

## Assessing the contributions of multiple interacting traits to plant reproductive success: environmental dependence

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### Abstract

The reproductive success of sibling cocklebur plants (Compositae: *Xanthium strumarium*) was monitored after growth at different levels of availability of water and nutrient resources. Variation in reproductive success among individual plants was related to physiological, structural, and phenological characteristics. Reproductive success increased with increased availability of resources, but the relative contribution of particular traits to reproductive success varied with resource availability. Allocation of biomass to different vegetative tissues, time to seedling emergence, degree of branching, transpiration rates, water use efficiency, the rate of decline in height growth after seedling emergence and final plant size all varied significantly with resource availability. However, the changes in each of these phenotypic traits across three garden environments did not always correlate with reproductive success. The shifts across environments in the apparent importance of somatic traits for reproductive success were attributed to plastic changes in the traits but also to changes in the phenotypic correlations of the traits with reproductive success.

### Introduction

A major challenge in evolutionary ecology lies in identifying the traits of a species that have the greatest influence on an individual's fitness across a wide range of environments. It is these key traits that best define the structural and functional interrelationships on which selection at the level of the whole organism depends. Identifying traits of possible ecological and evolutionary significance, gauging their contribu-

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tions to the major components of fitness, and settling on a parsimonious set of traits that effectively characterizes a species adaptation to its environment pose several substantial difficulties. These difficulties stem from two sources: the likely irrelevance to major components of fitness of most of the infinite measures of plant form and function and the environmental dependence of the contribution of a trait to fitness. In this paper we use data from cocklebur plants (Compositae: *Xanthium strumarium* L.) grown in experimental gardens of different resource availability to illustrate some approaches to overcoming these difficulties.

One might well argue at the outset that the rich body of theory on life history has already adequately defined an essential if not a complete set of traits appropriate for understanding the evolutionary ecology of most organisms. This is true in that the theory focuses on the interrelationships among recognizably major components of fitness such as survivorship, age at maturity, longevity, age-specific reproductive schedules, and investment in different modes of reproduction. Life history theory does not, however, address the evolution in metabolic rates, structural organization, timing of non-reproductive events, and similar somatic traits. Ironically, such traits, traditionally the concern of physiological ecologists and ecological anatomists, provide the functional underpinning of survival and reproduction. Stearns (1986) has recently emphasized the need to analyze this "intermediate structure" that defines the functional constraints on the relationship between genotype and phenotype. The possibility that the widespread assumption of negative correlations between investment in somatic versus reproductive function that underlies most of life history theory may not always hold (Bell and Koufopanou, 1986) emphasizes that the relative inattention of life history theory to the somatic basis for variation in the major components of fitness may be a significant shortcoming (Van Noordwijk and De Jong, 1986). The availability of resources to sustain growth and reproduction depends not only on resource availability in the local environment but also on an organism's investment in structures and metabolic activity associated with acquiring those resources from the environment. It is especially the somatic traits that determine this investment in *acquiring* resources relative to different patterns of resource allocation that have been undervalued in life history theory.

For example, contemporary theory on the allocation of resources to plant reproduction (Charnov, 1982; Goldman and Willson, 1986) is isolated from the rapid developments in theory on the functional basis for variation in rates of resource acquisition and their allocation to somatic function (Givnish, 1986). The theories of sex allocation partition a unit pool of resource to competing demands for alternate modes of reproduction (e. g. male versus female function) without consideration of how changes in the total resources available for reproduction might affect partitioning. The allometric dependence of reproduction on plant size (Samson and Werk, 1986; Bell and Lechowicz, ms) suggests reproductive modes will be affected by absolute resource availability. Conversely, theories of resource acquisition typically focus on the effect of partitioning to different somatic functions on the subsequent rates of resource accumulation and vegetative growth without concern for allocation to reproduction (Bloom et al., 1985). Only a very few analyses (King and Roughgarden, 1982 a, 1982 b; Chiarello and Roughgarden, 1984) bridge this gap and consider

directly how differences in resource uptake and allocation to both somatic and reproductive functions might affect plant fitness. Without a better understanding of the interrelationships between key somatic traits and the components of fitness incorporated into life history theory, we cannot predict their effect on phenotypic selection in a given environmental regime.

A correlational approach is frequently used to judge the importance of traits such as photosynthetic capacity or canopy architecture that are not themselves demonstrably major components of plant fitness. Correlations between such traits and major fitness components such as survivorship and fecundity are taken as evidence for the importance of these traits to fitness. These correlations may be based on individuals within a single species or population, on a group of species within a phylogenetic clade, or on a diverse and unrelated set of species. On the one hand, comparisons among conspecifics have the advantage that quantitative genetic analyses can potentially reveal the likely course of microevolution on a set of functionally interrelated traits (Lande, 1982; Arnold, 1983). On the other, any traits consistently correlated with fitness components across a wide range of species are likely to have adaptive significance despite the changes in other traits that often confound these interspecific analyses. This correlational approach can be applied equally well to traits like leaf size that are only tenuously connected to fitness or to traits known to be more directly important for plant function like photosynthetic capacity. The approach is intrinsically statistical in nature and is not intended to generate causal models of the mechanisms affecting fitness.

A second, contrasting approach to judging whether a trait has a positive effect on fitness is firmly grounded on a reductionist understanding of the contribution of traits to some aspect of plant function. The interactions among traits that achieve a particular functional end believed to be positively correlated with fitness are modelled and analyzed based on experimentally demonstrated functional relationships among traits. Applications of this approach to date have generally determined *only* the functional significance of traits, not their effect on survival and reproductive output, because the optimization criteria involved in the modelling efforts have involved somatic functions rather than major components of fitness (Givnish, 1986). The functional basis for variation in growth and reproduction has, however, been modelled in specific detail for a few particular agronomic and wild plant species (see review in Reynolds and Acock, 1986); it is entirely possible in concept to develop more general models predicting the somatic basis of plant survival or reproductive success across a range of species and environments, in essence mechanistic models delineating the contribution of somatic traits to fitness.

Both these approaches to recognizing the importance of traits for fitness are bedevilled by a troublesome complication: the contribution of traits to fitness can often depend on environment. This is why genotype  $\times$  environment interactions occur in the quantitative genetic analysis of plant performance and in turn are the basis for the analysis of plasticity in the expression of traits across a range of environments (Via and Lande, 1984; Schlichting, 1986). These shifts in the correlation between a trait and a major component of fitness can arise from plastic responses in either the trait itself, the fitness component, or both. Although we know that genotype

x environment interaction and plasticity are frequent in plants, the analysis of the functional patterns of the variations has not progressed much beyond the comparison of norm of reaction diagrams. Prediction of the nature and limits of plasticity in the major components of fitness has only just begun (Stearns and Koella, 1986), and analysis of the functional mechanisms and developmental constraints underlying these plastic responses pose a special challenge to evolutionary ecologists interested in how particular traits act on fitness (Stearns, 1982).

In this paper we use a correlational approach to screen a variety of phenological, physiological, and structural traits for their contribution to four measures of reproductive fitness in cocklebur plants grown under a range of nutrient and water availabilities. The traits studied are known to be functionally significant in a wide range of species (supporting references follow) and many were shown to have a direct effect on reproductive output in an earlier investigation of cocklebur grown in a single environment (Lechowicz, 1984). We analyze these data by three complementary methods to elucidate the effect of specific traits on reproductive output across the range of environments: 1) nonparametric, bivariate correlations among the somatic and reproductive traits, 2) calculation of the directional selection coefficients (Lande and Arnold 1983; Arnold and Wade, 1984) for fecundity of a selected subset of somatic traits, and 3) canonical correlations among two components of reproductive fitness and these somatic traits. Our primary purpose is to identify some of the key traits that have a direct effect on reproductive output in *Xanthium strumarium* regardless of the environment in which an individual cocklebur plant is grown. We leave the partitioning of phenotypic relationships into their genotypic and environmental components to the report of another experiment involving progeny from a crossing program (Farris and Lechowicz, in preparation).

## Materials and methods

### *Establishment of experimental gardens:*

In September 1981 fruits of *Xanthium strumarium* L. (Compositae) were collected from two randomly selected plants growing in each of 9 wild populations near Montreal, Quebec. The fruits were sown in three experimental gardens that varied in resource availability at the Emile Lods Agronomy Research Station, Ste-Anne-de-Bellevue, Quebec (45°26' N, 73°56' W). Fruits sown were randomly selected from the entire fruit production of each maternal parent subject to the constraint that the fruit was within 20% of the mean fruit weight for that parent. Five fruits were sown at 6 cm depth in each garden position on 27 May 1982, thinned to two plants per position on 5 July, and to one plant on 19 July. The final interplant distances were 2.0 meters and each garden was surrounded by two buffer rows of cocklebur. This planting design gave a total of 54 experimental plants: 2 maternal parents from each of 9 wild populations planted in three experimental gardens. The planting design included a split plot within each garden with one maternal parent from each of the 9 populations in each half-plot. Note that we chose to emphasize interpopulation

rather than intrapopulation differences in this initial survey of environmental response; individual parental effects are crossed with garden environments.

Experimental gardens were located within 100 meters of one another along a natural soil catena in an open farm field. Each garden received full insolation throughout the day but differed in the availability of water and nutrient resources. The resource poor garden was located on well-drained sandy loam (73 % sand, 20 % silt, 7 % clay) at the top of the catena while both the intermediate and resource rich gardens were located on loam (40 % sand, 43 % silt, 17 % clay) at the bottom of the catena. The resource poor garden was more subject to water stress due to both soil texture and position on the catena; plants in the intermediate and resource rich gardens had access to the local water table throughout much of the growing season. The 1982 growing season had a warmer and dryer spring and a cooler and wetter June and August than normal (Blais, 1984). Neither the resource poor nor the intermediate garden were fertilized, but their natural soils differed in soil nutrient concentrations (Table 1). The resource rich garden was fertilized before planting at 60 kg/ha N, 120 kg/ha P, and 120 kg/ha K in quick-release granules and 126 kg/ha N, 126 kg/ha P, and 126 kg/ha K in slow-release encapsulated form. Except for P concentration, which was notably high in the otherwise resource poor garden, the availability of major nutrient resources increased from the resource poor through the intermediate to the resource rich gardens (Table 1).

**Table 1.** Availability of soil nutrient resources in the upper 10 cm at the three experimental gardens. These are the means of composite samples taken on July 1, August 27, and October 22, 1982 and analyzed at the Macdonald College Soil Testing Laboratory of McGill University. All values are expressed as kg/ha.

GARDEN	NO <sub>3</sub>	NH <sub>4</sub>	P	K	Ca	Mg
Poor	15.86	1.72	135.7	97.3	1210	80.7
Intermediate	34.71	1.36	52.3	168.7	3080	788.3
Rich	52.59	24.00	99.3	198.0	3227	792.0

#### *Monitoring of phenological traits:*

Records were taken of the date of emergence (cotyledons free of soil), floral bud formation, anthesis, and senescence (onset of leaf yellowing in the fall) for each experimental plant. The first light frost occurred on October 11, 1982 but some plants had begun to senesce earlier. Rates of emergence (Kalisz 1986; Silvertown, 1984), timing of the switch from vegetative to reproductive growth (King and Roughgarden, 1982 a, 1982 b; Chiarello and Roughgarden, 1984), and timing of senescence (Hicks and Chabot, 1982) are all established as functionally significant for survival and reproductive success in a wide range of species.

*Monitoring of structural traits:*

Cotyledon area at emergence was estimated as twice the product of length and width for one of the cotyledons. Distance along the main stem from the apical bud to the ground was measured weekly throughout the growing season. The final asymptotic height was used as a measure of plant size. On 5 August the cumulative length of all branches was measured and used in conjunction with a concurrent height measurement to calculate an index of branching at flowering: cm of branch per cm plant height. Specific leaf weight was estimated from a series of 10 leaf discs collected during the assays of photosynthesis described below. Cotyledon area (Zimmerman and Weis, 1983), final plant size (Samson and Werk, 1986), canopy architecture (Lechowicz, 1984), and specific leaf weight (Jurik, 1986) have each been established as functionally significant for survival and reproductive success in a wide range of species.

Beginning on September 30 and continuing through October 22, individual plants were harvested as they senesced. The light frost on October 11 ( $-0.1^{\circ}\text{C}$ ) was followed by another on October 18 ( $-0.7^{\circ}\text{C}$ ), and thereafter remaining plants senesced rapidly. At harvest, root tissues were recovered only from a 40 cm circle centered on the plant stem to a depth of 30 cm; dry biomass of the roots recovered was taken as an index of overall biomass allocation to roots. Above-ground vegetative biomass was sorted into stem (including petioles) and leaf blade; essentially all above-ground tissues produced during the season were recovered at harvest. An alternative index of branching (g stem tissue per cm final plant height; Lechowicz, 1984) was calculated from these data. Allocation of biomass to different vegetative organs is well established as functionally significant for survival and reproduction in a wide range of species (Bazzaz et al., 1987; Lechowicz, 1987).

*Monitoring of physiological traits:*

Photosynthesis was assayed radiometrically on July 14, 15, 21, 23, 26, 30, August 3, 6, 16, and 18 following the protocol of Lechowicz (1984); additional methodological details are provided in Blais (1984). Transpiration rates and stomatal conductances for both the upper and lower leaf surfaces were measured at the same time as photosynthesis using a LiCor 1600 steady state porometer. The ratio of photosynthesis to total transpiration was taken as an estimate of the instantaneous water use efficiency (Schulze et al., 1987). It should be noted that all these parameters related to gas exchange are based on measurements made up to the time of anthesis, but not during the period of fruit maturation. The weekly data on height increase were fitted to a logistic curve to estimate two parameters: 1) the relative rate of increase in height at emergence and 2) the rate of decline in the relative rate of height increase over time (Kaufmann, 1981; Blais, 1984). Gas exchange parameters (Pearcy et al., 1987; Schulze et al., 1987) and rates of growth (Grime and Hunt, 1981) are both well established as functionally significant for survival and reproduction in a wide range of species.

*Monitoring of reproductive traits:*

Numbers of staminate inflorescences were counted 3 days after anthesis to estimate potential male reproductive success in this wind-pollinated, although usually selfing annual species (Weaver and Lechowicz, 1982). A comparable estimate of pistillate inflorescence numbers on each plant was made 7–10 days after anthesis. At the fall harvest all fruits were collected and air dried. A random 200 g sample of fruits from each plant was used to determine the ratio of mature (> 70 mg) to immature (< 70 mg) fruits. Mature cocklebur fruits contain two seeds (Weaver and Lechowicz, 1982). The ratio of mature to immature fruits together with the mean air dry mass of single fruits were used to estimate fecundity as the total number of mature fruits produced by each plant. The ratio of air dry to oven dry mass of the fruit subsample was used to convert the total air dry fruit biomass to its oven dry equivalent for comparison with oven dry vegetative biomass fractions. These four measures provide reasonable estimates of the quantity and quality of reproduction in cocklebur (Endler, 1986; Sutherland, 1986).

*Data analysis – univariate and bivariate analyses:*

The performance of plants in the three gardens was first compared using non-parametric methods in version 5.3 of SAS (SAS Institute, 1985). Wilcoxon rank sum tests (Proc NPAR1WAY) were used to test for the difference in median values of each measured phenological, structural, physiological, and reproductive trait across the three gardens. The pattern of significant relationships was unchanged if a Van der Waerden test was used. Spearman nonparametric correlations (Proc CORR) between each reproductive trait and the various somatic traits were calculated. Tabulation of the median rather than means and the use of these nonparametric analyses were preferred because of the relatively small sample sizes and disparate distributions of the monitored traits. Based on these results, certain somatic traits were selected and normalized as necessary (Proc UNIVARIATE) for subsequent parametric analyses.

*Data analysis – selection coefficients for fecundity:*

Our overall interest is in identifying the somatic traits most important in maximizing the quantity and quality of reproduction in cocklebur. The preceding bivariate correlation analysis cannot allow for the effects of collinearity that potentially confound interpretation of the importance to fitness of somatic traits that are themselves correlated (Lande and Arnold, 1983). As an alternative we use a multiple regression method (Lande and Arnold, 1983; Arnold and Wade, 1984) to estimate the directional components of phenotypic selection of the selected somatic traits in relation to fecundity. Sample sizes were inadequate to evaluate the effects of stabilizing or disruptive selection by inclusion of quadratic terms in the regression model (Lacey et

al., 1983; Endler, 1986). The independent variable in these regressions was an estimate of relative fitness (*sensu* Endler, 1986) calculated as the fecundity of each plant (measured as total number of fruits) relative to the mean fecundity in a given garden; the analysis was carried out separately for each of the gardens. The analysis is thus a regression of proportionate changes in fecundity on the set of somatic traits and the magnitude of effects on each trait in the different gardens can more easily be compared. The regressions were run in Proc REG of SAS to take advantage of the collinearity and influence diagnostics in that procedure (Belsley et al., 1980). Endler (1986, Chapter 6) provides a helpful discussion of the method and limits on its interpretation.

#### *Data analysis – canonical correlation:*

While the preceding analysis of selection coefficients allows for covariance between somatic traits, it does not address the simultaneous effects of somatic traits on multiple components of fitness. We therefore used canonical correlation (Proc CANCORR) to assess the relationships between two measures of reproductive success (number of fruits and mean fruit biomass) and selected somatic traits in each of the three gardens. This multivariate technique uniquely weights each variable to achieve the maximum possible correlation among the vector of reproductive traits and the vector of selected somatic traits (Cooley and Lohnes 1971; Gittins 1985). The magnitude of these weights, standardized to minimize the effects of different units of measurement, allows us to judge the relative importance of each somatic trait not simply to each individual component of reproduction but instead to the two primary quantitative and qualitative aspects of reproduction taken in concert. In this sense it is a logical extension of the preceding analysis of selection coefficients. Two aspects of the results are of interest in evaluating the importance of somatic traits for fitness: 1) what are the relative magnitudes of the standardized weighting coefficients for the different somatic traits in each garden, and 2) how do these standardized coefficients change from garden to garden. Basically, the greater is the absolute value of a coefficient for a trait, the greater is the impact of that trait (positive or negative as indicated by the sign of the coefficient) on both aspects of reproduction taken together.

## **Results**

### **Univariate and bivariate analyses**

#### *Reproductive traits:*

Both the male and female components of reproduction increase with increasing resource availability (Table 2).

**Table 2.** Median values of components of reproductive success for plants grown in experimental gardens differing in resource availability. Medians joined by lines do not differ significantly ( $p > 0.05$ ) by a non-parametric Wilcoxon rank sum test.

	Resource status of experimental garden		
	Poor	Intermediate	Rich
Number staminate inflorescences	455.0	786.5	750.0
Number pistillate inflorescences	1518.5	2364.5	2966.0
Number mature fruits	1601.0	2388.5	3133.5
Mean fruit biomass, mg	251	273	274

Inflorescence numbers are significantly greater in the resource rich garden compared to the resource poor garden. Numbers of mature fruits differ significantly in all three gardens, and increase steadily with increasing resource availability. Despite the significant differences in these quantitative aspects of reproduction, there are no significant differences in the quality of mature fruits as judged by their mean mass. Inflorescence and mature fruit numbers are strongly intercorrelated among themselves (Table 3). In the resource poor garden, the quantitative aspects of reproduction are all uncorrelated with fruit quality, but in the other more resource rich gardens the phenotypic correlation between reproductive quantity and quality is significantly negative (Table 3).

**Table 3.** Half matrix of Spearman rank order correlations among components of plant reproductive success in each of the three experimental gardens. Entries in bold type are significant at the 0.05 level or less ( $n = 18$  in all cases).

1. Number staminate inflorescences	–		Resource-poor
2. Number pistillate inflorescences	<b>0.957</b>	–	Garden
3. Number mature fruits	<b>0.985</b>	<b>0.977</b>	–
4. Mean fruit biomass	–0.155	–0.174	–0.127
1. Number staminate inflorescences	–		Intermediate
2. Number pistillate inflorescences	<b>0.895</b>	–	Garden
3. Number mature fruits	<b>0.907</b>	<b>0.971</b>	–
4. Mean fruit biomass	<b>–0.626</b>	<b>–0.716</b>	<b>–0.756</b>
1. Number staminate inflorescences	–		Resource-rich
2. Number pistillate inflorescences	<b>0.712</b>	–	Garden
3. Number mature fruits	<b>0.680</b>	<b>0.833</b>	–
4. Mean fruit biomass	–0.406	<b>–0.564</b>	<b>–0.773</b>

#### *Phenological, structural, and physiological traits:*

With the exception of minor changes in the timing of emergence, the phenological characteristics of *X. strumarium* do not vary significantly as a function of resource availability (Table 4). This is true whether phenologic events are gauged as calendar days or relative to the time since the plant emerged. Over a wide range of resource availabilities the typical life of a cocklebur plant was essentially the same in 1982 at the latitude of Montreal: about 10 days from planting to emergence, 53 days to formation of floral buds, and another 70 days to flower and mature fruits before the onset of senescence.

**Table 4.** Median values of somatic traits in experimental gardens with poor, intermediate, or rich levels of resource availability, and the Spearman rank order correlations of these somatic traits with reproductive traits in each experimental garden. Underlined groups of medians do not differ significantly at the 0.05 level in a Wilcoxon nonparametric rank sum test. Correlations in bold print are significant at the 0.05 level or less (n = 18 in all cases).

	Medians			Correlations with: # staminate inflorescences			Correlations with: # pistillate inflorescences			Correlations with: # mature fruits			Correlations with: mean fruit biomass		
	Poor	Inter	Rich	Poor	Inter	Rich	Poor	Inter	Rich	Poor	Inter	Rich	Poor	Inter	Rich
<b>Phenological traits: Julian days</b>															
Bud formation	211.0	209.0	209.0	-0.060	0.264	<b>0.521</b>	-0.080	0.326	<b>0.697</b>	-0.121	0.245	0.410	<b>0.622</b>	-0.367	-0.346
Anthesis	227.5	227.0	225.5	-0.044	0.373	0.449	-0.092	0.425	<b>0.677</b>	-0.137	0.336	0.305	-0.437	-0.388	-0.126
Senescence	271.0	269.5	268.0	0.213	<b>0.492</b>	<b>0.536</b>	0.199	<b>0.571</b>	<b>0.625</b>	0.208	<b>0.542</b>	0.355	-0.317	<b>-0.467</b>	-0.126
<b>Phenological traits: Age in days</b>															
Seeding to emergence	12.0	9.0	10.0	-0.542	-0.551	-0.644	-0.483	-0.627	-0.385	-0.500	-0.688	-0.443	-0.012	<b>0.651</b>	0.337
Emergence to bud formation	53.0	54.0	53.0	0.118	0.312	<b>0.720</b>	0.109	0.376	<b>0.723</b>	0.064	0.342	<b>0.509</b>	-0.696	-0.458	-0.367
Emergence to anthesis	69.5	71.5	69.0	0.030	0.432	<b>0.595</b>	-0.034	<b>0.480</b>	<b>0.692</b>	-0.068	0.442	0.370	-0.489	-0.568	-0.191
Emergence to senescence	125.0	123.5	122.0	0.213	<b>0.492</b>	<b>0.537</b>	0.199	<b>0.571</b>	<b>0.625</b>	0.208	<b>0.542</b>	0.355	-0.317	<b>-0.467</b>	-0.126
<b>Structural traits: size</b>															
Root biomass, g	23.7	29.5	32.5	<b>0.894</b>	<b>0.825</b>	<b>0.530</b>	<b>0.864</b>	<b>0.851</b>	0.364	<b>0.843</b>	<b>0.825</b>	0.242	0.044	-0.500	-0.083
Leaf biomass, g	96.2	151.0	179.8	<b>0.839</b>	<b>0.854</b>	<b>0.561</b>	<b>0.903</b>	<b>0.900</b>	<b>0.684</b>	<b>0.903</b>	<b>0.862</b>	<b>0.486</b>	0.026	-0.538	-0.055
Stem biomass, g	145.8	219.3	300.3	<b>0.872</b>	<b>0.845</b>	<b>0.575</b>	<b>0.942</b>	<b>0.900</b>	<b>0.631</b>	<b>0.936</b>	<b>0.864</b>	0.430	-0.003	-0.480	-0.038
Maximum height, cm	78.8	80.8	93.2	<b>0.626</b>	<b>0.705</b>	<b>0.262</b>	<b>0.645</b>	<b>0.649</b>	0.048	<b>0.612</b>	<b>0.662</b>	0.158	0.212	0.030	0.094
Cotyledon area, mm <sup>2</sup>	944	870	1024	0.114	0.409	0.343	0.174	0.368	0.086	0.106	0.336	0.144	0.148	0.037	0.295
<b>Structural traits: allocation</b>															
% vegetative biomass: roots	8.6	7.3	6.0	-0.563	-0.441	-0.046	-0.715	-0.480	-0.317	-0.703	-0.465	-0.303	-0.046	0.245	0.061
% vegetative biomass: leaf	36.7	36.6	34.2	0.447	-0.763	-0.124	-0.478	-0.692	0.195	-0.470	-0.688	0.373	-0.257	<b>0.480</b>	-0.287
% vegetative biomass: stems	53.9	55.2	59.7	<b>0.537</b>	<b>0.777</b>	0.087	<b>0.653</b>	<b>0.769</b>	0.018	<b>0.635</b>	<b>0.742</b>	-0.088	0.193	-0.453	0.232
% total biomass: reproduction	59.9	61.7	61.3	0.152	-0.269	-0.296	0.047	-0.458	-0.406	0.122	-0.223	-0.121	0.232	0.112	0.001
Branching at flowering, cm (branch)/cm (plant)	6.34	6.45	7.12	0.334	0.272	0.134	0.380	<b>0.470</b>	-0.114	0.393	0.439	-0.042	-0.248	-0.316	-0.100
Branching at harvest, g (stem)/cm (plant)	1.67	2.70	3.63	<b>0.784</b>	<b>0.783</b>	<b>0.469</b>	<b>0.868</b>	<b>0.845</b>	<b>0.635</b>	<b>0.895</b>	<b>0.816</b>	0.360	-0.013	-0.500	-0.103
Specific leaf weight, mg/cm <sup>2</sup>	5.401	5.820	5.488	0.240	-0.127	0.040	0.187	-0.063	-0.013	0.158	-0.156	-0.274	0.069	0.139	0.163
<b>Physiological traits: gas exchange</b>															
Maximum photosynthesis, mg CO <sub>2</sub> /dm <sup>2</sup> /h	40.8	41.8	41.5	0.351	0.309	0.087	0.390	0.185	-0.106	0.319	0.181	-0.129	0.407	0.001	0.221
Mean photosynthesis, mg CO <sub>2</sub> /dm <sup>2</sup> /h	33.6	33.5	32.6	0.289	0.259	-0.291	0.304	0.203	-0.412	0.300	0.265	-0.373	<b>0.785</b>	-0.391	0.250
Mean transpiration, g H <sub>2</sub> O/cm <sup>2</sup> /s	26.7	24.9	23.2	0.418	-0.115	-0.405	<b>0.517</b>	-0.090	-0.354	<b>0.474</b>	-0.053	-0.470	0.420	-0.088	0.277
Mean stomatal conductance, cm/s	2.21	2.08	1.96	0.423	0.144	-0.460	<b>0.488</b>	0.077	-0.432	<b>0.509</b>	0.148	-0.583	<b>0.484</b>	-0.197	0.431
Water use efficiency, mg CO <sub>2</sub> /g H <sub>2</sub> O	3.63	3.71	3.84	-0.450	0.331	<b>0.464</b>	-0.548	0.288	0.240	-0.498	0.306	0.457	0.084	-0.240	-0.309
<b>Physiological traits: growth</b>															
Relative growth rate (RGR) at emergence, cm/cm/day	0.082	0.083	0.081	0.402	0.069	-0.428	0.375	-0.042	-0.633	0.414	0.053	-0.395	<b>0.500</b>	0.030	0.249
Rate of decline in RGR, [RGR/cm]x10 <sup>3</sup>	1.064	1.025	0.890	-0.586	-0.598	-0.370	-0.614	-0.624	-0.286	-0.556	-0.564	-0.325	0.098	0.189	0.109

Cocklebur plants at maturity are bigger the more resources are available, but their proportionate investment in reproductive versus vegetative tissues does not vary significantly with resource availability (Table 4). In the most resource rich garden where plants are biggest, significantly more vegetative biomass is invested in stem and petiole tissues and less in leaf blade and root tissues. At the time of flowering the degree of branching of plants does not vary with resource availability, but by maturity this character increases significantly with increases in resource availability. Consistent with the uniformly high insolation in all gardens, the specific leaf weight does not vary with the availability of soil resources in the different gardens. Consistent with the fruit selection criterion at planting and the sib relationships of the garden plants, cotyledon area is also invariant with resource availability.

The photosynthetic capacity, mean seasonal photosynthetic rates, stomatal conductance, and initial relative growth rates of cocklebur do not vary significantly with resource availability. In the most resource rich garden, however, transpiration rates are significantly lower and water use efficiency higher than in the resource poor garden (Table 4). The decline in growth rate through the season is also significantly less in the resource rich garden.

*Phenotypic correlations between somatic and reproductive traits:*

Individual variation in the numbers of inflorescences and fruits is uncorrelated with specific leaf weight, maximal photosynthetic capacity, or average levels of photosynthetic activity prior to anthesis regardless of the availability of water and nutrient resources (Table 4). Similarly variation in cotyledon area among individual plants does not correlate with the quantitative components of reproductive success in any of the three gardens. Nor does individual variation in either cotyledon area or specific leaf weight correlate with mean fruit biomass, a qualitative measure of reproductive success in cocklebur (Zimmerman and Weis, 1983).

Even though the average phenological characteristics are invariant across the range of resource availabilities in the experimental gardens, individual variation in plant success within each garden is significantly associated with variation in phenological characteristics (Table 4). With the possible exception of the most resource rich environments, plants that emerge earlier produce more inflorescences and fruits. Earlier emergence is also associated with significantly greater mean fruit biomass in the intermediate garden environment. As resource availability increases, the quantitative components of individual reproductive success increase with the delay of both flowering and senescence. Conversely, the delay of flowering or senescence in less resource rich environments reduces fruit quality. In the most resource rich garden, apparent trends in the correlations among phenological and reproductive traits often weaken. As discussed subsequently, this appears related to the failure of the most productive individuals to mature their full fruit crop prior to induction of senescence by the first frosts.

The more biomass a cocklebur plant produces in any given resource environment, the greater will be its production of inflorescences and mature fruits (Table 4). This is

consistent with the advantage of earlier emergence in all resource environments, with the greater success of plants with slower rates of decline in height increase, and with the greater success of taller plants in all but the resource rich garden. There is some indication that in the resource rich garden plants with slower rates of increase in height but greater tendency to form lateral branches will be more successful if the growing season is long enough to allow all fruits to mature.

This possibility is consistent with the overall patterns of biomass allocation to different vegetative tissues at all levels of resource availability (Table 4). Except in the most resource rich environment, plants with a greater investment in stem rather than leaf or root tissues have greater numbers of inflorescences and fruits. Despite the lack of correlation with degree of branching at flowering, this trend is also reflected in the greater success of plants that show greater branching at maturity. It is likely that the incomplete extension of tertiary and quaternary branches at the time of flowering results in an underestimation of degree of branching on the most branched plants compared to the measurements at harvest. Again the weakening of these trends at high resource levels appears due to a failure of a few plants to fully mature all fruits before frost.

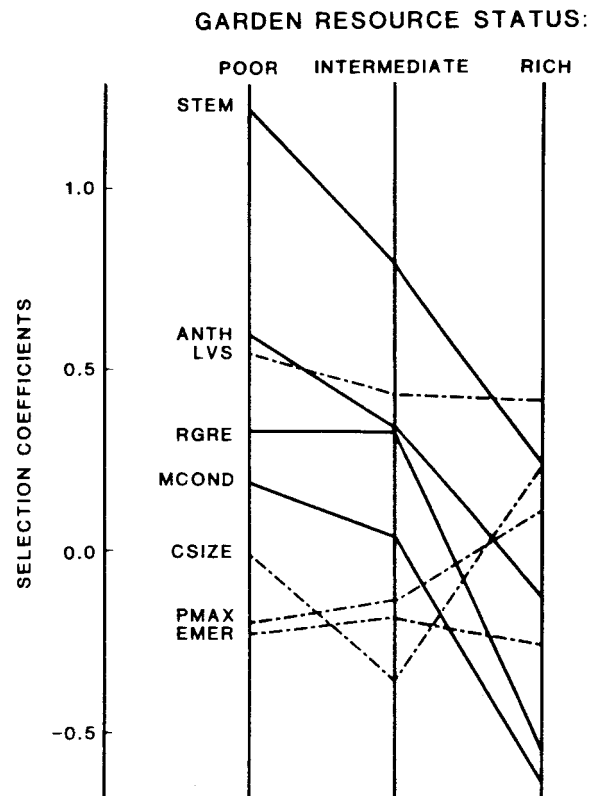
The correlations among gas exchange parameters and components of reproductive success (Table 4) suggest that selection on these physiological characters may vary with the availability of water and nutrient resources in the local environment. In resource poor environments cocklebur plants that maintain higher stomatal conductance, lose more water in transpiration, and actually have lower water use efficiency produce more mature fruits. In these resource poor environments plants that have higher photosynthesis and transpiration rates appear to produce fruits of higher mean biomass, but fruit quality is unaffected by water use efficiency. In the intermediate environment neither the quantity nor the quality of reproduction is significantly influenced by gas exchange parameters. In resource rich environments, the situation is exactly reversed from that in resource poor environments: low conductance, low transpiration, and high water use efficiency are associated with greater numbers of mature fruits. In resource rich environments fruit quality is unaffected by gas exchange characteristics.

### **Selection coefficients for fecundity**

The analysis of directional selection of somatic traits for fecundity (Fig. 1) clearly affirms the changing importance of individual traits as a function of resource availability, but also highlights the potentially misleading effects of covariance between somatic traits on the interpretation of the bivariate correlation analyses. For example, greater investments in stem and to some degree leaf biomass become progressively less important for reproductive success as the availability of water and nutrient resources increases. In the bivariate analyses, stem and leaf biomass partitioning appear oppositely correlated with fecundity (cf. Table 2) but the two somatic traits are themselves significantly correlated in all three gardens (unpublished). By considering all somatic traits simultaneously, the analysis of selection coefficients thus bet-

ter reflects the relative impact of a set of functionally interrelated traits on the quantitative aspect of reproductive success.

Other traits show some similar changes in relative importance in this analysis compared to the bivariate correlations. In the resource poor garden, rapid early relative



**Fig. 1.** The strength of directional fecundity selection of each of the selected somatic traits in each garden. The somatic traits include: STEM, the percentage of vegetative biomass in stem and petiole tissue at maturity; LVS, the percentage of vegetative biomass in leaf blade at maturity; ANTH, the number of days between emergence and anthesis; RGRE, the relative rate of height growth at emergence; MCOND, the stomatal conductance averaged across 10 sampling days prior to anthesis; CSIZE, the rate of decline in height increase as a function of size; PMAX, the maximal photosynthetic rate prior to anthesis expressed on an area basis; EMER, the number of days between planting and emergence.

The selection coefficients (selection gradients of Lande and Arnold 1983; Arnold and Wade, 1984) are the standardized regression coefficients from a multiple regression of the relative fecundity on the somatic traits. Relativized fecundity is the number of fruits produced by a plant divided by the mean number produced by plants in its garden (Endler, 1986); the analysis was done separately for each garden. In all but the rich garden, the regressions are significant with high  $r^2$  (0.83,  $p = 0.0096$ ; 0.86,  $p = 0.0039$ ; and 0.72,  $p = 0.07$  from poor to rich, respectively). There is some collinearity between somatic traits, but the pattern of collinearities is not consistent across the three gardens. Similarly, there are some particularly influential plants in the analyses, but these do not originate from consistent populations or maternal parents across the three gardens. The broken and solid lines emphasize traits with different trends in coefficient values across the three garden environments.

growth rate promotes fecundity, but the rate of decline in growth rate is less important than delay of the switch from vegetative growth to flowering in contributing to further increased fecundity. Conversely, in the resource rich garden individuals with relatively slow initial but sustained growth rates are more fecund with a slight further increase if flowering is not too long delayed. Only the tendency of early emerging plants to reproduce more is relatively invariant across the range of resource availabilities, as it also was in the bivariate analyses. Overall, despite the shifts in the effects of individual traits in the bivariate correlations versus selection of fecundity, the phenotypic relationships between fecundity and somatic traits clearly vary with the availability of water and nutrient resources.

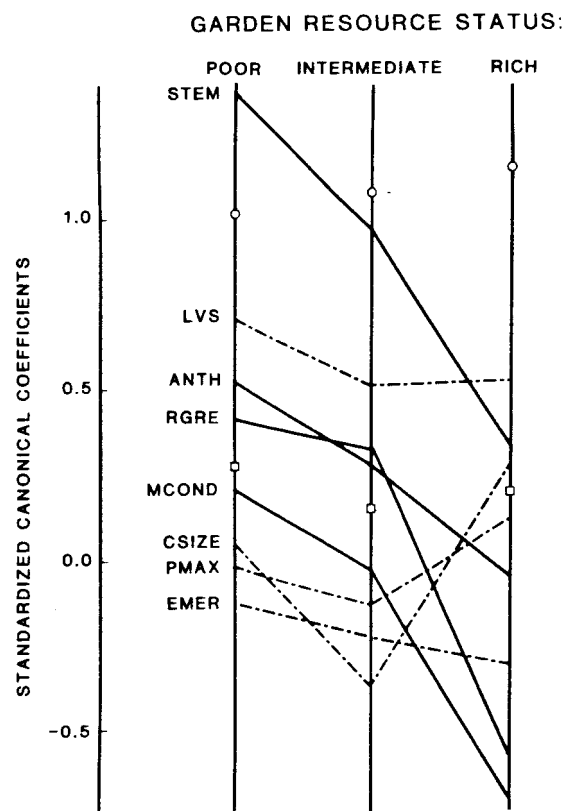
### **Canonical correlations between reproductive and somatic traits**

The results of the canonical correlation analysis (Fig. 2) extend and affirm the qualitative relationships between somatic traits and reproductive success in the three garden environments. While the relationship between the two components of fitness is generally negative (Table 3), their joint relationships with the somatic traits are essentially similar. Both components of fitness have positive canonical coefficients, but the larger coefficient for fruit numbers indicates its dominance in the canonical correlations with the somatic traits. Given the dominance of fruit numbers in the canonical relationships, it is perhaps not surprising that the canonical coefficients for the somatic traits follow a pattern very similar to that of the selection coefficients for fruit numbers (cf. Fig. 1). This similarity is not, however, a necessary result and its occurrence here suggests that selection of somatic traits is directly linked to the tradeoff between fruit numbers versus fruit size.

### **Discussion**

It is only the correlation between a trait and at least some fitness component that determines its adaptive significance, that is the effect of the trait on the process of phenotypic selection (Arnold, 1983; Endler, 1986). There are, however, very few studies that directly investigate the somatic basis of variations in major components of fitness among individuals in natural populations of wild plants, and these mostly concern a limited number of traits. Individual cocklebur in wild populations with shorter spines on their burs lost more seed to predation, but a variety of other morphological and chemical traits were unrelated to seed loss (Hare and Futuyma, 1978; Hare, 1980). Schmitt (1983) found that earlier and later flowering individuals of *Linanthus androsaceus* had a lower probability of setting seed than intermediate flowering individuals. Using the recently developed techniques for field estimations of selection (Lande and Arnold, 1983; Arnold and Wade, 1984), Kalisz (1986) showed that timing of germination in the winter annual *Collinsia verna* was under directional selection in one year and disruptive selection in the next. In *Cleome serrulata*, initial size and growth rate were under directional selection in a wild popu-

lation growing along a moisture gradient; at the drier end of the gradient, there was evidence that physiological traits associated with drought tolerance became more important for survival and reproduction than growth rates (Farris 1985, 1987). In *Impatiens pallida*, selection on a variety of characters associated with plant sized was in opposite directions in wet versus dry microsites in natural forest populations (Stewart and Schoen, 1987). These studies demonstrate that both viability and fecundity selection are operating on a variety of morphological, physiological, and phenological traits in natural populations of annual plants, but they reveal relatively



**Fig. 2.** The effects of resource availability on the canonical correlation between reproductive and somatic traits in cocklebur. The quantity of reproduction is measured as the number of mature fruits (open circles) and the quality as the mean mass of a single fruit (open squares). The acronyms for somatic traits are given in the caption of fig. 1. The contribution of each trait to the canonical correlation is graphed as the standardized coefficient for that trait in each garden. This removes the effects due simply to differences in units of measurement; the greater in absolute value is a coefficient, the greater the contribution (+ or - as signed) of that trait to the canonical correlation between the reproductive and somatic traits. The analysis was run separately for the plants in each garden. In all but the rich garden only the first canonical correlation was significant: 0.92 with  $p = 0.0135$  in the poor garden, 0.93 with  $p = 0.043$  in the intermediate garden, and 0.85 with  $p = 0.35$  in the rich garden. Despite the lack of statistical significance in the rich garden, the canonical coefficients still provide a good index of the strength of the relationships between the reproductive and somatic traits.

little about the functional interrelationships among traits that underlie this phenotypic selection.

Because of logistic difficulties and the high levels of uncontrolled environmental variance inherent in such field studies, it is difficult to screen large numbers of traits simultaneously and analyze their correlated effects in phenotypic selection. Comparisons among individuals of native species grown in experimental gardens provide more comprehensive and complementary data that can better address the functional basis for selection of characters observed in wild populations. These experimental designs are analogous to those in the extensive literature on breeding of cultivated species, but differ in their sole use of wild stock and frequently more extreme growing conditions. The designs can emphasize comparison of multiple traits in relation to fitness or the experimental manipulation of single traits to gauge effects on fitness. Werk and Ehleringer (1986) have used experimental manipulation of potted plants grown outdoors to demonstrate that the characteristic leaf orientation of *Lactuca serriola* contributes directly to plant reproductive success. Maddox and Antonovics (1983) analyzed the dependence of seed number and size on leaf area in two *Plantago* species grown under greenhouse conditions. In a garden comparison of the joint effects of somatic traits on flower and fruit production, only emergence time, leaf biomass, and stem biomass had significant bivariate correlations with components of reproduction in *Xanthium strumarium*; nonetheless complex functions involving stem, leaf and root biomass fractions, photosynthetic and transpiration rates, and plant height effectively predicted these components of reproduction (Lechowicz, 1984). The results reported in this paper further illustrate the complexity of interactions among traits that underlie fecundity selection and emphasize the environmental dependence of these interrelationships.

In the resource poor garden, the partitioning of more vegetative biomass to stem and leaf tissues, and higher stomatal conductances contributed to increased reproductive success. More rapid relative growth rate at emergence also contributed to increased reproductive success, but the subsequent rate of decline in growth rate had less effect than the delay of the switch from vegetative growth to flowering. Conversely, in the resource rich garden, individuals with relatively slow initial but more sustained growth rates have greater reproductive success; this is further increased if flowering is not too long delayed. Maintaining high stomatal conductance, however, reduces reproductive success. Partitioning more biomass to stem and leaf tissues still increases reproductive success, but less markedly than in the resource poor garden. Only the tendency of early emerging plants to reproduce more is relatively invariant across the range of resource availabilities. The complexity of the functional interactions among traits determining reproductive success across a range of environments complicates the identification of the importance of individual traits for fitness and the eventual recognition of any general patterns in the contribution of different types of traits to fitness.

Our experience with cocklebur suggests that the evaluation of the importance of many functionally interrelated traits in determining fitness is feasible, but two problems in experimental design and analysis must be directly confronted. First, the effect of a trait must be evaluated in a broad range of test environments, including

variations in plant density as well as resource levels, before the trait's importance for fitness can be fully appreciated. We may have found little contribution of photosynthetic capacity to reproductive fitness simply because all three gardens were unshaded and solar energy may not have ever been in sufficiently short supply for differences in photosynthetic capacity to express their effects on reproduction. Second, a problem of recognizing appropriate traits arises because we do not know *a priori* which of the infinite measurements we might make on an organism actually act, singly or in concert, to affect differential survival or reproductive success among individuals in a given environment. Only certain combinations or transformations of individual measurements may define a trait with robust and reliable interrelationships to major components of fitness. In this and a previous paper (Lechowicz, 1984), we used a variety of simple linear statistical approaches to screen the effects of traits on reproductive fitness, but these can easily be confounded by collinearities among traits (Belsley et al., 1980) that necessarily arise from their functional interrelationships. Another statistical alternative would be to employ structured equations that presume and allow for specific functional interrelationships (Li, 1975) among traits that directly or indirectly affect components of fitness. Such a structural approach has recently been successfully applied to the analysis of relationships among the components of fitness and leaf area at different life stages (Maddox and Antonovics, 1983).

In practical fact, it is the patterns of interspecific variation in somatic and reproductive function established in past studies in comparative ecology that offer the only available guide at this time to the design and interpretation of experiments intended to gauge those traits that most affect fitness in a given environment. Decisions on traits to screen for their effects on fitness invariably depend on information from earlier interspecific comparisons designed to test hypotheses in functional ecology. Similarly, while the functional significance of the widespread plastic adjustments in plant phenotypes (Schlichting, 1986; Schlichting and Levin, 1986) can be inferred from interspecific differences across habitats of different resource availability, determination of the contribution of plastic responses to fitness requires intraspecific comparisons to measure the correlations among somatic and reproductive traits. Our ultimate understanding of the evolution of traits is thus contingent on the application of both inter- and intraspecific comparisons across a range of environments differing in resource availability. Recognizing this interdependence, we should avoid facile inference of adaptive significance for traits studied only at the interspecific or interpopulation level. Only through analysis of patterns of individual variation in the relationships between somatic traits and the major components of fitness will we be able to predict the course of microevolution and better understand plant adaptation.

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## References

- Arnold, S. J. 1983. Morphology, performance, and fitness. *Am. Zool.* 23: 347–361.
- Arnold, S. J., and M. J. Wade. 1984. On the measurement of natural and sexual selection: theory. *Evolution* 38: 709–719.
- Bazzaz, F. A., N. R. Chiariello, P. D. Coley, and L. F. Pitelka. 1987. Allocating resources to reproduction and defense. *Bioscience* 37: 58–67.
- Bell, G., and V. Koufopanou. 1986. The cost of reproduction. *Oxford Surveys of Evolutionary Biology* 3: 83–131.
- Belsley, D. A., E. Kuh, and R. E. Welsch. 1980. *Regression diagnostics. Identifying influential data and sources of collinearity.* Wiley, New York.
- Blais, P. A. 1984. Phenological, morphological and physiological adaptations that control the reproductive output of the annual weed *Xanthium strumarium* L. Unpublished M. Sc. thesis, Department of Biology, McGill University, Montreal, Quebec.
- Bloom, A. J., F. S. Chapin III, and H. A. Mooney. 1985. Resource limitation in plants – an economic analogy. *A. Rev. Ecol. Syst.* 16: 363–392.
- Charnov, E. 1982. *The theory of sex allocation.* Princeton University Press, Princeton, New Jersey.
- Chiariello, N., and J. Roughgarden. 1984. Storage allocation in seasonal races of a grassland annual: optimal versus actual allocation. *Ecology* 65: 1290–1301.
- Cooley, W. W., and P. R. Lohnes. *Multivariate data analysis.* Wiley, New York.
- Endler, J. A. 1986. *Natural selection in the wild.* Princeton University Press, Princeton, New Jersey.
- Farris, M. A. 1985. Demographic variation and natural selection in an annual plant growing along soil moisture gradients. Unpublished Ph. D. dissertation. University of Colorado, Boulder.
- Farris, M. A. 1987. Natural selection on the plant-water relations of *Cleome serrulata* growing along natural moisture gradients. *Oecologia* 72: 434–439.
- Gittins, R. 1985. *Canonical Analysis. A review with applications in ecology.* Springer-Verlag, Berlin.
- Givnish, T. J. 1986 (ed.). *On the economy of plant form and function.* Cambridge University Press, Cambridge.
- Goldman, D. A., and M. F. Willson. 1986. Sex allocation in functionally hermaphroditic plants. A review and critique. *Bot. Rev.* 52: 157–194.
- Grime, J. P., and R. Hunt. 1975. Relative growth rate: its range and adaptive significance in a local flora. *J. Ecol.* 63: 393–422.
- Hare, J. D. 1980. Variation in fruit size and susceptibility to seed predation among and within populations of the cocklebur, *Xanthium strumarium* L. *Oecologia* 46: 217–222.
- Hare, J. D., and D. J. Futuyma. 1978. Different effects of variation in *Xanthium strumarium* L. (Compositae) on two insect seed predators. *Oecologia* 37: 109–120.
- Hicks, D. J., and B. F. Chabot. 1982. The ecology of leaf life spans. *A. Rev. Ecol. Syst.* 13: 229–259.
- Jurik, T. W. 1986. Temporal and spatial patterns of specific leaf weight in successional northern hardwood tree species. *Am. J. Bot.* 73: 1083–1092.
- Kalish, S. 1986. Variable selection on the timing of germination in *Collinsia verna* (Scrophulariaceae). *Evolution* 40: 479–491.
- Kaufmann, K. W. 1981. Fitting and using growth curves. *Oecologia* 49: 293–299.
- King, D., and J. Roughgarden. 1982 a. Multiple switches between vegetative and reproductive growth in annual plants. *Theoretical Population Biology* 21: 194–204.
- King, D., and J. Roughgarden. 1982 b. Graded allocation between vegetative and reproductive growth for annual plants in growing seasons of random length. *Theor. Pop. Biol.* 22: 1–16.
- Lacey, E. P., L. Real, J. Antonovics, and D. G. Heckel. 1983. Variance models in the study of life histories. *Am. Nat.* 122: 114–131.
- Lande, R. 1982. A quantitative genetic theory of life history evolution. *Ecology* 63: 607–615.
- Lande, R. and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37: 1210–1226.
- Lechowicz, M. J. 1984. The effects of individual variation in physiological and morphological traits on the reproductive capacity of the common cocklebur, *Xanthium strumarium* L. *Evolution* 38: 833–844.
- Lechowicz, M. J. 1987. Resource allocation by plants under air pollution stress: implications for plant-pest-pathogen interactions. *Bot. Rev.* 53: 280–299.

- Li, C. C. 1975. Path Analysis. Boxwood, Pacific Grove, California.
- Maddox, G. D. and J. Antonovics. 1983. Experimental ecological genetics in *Plantago*: a structural equation approach to fitness components in *P. aristata* and *P. patagonica*. *Ecology* 64: 1092–1099.
- Pearcy, R. W., O. Bjorkman, M. C. Caldwell, J. E. Keeley, R. K. Monson, and B. R. Strain. 1987. Carbon gain by plants in natural environments. *Bioscience* 37: 21–29.
- Reynolds, J. F. and B. Acock. 1985. Predicting the response of plants to increasing carbon dioxide: a critique of plant growth models. *Ecol. Model.* 29: 107–129.
- Samson, D. A., and K. S. Werk. 1986. Size-dependent effects in the analysis of reproductive effort in plants. *Am. Nat.* 127: 667–680.
- SAS Institute. 1985. SAS User's Guide: Statistics. SAS Institute, Cary, North Carolina.
- Schlichting, C. D. 1986. The evolution of phenotypic plasticity in plants. *A. Rev. Ecol. Syst.* 17: 667–693.
- Schlichting, C. D. and D. A. Levin. 1986. Phenotypic plasticity: an evolving plant character. *Biol. J. Lin. Soc.* 29: 37–47.
- Schmitt, J. 1983. Individual flowering phenology, plant size, and reproductive success in *Linanthus androsaceus*, a California annual. *Oecologia* 59: 135–140.
- Schulze, E.-D., R. H. Robichaux, J. Grace, P. W. Rundel, and J. R. Ehleringer. 1987. Plant water balance. *Bioscience* 37: 30–37.
- Silvertown, J. W. 1984. Phenotypic variety in seed germination behavior: The ontogeny and evolution of somatic polymorphisms in seeds. *Am. Nat.* 124: 1–16.
- Stearns, S. C. 1982. The role of development in the evolution of life histories. pp 237–258 in Bonner, J. T. (ed.) *Evolution and Development*. Springer Verlag, Berlin.
- Stearns, S. C. 1986. Natural selection and fitness, adaptation and constraint, pages 23–44 in D. M. Rays and D. Jablonski (eds.) *Patterns and Processes in the History of Life*, Springer Verlag, Berlin.
- Stearns, S. C. and J. C. Koella. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution* 40: 893–913.
- Stewart, S. C. and D. J. Schoen. 1987. Pattern of phenotypic viability and fecundity selection in a natural population of *Impatiens pallida*. *Evolution* 41: 1290–1301.
- Sutherland, S. 1986. Floral sex ratios, fruit set, and resource allocation in plants. *Ecology* 67: 991–1001.
- Van Noordwijk, A. J., and G. DeJong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. *Am. Nat.* 128: 137–142.
- Via, S., and R. Lande. 1985. *Genotype-environment interaction and the evolution of phenotypic plasticity*. *Evolution* 39: 505–522.
- Weaver, S. E., and M. J. Lechowicz. 1982. The biology of Canadian weeds – *Xanthium strumarium* L. *Can. J. Pl. Sci.* 63: 211–225.
- Werk, K. S., and J. Ehleringer. 1986. Effect of nonrandom leaf orientation on reproduction in *Lactuca serriola* L. *Evolution* 40: 1334–1337.
- Zimmerman, J. K., and I. M. Weis. 1983. Fruit size variation and its effects on germination and seedling growth in *Xanthium strumarium*. *Can. J. Bot.* 61: 2309–2315.

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