

Competition for Water in Two Populations of *Impatiens pallida* (Balsaminaceae) from Contrasting Water Environments

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수분환경이 다른 서식지에서 자란 *Impatiens pallida*의 두 개체군간 수분에 대한 경쟁

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ABSTRACT

We investigated the role of competition in adaptation to varying water availability levels for two ecotypically-differentiated populations of *Impatiens pallida* found naturally in low- vs. high-water environments. In a greenhouse experiment, seedlings were grown in pure cultures at two densities ($n=1$ and 2 plants per pot) and in mixed cultures ($n=2$) under low-, medium- and high-water treatments. The two populations were shown to be genetically distinct across the range of environmental conditions in the greenhouse experiment, confirming previous findings. The two populations had similar morphological responses to density and water availability in pure cultures and mixtures, but the population from the high-water environment showed a greater growth response to high water availability than did the population from the low-water environment and the difference in growth between the two populations decreased from the high-water to low-water treatment. Relative competitive ability of two populations were compared under three different water treatments and two densities. Differential response to watering treatment and density were not reflected in a difference in relative competitive ability. Relative yield totals were significantly greater than 1 overall. The niche differentiation suggested by RYT's > 1 may be responsible for the lack of differential competitive effects observed for populations in the three watering treatments.

Key words: Environmental conditions, *Impatiens pallida*, Relative competitive ability, Relative yield totals, Water availability

INTRODUCTION

In many natural environments, resource availability is a major factor affecting species composition and dynamics of plant communities. There is abundant evidence that competition for resources can have strong effects on survival, growth, and reproduction of individual plants (Harper 1977, Connell 1983, Roughgarden 1983, Schoener 1983, Strong 1983). The existence of these effects of interspecific competition in most ecological situations is widely recognized because all organisms within the plant community have the same basic requirements: they inevitably shade their neighbors and/or have somewhat overlapping root systems that draw from common, often limiting nutrient and water reserves. In particular, water is a significant factor limiting the plant productivity of both annuals and perennial shrubs (Ehleringer and Mooney 1983).

Topographic gradients can create substantial spatial variation in the reproductive success of annual plants. Along such gradients, water runoff creates a gradient in soil water availability (Pantastico-Caldas and Venable 1993), which in turn can directly determine plant growth and reproductive success. Pantastico-Caldas and Venable (1993) also showed that density response curves had different slopes in the different habitats along the water gradient in a competition experiment with *Plantago* and *Pectocarya*. Seed production of *Stipa capensis*, an annual plant of the Judean Desert in Israel, was found to be lowest on a dry slope, highest in wadi (wash), and moderate in shallow water-catching depressions (Kadamon and Shmida 1990a). Field studies frequently reveal significant correlations between available soil moisture and on a local scale, competition for water among neighboring plants in a population can be very intense (Fonteyn and Mahall 1978, 1981, Ehleringer 1984). In addition to the constraints on productivity imposed by abiotic factors, over the past two decades, many studies have concentrated attention on potential biotic limitations. Evidence from experimental studies has demonstrated that at least for annual plants competition may be important in determining survival, growth and fecundity (Friedman and Orshan 1974, Fowler 1986, Chesson and Huntly 1989, Pantastico-Caldas and Venable 1993). Specifically, a number of studies have demonstrated the existence of competition among desert annuals (Klikoff 1966, Inouye *et al.* 1980) and an increase in the intensity of competition along a gradient of increasing moisture availability (Del Moral 1983, Kadamon and Shmida 1990a, b).

This study was designed to test whether populations adapted to relatively low and high water environments have acquired superior competitive ability in their respective 'home site' water condition. We used a greenhouse experiment to test this "competitive reversal hypothesis" in order to isolate the effect of water availability from the other differences found along the natural gradient in the field. We chose a system in which ecotypic differentiation between adjacent populations has been clearly demonstrated (Bennington 1994). Superior growth and response to competition of the high water (floodplain) ecotype might

be expected, as many studies have demonstrated differences in competitive ability at the high end of resource gradients (Austin *et al.* 1988, McGraw and Chapin 1989, Campbell and Grime 1992). However, under low water conditions, does relative competitive ability reverse? The question is interesting since conservative water use patterns are often found in plants from low water sites (Gurevitch 1986). Conservative water use could be accomplished through a change in leaf area ratio, fewer or smaller stomates, and mid-day stomatal closure. Regardless of the mechanism, such a water-use pattern could make water relatively more available for a competitor if the net effect was to leave a larger reservoir of available water in the soil. Hence, we pose two questions in this study. First, are there genetic differences between populations in response to water availability? Second, if so, do their genetic differences confer increased competitive ability on the ecotypes from low and high water conditions (the "competitive reversal hypothesis"), or does the ecotype from high water conditions always outcompete the population from low water conditions (the "superior competitor hypothesis")?

MATERIALS AND METHODS

Impatiens pallida is a common annual, cleistogamous herb growing in moist habitats throughout eastern North America (Schemske 1978). Through experimental reciprocal transplant studies and population genetic analyses, it is known that these populations are ecotypically differentiated (Bennington 1994, Bennington and McGraw, submitted). The environments are also distinctive. The floodplain soil is a moderately well-drained Lobdell silt loam, which has a high available water capacity and high water table. Typically, the hillside soils have a moderate available water capacity with a much higher rate of runoff than the floodplain (Wright *et al.* 1982). These differences translated to much lower soil water availability on the hillside site, as assayed with pre-dawn water potentials on *Impatiens* plants at these sites (Bennington and McGraw, submitted).

Between July and September 1993, seeds were collected from plants in both a floodplain population (FP) and an adjacent hillside population (HL) at the West Virginia University Arboretum. All seeds were placed in individual wells in potting soil of plug trays, watered with distilled water, and stored at 4 °C. On 30 November 1993, after 2 to 4-months of cold stratification, seeds were germinated in the plug trays on a lighted lab bench using a 14 hour photoperiod and temperatures of 25~30 °C. On 10 December 1993, available seedlings were transplanted to 15 cm diameter and 15cm depth pots filled with Promix BX soil in the following five density/frequency treatments: 1) one HL plant, 2) two HL plants, 3) one FP plant, 4) two FP plants, and 5) one HL and one FP plant (2 rep.s of this pot type were included). The six pots containing all density/frequency treatments were placed together as a unit on the greenhouse bench. Three such adjacent units were considered a block. Each block replicated eleven times. Each unit within a block was randomly assigned to one of three watering levels. All pots were watered once daily during the in-

initial week. Treatments were imposed gradually in order to ensure survival to adult size and to roughly mimic the increasing effects of drought as the growing season progresses (Bennington and McGraw, submitted). Water treatments began on 17 December 1993. For five weeks, the following three treatments were imposed; 1) High water (once daily), 2) Medium water (once every two days), 3) Low water (once every three days). After this point, treatments were maintained as follows; 1) High water (once daily), 2) Medium water (once every three days), and 3) Low water (once every five days).

All seeds were collected from the onset of seed dispersal (28 February, 1994) until the end of the experiment. Height, basal diameter, leaf number and total leaf area were measured at the final harvest (24~26 March). Aboveground dry weight was measured after drying for a week at about 80 °C in a drying oven.

Competitive ability was measured using relative crowding coefficients (RCC, de Wit 1960):

$$RCC_{HF} = \frac{\left\{ \frac{\text{Mean Yield Per Plant of HL in Mixture}}{\text{Mean Yield Per Plant of FP in Mixture}} \right\}}{\left\{ \frac{\text{Mean Yield Per Plant of HL in Monoculture}}{\text{Mean Yield Per Plant of FP in Monoculture}} \right\}}$$

Values of $RCC_{HF} > 1$ indicate that the hillside population is more aggressive than, or is a superior competitor to, the floodplain population. If $RCC_{HF} < 1$, then the floodplain population is the superior competitor.

Relative yield totals were determined as a measure of niche separation of the two ecotypes:

$$RYT_{HF} = \left\{ \frac{\text{Mean yield of HL in mixture}}{\text{Pot yield of HL in pure culture}} \right\} + \left\{ \frac{\text{Mean yield of FP in mixture}}{\text{Pot yield of FP in pure culture}} \right\}$$

The expected value of RYT_{HF} is 1 if the resource use patterns are the same for the two ecotypes. A value greater than 1 suggests that the two ecotypes are exploiting limiting resources differently, and therefore more productivity is possible in the same environment than when the ecotypes are grown in pure culture.

Statistical analysis

To determine whether the two ecotypes respond differentially to watering treatments and density ($n=2$), we performed a three-way ANOVA in pure culture (main effects: population, watering treatment, and density). The main effects in the model were all considered fixed (Bennington and Thayne 1994). A second test of the response to watering treatment was done using two-way ANOVA for mixtures (main effects: population, watering treatment). In both analyses, of particular interest were the interaction terms

(population \times watering treatment and population \times density) which test for significant differential response of populations in terms of size parameters and seed production. All analyses were performed using SAS JMP (v. 3.0).

Relative crowding coefficients and relative yield totals were calculated separately for each block/treatment grouping. Means were then compared to 1 under each watering treatment and overall with a t-test (Sokal and Rohlf 1981) to test for deviation from the null hypothesis of equal competitive ability and resource use. Values of RCC and RYT were compared across environments using one-way analysis of variance to determine if competitive ability varied as a function of environment.

RESULTS

Density and water effects in pure cultures

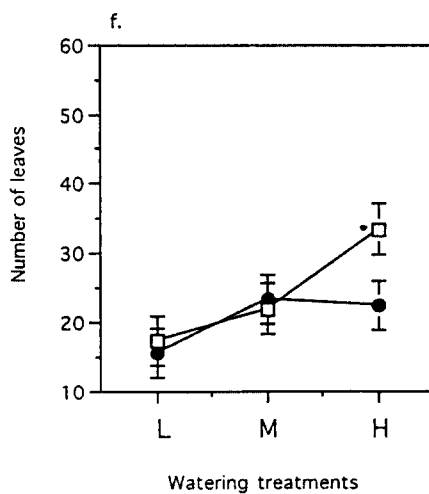
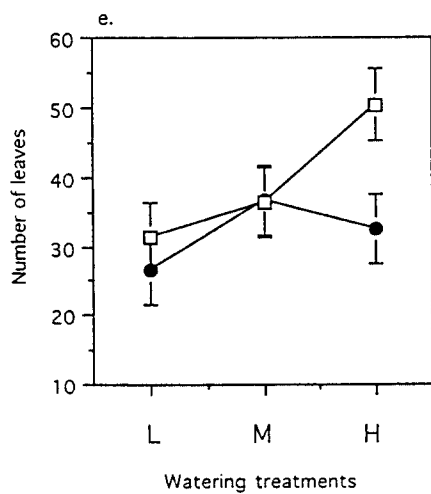
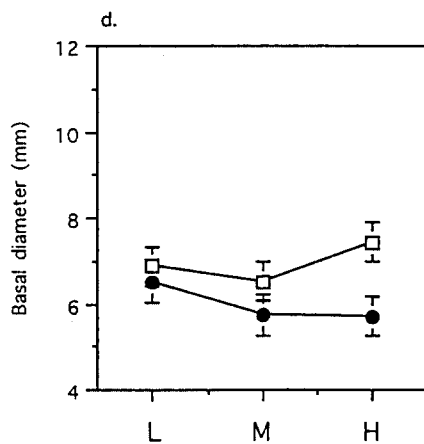
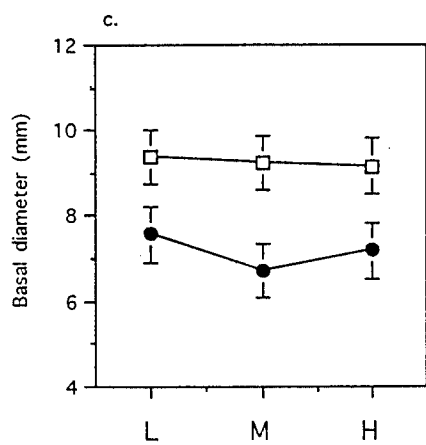
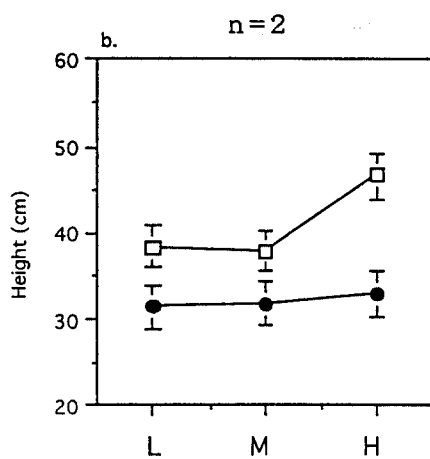
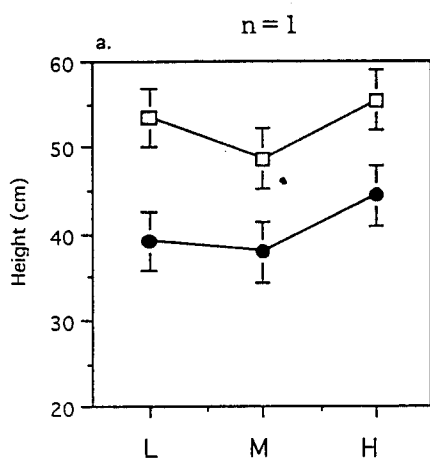
Plants in the high water environment were taller, and had greater leaf number, leaf area, seed number and total aboveground mass than plants grown in medium or low water environments (Fig. 1). Therefore, our watering treatments were significantly limiting plant growth (Table 1, Fig. 1). Individual plant size declined as density increased (Fig. 1), indicating that competition occurred at a density of 2. Likewise, seed number decreased as density increased.

In pure culture, plants from the floodplain population were larger than plants from the hillside population in all size measures except leaf area. However, the size difference depended on density and watering treatment. In general, floodplain plants were larger under high water conditions, and the plant sizes in the two populations converged under low water conditions (Fig. 1). The same pattern was found for density; at high density, the phenotypes converged.

Hillside plants produced more seeds than floodplain plants by the time the plants were harvested (Table 1). This difference in seed production did not depend on the watering treatment or density.

Density and water effects in mixtures

As in pure culture, when *Impatiens* plants were grown in mixture at lower water availability reduced height, number of leaves and aboveground dry mass in both populations (Fig. 2). Significant differences between populations existed in height, basal diameter, leaf area, seed number and aboveground mass (Table 2). Again, the tendency was for the size difference to be exaggerated under the high watering treatment, although the population \times environment interaction was significant only for aboveground biomass due to the smaller sample size within the single mixture treatment (Table 2). There was a tendency ($F = 3.68$, $p = 0.059$) for hillside plants to produce more seeds than floodplain plants, regardless of treatment.



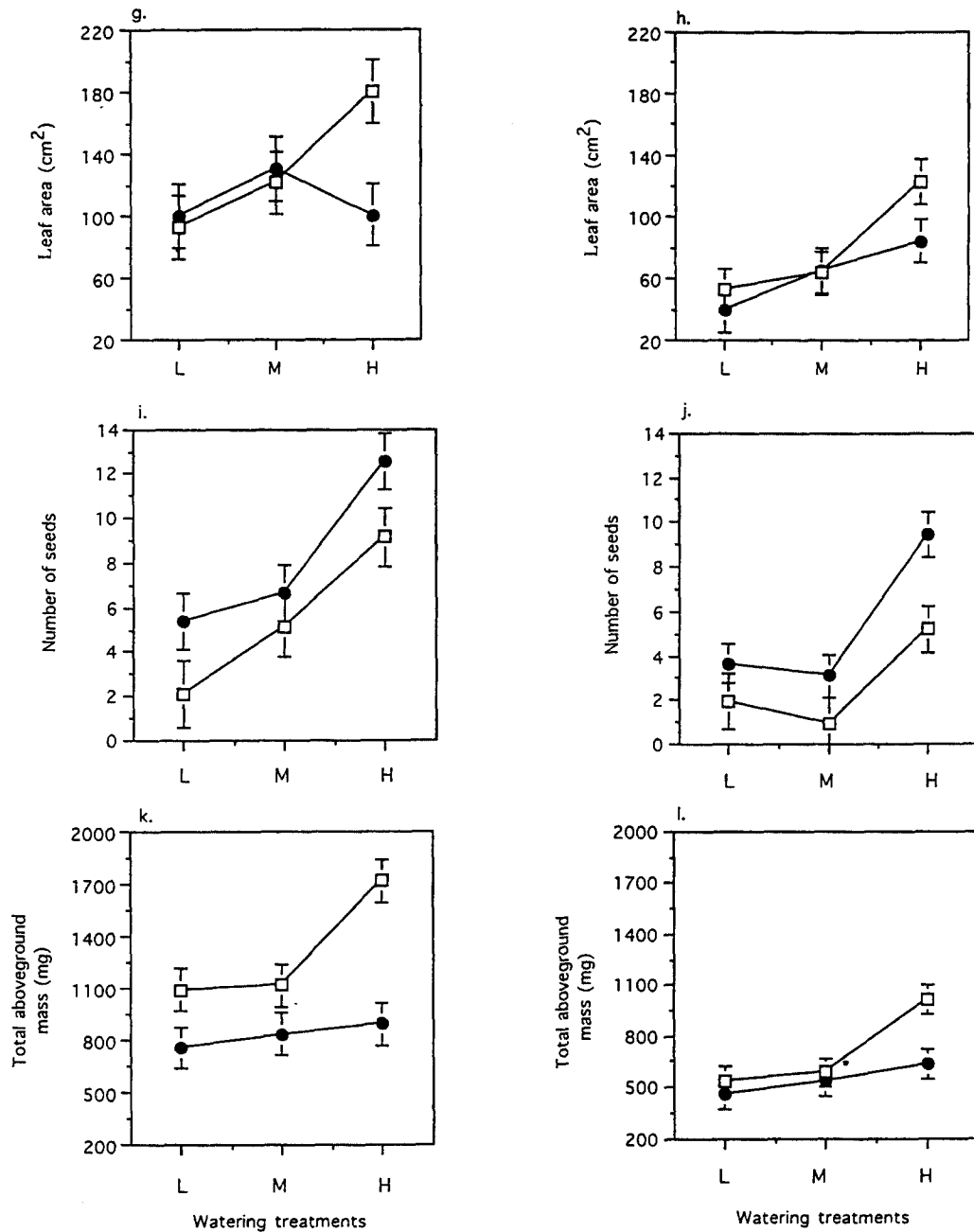


Fig. 1. Response of floodplain(□) and hillside(●) populations to water availability (L, low; M, Medium; H, high) at densities of 1 and 2 plants per pot in the competition experiment in pure culture. Means (±S.E.) are shown for height (a, b), basal diameter (c, d), number of leaves (e, f), leaf area (g, h), number of seeds (i, j), and total aboveground mass (k, l).

Table 1. F-values from ANOVAs showing the effect of population, density, and water regime on morphological traits, number of seeds and aboveground mass of *Impatiens pallida* grown in pure culture

Source of variation	df	Height	Basal diameter	Number of leaves	Leaf area	Number of seeds	Aboveground dry mass
Watering treatment	2	3.93*	0.87	7.39***	8.24**	28.24**	13.10***
Density	1	33.54***	29.23***	26.97***	24.03***	15.46***	53.80***
Population	1	36.10***	22.94***	5.18*	3.42	14.99***	28.87***
Watering treatment × Density	2	0.41	0.05	0.02	0.49	1.72	0.10
Population × Watering treatment	2	0.23	0.51	3.04	3.99*	0.72	5.32**
Population × Density	1	0.78	3.17	0.62	0.05	0.00	6.58*
Watering treatment × Density × Population	2	0.72	0.52	0.08	0.85	0.31	0.30

* p<0.05, ** p<0.01, *** p<0.001

Table 2. F-values from ANOVAs showing the effect of population and watering regime on morphological traits, number of seeds and aboveground mass of *Impatiens pallida* grown in mixed culture

Source of variation	df	Height	Basal diameter	Number of leaves	Leaf area	Number of seeds	Aboveground dry mass
Watering treatment	2	10.18***	1.98	3.79*	1.64	8.74***	6.26**
Population	1	19.58***	14.43***	1.08	5.51*	3.68	15.41***
Population × Watering treatment	2	0.36	1.42	2.46	2.25	0.06	3.51*

* p<0.05, ** p<0.01, *** p<0.001

Relative crowding coefficients and relative yield totals

Despite differential population responses to watering treatments and density, the relative crowding coefficients did not differ significantly from 1 under any watering condition (t-test). In addition, the crowding coefficient (Fig. 3a) was unaffected by watering treatment (ANOVA). Relative yield totals (Fig. 3b) were significantly greater than 1 overall (t=2.360, p=0.026), although there was no difference among environments in RYT (ANOVA).

DISCUSSION

In previous work, ecotypic differentiation between adjacent populations of *Impatiens pallida* was clearly demonstrated by field reciprocal transplant experiments (Bennington and McGraw, submitted). Genetic differences found in the field study were re-affirmed in the present greenhouse study: floodplain plants were consistently larger than hillside plants, regardless of treatment. Hillside plants flowered and produced seeds earlier than the floodplain plants and this accounted for their greater seed production, regardless of

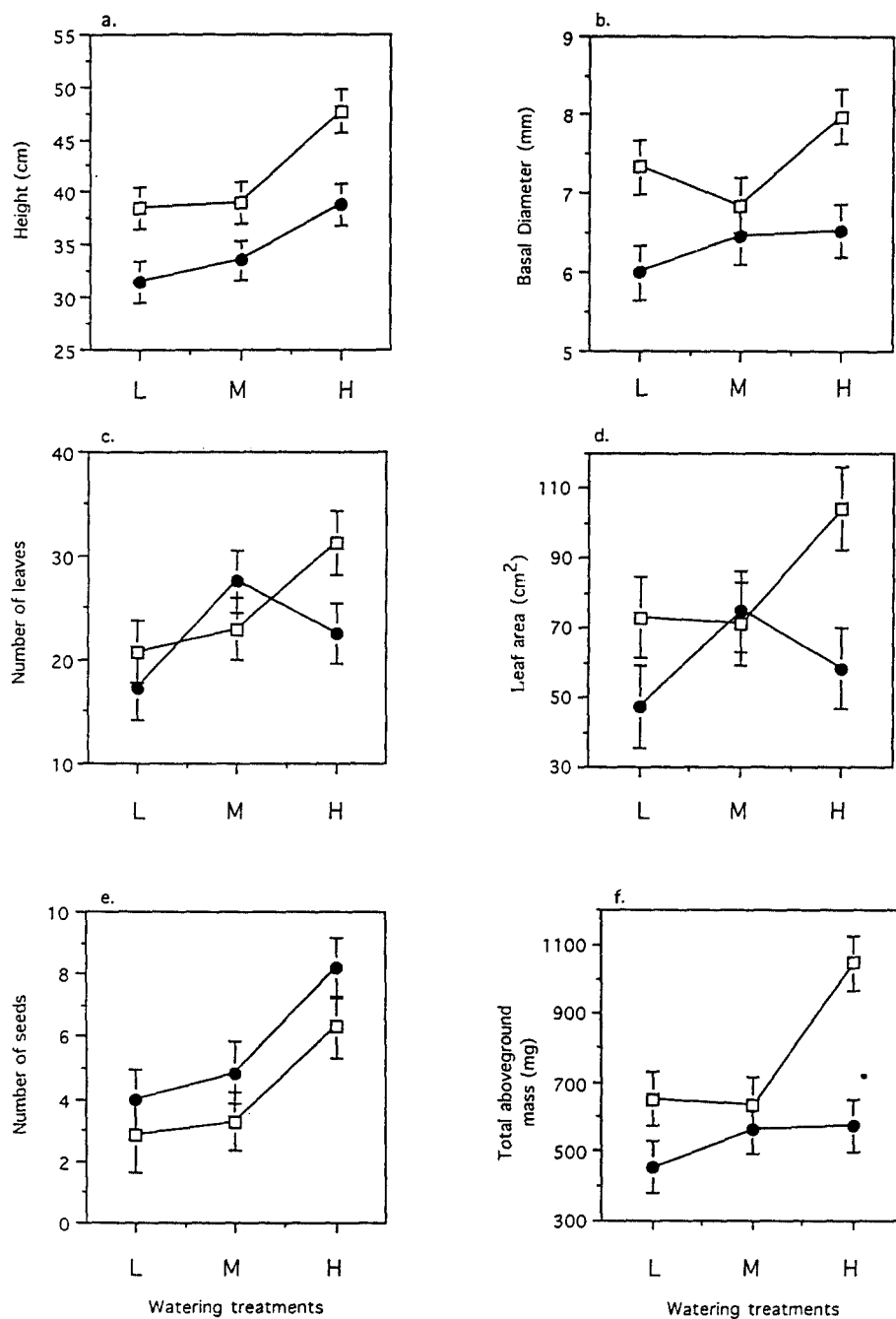


Fig. 2. Response of floodplain (□) and hillside (●) populations to water availability (L, low; M, medium; H, high) at density of 2 plants per pot in the competition experiment in mixed culture. Means (±S.E.) are shown for height (a), basal diameter (b), number of leaves (c), leaf area (d), number of seeds (e), and total aboveground mass (f).

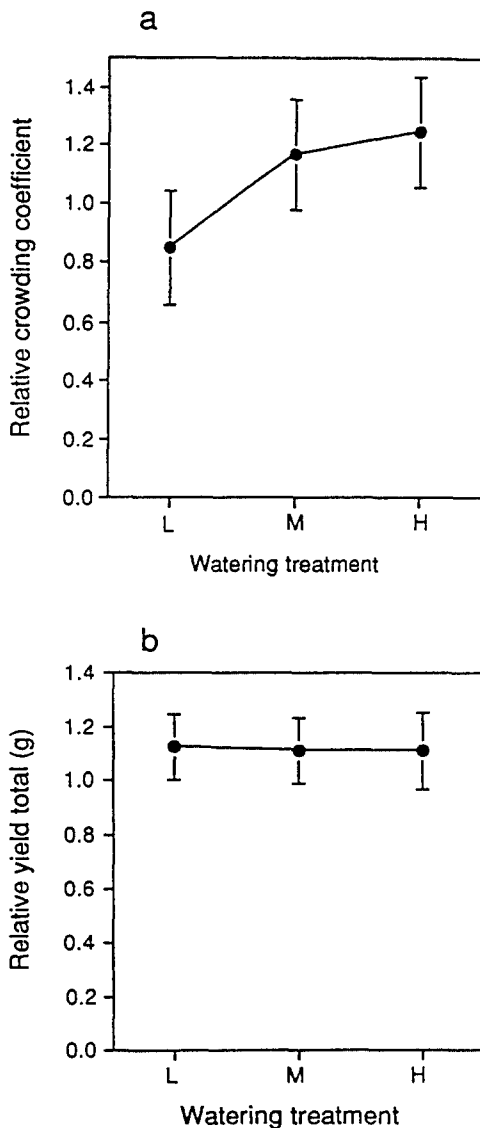


Fig. 3. Response of relative crowding coefficients (RCC, a) and relative yield totals (RYT, b) to watering regime. RCC and RYT were estimated using biomass as the measure of yield, eliminating all blocks having missing data.

high per plant whereas in undisturbed localities where plants approach the carrying capacity, resource levels per plant could be quite low despite being in a highly productive site. By contrast, in low resource sites, disturbances do not improve resource availability nearly so much due to abiotic limitations of site productivity.

watering treatment (the experiment was terminated well before most plants had begun to senesce).

The environmental gradient from hillside to floodplain is a complex one in which light, herbivory, disturbance and possibly nutrients vary as well as water. The present study, by examining response to water alone, demonstrates genetic differentiation in the ability of the two ecotypes to respond to high water availability in a manner consistent with that observed along the multifactorial gradient in the field. The floodplain ecotype grew larger than the hillside ecotype when given high amounts of water but the two ecotypes were similar under low water conditions. This pattern, in which a population adapted to relatively high resource levels is more plastic in response to gradients, has been observed in many other studies of ecotypic variation (Gurevitch *et al.* 1986, McGraw 1987, Fletcher and Shaver 1990, Bennington and McGraw, submitted).

Higher levels of plasticity are advantageous when the environment is spatially heterogeneous and a plant with the ability to respond to this heterogeneity will therefore have superior fitness (Bradshaw 1965, Schlichting 1986, Sultan 1987). In the case of the contrast between low and high resource environments, it is likely that high resource environments are more variable because in local scale disturbances (e.g., flooding in the floodplain) that reduce plant density, resource availability will be very

Differential growth rates in the high water treatment might be expected to result in asymmetrical competition, with suppression of the smaller plants by larger plants (Weiner and Thomas 1992). The fact that the index of competitive ability (RCC) was not significantly different from 1 indicates that this did not occur; despite being larger, floodplain plants did not gain a relative competitive advantage in mixture. Thus, the 'superior competitor hypothesis' was not supported. The fact that RCC did not change significantly across watering treatments provides no support for the alternative 'competitive reversal hypothesis' either. This contrasts with earlier findings of altered competitive ability as a function of resource availability (McGraw and Chapin 1989).

One possible explanation for the lack of competitive shifts with watering treatment may have to do with the fact that niches of the two ecotypes were found to be significantly different ($RYT > 1$; Harper 1977). For example, in the high water treatment, the competitive effect of larger-statured floodplain plants may have been countered by niche differences belowground, such that different soil resources were being exploited. One mechanism for this could be different rooting-depths (Berendse 1982).

Although this study did not implicate competitive ability as a significant factor in adapting the two ecotypes to distinctive moisture regimes, the differences could become more pronounced at high densities and in field soils. It does appear from previous work that the primary adaptation of hillside plants to drought is a distinct hastening of the development rather than water conservation (Schulz *et al.* 1993, Bennington and McGraw, submitted). By this mechanism, flowering and seed production are achieved prior to onset of summer drought. However, selection favors large size on the floodplain (Bennington and McGraw, submitted). Given the manifold reduction in density that occurs through self-thinning during development of a pure stand on the floodplain, it is logical that part of the cause for such selection is competition. Manipulations of density and ecotype frequency in the field would be helpful in order to clearly show the importance of competition in *Impatiens pallida* adapted to low and high resource sites.

적 요

본 연구는 수분환경이 다른 생육지에서 자란 *Impatiens pallida*의 두 생태형간의 수분함량의 변화에 대한 적응능력에 있어서의 경쟁의 역할을 조사했다. 온실에서 유묘들은 저, 중, 고수분 조건을 유지하며, 순수배양에서 pot 당 1과 2 개체의 밀도로, 그리고 혼합배양에서 pot 당 2개체의 밀도로 길러졌다. 두 개체군들은 본 실험에서 일련의 수분환경의 구배에 따라 유전적으로 차이를 보였는데, 이것은 앞선 연구결과와 일치하였다. 두 개체군들은 순수배양에서 밀도와 수분함양에 대해 유사한 형태적인 반응을 보였으나, 고수분환경에서 생육했던 개체군이 저수분환경에서 생육했던 개체군보다 고수분조건에서 더 큰 성장을 나타냈다. 이러한 두 개체군간 성장의 차이는 고수분조건에서 크게 나타났고, 저수분조건으로 갈수록 낮아졌다. 두 개체군들의 상대적인 경쟁능력이 3가지 수분조건과 2가지 밀도에서 비교되어 졌다. 수분조건과 밀도에 대한 다른반응은 상대적인 경쟁차를 나타낸 것은 아니다. 상대적인 총생산력은 1보다 컸다. RYT가

1보다 큼으로써 시사된 생태적 지위의 차이는 개체군들이 3가지 수분조건에서 관찰된 다른 경쟁적 영향의 부족을 설명할 수 있을 지 모른다.

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