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ENVIRONMENTAL CORRELATES OF HABITAT DISTRIBUTION AND FITNESS COMPONENTS IN *IMPATIENS CAPENSIS* AND *IMPATIENS PALLIDA*

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SUMMARY

(1) We correlated aspects of the growth and reproduction of *Impatiens capensis* and *I. pallida* (Balsaminaceae) with a broad range of availabilities of water, light and inorganic nutrients in diverse microhabitats on Mont St. Hilaire, Quebec, Canada.

(2) Both species have distinct but overlapping distributions along environmental gradients on Mont St. Hilaire. Compared to *I. capensis*, *I. pallida* predominantly grows in a narrower range of habitats that are both significantly drier and richer in nitrate and phosphorus. Sites dominated by *I. pallida* also tend to be richer in potassium, to be relatively poor in calcium and magnesium, and to have significantly lower soil pH.

(3) In the habitats on Mont St. Hilaire where each species commonly grows, *I. pallida* attains a significantly greater biomass and has higher fecundity than *I. capensis*, although the two species do not differ in numbers of cleistogamous capsules produced per plant.

(4) Growth and reproduction are greatest on sites rich in potassium and phosphorus, and high in organic matter for *I. capensis*, and on sites rich in calcium and magnesium with high insolation for *I. pallida*. In *I. pallida*, fecundity increases with the availability of nitrate but decreases with ammonium. Waterlogged soils are detrimental to both species, but plant performance in most natural habitats of *Impatiens* on Mont St. Hilaire is not affected by water shortages in years of normal precipitation.

(5) Based on these correlations, we believe that both the distribution of *Impatiens* in eastern deciduous forest ecosystems and the fitness of individuals in different habitats are mediated by the availability of inorganic nutrient resources to a greater degree than has previously been appreciated. Experimental investigations are necessary to actually define the interacting effects of different inorganic nutrients on growth and fecundity for both *I. capensis* and *I. pallida*.

INTRODUCTION

Plant growth, survival and reproductive success hinge on the effective acquisition and allocation of carbon, water and inorganic nutrient resources. The acquisition of these essential resources depends on their availability in the microenvironment where the plant is rooted and on the plant's requirement for each particular resource. Plants can adjust somatic allocation to increase the rates of acquisition of resources which are in high demand, but have low availability (Bloom, Chapin & Mooney 1985). The overall availability of resources can limit plant size and consequently absolute levels of reproduction (Samson & Werk 1986). The balance of resource demand and availability can also be modulated by qualitative shifts between reproductive modes that differ in resource requirements (Willson 1983). Because such dynamic and plastic responses to resource availability can be principal determinants of plant fitness, it is important to define the patterns of resource availability, resource requirements and responses to

different resource availabilities that prevail among co-occurring plants in natural habitats.

Surprisingly few studies have considered the responses of native plant species to the availability of a broad array of essential resources. The effects of one or at most a few resources with special emphasis on the availability of solar energy, carbon and water resources, and more recently nitrogen, has received most attention. For example, the growth and reproductive success of understorey species in temperate deciduous forests is usually considered to be affected by the solar radiation regime (Ashmun & Pitelka 1984; Pitelka, Ashmun & Brown 1985) or by both solar radiation and water availability (Waller 1980; Menges & Waller 1983; Cid-Benevento & Werner 1986). The possibility that the availability of inorganic nutrient resources might regulate or limit components of plant performance in forest understorey habitats has not often been considered in North America despite the suggestion of their importance in a number of phytosociological analyses (Peet & Loucks 1977; Peet & Christensen 1980) and their well recognized importance in European forests (Ellenberg 1982).

We have therefore investigated the association between key aspects of plant growth and reproduction and the availability of all major resources in the local environment for two annual herbs common in the eastern deciduous forests of North America: *Impatiens capensis* Meerb. and *Impatiens pallida* Nuttall. The responses of these two *Impatiens* species to environmental resource gradients have recently been the focus of a series of evolutionary and ecological investigations (Abrahamson & Hershey 1977; Rust 1977; Schemske 1978, 1984; Waller 1979, 1980, 1982, 1984, 1985; Bell *et al.* 1984; Schmitt, Ehrhardt & Swartz 1985; Simpson Leck & Parker 1985; Cid-Benevento & Schaal 1986; Cid-Benevento & Werner 1986; Schoen *et al.* 1986; Stewart & Schoen 1987). Despite the current interest in the evolutionary ecology of *Impatiens*, we do not know the limits of plastic adjustments by either species to variations in the environmental availability of major resources, nor do we know the abiotic factors most consistently affecting the fitness of individuals in natural populations of *Impatiens*. Our goals in this initial investigation were to provide direction for subsequent manipulative experiments, designed to elucidate both the factors controlling habitat separation of the two *Impatiens* species in nature and the important factors underlying fitness variation between individuals in natural populations of both species.

METHODS

Study location

All the sampled populations of *Impatiens* grew on Mont St Hilaire (45°32'N, 73°8'W), a low mountain that rises abruptly above the St Lawrence River valley near Montreal, Quebec, Canada. The mountain consists of eight forested peaks surrounding Lac Hertel, a 29-ha lake fed entirely by drainage from the interior slopes. Because of differences in slope, aspect and soil depth, the microclimate and hydrology of Mont St Hilaire have high spatial and temporal variance (Rouse & Wilson 1969; Enright & Lewis 1985). The bedrock of the eastern half of the mountain is nepheline syenite, and the western half is essexite with some localized deposits of limestone (Currie 1976; Greenwood 1983). Soils on the mountain include dystochrepts, eutrochrepts and haplaquepts (T. R. Moore, personal communication) and those developed on the syenitic bedrock are richer in K, Zn and Mn, while those on essexite are richer in Ca and Fe (Webber & Jellema 1965). The

outer flanks of the mountain have a rim of baked limestones (hornfels) which originated when the igneous plugs now forming the mountain peaks first intruded into the sedimentary deposits of the region. Northern hardwood forest communities dominated by mixtures of *Acer saccharum* Marsh., *Fagus grandifolia* Ehrh., *Betula alleghaniensis* Britt., *Fraxinus americana* L., *Tilia americana* L., *Quercus rubra* L. and *Tsuga canadensis* (L.) Carr. occur on Mont St Hilaire (Maycock 1961; Enright & Lewis 1985). Most of the forests are mature, some largely undisturbed by human activity for centuries, and have species-rich and ecologically diverse understorey communities (Holland 1971, 1978). Contrasting edaphic conditions, topographically induced microclimatic variation, and the diverse vegetation provide an unusually wide array of different habitats for establishment of *Impatiens* in a contiguous area of about 900 ha.

Monitoring of plants and microenvironment

Impatiens capensis and *I. pallida* are both widespread and abundant on Mont St Hilaire. In May 1984 we established fifty-one study sites at twenty-six localities, chosen randomly from among 228 localities representing all the known habitats and sections of the mountain where *Impatiens* commonly grew. Localities are areas where local topography has resulted in recognizably discrete populations of *Impatiens* up to a few hectares in extent. At each of the twenty-six localities we randomly chose two 1-m² study sites, one high and the other low on the local microtopographic gradient. For example, one site might be randomly placed along a stream-side and the other on the adjacent upland drained by that stream. Each study site was dominated by *Impatiens* seedlings, all of which were then too young to be identified to species. At each site ten seedlings were randomly selected and tagged. We monitored the height growth, survivorship, flower numbers and capsule production of these individuals weekly from 27 June until 15 September 1984 when all surviving plants were harvested. Individuals were identified to species as they developed chasmogamous flowers, or in a few cases by inference when all flowering plants in a locality were of the same species. The dry biomass of each individual was measured at harvest. Capsules originating from cleistogamous versus chasmogamous flowers were distinguished by marking pedicels of individually monitored flower buds with spots of acrylic paints and following these to abortion or fruit set.

We estimated the mean soil moisture at each site from ten samples taken through the growing season in the rooting zone of *Impatiens*; gravimetric soil moisture is expressed as $g(H_2O) g^{-1}$ (dry soil) following Slavik (1974). Insolation at each site was measured twice during the flowering period of *Impatiens* by exposing packets of diazochrome film mounted horizontally at the top of the *Impatiens* canopy in each site for one to two days (Friend 1961); the number of layers of film exposed at each site was expressed as a percentage of simultaneous exposure under full sunlight. Although the spectral response of diazochrome film differs dramatically from the absorption spectrum of foliage, this method does provide useable, comparative data on insolation across many sites at reasonable cost. We gathered composite samples of the top 6 cm of soil from each site in mid-July 1984; this sampling depth, which included both organic and upper mineral soil horizons, was chosen because the roots of *Impatiens* plants are most densely distributed in this zone. A soil sample taken at a single point in time does not necessarily represent the availability of mineral resources at a site over the entire growing season, especially for dynamic resources pools like nitrate or ammonium (Barber 1984; Mengel 1985). Nonetheless, by sampling soil nutrient resources at the onset of peak flowering in *Impatiens* and across a wide range of habitats, we believe that one can make meaningful, if

preliminary, assessments of the nutrient dependence of plant performance in these two forest species. It was neither practical nor consonant with the goals of this initial investigation to sample environmental factors across sufficient sites at the necessary intervals to fully define temporal as well as spatial variation in resource availability.

Soil samples were rapidly frozen (Nelson & Bremner 1972) and then stored for subsequent analysis by the Soil Testing Laboratory, Macdonald College of McGill University. The KCl extractable fractions of nitrate (Kamphake, Hannah & Cohen 1967) and ammonium (O'Brien & Fiore 1962) were assayed. Nitrate and ammonium availabilities were measured separately because the energetic costs of assimilating nitrogen from these two sources differ and not all species can utilize both forms of nitrogen (Haynes & Goh 1978). The available phosphorus assay follows Method 2 of Bray & Kurtz (1945) with extraction in HCl and NH_4F . Potassium, calcium and magnesium were assayed by atomic absorption spectrophotometry following Jackson (1964). Percentage organic matter was determined by loss-on-ignition (Bell 1964). We measured soil pH as a 1:1 slurry in H_2O on the same soil samples following McLean (1982).

Statistical analyses

SAS, Version 5 (SAS Institute 1985) was used to screen, normalize, describe and analyse our data. Because our environmental sampling was designed to represent average conditions within each m^2 site, we treated the site as our experimental unit; the plant performance variables used in the analyses are therefore the mean values based on the ten individuals sampled within each m^2 site. Because of high levels of fine-scale spatial and temporal heterogeneity in insolation (Hutchison & Matt 1977; Baldocchi *et al.* 1986) and edaphic conditions (Frankland, Orington & Macrae 1963; McFee & Stone 1965; Mollitor, Leaf & Morris 1980), the m^2 study sites at a common locality can be considered statistically independent in the analyses that follow. We used non-parametric correlations and least square regression on normalized data to describe the performance and environmental distribution of each species at Mont St Hilaire.

To illustrate the distribution of the two *Impatiens* species along environmental gradients and the primary environmental factors correlated with the distribution of each species, we use a multivariate technique, biplot analysis (Gabriel 1971), that involves the canonical decomposition of a principal components analysis. In the biplot analysis of these data each m^2 site is described by the deviation of its environmental characteristics from the grand mean of all fifty-one sites; only environmental variables, not species composition or plant performance, determine the outcome of the analysis. Subsequently each field site was identified in the biplot graph as pure *I. capensis*, pure *I. pallida*, or a mixture of the two species. Sites at a common locality were also coded by superscripts to help assess the level and pattern of environmental variation within and between the localities where *Impatiens* grew on Mont St Hilaire. K. R. Gabriel (University of Rochester, N.Y.) wrote and supplied the FORTRAN program used in the biplot analysis.

RESULTS

Impatiens capensis and *I. pallida* have distinct, but overlapping environmental distributions at Mont St Hilaire (Fig. 1, Table 1). Compared to *I. capensis*, *I. pallida* grows in a somewhat narrower range of habitats that are both significantly drier and richer in nitrate and phosphorus (Table 1). Sites dominated by *I. pallida* also tend to be richer in potassium

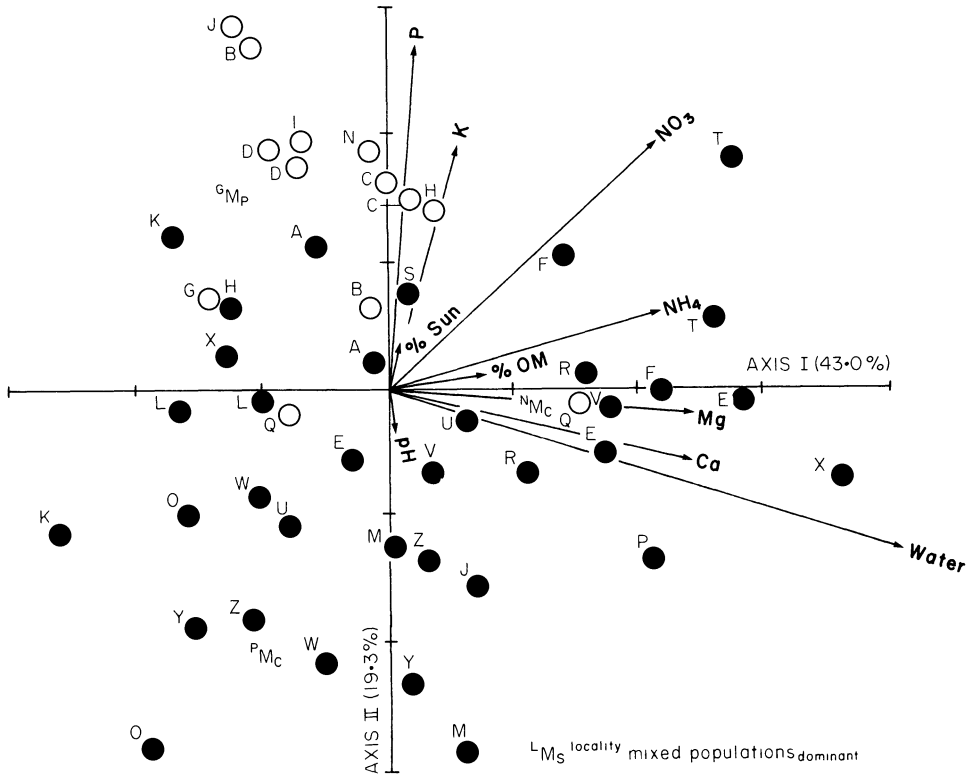


FIG. 1. Canonical decomposition (Gabriel 1971) of the site \times environment deviations matrix describing the distribution of *Impatiens capensis* (●) and *Impatiens pallida* (○) at Mont St Hilaire, Quebec. The points in the graph represent the individual study sites characterized by only their abiotic environmental conditions; in general, the closer together are two points, the more environmentally similar are the two sites. Sites from the same locality share a common superscript; subscripts on the three mixed-site symbols indicate the locally dominant species. The grand mean of all sites is at the origin of the graph. The vectors represent the influence of individual environmental factors in distinguishing one site from another; the longer a vector, the greater its influence. Perpendicular projections from each point to a particular vector give the ordering of the individual sites along that environmental factor from low to high values in the direction the vector points. The cosine of the angle between any two vectors approximates the correlation between those two environmental factors in these data. Acronyms for the environmental vectors are given in Table 1.

and phosphorus, to be relatively poor in calcium and magnesium, and to have significantly lower soil pH. The habitats of *Impatiens* at Mont St Hilaire encompass a wide range of soil organic matter contents and insolation regimes, but the two species do not differ significantly in their distribution along these two environmental gradients. Species dominance in the three sites containing both species reflects the same overall environmental correlations as species distribution: *I. capensis* dominates all but the one mixed site nearest the primary cluster of *I. pallida* sites in the biplot graph (Fig. 1).

Although *I. pallida* occurs in a narrower range of environments than *I. capensis* on Mont St. Hilaire, on average it attains a significantly greater biomass and higher fecundity (Table 2). The two species do not differ in the number of cleistogamous capsules they produce, but *I. pallida* produces more chasmogamous flowers and capsules. *Impatiens*

TABLE 1. Environmental characteristics at sites dominated by *Impatiens capensis* vs. *Impatiens pallida*. Values for the mean \pm S.D., the median, and the minimum and maximum (sample size) are tabulated and tested for interspecific differences by a Wilcoxon rank sum test.

Acronym	Variable	<i>I. capensis</i>	<i>I. pallida</i>	$P(H_0: I_c = I_p)$
H ₂ O	g(H ₂ O) g ⁻¹ (dry soil)	2.31 \pm 1.50, 1.98, 0.41–5.81(35)	1.17 \pm 0.68, 0.98, 0.39–2.95(13)	0.007**
SUN	% full sunlight	74 \pm 15, 73, 42–100(38)	80 \pm 16, 83, 51–100(13)	0.198
NO ₃ ⁻	μ g(NO ₃ ⁻) g ⁻¹ (dry soil)	18.9 \pm 25.3, 8.8, 0.6–112.9(35)	20.0 \pm 10.7, 18.1, 4.9–42.0(13)	0.049*
NH ₄ ⁺	μ g(NH ₄ ⁺) g ⁻¹ (dry soil)	42.6 \pm 42.8, 30.9, 6.7–245.3 (35)	45.2 \pm 20.4, 45.6, 13.5–90.5(13)	0.219
P	μ g(P) g ⁻¹ (dry soil)	61.9 \pm 45.3, 54.0, 13.0–199.0(35)	173.8 \pm 135.5, 100.0, 34.0–450.0(13)	0.002**
K	μ g(K) g ⁻¹ (dry soil)	258 \pm 222, 175, 37–1078(35)	343 \pm 253, 297, 63–1050(13)	0.174
Ca	μ g(Ca) g ⁻¹ (dry soil)	3427 \pm 2811, 2482, 260–11396(35)	2440 \pm 2404, 1170, 620–8382(13)	0.150
Mg	μ g(Mg) g ⁻¹ (dry soil)	479 \pm 561, 325, 62–3048(35)	272 \pm 190, 150, 75–666(13)	0.164
pH	Soil pH	5.89 \pm 0.50, 5.97, 4.30–6.65(38)	5.49 \pm 0.63, 5.35, 4.56–7.00(13)	0.009**
OM	% organic matter	32.6 \pm 18.3, 29.6, 2.1–81.8(35)	30.6 \pm 11.8, 29.2, 14.4–58.2(13)	0.908

* 0.01 < P \leq 0.05.

** 0.001 < P \leq 0.01.

TABLE 2. Mean plant performance at sites with monospecific stands of *Impatiens capensis* or *Impatiens pallida*. Values for the mean \pm S.D., the median, and the minimum and maximum (plus sample size) are tabulated and tested for interspecific differences by a Wilcoxon rank sum test.

Acronym	Variable	<i>I. capensis</i>	<i>I. pallida</i>	$P(H_0: I_c = I_p)$
CH	Chasmogamous flowers	7.1 \pm 18.0, 2.7, 0.0–110.4(35)	17.9 \pm 14.6, 14.0, 2.1–62.8(13)	0.0001***
CHC	Chasmogamous capsules plant ⁻¹	3.9 \pm 11.3, 1.2, 0.0–69.7(35)	8.8 \pm 6.5, 7.2, 0.5–27.9(13)	0.0002***
CLC	Cleistogamous capsules plant ⁻¹	9.3 \pm 8.1, 6.7, 1.0–33.2(35)	9.9 \pm 6.9, 6.5, 4.0–27.9(13)	0.503
TC	Total capsules plant ⁻¹	13.2 \pm 17.4, 7.4, 1.0–102.9(35)	18.7 \pm 10.6, 12.6, 4.5–40.9(13)	0.022*
BM	Dry biomass plant ⁻¹ (g)	0.89 \pm 1.08, 0.61, 0.15–6.53(35)	1.64 \pm 1.32, 1.36, 0.18–5.47(13)	0.009**
HT	Plant height (cm)	55 \pm 27, 50, 19–126(35)	52 \pm 15, 54, 16–78(13)	0.871
LIFE	Julian day of death	244 \pm 6, 247, 228–250(35)	238 \pm 7, 238, 226–249(13)	0.012*

* 0.01 < P \leq 0.05.

** 0.001 < P \leq 0.01.

*** P \leq 0.001.

pallida achieves this greater growth and fecundity despite senescing significantly earlier in the growing season than *I. capensis*. Consistent with the distinctive environmental distributions of *I. capensis* and *I. pallida* on Mont St. Hilaire, these contrasting patterns of growth and reproduction stem from differences in responses to environmental factors in the two species (Table 3).

Greater plant size in *I. capensis* is primarily associated with greater availability of K on sites rich in organic matter but not prone to waterlogging (Table 3). *Impatiens pallida* tends to grow larger at well-lit, Ca-rich sites that are not too wet. Sites promoting growth in *I. pallida* are also associated with early senescence, apparently tied to a likelihood of late season water shortages (unpublished data).

In *I. capensis*, numbers of chasmogamous flowers and capsules increase with concentrations of soil K and higher soil organic matter, but decrease on waterlogged sites (Table 3). In *I. pallida* the numbers of chasmogamous flowers increase at Ca-rich sites. In *I. pallida* the maturation of chasmogamous capsules is enhanced by higher insolation and

TABLE 3. Least square regressions relating components of fitness to environmental variables. Models were developed by stepwise regression using the max r^2 technique (PROC STEPWISE: SAS Institute 1985) and subsequent analyses of collinearity, influence statistics, and partial residual plots (PROC REG: SAS Institute 1985). All model parameters are significant at $P \leq 0.05$ with a few exceptions ($P \leq 0.10$). No significant regressions could be developed to predict LIFESPAN. Acronyms and units appear in Tables 1 and 2.

Impatiens capensis ($n = 35$ sites)

$$\begin{aligned} \ln \text{BM} &= 0.33 \ln \text{K} + 2.16 \arcsin \sqrt{\text{OM}} - 0.86 \ln \text{H}_2\text{O} - 2.93, r^2 = 0.28, P = 0.15 \\ \ln \text{CH} &= 0.41 \ln \text{K} + 3.08 \arcsin \sqrt{\text{OM}} - 1.03 \ln \text{H}_2\text{O} - 1.90, r^2 = 0.30, P = 0.011 \\ \ln \text{CHC} &= 0.31 \ln \text{K} + 2.58 \arcsin \sqrt{\text{OM}} - 0.93 \ln \text{H}_2\text{O} - 1.60, r^2 = 0.26, P = 0.023 \\ \ln \text{CLC} &= 0.26 \ln \text{K} + 2.57 \arcsin \sqrt{\text{OM}} - 0.56 \ln \text{H}_2\text{O} - 0.45 \ln \text{Mg} + 2.16, r^2 = 0.37, P = 0.006 \\ \ln \text{TC} &= 0.34 \ln \text{K} + 3.04 \arcsin \sqrt{\text{OM}} - 0.73 \ln \text{H}_2\text{O} - 0.47 \ln \text{Mg} + 1.87, r^2 = 0.37, P = 0.007 \end{aligned}$$

Impatiens pallida ($n = 13$ sites)

$$\begin{aligned} \ln \text{BM} &= 0.96 \ln \text{Ca} + 2.15 \arcsin \sqrt{\text{SUN}} - 0.89 \ln \text{H}_2\text{O} - 0.81 \ln \text{NH}_4^+ - 6.38, r^2 = 0.80, P = 0.007 \\ \ln \text{CH} &= 0.42 \ln \text{Ca} - 0.41, r^2 = 0.31, P = 0.048 \\ \ln \text{CHC} &= 0.91 \ln \text{Ca} + 3.15 \arcsin \sqrt{\text{SUN}} + 0.67 \ln \text{K} + 0.58 \ln \text{NO}_3 - 1.39 \ln \text{NH}_4^+ - 8.61, r^2 = 0.78, P = 0.029 \\ \ln \text{CLC} &= 0.94 \ln \text{Ca} + 2.55 \arcsin \sqrt{\text{SUN}} - 0.76 \ln \text{H}_2\text{O} - 1.07 \ln \text{Mg} - 0.68 \ln \text{P} + 1.44, r^2 = 0.72, P = 0.064 \\ \ln \text{TC} &= 0.67 \ln \text{Ca} + 2.10 \arcsin \sqrt{\text{SUN}} - 0.43 \ln \text{H}_2\text{O} - 0.86 \ln \text{NH}_4^+ - 1.35, r^2 = 0.80, P = 0.007 \end{aligned}$$

increased availability of nitrate-N, but is suppressed by increased levels of ammonium-N (Table 3).

Production of cleistogamous capsules in *I. capensis* increases with K availability and soil organic matter content, but is suppressed on wetter, Mg-rich sites. In *I. pallida* cleistogamy increases in sunny, Ca-rich sites that are relatively dry and low in Mg and P (Table 3).

In terms of overall fecundity, the capsule numbers in both species decrease as soil moisture increases (Table 3). In *I. capensis*, increasing soil K and higher soil organic matter content with decreasing soil Mg concentrations also are associated with an increase in capsule numbers. In *I. pallida* capsule numbers increase on Ca-rich sites with greater insolation, but decrease with high soil concentrations of ammonium-N.

DISCUSSION

Inorganic nutrients may be more important than has generally been recognized in regulating and sometimes limiting the growth and reproduction of *Impatiens* in eastern North America. In a glasshouse experiment Waller (1980) found no response of *I. capensis* to NPK fertilization, but his experimental plants were grown in a commercial potting mix that probably already contained sufficient nutrients. Although Simpson, Leck & Parker (1985) reported no significant correlations of soil nitrogen or phosphorus concentrations with the growth or reproduction of *I. capensis*, they sampled only eight natural populations and did not sample plant performance and soil characteristics at the same spatial scale. In contrast, Graves & Monk (1982) did find significant correlations between percentage cover and soil N, Ca and Zn concentrations at microsites sampled within a Georgia population of *Impatiens* sp. Peterson & Rolfe (1982) found that *I. pallida* had the highest tissue concentrations of N, K and Ca of the dominant herbs in an Illinois oak-hickory forest, which suggests the species requirement for these nutrient resources may be substantial. Similarly, *I. parviflora*, a species native to shaded, moist habitats in central Asia (Coombe 1956), has the highest tissue concentrations of P of the herbs in a

Czechoslovakian flood plain forest (Penka *et al.* 1985, p. 428). Peace & Grubb (1982) showed that the growth of *I. parviflora* was limited by the availability of P. Finally, the early experiments of both Carroll (1919) with *I. capensis* and Goebel (1904) with the similar Eurasian species, *I. noli-tangere*, demonstrated that growth and mode of reproduction vary with the availability of inorganic nutrients.

Our results provide additional evidence for the critical dependence of *Impatiens* distribution and performance on the availability of inorganic nutrients. At Mont St. Hilaire, *Impatiens capensis* grows on more Ca-rich sites poorer in nitrate-N, P and K than sites dominated by *I. pallida*. Increased availability of Ca enhances all aspects of growth and fecundity in *I. pallida*, and K availability has a similar effect on *I. capensis*. It is noteworthy that the performance of *I. pallida*, which occurs on sites lower in Ca than those dominated by *I. capensis*, increases with Ca availability. Higher soil organic matter contents, which serve as reservoirs of gradually released inorganic nutrients, are also associated with greater growth and fecundity in *I. capensis*. Other nutrients play less significant, or perhaps more subtle, roles. Considering the experimental evidence that the availability of N and P regulates plant performance in *I. parviflora* (Peace & Grubb 1982), it is perhaps surprising that the growth of neither *I. capensis* nor *I. pallida* shows significant correlations with the local availability of these resources. Stewart & Schoen (1987) did find a significant positive correlation between fecundity and soil P concentration for *I. pallida* growing at twenty-four microsites within a single locality at Mont St. Hilaire. The correlations of growth and fecundity with Ca and K observed across a broader range of localities at Mont St. Hilaire might actually reflect the frequent covariance of these nutrients with the availability of N and P in soils (Barber 1984; Mengel 1985; Sumner & Farina 1986). For example, the rate of mineralization of N, a critical variable determining the seasonal variation in N availability that we did *not* measure, is typically positively correlated with Ca (Rorison & Robinson 1984). Thus, the positive correlation of growth and fecundity in *I. pallida* may actually indicate a strong dependence on the seasonal availability of N, consistent with the results of Peace & Grubb (1982) for *I. parviflora*. In our data for soils on Mont St. Hilaire it is also clear that soils high in K also tend to be high in P (Fig. 1); the statistically significant correlations of K with the success of *Impatiens capensis* may well actually arise from functional dependencies on the availability of P with which K availability is positively covariant at Mont St. Hilaire. The collinearity between Ca and Mg at Mont St. Hilaire may similarly mask functional dependencies on Mg in the regression analyses for performance in *Impatiens pallida*. By their nature, the correlations in our survey data cannot define such subtle interactions in the quantitative regulation of *Impatiens* growth and reproduction by inorganic nutrient resources, but together with earlier reports (Goebel 1904; Carroll 1919; Graves & Monk 1982; Peace & Grubb 1982; Peterson & Rolfe 1982) they clearly demonstrate the need for experimental investigations of the nutritional ecology of *I. capensis* and *I. pallida*.

Although the habitats of the two *Impatiens* species did not differ significantly in insolation, we found that only the growth and reproduction of *I. pallida* increased with the availability of solar radiation at Mont St. Hilaire in 1984. Contrary to earlier reports (Waller 1980; Simpson, Leck & Parker 1985) that considered insolation levels as low as a few per cent of full sun, the growth and reproduction of *I. capensis* was not significantly correlated with insolation levels that ranged from 42 to 100% of full sunlight at Mont St. Hilaire in summer 1984. Almost all our study sites received unusually high insolation as a result of a severe glaze ice storm in December 1983 which stripped many large branches from canopy trees (Melancon & Lechowicz 1987). The increased growth and fecundity of

I. pallida under increased solar radiation (this study; Schemske 1978; Cid-Benevento & Schaal 1986) and the increasing population densities of *I. pallida* following opening of the canopy by a windstorm (Riemenschneider & Blodgett 1983), all indicate the ability of *I. pallida* to utilize even full sunlight effectively. Stewart & Schoen (1987), however, did find that the mortality of *I. pallida* increased with insolation. Conversely, while the growth and reproduction of *Impatiens capensis* is limited by very low light levels (Waller 1980; Simpson, Leck & Parker 1985; Cid-Benevento & Werner 1986), the present results suggest this species is unable to exploit high levels of insolation fully. Cid-Benevento & Werner (1986) found that in greenhouse shading experiments the fecundity of *I. capensis* was actually inhibited at insolation levels above about 25% of full sunlight.

In accord with earlier reports (Struik & Curtis 1962; Wheeler & Kapp 1978; Menges & Waller 1983), we found water availability to be an important control on the distribution of *Impatiens* at Mont St Hilaire. Although both species occur in dry and mesic sites, only *Impatiens capensis* grows in wetter sites at Mont St Hilaire. Contrary to some earlier reports (Waller 1980; Simpson, Leck & Parker 1985), the growth and fecundity of both species actually appears to decrease as soil moisture increases beyond a certain threshold. This is consistent with field observations by Abrahamson & Hershey (1977) who found that the survivorship and growth of *I. capensis* were markedly reduced on waterlogged sites. Our results might, therefore, be explained if summer 1984 was unusually wet and sites were prone to periodic inundation or waterlogging. Precipitation levels at nearby St Hubert (Environment Canada 1984), however, were normal in early summer 1984 and unusually dry in later summer: 74 mm in April, 114 mm in May, 103 mm in June, 62 mm in July, 112 mm in August and 33 mm in September. We conclude that while water availability limits the distribution of both *Impatiens* species at Mont St Hilaire, the growth and fecundity of plants is adversely effected by increasing water availability, especially at higher levels of soil water content.

The contribution of these differences in resource utilization between and within the two *Impatiens* species to their distribution and abundance requires direct experimental investigation. The environmental correlates of intraspecific variation in growth and aspects of reproduction associated with plant fitness also differ between the two *Impatiens* species. It is noteworthy that the more widespread *I. capensis* not only differs in resource response from *I. pallida*, but also has a higher intraspecific variance in growth and reproduction (Table 2). Recent transplant experiments (Schoen *et al.* 1986) have established that the environmental component of the phenotypic variance in the fitness of both *I. pallida* and *I. capensis* has an abiotic basis in part. Given the association between the availability of resources and the growth and reproduction of both *Impatiens* species, it seems likely that differences in resource utilization among individuals in a population of either species will act as a proximate mechanism underlying this environmental variance in fitness. Any investigation of these evolutionary and ecological implications of resource economy in *Impatiens* will, therefore, have to consider not only water and light, but also the availability of the principal inorganic nutrients.

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REFERENCES

- Abrahamson, W. G. & Hershey, B. J. (1977). Resource allocation and growth of *Impatiens capensis* (Balsaminaceae) in two habitats. *Bulletin of the Torrey Botanical Club*, **104**, 160–164.
- Ashmun, J. W. & Pitelka, L. F. (1984). Light-induced variation in the growth and dynamics of transplanted ramets of the understory herb, *Aster acuminatus*. *Oecologia*, **64**, 255–262.
- Baldocchi, D., Hutchison, B., Matt, D. & McMillen, R. (1986). Seasonal variation in the statistics of photosynthetically active radiation penetration in an oak-hickory forest. *Agricultural and Forest Meteorology*, **36**, 343–361.
- Barber, S. A. (1984). *Soil Nutrient Bioavailability. A Mechanistic Approach*. Wiley, New York.
- Bell, D. F. (1964). Loss-on-ignition as an estimate of organic matter and organic carbon in non-calcareous soils. *Journal of Soil Science*, **12**, 84–92.
- Bell, G., Lefebvre, L., Giraldeau, L. A. & Weary, D. (1984). Partial preference of insects for the male flowers of an annual herb. *Oecologia*, **64**, 287–294.
- Bloom, A. J., Chapin, F. S. III & Mooney, H. A. (1985). Resource limitation in plants—an economic analogy. *Annual Review of Ecology and Systematics*, **16**, 363–392.
- Bray, R. H. & Kurtz, T. (1945). Determination of total, organic, and available forms of phosphorus in soils. *Soil Science*, **59**, 39–45.
- Carroll, F. B. (1919). The development of the chasmogamous and the cleistogamous flowers of *Impatiens fulva*. *Contributions of the Botanical Laboratory of the University of Pennsylvania*, **4**, 144–184.
- Cid-Benevento, C. R. & Schaal, B. A. (1986). Variation in population growth rate in the woodland annual *Impatiens pallida* (Balsaminaceae). *American Journal of Botany*, **73**, 1031–1042.
- Cid-Benevento, C. R. & Werner, P. A. (1986). Local distributions of old-field and woodland annual plant species: demography, physiological tolerances, and allocation of biomass of five species grown in experimental light and soil-moisture gradients. *Journal of Ecology*, **74**, 857–880.
- Coombe, D. E. (1956). Biological flora of the British Isles: *Impatiens parviflora* D.C. *Journal of Ecology*, **44**, 701–713.
- Currie, K. L. (1976). The alkaline rocks of Canada. *Geological Survey of Canada Bulletin*, **239**, 50–52.
- Ellenberg, H. (1982). *Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht*. Ulmer, Stuttgart.
- Enright, N. J. & Lewis, J. E. (1985). Aspect-related vegetation patterns and climate at Mont St. Hilaire, Quebec. *Canadian Geographer*, **29**, 249–256.
- Environment Canada (1984). *Monthly Weather Review*. Atmosphere Environment Service, Downsview, Ontario.
- Frankland, J. C., Orington, J. D. & Macrae, C. (1963). Spatial and seasonal variations in soil, litter, and ground vegetations in some Lake District woodlands. *Journal of Ecology*, **51**, 97–112.
- Friend, D. T. C. (1961). A simple method of measuring integrated light values in the field. *Ecology*, **42**, 577–580.
- Gabriel, K. R. (1971). The biplot graphic display of matrices with application to principal components analysis. *Biometrika*, **58**, 453–467.
- Goebel, K. (1904). Die Kleistogamen Blüten und die Anpassungstheorien. *Biologische Centralblatt*, **24**, 673–697, 737–753, 769–786.
- Graves, J. H. & Monk, C. D. (1982). Herb-soil relationships on a lower north slope over marble. *Bulletin of the Torrey Botanical Club*, **109**, 500–507.
- Greenwood, R. C. (1983). *Petrogenesis of the gabbroic suite, Mont St. Hilaire, Quebec*. M.Sc. thesis, Department of Geology, University of Western Ontario, London, Ontario.
- Haynes, R. J. & Goh, K. M. (1978). Ammonium and nitrate nutrition of plants. *Biological Review*, **53**, 465–510.
- Holland, P. G. (1971). Seasonal changes in forest plant patterns of deciduous forests in southern Quebec. *Oikos*, **22**, 137–148.
- Holland, P. G. (1978). Species turnover in deciduous forest vegetation. *Vegetatio*, **38**, 113–118.
- Hutchison, B. A. & Matt, D. R. (1977). The distribution of solar radiation within a deciduous forest. *Ecological Monographs*, **47**, 185–207.
- Jackson, M. L. (1964). *Soil Chemical Analysis*. Prentice Hall, Englewood Cliffs, New Jersey.
- Kamphake, L. J., Hannah, S. A. & Cohen, J. M. (1967). Automated analysis for nitrate by hydrazine reduction. *Water Resources*, **1**, 205–216.
- Maycock, P. F. (1961). Botanical studies on Mont St. Hilaire, Rouville County, Quebec. General description of the area and a floristic survey. *Canadian Journal of Botany*, **39**, 1293–1325.
- McFee, W. W. & Stone, E. L. (1965). Quantity, distribution, and variability of organic matter and nutrients in a forest podzol in New York. *Soil Science Society of America, Proceedings*, **29**, 432–436.

- McLean, E. O. (1982). Soil pH and lime requirement. *Agronomy Monograph No. 9* (Ed by A. L. Page, R. H. Miller & D. R. Keeney), pp. 199–224. American Society of Agronomy, Madison, Wisconsin.
- Melancon, S. & Lechowicz, M. J. (1987). Differences in the damage caused by glaze ice on codominant *Acer saccharum* and *Fagus grandifolia*. *Canadian Journal of Botany*, **65**, 1157–1159.
- Mengel, K. (1985). Dynamics and availability of major nutrients in soils. *Advances in Soil Science*, **2**, 65–131.
- Menges, E. S. & Waller, D. M. (1983). Plant strategies in relation to elevation and light in floodplain herbs. *American Naturalist*, **122**, 454–473.
- Mollitor, A. V., Leaf, A. L. & Morris, L. A. (1980). Forest soil variability on Northeastern flood plains. *Journal of the Soil Science Society of America*, **44**, 617–620.
- Nelson, D. W. & Bremner, J. M. (1972). Preservation of soil samples for inorganic nitrogen analysis. *Agronomy Journal*, **64**, 196–199.
- O'Brien, J. E. & Fiore, J. (1962). Ammonia determination by automatic analysis. *Wastes Engineering*, **33**, 352–353, 377.
- Peace, W. J. H. & Grubb, P. J. (1982). Interactions of light and mineral nutrient supply in the growth of *Impatiens parviflora*. *New Phytologist*, **90**, 127–150.
- Peet, R. I. C. & Loucks, O. L. (1977). A gradient analysis of southern Wisconsin forests. *Ecology*, **58**, 485–499.
- Peet, R. I. C. & Christensen, N. L. (1980). Hardwood forest vegetation of the North Carolina Piedmont. *Veröffentlichungen des Geobotanischen Institutes der Eidgenössische Technische Hochschule Stiftung Rübel in Zürich*, **69**, 14–39.
- Penka, M., Vyskot, M., Klimo, E. & Vašiček, F. (1985). *Floodplain Forest Ecosystem. I. Before Water Management Measures*. Elsevier, Amsterdam.
- Peterson, D. L. & Rolfe, G. L. (1982). Nutrient dynamics of herbaceous vegetation in upland and floodplain forest communities. *American Midland Naturalist*, **107**, 325–339.
- Pitelka, L. F., Ashmun, J. W. & Brown, R. L. (1985). The relationships between seasonal variation in light intensity, ramet size, and sexual reproduction in natural and experimental populations of *Aster acuminatus* (Compositae). *American Journal of Botany*, **72**, 311–319.
- Riemschneider, V. & Blodgett, T. D. (1983). Post wind damage survey of herbaceous level in Bendix Woods Nature Preserve. St. Joseph County, Indiana. *Proceedings of the Indiana Academy of Sciences*, **93**, 199–206.
- Rorison, I. H. & Robinson, D. (1984). Calcium as an environmental variable. *Plant, Cell and Environment*, **7**, 381–390.
- Rouse, W. R. & Wilson, R. G. (1969). Time and space variations in the radiant energy fluxes over sloping terrain and their influence on seasonal heat and water balances at a middle latitude site. *Geografiska Annaler*, **51A**, 160–175.
- Rust, R. W. (1977). Pollination in *Impatiens capensis* and *Impatiens pallida* (Balsaminaceae). *Bulletin of the Torrey Botanical Club*, **104**, 361–367.
- Samson, D. A. & Werk, K. S. (1986). Size-dependent effects in the analysis of reproductive effort in plants. *American Naturalist*, **127**, 667–680.
- SAS Institute (1985). *SAS User's Guide: Statistics, Version 5 Edition*. SAS Institute, Cary, North Carolina.
- Schemske, D. W. (1978). Evolution of reproductive characteristics in *Impatiens* (Balsaminaceae): the significance of cleistogamy and chasmogamy. *Ecology*, **59**, 596–613.
- Schemske, D. W. (1984). Population structure and local selection in *Impatiens pallida* (Balsaminaceae), a selfing annual. *Evolution*, **38**, 817–832.
- Schmitt, J., Ehrhardt, D. & Swartz, D. (1985). Differential dispersal of self-fertilized and outcrossed progeny in jewelweed (*Impatiens capensis*). *American Naturalist*, **126**, 570–575.
- Schoen, D. J., Stewart, S. C., Lechowicz, M. J. & Bell, G. (1986). Partitioning the transplant effect in reciprocal transplant experiments with *Impatiens capensis* and *Impatiens pallida*. *Oecologia*, **70**, 149–154.
- Simpson, R. L., Leck, M. A. & Parker, V. T. (1985). The comparative ecology of *Impatiens capensis* Meerb. (Balsaminaceae) in central New Jersey. *Bulletin of the Torrey Botanical Club*, **112**, 295–311.
- Slavik, B. (1974). *Methods of Studying Plant Water Relations*. Springer-Verlag, Berlin.
- Stewart, S. C. & Schoen, D. J. (1987). Pattern of phenotypic viability and fecundity selection in a natural population of *Impatiens pallida*. *Evolution*, **41**, 1290–1301.
- Struik, G. J. & Curtis, J. T. (1962). Herb distribution in an *Acer saccharum* forest. *American Midland Naturalist*, **68**, 285–296.
- Sumner, M. E. & Farina, M. P. W. (1986). Phosphorus interactions with other nutrients and lime in field cropping systems. *Advances in Soil Science*, **5**, 201–236.
- Waller, D. M. (1979). The relative costs of self- and cross-fertilized seeds in *Impatiens capensis* (Balsaminaceae). *American Journal of Botany*, **66**, 313–320.
- Waller, D. M. (1980). Environmental determinants of outcrossing in *Impatiens capensis* (Balsaminaceae). *Evolution*, **34**, 747–761.
- Waller, D. M. (1982). Factors influencing seed weight in *Impatiens capensis* (Balsaminaceae). *American Journal of Botany*, **69**, 1470–1475.
- Waller, D. M. (1984). Fitness differences between seedlings derived from cleistogamous and chasmogamous flowers in *Impatiens capensis*. *Evolution*, **38**, 427–440.

- Waller, D. M. (1985).** The genesis of size hierarchies in seedling populations of *Impatiens capensis* Meerb. *New Phytologist*, **100**, 243–260.
- Webber, G. R. & Jellema, J. V. (1965).** Comparison of chemical composition of soils and bedrock of Mont St. Hilaire, Québec. *Canadian Journal of Earth Sciences*, **2**, 44–58.
- Wheeler, R. H. & Kapp, R. O. (1978).** Vegetational patterns on the Tittabawasee floodplain at the Goetz Grove Nature Center, Saginaw, Michigan. *Michigan Botanist*, **17**, 91–99.
- Willson, M. F. (1983).** *Plant Reproductive Ecology*. Wiley, New York.

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References

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Biometrika, Vol. 58, No. 3. (Dec., 1971), pp. 453-467.

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<http://links.jstor.org/sici?sici=0006-3444%28197112%2958%3A3%3C453%3ATBGDOM%3E2.0.CO%3B2-F>

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- Page 3 of 6 -



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<http://links.jstor.org/sici?sici=0012-9658%281977%2903%3A3%3C485%3AAGAOSW%3E2.0.CO%3B2-Q>

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<http://links.jstor.org/sici?sici=0003-0031%281982%2902%3A2%3C325%3ANDOHVI%3E2.0.CO%3B2-U>

LINKED CITATIONS

- Page 4 of 6 -



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American Journal of Botany, Vol. 72, No. 2. (Feb., 1985), pp. 311-319.

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Pollination in *Impatiens capensis* and *Impatiens pallida* (Balsaminaceae)

Richard W. Rust

Bulletin of the Torrey Botanical Club, Vol. 104, No. 4. (Oct. - Dec., 1977), pp. 361-367.

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Ecology, Vol. 59, No. 3. (Late Spring, 1978), pp. 596-613.

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Population Structure and Local Selection in *Impatiens pallida* (Balsaminaceae), A Selfing Annual

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Evolution, Vol. 38, No. 4. (Jul., 1984), pp. 817-832.

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<http://links.jstor.org/sici?sici=0014-3820%28198407%2938%3A4%3C817%3APSALSI%3E2.0.CO%3B2-S>

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- Page 5 of 6 -



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Johanna Schmitt; David Ehrhardt; Daniel Swartz

The American Naturalist, Vol. 126, No. 4. (Oct., 1985), pp. 570-575.

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The Comparative Ecology of *Impatiens capensis* Meerb. (Balsaminaceae) in Central New Jersey

Robert L. Simpson; Mary Alessio Leck; V. Thomas Parker

Bulletin of the Torrey Botanical Club, Vol. 112, No. 3. (Jul. - Sep., 1985), pp. 295-311.

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<http://links.jstor.org/sici?sici=0040-9618%28198507%2F09%29112%3A3%3C295%3ATCEOIC%3E2.0.CO%3B2-P>

Pattern of Phenotypic Viability and Fecundity Selection in a Natural Population of *Impatiens pallida*

Steven C. Stewart; Daniel J. Schoen

Evolution, Vol. 41, No. 6. (Nov., 1987), pp. 1290-1301.

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Herb Distribution in an *Acer saccharum* Forest

Gwendolyn J. Struik; J. T. Curtis

American Midland Naturalist, Vol. 68, No. 2. (Oct., 1962), pp. 285-296.

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The Relative Costs of Self- and Cross-Fertilized Seeds in *Impatiens capensis* (Balsaminaceae)

Donald M. Waller

American Journal of Botany, Vol. 66, No. 3. (Mar., 1979), pp. 313-320.

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Environmental Determinants of Outcrossing in *Impatiens capensis* (Balsaminaceae)

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Evolution, Vol. 34, No. 4. (Jul., 1980), pp. 747-761.

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Donald M. Waller

American Journal of Botany, Vol. 69, No. 9. (Oct., 1982), pp. 1470-1475.

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Differences in Fitness Between Seedlings Derived from Cleistogamous and Chasmogamous Flowers in *Impatiens capensis*

Donald M. Waller

Evolution, Vol. 38, No. 2. (Mar., 1984), pp. 427-440.

Stable URL:

<http://links.jstor.org/sici?sici=0014-3820%28198403%2938%3A2%3C427%3ADIFBSD%3E2.0.CO%3B2-E>

The Genesis of Size Hierarchies in Seedling Populations of *Impatiens capensis* Meerb

D. M. Waller

New Phytologist, Vol. 100, No. 2. (Jun., 1985), pp. 243-260.

Stable URL:

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