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# Environmentally induced carry-over effects on seed production, germination and seedling performance in *Bunium bulbocastanum* (Apiaceae)

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## Summary

This study investigates the effects of differences in resource supply to parent plants on seed production, seed germination and seedling performance in the tuber-forming geophyte *Bunium bulbocastanum* L. (Apiaceae). Parent plants were grown in a factorial design with two levels of light and nutrient supply, respectively. All plants flowered and set seeds in the second growing season. For each treatment, seeds were split into three weight classes and 100 seeds of each group (3 weight classes × 4 treatments) were planted. The emerging seedlings were grown under uniform conditions for one growing season.

Resource availability strongly affected the number, but not the size of seeds produced. Nevertheless, seeds of equal size originating from different maternal light and nutrient treatments showed marked differences in germination rate, seedling performance and final tuber weight, indicating the presence of environmentally induced carry-over effects in *B. bulbocastanum*. Shading of parent plants had generally negative effects on offspring performance, while low nutrient supply tended to increase germination and seedling growth. Environmental carry-over effects influenced final tuber weight via seedling characteristics in a complex way, thereby impeding clear predictions of offspring performance from seed size alone.

Key words: Environmental carry-over effects, light, maternal resource availability, nutrients, path analysis, seed size

## Introduction

Seed production, seed germination and seedling development are crucial stages in the life cycle of sexually reproducing plants, determining the dynamics of populations and affecting their fitness to a large extent. In many plant species the number and size of seeds, their germinability and the performance of seedlings depend at least partly on the conditions under which seeds mature on the mother plant. Such effects are commonly referred to as environmentally induced carry-over effects (BULLOCK et al. 1993; ROACH & WULFF 1987) and include non-genetical components of the relationship between parent plants and their offspring. Sometimes, these effects are also called maternal effects. This term is avoided here because it may refer to genetical as well as to environmental effects (MAZER 1987; ROACH & WULFF 1987; SCHAAL 1984; SCHMID & DOLT 1994). Considerable amounts of data are available showing

effects of environmental conditions on seed production (i.e., seed sizes and numbers; cf. FENNER 1992; ZHANG & MAUN 1993) on one hand, and effects of seed size on seedling growth and development on the other (cf. CIDECIYAN & MALLOCH 1982; DOLAN 1984; GROSS & SMITH 1991; MONTALVO 1994; STANTON 1984; WINN 1985). However, only few experimental studies (cf. AMZALLAG 1994; MIAO et al. 1991 a, b; PARRISH & BAZZAZ 1985; WULFF 1986 a, b, c; see review by ROACH & WULFF 1987) have specifically investigated to what extent environmental carry-over effects influence seed germination and/or seedling performance, i.e. how they translate into fitness-related parameters of the offspring generation.

Variation in seed size due to environmental and developmental conditions represents the most obvious carry-over effect. Various studies have shown that the size of seeds can be affected by plant size, plant density, by the position on the parent plant and by resource avail-

ability (HENDRIX 1984; HENDRIX & SUN 1989; OBESO 1993; PARRISH & BAZZAZ 1985; WULFF 1986a). Effects of resource shortage on seed size are often counteracted by a variable number of seeds (FENNER 1986; MEHLMAN 1993; STEPHENSON 1984), which is usually interpreted as a strategy to minimize negative carry-over effects on the offspring generation (LLOYD 1987; SILVERTOWN & LOVETT DOUST 1993: 164; SMITH & FRETWELL 1974). In this way plants are able to trade the number of offspring against their size, which may be an important determinant of seed germinability and seedling growth and establishment (FENNER 1991; GUTTERMAN 1992; HAIG & WESTOBY 1988; LLOYD 1987).

Large seeds usually have a higher germination percentage than small seeds of the same species (HENDRIX 1984; HENDRIX & TRAPP 1992; STANTON 1984; VERKAAR & SCHENKEVELD 1984; but see MANASSE 1990; MONTALVO 1994; SCHMITT & ANTONOVICS 1986; ZHANG & MAUN 1993) and they may produce larger seedlings with higher survival chances (FENNER 1992; MANASSE 1990; WULFF 1986b; ZHANG & MAUN 1993; but see HENDRIX et al. 1991). This advantage could be amplified in successive generations if plants deriving from large seeds again have a higher seed production or germinate earlier than plants deriving from small seeds (SCHAAL 1984; STANTON 1984; but see WULFF 1986 a, c). However, such a positive relationship between seed size and future reproductive success may be counterbalanced by the fact that small seeds germinate earlier and seedlings originating from them may gain a competitive advantage over later germinating individuals (FENNER 1992; HENDRIX 1984).

Apart from seed size, germinability can also be influenced by different aspects of the maternal environment (i.e. growth conditions experienced by parent plants) including day length, temperature, light quality, water availability and altitude (FENNER 1991; GUTTERMAN 1992; ROACH & WULFF 1987). However, only limited information is available (cf. MIAO et al. 1991 a, b; PARRISH & BAZZAZ 1985) about carry-over effects caused by different levels of nutrient and light supply and about the interaction between seed size and other, not size-related carry-over effects.

The experiment reported here was designed to answer the following questions:

- (a) How do differences in light and nutrient supply affect seed production (number, size and nutrient content of seeds)?
- (b) How do seed size and size-independent carry-over effects influence seed germination and seedling performance during their first year of life?
- (c) To what extent can variation in seedling performances (measured as tuber size at the end of the first growing season) be explained by differences in ger-

mination time, and by the size and life span of cotyledons?

- (d) How are the traits mentioned in (a)–(c) influenced by environmentally induced carry-over effects?

An attempt is made to summarize the impact of carry-over effects on plant performance by estimating relative fitness values for seed production, germination and seedling growth. This should give an indication of how differences in the maternal environment translate into differences in fitness among individuals in the next generation.

## Material and methods

### The species

*Bunium bulbocastanum* L. (Apiaceae) is a geophyte of sub-mediterranean origin (MEUSEL et al. 1978). Seeds, which after cold-stratification in the field show no dormancy (WILLEMS, unpubl. data), germinate in early spring. Every seed gives rise to one lanceolate cotyledon (secondary monocotyledony) which produces a small spherical tuber during the first growing season (cf. HUBER 1992). The tuber represents the only perennating organ of the species. It steadily becomes bigger as the plant ages and it can reach a diameter of 4–5 cm in old individuals. Since tuber size is likely to be positively correlated with vegetative growth and reproduction in juvenile individuals (cf. BOEKEN 1989, 1990; HUBER, pers. observation), this parameter will be used as a fitness estimate of one year old plants in this study. Rosette leaves are produced in the second year and flowering can occur from the third year onwards, depending on the size of the tuber.

As a spring geophyte, *B. bulbocastanum* has a short yearly growth season. In early spring (i.e., late February in the Netherlands) 4 to 15 rosette leaves emerge from the tuber and they die back in late May or in June (HUBER 1992). Bolting usually occurs at the end of April and the seeds ripen in July, when all above-ground parts die back. Individual plants may flower many times, but intermittent years without flower and seed production are common in the field (HUBER, pers. observation).

In the past *B. bulbocastanum* was relatively widespread in Mid-Europe (including the Netherlands) and occurred as a weed in extensively managed arable fields. Due to intensified agricultural practices the species has become rare during the last decades. Nowadays, it is mainly restricted to chalk grasslands and dune areas which serve as refuge habitats for *B. bulbocastanum* in the Netherlands.

All plant material used in this experiment was derived from a population in the chalk grassland nature reserve "Wrakelberg", which used to be an arable field (for a site description see BOBBINK & WILLEMS 1987; WILLEMS & BOBBINK 1990), situated in the southern parts of the Netherlands (50° 52' N, 5° 55' E).

*Bunium bulbocastanum* L. proved to be especially suitable for investigating environmental carry-over effects for the following three reasons: (1) this species maintains a generally

high seed production under different environmental conditions, (2) each seed produces one single cotyledon and no foliar leaves in the first growing season (which facilitates comparisons among plants), and (3) each cotyledon produces a small over-wintering tuber during the first growing season, which can be used as a good estimate of plant survival and of juvenile fitness (WILLEMS & HUBER, unpubl. data).

## The experiment

In 1986, adult tubers of *B. bulbocastanum* were excavated in the field and transplanted to the botanical garden of the Utrecht University, where they were grown outside under uniform conditions for two years. Seeds produced in summer 1988 were collected and germinated in spring 1989. Seedlings were grown for one year under uniform conditions. In February 1990, one year old tubers with an average fresh weight of 72 mg ( $\pm$  15.5) were planted in separate pots (diameter: 13 cm) filled with a substrate containing two parts of river sand and one part of soil collected at the original field site.

Before starting the experiment 10 to 14 plants were randomly assigned to each of four treatments. The experimental set-up consisted of two light and two nutrient levels arranged in a factorial design. The two light levels were full daylight (L+) and a shading treatment (L-) where light intensity (PAR) was reduced to 30% of full daylight. Shading was done by cages covered with black shade cloth which did not affect the spectral composition of the transmitted light. Plants grown under conditions of high-nutrient supply (N+) were fertilized weekly with a modified Hoagland solution (amounts equivalent to 100 kg nitrogen per ha and per growing season). Plants exposed to low nutrient conditions (N-) did not receive any fertilization throughout the experiment. Plants were grown outside in the experimental garden and they were watered regularly.

These treatments were applied for two successive years. In the second year all plants flowered. To avoid positional effects only seeds of the primary umbel of each plant were harvested, counted, and their total weight measured. Fifteen randomly chosen seeds of each umbel were weighed individually. Seed nitrogen and phosphorus concentrations were determined colorimetrically with a continuous flow auto-analyzer after digestion of seeds with diluted sulphuric acid.

The harvested seeds were pooled within treatments and then divided into three weight classes: small seeds (< 1.5 mg), medium-sized seeds (1.7–1.9 mg), and large seeds (> 2.0 mg). After an 8-weeks' period of cold stratification in the field, 100 randomly chosen seeds of each of the 12 groups (four treatments  $\times$  three size classes) were planted into individual pots in February 1993. A mixture of sand (1/3) and potting compost (2/3) was used as substrate. Some chalk was added to increase the pH to values found under field conditions. The pots were randomized and placed under uniform conditions (full daylight without additional fertilization) outside in the experimental garden. During the growing season emergence and dying back of the cotyledons was recorded twice a week. The variable called 'germination delay' refers to the time-lag (in number of days) between the emergence of individual seedlings and the emergence of the first seedling in the whole experiment (high values, thus, indicate delayed germination). The

cotyledon life span is defined as the number of days between emergence and disappearance of a cotyledon. The length of the cotyledons was measured at the beginning of June, when cotyledons had reached their full length. At the end of July all tubers were harvested, dried to constant mass at 72 °C, and weighed.

## Statistical analysis

All variables were tested for normality and log-transformed when necessary. Data on seed number, seed weight and nutrient content were analyzed by means of two-way analysis of variance (ANOVA), with light and nutrient availability as the main effects. The weight of individual seeds was analyzed with a nested ANOVA (plants nested within treatments). Three-way ANOVA was used to test for effects of the maternal light and nutrient environment and of seed size on germination delay, cotyledon life span, cotyledon size, and tuber size at the end of the season. Treatment effects on germination rate (i.e. percentage of seeds emerged) were tested with a logistic regression (SOKAL & ROHLF 1981). The program package SAS (SAS Institute 1988) was used for these analyses.

In addition, a path analysis (cf. GROSS & SMITH 1991; SILVERTOWN & LOVETT DOUST 1993: 20; SOKAL & ROHLF 1981: 642) using multiple regressions was used to evaluate treatment (i.e. light, nutrient availability to parent plants) and seed size effects on germination delay, cotyledon life span and cotyledon size and to analyze effects of these parameters on tuber size. Interaction effects between maternal treatments and seed size were not included in the path analysis. Correlation coefficients and standardized regression coefficients were calculated for all variables in the path analysis. Coefficients of determination (i.e., percent of variation explained by the model) were obtained for the two steps in the path. The statistical program package SPSS (1993) was used for these analyses.

## Results

Seed production was significantly affected by light and nutrient supply. Shaded plants produced on average 35% fewer seeds than plants grown in full daylight. Low nutrient availability also led to a reduced number of seeds, especially in plants which grew in full daylight (Fig. 1a). The average weight of seeds was not significantly affected by changes in the availability of light and nutrients (Fig. 1b). Seeds produced in shade showed significantly higher nitrogen and phosphorus concentrations than seeds produced in full daylight. Nutrient addition increased the nitrogen content of seeds (Table 1).

Germinability was close to 100% for seeds produced under high-light conditions, but this value dropped to about 54% for seeds originating from shaded plants (Fig. 2). Fertilization had no main effect on seedling emergence, while seed size generally tended to increase

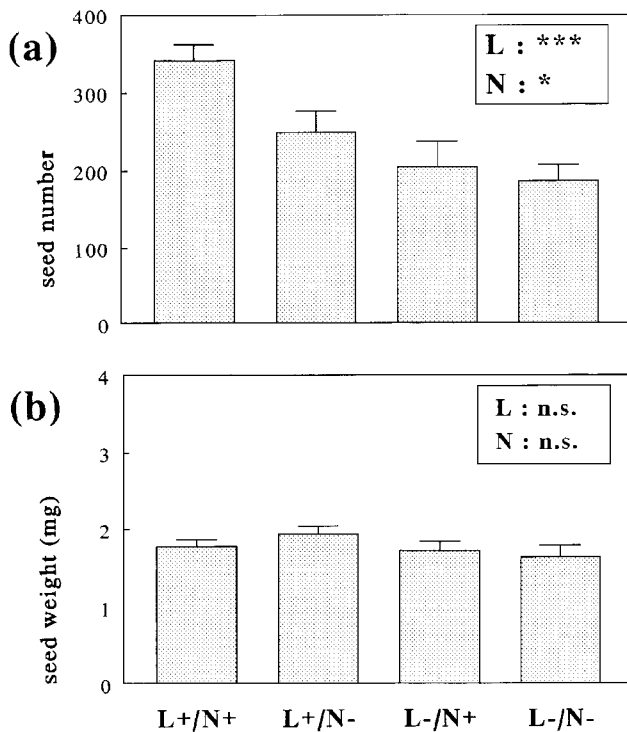


Fig. 1. Mean number of seeds (a), and mean weight of individual seeds (b). Error bars give one SE of the mean. Boxes give the results of significance tests for the effects of light (L) and nutrient availability (N). There were no significant interactions between light and nutrients.

Table 1. Nitrogen and phosphorus concentrations of seeds produced in 1991; (a) mean values  $\pm$  SE, and (b) results (p-values) of a two-way ANOVA testing the effect of light (L) and nutrient (N) availability.

variables	nitrogen	phosphorus
(a) nutrient concentration in % ( $\pm$ SE)		
L+/N+	2.61 $\pm$ 0.02	0.46 $\pm$ 0.01
L+/N-	2.47 $\pm$ 0.06	0.47 $\pm$ 0.02
L-/N+	3.96 $\pm$ 0.04	0.77 $\pm$ 0.01
L-/N-	3.77 $\pm$ 0.02	0.70 $\pm$ 0.16
(b) significance		
L	< 0.0001	< 0.0001
N	0.0004	0.0551
L*N	0.4900	0.0058

germinability of seeds (Fig. 2; Table 2). The latter effect, however, was reversed in large seeds produced under shaded, nutrient poor conditions, where large seeds showed considerably lower emergence rates than smaller seeds.

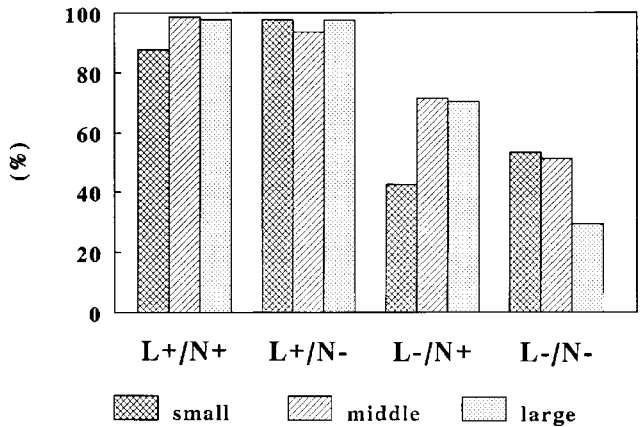


Fig. 2. Percentage of seeds germinating. For significant differences between treatments and size classes see Table 3.

Table 2. Performance of seedlings. Means values ( $\pm$  SE) for the variables germination delay (in days after the first seedling emerged), cotyledon life span (number of days between emergence and senescence of the cotyledon), cotyledon length and tuber weight. For significance of the differences see Table 3.

seed size:	small	middle	large
germination delay (in days)			
L+/N+	20.71 $\pm$ 0.78	18.09 $\pm$ 0.74	17.34 $\pm$ 0.53
L+/N-	16.05 $\pm$ 0.69	16.39 $\pm$ 0.64	18.38 $\pm$ 0.54
L-/N+	21.23 $\pm$ 1.11	23.03 $\pm$ 0.83	23.67 $\pm$ 1.05
L-/N-	19.71 $\pm$ 1.18	18.14 $\pm$ 0.90	22.25 $\pm$ 1.36
cotyledon life span (in days)			
L+/N+	69.36 $\pm$ 2.06	73.72 $\pm$ 2.12	73.73 $\pm$ 1.82
L+/N-	76.86 $\pm$ 2.11	81.39 $\pm$ 1.72	77.23 $\pm$ 2.36
L-/N+	69.68 $\pm$ 2.92	66.62 $\pm$ 2.50	68.96 $\pm$ 2.29
L-/N-	70.57 $\pm$ 2.94	81.97 $\pm$ 3.06	68.94 $\pm$ 3.63
cotyledon length (mm)			
L+/N+	27.93 $\pm$ 0.97	37.06 $\pm$ 1.01	37.21 $\pm$ 0.88
L+/N-	29.54 $\pm$ 0.94	35.79 $\pm$ 1.03	36.13 $\pm$ 0.86
L-/N+	33.33 $\pm$ 1.67	33.39 $\pm$ 1.01	34.88 $\pm$ 1.38
L-/N-	30.01 $\pm$ 1.10	39.30 $\pm$ 1.79	37.14 $\pm$ 2.06
tuber weight (mg)			
L+/N+	21.95 $\pm$ 1.89	39.26 $\pm$ 2.66	42.34 $\pm$ 3.17
L+/N-	31.29 $\pm$ 3.13	39.40 $\pm$ 2.84	39.28 $\pm$ 2.30
L-/N+	30.45 $\pm$ 3.30	24.91 $\pm$ 2.04	32.73 $\pm$ 3.03
L-/N-	25.31 $\pm$ 2.52	45.70 $\pm$ 4.28	30.24 $\pm$ 3.43

Seeds produced under high-light conditions germinated earlier than seeds produced in shade (Tables 2, 3). This effect was more pronounced in large and medium-sized seeds than in small seeds. Nutrient addition to mother plants delayed germination of small, and to a lesser extent also of larger seeds (Tables 2, 3). There was a tendency for large and medium-sized seeds to emerge

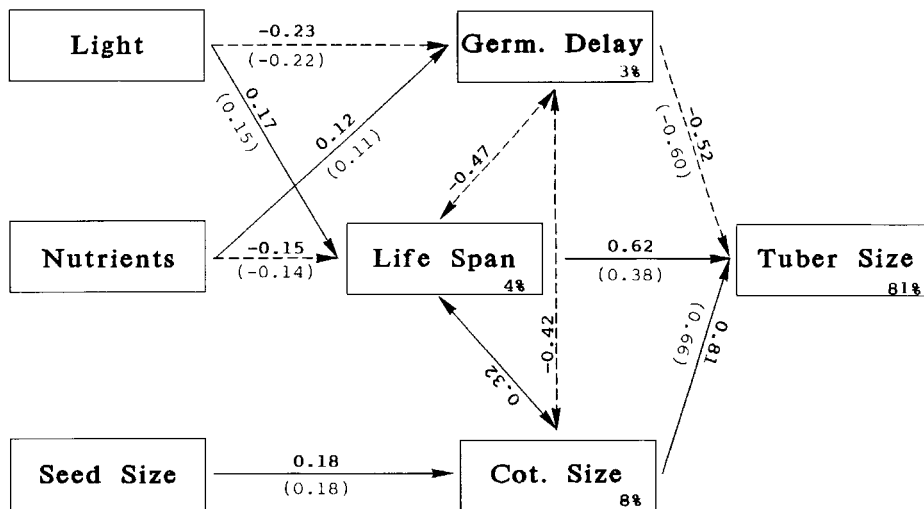


Fig. 3. Results of the path analysis. Bold numbers give the correlation coefficients, numbers in brackets indicate the standardized regression coefficients. Numbers within boxes give the coefficients of determination (i.e. percentage of explained variation). Only significant relationships are connected with lines, positive relations are indicated with full lines, negative relations are indicated by dashed lines.

later than small seeds. This pattern, however, was not consistent among treatments which is reflected by significant interaction terms (Table 3).

High-light supply to parent plants significantly increased the cotyledon life span of their offspring, while nutrient addition had the opposite effect (Tables 2, 3). This negative influence of fertilization was pronounced in the two lower categories of seed size but it was not significant in large seeds. Under nutrient poor conditions cotyledons produced by medium-sized seeds had a higher life expectancy than cotyledons of small and large seeds (Tables 2, 3).

The average size of cotyledons was not directly (but see significant interaction effect, Table 3) affected by maternal light and nutrient treatments, but it showed a positive relationship with seed size. The significant three-way interaction indicates that this response was different for the different light and nutrient treatments (Tables 2, 3).

Table 3. Performance of seedlings. Results of significance tests for the main effects light availability (L), nutrient supply (N), and seed size (S) and for the interactions. Significance levels: \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ , n.s. =  $p > 0.05$ .

variables	L	N	S	L*N	L*S	N*S	L*N*S
germination rate (%)	***	n.s.	*	n.s.	n.s.	***	n.s.
germination delay	***	***	*	n.s.	n.s.	*	*
cotyledon life span	**	***	*	n.s.	n.s.	**	n.s.
cotyledon length	n.s.	n.s.	***	n.s.	n.s.	n.s.	**
weight of the tuber	*	**	***	n.s.	**	*	***

### Path analysis

The three seedling parameters, germination delay, cotyledon life span and cotyledon size had significant effects on the size of the tuber at the end of the first growing season (Fig. 3), explaining more than 80% of the variation in this variable. Early germination, a long life span and a large size of the cotyledons had positive effects on tuber size, the last variable having the strongest impact (Fig. 3). The three seedling characteristics appeared to be significantly inter-correlated: seedlings emerging later in the season produced smaller cotyledons with a lower life expectancy, and large cotyledons tended to live longer than small ones (Fig. 3).

The path analysis summarizes the complex relationships between seedling parameters, the maternal treatments and seed size on one hand, and their impact on the size of the tuber on the other (Fig. 3). The germination date of seeds and the life span of cotyledons was significantly affected by light and nutrient supply to parent plants, while the size of cotyledons showed a significant positive relationship with seed size. The coefficients of determination for the three seedling parameters were generally low. The weight of tubers at the end of their first growing season was largely determined by the three seedling parameters (Fig. 3).

In combination the two steps of the path analysis show that a high-light supply to mother plants had positive effects on the weight of the first-year tubers, mediated by the germination delay and by the life span of cotyledons, while nutrient addition negatively affected tuber

size via the same traits. Seed size had mainly positive effects on the size of the tuber which were mediated by the size of cotyledons. There was also a tendency for seed size to decrease tuber size via delayed germination and via a decreased life expectancy of cotyledons (Fig. 3). Tuber size at the end of the first growing season was the result of complex interactions (see Table 3 for statistical interaction terms) between environmental factors, seed size and various components for seedling growth.

## Discussion

The light and nutrient environment which parent plants were exposed to significantly affected seed production, seed germination and seedling performance in *Bunium bulbocastanum*. Especially shading resulted in strong negative carry-over effects on all three investigated stages of the life cycle, while low nutrient levels generally tended to enhance germination rates and offspring performance. The tuber weight of offspring individuals at the end of their first growing season, which was used as a fitness estimate in this study, was significantly affected by the maternal treatments and by seed size. These results provide further evidence for the notion that carry-over effects may persist for prolonged periods of time (BULLOCK et al. 1993; MIAO et al. 1991 a, b; SCHAAL 1984), and that seed size significantly affects juvenile traits, which has also been reported for a number of other species (ROACH & WULFF 1987; STANTON 1984; WINN 1985; ZHANG & MAUN 1993). The relationship between tuber weight on one hand and maternal treatments, seed size and juvenile traits on the other, was not straightforward but characterized by highly significant interaction terms (cf. Table 3), indicating that carry-over effects influence the performance of offspring individuals in a complex way. This is in agreement with results of other studies which also showed maternal treatments to affect offspring traits in a very intricate way (BULLOCK et al. 1993; MIAO et al. 1991 a, b).

## Seed production

The average size of seeds was not affected by differences in light and nutrient supply to parent plants, while the number of seeds decreased considerably under conditions of resource shortage (cf. Fig. 1). Such size-number trade-offs in seed production have been found by various authors (cf. FENNER 1986; ROACH & WULFF 1987) and they are generally interpreted as a mechanism to buffer negative carry-over effects on seed size (LLOYD 1987; SILVERTOWN & LOVETT DOUST 1993). Such a trade-off carries evolutionary

advantages whenever the size of seeds is positively related to germination rates and to the survival chances of the offspring. Our results on germination and seedling performance suggest such advantages for *B. bulbocastanum*.

## Germination and seedling performance

The quality of the maternal environment strongly affected seed germination and seedling performance, in spite of the absence of significant differences in seed size among treatments. This implies that seeds of the same size produced under different environmental conditions did not perform equally well. Seed size alone can, therefore, be considered as a poor predictor of the reproductive success in *B. bulbocastanum*.

Although small seeds showed a slight tendency to germinate earlier and they reached higher emergence rates in one of the treatments (Fig. 3, Table 2), this advantage of small over bigger seeds was (more than) offset by consistently positive effects of seed size on the length of cotyledons and, eventually, on tuber size (Fig. 3). It should be noted, however, that large seeds do **not** produce larger cotyledons than medium-sized seeds. Large seeds showed strongly depressed germination rates under one set of maternal conditions (L–N–) as compared to smaller seeds, and their cotyledons had a lower life expectancy than those emerging from medium-sized seeds. Thus, averaged over all treatments, medium-sized seeds performed best, suggesting that plants could not gain advantages from producing big rather than medium-sized seeds. Studies on the effects of seed size differences on offspring performance suggest that this relationship may considerably differ between species. Some authors report positive effects of seed mass on germination and seedling growth (cf. AMZALLAG 1994; SCHAAL 1984; ZHANG & MAUN 1993), while others did not find evidence for such correlations (CIDECIYAN & MALLOCH 1982; MONTALVO 1994). Our results indicate that in *B. bulbocastanum* directional selection for large seeds may be counteracted by various factors. The production of large instead of medium-sized seeds would cause biomass costs but would have no clear benefits in terms of seed germination and seedling performance.

More than 80% of the variation in final tuber weight was explained by the three seedling characteristics, germination delay, cotyledon length and cotyledon life span, which corroborates findings that juvenile traits may strongly determine early seedling growth and biomass production in various species (GROSS & SMITH 1991; SCHAAL 1984). Tuber size at the end of the first growing season is a fitness-relevant parameter which determines the success of newly recruited individuals (e.g. survival and onset of reproduction). Our data,

hence, suggest the occurrence of strong selection pressures on early germination and the production of big long-lived cotyledons in *B. bulbocastanum*, which ultimately lead to the production of bigger tubers.

Variation in these juvenile traits, however, is likely to be restricted by prevailing environmental conditions in the natural environment of the species. Early germination and late senescence of the cotyledons, although positive for tuber growth, carry the risk of seedlings being killed by frost or drought, respectively, while bigger cotyledons may run a greater risk of herbivory.

### Carry-over effects on offspring fitness

The impact of environmental carry-over effects on reproduction and seedling establishment in *B. bulbocastanum* can be summarized by extrapolating the results of this study to the life cycle of hypothetical individuals growing under different conditions of resource supply (Table 4). If a parent plant produced 100 seeds under high-light and high-nutrient conditions it would only produce 73, 60 and 54 seeds under conditions of restricted nutrient and/or light availability (Table 4, row 2). These effects would be reinforced in the same direction by carry-over effects on seed germination. From the 100 original seeds only 24 (low nutrient supply, N-) and 37 (high-nutrient supply, N+) would emerge if produced in shade as compared to 71 (N-) and 95 (N+) for seeds produced in full daylight. Compared to these enormous differences, carry-over effects

Table 4. Estimate of carry-over effects of light and nutrient supply to parent plants on relative fitness of offspring individuals, defined as cumulative effect of seed production, seed germination and tuber size at the end of the first year of seedling growth. Figures within brackets give relative fitness values for every step in the life cycle (scaled to 100). The last row gives the relative fitness values (scaled to 100) resulting from the cumulative effects of treatments on the studied processes. See text for more details.

	treatments				
	L+N+	L+N-	L-N+	L-N-	
parent plant	1	1	1	1	
seed production	100	73	60	54	Fig. 1 a
seedling emergence	95	71	37	24	Fig. 2
	(100)	(75)	(39)	(25)	
tuber size	35.1	36.6	29.3	34.3	Table 2
	(96)	(100)	(80)	(94)	
number of seedlings x tuber size (relative fitness)	3325	2556	1073	816	
	(100)	(78)	(32)	(25)	

on tuber size seem less pronounced, although statistically significant. Tuber size was reduced both by shading and by adding nutrients to the parent plants, resulting in highest values for this variable under parental conditions of low nutrient and high-light supply (Table 4, row 4). Since the reproductive success of plants is determined both by the number and by the performance of seedlings, mean tuber size was multiplied by the number of seeds germinated to get an integral estimate of relative fitness (Table 4, last row). These values show that especially shading has detrimental carry-over effects on reproduction and establishment in *B. bulbocastanum*, reducing relative fitness values to as much as a third of that of unshaded plants. These values may even underestimate the effects of the treatments, because small differences in tuber size might lead to a delay of juvenile plants entering the reproductive phase, or to a lower seed production.

### Conclusions

Greenhouse studies and field observations have shown that *B. bulbocastanum* does not benefit from additional nutrient supply (HUBER 1992) and that shading generally leads to the gradual disappearance of the species in its natural habitats. Based on the results of our experiment we conclude that light and nutrient availability not only affect the species via direct impacts on plant performance but that resource supply to adult individuals is likely to influence the long-term survival of *B. bulbocastanum* populations via indirect, environmentally induced carry-over effects.

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## Buchbesprechung

**Vegetation science in forestry: global perspective based on forest ecosystems of East and Southeast Asia.** Ed. by E. O. BOX with R. K. PEET, T. MASUZAWA, I. FUJIWARA, and P. F. MAYCOCK. Handbook of vegetation science vol. 12/1. – Dordrecht, Boston, London: Kluwer 1995. – X, 663 S., 237 Abb., 113 Tab., gebunden, US\$ 262.00 – ISBN 0-7923-2679-2.

Es erstaunt im ersten Moment, wenn man als Untertitel eines Bandes eines Handbuches liest: "Papers from four symposia from the International Congress of Ecology, Yokohama 1990". Mithin basiert dieser Band (vol. 12/1) des "Handbook of Vegetation Science" auf Symposiumsbeiträgen. Die Erklärung dafür liefert der verantwortliche Herausgeber des Handbuches, H. LIETH, im Vorwort.

Ausgehend davon, daß der von GISELA JAHN bearbeitete Band 12 zur forstlichen Vegetationskunde mehr pflanzensoziologisch ausgerichtet war (entsprechend der Konzeption des Begründers des Handbuches, R. TÜXEN) und weitgehend nur die europäischen Wälder behandelte, entstand während der INTECOL-Symposia in Japan die Idee, ihn durch einen neuen, thematisch und geographisch weit darüberhinausgehenden Band zu ergänzen. Der nun (1/2 Jahrzehnt nach den Symposien) erschienene Band 12/1 deckt inhaltlich ein wesentlich weiteres Spektrum der Waldvegetationskunde ab, bereichert insbesondere um vielfältige ökologische Problemstellungen, so zur Aut- und Synökologie, Populationsökologie, Ökosystemstruktur und -dynamik. Es sind alle Waldformationen, die in Ost- und Südostasien eine besondere Bedeutung haben, und die alpine Vegetation berücksichtigt. Die Darstellungen konzentrieren sich, beschränken sich aber nicht auf die sinojapanischen und südostasiatisch-malayischen Regionen, wobei die entsprechenden Vegetationsformationen verschiedentlich auch weltweit analysiert werden oder zumindest andere Kontinente vergleichend einbezogen sein können. Afrika, aber auch die Neotropis, bleiben weitestgehend unberücksichtigt.

Der Band enthält 35 Einzelarbeiten, die in fünf (allerdings nur im Inhaltsverzeichnis, nicht im Text ausgewiesene) Themenkomplexe gegliedert sind:

- Überblicksbeiträge zu Klima und Waldvegetation sowie floristischer Diversität in Ost- und Südostasien,
- „Region immergrüner Wälder“ (Beiträge zu außertropischen immergrünen Breitlaubwäldern einschließlich Monsun- und Lorbeerwäldern Asiens, des südlichen Südamerikas, Australiens und Neuseelands bis zu mediterranen Hartlaubwäldern und ostasiatischen Kiefernwäldern),
- „Region sommergrüner Wälder“ (Beiträge zu Laub- und Laub-/Nadelmischwäldern Europas, Chinas und Koreas, Eichenwäldern südchinesischer Gebirge, mexikanischen Buchenwäldern),
- „Montane und boreale Region“ (Beiträge zu chinesischen Fichtenwäldern, japanischen Birken- und Nadelwäldern sowie zur alpinen Vegetation aus globaler Sicht),
- „Region tropischer Wälder“ (Beiträge besonders zu Regenwäldern, Mangroven und Moorwäldern des tropischen Asiens, zu *Dipterocarpus*- und *Hopea*-Wäldern, aber auch zu künstlich begründeten *Eucalyptus*- und *Acacia*-Beständen Thailands).

Die Autoren (etwa zur Hälfte aus Japan und China) verfolgen unterschiedlichste methodische Ansätze der Analyse der Waldvegetation. Neben klassischen vegetationskundlichen bzw. pflanzengeographischen (z. B. Vergleich europäischer und asiatischer sommergrüner Breitlaubwälder, Besonderheiten der Nadelwälder Hokkaidos im Vergleich zu borealen Wäldern Nordamerikas und Eurasiens, neuer Klassifikationsvorschlag für zonale Tieflandwälder des tropischen Asiens) finden sich vegetationsökologische bzw. ökosystemare Darstellungen (z. B. zu Bestandesstruktur und -dynamik, Netto-primärproduktion oder Phytomasse verschiedenster Waldtypen, Verteilung der Wurzelmasse durch Ermittlung der Feinwurzelbiomasse in Mangroven-Jungbeständen). Mehrere