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Partitioning the transplant site effect in reciprocal transplant experiments with *Impatiens capensis* and *Impatiens pallida*

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Summary. Modified reciprocal transplant experiments were conducted with the annual plant species *Impatiens capensis* and *I. pallida* to partition the influence of environment on fitness into two components; that of (1) conspecific neighbours occupying each transplant site, and (2) the abiotic and biotic features of each site exclusive of the conspecific neighbours. In the within-species reciprocal transplant series, differences in survivorship and fruit production by cleistogamous flowers were attributable primarily to the effect of conspecific neighbours. In addition, plants surrounded by neighbours from the site of origin produced significantly more fruit from chasmogamous flowers compared with plants surrounded by neighbours from the alien site. In the between-species reciprocal transplant series, one transplant site was consistently associated with greater survivorship and fruit production regardless of the identity of neighbouring plants. The results suggest that different aspects of the environment in these reciprocal transplant experiments (conspecific neighbours, other species, physical factors) determine fitness in different situations.

Key words: Transplant experiment – Survivorship – Fruit production – Neighbour effects – *Impatiens capensis* – *Impatiens pallida* – Balsaminaceae

The decomposition of fitness variation into genotypic and environmental components is fundamental to the study of population biology. For plant populations, reciprocal transplant experiments offer an effective design, and have revealed that environmental influences on plant fitness may be large or small relative to genetic ones (Turesson 1930; Clausen et al. 1948; Fowler and Antonovics 1981; Antonovics and Primack 1982; Schmidt and Levin 1985). Yet, in these designs the environmental component of variation remains complex, being composed not only of features of the physical environment (e.g. soil moisture level, nutrient status of the soil, light availability), but also of interactions with individuals of the same and other species. If ecological hypotheses regarding these factors are to be tested experimentally, further partitioning of the environmental component is needed. Such experiments will help to reveal the variety and relative importance of responses to abiotic and biotic habitat features.

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We report here the results of modified reciprocal transplant experiments involving the annual plant species *Impatiens capensis* and *I. pallida* (Balsaminaceae). Much is known about the reproductive biology and demography of these species (Rust 1977; Schemske 1978; Waller 1979, 1980, 1984; Leck 1979; Windsor 1983; Bell et al. 1984; Mitchell-Olds and Waller 1985; Schmitt et al. 1985), and recent studies of phenotypic differentiation among populations point to the importance of the environment in determining the expression of phenotypic variation (Schemske 1984). The basic experimental design of our study differs from that of previous reciprocal transplant experiments in that we transplant not only single individuals into sites, but a set of neighbouring individuals as well. This modification allows the effect of alien versus like neighbours to be studied independent of other effects of site. In particular, our present study discriminates between two types of environmental effects; that of neighbours (conspecific or congeneric) and that of abiotic and other biotic features of the home and away sites exclusive of neighbours. The effects of neighbours on plant performance is of particular relevance to the biology of *Impatiens* in southern Quebec. There the species usually occur in dense monospecific stands, or occasionally in mixtures composed of *I. capensis* and *I. pallida*.

Methods

The work was done at the McGill University Research Reserve at Mont St. Hilaire, Québec, Canada (Maycock 1961). We sampled populations from four sites. All are located in wet areas in beech-maple forest, and separated from one another by 0.5 to 1 km. Three of the populations, referred to below as c1, c2, c3, were comprised of *Impatiens capensis*, and the remaining population, p1, was comprised of *I. pallida*. While these extensive populations do not have discrete boundaries, for convenience we limited our sampling to areas of 300–400 m² within each population.

The modified reciprocal transplant experiments were concerned with how survival and fruit production is influenced by three factors: (1) site of transplant; (2) site of origin; and (3) site of neighbours. Two separate experiments were carried out. In the first, neighbours were conspecific. In the second, neighbours were of the opposite *Impatiens* species. The two experiments are referred to below as the within-species and between-species experiments, respectively. The within-species reciprocal transplants were

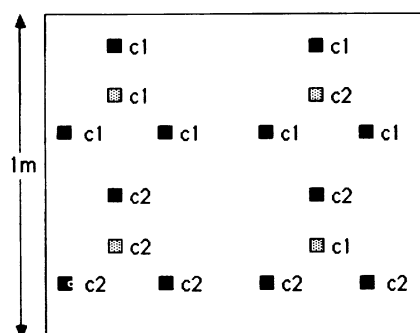


Fig. 1. Physical layout of quadrats used in reciprocal transplant studies. Shaded squares represent targets. Black squares represent neighbours. Target-neighbour distances not drawn to scale; actual distances were 6 cm between target and neighbour stems

between populations c1 and c2. The between species transplants were between populations c3 and p1.

Material for the experiments was obtained by transplanting seedlings from each of the populations. This involved inserting a 7 cm diameter metal core 6 cm into the soil surrounding the seedling, and withdrawing both seedling and soil core. Seedlings at this stage had exposed cotyledons and their first pair of vegetative leaves. After removal, but before replanting, the seedlings were tagged and stored for 4–6 h in styrofoam cups. When replanting, the soil coring instrument used originally to remove seedlings was used again to remove soil from specified locations where seedlings were replanted.

The design for the within-species transplant series was as follows. Four seedlings were selected from random positions in twenty 1 m² quadrats in each of the two populations of the series. From each of the twenty quadrats, two of the selected individuals were removed and replanted in a quadrat in the opposite population, while the other two were removed and replanted into the quadrat from which they had originated, as a control for the handling effect. The seedlings are referred to below as “targets”. Each target was then surrounded with three replanted seedlings. These are referred to below as “neighbours”. Neighbour seedlings were obtained and treated in the same manner as the targets. Thus, neighbour seedlings were taken from either the same quadrat as the target or from a quadrat in the other site, and were planted at the same time as the targets. They were positioned to form the vertices of an equilateral triangle 6 cm from the target. A quadrat in the within-species transplant series therefore included the following target-neighbour combinations: (1) c1 surrounded by c1; (2) c1 surrounded by c2; (3) c2 surrounded by c1; and (4) c2 surrounded by c2 (Fig. 1). The quadrats of the between-species transplant series were of a similar arrangement except that populations c3 and p1 were utilized.

Three days were required to complete all of the transplants. Seedlings dying within 1 week after transplanting were replaced, as deaths at this stage were inferred to be due to transplant shock. From this point on, the survival of transplanted target individuals was monitored weekly. The lifetime fruit production of each target individual was also recorded. Cleistogamous (CL) and chasmogamous (CH) flowers were marked on the pedicel, and fruit deriving from CL and CH flower types (CL and CH fruit, respectively) were scored separately.

Both reciprocal transplant series were analyzed as split-plot experimental designs, where whole plots were the individual 1 m² quadrats and all factors were considered fixed effects. Classification data, such as survival to a given date, can be analyzed using this procedure because fixed effects models are robust to the effects of non-normality and heteroscedasticity of errors (Scheffé 1959; Kendall et al. 1983).

Elevation of each site was measured with a Terra model SA-1 altimeter. In August of 1984, the relative amount of light penetrating the canopy during two diurnal periods was estimated by exposing layers of diazochrome film at each population and relating light availability to that observed when film was exposed outside the canopy. Gravimetric water content of soil at each site was measured 10 times between June and September 1984. Soil samples collected in July and immediately frozen were analysed at the MacDonald College Soil Testing Laboratory for nitrate (Kamphake et al. 1967), ammonium, phosphorous (Bray and Kurtz 1945), potassium, calcium, and magnesium (Jackson 1973), and percent organic matter (Bell 1964). Soil pH was measured following McLean (1982). Two samples were taken at each site to represent the local microtopographic extremes in which the plants grew, i.e. streambed and streambank habitats.

Results

Data from the two transplants series are presented separately below. Three classes of response by target individuals are analysed separately: (1) survivorship to 16 July 1984 (when plants first produced fruit); (2) total lifetime CL fruit production of individuals alive on 16 July; and (3) total lifetime CH fruit production of individuals alive on 16 July. In the latter two analyses, untransformed data, log transformed data, and square root transformed data yielded similar results. We present only the analyses of untransformed data.

Within-species transplants. The site from which *I. capensis* individuals originated and the site into which these individuals were transplanted did not significantly effect survivorship or fruit production by either flower type (Tables 1 and 2). Neighbouring plants, however, did have a significant effect both on survivorship and CL fruit production. Indi-

Table 1. Analysis of variance for the within-species transplant involving populations c1 and c2. Survivorship to 16 July 1984^a

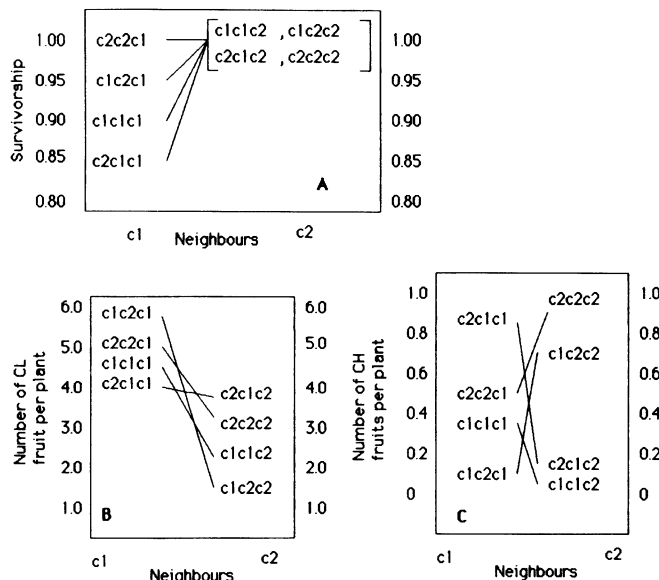
Source of variation	df	MS	F ratio
Site of Transplant	1	0	0
Error (whole plots)	38	0.034	
Neighbour	1	0.225	6.43*
Site of Origin	1	0.100	2.85
Transplant × Neighbour	1	0	0
Transplant × Origin	1	0.025	0.71
Neighbour × Origin	1	0.100	2.85
T × N × O	1	0.025	0.71
Error (subplots)	114	0.035	
Total	159		

^a Survivorship of each individual coded as a binary variable with 0 indicating the plant was alive and 1 indicating the plant was dead on 16 July 1984

* $P < 0.05$

Table 2. Analysis of variance for the within-species transplant involving populations c1 and c2. CL and CH fruit production

Source of variation	df	CL fruits		CH fruits	
		MS	F ratio	MS	F ratio
Site of Transplant	1	2.4	0.12	2.94	2.12
Error (whole plots)	32	19.6		1.39	
Neighbour	1	102.4	10.8**	0.11	0.08
Site of Origin	1	0	0	1.44	1.11
Transplant	1	16.9	1.8	0.03	0.02
xNeighbour					
Transplant x Origin	1	0.03	0.0	0.12	0.08
Neighbour x Origin	1	28.3	3.0	7.53	5.79*
T x N x O	1	1.9	0.2	0.74	0.57
Error (subplots)	96	9.45		1.30	
Total	135				

* $P < 0.05$ ** $P < 0.01$ **Fig. 2A–C.** Responses of target individuals in the within-species transplant experiment to treatment combinations. Order of letters indicates site of transplant, site of origin, and site of neighbour, respectively. **A** Survivorship to 16 July 1984 ($n=20$ seedlings per treatment combination); **B** Mean CL fruit production per individual surviving to 16 July 1984; **C** Mean CH fruit production per individual surviving to 16 July 1984

viduals neighbored by plants from c2 had on average a 0.075 higher probability of surviving to 16 July ($P < 0.02$) but set on average 1.74 fewer CL fruits ($P < 0.01$) than individuals with c1 neighbours (Tables 1 and 2, Fig. 2A, B). CH fruit production interacted with the sites and neighbouring plants (Table 2, Fig. 2C). On average, individuals with neighbours from the same population as themselves produced 0.5 more CH fruits than individuals whose neighbours were from the other population (Table 2, $P < 0.05$).

Between-species transplants. Environmental features of the transplant site other than the neighbours significantly influenced survivorship of individuals and fruit production by both flower types in *I. capensis* and *I. pallida*. Individuals

Table 3. Analysis of variance for the between-species transplant involving populations c3 and p1. Survivorship to 16 July 1984*

Source of variation	df	MS	F ratio
Site of Transplant	1	1.406	13.02***
Error (whole plots)	38	0.108	
Neighbour	1	0.056	0.20
Site of Origin	1	0.056	0.20
Transplant x Neighbour	1	0.006	0.02
Transplant x Origin	1	0.156	0.55
Neighbour x Origin	1	0.006	0.02
T x N x O	1	0.056	0.20
Error (subplots)	114	0.284	
Total	159		

* Survivorship of each individual coded as a binary variable with 0 indicating a plant was alive and 1 indicating a plant was dead on 16 July 1984

*** $P < 0.001$

transplanted into site c3 had on average a 0.16 lower probability of surviving to 16 July ($P < 0.001$), set on average 17.0 fewer CL fruits per individual ($P < 0.01$), and set on average 10.3 fewer CH fruits per individual ($P < 0.01$) than individuals transplanted into site p1, regardless of the site of the neighbours (Tables 3 and 4, Fig. 3A–C). In addition, the environment of the transplant site, the site of origin, and site of neighbours interacted to produce an important ecological response. Specifically, individuals transplanted back into the site from which they originated had on average 10.2 more cleistogamous fruits per individual if their neighbours were *I. pallida*, than if their neighbours were *I. capensis*. In contrast, individuals transplanted into the site which was not the site of origin showed no significant effect of neighbours on survival of fruit production of either flower type (Fig. 3B). The three-way interaction sum of squares of Table 4 averages these two contributions and is not significant ($P < 0.05$). Nevertheless, the observed response is of ecological interest, and *a posteriori* tests show that treatment means of p1p1p1 and c3c3p1 are significantly greater than those of p1p1c3 and c3c3c3, respectively ($P < 0.05$; lsd = 15.5).

Physical characteristics of the sites. Table 5 summarizes several physical features of the sites occupied by the populations. Of the sites occupied by the within-species transplant series, c1 was shadier, drier, and less rich in organic matter than c2. The lowest soil nitrate, potassium, phosphorous, and calcium concentrations also occurred in c1 in comparison to c2. Of the sites occupied by the between-species transplant series, c3 was shadier, and had lower concentrations of almost all inorganic nutrients in comparison to p1. These interspecific differences parallel the results obtained in a broader survey of site occupied by *Impatiens capensis* and *I. pallida* on Mont St. Hilaire (Lechowicz et al. unpublished work).

Discussion

The reciprocal transplant experiments reveal the complexity of the environmental influence on the expression of characteristics associated with fitness. In the within-species transplant series, the depressive effects of site c1 on survivorship,

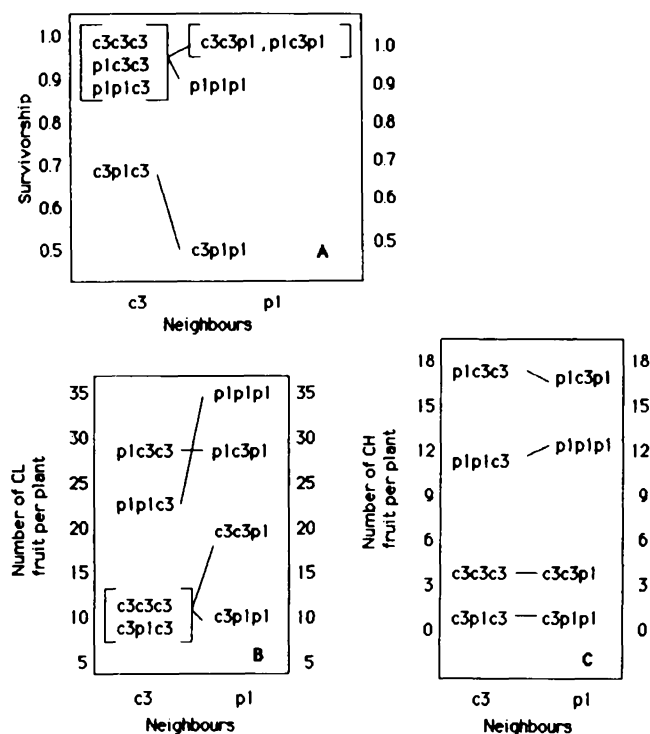
Table 4. Analysis of variance for the between-species transplant involving populations c3 and p1. CL and CH fruit production

Source of variation	df	CL fruits		CH fruits	
		MS	F ratio	MS	F ratio
Site of Transplant	1	6,218.1	10.1**	2,563.0	7.94**
Error (whole plots)	23	615.5		322.8	
Neighbour	1	912.0	2.7	10.9	0.1
Site of Origin	1	51.8	0.2	278.9	0.6
Transplant × neighbour	1	100.0	0.3	5.1	0.03
Transplant × Origin	1	258.2	0.8	11.0	0.1
Neighbour × Origin	1	144.0	0.4	34.8	0.2
T × N × O	1	644.2	1.9	13.1	0.1
Error (subplots)	69	342.0		174.4	
Total	99				

** $P < 0.01$ **Table 5.** Physical characteristics of transplant sites

Pop.	Sample number	Elevation (m)	%full sunlight	Soil moisture (g H ₂ O/ g soil)*	NO ₃ (µg/ g soil)	NH ₄ (µg/ g soil)	K (µg/ g soil)	Ca (µg/ g soil)	Mg (µg/ g soil)	P (µg/ g soil)	% organic matter
c1	1	169	67	0.77	7.2	20.9	75	1,476	200	30	12.3
c1	2	169	64	0.77	0.6	16.5	176	1,798	264	13	12.5
c2	1	164	79	5.34	2.6	107.6	289	3,744	257	123	41.8
c2	2	166	63	1.49	5.3	10.6	123	2,976	113	13	20.3
c3	1	185	52	4.06	2.7	40.7	75	984	363	26	29.1
c3	2	185	82	1.75	6.9	37.4	151	3,872	427	25	29.6
p1	1	206	92	0.80	12.6	40.4	150	5,808	325	450	21.8
p1	2	204	85	2.22	16.3	62.8	192	6,150	724	58	38.4

* Mean of 10 samples over the growing season

**Fig. 3A–C.** Responses of target individuals in the between-species transplant experiment to treatment combinations. Data presented as in Fig. 2

and site c2 on CL fruit production are attributable to the plants of *Impatiens capensis* which occupy these sites (or possibly to the soil transported with these plants), rather than to other biotic and abiotic features of the sites (Tables 1 and 2, Fig. 2A, B). Indeed, the targets do not appear to respond to the differences among the pair of sites in water status, light level, and nutrient concentrations (Table 5). The biological basis of the neighbour effect is not yet clear. Since mortality and fecundity of individuals respond differently to neighbours, several components are probably responsible. One explanation for the higher mortality seen when plants are surrounded by individuals from population c1 is transmission of pathogens from the neighbours (or the soil surrounding them) to the target. Competition can probably be ruled out due to the small size and consequent lack of interaction between target and neighbours at this early stage of the life cycle. The biological basis of reduced CL seed production when plants are surrounded by individuals from population c2 is also uncertain. Since plants are larger at this stage, there is greater potential for competitive interactions between target and neighbours. If competition is a factor, the results suggests that there may have been genetic differentiation among the populations for competitive ability, with plants from c2 being the more vigorous competitors. Genetic differentiation in a variety of traits over short distances has been documented by Schemske (1984) in *Impatiens pallida*, and evidence exists for other species to suggest that certain geno-

types can be competitively superior to others (Sakai and Gotoh 1955; Mather and Cooke 1962).

Another result from the modified design of the within-species transplants is the observation that CH fruit production is higher when surrounded by neighbours from the home versus away site (Table 2, Fig. 2C). This is an important refinement of the home site advantage. Home site advantages have been reported by other researchers utilizing reciprocal transplant designs (Primack and Antonovics 1982; Schemske 1984; Schmidt and Levin 1985). In the present case, however, because the transplant site effect can now be partitioned into the effect of conspecifics and other effects, it is seen that the home site advantage pertains to interactions with the conspecifics which occupy the site, rather than to other site characteristics. The result is similar to that reported by Turkington and Harper (1979) who concluded that the home site advantage in *Trifolium repens* arises from biotic interactions between specific genotypes, in particular, those related to ecological combining ability.

In contrast to the within-species experiments, differences in survivorship and fruit production in the between-species transplant series are attributable primarily to features of the site of transplant other than the interaction with neighbours. One of the two sites, p1, is superior for the growth and reproduction of both species. This site is sunnier, wetter, and richer in inorganic nutrients than c3. As in the within-species transplants, the result suggests that environment (in this case, features other than interactions with neighbours) plays a larger role than genotype in determining fitness, as seen by Hickman (1975) for *Polygonum cascadenae*, Gottlieb (1977) for *Stephanomeria exigua*, Sobrig (1981) for *Viola sororia*, and Primack and Antonovics (1982) for *Plantago lanceolata*. The possibility that environment plays a larger role than genotype in determining fitness in general in these species needs further corroboration, however, as relatively few populations and sites were studied in the work reported here.

Issues pertaining to the evolution and maintenance of sexual reproduction can also be addressed using our experimental design (Ghisselin 1974; Williams 1975; Maynard Smith 1978; Bell 1982). One component of current theory for the evolution of sexual reproduction postulates an advantage for individuals which are genetically different from their neighbours (Levin 1975; Jaenike 1978; Glesener 1979; Lloyd 1980; Price and Waser 1982; Bell 1982). This advantage could be mediated by plant-herbivore and/or pathogen-plant interactions, with the rarer type suffering less parasitism and herbivory (Clarke 1976; Antonovics and Ellstrand 1984), or by competitive interactions, with the rarer type using a different set of resources than the more common type. According to the theory, we would then expect to find the lowest mortality and highest fecundity in targets surrounded by unlike neighbours. In neither of the reciprocal transplants, was the site of neighbour \times site of origin interaction statistically significant. In the within species transplants, the interaction was, however, marginally significant ($P < 0.10$), and in the direction hypothesized by the theory, for both survivorship and CL fruit production (Tables 1 and 2; Fig. 1).

In a recent article, Primack and Antonovics (1982) argue that one of the strengths of reciprocal transplants is that "phytometers" (Clements and Goldsmith 1924) can be used to characterize the environment, thereby making operational such terms as environmental heterogeneity and environ-

mental stress. We endorse this viewpoint, and would add that with further refinements of the type used here, one may begin to determine which aspects of the environments are heterogeneous or stressful, and how different genotypes respond to these environmental features. As our own results suggest, the environmental effect on fitness is a complex one, acting differentially upon separate fitness components, and sometimes consisting of several interacting elements. Experiments of this type will, therefore, be useful in further determining the basis of fitness variation among and within populations.

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