self-maintaining populations at each elevation; and (iv) assess the likelihood that climate currently limits the species' distributions in the study region.

Methods and materials

STUDY SPECIES

Impatiens glandulifera Royle (Balsaminaceae) and *Heracleum mantegazzianum* Sommier et Levier (Apiaceae) are both highly successful, non-indigenous species in the British Isles, with similar native habitat but different life histories (Table 1). The species (hereafter *Impatiens* and *Heracleum*) are currently consolidating their ranges in the British Isles, although both now occur throughout most regions. The two species are also widespread NI species through much of western and central Europe, *Heracleum* also having naturalized in North America and Canada (Beerling & Perrins 1993; Tiley, Dodd & Wade 1996). The ecology and history of the species' invasion in the UK have been reviewed by Beerling & Perrins (1993) and Tiley, Dodd & Wade (1996).

The spatial distribution of both species in the British Isles, and specifically north-east England, is correlated with climate, particularly the annual heat sum (Collingham *et al*. 2000). Nevertheless, additional variables such as land use, geology and human settlements are also important (Collingham *et al*. 2000).

SITE LOCATIONS AND EXPERIMENTAL DESIGN

Species introduction experiments were used to test the extent to which climate variables limit the establishment and performance of the species within and beyond their current range. Six elevation stations were established across a representative elevational gradient in north-east England, including sites outside the current range of the species (Fig. 1). To prevent the accidental introduction of the species into the wild, seeds were sown under natural conditions in plastic containers at each station and, following flower senescence, inflorescences were bagged and seeds collected prior to dispersal.

Plastic containers were 25 cm in diameter and 25 cm deep, with drainage holes drilled into their base. These were filled with standard potting compost (Crowpost, Ken Crow, Eastcroft, UK) into which 20 seeds of one of the species (collected locally) were sown in the autumn. Ten replicate containers were established for both species at all six stations in each of two years, 1996 and 1997. Due to the annual life history of *Impatiens*, containers established in 1996 were replaced with new ones in 1997, whereas for *Heracleum* an

Table 1. Origins and life history traits of *Impatiens glandulifera* and *Heracleum mantegazzianum*

Trait	*I. glandulifera*	*H. mantegazzianum*
Family	Balsaminaceae	Umbelliferae
Life form	Annual*	Monocarpic perennial†
Mode of dispersal	Ballistic, water*	Wind, water†
Height (m)	1–2*	2–5†
Pollinators in UK	*Bombus* spp.‡	Many insects (non-specialized)§
Seed number	800*	10–100 000†
Seed bank	Transient¶	Persistent¶
Natal area	Himalayas*	Caucasus†
Natural habitat	Montane streams*	Montane streams†
Date of first UK record	1839**	1828†
Source of most introductions	Garden plant*	Garden plant†

*Beerling & Perrins (1993).
†Tiley *et al*. (1996).
‡Dunn (1977).
§Grace & Nelson (1981).
¶Thompson, Bakker & Bekker (1997), although Beerling & Perrins (1993) provide limited evidence of a short-lived seed bank for *I. glandulifera*.
**Coombe (1956).

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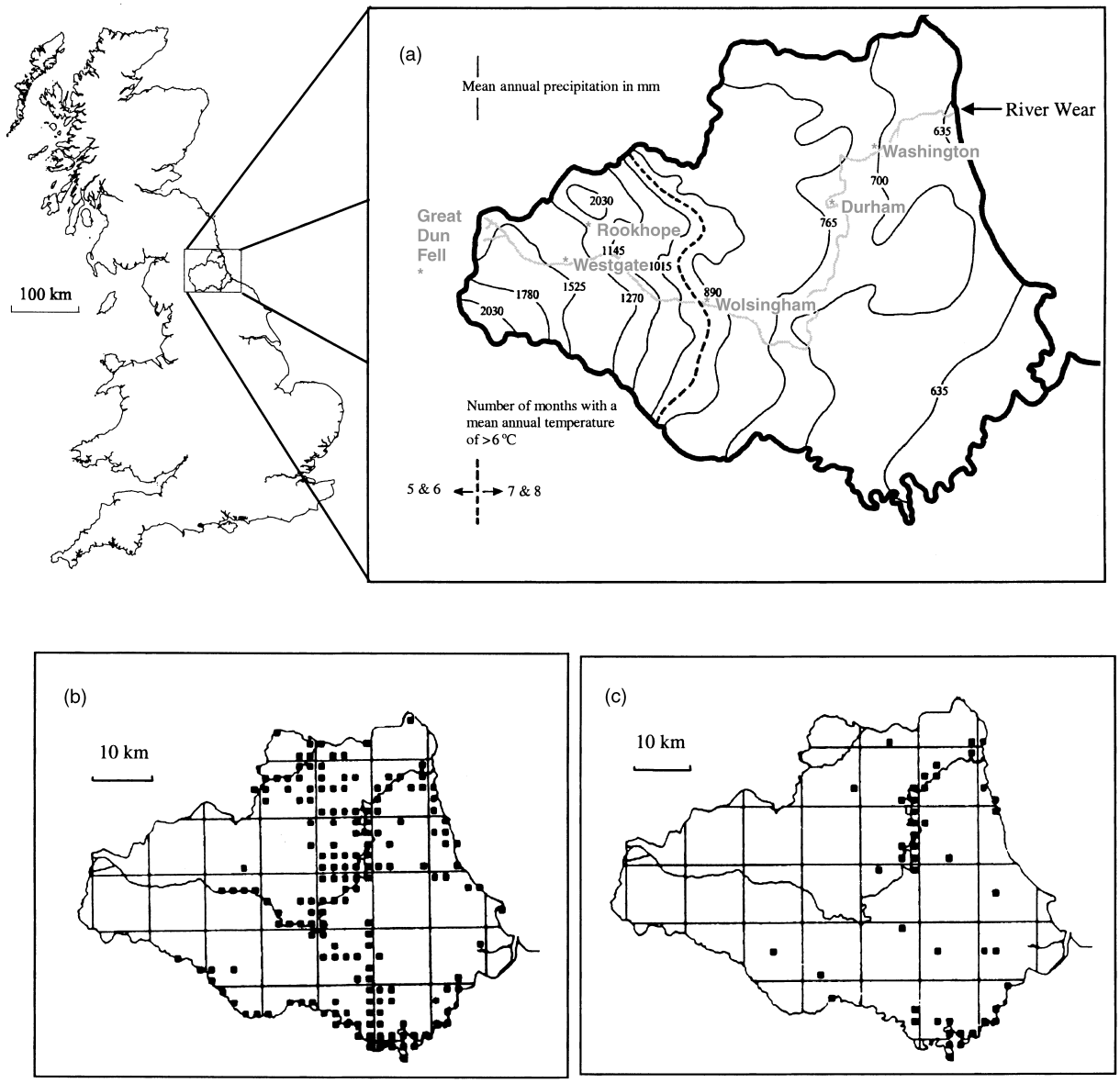


Fig. 1. Location of County Durham, north-east England. (a) County Durham outline showing study stations locations along the River Wear and climatic gradient from east to west. The six stations encompass a wide elevational gradient: Washington (10 m a.s.l.), Durham (30 m a.s.l.), Wolsingham (130 m a.s.l.), Westage (270 m a.s.l.), Rookhope (330 m a.s.l.) and Great Dun Fell (600 m a.s.l.). Distributions of (b) *Impatiens*; (c) *Heracleum* (distributions and climate gradient from Graham 1988).

additional 10 containers were established in 1997. This enabled the performance of the 1996 *Heracleum* cohort to be followed over 2 years. Each elevation station was fenced to prevent grazing by mammals, and molluscicide pellets were added to control mollusc herbivory. At the completion of the experiments in autumn 1998, all remaining plant material was collected and incinerated, and compost was autoclaved prior to disposal to a municipal waste site.

Fortnightly censuses assessed the timing and proportion of seeds germinating, as well as seedling and adult survival. Plants were classed as seedlings until the appearance of the first true leaves, after which point they were regarded as adults. Fecundity of surviving adult *Impatiens* plants was assessed by counting the total number of seed pods produced. Estimates of *Heracleum* fecundity could not be made from a 2-year study, hence the fecundity of a sample of 30 flowering plants was assessed at both the highest (120 m a.s.l.) and lowest (30 m a.s.l.) elevation of populations along the transect. In the experiment, two correlated measures of performance were assessed: plant height and biomass. Plant height was estimated as the length of the straightened stem of a plant, including the length of the terminal leaf (or the terminal inflorescence for *Impatiens*). Owing to difficulties in assessing the biomass of senescing *Impatiens* plants, the relationship between biomass and plant height was derived from sampling 70 wild plants from a representative riparian habitat. Harvesting of *Heracleum* in May 1998 enabled estimation of above- and below-ground biomass of both 1996 and 1997 cohorts.

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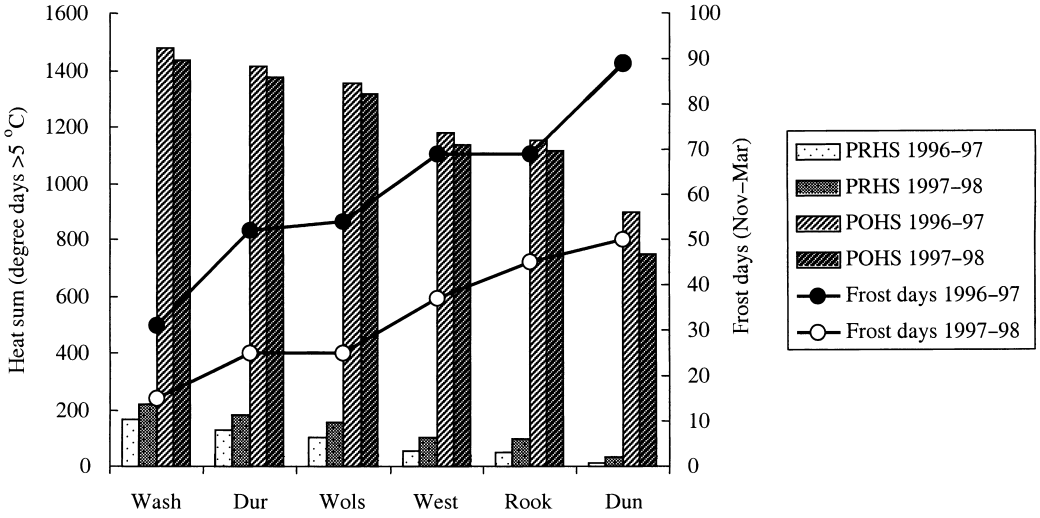


Fig. 2. Variation along elevation stations in the interpolated climate variables: pre-emergence heat sum >5 °C (PRHS); post-emergence heat sum >5 °C (POHS), and frost days. Stations (in order of increasing elevation): Wash (Washington); Dur (Durham); Wols (Wolsingham, note 1996 cohort damaged); West (Westgate); Rook (Rookhope); Dun (Great Dun Fell).

METEOROLOGICAL DATA

Climate data over the study period (October 1996–October 1998) were obtained from a standard meteorological station at the Durham Observatory and an automated station on Great Dun Fell (Fig. 1). From these it was possible to derive daily maximum, mean and minimum temperatures over the experimental period. These data were used in conjunction with interpolated 30-year (1961–90) national climate data (Barrow, Hulme & Jiang 1993) on a 10 km grid to simulate daily maximum and minimum temperatures for the other sites where temperature observations were not available. This was undertaken using an interpolation method similar to that described and validated by Parker, Legg & Folland (1992). Interpolation enabled the estimation of two key variables for each of the stations over the study period: frost days and heat sums (degree days >5 °C) (Fig. 2). Frost days were calculated over the vernalization period (November–March). Pre-emergence heat sums (PRHS) were calculated to examine for effects on emergence, this period being from January to March (which was a much better predictor than the entire pre-emergent period, i.e. November–March). Post-emergence heat sums (POHS) were calculated for the period April–September inclusive. Interpolated estimates of precipitation and wind speed would also have been desirable, but these variables cannot be as reliably interpolated between sites (Hulme *et al.* 1995).

ANALYSES

Variation in plant traits across the experimental gradient was assessed using nested ANOVA (Norusis 2000). Traits that varied significantly across the elevational gradient were further examined in relation to the interpolated climate variables using mixed-model ANOVA (Norusis 2000) on the means for each elevation station, with year as a factor and individual climate traits as covariates. Non-linear regressions were applied only when they resulted in significantly better fits than linear models.

For *Impatiens*, it was possible to calculate the finite rate of increase (λ) for populations at each site:

$$\lambda = g(1 - d)F \qquad \text{eqn 1}$$

where λ is the finite rate of increase; g is the proportion of seeds germinating in spring; d is the proportion of seedlings that die before seeding; and F is the mean number of seeds produced per surviving plant.

Following Crawley *et al.* (1993), the probability of *Impatiens* establishing an invasive population at each site was assessed by the degree to which λ > 1.

Results

SURVIVORSHIP

The timing of seedling emergence differed significantly, among elevations in any year (*Impatiens*: $F_{5,1003} = 26{\cdot}3$, $P < 0{\cdot}001$; *Heracleum*: $F_{5,1962} = 160$, $P < 0{\cdot}001$) and between years (*Impatiens*: $F_{1,1003} = 563{\cdot}9$, $P < 0{\cdot}001$; *Heracleum*: $F_{1,1962} = 8251$, $P < 0{\cdot}001$). An increased mean germination rate in relation to increasing PRHS was observed for *Heracleum* in both years, and for the 1997 cohort of *Impatiens* [*Heracleum*: $F_{1,11} = 26{\cdot}97$, $P = 0{\cdot}001$, mixed model (mm), R^2 (mm) = 0·962; *Impatiens* (both years): $F_{1,11} = 4{\cdot}74$, $P = 0{\cdot}057$, R^2(mm) = 0·755; *Impatiens* (1997 cohort): $F_{1,5} = 38{\cdot}44$, $P < 0{\cdot}01$, $R^2 = 0{\cdot}882$; Fig. 3].

Overall germination of *Heracleum* seeds was >80% (Fig. 4) and differed significantly between years (1996 cohort = 85 ± 1·1%, 1997 = 80 ± 1·1%, $F_{1,194} = 3{\cdot}45$, $P < 0{\cdot}001$) but not among elevations ($F_{5,194} = 11{\cdot}98$,

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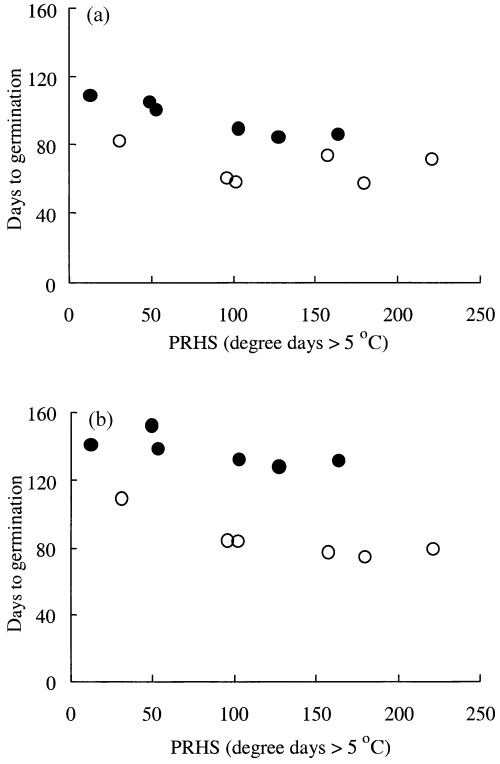


Fig. 3. Germination time (measured as days from 1 January) of seedlings of (a) *Impatiens* and (b) *Heracleum* in relation to pre-emergence heat sum (PRHS) (Jan–Mar) at a site. Means are derived from plants grown along the elevation transect during 1997 (●) and 1998 (○). Standard error bars are smaller than markers.

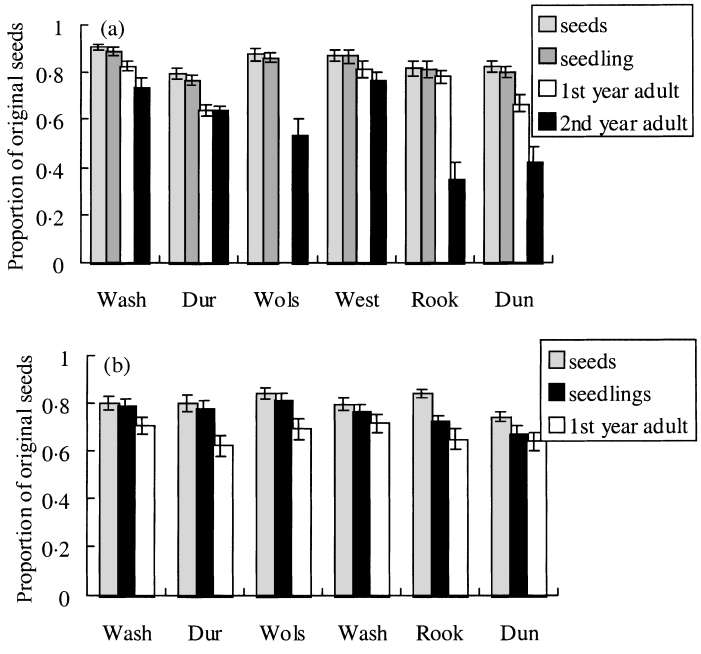


Fig. 4. Proportion of seeds germinating and survival of seedling and adult *Heracleum* plants across the elevation transect from cohorts of 20 seeds sown in (a) 1996; (b) 1997. Proportions are calculated as a proportion of the original seed sown, not the previous life stage. The survival categories are: seeds (survival to germination); seedling (survival to true leaf); first-year adult (survival to autumn senescence); second-year adult (survival to harvest). Only the 1996 cohort was studied through to produce second-year adults. Site abbreviations follow Fig. 2.

NS). Mortality was higher for adults than seedlings, and for first-year adults was similar among elevations and between years. Mortality of second-year adults was more marked and reflected significant differential overwinter survivorship among sites, with greatest mortality at the upper (and coldest) stations. Nevertheless, even at these upper elevations ≈30% of plants survived through their second year. Unfortunately the 1996 cohort in Wolsingham was damaged by grazing cattle.

Germination of *Impatiens* seeds varied considerably among elevations and between years ($F_{5,194} = 119{\cdot}5$, $P < 0{\cdot}001$ and $F_{1,194} = 3185$, $P < 0{\cdot}001$, respectively, Fig. 5), which could not be accounted for by the temperature variables. After poor germination of the 1996 cohort ($10{\cdot}5 \pm 1{\cdot}1\%$), the majority of seedlings survived through adulthood to flower. In contrast, in the following year the high germination ($73{\cdot}9 \pm 3{\cdot}9\%$) at most sites was followed by poor seedling survival and even lower adult survival. Consequently, final adult plant densities were similar in both years, suggesting compensatory density-dependent survival. Densities in the majority of containers ranged between 20 and 80 plants m^{-2} (88% of containers), which is similar to wild populations (50–70 m^{-2}, Perrins, Fitter & Williamson 1993; 30–40 m^{-2}, Beerling & Perrins 1993).

PERFORMANCE

The maximum height of both species in their first growing season varied significantly among elevations and between years (*Heracleum*: $F_{4,118} = 145{\cdot}8$, $P < 0{\cdot}001$, $F_{1,118} = 484{\cdot}1$, $P < 0{\cdot}001$; *Impatiens*: $F_{4,95} = 16{\cdot}77$, $P < 0{\cdot}001$, $F_{1,95} = 88{\cdot}08$, $P < 0{\cdot}001$ for site and year, respectively). Plant height was positively correlated with POHS [*Heracleum*: $F_{1,11} = 10{\cdot}32$, R^2 (mm) $= 0{\cdot}628$, $P = 0{\cdot}012$; *Impatiens*: $F_{1,11} = 7{\cdot}93$, R^2 (mm) $= 0{\cdot}719$, $P = 0{\cdot}023$; Fig. 6]. The biomass of harvested 2-year-old *Heracleum* plants varied significantly among elevations ($F_{5,50} = 3{\cdot}86$, $P < 0{\cdot}01$). Comparison of mean plant biomass with the total POHS for the 2 years (up to the point of harvest) revealed a significant quadratic relationship ($F_{1,5} = 79{\cdot}39$, $R^2 = 0{\cdot}982$, $P < 0{\cdot}01$; Fig. 7). This suggests an optimal POHS of ≈1700 degree days >5 °C, which corresponds to a position along the elevational transect between Westgate and Wolsingham, a region far upstream of the species' current distribution limit. The optimal POHS tallies with the only observed flowering of *Heracleum* (at Wolsingham) during the study. In addition, *Heracleum* at higher elevations (and hence lower POHS) allocated a significantly greater proportion of resources to above-ground biomass (Mann–Whitney *U*-test, $Z_{242} = 2{\cdot}71$, $P < 0{\cdot}01$). Although *Impatiens* plants were not weighed (as explained previously), plant height and mass in wild plants were significantly related ($F_{1,68} = 496$, $R^2 = 0{\cdot}879$, $P < 0{\cdot}001$; mass $= 4{\cdot}0207e^{(0{\cdot}0262)\text{Height}}$), so a similar trend between plant biomass and POHS might be expected as that found for height.

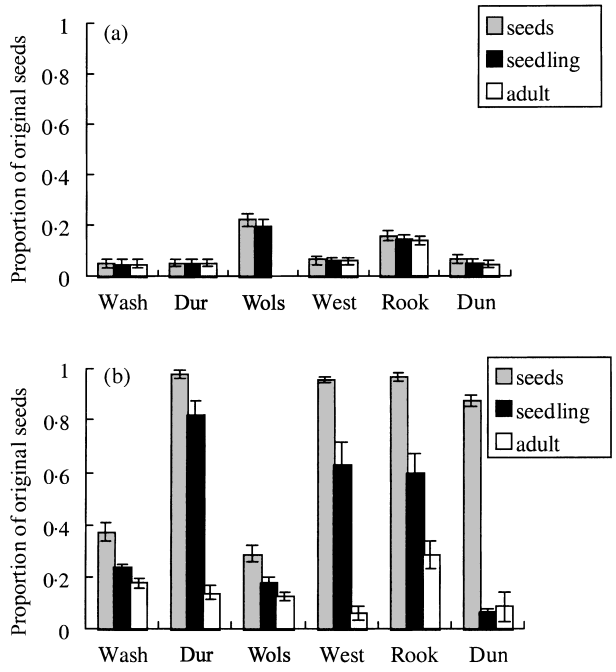


Fig. 5. Proportion of seeds germinating and survival of seedling and adult *Impatiens* plants across the elevation transect from cohorts of 20 seeds sown in (a) 1996; (b) 1997. Proportions are calculated as a proportion of the original seed sown, not the previous life stage. The survival categories are: seeds (survival to germination); seedling (survival to true leaf); adult (survival to autumn senescence). Site abbreviations follow Fig. 2.

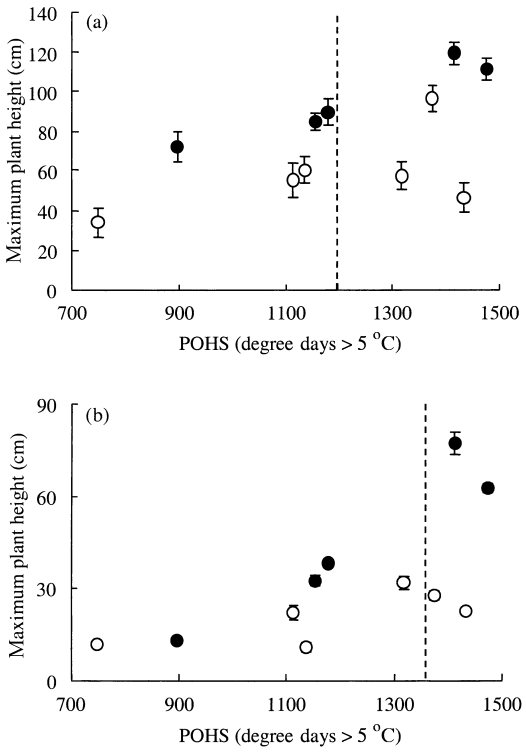


Fig. 6. Maximum heights of (a) *Impatiens*; (b) 1-year-old *Heracleum*, in relation to post-emergence heat sum (POHS) (Apr–Sep) at sites along the elevation transect during 1997 (●) and 1998 (○). Displayed values are means (with SE) from each of the study plots in a particular year. Dotted lines indicate approximate current lower heat-sum limit of each species in County Durham.

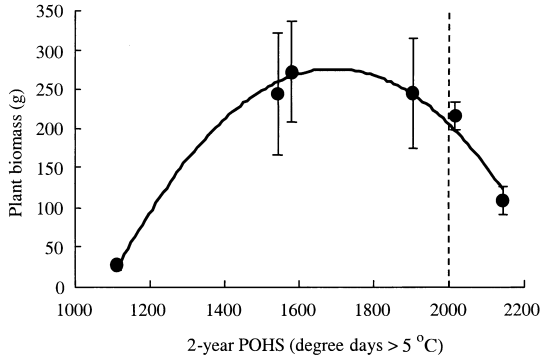


Fig. 7. Biomass of 2-year-old *Heracleum* plants along the elevation transect in relation to the post-emergence heat sum (POHS) over the period of growth in the 2 years since sowing. Plants were grown from seeds sown in 1996 and sampled in late May 1998. Dotted line indicates approximate current lower heat-sum limit of the species. Equation: $y = -0{\cdot}0007x^2 + 2{\cdot}5362x - 1869$.

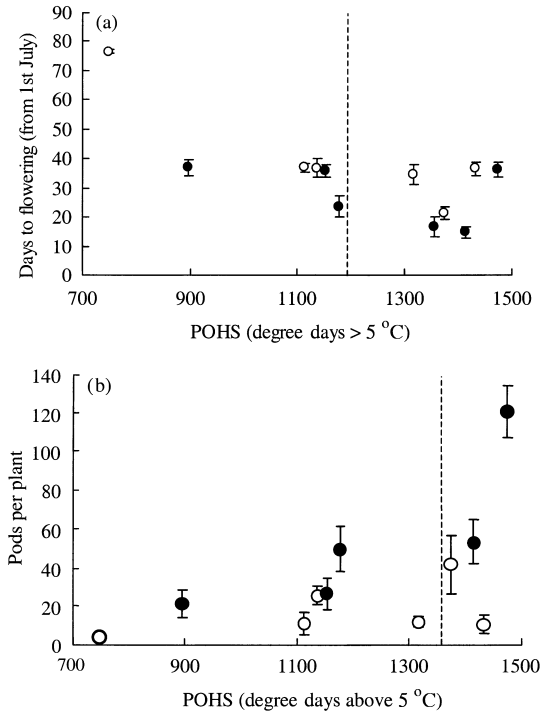


Fig. 8. (a) Relationship between the day of first flowering of *Impatiens* at the elevation stations over the 2 years of study and the associated post-emergence heat sums (POHS). (●) 1996 cohort; (○) 1997 cohort. Displayed values are means (with SE) for a station. (b) Pod production of *Impatiens* plants in relation to post-emergence heat sum (POHS) at elevation stations along the elevation transect over the 2 years of study. Displayed values are means (with SE) from each of the stations in a particular year. Dotted vertical line indicates approximate current lower heat-sum limit of the species.

FECUNDITY

The timing of *Impatiens* flowering varied significantly among elevations and years ($F_{4,211} = 29{\cdot}48$, $F_{1,211} = 51{\cdot}72$ for elevation and year, respectively; both $P < 0{\cdot}001$). However, none of the available climate variables was correlated with timing of flowering, particularly if the outlier of the 1997 cohort at Dun Fell is omitted (Fig. 8a).

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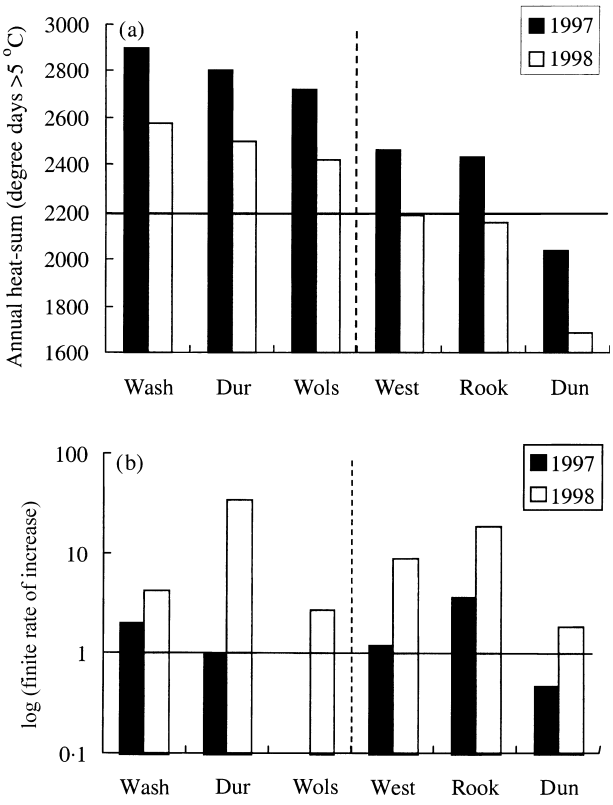


Fig. 9. (a) Annual heat sums of elevation stations (degree days >5 °C) compared to the predicted climatic limits of *Impatiens* (solid line) suggested by Beerling (1993). (b) Finite rate of increase of *Impatiens* at sites over the two study years (see text for details). Solid line at $y = 1$ indicates the point at which the invasion criterion is reached (Crawley *et al*. 1993). Data for Wolsingham 1997 are missing due to grazing damage. Dotted vertical lines indicate the approximate current upper limit of the species.

At the lower elevation stations, *Impatiens* developed seeds at an earlier date than upland stations and, in 1998 at least, plants in the uplands failed to ripen seeds in any quantity before the end of September. There was significant variation in pod production of plants among both elevations and years ($F_{4,145} = 11{\cdot}05$, $F_{1,145} = 58{\cdot}90$, respectively; both $P < 0{\cdot}001$), mean pod production being positively correlated with POHS [$F_{1,11} = 9{\cdot}49$, R^2 (mm) = 0·68, $P = 0{\cdot}015$; Fig. 8(b)]. However, the variation displayed in Fig. 8(b) suggests that heat sum is not the only factor affecting pod production and hence seed output.

Sampling of wild-grown *Heracleum* at its upper and lower elevation limit in County Durham, north-east England (30 and 120 m a.s.l.) indicated that fecundity was no different between the two extremes ($t_{30} = 0{\cdot}598$, NS).

THE INVASION CRITERION

A comparison of the annual heat-sum figures for the sites over the study period with Beerling's (1993) predicted threshold for occurrence of *Impatiens* indicates that the suitability of sites for this species varied between years (Fig. 9a). This suggests that the threshold must be exceeded in most years for populations to persist at a site. However, comparisons of the finite rate of increase of the populations highlights that the magnitude of the invasion criterion does not reflect the requirement of a heat-sum threshold (Fig. 9b).

Discussion

The high germination, seedling and adult survivorship of *Heracleum* across a wide range of elevation is consistent with the species' native montane habitat, where cold winters occur (Mandenova 1950; in Tiley *et al*. 1996). Adult survivorship and biomass were lowest at the highest elevations, yet plants were capable of considerable growth. However, based on the rate of biomass production it is unlikely that flowering would occur within 3–4 years at the most upland sites. Although plants flowered only at one mid-elevation station, the growing season may be too short for seed maturation at higher elevations (Tiley *et al*. 1996 state that plants flowering in September may fail to set seed). While climate may determine the absolute distribution of a species, this study indicates that the current lowland distribution of *Heracleum* in the UK may, as in the Czech Republic (Pysek 1994), primarily reflect dispersal limitations and human influences, rather than climatic limits.

Climate, particularly heat sum, was important in determining the rate of germination, performance and fecundity of *Impatiens*. Germination, seedling and adult survival, and initiation of flowering were not related directly to the elevation gradient (and hence climate). Irrespective of the reasons for mortality of *Impatiens* plants, the resulting survival to flowering was similar in both years and among all elevations. Density-dependent survivorship may enable high-density populations to compensate for mortality factors acting on particular life stages. Natural populations of *Impatiens* also undergo similar self-thinning (Prach 1994; Willis 1999). Compensatory survivorship will mask individual sources of mortality, yet highlights that populations are likely to be robust to the loss of individuals.

Several authors studying native species towards their distributional limit have observed delayed flowering (e.g. Pigott 1970; Pigott & Huntley 1981; Prince & Carter 1985). Although timing of flowering by *Impatiens* did not alter significantly beyond its current range limit, timing of pod production indicated that much of the seed output occurred at the end of the growing season at the more marginal, upland stations. It would require only a slightly shorter growing season at the upper two sites to prevent seed output. It is likely that, at the higher elevations, seed output will be irregular and usually insufficient to compensate for overwinter seed mortality and seed loss through herbivory, flooding, etc.

The distribution of *Impatiens* in north-east England coincides with the annual heat-sum threshold described by Beerling (1993). The coincidence of the

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predicted heat-sum threshold with the actual distribution limit of *Impatiens* is expected, as distribution data were used to derive the threshold. This study reveals that, if such a threshold exists, it is a minimum that must be exceeded in most years for populations to persist. An annual heat-sum threshold is a less appropriate measure than seasonal heat sums (e.g. PRHS, POHS). Surprisingly, the annual heat-sum threshold does not coincide with significant reductions in plant performance or finite rate of increase. While climate may set an absolute limit on species' distributions, the demographic evidence suggests that both species should be able to persist beyond the heat-sum threshold. The reason for this discrepancy may lie in the correlative approach adopted by Beerling (1993). A fundamental assumption in correlative modelling of species distributions is that species should be in equilibrium with their environment (Franklin 1995). In the British Isles, the distributions of both non-indigenous species are still increasing (Collingham *et al*. 2000; Rich & Woodruff 1996), and this non-equilibrium distribution will limit the predictive power of correlative analyses. The absence of many NI species from upland environments may reflect the greater frequency of species introductions in lowland environments, and the occurrence of settlements and major transport networks (Collingham *et al*. 2000).

This study focused on temperature (e.g. frost-free days, heat sum) as the principal climatic driver influencing plant performance. However, climatic variables are generally correlated with one another (Ford & Milne 1981). An apparent correlation between a plant trait and a climatic variable may be caused by correlations with other climatic factors such as precipitation and wind speed. Motion *per se* is a potent inhibitor of growth (Grace 1981), and wind will also reduce ambient temperatures and increase evapotranspiration during the growing season. The increased wind speed at the upper extremes of the transect during much of the year may explain the observed patterns of reduced plant performance at these sites. Beerling, Bailey & Conolly (1994) suggested that shelter from wind damage could influence the altitudinal limit of another non-indigenous plant species, *Fallopia japonica*. Wind data were available for two extremes of the transect (Dun Fell and Durham), but were less correlated with plant traits than was temperature. The reduced precipitation at the lowest elevations during midsummer may have deleterious effects on the growth of the species, both of which are drought-intolerant to varying extents (Beerling & Perrins 1993; Tiley *et al*. 1996). Beerling & Perrins (1993) suggest that soil moisture determines whether *Impatiens* plants grow into small or large phenotypes, and growth may be directly proportional to soil water availability (Koenies & Glavec 1979). There was a strong negative correlation between POHS and precipitation at the two sites where the latter was measured, such that the perceived inhibitory effects of high POHS on *Heracleum* biomass may be an artefact of the correlation with low precipitation. The significant effects observed between years are likely to arise from between-year variation in the unmeasured climate variables. Nevertheless, while these additional factors are important, temperature is a major determinant of the distributions of these two species (Collingham *et al*. 2000).

Both species grew and survived at relatively high elevations. Does this mean that the species are likely to expand up to 600 m a.s.l. (the elevation of the Dun Fell site) in the UK? This is unlikely. Even if climate is insufficient to prevent plant growth and survival, it will interact with other environmental factors that will curtail the potential distribution of the species. For example, the ability of plant species transplanted outside their range to produce viable seed has been reported for other species (e.g. Prince & Carter 1985), the actual limits being ascribed to secondary effects on populations and metapopulations, rather than effects on individuals. Such an explanation could equally be offered for the species studied here. Prince & Carter (1985) detected an increased allocation of resources to leaves in *Lactuca serriola* when transplanted beyond its natural range, a result mirrored in *Heracleum* at the high elevations in this study. Upland soils generally have a pH and drainage regime different from lowland soils, which will have a major impact on plant performance and will modify the impact of climate on plant survivorship. Similarly competitive effects in natural habitats may also modify the species' performance. The experiments undertaken here, in relatively well drained, nutrient-rich compost of optimum pH, merely indicate where the species could potentially grow, given that all other conditions were suitable.

Our results suggest that seasonal temperature variation is not the only factor limiting these long-established species in their current distribution. Other factors, such as proximity to settlements, soil type and habitat availability, will also be important, as has been shown elsewhere (Collingham *et al*. 2000; Pysek & Prach 1993; Pysek *et al*. 1998; Willis *et al*. 1997). Conversely, given the similar germination and successful seed production by flowers at all sites, factors such as winter climate and pollinator limitation are suggested to be non-limiting. Caution should therefore be exercised in extrapolating data from current non-indigenous species distributions to predict their potential ranges elsewhere (Collingham *et al*. 2000). The evidence presented here, along with continuing local (Willis 1999) and national (Collingham *et al*. 2000) expansions, indicates that both species remain in a state of non-equilibrium distribution and may be capable of further spread if introduced at higher elevations. This has important conservation implications regarding the transport of seeds and the potential vulnerability of sites beyond the species' current ranges. Seed transplanted beyond current range margins may lead to further episodes of expansion of the species to the detriment of others (Chittka & Schürkens 2001); and once

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established, such species are extremely difficult to eradicate (Wadsworth *et al*. 2000).

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