

INHERITANCE AND NATURAL SELECTION ON FUNCTIONAL TRAITS

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We surveyed the literature published since 1985 for evidence of natural selection and heritability in vegetative functional traits and performance. Our goals were to (1) review patterns of selection on specific functional traits and (2) assess general evolutionary questions about selection and heritability for broad classes of traits. While generalizations about the functional significance of specific traits are premature, several functional hypotheses are supported. For example, herbivores can exert strong selection on secondary chemistry and mechanical defenses, but costs of resistance and negative correlations between defense traits may constrain their evolution. Competitive interactions select for early germination and favor stem elongation and shifts in flowering time where such responses actually minimize competitive effects. In the very few studies of physiology, selection on gas exchange and leaf size is clearly environment dependent. More generally, in reciprocal transplant experiments, populations often are locally adapted, and selection favors the native phenotype. These results suggest that selection is important in functional trait evolution and population differentiation. At the same time, selection often varies in space and time and across life-history episodes. This variation could slow the rate of evolutionary change, maintain genetic variation within populations, and select for plasticity. Analyses of general questions revealed that indirect selection through correlated characters accounts for a substantial portion of total selection on traits and often appears to reinforce the pattern of direct selection. This could be due to environmental effects on multiple phenotypic traits and fitness. Alternatively, indirect selection could contribute to the rapid evolution of suites of traits. We found only weak evidence that traits under strong selection have low heritability, a pattern that has been reported for animals and predicted by some theory. Thus, the rate of evolutionary change may well differ among traits. The strength of selection also depended on the fitness measure, being stronger selection through cumulative fitness than fertility or vegetative performance. Attributes of species' biology and experimental design affected selection and heritability estimates. Heritability was lower in inbreeding species relative to outbreeders, as expected. Heritabilities in controlled environments substantially overestimate estimates from the wild and should not be used as reliable predictors of the rate of adaptive evolutionary change in natural populations. Likewise, broad-sense heritability overestimates narrow-sense heritability and is thus unreliable for predicting evolutionary change in outbreeding species. Future studies of functional trait evolution should focus on physiology and a broader array of phenological and developmental traits. Long-lived species are severely underrepresented in microevolutionary studies, no doubt for practical reasons. Finally, an emphasis should be placed on exploring the nature and effect of trait interactions on fitness, since these are likely to be very important in shaping the course of evolution.

Keywords: adaptation, direct selection, evolution, fitness, genetic variation, heritability, indirect selection, performance, selection coefficients.

Introduction

A major focus of plant functional biology is the study of evolutionary adaptation and its basis in traits such as photosynthetic physiology, morphology, and development. A long-standing approach to the study of adaptation is to compare traits among taxa that differ in or share a common ecology (Ackerly et al. 2000). The comparative approach to the study of adaptation has a long and distinguished history (Darwin 1867; Harvey and Pagel 1991) and is motivated by observa-

tions of divergence in form and function among taxa from different environments or life forms and of convergence among taxa from similar environments or life forms (Grime and Hunt 1975; Mooney 1977; Ehleringer et al. 1981; Grime et al. 1988; Ehleringer and Monson 1993; Garnier and Laurent 1994; Beerling and Kelly 1996; Monson 1996; Reich et al. 1997, 1999; Ackerly and Donoghue 1998; Ackerly and Reich 1999; Cunningham et al. 1999).

In the last several decades, there has also been a push for studies of adaptive evolution in functional traits within populations, i.e., for microevolutionary studies of functional adaptation (McGraw and Wulff 1983; Ackerly et al. 2000; Arntz and Delph 2001). Microevolutionary studies are essential because adaptive divergence and convergence ultimately depend

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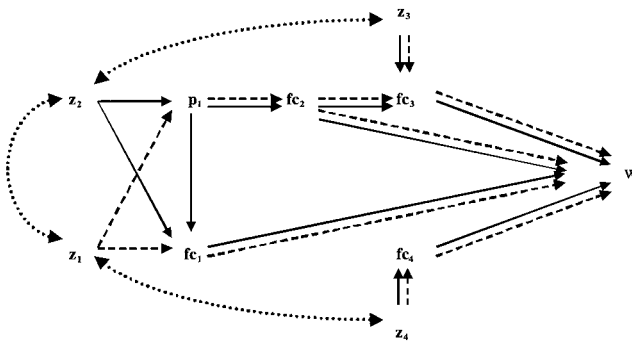


Fig. 1 Pathways of influence of functional traits (z_i) on relative fitness, w , via performance traits (p_i) and fitness components (f_{c_i}). Double-headed arrows indicate correlations between phenotypic traits, while single-headed arrows represent causal effects. For example, suppose that z_1 = water use efficiency (WUE), z_2 = leaf size, z_3 = ovary size, z_4 = nectar production, p_1 = vegetative growth rate, f_{c_1} = survivorship, f_{c_2} = vegetative biomass, f_{c_3} = fertility, f_{c_4} = mating success, and w = relative fitness. Leaf size and WUE affect survival and growth, ovary size affects fertility, and nectar production affects mating success through pollinator attraction. Leaf size and WUE may be correlated (dotted double-headed arrow) because of scaling between photosynthetic rates and transpiration rates per unit leaf area. Leaf size may be correlated with ovary size because of common developmental pathways. In addition, WUE, to the extent that it is also a function of the plant's ability to take up water, may be correlated with nectar production that depends on plant water status. Growth rate affects survivorship and vegetative biomass, and each fitness component may influence final relative fitness (w) directly or indirectly via other fitness components. Thus, leaf size and WUE may evolve because of direct effects on fitness (solid lines) and indirect effects via correlated traits (dotted and dashed lines).

on the existence of population-level genetic variation in and fitness consequences to these traits. In this article, we review evidence of the potential for microevolution in plant functional traits.

The process of evolution by natural selection can be divided into two phases: (1) changes in the distribution of a phenotypic trait within a generation from differences in survivorship, growth, fertility, or mating success among parents with different phenotypes and (2) the evolutionary response to selection between generations, consisting of genetically based changes in trait distribution in offspring that result from fitness differences among parental phenotypes. An understanding of adaptive trait evolution therefore requires an assessment of the form and magnitude of selection on traits and of the heritable basis of phenotypic variation in traits. Using a survey of published literature, we ask whether plant functional traits are under selection, examine the form of selection on these traits, and survey the evidence for heritable variation in functional traits.

Definition of Functional Traits

In the broadest sense, a functional trait can be defined as any phenotypic character that influences organismal fitness through biochemical, physiological, morphological, developmental, or behavioral mechanisms. Most often, a functional trait affects fitness through performance measures, such as

growth rate, competitive ability, herbivore resistance or tolerance, attractiveness to pollinators, and so on (fig. 1; Arnold 1983). The performance measures, in turn, affect fitness components, such as age-specific rates of survival, growth, fertility, or mating success, and, eventually, lifetime fitness (fig. 1). In addition, many functional traits not only have direct effects on fitness (solid arrows) but also influence fitness indirectly because they are correlated to other functional traits (dotted double-headed arrows) that are also under selection (dashed arrows). Thus, the influence of a functional trait on final fitness can be complex.

In practice, the distinctions between functional and performance traits and between performance and fitness components are difficult and subjective because the designations will often differ between researchers investigating different levels of function. For example, leaf size is often considered a functional trait by ecologists, whereas a developmental biologist might view it as a performance measure because it is the outcome of leaf meristem size and rates of cell division and expansion. Leaf photosynthetic rate is also considered a functional trait by ecologists and many ecophysiologicals, but as a measure of net carbon gain it can also be viewed as a performance trait that is determined by biochemical and transpiration properties of leaves (Geber and Dawson 1997).

In our article and in others in this issue, we focus on traits related to vegetative function that affect survival, vegetative growth and size, and fertility. We do not address functional traits affecting mating success, i.e., sexually selected traits.

Review Goals

We had two aims in surveying the literature. The first was to assess the adaptive significance and the environmental dependence of fitness-trait relationships for specific functional traits. For example, does secondary chemistry or mechanical defense confer herbivore resistance to plants? Does selection under stressful conditions favor avoidance through rapid development or tolerance through slow growth? Is water use efficiency (WUE) uniformly favored in arid environments? Or does the adaptive value of high WUE differ for short- versus long-lived plants (Geber and Dawson 1990, 1997; Arntz and Delph 2001)? While generalizations about the functional significance of specific traits are premature because few studies focused on the same trait across populations, taxa, and environments, we were able, nevertheless, to assess support for hypotheses about function.

Our second goal was to seek generality on patterns of selection and heritable variation for broad categories of functional traits (e.g., physiology, morphology) and fitness measures (e.g., vegetative fitness, fertility). We addressed six questions of general significance to studies of adaptive evolution, most of which have not been examined in any systematic fashion in plants (but see Kingsolver et al. 2001 for questions 2 and 5). The analytical portion of our article is aimed at answering these general questions:

1. Is selection on a functional trait largely due to its direct influence on fitness, or is it the result of indirect influences via other correlated characters (fig. 1)? The answer to this question is fundamental to an understanding of the actual mode of action of functional traits. In addition, the rate of selection

may be retarded or accelerated depending on whether indirect selection opposes or reinforces direct selection.

2. Does selection differ for different types of traits? Whole plant-level traits, such as measures of vegetative performance, are expected to have more direct connections to fitness and should therefore be under stronger directional selection than organ-level traits (e.g., physiology, morphology) (Houle 1992; Merilä and Sheldon 1999; Kingsolver et al. 2001). By contrast, organ-level traits or development may experience optimizing selection (Houle 1998).

3. Does heritable variation differ for different types of traits? Heritability, a measure of the portion of the phenotypic variance that is attributable to genetic variation (Falconer 1981), is inversely related to the magnitude of environmental effects on trait expression and so is expected to be low for highly plastic traits (e.g., leaf-level physiology) or for “high-level” traits that are the cumulative expression of many intervening traits (e.g., phenology, vegetative performance) (Price and Schluter 1991; Stratton 1992b; Merilä and Sheldon 1999, 2000; Stirling et al. 2002; but see Bennington and McGraw 1995). It has also been argued that traits that are under stronger directional selection (e.g., fitness-related traits) will have reduced genetic variance compared with traits with more distant connections to fitness (Fisher 1930; Falconer 1981; Mousseau and Roff 1987; Roff and Mousseau 1987). An alternative view is that high-level traits are expected to have large genetic variance because of mutational inputs from the many loci that affect their expression (Charlesworth 1987; Houle 1991, 1992, 1998; Houle et al. 1996).

4. Are the traits that are under strongest selection also the ones with the highest heritabilities? If true, evolutionary change in these traits could proceed rapidly. However, if strong directional selection reduces genetic variance so that traits tightly associated with fitness are less genetically variable, then the strength of selection will be inversely related to heritability and the rate of adaptive evolutionary change may be similar across traits in the short term.

5. Does that strength of selection differ via different fitness components? If true, then selection during some life-history episodes may dominate the course of evolution (Kingsolver et al. 2001).

6. Finally, we examined whether estimates of selection coefficients and heritable variation are influenced by experimental protocol and whether attributes of the species' biology influenced the magnitude of genetic variation. All previous reviews of selection have been limited to studies of natural populations in their native environment. While these studies are the only ones that can describe actual patterns of selection in the wild, by their very nature, they may not identify the causes of selection. A better understanding of cause may come from studies that manipulate the environmental factors that are thought to engender selection on traits (Wade and Kalisz 1990). Likewise, studies that manipulate trait variation, especially those that manipulate single traits independently of variation in correlated characters or disrupt character correlations among traits, may be better suited for identifying direct selection of individual traits on fitness (Wade and Kalisz 1990; Jordan 1991; Andersson and Shaw 1994; Nagy 1997; Arntz et al. 2000a, 2000b). Last, the full form of the relationship between trait and fitness may be more accurately described in

studies that extend the range of phenotypic variation beyond the natural range (Schluter 1988; Wade and Kalisz 1990; Jordan 1991; Bennington and McGraw 1995, 1996; Dudley 1996a; Dudley and Schmitt 1996; Nagy 1997; Roy et al. 1999; Donohue et al. 2000; Dorn et al. 2000; Juenger and Bergelson 2000; Stanton et al. 2000; Arntz and Delph 2001). In sum, experimental studies may be better at detecting selection and may yield larger selection coefficients than observational studies.

Estimates of heritable variation are also predicted to depend on experimental protocol. Thus, broad-sense heritability estimates, which include nonadditive sources of genetic variation, are likely to be larger than narrow-sense estimates. This is an obvious prediction (Falconer 1981), but evidence in support of it is not terribly strong (Mousseau and Roff 1987; Roff and Mousseau 1987; Stirling et al. 2002). Broad-sense heritability is appropriate to predictions of rates of evolution for inbreeding species, whereas narrow-sense heritability is the relevant measure for outbreeders. Heritabilities measured in more controlled environments, where environmental variance is reduced, are also predicted to be larger than estimates from the wild (Falconer 1981; but see Weigensberg and Roff 1996). As others have pointed out (Mitchell-Olds and Rutledge 1986; Weigensberg and Roff 1996), inflated estimates of heritability from controlled environments will then yield poor predictions on the possibility for and rates of trait evolution.

With respect to biology, we asked whether inbreeders are less genetically variable than outbreeders. While such a difference is expected (Charlesworth and Charlesworth 1995) and has been substantiated in studies of molecular variation (Hamrick and Godt 1996; Liu et al. 1999), there is surprisingly little direct evidence of low levels of quantitative genetic variation in populations of inbreeders, and the relationship between molecular and quantitative variation may be weak (McKay and Latta 2002; see Merilä and Crnokrak 2001). Annual species may also have lower levels of heritable variation than perennials because their population sizes are often much more variable. Variable population size leads to lower genetic effective size and a reduction in heritable variation.

Our article is not the first to review evidence of selection and heritable variation or to address the general hypotheses listed above. Endler (1986), in his book *Natural Selection in the Wild*, reviewed the literature published through 1983 on selection studies in natural populations. Kingsolver et al. (2001) updated Endler's work in a survey of field studies published since 1984 on vertebrates, invertebrates, and plants and examined variation in selection among trait types and via different fitness measures. Endler (1986) and Kingsolver et al.'s (2001) surveys were both limited to nonexperimental studies in the wild. Arntz and Delph (2001) recently reviewed evidence of selection and heritable variation in photosynthetic physiology. A number of surveys of heritable variation have been published (Mousseau and Roff 1987; Roff and Mousseau 1987; Houle 1992; Weigensberg and Roff 1996; Stirling et al. 2002), but they deal exclusively with animals. Last, the relationship between heritable variation and selection among traits (question 4), a topic of long-standing interest to evolutionary biologists, has been examined in a few animal taxa (see Houle 1998; Merilä and Sheldon 1999, 2000). Our article provides the most comprehensive review of selection studies in plants

(44 studies as compared with 18 in Kingsolver et al.'s [2001] review) and the only extensive review of heritable variation in plants.

For an entry into the literature on the theory and measurement of natural selection, readers should consult Lande and Arnold (1983), Arnold and Wade (1984a, 1984b), Endler (1986), Mitchell-Olds and Shaw (1987), Schluter (1988), Phillips and Arnold (1989), Wade and Kalisz (1989, 1990), Rausher (1992a), Schluter and Nychka (1994), Brodie et al. (1995), and Stinchcombe et al. (2002). The theory and measurement of quantitative genetic variation are covered in Falconer and Mackay (1996) and Lynch and Walsh (1998).

Methods

Literature Survey

For selection studies, we surveyed the tables of contents of 10 journals from 1985 to May 2002 (except where noted): *American Journal of Botany*, *The American Naturalist*, *Biological Journal of the Linnean Society*, *Ecology*, *Evolution*, *International Journal of Plant Sciences* (1992 to May 2002), *The Journal of Ecology*, *Journal of Evolutionary Biology* (1988 to May 2002), and *Oecologia*. For studies of heritability, we surveyed six journals, again from 1985 to May 2002 (except where noted): *American Journal of Botany*, *The American Naturalist*, *Ecology*, *Evolution*, *Heredity* (1990 to March 2002), and *Journal of Evolutionary Biology* (1988 to March 2002).

If the title indicated that the study might include estimates of selection coefficients or heritabilities in vascular plants, we read the abstract and carefully scanned the article for these estimates. We supplemented the table of contents searches with keyword searches in JSTOR (<http://www.jstor.org>) by scanning all available articles (back to 1985) for which the terms "selection differentials," "selection gradients," or "heritability" appeared in the full text.

Our surveys yielded 45 articles on selection from 11 journals and 74 articles on heritability from 13 journals (table 1). The largest number of articles came from the journal *Evolution* (43% of selection studies and 35% of heritability studies). A total of 67 species from 27 families were represented in our survey (28 species in selection studies and 51 species in heritability studies). Only 12 species appeared in both types of studies (table 1). The two data sets can be obtained from M. A. Geber.

Table 1

Number of Studies and Taxonomic Diversity in Selection and Heritability Data Sets (1985–2002)

Number in survey	Natural selection	Heritability	Both studies
Studies	45	74	...
Species	28	51	12
Genera	25	44	10
Families	18	21	11

Measures of the Strength and Form of Selection and of Heritable Variation

We used standardized selection differentials and gradients to characterize the form of selection on traits. Standardized selection coefficients allow comparisons of the strength of selection on traits that are measured on very different scales. The selection differential measures net or total selection, whereas the gradient measures direct selection on a trait, independent of indirect selection via correlated traits. Linear selection coefficients measure directional selection and indicate whether selection favors larger or smaller trait values. Quadratic coefficients measure curvature in the trait-fitness relationship. Negative quadratic coefficients indicate a decelerating relationship between fitness and trait value that corresponds to stabilizing selection if there is fitness maximum at an intermediate trait value within the measured range of phenotypes (Mitchell-Olds and Shaw 1987). Positive coefficients indicate an accelerating relationship between fitness and trait that corresponds to disruptive selection for extreme trait values if there is a fitness minimum at an intermediate trait value within the measured range of phenotypes. Not all studies tested for fitness maxima or minima within the range of phenotypes when significant quadratic selection was detected. Correlational selection gradients, reflecting selection for particular combinations of traits, were not analyzed because of limited sample size.

We used heritability (h^2)—the ratio of additive genetic variance (V_A) (or total genetic variance [V_G]) to phenotypic variance (V_P)—as a measure of a trait's ability to evolve by natural selection. Houle (1992, 1998) has argued that the additive genetic variance (V_A)—or, more precisely, the coefficient of additive genetic variance, $CV_A^2 = 100[V_A/\text{mean}(z)]^2$ —is a better measure of a trait's evolvability than is heritability because it provides a scale-independent estimate of actual genetic variance, independent of environmental effects on traits. It may be better suited to evaluating a trait's long-term potential for change. We were unable to use CV_A as a measure of evolvability because V_A and trait means are rarely reported. Heritability is still appropriate for predictions of evolutionary response to selection in the short term (Falconer 1981).

Exclusions from the Data Set

We did not include studies from journals of forestry or of cultivated crops because the source of plant phenotypes and genotypes was often unclear. In the end, we excluded studies of woody plants because they were few in number (three each for studies of selection and heritability). We omitted heritability estimates obtained from pooling genotypes from distinct populations. We also eliminated studies that focused exclusively on reproductive characters related to mating success and breeding system (e.g., floral morphology, nectar production, outcrossing rate) and did not include these characters from studies that also considered vegetative traits. We excluded selection studies focused on discrete characters (e.g., flower color, solar tracking vs. nontracking leaves or flowers) and omitted these traits from studies that also measured selection on continuously varying traits. Last, we omitted selection and heritability studies on trait plasticity (Donohue 2003). We did not include genetic correlations among traits because they are rarely reported.

Data Compilation

In addition to the selection coefficients and heritabilities, we extracted the following information from each species in each study: (1) the plant family, (2) the life history (annual or herbaceous perennial), (3) the breeding system of the species (selfing, outcrossing, or mixed mating system), (4) the growth environment (greenhouse/growth chamber, modified outdoor environment such as a common garden, or natural setting), and (5) the traits for which selection coefficients and/or heritability estimates were obtained.

For selection studies, we also recorded (6) the measure of fitness used in the selection analysis and (7) whether an expanded range of phenotypes was included. The natural range of phenotypes in a single population may be expanded when plants from multiple populations, or progeny from crosses between populations, are grown in the same environment and pooled to estimate selection coefficients.

For heritability studies, we recorded (9) the experimental design used to obtain the estimates (full-sib, half-sib, diallel, parent-offspring regression, clonal or selfing inbred lines, selection experiment, or molecular-based method) and classified the designs into those that yielded broad- versus narrow-sense heritabilities. Since heritability varies between 0 and 1, we substituted 0 for negative estimates and 1 for estimates greater than 1. If intraclass correlations (i.e., ratios of between-family variance to the sum of within- and between-family variances) were reported, we calculated heritability by multiplying these correlations by 4 for half-sib designs, 2 for full-sibs, and 1 for inbred family lines (Falconer and Mackay 1996).

We classified traits into four categories: (1) physiology/chemistry, (2) morphology of vegetative organs and of plant form, (3) developmental phenology, and (4) measures of vegetative performance. The latter group of traits does not really qualify as functional traits but was commonly included in studies of selection and heritability. Exemplars and sample sizes of specific traits included in each broad category are listed in table 2.

We classified fitness measures into three categories: (1) vegetative fitness, (2) fertility, and (3) cumulative fitness (table 3). Vegetative fitness measures aspects of vegetative success, such as survivorship, vegetative biomass, and herbivore resistance and tolerance when the latter are measured, respectively, as the reduction in herbivore attack and the reduction in fitness in the presence versus the absence of herbivores (Rausher 1992b; Mauricio 2000). Thus, measures of vegetative fitness overlap with traits categorized as measures of vegetative performance (cf. tables 2, 3). Within a given study, the same trait was obviously not used as both a performance and a fitness measure.

Fertility measures reproductive output of plants that have survived to flowering (or were reproductive when measured) and does not include variation in vegetative survival or performance before reproduction. Cumulative fitness is a measure of reproductive output that does account for vegetative performance, fertility, and mating success and can only be obtained on plants that are followed from seed (or seedling) to the end of life. In all studies, cumulative fitness was measured as cumulative reproductive success through female function (seed number, fruit number, or reproductive biomass) and did

not include reproductive success through male function. Cumulative female fitness is appropriate in selfing and apomictic species but is incomplete, and possibly biased, in outcrossing taxa if male and female fitnesses differ within or among individuals (Campbell 1998).

Statistical Comparison of Net and Direct Selection

For studies that measured both selection differentials and gradients (either linear or quadratic) on the same traits, we used reduced major axis regression (RMA) to examine the relationship between differentials and gradients. RMA regression is appropriate when both dependent and independent variables are measured with error, as is the case with selection differentials and gradients (Sokal and Rohlf 1981; McArdle 1988). RMA slopes and confidence intervals were estimated with software for reduced major axis regression (Bohaneck 2002).

Statistical Analysis of Selection Coefficients and Heritabilities

We analyzed selection coefficients and heritabilities with multivariate ANOVAs that included, as independent variables, many of the factors recorded on each study. We used multivariate analysis because our data sets were unbalanced in that each study was characterized by a particular combination of factor levels, and certain combinations of factor levels occurred more frequently than others. Multivariate ANOVAs allowed us to better test for the effect of one factor on selection or heritability while controlling for other factors. We were unable to test for interactions among factors because of limited sample size. All analyses were performed with SAS statistical software (SAS Institute 1996).

We performed separate analyses on the actual values and the absolute values of the selection coefficients. Analyses of actual values test whether selection varies in sign. For questions about the magnitude of selection, absolute values of coefficients are the relevant measure because the sign of the selection coefficient is immaterial. ANOVAs of the absolute values of selection coefficients were \log_e transformed ($\log_e[|\text{coefficient}| + 0.001]$) to improve normality of errors.

The ANOVA models for the actual values of selection coefficients included trait type as the independent variable. The models for the absolute values also included the fitness measure, the range of phenotypes (expanded or not), and the growth environment as independent factors. Because we tested the same factors in multiple analyses on nonindependent data, the statistical significance of a factor across all analyses was adjusted by the sequential Bonferroni procedure (Rice 1989). Heritabilities were analyzed by ANOVA in a model that included trait type, life history, breeding system, type of heritability estimate (broad or narrow sense), and growth environment as independent factors. Heritability values were arcsine-square root transformed.

Outliers

For all analyses, extreme outliers, as judged by measures of influence (Cook's D, DFFITS, and DFBETAS), were eliminated

Table 2

Trait Types and Sample Sizes of Selection Coefficients and Heritability Estimates

Category, subtype, and trait	Selection coefficients		Heritability	
	Number of estimates	Number of studies	Number of estimates	Number of studies
Physiology/chemistry:				
Secondary chemistry:				
Secondary chemistry	24	5	140	8
Gas exchange and water use efficiency:				
Photosynthesis	6	2	3	2
Transpiration	2	1	3	2
Water use efficiency	2	1	3	2
Carbon isotope discrimination	0	0	2	1
Metal tolerance:				
Metal tolerance	0	0	10	2
Total number:				
Total number	34	7	161	14
Morphology:				
Leaf/bract size and shape:				
Leaf size	50	10	114	21
Leaf shape or thickness	24	4	36	9
Stomatal density	3	1	0	0
Bract or ligule morphology	0	0	29	2
Seed/seedling morphology:				
Seed morphology	28	4	75	18
Seedling morphology	1	1	19	2
Cotyledon morphology	12	1	41	7
Mechanical defense:				
Mechanical herbivore defense	45	4	3	2
Architecture:				
Growth habit, internode length, stem diameter	39	3	24	8
Total number:				
Total number	202	20	338	39
Phenology/development:				
Germination date:				
Germination date	196	12	68	17
Flowering/fruiting time:				
Flowering time	80	19	134	32
Onset or duration of fruiting	1	1	4	1
Node of first flower	0	0	1	1
Meristem activity:				
Axillary bud activation	0	0	1	1
Node of first flower	0	0	1	1
Total number:				
Total number	277	27	208	42
Vegetative performance:				
Plant size:				
Plant, shoot, tiller, rosette height or width, root length	157	17	193	30
Total leaf area	16	5	18	5
Leaf biomass	6	2	12	2
Root biomass	4	1	15	8
Stem, shoot, above ground, or total mass	10	4	64	18
Branch, stem, tiller, leaf, or node number	64	22	126	15
Growth rate:				
Growth, expansion rate	53	5	40	9
Allocation:				
Biomass allocation	0	0	10	6
Herbivore defense:				
Herbivore tolerance	6	2	0	0
Herbivore resistance	42	7	6	3
Survival:				
Survival or germination percent	0	0	20	6
Total number:				
Total number	358	32	504	49

Table 3
Fitness Measures and Sample Sizes in Selection Studies

Fitness measure, subtype, and trait	Selection coefficients	
	Number of estimates	Number of studies
Cumulative fitness: ^a		
Reproductive biomass:		
Reproductive or total seed biomass	58	3
Flower/fruit number:		
Flower or inflorescence number	16	3
Fruit number	86	7
Seed number:		
Seed number	253	21
Total number of estimates:		
Total number of estimates	413	32
Fertility: ^b		
Seeds per fruit:		
Seeds per fruit	13	1
Reproductive biomass:		
Reproductive biomass	16	1
Flower/fruit number:		
Flower or spikelet number	24	2
Fruit number	15	2
Seed number:		
Seed number	101	8
Total number of estimates:		
Total number of estimates	169	12
Vegetative fitness:		
Survivorship:		
Seed germination percent or seedling establishment	29	3
Percent survival	211	8
Growth rate:		
Growth rate	20	2
Plant size:		
Plant biomass or size	11	2
Herbivore defense:		
Herbivore or parasite resistance	18	1
Total number of estimates:		
Total number of estimates	289	12

^a Cumulative fitness includes survival to reproduction.

^b Fertility does not include survival to reproduction.

from the ANOVAs (0–5 data points out of sample sizes of 100–680; SAS Institute 1996).

Caveats about Analyses

The results of our analyses must be interpreted with caution. First, because estimates of selection coefficients and heritabilities on multiple traits within a study are not independent of one another, it is actually inappropriate to conduct ANOVAs in which each estimate is taken as an independent data point (Gurevitch and Hedges 1999; Kingsolver et al. 2001). It would have been preferable to conduct meta-analyses across studies (Gurevitch and Hedges 1999), but the relevant information for such analyses (phenotypic variances and covariances among traits) was not available. Kingsolver et al. (2001) opted to forgo formal parametric analyses of survey data on selection coefficients in favor of more heuristic comparisons of frequency distributions of selection coefficients. Mousseau and

Roff (1987) and Roff and Mousseau (1987) compared the cumulative distributions of heritabilities among trait types. We have already alluded to the second limitation of our analyses. It is difficult to claim that multiple studies on similar traits or with similar fitness measures are true replicates of one another because biological and experimental factors differed across studies. In addition, not all combinations of factors were equally represented in the data sets.

Results

We first report summary information on the data sets and the frequency distributions of selection coefficients and heritabilities. Using the results of the statistical analyses, we then address the six questions posed in the introduction.

Summary of Data Sets

Our survey of the literature yielded 871 traits for which selection coefficients were estimated. The data set contained 506 linear selection differentials, 653 linear gradients, 111 quadratic differentials, and 214 quadratic gradients (table 4). Heritabilities were estimated for 1214 traits.

The distribution of estimates among trait types was similar for linear selection coefficients and heritabilities. Approximately 40% of the estimates were measured on vegetative performance traits, ca. 30% on morphology, 20% on phenology, and only 4%–13% on physiological/chemical traits (table 2).

The breakdown of selection and heritability estimates into subtypes of broad trait categories was also similar. Between 72% and 86% of the estimates on vegetative performance were on measures of plant size (height, number of parts, leaf area or biomass), 8%–15% were on growth rate, and 1%–13% were on herbivore tolerance or resistance. Among morphological traits, selection coefficients and heritabilities were most frequently measured on leaf or bract morphology (size or shape; 37% and 53%, respectively). Seed and seedling morphology accounted for 15% and 35% of the selection coefficients and heritabilities, respectively; 24% of the selection coefficients but less than 1% of heritabilities were on mechanical defense traits (e.g., trichomes); and 7%–17% of the heritabilities and selection coefficients were on traits related to plant architecture (e.g., branching pattern, internode length). Two traits, germination time (66% vs. 36%) and flowering time (33% vs. 63%), accounted for virtually all of the selection coefficients and heritabilities on phenology. The most common physiological/chemical trait among selection coefficients and heritabilities was secondary chemistry (66% and 89%), with the remainder consisting mostly of gas exchange parameters and water use efficiency.

The most common fitness measure in selection studies was cumulative fitness (47%), while 33% and 20% of the coefficients were based on vegetative performance and fertility as fitness measures (table 3). Cumulative fitness, which includes survival to reproduction, and fertility, which does not, were measured by total seed number (60%–62%), flower or fruit number (23%–24%), or reproductive biomass (9%–14%). The most common measure of vegetative fitness was survivorship (73%), with 3%–10% for emergence date, biomass, growth rate, and herbivore/parasite resistance. Thus, although

Table 4

Sample Size (<i>n</i>), Means \pm SE, and Medians of Selection Coefficients and Heritabilities				
Selection coefficient or heritability	<i>n</i>	Mean \pm SE	Median	Mean vs. median
Actual value:				
Linear selection differential	506	0.085 \pm 0.020 ^{ns}	0.012	***
Linear selection gradient	653	0.049 \pm 0.013 ^{ns}	0.010	***
Quadratic selection differential	111	0.029 \pm 0.021 ^{ns}	0.007	ns
Quadratic selection gradient	214	-0.010 \pm 0.010 ^{ns}	-0.001	ns
Absolute value:				
Linear selection differential	506	0.270 \pm 0.16 ^{***}	0.132	***
Linear selection gradient	653	0.201 \pm 0.011 ^{***}	0.118	***
Quadratic selection differential	111	0.125 \pm 0.018 ^{***}	0.049	***
Quadratic selection gradient	214	0.083 \pm 0.008 ^{***}	0.029	***
Heritability	1214	0.362 \pm 0.297 ^{***}	0.300	***

Note. Significance values in the last column indicate whether means differ from the medians.

*** Significance values ($P < 0.01$) indicate whether means differ from 0.

there is considerable overlap in the traits subsumed under the categories of vegetative performance and vegetative fitness (tables 2, 3), selection on vegetative performance traits emphasized measures of plant size, whereas selection via vegetative fitness focused on survivorship.

Frequency Distributions of Selection Coefficients and of Heritabilities

The mean value of linear and quadratic selection coefficients did not differ significantly from 0 (table 4), and the frequency distributions of the coefficients also had a strong mode at 0 (not shown). As reported by the authors of the studies, many, if not most, of the selection coefficients did not differ significantly from 0 (48% of the linear selection differentials, 59% of the linear gradients, 83% of the quadratic differentials, and 84% of the quadratic gradients). The concentration of linear coefficients around 0 led to median values that were significantly smaller than mean values. At the same time, the frequency distributions of the selection coefficients had long tails

of both positive and negative values. As a result, the mean and median magnitudes (absolute values) of the coefficients were significantly greater than 0 (table 4).

The average heritability differed significantly from 0 but was significantly greater than the median value (table 4). This is because low heritabilities ($b^2 \leq 0.15$) accounted for nearly 50% of the values.

Question 1: Direct or Indirect Selection on Traits?

We were able to compare linear gradients versus differentials for 278 traits and quadratic gradients versus differentials for 47 traits. In both comparisons, gradients were significantly positively correlated with differentials, but the slopes from reduced major axis regression were significantly less than 1 (fig. 2). Within three trait types—morphology, phenology, and vegetative performance—the regressions slopes between linear gradients and differentials were also less than 1 and did not differ from each other or from the overall slope (RMA slope for morphology: 0.60 ± 0.10 SE; for phenology: $0.85 \pm$

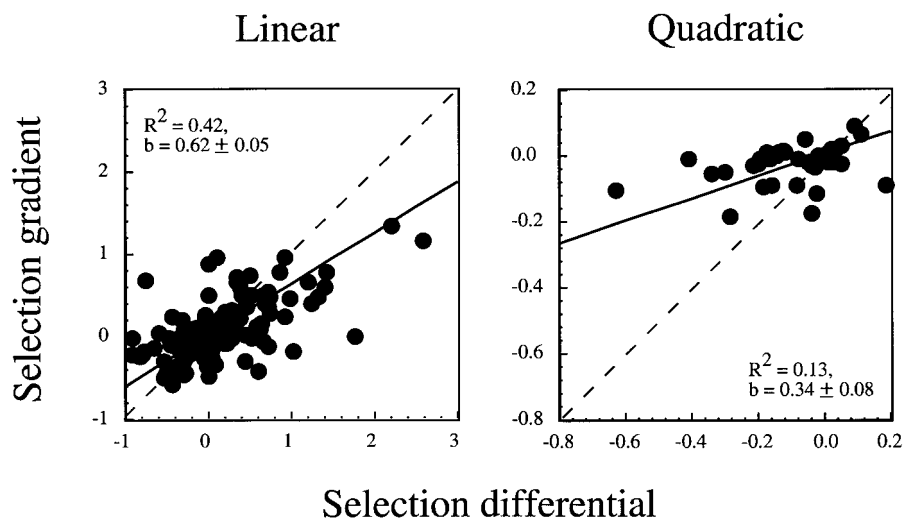


Fig. 2 Reduced major axis regressions of selection gradients on selection differentials (solid line). The R^2 , jackknifed slope, and standard errors are shown. The dashed line represents a one-to-one relationship between gradients and differentials.

Table 5
F Statistics from ANOVA of Linear and Quadratic Selection Differentials and Gradients

Source	Form of selection					Magnitude of selection				
	df	Linear		Quadratic		df	Linear		Quadratic	
		Net <i>F</i>	Direct <i>F</i>	Net <i>F</i>	Direct <i>F</i>		Net <i>F</i>	Direct <i>F</i>	Net <i>F</i>	Direct <i>F</i>
Trait type	3	60.7 ^a	9.8 ^a	3.6	1.6	3	11.8 ^a	5.7 ^a	0.3	1.7
Fitness measure	2	12.3 ^a	3.0	7.1 ^a	2.1
Phenotypic range	1	1.1	14.8 ^a	0.4	11.8 ^a
Environment	2	16.5 ^a	7.0 ^a	9.1 ^a	6.6 ^a
Denominator df		505	642	108	213		498	636	104	201
Adjusted <i>R</i> ²		0.27	0.04	0.06	0.02		0.18	0.10	0.18	0.15

Note. Analyses were performed on the actual and absolute values of coefficients. Absolute values were log_e transformed. Numerator degrees of freedom (df): trait type df = 3, except for net quadratic selection, where it is equal to 2; fitness measure df = 2, except for net quadratic selection, where it is equal to 1; phenotypic range df = 1; environment df = 2. Denominator df and *R*² for each analysis appear in bottom rows.

^a Statistically significant $\alpha = 0.05$, after Bonferonni correction.

0.15; for vegetative performance: 0.61 ± 0.06). These results indicate that, overall as well as for these three trait types, direct selection accounts for only part of total selection. In addition, because most data points fall below the one-to-one line for linear coefficients (fig. 2), indirect selection appears to reinforce (i.e., is of the same sign as) direct selection. For chemistry, where there were only eight cases for which both linear differentials and gradients were reported, the RMA slope was much higher, as was the standard error (23.5 ± 30.8). If chemistry is generally characterized by very high direct relative to net selection, it would mean that indirect selection opposes direct selection. With quadratic selection, indirect selection overall appears to oppose direct selection, since most data points fall above the one-to-one line (fig. 2).

Question 2: Do Selection Coefficients Differ among Trait Types?

The sign and magnitude of linear selection differed among trait types, but quadratic selection did not (table 5; fig. 3). As expected, net directional selection was strongest on vegetative performance, and the direction of selection on this trait was positive. Direct linear selection on performance was also positive, but no stronger than on other trait types. The sign of both net and direct linear selection on phenology was negative, meaning that early development (i.e., early germination or flowering time) was consistently favored. Quadratic selection on phenology was significantly positive. In most studies that detected positive quadratic selection on phenology, there was no fitness minimum within the range of measured phenotypes. Thus, positive quadratic selection appears to be due to a convex fitness function that favors early development. On average, there was no net directional or quadratic selection on physiology or morphology.

There were discrepancies between the strength of net and direct linear selection for some traits. In the case of vegetative performance, net selection was considerably stronger than direct selection. This difference suggests that indirect selection on other traits, which themselves enhance vegetative vigor, contribute to net selection on performance. With physiology/chemistry, net linear selection was weak compared with direct selection. The discrepancy was entirely due to strong di-

rect selection on secondary chemistry ($\log_e |\beta|_{\text{chemistry}} = -1.9 \pm 0.4 \text{ SE}$) because direct selection on gas exchange and WUE was weak ($\log_e |\beta|_{\text{gas exchange physiology}} = -3.0 \pm 0.6$). In other words, indirect selection on secondary chemistry opposes direct selections, and, aside from secondary chemistry, the strengths of net and direct selection rank in the same order among traits (i.e., vegetative performance > phenology = morphology > gas exchange physiology).

Question 3: Do Heritabilities Differ among Trait Types?

Average heritability also differed among trait types. Surprisingly, the heritability of physiology was significantly larger than for other traits (fig. 4), but this was again due to secondary chemistry ($0.57 \pm 0.001 \text{ SE}$, back transformed from arcsine-square root values). The mean heritability for gas exchange physiology (0.13 ± 0.01) did not differ from that of phenology and vegetative performance ($0.20\text{--}0.21 \pm 0.001$). The heritability of morphology (0.26 ± 0.001) was intermediate between that of secondary chemistry and other traits.

Question 4: Are the Magnitudes of Selection and Heritability Correlated?

Even though few studies measured both selection and heritability, we were able to compare their magnitudes because, across the entire data sets, these parameters were both estimated on the same broad trait categories and trait subtypes at relatively equal frequencies.

The magnitudes of net directional selection and heritability were inversely related among the four broad trait categories ($r = -0.95$; fig. 3 vs. fig. 4) and the trait subtypes identified in table 2 ($r = -0.74$, $df = 9$, $P < 0.02$). The strength of the negative correlation between selection and heritability was strongly influenced by secondary chemistry (low net directional selection, very high heritability). With chemistry removed, the correlation among trait subtypes remains negative ($r = -0.31$, $df = 7$, $P > 0.2$) but not statistically significant. Thus, while strongly selected traits appear to have low heritability, the negative correlation may be driven by a few types of traits. The relationship between direct linear selection strength and heritability among trait subtypes was actually positive ($r =$

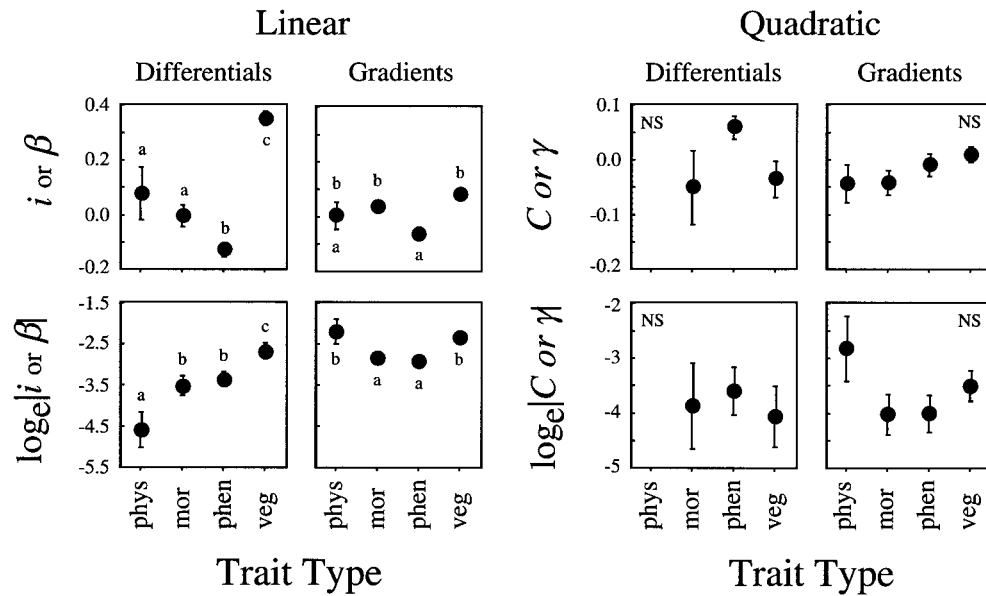


Fig. 3 Effect of trait type on the form and magnitude of selection. Least squares means \pm SE for actual values and (\log_e -transformed) absolute values of selection coefficients are shown (i = linear selection differential; β = linear selection gradient; C = quadratic selection differential; γ = quadratic selection gradient). The average magnitude of selection is zero when the least squares mean is -6.91 . Means with different letters are significantly different from one another. NS = no statistically significant effect of trait type on selection coefficients. Trait type: *phys* = physiological/chemical; *mor* = vegetative morphology; *phen* = phenology/development; *veg* = vegetative performance.

0.47, $df = 10$, $P < 0.15$) but, again, was driven largely by chemistry. With chemistry removed, the correlation falls to 0.12.

Question 5: Does the Fitness Measure Affect the Form and Magnitude of Selection?

The magnitude of net selection depended on the fitness measure that was used (table 5; fig. 5). Directional and quadratic

selection was stronger via cumulative fitness than through other fitness components. These differences in selection strength are unlikely to be explained by differences in the kinds of traits on which selection was measured. At least for directional selection, the frequency of the four trait types was very similar across the three fitness components.

Question 6: Do Experimental Conditions or Species Attributes Affect Selection and Heritability?

We expected that studies with an expanded range of phenotypes would be more likely to detect selection than studies on the natural, more restricted phenotypic range, but we found the opposite to be true (table 5; $\log_e |\beta|$ expanded range = -2.4 ± 0.1 SE, $\log_e |\beta|$ nonexpanded range = -2.8 ± 0.25 SE; $\log_e |\gamma|$ expanded range = -2.8 ± 0.3 SE, $\log_e |\gamma|$ nonexpanded range = -4.3 ± 0.4). We also did not find support for the prediction that selection might be more easily detected in studies conducted in controlled settings (greenhouse, common environment). Although the magnitudes of both net and direct linear and quadratic selection differed across environmental settings, they were always smaller in common gardens than in either greenhouse or the wild and tended to be largest in the greenhouse.

Our expectations concerning heritability estimates were largely confirmed (table 6). Broad-sense heritabilities (0.32 ± 0.001) were larger than narrow-sense estimates (0.23 ± 0.001). Heritabilities measured in controlled environments were also larger than those measured in the wild (h^2 greenhouse = 0.42 ± 0.00 SE; h^2 outdoor common garden = 0.22 ± 0.001 ; h^2 field = 0.12 ± 0.001). Last, heritabilities were larger in species with outcrossing or mixed mating systems ($h^2 = 0.29 \pm 0.001$ for both mating systems) compared with inbreeding spe-

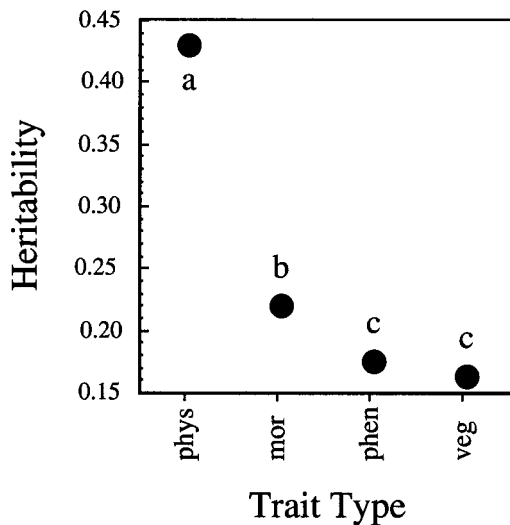


Fig. 4 Effect of trait type on heritability. Least squares means \pm SE of heritability are shown as a function of trait type. Means with different letters are significantly different from one another. Means were back transformed from arcsine-square root values. Trait types as in fig. 3.

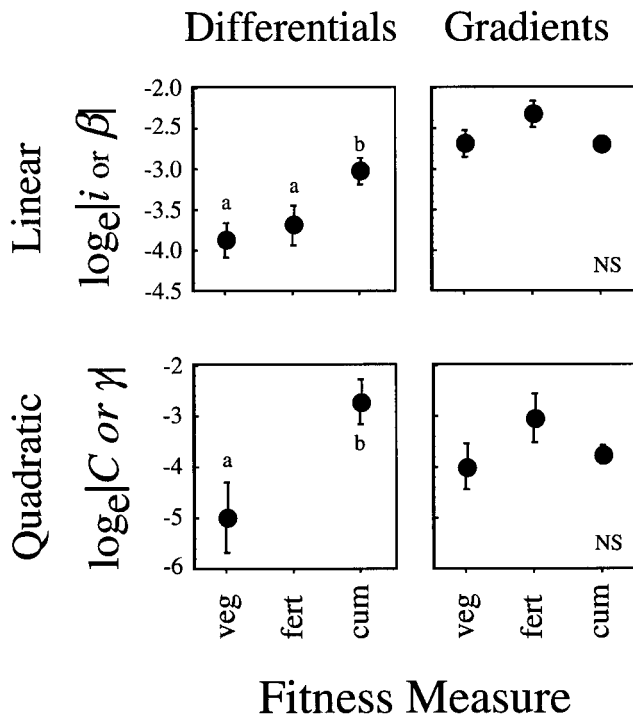


Fig. 5 Effect of fitness measure on the magnitude of selection. Least squares means \pm SE for the (\log_e -transformed) absolute values of selection coefficients are shown (i = linear selection differential; β = linear selection gradient; C = quadratic selection differential; γ = quadratic selection gradient). The average magnitude of selection is zero when the least squares mean is -6.91 . Means with different letters are significantly different from one another. *NS* = no statistically significant effect of fitness measure on selection coefficients. Fitness measure: *veg* = vegetative fitness; *fert* = fertility; *cum* = cumulative fitness. Fertility was not used as a fitness measure in studies reporting quadratic selection differentials.

cies ($b^2 = 0.15 \pm 0.001$). Annuals and perennials, however, did not differ in the magnitude of heritable variation (b^2 annual = 0.25 ± 0.001 ; b^2 perennial = 0.23 ± 0.001).

Discussion

Characterization of the nature and strength of selection and heritability in functional traits is still rather limited in scope, if one considers that a decided majority (>70%) of estimates come from high-level performance attributes. The good news is that there is room for a lot more work; the bad news is that we remain ignorant of microevolution of many functional traits, in spite of vast evidence of population and interspecific differentiation in functional attributes. Studies of functional traits are heavily biased toward morphology and a limited number of developmental traits. Physiology in plants, as in animals, is a neglected area of investigation (Mousseau and Roff 1987; Roff and Mousseau 1987; Kingsolver et al. 2001).

Adaptive Significance of Functional Traits

Herbivore-mediated selection. Some of the most directed work on adaptive evolution centers on herbivore/pathogen-

mediated selection in plants. The role of herbivores as selective agents on plant secondary chemistry and mechanical defenses has been debated at length and has spawned a large research program in ecology, evolution, and molecular biology (Simms and Rausher 1987; Simms 1992; Berenbaum 1995; Strauss and Anurag 1999; Heil and Baldwin 2002; Whittstock and Gershenzon 2002). Our survey includes only a limited sample of these studies because many do not report selection coefficients on putative defense traits.

Of the 45 studies in our survey, 15 focused on herbivore-plant interactions. In five of these, the principal aim was not to test the value of specific functional traits (e.g., secondary chemistry or mechanical defense) for herbivore resistance or tolerance. Rather, research was focused on questions of a more general (less trait-based) nature, such as the following: Are there fitness costs to tolerance or resistance in the absence of herbivores (Tiffin and Rausher 1999)? Are there optimal levels of tolerance or resistance because of these costs (Rausher and Simms 1989; Tiffin and Rausher 1999)? Are tolerance and resistance alternative defensive strategies (Mauricio et al. 1997)? Is selection on tolerance or resistance to one herbivore changed in the face of plant attack by multiple herbivores (Pilson 1996; Juenger and Bergelson 1998; Stinchcombe and Rausher 2001)? These questions are fundamental to an understanding of the evolution of defensive strategies but do not necessarily inform us about selection on specific defensive traits.

In the 10 remaining studies, selection on specific chemical, mechanical, developmental, or phenological traits was evaluated. An effective method of demonstrating that herbivores can act as selective agents is to compare selection on putative defense traits in the presence versus the absence of herbivores (Mauricio and Rausher 1997). Using this approach, Mauricio and Rausher (1997; also Mauricio et al. 1997) have shown that herbivores favor increased glucosinolate content in leaves of *Arabidopsis thaliana* in spite of costs (Mauricio 1998). In *Datura stramonium*, however, herbivore-mediated selection favors intermediate levels of hyoscyamine but reduced levels of scopolamine, two alkaloids derived from the same biosynthetic pathway (Shonle and Bergelson 2000). Optimizing selection on hyoscyamine may result from a cost of defense, while directional selection against scopolamine may result from the action of this chemical as an attractant to specialist flea beetles. In the presence of herbivores, Berenbaum et al. (1986) found that furanocoumarins enhance plant resistance to herbivores

Table 6

<i>F</i> Statistics from ANOVA of Heritabilities		
Source	df	Heritability <i>F</i>
Trait type	3	23.6 ^a
Life history	1	0.9
Breeding system	2	10.9 ^a
Estimate type	1	16.1 ^a
Environment	2	61.3 ^a
Denominator df		1204
Adjusted <i>R</i> ²		0.18

Note. Analysis was performed on arcsine-square root values.

^a Statistically significant at $\alpha = 0.05$.

in *Pastinaca sativa*, but the evolution of increased levels of defense may be constrained because of costs associated with the production of defense (Zangerl and Berenbaum 1997) and because levels of different furanocoumarins are negatively correlated. In an observational study on Ponderosa pine (one of the few selection studies of trees), resin flow rates and concentrations of several monoterpenes were positively correlated with long-term growth rate and, indirectly through growth, with male cone production (Latta and Linhart 1997). However, negative correlations among monoterpene fractions would limit evolutionary increases in the concentration on individual monoterpenes. Furthermore, there was little evidence that resin characteristics negatively affected herbivore damage by deer, aphids, porcupines, and cone predators. Latta and Linhart (1997) therefore question the role of herbivores as selective agents in this Colorado population.

Herbivores have also been shown to exert selection on mechanical defenses, albeit to varying degrees among populations of a single species and across taxa. In *A. thaliana*, there is a fitness advantage to increased trichome production, along with glucosinolates, in the presence of herbivores (Mauricio and Rausher 1997; also Mauricio et al. 1997). In *D. stramonium*, the selection pressure exerted by herbivores on trichomes varies among populations (Valverde et al. 2001). Leaf trichome density is positively correlated with resistance to herbivore attack in five of six study populations of *D. stramonium* and across all six populations, but plant resistance to herbivores was associated with higher plant fitness at only three of the six sites. In columnar cacti of the genus *Echinops*, spines are only a weak deterrent to birds that disperse the seeds of parasitic mistletoes to cacti, and this is in only one out of two *Echinops* species (Medel 2000).

Last, plants may escape herbivores in time through changes in phenology or compensate for herbivore damage through developmentally mediated changes in growth. Thus, in the absence of late-season seed herbivores, late-flowering sunflowers (*Helianthus annuus*) have higher fitness, but in their presence, selection for late flowering disappears (Pilson 2000). Similarly, in *Ipomopsis aggregata*, selection for early flowering is intensified in the presence of simulated damage, and damage alters the pattern of selection on apical dominance. Reduced apical dominance (increased branching) is favored in the presence of herbivory since it enhances the regrowth potential of damaged plants (Juenger and Bergelson 1997, 2000).

Since many of the defensive traits in these studies exhibit genetic variation, adaptive evolution in response to herbivore or parasite pressure is theoretically possible. At the same time, most estimates of selection on chemical traits were of direct selection, and our survey suggests that indirect selection may constrain evolutionary response in chemistry. It is interesting, in this regard, to note that opposing trait correlations among chemical compounds were reported in several studies. It is also clear that the selection pressure exerted by herbivores and pathogens can be highly variable in space and time and that the identity and interactions among herbivores may affect the pattern of selection on defense traits. It is still an open question whether variation in selection pressure, cost of defense, and opposing indirect selection contributes to the maintenance of variation in defense attributes within populations and to diversification between populations and taxa.

Habitat factors, abiotic environment, and competition as agents of selection. The biological context, selective agent, functional trait, and specificity of question all varied in the remaining studies in our survey. The most general studies asked whether natural selection in the wild varies spatially or temporally (Kalisz 1986; Brassard and Schoen 1990; Stratton 1992a; Kelly 1993; Gross et al. 1998) without regard to obvious habitat variation. Ecotypic differentiation of plant populations provided the impetus for 10 studies (Clausen et al. 1948; Bradshaw 1984; Geber and Dawson 1993; Linhart and Grant 1996). In these studies, transplant experiments were often used to evaluate patterns of selection and local adaptation. The most general question addressed by these studies was whether selection differs among the habitats occupied by different ecotypes (Biere 1991; van Tienderen and van der Toorn 1991; Andersson and Shaw 1994). More focused studies asked whether the pattern of selection in each habitat favors the trait values of the native ecotype and therefore might account for ecotypic differentiation in these traits (Scheiner 1989; Jordan 1991; Bennington and McGraw 1995, 1996; Nagy 1997). The most directed studies began with hypotheses concerning the adaptive significance of specific traits in relation to specific habitat differences (Dudley and Schmitt 1996; Donohue et al. 2000). In a third class of study, the focus was on the role of specific abiotic or biotic factors (e.g., drought, temperature, salt, light, competition) as agents of selection; two of the studies were motivated by spatial or seasonal variation in abiotic factors in natural populations (Dudley 1996a; Winn 1999), while six studies used synthetic populations in experimental environments (Miller et al. 1994; Totland 1999; Arntz et al. 2000a; Dorn et al. 2000; Stanton et al. 2000; Weinig 2000). Last, several studies focused on selection in one environment (seed size: Mojonier 1998; Winn 1988; germination time: Kalisz 1986; flowering time: Mitchell-Olds 1990, 1996).

Patterns of selection were often variable over small and large spatial (e.g., plot, transect, nearby sites) and temporal (seasons, years) scales (Kalisz 1986; Biere 1991; Stratton 1992a; Kelly and Levin 1997; Gross et al. 1998; but Winn 1988; Brassard and Schoen 1990). This is an important result because variable selection can maintain genetic variation in functional traits within or between populations (Hedrick et al. 1976) or select for adaptive plasticity in functional traits (Via and Lande 1985). Selection coefficients also differed in virtually all comparisons among habitats or treatments for at least some traits (but Winn 1999). Most interestingly, in virtually all ecotypic studies, selection at a site generally favored trait values of native populations, but again for only a subset of the measured traits (Scheiner 1989; Jordan 1991; Bennington and McGraw 1995, 1996; Dudley 1996a; Dudley and Schmitt 1996; Nagy 1997; Donohue et al. 2000). In other words, current patterns of selection might account for some but not all of the phenotypic differentiation among populations.

Some of the most elegant work on functional adaptation comes from a series of experimental studies on phytochrome-mediated responses to shade from competing plants (Dudley and Schmitt 1995, 1996; Schmitt et al. 1995; Donohue et al. 2000; Dorn et al. 2000; Weinig 2000). Many plant species exhibit a range of responses to changes in light quality (red : far red [R : FR] ratio) and light quantity that are indicative of the presence of neighbors. R : FR responses, such as

stem elongation and changes in flowering time, have been shown to be adaptive in the presence of neighbors but not in their absence, while experimental suppression of these responses is maladaptive with but not without neighbors (Dudley and Schmitt 1995, 1996; Schmitt et al. 1995; Donohue et al. 2000; Dorn et al. 2000). Reciprocal fitness relations in the absence versus presence of competition arise because shade-avoidance responses minimize competition but may also carry costs. Dudley and Schmitt (1995) also show that populations are genetically differentiated in the level of R : FR response, with populations from open habitats responding more strongly to shifts in light quality compared with populations from woodland habitats where elongation is not effective in overtopping the canopy.

Only one additional study examined the role of competition as a selective agent, in spite of the importance attached to competition in driving the evolution of life history, resource use and acquisition, and effect and response to competition. Miller et al. (1994) found support for the hypothesis that early germination is advantageous in competitive environments because it gives seedlings a head start against competitors (Miller et al. 1994).

A heavy emphasis in plant ecophysiology has always been on adaptation and acclimation in relation to the abiotic environment, and yet very few selection studies are aimed at these issues. Only two studies in our survey measured selection on gas exchange physiology. Dudley (1996a, 1996b) found support for the hypothesis that selection in *Cakile edentula* favors higher water use efficiency and smaller leaf size in dry relative to wet habitats. Furthermore, heritable variation in these traits would allow for fairly rapid evolution between trait optima for the two environments, in spite of positive correlations between water use efficiency and leaf size. The value of high integrated water use efficiency under water-limiting conditions is supported by work on *Encelia farinosa*, a desert shrub, in which survivorship during a prolonged drought was higher for more water use efficient plants (Ehleringer 1993). However, work by Donovan and Ehleringer (1994) on another desert shrub did not find evidence of selection for higher water use efficiency under drought. In short-lived species, evidence suggests that a variety of stress factors, including water stress, favor accelerated development (McGraw and Bennington 1995; Stanton et al. 2000), and accelerated development may be associated with higher photosynthetic rates and lower water use efficiency (Geber 1990; Geber and Dawson 1990, 1997; Arntz and Delph 2001). The second study in our survey to measure selection on physiology made use of a photosynthetic mutant in *Amaranthus hybridus* to measure selection on photosynthesis. In one of the few studies to actually demonstrate an effect of photosynthetic rate on fitness, Arntz et al. (2000b) found that mutants, with lower photosynthetic rates, had lower survivorship and fertility, mediated through effects of photosynthesis on growth (see also Arntz et al. 1998, 2000a; Arntz and Delph 2001).

There is clearly a need for further tests of functional hypotheses of selection mediated by both biotic and abiotic factors. These studies should also explore the nature and effect of trait interactions on fitness, since these are likely to be very important in shaping the course of evolution.

General Questions on the Nature of Selection and Heritability

Through the compilation of data from the literature, we were also able to address some very general questions about patterns of selection and heritable variation in plants. While these questions do not speak to specific functional hypotheses, they are relevant to the process of adaptive evolution in functional traits and can be informative about likely rates of evolution for different kinds of functional traits. In the remainder of the article, we discuss our findings in relation to these general questions.

Direct versus indirect selection. The pattern of net selection on a trait determines the course of its evolution in the short term, assuming the existence of heritable variation. Still, it is the pattern of direct selection that best describes the functional basis of selection on the trait. The difference between patterns of direct versus net selection is indicative of how a trait's influence on fitness is mediated through correlated traits and how trait evolution is altered by indirect effects.

Our analysis indicates that, while net and directional selection are positively correlated, indirect selection accounts for nearly 40% of total linear selection and 65% of quadratic selection (fig. 2). In contrast to our study, Kingsolver et al. (2001) reported a one-to-one relationship between linear differentials and gradients from their survey of selection studies in the wild. The discrepancy between the two results is not likely to be explained by our inclusion of studies from controlled environments, because there was a one-to-one relationship between linear differentials and gradients in experimental studies (RMA slope for experimental studies: 1.02 ± 0.09 ; for studies in the wild: 0.58 ± 0.04). One possible explanation for the difference is that Kingsolver et al.'s (2001) analysis included both animal and plant data, and indirect selection may be weaker in animals. Second, their survey also included functional traits affecting mating success, and indirect selection may be weaker on sexually selected traits whose connection to reproductive success and fitness may be more immediate.

We are not surprised by evidence of indirect selection in plants. The modular and indeterminate nature of plant development means that organ-level traits (i.e., physiology, secondary chemistry, morphology) are likely to have repeated and interactive effects over the growth cycle and on the expression of higher-level traits (i.e., vegetative performance) (fig. 1; Ackery et al. 2000; Arntz and Delph 2001). As a result, the opportunity for multiple pathways of influence of traits on fitness is likely to be enormous and could contribute to indirect selection. Many animals, by contrast, do not have variable numbers of "parts" and have a more determinate development. This may decrease the number of pathways of interaction between traits and/or enhance the direct effects of traits on fitness.

Some interesting implications and questions emerge from the relationship of net and direct linear selection in plants. First, apart from chemical traits, the reinforcing nature of indirect linear selection (fig. 2) in the wild implies that traits that are positively correlated with the target trait are subject to the same pattern of selection (i.e., same sign of selection coefficients) as the target, while negatively correlated traits are subject to opposing patterns of selection. In other words, there

do not appear to be conflicting selection pressures and a constraining correlation structure among traits. If this is true, selection in plants should lead to the evolution of coordinated suites of traits, and adaptive differentiation among populations may often consist of divergence in suites of traits. Studies focused on microevolution of interacting sets of functional traits will be required to understand their functional interdependence, to partition direct and indirect pathways of influence among these traits, and to quantify the strength and pattern of selection on suites of traits (i.e., correlational selection) (Lechowicz and Blais 1988; Farris and Lechowicz 1990; Jordan 1991; Bennington and McGraw 1995; Dudley 1996a; Mauricio et al. 1997; Kelly and Levin 1997; Ackerly et al. 2000; Arntz et al. 2000b; Donohue et al. 2000; Juenger and Bergelson 2000; Scheiner et al. 2000; Arntz and Delph 2001).

There is, however, another compelling explanation for reinforcing indirect selection in the wild. Rausher (1992a) has argued that measurements of phenotypic selection (i.e., of the relationship between an individual's phenotype and fitness) may be biased if fitness and phenotype are both influenced by the environment and if environments vary among individuals. For example, if individuals are distributed across environments of differing quality, and quality simultaneously affects fitness and phenotype (e.g., many seeds, big leaves in good environments, and vice versa in poor environments), there will be apparent directional selection on leaf size even in the absence of any true effect of this trait on fitness. If multiple phenotypic traits, such as leaf, stem, and branch size, respond in the same manner to environmental quality, then indirect selection will appear to be reinforcing. Apparent reinforcement of direct selection may be reduced in experimental settings where environmental variance and environmentally mediated trait correlations are lessened.

To get around the problem of environmentally induced bias in phenotypic selection analyses, Rausher (1992a) has advocated a genotypic analysis of selection in which selection is measured as the covariance between the breeding values of fitness and trait among genotypes. In a comparison of phenotypic and genotypic analyses of three data sets on herbivore-mediated selection (Mauricio and Rausher 1997; Tiffen and Rausher 1999; Stinchcombe and Rausher 2001), Stinchcombe et al. (2002) report a 25%–30% bias in phenotypic relative to genotypic gradients. We were unable to estimate environmentally mediated bias in our survey because very few studies reported both types of analyses. Additional comparisons of genotypic versus phenotypic selection analyses are clearly warranted in view of the profound effects of environment on plant phenotypes.

Environmentally mediated changes to both phenotype and fitness may not only lead to overestimates of directional selection but they can also mask the existence of stabilizing selection (Price et al. 1988; Travis 1989). For example, even if selection favors intermediate photosynthetic rates, because of trade-offs between carbon gain and water loss, selection may appear to be directional for higher photosynthetic rates if plants in sites with more favorable water balance have both elevated photosynthetic rate and fitness. It is impossible to judge, at this point, whether environmentally induced bias in selection estimates accounts for the apparent absence of strong

quadratic selection or for the fact that indirect quadratic selection appears to oppose direct quadratic selection (fig. 2).

Form and magnitude of selection on traits. The first prediction that directional selection would be both strong and the dominant form of selection on vegetative performance—a fitness-related trait—was confirmed (table 5; fig. 3). Indeed, evidence of strong positive directional selection for increased vegetative performance is only to be expected. The consistently negative directional selection on phenology and evidence of convex (accelerating) rather than concave (decelerating) quadratic on this trait was unexpected. The phenological traits in our survey were of two types, emergence or establishment time of seedlings (196 selection estimates) and the length of the vegetative phase (82 estimates), and negative directional selection means that early emergence and a short vegetative phase were favored. Consistent directional selection for early development may reflect the fact that annuals and short-lived perennials comprised the bulk of the data set and that accelerated development is often at a premium in short-lived taxa (Kalisz 1986; Geber 1990; Geber and Dawson 1990; Kelly 1992; Stratton 1992a; Bennington and McGraw 1995; Donohue et al. 2000; Stanton et al. 2000).

The second prediction that optimizing selection would be stronger on lower-level traits was not supported (table 5; fig. 3). In fact, we detected no effect of trait type on either the form or magnitude of quadratic selection, and none of the quadratic selection coefficients, except for positive net selection on phenology, differed from zero. Quadratic selection may simply be rare. It is also notoriously difficult to detect without very large samples sizes within studies (Mitchell-Olds and Shaw 1987; Travis 1989; also Kingsolver et al. 2001), and our data set contained many fewer estimates of quadratic coefficients than linear coefficients, perhaps because authors tend not to report insignificant results. Much of the thinking and modeling in evolutionary ecology is based on optimizing selection, in part because trade-offs are assumed to be common (e.g., higher defense levels reduce herbivory but are also costly) (Travis 1989). It is of theoretical and biological interest therefore to distinguish between a real absence of quadratic selection versus a statistical inability to detect it (Travis 1989).

Heritability of traits. In our survey, as in surveys of animal data (Falconer 1981; Mousseau and Roff 1987; Roff and Mousseau 1987), heritability is generally higher of morphology than of life history/vegetative performance and phenology/development (fig. 5). We were surprised, however, by the high heritability of physiological/chemical traits. In animals, heritability of physiology tends to be intermediate between that of life history and morphology (Mousseau and Roff 1987; Roff and Mousseau 1987). The high heritability of physiology/chemistry in our survey was due to secondary chemistry. It is not clear whether chemical traits generally have higher genetic variance (or lower environmental variance) than other organ-level traits in plants. The data in our survey came from only seven species, and >60% of the estimates came from a single species, *Pastinaca sativa* (Berenbaum et al. 1986; Zangerl and Berenbaum 1990, 1997).

Selection versus heritability. Our survey provided relatively weak evidence that the traits under strongest directional selection are the ones with the lowest heritabilities, with the implication that all traits can evolve at similar rates. Although

there was a negative correlation between the magnitudes of linear differentials and heritabilities across traits and trait subtypes, the strength of the correlation was heavily influenced by a single trait type, namely secondary chemistry. In addition, the strength of direct linear selection was either positively correlated or uncorrelated with heritability, depending on whether secondary chemistry was included or not. Thus, there is little evidence that short-term evolutionary change will proceed at similar rates across different traits.

Negative correlations between heritability and selection strength have been reported in animals (for review, see Merilä and Sheldon 1999, 2000). The pattern of selection across trait types is generally not in dispute, with traits closer to fitness being subject to stronger directional selection than other traits. The question is whether low heritability of fitness-related traits is the result of low additive genetic variance (V_A) or high residual variance (V_R ; i.e., nonadditive genetic or environmental variance). The traditional view, that fitness-related traits have low heritability because of a history of strong directional selection (Fisher 1930; Falconer 1981), is in dispute. In particular, fitness-related traits harbor high levels of genetic variation because of high inputs of mutational variance from the many loci that determine their expression (Houle 1992, 1998; Kondrashov and Houle 1994; Houle et al. 1996; Merilä and Sheldon 1999, 2000); in contrast to heritability, the coefficient of additive genetic variance (CV_A) is positively correlated with selection strength (Houle 1992; Merilä and Sheldon 1999, 2000).

The low heritability of fitness-related traits is then the result of high residual variance. The V_R is high for fitness traits because of the compounding of nonadditive genetic or environmental variance across loci (Price and Schluter 1991; Houle 1992, 1998; Merilä and Sheldon 1999, 2000; Stirling et al. 2002). The few studies that have examined the source of low heritability in fitness traits in plants have found it to be due to high environmental variance (Stratton 1992*b*; Campbell 1997). Future studies of genetic variation should report estimates of V_A , V_R , trait means, and heritability (Houle 1992, 1998).

Selection and fitness measures. The strength of directional and quadratic selection was stronger via cumulative fitness than through vegetative fitness or fertility, results that largely parallel those of Kingsolver et al. (2001). Vegetative fitness was composed mostly of measures of survival, and selection via this component has been weak in other studies as well (Endler 1986; Kingsolver et al. 2001). Weak selection via survivorship may be due to the highly stochastic nature of survival, especially in short-lived plants subject to high-levels of disturbance.

Kingsolver et al. (2001) found selection to be strongest via mating success—a component that was not included in our study—while selection strength via fertility was intermediate. The latter category corresponds to a combined category of fertility and cumulative fitness in our study. Selection strength on this combined category is also higher than that on vegetative performance in our data set.

There are two implications that emerge from differences in selection strength via different fitness components. First, selection studies on individual components provide a very incomplete picture of lifetime selection; second, certain life-history episodes

may have dominant effects on the course and rate of trait evolution.

Experimental and biological factors in studies of selection and heritability. One of the tenets of modern biology is that scientific hypotheses are better tested through experimentation than observation. And yet it is easy to conduct experiments in settings that have little relevance to the real world. A case in point is that heritability estimates in controlled environments overestimate heritabilities in the wild by two- to fourfold, according to our survey. Projections of evolutionary response in the wild based on heritabilities measured in controlled environments must therefore be tempered considerably. The use of broad-sense heritabilities for purposes of projecting evolutionary response in outcrossing taxa will also overestimate the rate of evolution by 30%–40%.

Experimental studies of selection are of value in two ways. The role of a particular environmental factor as a selective agent is perhaps best evaluated by experimental manipulation of the factor (e.g., herbivory). Many, though not all, of the experimental studies in our survey did detect differences in selection among treatments. Whether experiments are conducted in the wild, common garden, or greenhouse does not appear to have a systematic effect on the magnitude of selection, although no study directly compared selection across two or more of these environments. The second important role of experiments in selection studies is the experimental manipulation to extend the range of phenotypes beyond what is normally found in a single population. Inclusion of individuals with extreme phenotypic values should make it easier to describe the full form of the fitness function on a trait. We hypothesized, therefore, that studies with an extended phenotypic range would have better power to detect selection and would yield larger estimates of selection coefficients than studies with the normal phenotypic range. We actually found the opposite to be true—selection was weaker in studies with extended phenotypes—but, again, no study compared selection between experimental groups with a large versus narrow range of phenotype.

Heritability was influenced by plant mating system but not by life history in this admittedly narrow sample of life histories. Not unexpectedly, the heritability of traits in inbreeding species was lower by ca. 50% compared with species with some degree of outcrossing. This finding supports the idea that selfing lineages are less able to evolve in the face of novel environments and are thus evolutionary dead ends (Schoen et al. 1997; Takebayashi and Morrell 2001). Interestingly, species classified by the authors as having a mixed mating system had heritabilities as large as outbreeders. Because outcrossing rates were not reported for any taxon, we do not know how much outcrossing takes place in taxa with mixed mating systems. Theory would suggest that only small amounts of outcrossing can maintain substantial levels of genetic variation.

Future directions. It is clear from our survey that functional traits and vegetative performance are both heritable and under selection and that both abiotic and biotic (herbivores, competitors) factors exert important selective pressure on traits. Furthermore, patterns of selection in different environments are frequently congruent with observed phenotypic and genotypic differentiation for some traits and so support the view that population differentiation is frequently driven by divergent selection. At the same time, we are not yet at the

point of making predictions about the likelihood and rate of adaptive evolutionary change because of insufficient information on genetic variation and covariation among traits in most studies. In view of the apparent importance of indirect selection on traits, knowledge of trait covariances is essential to predictions of adaptive evolution.

Several areas are in need of further investigation. First, evolutionary biologists measure selection and heritability most frequently on vegetative performance traits rather than on true functional traits, and among functional traits, physiology is rarely studied. Studies of phenology also deal with a very limited number of traits (the timing of germination and flowering) and should be expanded to consider the timing of other life-history events (e.g., timing of bud determination, leaf expansion, or leaf senescence). The bias away from physiology and development most likely reflects the fact that few evolutionary biologists are trained in physiology and development (and few physiological ecologists are trained in evolutionary methods). We hope that collaboration between scientists in these two fields will help correct the imbalance. Second, the sample of taxa is very biased in favor of annuals and short-lived perennials because it is difficult to estimate heritability and fitness

in long-lived taxa. Only with the inclusion of a broader range of long-lived species, and especially woody plants, can one explore life-history effects on patterns of selection and heritability. Third, because indirect selection appears to be quite common, a more detailed approach to studying trait linkages (fig. 1) would be helpful in piecing together the various modes of action of traits on fitness. Path analysis (Pedhazur 1982; Jordan 1991; Kingsolver and Schemske 1991; Dudley 1996a; Juenger and Bergelson 1997; Mojonner 1998; Arntz et al. 1998; Scheiner et al. 2000; Weinig 2000) offers a statistical approach to quantifying these linkages that can be compared with the net (total), direct, and indirect pathways of selection on traits.

From a more general perspective, it would be helpful to better understand the relationship between levels of genetic variation and selection strength, since this relationship affects the long-term evolvability of traits. Last, it is of interest to know whether selection over the lifetime is dominated by certain life-history episodes and how the latter might vary with life span and across environments, because it is these episodes that are most likely to explain population divergence.

Appendix

Studies in Selection (s) and Heritability (h) Data Sets

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- 1996 Floral variation in *Saxifraga granulata*: phenotypic selection, quantitative genetics and predicted response to selection. *Heredity* 77:217–223. (h)
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