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Environmental severity and variation in the reproductive traits of *Impatiens glandulifera*

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Summary

1. Seed mass is widely regarded as a key plant trait, yet is notoriously variable within an individual species. This study reports the first field experiments to disentangle the relative importance of four major correlates of seed mass variation: resource limitation; plant height; seed number; and seasonality.

2. Variation in reproductive traits in *Impatiens glandulifera* Royle was partitioned among six populations established across an elevation gradient, among plants at each elevation and within individual plants.

3. Seed mass was the least variable trait both at the individual and population levels, while the number of pods per plant varied most. Seed mass variation was greatest among individual plants (42%) and was least among populations (28%).

4. Taller plants produced proportionally more seed pods and more seeds per pod. Seed mass was not related to the number of pods per plant, or the number of seeds per pod. Thus with increasing resources, *I. glandulifera* allocated resources to produce more seeds rather than larger seeds.

5. Seed mass was negatively correlated with the heat sum over the period of seed maturation, explaining increased seed mass at higher elevations and increasing seed mass over time at most elevations. This may indicate that environmental condition pre- and post-fertilization determines the relationship between seed mass and elevation, thereby limiting the potential for evolutionary selection for seed-size optima.

6. The study warns against correlative studies of seed mass variation that select arbitrary populations or ignore the temporal dynamics in seed mass, as these may generate spurious correlations among life-history traits.

7. The success of *I. glandulifera* as an invasive species may reflect the extended period of seed release, considerable seed mass variation and large seed size under conditions of environmental severity. These traits will facilitate the exploitation of spatially and temporally heterogeneous natural environments commonly found in riparian ecosystems.

Key-words: biological invasions, climate, elevation, reproductive allocation, seed size trade-offs

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Introduction

Seed mass is widely recognized as a key trait in plant population dynamics and community structure (Rees 1993, 1995; Guo *et al*. 2000; Leishman 2001; Jakobsson & Eriksson 2002). Within a species, a larger seed mass increases the germination rate, vigour and competitive ability of seedlings (Black 1958; Bretagnolle *et al*. 1995; Gan & Stobbe 1995; McKee & Richards 1996; Roy *et al*. 1996; Eriksson 1999). Alternatively, a small seed mass may be an effective defence against seed predators (Hulme & Benkman 2002); assist seed dispersal (Schippers *et al*. 2001); and, through trade-offs with seed number, facilitate colonization (Leishman & Murray 2001). However, the view that seed mass may reflect selective optima or selective compromises (Haig & Westoby 1988; Rees & Westoby 1997) is at odds with the considerable intraspecific variation in seed mass found in wild plants (Silvertown 1989; Mehlman 1993; Obeso 1993; McKee & Richards 1996). Often, seed mass variation is as great within individuals as between individuals or populations (Waller 1982; Briggs 1991; Kang & Primack 1991; Obeso 1993; Crochemore *et al*. 1994; Krannitz 1997; Telenuis & Torstensson 1999; Buckley *et al*. 2003). Such phenotypic plasticity suggests only a limited opportunity for an evolutionary response in seed mass, despite strong selection pressures (Waller 1982; Winn 1988; Silvertown 1989; Susko & Lovett-Doust 2000). However, from a demographic perspective, by

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increasing the similarity in seed mass of co-occurring species and hence overlap in the regeneration niche, a high level of intraspecific variation in seed mass may limit species coexistence (Leishman & Murray 2001; Schippers *et al*. 2001). Thus knowledge of the environmental circumstances that increase or decrease seed mass variation may be essential for understanding the structure of plant communities.

For any one species, variation in seed mass can occur among different populations (McWilliam, Landers & Mahlstede 1968; McKee & Richards 1996); among individuals within a population (Mehlman 1993); and also within a single plant (Obeso 1993; Navarro 1996; Yanful & Maun 1996). Plasticity in seed mass often arises as a consequence of resource limitation. In general, resource limitation will reduce the mean but increase the variance in seed mass (Michaels *et al*. 1988). Within a species, taller plants generally have larger seeds (Waller 1982; McKee & Richards 1996), and along environmental severity gradients (e.g. elevation) both mean plant height and seed mass decline (Totland & Birks 1996). Similarly, the observed decline in mean seed mass with increasing latitude in both Northern (Moles & Westoby 2003) and Southern (Murray *et al*. 2003) hemispheres is believed to arise from resource limitation (shorter growing season). Within an individual plant, competition for maternal resources is responsible for proximate inflorescences producing heavier seeds than distal ones (Waller 1982; Obeso 1993; Navarro 1996; Velasco *et al*. 1998; Susko & Lovett-Doust 2000) and observed declines in mean seed mass during the flowering season (Lee 1988; Wolfe 1995).

In summary, although stabilizing selection should limit seed mass variation within a species, such variation occurs due to trade-offs between seed number and mass (Wolf *et al*. 1986; Lalonde & Roitberg 1989; Wolfe 1995) and from resource competition (Wulff 1986; Ågren 1989; Wolfe 1995; Vaughton & Ramsey 1997), which limit the opportunities for plants to optimize seed mass (Vaughton & Ramsey 1998). At the level of the individual plant, competition for resources has been hypothesized to influence seed mass variation in at least four ways (Lee 1988; Michaels *et al*. 1988; Shaanker *et al*. 1988; Aarssen & Jordan 2001; Henery & Westoby 2001).

1. Seed mass should decrease (and its variation increase) with increasing resource limitation due to increased sibling competition.
2. Seed mass should increase (and its variance decrease) with increasing plant height as a result of an allometric relationship between these variables (Thompson & Rabinowitz 1989).
3. Seed mass should decrease (and its variance increase) with total number of seeds produced because, for a given amount of resources, increases in seed mass may come at the expense of producing fewer seeds.
4. Seed mass should decrease (and its variance increase) through the season (due to an ever shorter period available for seed maturation and/or asymmetric competition for resources from seeds formed earlier).

The considerable literature on seed mass variation provides support both for and against these hypotheses, and reflects the intricate interplay between resource competition and pollination rates, physiological responses and development constraints (Leishman *et al*. 2000). Current insights into seed mass variation rely heavily on correlative rather than experimental approaches, and no comprehensive field tests of all four hypotheses exist. Rather, present knowledge is drawn from a catalogue of disparate studies each tackling different hypotheses, often on markedly different plant species. This has led to conflicting results and has limited the opportunities for synthesis. This study aims to address this heterogeneous background by testing all four hypotheses simultaneously in order to provide a foundation for an integrated, functional understanding of seed mass variation.

To test these predictions requires variation in seed mass to be partitioned among populations spanning a marked environmental gradient, among plants within these populations, and within the individual plants themselves. Although several studies have attempted to partition seed mass variation, most have examined only a single population (Winn 1991; Mehlman 1993; Obeso 1993; Eriksson 1999). Where more than one population has been examined, only occasionally has a study covered an explicit environmental gradient (Ågren 1989; Stocklin & Favre 1994; Susko & Lovett-Doust 2000). Even these studies suffer from a correlative approach that may confound effects due to local adaptation (Susko & Lovett-Doust 2000), or fail to tease apart the impacts on seed mass of multiple covarying environmental gradients such as shade (Wulff 1986; Ågren 1989); plant density (Winn & Miller 1995); soil nutrient status (Wulff 1986); soil pH (Susko & Lovett-Doust 2000). In the past these limitations have been addressed by collecting seeds from the field and examining allocation patterns of the resulting plants under laboratory conditions (Wulff 1986; Winn & Gross 1993; Susko & Lovett-Doust 2000). However, extrapolation of results back to the field is often problematic (Wulff 1986). The foregoing highlights the piecemeal state of the current understanding of seed mass variation and the need for a different approach.

The present study reports the results of a novel approach in which patterns of seed mass variation were examined in plants arising from the experimental sowing of *Impatiens glandulifera* Royle (Balsaminaceae) along a marked climate gradient. Our aims were to:

1. test the hypotheses regarding seed mass variation within and between individuals as well as among populations distributed across a climatic gradient;
2. assess the extent of compensation in seed allocation in response to resource limitation;
3. elucidate the environmental drivers of variability in seed mass.

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Impatiens glandulifera (hereafter *Impatiens*) is suitable for such analyses because of its discrete packaging of seeds within pods, its annual life history, and the important role climate plays on plant performance (particularly reproductive traits) and distribution (Collingham *et al*. 2000; Willis & Hulme 2002).

Materials and methods

STUDY SPECIES

Impatiens glandulifera is the tallest (up to 3 m) annual species in the British flora (Grime *et al*. 1988), having become naturalized in the late 19th century following its introduction from Asia (Beerling & Perrins 1993). Detailed information on the floral biology can be found in Beerling & Perrins (1993). Spurred, helmet-like flowers are produced in few-flowered racemes in leaf axils. Flowers produce substantial volumes of nectar and are highly attractive to pollinators, often to the detriment of neighbouring species (Chittka & Schurkens 2001). Although flowers are hermaphrodite and self-compatible (Valentine 1978), widespread *Bombus* spp. readily visit the flowers and deposit sufficient pollen to result in often 100% seed set (Titze 2000). Flowers and resulting multiseeded capsules (pods) are produced sequentially over a period extending from July–October When ripe the capsules explode at the slightest touch, dispersing seeds ballistically over a radius of 5 m. Seeds are among the largest for annual plants in the British flora, and weigh on average 22 mg (range 2–35 mg). Pods may contain between four and 16 seeds with, on average, between five and six ripe seeds per pod (Beerling & Perrins 1993). Plants produce a terminal inflorescence at the start of the flowering period and then, given adequate resources and space, can subsequently produce lateral inflorescences arising from branches off lower nodes of the main stem. Flowers and seed pods develop sequentially on florets within an inflorescence, with the distal flowers developing first and proximal flowers developing last, opposite to the development pattern of many plant species (reviewed by Lee 1988). In dense stands *Impatiens* produces almost all its seed pods on the terminal inflorescence, with very little production of pods from lateral inflorescences. However, when conditions allow, the lower inflorescences may produce the majority of seed pods.

SITE LOCATION AND EXPERIMENTAL DESIGN

Ripe seeds of *Impatiens* were collected from a single population in Durham City and sown along an elevation transect in north-east England (Table 1). Six stations were established in the River Wear catchment, including sites beyond the species' current range

Table 1. Summary statistics for each of six elevation stations with regard to the number of pods per plant, seed content per pod and seed mass for experimentally sown *Impatiens glandulifera*

	Elevation station					
Parameter	Washington	Durham	Wolsingham	Westgate	Rookhope	Dun Fell
Elevation (m)	10	30	130	270	330	600
Latitude (N)	54°54′	54°47′	54°43′	54°44′	54°46′	54°40′
Longitude (W)	01°30′	01°34′	01°51′	02°07′	02°05′	02°27′
Number of pods per plant						
Mean	10·7	41·7	12·1	25·9	18·5	4·00
Range	1–99	3–270	2–49	9–55	2–164	1–10
N	21	18	16	12	15	6
SE	4·67	15·0	2·97	4·63	10·5	1·51
Skew	3·91	3·13	2·11	0·70	3·74	0·86
Population CV (%)	201	152·0	95·5	61·9	220	100
Seed content per pod						
Mean	3·57	8·23	4·84	5·73	5·23	5·33
Range	1–9	1–19	1–9	2–13	1–11	2–7
N	89	477	49	79	69	3
SE	0·18	0·17	0·29	0·28	0·31	1·67
Skew	0·93	0·54	0·15	0·71	0·19	–
Population CV (%)	46·2	45·6	41·4	42·6	48·6	–
Mean individual CV (%)	33·4	28·8	35·2	23·8	29·6	–
Individual seed mass						
Mean	175	195·7	194·7	265·0	232·9	352
Range	33–358	35–419	50–466	73–664	79–478	294–410
N	283	1367	225	405	252	2
SE	4·06	2·07	5·38	5·54	5·21	–
Skew	0·26	0·42	1·08	1·00	0·48	–
Population CV (%)	38·5	39·1	40·2	42·0	35·5	–
Mean individual CV (%)	23·6	23·9	25·6	26·1	19·9	–

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(Rookhope and Dun Fell). Details of the station locations and design are described more fully by Willis & Hulme (2002). Twenty seeds were planted in 10 replicate pots containing a similar soil/compost mixture at each station, reducing much of the variation associated with natural stands. Seeds were planted in October 1997, and the resulting plants followed during the 1998 growing season. Mortality of seeds and seedlings led to similar flowering plant densities at all stations (20–80 plants m^{-2}), which were comparable to natural densities (Willis & Hulme 2002).

Plant performance was assessed fortnightly by recording plant height as well as seed-pod and flower production. To enable cross-pollination but prevent seed dispersal, flowers were left open until the initiation of pod formation, at which point seed pods were enclosed in muslin bags. Seeds were collected from plants on a regular basis through the summer in order to record seed numbers from all pods produced. A subsample of the seeds collected was weighed on the day of collection. Seeds and pods were recorded as originating from either the terminal inflorescence or a lateral inflorescence. At the Durham City station, the sequence of ripe pod production along terminal and lateral inflorescences was recorded, along with corresponding values for seed number and mass.

METEOROLOGICAL DATA

Climate data over the study period (October 1997–October 1998) were obtained from a standard meteorological station at Durham City and an automated station on Great Dun Fell. From these it was possible to interpolate daily temperature at the remaining stations and derive bioclimate variables (for details see Willis & Hulme 2002). Daily heat sums, measured as growing degree-days >5 °C (GDD5), were calculated. From these data heat sums were estimated for the period up to seedling emergence (pre-emergent heat sum, PRHS, Jan–Mar); for the growth season (post-emergent heat sum, POHS, April–September); for the entire year from sowing (ALLHS); and for periods from seedling emergence up to the day of seed set (SEEDHS). Finally, as data collected from the study stations indicated that the usual time to produce a flower, ripen the pod and set seed was ≈4 weeks, an additional variable was created summing GDD5 for the periods of flowering to seed set (4WKHS). Estimates of wind speed and precipitation would also have been desirable, but these variables could not be as reliably interpolated between stations (Hulme *et al*. 1995). However, at the two meteorological stations there was a strong negative correlation between GDD5 and precipitation.

ANALYSES

Data were examined using nested ANOVA and regression analyses (Norusis 2000). Regressions used mean data from individual plants to examine relationships (e.g. plant height and seed traits). Nested ANOVAs were undertaken on measurements of individual seeds and pods, unless stated otherwise. To produce balanced models, the analysis of seed number per pod among stations and among plants eliminated the highest elevation station and used five randomly selected pods per plant. Analysis of seed mass between plants and stations similarly used 10 random seeds per plant with the number of stations reduced to four, eliminating the two high elevation stations. Analyses were undertaken using each of the bioclimate variables separately as explanatory variables.

Results

PARTITIONING VARIATION IN REPRODUCTIVE TRAITS BETWEEN STATIONS AND PLANTS

Over the entire 1998 flowering period, individual plants differed across two orders of magnitude in the number of pods they produced, ranging from one to 270 (Table 1). The considerable interplant differences within individual elevation stations accounted for 72% of the variation in pod production in the experiments, although significant differences among elevation stations were still found ($F_{4,102} = 7{\cdot}63$, $P < 0{\cdot}001$, ANOVA on log-transformed number of pods per plant). There was no significant trend with elevation in either the mean or variance in pod production, and no correlation between mean pod production at a station and interplant variation ($r_s = 0{\cdot}021$, df = 4, $P > 0{\cdot}1$; Table 1). The number of seeds per pod ranged from one to 19 (Table 1) and varied significantly both within and among stations (nested ANOVA: within station, $F_{20,75} = 4{\cdot}45$, $P < 0{\cdot}001$; among station, $F_{4,20} = 11{\cdot}28$, $P < 0{\cdot}001$), with 41·9 and 27·7% of variation explained within and among stations, respectively). There was no significant trend with elevation in either the mean or variance in seed number per pod, and no correlation between mean pod production at a station and interplant variation ($r_s = 0{\cdot}009$, df = 4, $P > 0{\cdot}1$). Seed mass varied significantly within and between stations (nested ANOVA: within station, $F_{36,399} = 21{\cdot}99$, $P < 0{\cdot}001$; among station, $F_{3,399} = 56{\cdot}22$, $P < 0{\cdot}001$), with 60·0 and 13·0% of variation explained within and among stations, respectively. Seed mass distributions were all positively skewed, which was attributable to one or a few large-seeded individuals in each population (Fig. 1). A significant trend of heavier seeds at higher elevations was found ($r_s = 0{\cdot}955$, df = 4, $P < 0{\cdot}01$; Table 1; Fig. 1). Although the coefficients of variance (CV) did not differ significantly among stations (Kruskall–Wallis df = 4, $\chi^2 = 5{\cdot}051$, $P > 0{\cdot}1$), the range in seed mass (as described by the ratio of largest to smallest seed) declined progressively from almost 12 at Durham City to less than 2 at Dun Fell (Table 1). Overall, the highest population variation in reproductive traits was found in the number of pods per plant, and the least in individual seed mass.

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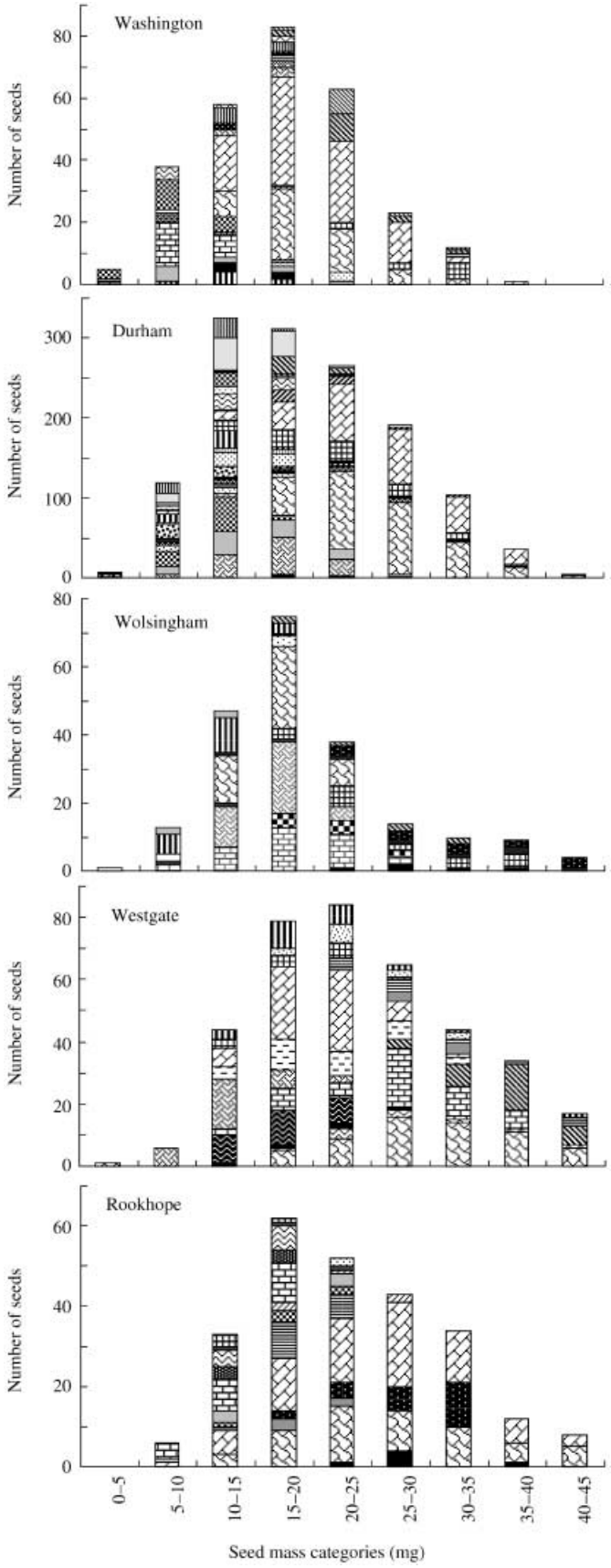


Fig. 1. Histograms of seed mass distributions at each of five elevation stations. Each shading pattern refers to the seed mass distribution of an individual plant, facilitating comparisons of both population and individual seed mass distributions. Values of skew are 0·255, 0·415, 1·083, 1·004 and 0·475 for Washington, Durham, Wolsingham, Westgate and Rookhope, respectively (too few seeds were produced at Dun Fell to merit plotting).

SEASONAL VARIATION IN REPRODUCTIVE TRAITS

Following individual plants throughout the 2 month fruiting period highlighted changes in seed output and quality over time. Pod production was initiated and subsequently peaked progressively later with increasing elevation (Fig. 2). Although facing a shorter season at higher elevations, plants at all but the highest elevation compensated by producing, on average, more pods per unit time once pod production began. Thus while, in late August, a negative relationship existed between elevation and numbers of pods per plant ($r_s = -0{\cdot}964$, df = 4, $P < 0{\cdot}01$), the trend had disappeared by late September ($r_s = 0{\cdot}297$, df = 4, $P > 0{\cdot}05$). Number of seeds per pod varied during the fruiting period (Fig. 3), being highest at the start of the fruiting period, declining as fruiting progressed, and increasing towards the end of the period. This trend may reflect within-plant allocation patterns, as revealed by more detailed sampling at the Durham City station where, within individual plants, pods produced earlier had more seeds than later pods on the same inflorescence ($t_{39} = 6{\cdot}94$, $P < 0{\cdot}001$). Although, on average, low-elevation stations produced smaller seeds than stations at higher elevations (Table 1), seed mass varied seasonally (Fig. 4). Over the fruiting period, the mean seed mass of the lower elevation stations increased towards a maximum of ≈25 mg, such that at the end of the season mean seed mass was similar at all stations.

CORRELATES AMONG REPRODUCTIVE TRAITS

Not surprisingly, taller plants produced proportionally more seed pods ($r_s = 0{\cdot}85$, df = 99, $P < 0{\cdot}001$; Fig. 5a) as a result of an increased number of lateral inflorescences. Plants that produced more seed pods, however, also produced more seeds per pod ($r_s = 0{\cdot}50$, df = 68, $P < 0{\cdot}001$; Fig. 5b). This trend arises partly as a result of pods on lateral inflorescences containing more seeds per pod than those on the terminal inflorescence (lateral mean = $8{\cdot}49 \pm 0{\cdot}41$ seeds per pod; terminal mean = $7{\cdot}04 \pm 0{\cdot}37$ seeds per pod; paired *t*-test, $t_{34} = 4{\cdot}87$, $P < 0{\cdot}001$). Individual seed mass was not related to either the number of pods per plant ($r_s = 0{\cdot}17$, df = 66, $P > 0{\cdot}1$) or the number of seeds per pod ($r_s = 0{\cdot}18$, df = 61, $P > 0{\cdot}1$). There was no difference in seed mass between seeds originating from terminal *vs* lateral inflorescences of the same plant at any given time (*t*-tests of plants with 30 or more seeds from both terminal and lateral inflorescences were all non-significant). Thus with increasing resources, *Impatiens* allocates resources to produce more, rather than larger, seeds.

IMPACT OF CLIMATE ON REPRODUCTIVE OUTPUT

None of the measures of heat sum (PRHS, POHS, ALLHS) explained significant variation in the number

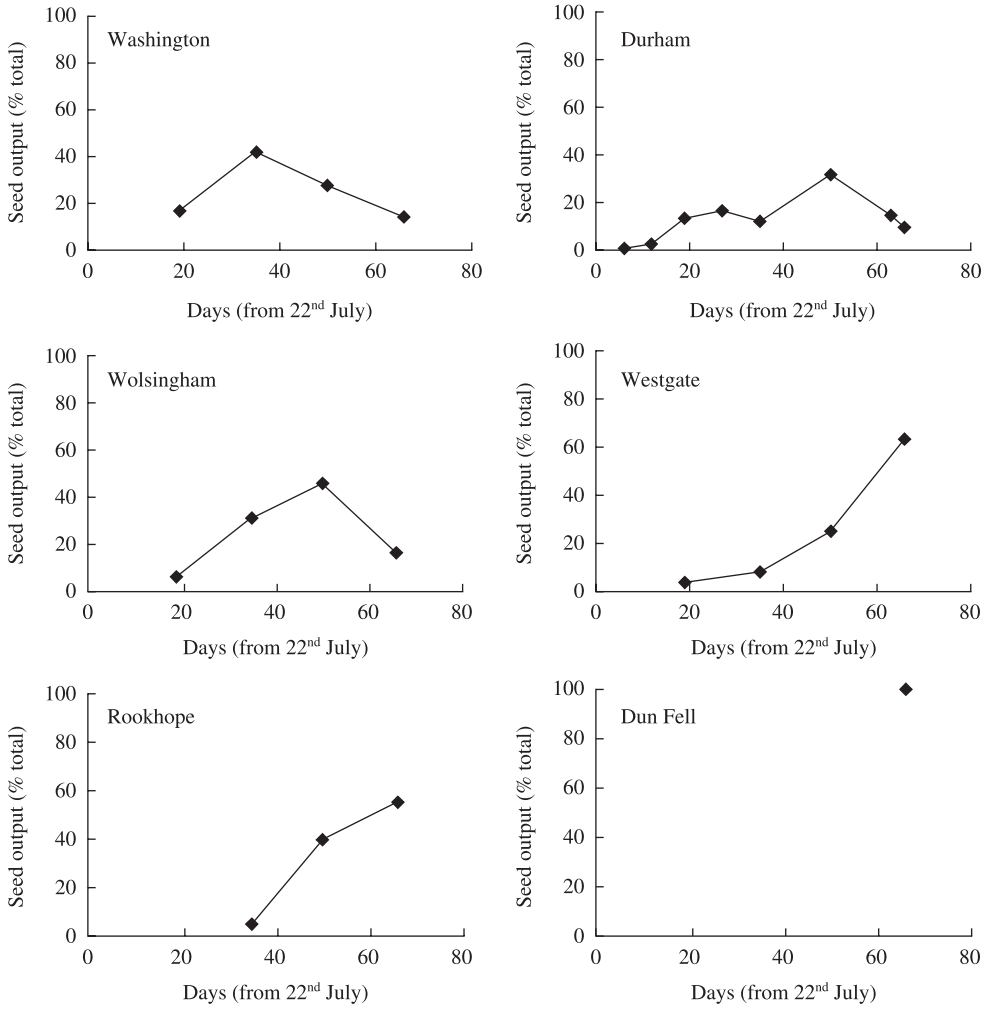


Fig. 2. Temporal changes in production of ripe *Impatiens* pods at each elevation measured in days from the period of first pod production (22 July). Pod production is plotted as a percentage of total pods produced at the station over the fruiting period.

of pods produced per plant during the 1998 growing season. The heat sum over the period of flowering and seed development (4WKHS) was by far the best predictor of seed mass, and revealed a strong negative relationship between heat sum and mass of seeds produced ($r^2 = 0{\cdot}717$, $F_{1,22} = 55{\cdot}74$, $P < 0{\cdot}001$; Fig. 6).

Discussion

The reproductive traits in *Impatiens*, as in numerous plant species (Michaels *et al.* 1988; Leishman *et al.* 2000), show marked intraindividual and intrapopulation variation. Of the three reproductive traits, seed mass was the least variable at both individual and population levels, while the number of pods per plant varied most. This pattern is consistent with the general finding that seed mass is the least variable component of yield (Harper *et al.* 1970; Haig & Westoby 1988). However, although seed mass was the least variable trait, it still exhibited significant variation. The mean population CV in seed mass was over 39%, and is high compared to an average of 28% for 39 plant species in eastern-central Illinois (Michaels *et al.* 1988). The detailed experimental approach in this study presents a unique opportunity to assess the correlates of seed mass variation and their adaptive significance.

Partitioning the variation in seed mass revealed the greatest source to be that arising among individual plants (42%) within a station, while the least was found among elevation stations (28%). Within an elevation station, over 53% of the variation in seed mass occurred among plants and, compared to an average of 38% for the species examined by Michaels *et al.* (1988), represents a relatively high percentage. This finding is striking for at least two reasons. First, it is contrary to what might be seen as the norm for herbaceous plants; second, it is maintained even in the face of a marked elevational trend that led to a doubling in mean seed mass and a tenfold reduction in its range (Table 1). Although no information was available on genotypic variation, marked variation in seed mass among individual plants may reflect an adaptive response to changes in resources.

At all elevations, self-thinning led to significant plant-size hierarchies. The interplant variation in seed

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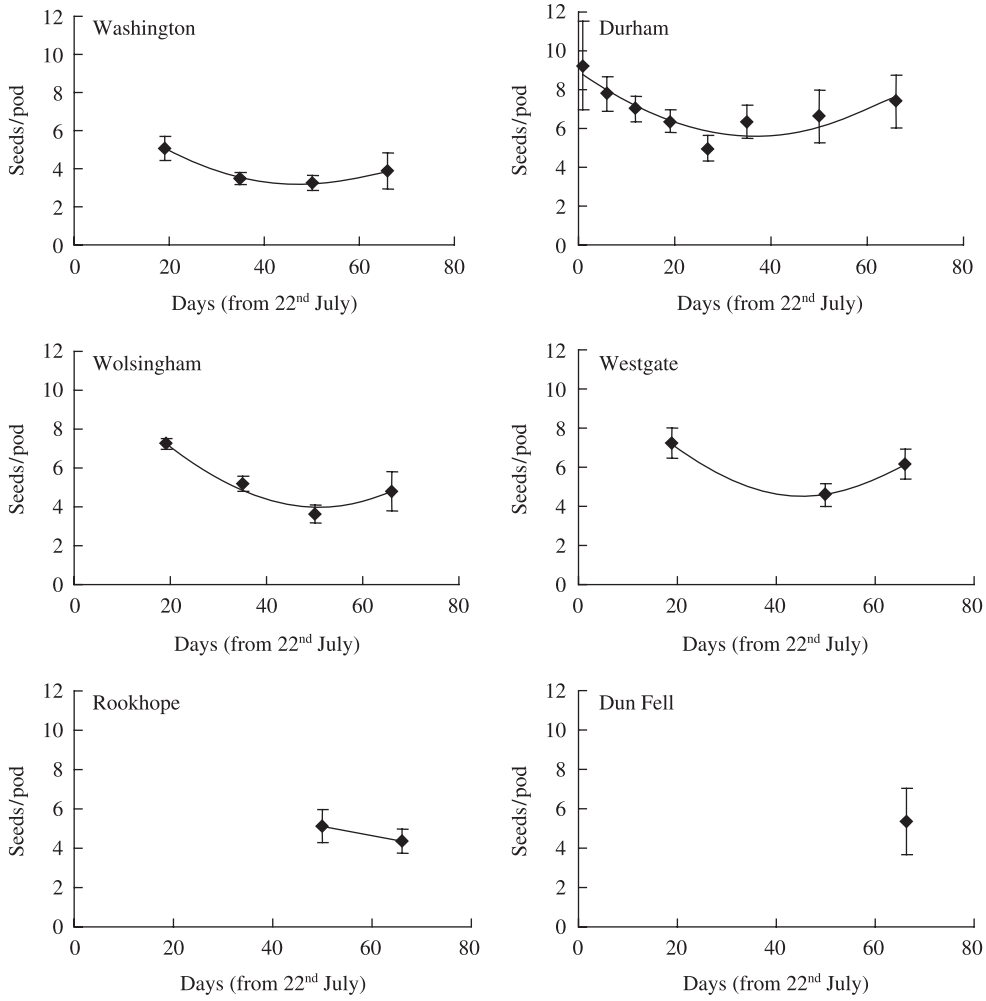


Fig. 3. Temporal changes in seed content per pod of *Impatiens* pods from plants grown at stations along the elevation gradient, measured in days from the period of first pod production (22 July). Means are calculated from median pod mass of each replicate plant to standardize for varying pod output per plant. Second-order polynomials fitted to means for the four lowest stations are: Washington, $y = 0{\cdot}0023x^2 - 0{\cdot}2168x + 8{\cdot}3596$, $r^2 = 1$; Durham, $y = 0{\cdot}0025x^2 - 0{\cdot}1808x + 8{\cdot}9807$, $r^2 = 0{\cdot}82$; Wolsingham, $y = 0{\cdot}0033x^2 - 0{\cdot}3341x + 12{\cdot}533$, $r^2 = 0{\cdot}96$; Westgate, $y = 0{\cdot}0039x^2 - 0{\cdot}3574x + 12{\cdot}621$, $r^2 = 1$.

mass could simply reflect that larger plants produce larger seeds, and it is evident that one or two plants in each population had markedly larger seeds than the rest (Fig. 1). Both the number of pods per plant and the seeds produced per pod were a function of plant height, and resulted in seed production varying by between two and three orders of magnitude among plants at the same elevation. Yet even with considerable variation in seed number, there was no evidence of a trade-off with seed mass and it appears that, with increasing resources, *Impatiens* tends to produce more rather than larger seeds. Although there is empirical support for a trade-off in seed mass and number across different species (Shaanker *et al.* 1988; Henery & Westoby 2001; Leishman 2001), within species there is evidence for (Ågren 1989; Vaughton & Ramsey 1998; Eriksson 1999; Parciak 2002); and against (Wulff 1986; Winn & Gross 1993; Mendez 1997; Simons & Johnston 2000) such a trade-off. The *Impatiens* data argue against such a trade-off, as plant size strongly determined seed number but not seed mass. By simultaneously assessing the covariance among reproductive and somatic traits and controlling for resource limitation, this study provides the first experimental support for models of optimum seed mass that predict plants responding to changes in resource supply by a change in seed number rather than mass (Haig & Westoby 1988).

While seed mass did not vary with either plant height or seed number, a significant trend of increasing seed mass with higher elevations was found. Could such variation reflect selection on individual plant traits? Seed mass has previously been found to increase (Hurka & Benneweg 1979; Oyama 1993; Lord 1994; Murray *et al.* 2003); decline (Baker 1972; Totland & Birks 1996; Kollmann & Pflugshaupt 2001; Murray *et al.* 2003); or be invariant (Greimler & Dobes 2000; Buckley *et al.* 2003; Murray *et al.* 2003) with elevation. This indicates that the selective advantages of a large seed mass in the face of environmental severity at higher elevations (Hurka & Benneweg 1979; Lord 1994) are finely balanced

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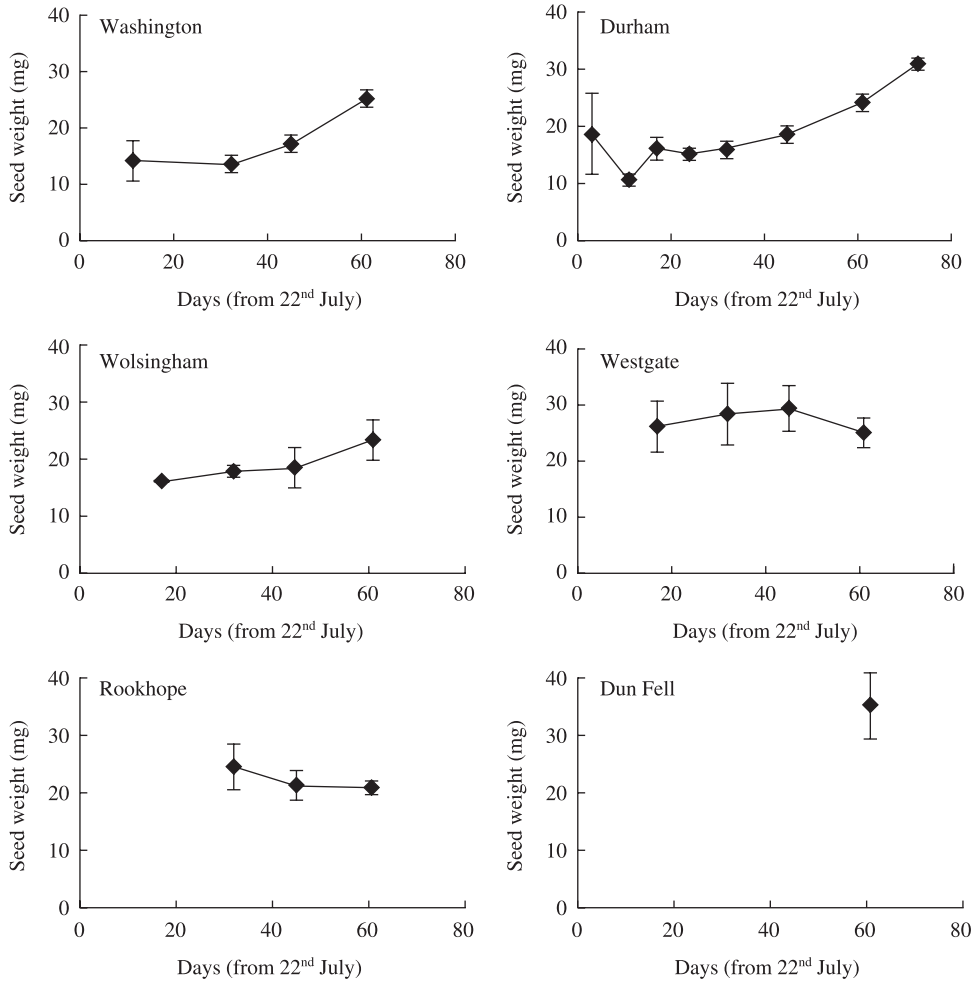


Fig. 4. Temporal changes in seed mass of *Impatiens* pods from plants grown at stations along the elevation gradient, measured in days from the period of first pod production (22 July). Values are calculated from means of each replicate plant to standardize for varying seed output per plant.

by a shorter growing and seed-maturation period (Baker 1972). However, previous studies of seed mass variation along elevation gradients have not assessed the role of climate on seed mass. This study highlights that lower heat sums at higher elevations explain most of the variation in seed mass along the elevation gradient, and the trend is consistent with laboratory studies that have revealed low temperatures to increase seed mass (Wulff 1986; Lacey 1996). The timing of changes in resource supply may be crucial and, if occurring after seed number is determined, a response in seed mass might be expected (Harper *et al*. 1970; Haig & Westoby 1988; Eriksson 1999). Post-zygotic parental temperatures strongly determine seed mass (Lacey 1996), and this may explain why, in *Impatiens*, the heat sum over the 4 weeks preceding seed maturation rather than over the entire growing season was most strongly correlated with seed mass. This effect of temperature was seen both in comparisons of mean seed mass across the elevation gradient and also over time within a population. Thus any adaptive explanations regarding improved performance at higher elevations are not convincing arguments for seasonal variation within an elevation. Why, then, does seed mass sometimes decline with elevation? A tentative hypothesis regarding declines in seed mass with elevation is that, in these species, allocation patterns are determined pre- rather than post-fertilization (McKee & Richards 1996). This may explain why declines in seed mass with elevation can coincide with a reduction in seed number (Totland & Birks 1996; Kollmann & Pflugshaupt 2001). However, it should also be borne in mind that simple differences in the timing of seed collection in correlative studies may produce artefactual relationships between seed mass and elevation. So, while adaptive explanations may be sought for such trends in seed mass, these must be viewed in the context of physiological and developmental constraints relating to direct temperature effects. Whether the variations in seed traits driven by such constraints actually result in increased, decreased or invariant consequences for success requires further work.

It appears that *Impatiens* does not fit the expectation as to how resources might influence seed mass

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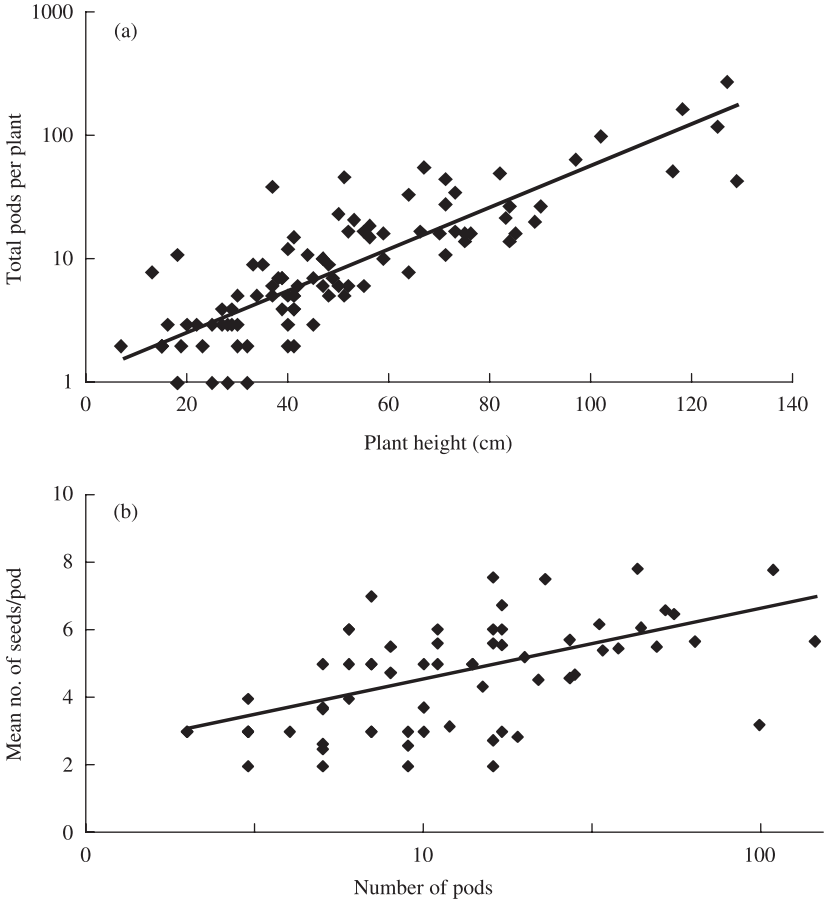


Fig. 5. Relationships between (a) mean number of seeds per pod and plant height ($F_{68} = 21{\cdot}02$, $r^2 = 0{\cdot}24$, $P < 0{\cdot}001$); (b) mean number of seeds per pod and pod production. $F_{68} = 21{\cdot}22$, $r^2 = 0{\cdot}23$, $P < 0{\cdot}001$ for *Impatiens* plants grown along the elevation gradient.

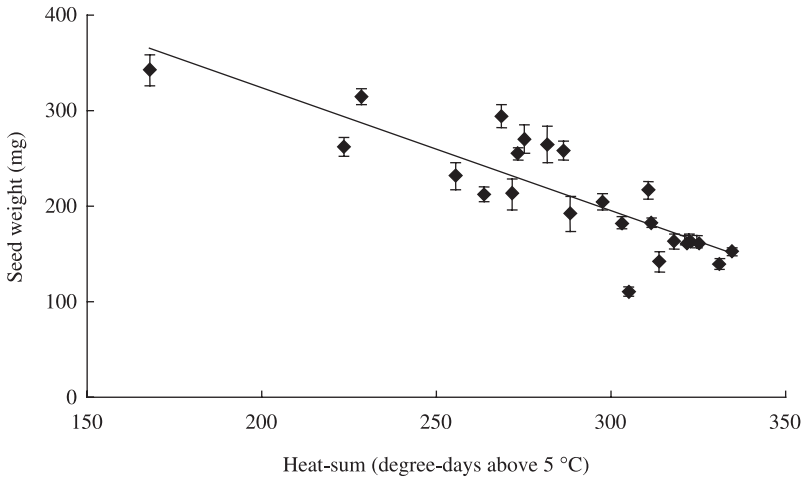


Fig. 6. Mass of seeds from *Impatiens* plants grown at stations along the elevation gradient in relation to heat sum over the preceding 4 weeks. Displayed values are means (with SE) from each of the study plots separated by different collection dates.

variation (Lee 1988; Michaels *et al.* 1988; Leishman *et al.* 2000). Seed mass increased, rather than decreased, with increasing resource limitation at higher elevations; was not related to plant height or fecundity; and seeds produced late in the season were often larger than the first seeds to mature. In addition, while intra-individual seed mass variation was high, there were marked differences in seed mass among individual plants. However, rather than obscure the search for general trends, the experimental approach and detailed monitoring have significantly advanced understanding of the interplay between allocation patterns and the environment. Of

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particular importance is the identification of climate as a crucial influence on both mean and variance in seed mass. The study also warns against correlative studies of seed mass variation that fail to account for environmental gradients by selecting arbitrary populations, or that ignore the temporal dynamics in seed mass by sampling populations on a single occasion. Had this study followed a correlative approach using natural populations, it is likely that trends in increased seed mass at higher elevations and significant individual variation in seed mass would probably have been detected. However, this combination of trends could lead to adaptive explanations of increased selection for larger seed mass at higher elevations. The experimental approach adopted here argues against an adaptive explanation. Thus, while individual plants may vary in mean seed mass, this does not appear to be related to increased fitness (plant size and fecundity), nor to increased survival in the face of environmental severity (Moles & Westoby 2004). Rather, the results reiterate increasing evidence that plasticity in seed mass may be as important a life-history characteristic as mean seed mass, and comparative analyses based solely around means and not variances may miss fundamental aspects of plant ecology (Geritz 1995). For example, the success of *Impatiens* as an invasive annual species may reflect intraindividual variation in seed mass that potentially facilitates the exploitation of heterogeneous environments (Venable & Brown 1988; Rees & Westoby 1997), especially in wetland ecosystems (Yanful & Maun 1996). Thus the extended period of seed release, considerable variation in seed mass, and increased seed mass in response to environmental severity are all likely to maximize the opportunities for colonization and establishment in this invasive species.

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