

ty is the property of a geno-  
fferent phenotypes in response  
mental conditions (Bradshaw  
nuth, this volume, chapter 2).  
of phenotypic plasticity deal  
(genes) and nurture (environ-  
ld the anatomy, morphology,  
ng organisms. Of course, not  
d differentially to changes in  
not all environmental changes  
otype given a particular geno-  
while the distinction between  
type is in principle very clear,  
g factors immediately ensue.  
otype can be modified by en-  
as in the case of DNA methyl-  
Sano et al. 1990; Mazer and  
, chapter 2). More intuitively,  
re constantly changed by the  
in them, the genetic consti-

of the environmental  
with small wings at lo  
phenotypic value at the  
treme (say, large wings  
type 3, however, does  
notype 2 is unresponsive  
always producing the  
of the conditions (wi  
ments considered).

Even though the ca  
very simple (notice, fo  
norms are linear, whi  
tions), several general  
stood following a close

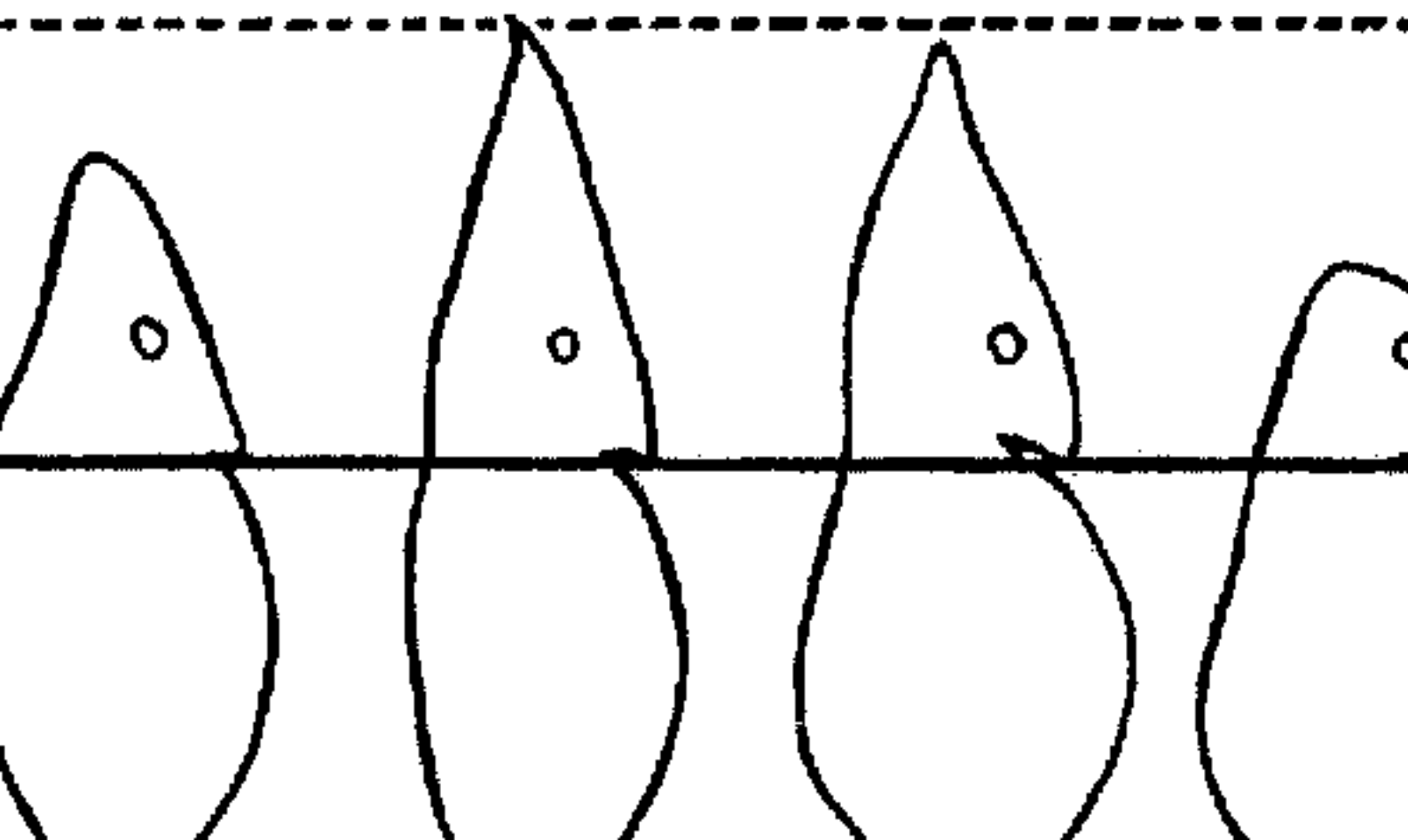
1. Let us consider t  
*notypic plasticity* and  
two terms are often u  
clearly not. A reaction  
vironment-phenotype  
given genotype: plasti



Woltereck erroneously be-  
cause of reaction norms falsified  
fundamental distinction be-  
phenotype proposed a few  
nsen. The reasoning was that  
ould alter the phenotype pro-  
otypes, then the genotype it-  
from the phenotype it pro-  
911) published a masterful  
showed why the idea of reac-  
ntradict the genotype-pheno-  
the contrary, it allows us to

which are still being inv  
and Pigliucci 1998).

Nevertheless, it was  
lished a very influential  
search on phenotypic p  
the realm of applied sci  
ticular have always bee  
come" effects of the en  
and into the main sta  
Bradshaw was the first  
mental concepts conce  
plasticity. First, plastici



also actively explored the theoretical work was paper, which incorporated norms within the new quantitative genetics. Thus, they treated reaction norm genetic correlations. The expression of one environment as a trait distribution of the same character in therefore, they could calculate between the two "traits" of the degree to which genetic expression (if the significantly less than unity, the trait in one environment—but see Schlichting and of this approach).

space here to discuss the punctuated the field before the early 1990s, but there plenty of challenges of the best classical evolutionary the evolution of complex (1986), plasticity as an adaptation the macroevolutionary

condition, it will do significantly better than other condition. Depending on the two environments, the phenotype favored over the long run. Moving about the plasticity of fitness, not of fitness itself. reaction norm for fitness to as possible across environments be successful.

An example of testing hypothesis is the work of (1996) on shade avoidance of plasticity in which an individual presence of other plants (and competition) by means of different spectral quality of incident light. Red light is absorbed by neighboring is photosynthetically active reflected because it is of too high in plants' metabolism. The plant under sunlight is different plant under shade, in that advantageous to grow tall and accelerate the time of Schmitt manipulated the environment individuals of *Impatiens cap*

gh

LOW

## Density

cy of cumulative fitness in  
 on neighbor's density. Sup-  
 er than elongated ones at low  
 an exploit the lack of compe-  
 ructurally more sturdy, but  
 where they cannot outgrow  
 search of light. (From Dudley

es will fare better on average

cept concerning modern the-  
 arch on phenotypic plasticity  
 icity does not come free of  
 e to ask if the ability to mon-  
 nditions and to alter the de-  
 in response to changes in  
 s costs that might somewhat  
 a plastic genotype. In fact, to

reduced canalization  
 each environment  
 cision”

*Genetic:* due to dele  
 genes through lin  
 with other genes

To these, one can add:

## Limits of Plasticity

*Information reliability:*  
 may be unreliable  
*Lag time:* The respo  
 pared to the tim  
 mental change, le  
 ticity.

*Developmental range:*  
 not be able to ex  
 equivalent to tha  
 ulation of special

*Epiphenotype prob*  
 could have evolu  
 tion more like an  
 velopmental mac  
 unit. As such, it

be. The latest definition  
alizes them as “regula-  
nd to a specific environ-  
ing a specific series of  
gliucci 1996, p. 169).  
r that only this category  
variation for plasticity  
the contrary, many dif-  
ling transduction signal  
rs (e.g., responding to  
contribute. But these  
ult to pin down as pri-  
icity (and therefore as  
hat purpose) since they  
of other functions as

y genes? So far, two ma-  
posed. On the one hand,  
genes” based on previ-  
ction of gene products  
tified by mutagenesis or  
ther hand, the increas-  
e of QTL (quantitative  
e used to identify genes  
phenotypic plasticity in  
apping could eventually  
t function of such genes

some regulatory switches are  
changes in the environment.”  
will cause batteries of genes  
specific subset of environm  
not in others.

Wu reckoned that QTLs t  
one environment may consti  
of regulatory plasticity, while  
across environments, but w  
the phenotype changes in an  
manner, may be good candi  
tivity. Indeed, he found that  
covered by his analyses fel  
plasticity category, with som  
sensitivity. These results are n  
as they may sound, because  
largely a statistical approach  
anything directly about gene  
the environment-specific Q5  
manner must be part of th  
turned on or off, but they a  
primary switches themselves  
ably active across all environ

These difficulties notwith  
plasticity genes has direct re  
ary questions concerning rea  
they change. While it is po

## Phenotype

Investigation of phenotypic plasticity in the literature for many years has seen varied attempts at a better understanding of the plasticity of phenotypic integration across environments and genotypes. The relationship among several traits and the whole-organism phenotype is the focus of this line of research because once one reflects on the fact that traits are not just a collection of independent traits that evolve separately from each other, but that all traits are linked to each other to some degree by the existence of genes, it becomes clear that the relationships among the traits themselves. In fact, the study of how sets of correlated traits are broken up and disassembled by natural selection is one of the most promising avenues for understanding the appearance of phenotypic nov-

elty. Genetic correlation is a statistical measure that quantifies the overlap in the genetic architecture of two traits. If most of the same genes affect both traits, the genetic correlation will be high, either positive or negative, depending on whether the genes have the same or opposite effects on the two

traits. While the allelic effects of the genes may differ, the resulting genotypes will have similar effects on the traits. The dramatic functions of the genes on the traits are the same. The covariances between the traits can then be readily shown to be positive or negative, depending on the direction of the effects toward the middle of the distribution. It remains to be seen how far this result can be generalized to more ecologically realistic cases, but it is clear that it is in demonstrating that the complex patterns of genetic integration are the result of a very simple mechanism of action on trait covariances.

Clear experimental evidence that the environment can indeed affect the genetic architecture has been published, for example by Lande (1994), who studied the genetic architecture of the tropical butterfly *Bicyclus an*, which I will return to later. The analysis (figure 5.4) of the relationships in these analyses shows that temperature (on PC2) and precipitation dramatically alter the genetic architecture. In the diagram, the vectors represent the phenotypic variables, and the lengths are proportional to the

ASONAL FORM

PC2 =  
-0.5

THERMAL FORM

variation induced by genotype-environment interaction in  
variation is summarized by principal components axes, the  
forms, the vertical ones separating the thermal forms. (Fr

revealing fashion. The re-  
developmental time and  
form was significant in the  
cause of a trade-off due to  
producing the wet pattern.  
er, disappeared during the  
corresponding wing pattern  
to make. This is an exam-  
mechanism potentially un-

case, it might contribute  
due to predation. Conver  
the butterflies might dev  
adapted for survival (lar  
suited for reproduction (a  
and several other details  
particularly good and rare  
integration within the fran  
system.



# Canopies

## ots

s discussed in the preceding can be seen interwoven with particularly clear case studies of the adaptive reaction of ed by neighboring individuals *shade avoidance response*, and of the eyespot on the wings will therefore examine these more detail here as illustrative of research on phenotypic

## and Ecology

and ecologists have long been at some plants respond in a way to canopy shade and that ated by one or more specific ever, the two ends (ecological s field of research had rarely y.

ove, shade avoidance is best

phytochrome A and phytochrome C play a role in cal response.

While morphological known in understory p tage of canopy gaps, mostly been studied in *bidopsis thaliana*, which instead of overtopping its *A. thaliana* does have a it is usually credited while its shade avoidance than that of some of its is found in a variety of ter- and intraspecific occur.

Given all of the above *thaliana* provides the rare opportunity to examine basis of ecologically re Schmitt and I took advantage by studying the reaction ble mutants affected in shade avoidance receptor systems. Figure 5.5, for example phytochrome B (the

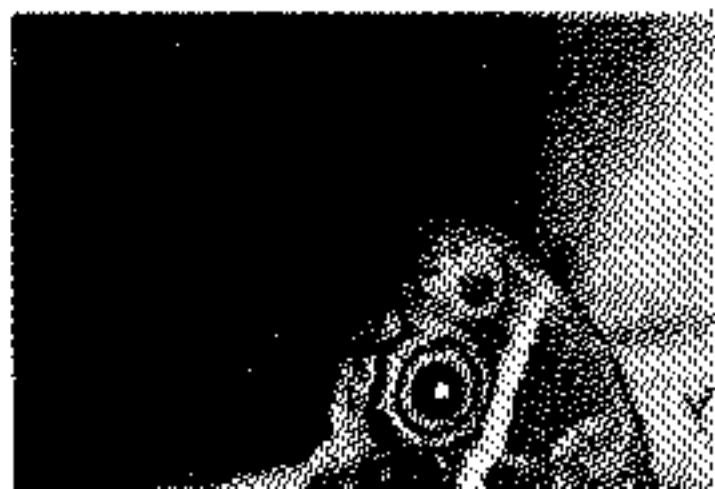
ns of single-gene mutants  
ception in *Arabidopsis*  
ered here is leaf produc-  
phase of the life cycle in  
ow R:FR ratio simulating  
ors. Notice the opposite  
wild type, in high light) of  
otted line) compared to a  
mutants (broken lines). The  
wild type. (Modified from  
9.)

otype. Second, under high  
actually acts in opposition  
ted line) in respect to the  
that eliminating its func-  
s the vegetative phase in  
onal analyses revealed the  
s on reproductive fitness,  
ocused on the epistatic ef-  
e genotypes are subjected  
y relevant conditions.

erstand that the point of  
investigate the genetic basis  
lasticity—an issue that can

perience a regular alternati  
sons, which brings about  
ecology in this species. Dur  
ditions are such that the  
about, being mostly intent  
ditions improve. In this cas  
hardly visible, so the anima  
vironmental background ar  
ure 5.6 *left*). When the wet  
ditions are completely diff  
butterflies are most actively  
their defense strategy char  
5.6 *right*). The eyespot is n  
has the potential to benefit  
predatory birds toward non

Brakefield and coworker  
pressive amount of inform  
characterizing the basic eco



spot patterns can evolve in a short period of time. This evolution from a series of selection experiments from comparisons of closely related *Drosophila* species whose evolutionary relationships are well understood. The outcome showed that the evolution of spot patterns to selection can be accounted for by changes in the frequencies at one or very few regulatory loci, controlled by major regulatory action. This work points toward a potential convergence of the study of regulatory genes and the study of evolutionarily relevant genes. This field was neglected until a few years ago.

## Future:

To predict the future, especially in fields of inquiry such as developmental biology. However, one can reasonably predict that some of the most promising research will develop into within-species comparisons. At best, this prediction might encourage students and active researchers to consider possible research programs.

Regulatory genes in evolutionarily conserved genes have been considered. The consequences of their evolution are not clear for there to be any allometry. Recently, however, non-coding DNA has been implicated in major evolutionary changes (Carroll et al. 1995), but the role of within-species sequence variation is not yet exploited by natural selection. This is a new phenotype (e.g., Purugganan et al. 1995). Should these preliminary results spread, they will force a re-evaluation of our current understanding of evolution (Schlichting and Pigliucci 1998).

Another area of plasticity that has been neglected because of methodological difficulties is the evolution of reaction norms. The evolution of plasticity in reaction norms is an important reaction norm variation. Plasticity in a group's reaction norm with a flat, no-plasticity reaction norm. The latter may make more sense in terms of functional ecological variation. This hardly represents a good model of patterns. However, when we do compare different species

onically, we really need understanding the ecology after the gargantuan pio- ausen, Keck, and Hiesey century, we have seen a research under controlled studies of phenotypic an ecologically realistic on of modern quantita- us to quantify the inten- ection under field condi- Reeve, this volume) we mples of adaptive pheno- terophylly in plants and is in salamanders, with they actually *are* under logistics of these experi- , and they represent for- e point of view of statis- les have appeared in the

the new merging of molecu search programs will contin in this area. Furthermore, t environment interactions pr cal framework for a better man nature itself, as well a our research into its biologi

### Notes

1. "Narrow-sense herita ditive genetic to phenotypic generally symbolized by  $h^2$ . ity," the ratio of total genet ances ( $\sigma_G^2/\sigma_P^2$ ), is symbolized
2. A quantitative trait loc chromosome, defined by lin cus, that has a significant ef trait. The phenotypic effects detected through crosses be fering in average expression trait.