

# Phenotypic plasticity and plant adaptation\*

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## SUMMARY

This paper focuses on phenotypic plasticity as a major mode of adaptation in plants. A methodological critique examines difficulties in studying plasticity, including the conceptually critical distinction between functionally adaptive and inevitable aspects of response. It is argued that plasticity studies depend critically upon the genotypic sample, the choice of environmental factors and factor states, and the definition of phenotypic traits. Examples are drawn from recent studies showing adaptive response by genotypes to physical aspects of the environment, as well as to biotic factors such as neighbour density and the presence of bacterial symbionts. Alterations of offspring traits by parental plants of *Polygonum persicaria* are discussed as a cross-generational aspect of plastic response to environment. Finally, individual plasticity and local ecotypes are examined as alternative bases of species ecological breadth, and methodological problems in distinguishing these alternatives are discussed.

*Key-words:* adaptation, maternal effects, norm of reaction, phenotypic plasticity, *Polygonum*, species distribution.

## INTRODUCTION

Natural environments inevitably vary, both spatially and temporally. According to the classic neo-Darwinian model, organisms accommodate that variation by means of natural selection, which through evolutionary time matches specific genotypes and environments. By assuming a simple Mendelian relationship of genotype to phenotype, this powerful model provides a genetic mechanism for adaptive phenotypic changes in populations. In this paper I wish to focus on a second major mode of adaptation, one which is becoming particularly well understood in plants: the capacity of a single genotype to produce different, functionally appropriate phenotypes in different environments, or *adaptive phenotypic plasticity*. This property of short-term individual response offers an 'alternative picture' of the way that organisms adapt to their environments (Bradshaw & Hardwick 1989). By virtue of phenotypic plasticity, adaptation occurs through individual development and physiology as well as through change in population gene frequencies. Thus, a single genotype may be able to maintain function and hence reproductive fitness under a variety of environmental conditions. For this reason, individual adaptive response has important implications for our

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\*This paper is based on a lecture presented at a symposium on 'Plant and Evolution' held on 18 May 1995 in celebration of the 150th anniversary of the Royal Botanical Society of The Netherlands.

understanding of natural selection and evolutionary diversification (reviewed in Bradshaw 1965; Schlichting 1986; Sultan 1987; West-Eberhard 1989; Stearns 1989; Scheiner 1993).

## THE STUDY OF ADAPTIVE PHENOTYPIC PLASTICITY

### *The norm of reaction approach*

In the new-Darwinian view, the expressed phenotype is considered a result of environmental interference superimposed on the 'inner reality' of the genes, which are seen as the basis of all evolutionarily meaningful variation (see critiques in Allen 1979; Sultan 1992). According to this model, adaptive diversity is best studied in a uniform environment, where genetic variation will be most clearly revealed. Alternatively, the genotype may be understood as a developmental system which will produce one of a number of possible phenotypes depending on its environmental circumstances (Schmalhausen 1949). To the extent that the various phenotypes are functionally adaptive to the environments in which they are produced, the individual's phenotypic repertoire in itself comprises a significant mode of adaptation to environment (Wright 1931; Bradshaw 1965).

This view of the phenotype as determined jointly by genotype and environment implies quite a different research approach, one designed to reveal the genotype's entire repertoire of responses. The phenotypic response pattern or *norm of reaction* of a genotype can be determined by cloning the genotype and measuring traits of interest in a specific set of environments. A two-dimensional plot of trait values in each environment thus specifies both the genotype and the environment associated with each phenotypic state. Norms of reaction for a group of genotypes can be plotted together to show graphically the relative magnitude of phenotypic differences among genotypes and among environments as sources of variation (e.g. Gupta & Lewontin 1982; Van Noordwijk 1989; Sultan & Bazzaz 1993a-c).

### *Adaptive versus inevitable plasticity*

One difficulty that arises immediately in plasticity research is the interpretation of these phenotypic responses to environment. As a result of physical and biochemical effects on metabolic and developmental processes, plants in unfavourable or resource-poor environments inevitably show reduced growth. Thus, although phenotypes produced in sub-optimal environments may include alterations that adaptively maximize function in those environments, they will necessarily reflect growth limits as well (Sultan & Bazzaz 1993a). For this reason, all of the phenotypic change associated with different environmental conditions cannot be assumed to represent adaptive plastic adjustment (Stearns 1982; Taylor & Aarssen 1988).

The recent literature on plant plasticity reveals two distinct approaches to this problem. The approach taken by most authors is to use the term 'phenotypic plasticity' to denote all phenotypic change across environments (e.g. De Jong & Stearns 1991; Markwell & Osterman 1992; Scheiner 1993). In other words, these authors use the terms 'phenotypic plasticity' and 'norm of reaction' interchangeably. In these studies, plasticity is simply a neutral metric of phenotypic differences in various environments, of unknown and possibly little functional significance (Zhang & Lechowicz 1994). Such studies address the question: 'How do phenotypes change from environment to

environment in this sample of genotypes? This approach thus provides information as to the amount and pattern of phenotypic variability, but does not address the selective impact of that variability.

A second approach is to conceptually distinguish aspects of phenotypic response to environment that are functionally adaptive from those that are developmentally or biochemically inevitable. This distinction is essential if we wish to know whether the phenotypic responses of genotypes may constitute adaptations. Hence, one can choose to focus specifically on *adaptive* phenotypic plasticity, defined as phenotypic response to an environment that enhances plant function and therefore fitness in that environment (Sultan 1987). According to this more precise definition, adaptive plastic variation will be a subset of the variation catalogued by norm of reaction data for any organism. The guiding question of the research then becomes: 'Given the growth limits posed by this set of environments, do individuals respond phenotypically in ways that specifically avoid or offset those limits?'

In the absence of historical information as to the course of natural selection, and since correlations with fitness will be negative rather than positive in these cases (the 'silver spoon' effect *sensu* Grafen 1988; discussed in Sultan & Bazzaz 1993a), the argument that a given phenotypic response is adaptive (functionally appropriate) must rest on engineering principles and ecophysiological interpretation (Lewontin 1982; Sultan & Bazzaz 1993a). For instance, the rate of photosynthesis per unit leaf area will inevitably be drastically reduced in conditions of low photon flux density, such that plants grown in reduced light intensities produce only a fraction of the biomass of plants given ample light. In the case of light-deprived plants, then, the functionally adaptive plastic response would be to maximize photosynthetic surface area relative to biomass, thereby increasing light interception per gram of plant tissue. After determining genotypic norms of reaction to a range of light levels, one may examine the relevant allocational and morphological traits to determine whether the phenotypes of light-deprived plants include such appropriate trait adjustments along with the inevitable biomass reduction.

In practice, this conceptually critical distinction may be quite difficult to make. In many cases, the plant physiological and ecophysiological literature provides a strong basis on which to evaluate the functional significance of changes in specific allocational, morphological, and metabolic traits. However, for some traits and environments relevant ecophysiological data on the functional effect of variation may be lacking. Furthermore, a given trait response may simultaneously reflect *both* inevitable and adaptive aspects. For instance, *Calamagrostis canadensis* plants produce fewer and shorter rhizomes in low-temperature soil treatments. This results in preferential clonal expansion into more favourable microsites, and more extensive exploitation of those sites once entered (Macdonald & Lieffers 1993). Although such a developmental response clearly cannot be classified as solely either 'inevitable' or 'adaptive', the conceptual distinction permits both aspects of the response to be recognized, and hence allows a clearer focus on both the response mechanism and its ecological impact than would a purely neutral measurement of phenotypic variability across temperature treatments.

Adaptive interpretation of trait plasticity is further complicated by the fact that fitness results from many aspects of the phenotype (Schlichting 1989). Thus, it is often necessary to consider interactions among sets of functionally related traits in order to evaluate the fitness effect of change in a particular trait (see examples and discussion in Sultan & Bazzaz 1993a). In some cases, how a trait is defined affects the interpretation

of plastic response. For example, Eiguchi *et al.* (1993) predicted that a flood-intolerant strain of cultivated rice would be found to lack the ability to adaptively elongate in response to shoot submergence. Their study revealed that the genetic difference between this strain and its wild progenitor did not affect the amount of elongation response, but rather the *timing* of the response. In the cultivated genotype, the shoot elongates too late to ensure survival if flooding occurs early in the life-cycle (Eiguchi *et al.* 1993). Thus, the plastic character of greatest adaptive importance was not amount of shoot elongation but the time required to initiate elongation after the submergence cue.

*The specificity of phenotypic response and its implications for experimental design*

Genotypes cannot be classified as more and less 'plastic', since the amount of phenotypic variability across environments will vary from trait to trait in the same individual (Bradshaw 1965; Sultan 1987). Reproductive traits such as fruit size and number are well known to show different amounts of phenotypic variability (Salisbury 1942; e.g. Marshall *et al.* 1986). In Composites, traits such as the number of organs per floret may be quite canalized, while in the same genotypes the number of florets per inflorescence may vary from one environment to another (Battjes & Bachmann 1994). Reaction norms of different traits may also vary in the direction or pattern of response to a given environmental range (Schlichting & Levin 1986). For instance, in response to increased soil nutrient supply, a given genotype of *Polygonum persicaria* may increase the mean size of leaves, decrease allocation to roots, and hold constant individual achene mass (Sultan & Bazzaz 1993c). Finally, phenotypes will vary ontogenetically, so the timing of trait measurements may also shape the results (Sans & Masalles 1994; Pigliucci & Schlichting 1995).

Adaptive interpretation of plastic response is particularly complex when traits that interact in their effect on fitness, such as leaf size and number, show different amounts and/or directions of response to an environmental change. Since phenotypic traits respond differently to a given change in environmental conditions, both the strength and the direction of correlations among traits are environmentally dependent (Schlichting 1989 and references). A further implication of this trait specificity is that correlations of particular functionally important traits with fitness will also vary from one environment to another. As a result, the intensity of selection on each correlated trait will vary among environments (Schlichting 1989). In neo-Darwinian terms, this poses a major constraint on natural selection in plant populations (Antonovics 1976). An ecophysiological perspective suggests that the functional importance of a given trait to fitness will indeed depend on environmental circumstances. For instance, relative biomass allocation to root tissue may strongly correlate with fitness when soil moisture or nutrients are in short supply, but not in more favourable soil environments (compare Sultan & Bazzaz 1993a–c). The environmental specificity of such correlations may suggest clarifications in trait definition and in adaptive predictions. For example, the correlation of water use efficiency (the ratio of photosynthetic carbon gain to transpirational water loss) with plant fitness varies not only in strength but in sign depending on environmental conditions, in a number of taxa (Donovan & Ehleringer 1994). One explanation for this paradoxical result is the fact that an increase in this ratio can be produced either by stomatal limitation that reduces carbon fixation along with water loss, or by an increased photosynthetic rate (Donovan & Ehleringer 1994). Depending on the severity of drought stress, these alternative physiological changes will have very different adaptive consequences.

For a given trait and set of environments, the magnitude and direction of phenotypic response may vary from genotype to genotype, as well as among populations and taxa (Counts 1993 and references). In populations that encounter variable environments, such genotype by environment interaction (revealed graphically as non-parallel norms of reaction) can retard selection for particular norms of reaction (Via 1987; Van Tienderen 1991) and maintain genetic variation even if genotypes differ on average for fitness-related traits (Via & Lande 1985; Mitchell-Olds & Rutledge 1986), since different genotypes will have relatively higher fitness in different environmental states (Gillespie & Turelli 1989; see Stearns & Koella 1986; De Jong 1990; and Gomulkiewicz & Kirkpatrick 1992 for further theoretical treatments of the evolution of norms of reaction in multiple environments). Norm of reaction studies of plant, animal, and algal populations typically reveal this type of interaction in response to both biotic and abiotic variation in environment (e.g. Bell *et al.* 1991; Gupta & Lewontin 1982; Shaw 1986; Mazer & Schick 1991; Sultan & Bazzaz 1993a–c; Schmitt 1993; Thomas & Bazzaz 1993; Windig 1994; Andersson & Shaw 1994). Thus, genotype by environment interaction rather than consistent between-genotype fitness differences across environments may typify patterns of genetic diversity in natural populations (Haldane 1946).

Within a particular genotype, patterns of phenotypic response vary depending not only on the trait measured, but on the precise set of experimental environments (Bradshaw & Hardwick 1989). As a result of this specificity, the relative magnitudes of among-genotype (or population) and among-environment sources of variation, as well as the mean phenotypic values and covariance patterns, depend entirely on the set of genotypes and environments used (Lewontin 1974; De Jong & Stearns 1991; Mazer & Schick 1991). The design of both the genetic sample and experimental environments is thus of crucial importance to norm of reaction studies. If the information is to be interpreted in an evolutionary context, it is clearly essential to study genotypes sampled from natural populations in a range of conditions relevant to the environmental variability that exists in the field. Moreover, the specific subset of natural populations, genotypes, and environments chosen for any study will profoundly shape the results and conclusions. For instance, the rapid-flowering *Arabidopsis thaliana* strains used in many laboratory studies have highly invariant (canalized) norms of reaction relative to other natural populations of the species. Researchers are thus inadvertently studying genetic lines with atypically low plasticity (Zhang & Lechowicz 1994).

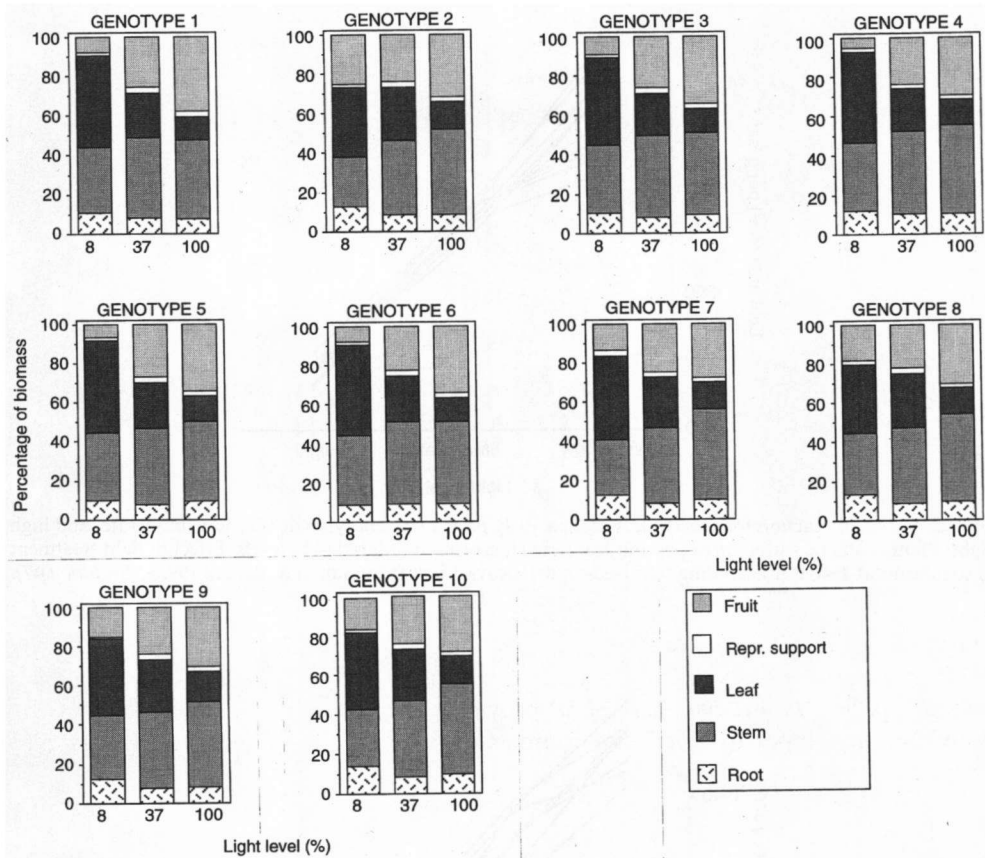
With respect to experimental environments, studies that manipulate ecologically important resources or stresses provide information of far greater interest than those which vary an easily controlled but otherwise arbitrary parameter (Van Noordwijk 1989). In addition to major abiotic factors such as light, moisture availability, macronutrients, and soil pH, biotic factors such as the density and size of neighbouring plants may represent key environmental pressures to which plants respond phenotypically (e.g. Platenkamp & Foin 1990; Mazer & Schick 1991). However, it is not always clear which environmental variable is most important. For example, although plants of *Murdannia keisak* in thermally polluted wetlands are phenotypically different from those in sites with lower water temperature, glasshouse studies showed that water temperature had no significant effect on phenotype (Dunn & Sharitz 1991). Further investigation suggested a more complex chain of causation: high water temperatures kill the overstorey vegetation, thus increasing the amount of light reaching the *Murdannia* plants. The phenotypic changes in the thermally polluted sites are due to this change in light intensity and not to increased temperature *per se* (Dunn & Sharitz 1991).

Although norms of reaction are plotted as continuous phenotypic curves, they are necessarily based on phenotypic means taken in a finite and usually quite small number of environmental treatments. Since reaction norms can by no means be assumed to be linear (Scheiner 1993), the precise levels of environmental factors used may strongly affect the patterns of phenotypic variation that emerge. Ideally, treatments will be chosen to reflect the actual variability of that factor in the area or populations of interest. Thus, a sampling protocol is required that will characterize not site means but site variability in the salient aspects of the environment. This may call for extensive sampling, as natural environments are extraordinarily variable not only spatially (Bazzaz & Sultan 1987; Bell *et al.* 1991; Thomas & Bazzaz 1993) but temporally, within as well as between growth seasons (Bazzaz & Morse 1991; Sans & Masalles 1994). Indeed, seedling cohorts that germinate in the same site during a single growth season, but at different times within that season, will express the phenotypic effects of growing in different environments (Sans & Masalles 1994; see also Billington *et al.* 1990).

#### ADAPTIVE PLASTICITY TO THE IMMEDIATE ENVIRONMENT

Numerous studies in a broad range of plant taxa and life forms have shown adaptive plasticity in such traits as tissue allocation, morphology, defence biochemistry, and metabolic pathways and rates (reviewed in Bradshaw 1965; Schlichting 1986; Sultan 1987; Bradshaw & Hardwick 1989). A study of norms of reaction in the widespread annual species *Polygonum persicaria* provides examples of adaptive response by individual genotypes to several environmental factors in growth traits important to resource acquisition.

In one experiment, 10 genotypes from an old-field population of *P. persicaria* were cloned and grown in the glasshouse at three light levels, covering the range of light availabilities measured in the field (from 100% to 8% of full summer sun). Other aspects of the environment were held constant at favourable levels. As expected, plants deprived of light showed reduced growth. Total plant biomass was reduced by 98% in clones grown at very low light (8%) compared with those given full sun (Sultan & Bazzaz 1993a). Of far greater interest were the functionally appropriate allocational and morphological changes made by all of the genotypes in response to reduced light intensity. In moderately and severely reduced light, genotypes respectively doubled and tripled their proportional allocation of biomass to leaf tissue (Fig. 1), thus increasing relative allocation to the organ collecting the limiting resource (see Chapin *et al.* 1987). Light-deprived plants also expressed great plasticity for leaf morphology by increasing specific leaf area (surface area per gram of leaf tissue; Fig. 2). This thin spreading of leaf tissue is known to enhance light-harvesting efficiency under conditions of low photon flux density (Björkman 1980 and accompanying references). The combined effect of these phenotypic changes under moderate and low light was to dramatically increase leaf area relative to plant biomass. As a result, despite the inevitable severe decreases in photosynthetic rate per unit leaf area, the relative photosynthetic efficiency of the plants (mg CO<sub>2</sub> fixed per gram plant tissue per unit time) remained constant or even increased. Furthermore, all 10 genotypes survived and produced viable achenes across the full range of light environments (Sultan & Bazzaz 1993a). Thus, these phenotypic responses were associated with a very broad range of tolerance for variability in light conditions within individual genotypes.



**Fig. 1.** Proportional biomass allocation in 10 *Polygonum persicaria* genotypes cloned and grown at very low, moderate, and high light. Each box represents one genotype; each column within the box shows the mean biomass proportions of six replicates at the specified light treatment (columns sum to 100% of total biomass). Proportional allocation to leaf tissue increases steeply with reduced light. The effect of light treatment is significant at  $P < 0.001$  for all five biomass fractions according to MANOVA (data from Sultan & Bazzaz 1993a, *Evolution* 47).

The phenotypes of light-deprived *P. persicaria* plants thus showed inevitable growth reductions as well as alterations that maximized photosynthetic surface area relative to plant biomass. In order to interpret these latter changes as plastic adaptations to low light, it is necessary to determine that they occurred specifically in response to low-light conditions rather than as a general ‘stress phenotype’ produced in any sub-optimal environment. To investigate this question of resource specificity, a second experiment was performed in which genotypes from the same population were grown at four soil moisture treatments: severe drought (daily wilting), moderate drought (occasionally wilting); field capacity (soil both moist and aerated), and flooded (pots submerged to soil level). Again, other aspects of the environment such as light, temperature, ambient humidity, and soil nutrients were maintained at constant, favourable levels (Sultan & Bazzaz 1993b).

One specific response appropriate to drought stress would be to increase biomass allocation to the root system relative to vegetative tissues, which maximizes the supply of water available to those tissues (Fitter & Hay 1981 and references). All of the

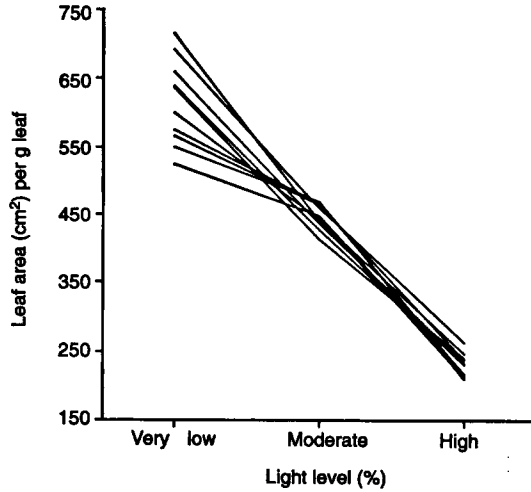


Fig. 2. Norms of reaction for specific leaf area in 10 *P. persicaria* genotypes at very low, moderate, and high light. Photosynthetic surface area per unit leaf tissue increases at reduced light levels. Effect of light treatment is significant at  $P < 0.001$  according to mixed-model ANOVA (data from Sultan & Bazzaz 1993a, *Evolution* 47).

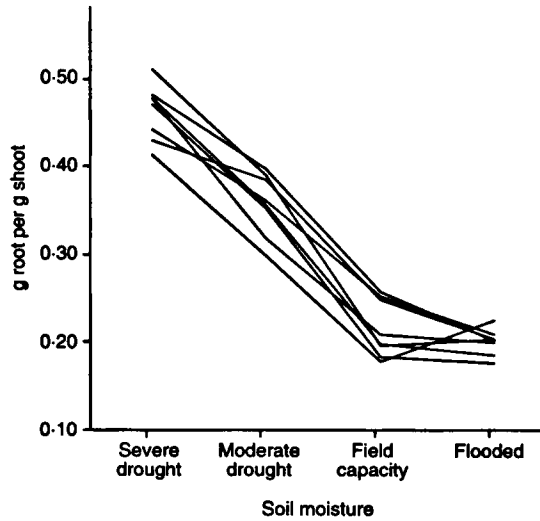


Fig. 3. Norms of reaction for root to shoot biomass ratio in eight *P. persicaria* genotypes cloned and grown at four soil moisture levels. Allocation to roots increases sharply relative to vegetative tissue with decreasing soil moisture. The effect of moisture treatment is significant at  $P < 0.001$  according to mixed-model ANOVA (data from Sultan & Bazzaz 1993b, *Evolution* 47).

*P. persicaria* genotypes showed this plastic adjustment to moisture limitation, increasing root-to-shoot biomass ratio by *c.* 70% in moderately droughted soil, and by more than 100% in extremely dry soil relative to plants of the same genotypes given ample soil moisture (Fig. 3). In contrast to clones of closely related genotypes deprived of light, plants subjected to drought did not alter specific leaf area or change tissue allocation to leaves compared with well-watered plants (Sultan & Bazzaz 1993b). Phenotypic responses were thus specific to the limiting resource, in this case soil moisture.



The plastic responses of the *Polygonum* genotypes to waterlogged soil were even more dramatic. Due to the low energy efficiency and phytotoxic end products of anaerobic metabolism, flooded soil represents an extreme plant environment, and one in which many species suffer drastic growth reductions or mortality (Levitt 1980; Kramer 1983). Surprisingly, the *Polygonum* plants grew and reproduced equally well in the flooded treatment as at the optimal treatment (Sultan & Bazzaz 1993b). When plants from the water-logged treatment were examined, they were found to have radically altered root system morphology and deployment. The flooded *Polygonum* produced dense mats of extremely fine adventitious and superficial roots just at the surface of the soil and around the interior of the clay pots. This root morphology did not occur in any of the other 10 experimental environments in which these genotypes were raised (Sultan 1990). The production of such root systems in response to soil flooding is a well known feature of specialized, flood-tolerant wetland species. Such species avoid the deleterious effects of root oxygen deficits by creating superficial roots with aerenchymatous channels to internally transport oxygen from the soil surface to the deeper roots and rhizosphere (Blom *et al.* 1994). Again, all of the genotypes survived and reproduced in every moisture treatment, from extreme drought to flooding (Sultan & Bazzaz 1993b). In *P. persicaria*, a broad range of adaptive diversity for contrasting moisture conditions evidently exists within single genotypes.

The ability of *P. persicaria* genotypes from the old-field population to respond plastically to flooding was particularly surprising because the population inhabits a hilltop site, where it has been established for between 20 and 200 years (Sultan 1990). Although the population may well have originally been colonized by immigrants from a lowland area subject to periodic flooding, such flooding cannot have occurred at the old-field site for many generations. Thus, the capacity to recognize and respond plastically to root submergence has evidently persisted in this population in the absence of on-going selection pressure (Sultan & Bazzaz 1993b). This raises the question of whether the capacity for plastic response carries a fitness cost to the genotype (see discussion and references in Sultan 1992). This question is of key theoretical importance because the conditions under which natural selection is expected to lead to adaptive plasticity rather than canalized adaptations depend largely on relative costs and benefits (Lewontin 1957; Levins 1968; Moran 1992). Although very little is known empirically about the magnitude of such costs, they are usually hypothesized to be substantial (Van Tienderen 1990). However, the result described above is consistent with the possibility that having once evolved, the capacity for plastic response to flooding may bear no fitness cost (Sultan & Bazzaz 1993c).

As plant biologists increasingly study phenotypes in more than one environment, more subtle aspects of plasticity may come to light. For example, under different environmental stresses, plants may alter anatomical as well as morphological traits. In xeric sites, leaves of the Patagonian forage grass *Festuca pallelescens* change not only in size and shape, but unlike the leaves of this species in moist habitats, they have continuous bands of sclerenchyma cells under the leaf epidermis (Oliva *et al.* 1993). This distribution of sclerenchyma is thought to enhance drought-tolerance (Oliva *et al.* 1993). Another aspect of plasticity that demands meticulous study is that of mineral rather than biomass allocation. Patterns of mineral allocation within the plant body have a strong impact on efficient carbon fixation and other aspects of plant function, and may be quite complex (Chapin *et al.* 1987). In highly productive herbaceous species such as *Carex acutiformis*, plants respond to increased nitrogen supply by enhanced

translocation to leaves in the upper, most highly illuminated portion of the plant canopy. This mineral reallocation creates a leaf nitrogen gradient that conforms to the steep gradient in photon flux density available to differently positioned leaves (Aerts & Caluwe 1994). This pattern of leaf nitrogen redistribution conforms to the optimal pattern for maximum carbon gain, which depends on both mineral supply and light availability (Bazzaz & Harper 1977; Field & Mooney 1986; additional references in Aerts & Caluwe 1994).

Many remarkable instances of plasticity entail plant response to biotic elements of the environment. Not only are plastic (inducible) chemical defences in response to herbivory far more widespread than previously believed (reviewed in Karban & Myers 1989), but in at least one case, structural defences may also be produced in response to vegetative damage. Ecologists in Kenya found that branches of *Acacia seyal* trees subjected to grazing by giraffes produced longer and more densely distributed defensive thorns than did branches out of reach of giraffes (Milewski *et al.* 1991). Controlled experiments showed that the presence and increased length of these thorns effectively deterred browsing (Milewski *et al.* 1991). Genotypes of *Impatiens capensis* respond plastically to a more delicate biotic cue. The stems of individuals in dense stands are greatly elongated, a phenotype which enhances fitness under crowded conditions. This adaptive elongation is cued by a phytochrome-mediated response to the change in light quality that occurs under vegetative shade (S. Dudley & J. Schmitt, unpublished).

The leguminous herb *Lupinus nanus* also adjusts plastically to the presence or absence of a neighbour that strongly affects its function: nitrogen-fixing bacteria of the genus *Bradyrhizobium*. These bacteria induce the formation of root nodules which they thenceforward inhabit, contributing significantly to the plant's nitrogen supply. The symbiotic relationship between leguminous plants and their nodulating bacteria is generally considered to be a mutualistic one; it is of undoubted benefit to the plant, particularly so in low-nitrogen soils (Fitter & Hay 1981). In a glasshouse study of nitrogen-deprived *L. nanus*, plants grown without soil inocula increased by 94% the proportion of biomass allocated to roots compared with those grown in the presence of bacteria ( $F=65.2$ , difference significant at  $P<0.001$ ; unpublished data of A. Wilczek and E. Simms). Among the plants in inoculated soils, individuals with fewer bacterial nodules allocated proportionally more biomass to roots than did more heavily nodulated individuals. Thus, plants responded to the paucity or absence of symbionts that supply usable nitrogen by increasing their production of nitrogen-gathering organs (roots) relative to other plant tissues (A. Wilczek, unpublished).

## PLASTICITY ACROSS GENERATIONS

Environmental conditions may affect not only the plant itself but its progeny (reviewed in Roach & Wulff 1987). Each seed's nutrient reserves are provided by the maternal plant, and their abundance and quality will be influenced by its carbohydrate and mineral status. The seed coat and associated fruit tissues are in fact tissues of the maternal plant (Westoby 1981). Hence, it is often assumed that plants in unfavourable growth conditions will produce not only fewer but smaller, poorly provisioned seeds. Because of the central importance of seed size and quality to seedling establishment (Salisbury 1942; Harper *et al.* 1970; Silvertown 1984; McGinley *et al.* 1987; Forbes 1991; Stephenson 1992), limits to maternal resources might thus be expected to cause reduced fitness in the next generation (e.g. Parrish & Bazzaz 1987; Stratton 1989; additional

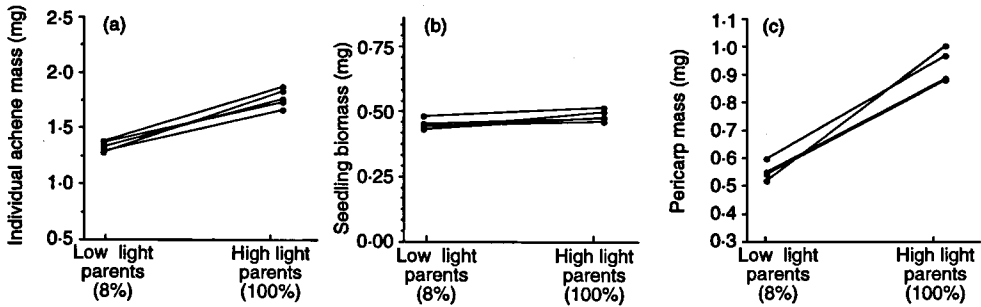


Fig. 4. Norms of reaction for offspring traits in five parental *P. persicaria* genotypes cloned and grown to reproductive maturity at very low (8%) and high (100%) light (means of 12 offspring per parent per treatment). Light-deprived parents produce achenes that weigh less individually due to reduced pericarp, not reduced seed reserves (S. E. Sultan, unpublished data). (a) Mass of individual achenes produced by low-light versus high-light parents. Effect of parental light treatment significant at  $P < 0.001$  according to ANOVA ( $F = 68.62$ ). (b) Total seedling biomass at 72 hours of offspring produced by low-light and high-light parents. Effect of parental light treatment not significant ( $F = 2.65$ ;  $P \leq 0.11$ ). (c) Mass of pericarp tissue surrounding each seed in achenes of low-light versus high-light parents. Effect of parental light treatment significant at  $P < 0.001$  ( $F = 243.80$ ).

references in Roach & Wulff 1987). An alternative possibility is that in some taxa, resource-limited maternal plants may adjust offspring traits so as to maximize offspring quality despite those limits, and thus mitigate the negative carry-over effect of poor parental conditions (treated theoretically by Lloyd 1987; Haig & Westoby 1988; Kirkpatrick & Lande 1989). Thus, variation in the structure and composition of propagules in different parental environments may constitute a second, cross-generational aspect of adaptive plasticity (Lacey 1991; Schmitt *et al.* 1992). Like other aspects of response to environment, the amount and patterns of plasticity for offspring traits are likely to vary among genotypes, taxa, traits, and environmental states (Roach & Wulff 1987; Schmitt *et al.* 1992; Platenkamp & Shaw 1993).

The achenes produced by cloned *Polygonum persicaria* genotypes grown in contrasting environments provide ideal material for a study of the effects of parental environment on offspring traits. (Plants are referred to as 'parental' rather than maternal, since the achenes were produced by self-pollination.) The smaller *P. persicaria* plants grown at very low light produced fewer achenes than did plants of the same genotype given full sun (cf. the developmentally inevitable reduction in plant biomass noted above), and the achenes weighed less individually (Fig. 4a). To determine whether these light-deprived plants did indeed provision their offspring less well, achenes from high-light and low-light grown parents were germinated in sterile sand in a dark growth chamber, and each seedling weighed 72 hours after its emergence. Because the seedlings were given no light or added minerals, seedling dry weight provided a good indicator of initial provisioning by the parental plant.

Surprisingly, parental light deprivation had no effect whatsoever on mean seedling biomass (Fig. 4b; S. E. Sultan, unpublished data). In other words, provisioning to individual seeds by parental plants remained constant despite a 92% reduction in available light. The difference in achene mass was due not to reduced offspring provisioning, but to a change in fruit structure. The *Polygonum* fruit is an achene ('nutlet') consisting of a seed, with its embryo and nutritive endosperm, enclosed in a thick outer pericarp or shell. Plants grown in low light reduced the amount of pericarp tissue by approximately one-half, compared with fully insulated plants (Fig. 4c; S. E.

Sultan, unpublished data). This alteration in fruit structure suggests that under severe light limitation, parental plants conserved nutrient provisioning to seeds, and economized on carbon-based pericarp tissue. The relative thickness of pericarp affects germination behaviour (S. E. Sultan, unpublished data) and perhaps achene longevity in the soil, but is less critical to offspring survival and establishment than is seed provisioning. This response by parent plants evidently constitutes functional homeostasis: adaptive constancy of phenotypic traits central to fitness, achieved by plasticity in developmentally related traits (Sultan & Bazzaz 1993c and references therein). As in the case of immediate phenotypic response to environment, this response was resource-specific. For instance, plants produced in very dry soil also had lower total biomass and produced fewer achenes, but did not alter the pericarp thickness of those achenes (S. E. Sultan, unpublished data).

### ADAPTIVE PLASTICITY AND SPECIES DISTRIBUTION

Because phenotypic plasticity lends adaptive diversity to individual genotypes, it is likely to influence both the ecological distribution of species and their patterns of diversification. This issue is being studied in a monophyletic group of annual plants in the genus *Polygonum* (S. E. Sultan, unpublished). Species in section *Persicaria* share a common life-history, breeding system, habit, and morphology, but differ markedly in their ecological breadth (the range of habitats in which they can successfully grow and reproduce). *P. persicaria* and *P. lapathifolium* are ecological 'generalists', while *P. hydropiper* and *P. cespitosum* are narrow 'specialists'. *P. persicaria* (the annual species that earlier provided several examples of adaptive plasticity) occurs naturally in a wide diversity of light, moisture, edaphic, and density conditions, in such contrasting habitats as open wetlands, forest trails, cultivated fields, sandy roadsides, and chalk pits (Table 1; Simmonds 1945a; Lousley & Kent 1981; Staniforth & Cavers 1979; Sultan 1990). Its close relative *P. lapathifolium* also occurs in a range of habitats (Simmonds 1945b; Sultan 1990). Both of these species are so widespread and invasive as to be considered serious agricultural weeds in many temperate regions (Holm *et al.* 1979). In contrast, *P. hydropiper* and *P. cespitosum* are ecologically quite narrow, and occur only in very moist and shaded sites, respectively (Table 1; Lousley & Kent 1981; Staniforth & Bergeron 1990; S. E. Sultan, unpublished observations). What accounts for the very broad ecological range of species such as *P. persicaria* and *P. lapathifolium* compared with otherwise similar, closely related congeners?

One possible explanation for this kind of within-species ecological breadth is the concept of the locally adapted ecotype (reviewed in Bradshaw 1984). According to this model, each population once established undergoes differential change in allele frequencies as a result of local selective pressures (acting in conjunction with genetic drift and other structuring forces). Environmental differences from one habitat to another are thus accommodated by the evolution of specially adapted genetic entities (see references and critique in Sultan 1987), and the ecological breadth of the species will arise from the aggregate total of these locally adapted populations. An alternative model is one in which each genetic individual in the species is sufficiently plastic as to be in itself broadly tolerant of environmental diversity (Baker 1965). In this case, the ecological range of the species would arise from the response breadth of its individuals (Salisbury 1940; Lewontin 1957; Brown & Marshall 1981; Gross 1984; Bazzaz & Sultan 1987).

**Table 1.** Ecological distribution of *P. persicaria*, *P. lapathifolium*, *P. hydropiper* and *P. cespitosum* in North America, Europe and Asia

Habitat	<i>P. persicaria</i>	<i>P. lapathifolium</i>	<i>P. hydropiper</i>	<i>P. cespitosum</i>
Cultivated fields	✓	✓	No	No
Open wetlands	✓	✓	✓	No
Swampy meadows, bogs	✓	✓	✓	No
Occasionally flooded riverbanks and ditches	✓	✓	✓	If shaded
Wet acidic peat	✓	✓	No	No
Dry roadsides	✓	✓	No	If shaded
Open sand beaches	✓	No	No	No
Waste ground	✓	✓	If moist	If shaded
Chalk pits	✓	✓	No	No
Shaded wetland	✓	No	✓	✓
Forest trails	Rare	No	Rare, if wet	✓
Major weed?	Yes	Yes	No	No

Habitats marked with a tick (✓) are those in which the species typically occurs.

Rare=small populations of the species are occasionally found in these habitats.

Based on examination of herbarium collections in the Gray Herbarium of Harvard University and the New England Botanical Club, on unpublished field observations, and on references cited in the text.

A good deal of theoretical work has identified conditions under which the evolution of individual plasticity should be favoured over ecotypic divergence (Levins 1968; Van Tienderen 1990). If the range of plastic response within individuals strongly affects the overall ecological breadth of a species (Lewontin 1957; Baker 1965; Bradshaw 1965; Sultan 1987), differences in phenotypic response capacities for functionally important traits may be a major factor distinguishing 'generalists' and 'specialists' (discussed in Salisbury 1940; Thoday 1975; Scheiner & Goodnight 1984; Crick & Grime 1987; Macdonald *et al.* 1988; Bradshaw & Hardwick 1989; relevant models reviewed in Futuyma & Moreno 1988). Although 'specialists' are usually considered to possess superior adaptation to their native environments, ecologically restricted species may in fact represent the failure of species to evolve adaptive plasticity (Sultan 1992).

In plants, these evolutionary alternatives are often tested through common garden and reciprocal transplant studies on populations of ecologically widespread and phenotypically diverse species (references in Galen *et al.* 1991). Such studies are designed to show whether the phenotypic differences between plants in different sites reflect genetic differentiation rather than immediate environmental effects, and if so, whether these genetic differences among populations constitute local adaptation to their respective environments. Although many studies have revealed genetic divergence among populations for patterns of environmental response as well as trait means (Schlichting & Levin 1988; Taylor & Aarssen 1988); the adaptive nature of those differences is generally far from clear (Bradshaw 1984; Macdonald & Chinnappa 1989; Billington *et al.* 1990; Van Tienderen 1990; Winn & Evans 1991; Schmitt 1993; Galloway, unpublished; but see Emery *et al.* 1994).

Dramatic *in situ* phenotypic differences among conspecific populations may disappear when plants are transplanted to a common environment (e.g. Oliva *et al.* 1993). Such

results underscore the tremendous variability expressed by plant genotypes in different growth conditions, but do not permit the ecotype explanation to be rejected as the source of each population's environmental tolerance. Populations may converge phenotypically in a favourable environment, yet respond very differently and with varying degrees of functional success to other environmental circumstances and stresses. Because selective differentiation among as well as within populations depends on fitness differences relative to the distribution of environments (and on gene flow; Van Tienderen 1990), those differences must be assessed for the entire set of relevant environmental states (discussion and references in Sultan 1987).

Somewhat more compelling evidence for the relation of adaptive plasticity to the ecological amplitude of species is found in cases where conspecific populations from contrasting habitats express remarkably similar patterns of environmental response to a relevant range of environments (Schlichting & Levin 1988). For instance, amounts and patterns of phenotypic response to temperature did not differ among populations of *Zizania aquatica* evolved in very different climates (New Brunswick, north-eastern Canada versus Georgia, in the south-eastern United States; Counts 1993). Similarly, Zhang & Lechowicz (1994) found that populations of *Arabidopsis thaliana* from latitudes as different as 16°N and 56°N showed very similar patterns of morphological alteration in response to nutrient availability. Studies focusing on aspects of phenotypic response that affect function in different habitats are particularly likely to illuminate the basis of ecological breadth. Populations of *Prunella vulgaris* from shaded and insolated sites shared similar responses to light intensity for functionally key traits such as photosynthetic capacity and water use efficiency, although they differed in norms of reaction for morphological traits of uncertain relevance to fitness (Winn & Evans 1991). Thus, disjunct populations may diverge genetically in selectively trivial traits, but continue to share patterns of functionally important plasticity.

The strongest possible experimental support for the plasticity hypothesis would be a case where populations showed equivalent fitness across a set of conditions based on measured environmental differences among their sites of origin, along with functionally interpretable phenotypic responses to those conditions. However, the absence of habitat-specific fitness differences among populations in experimental environments does not falsify the ecotype hypothesis. Under experimental conditions, it is never certain that the environmental factor in response to which the populations have differently evolved has been correctly identified, or if identified has been tested at the appropriate levels, or with the relevant states of interacting environmental factors. Once the extraordinary specificity of environmental response is recognized, the assumption that experimental results can be extrapolated to the real world becomes a more tenuous one.

A more robust test of the hypothesis that the plasticity of individuals can accomplish adaptation to different habitats can be made through reciprocal transplants of genotypes from different populations into the field sites of origin. In one such field test, there was no between-population component of variation in survival for *Anthoxanthum odoratum* populations from dry and mesic sites, suggesting that ecotypic differentiation had not occurred for this aspect of the habitat (Platenkamp 1990). This result is particularly intriguing because it is in this same species that the paradigmatic case of fine-scale ecotypic differentiation (for heavy-metal soil contamination) was described (references in Bradshaw 1984).

A two-step approach to this issue may prove particularly fruitful: testing differences among populations in realized fitness through reciprocal transplant studies in the field, as well as examining growth across a relevant range of controlled environments to permit ecophysiological interpretation of phenotypic differences. Such a combined approach would permit both a meaningful assessment of realized fitness to test the ecotype hypothesis as the source of adaptation to field conditions, and ecophysiological insight to more carefully interpret environmentally-induced phenotypic variation. Note, however, that even reciprocal field studies will not permit the ecotype hypothesis to be rejected as a possible mode of differential adaptation, since the salient environmental pressure may be a rare climatic or biotic event unlikely to occur even in an experiment lasting many years. Such rare, severe selective events may have great impact on the genetic composition of populations (Travis & Mueller 1989). Thus, the ecotype explanation cannot be falsified because it is impossible to test relative fitness in all potential environments. Although this limitation should be recognized, it may not be as great an obstacle to a deeper understanding of species' ecological breadth as it first appears. Ecotypic differences and adaptive plasticity may be complementary rather than mutually exclusive ways that organisms evolve to accommodate environmental variability. Indeed, it is likely that some degree of selective differentiation will accompany the process of genetic divergence between populations (depending on the occurrence of appropriate mutations (Al-Hiyaly *et al.* 1993), population structure and gene flow, and selective pressures). This in no way diminishes the importance of understanding the role of individual phenotypic plasticity in the environmental tolerance and ecological distribution of species.

In addition to illuminating the basis of present-day species distributions, the relation of individual plasticity to ecological breadth may significantly influence subsequent patterns of evolutionary diversification. If ecological amplitude rests upon individual plasticity, species in which individuals are less plastic would be expected to show greater selective divergence into local ecotypes and ultimately adaptively differentiated species (Thoday 1953; Bradshaw 1965; Jain 1979). Conversely, many aspects of adaptive differentiation may be obviated in taxa with functionally appropriate phenotypic flexibility in response to key environmental pressures (Sultan 1987). Consistent with this idea, in the widespread introduced species *Bromus tectorum*, 60 populations from diverse arid environments across North America showed remarkably little genetic divergence (Novak *et al.* 1991). Based on protein electrophoresis for 25 isozyme loci, the mean genetic identity coefficient (Nei's  $I$ ) was calculated to be 0.98. This was particularly surprising because the species is self-pollinating, which would facilitate differentiation among populations (Novak *et al.* 1991). However, quantitative growth traits were extremely variable within families due to environmental response. This highly successful species may thus be composed of numerous genetically similar populations, each consisting of 'general-purpose', adaptively plastic genotypes (Novak *et al.* 1991).

## CONCLUSIONS

It is becoming increasingly clear that a great deal of adaptive phenotypic diversity may exist within as well as between genetic individuals. The highly specific nature of phenotypic response dictates that effective studies of this aspect of diversity be carefully designed with respect to functional traits, genetic sample, and environmental treatments. Phenotypic plasticity may be especially dramatic in sessile organisms such as

plants (as well as clonal invertebrates; Harvell 1990), which must tolerate environmental fluctuations. Plant response to immediate environment is particularly flexible because plants can vary the number as well as the size of parts, and can differently allocate and reallocate resources to various tissues. Studies of alterations to offspring traits under different parental treatments suggest that this individual adjustment to environment may extend across generations as well.

The ecological distribution of a species may be partly determined by the capacity for individual adaptation shown by its individual members. A further possible implication of this point is that population divergence and ultimately allopatric speciation under local selection pressures may be obviated by this property of individual plasticity. Thus, the degree to which individuals of a species tolerate environmental variability through plastic response may shape its patterns of evolutionary diversification. Further insight into the relation of phenotypic plasticity to ecological breadth may illuminate differences between generalist and specialist taxa. If this is one reason certain groups are relatively less speciose than others, such insight may also clarify the relation between species diversity and adaptive diversity, which is clearly more complex than that proposed by Darwin in his selective theory of species divergence.

Plants undoubtedly provide excellent systems in which to study phenotypic plasticity, as they may in many cases be replicated clonally and subjected to environmental manipulations. It should be noted, however, that the ecological and hence evolutionary role of individual adaptability is likely to be extremely important in other organisms as well. Phenotypic plasticity has been documented in organisms as diverse as algae (van Alstyne 1988; Egan & Trainor 1991), fish (Meyer 1987; Brönmark & Miner 1992), sessile and planktonic crustaceans (Lively 1986; Ebert *et al.* 1993), marine bryozoans (Harvell 1986), insects (Scharloo 1987), and small mammals (Negus *et al.* 1992). As is the case with plants, these responses are rapid (Harvell 1992) and trait-specific (Ebert *et al.* 1993; Ford & Siegel 1991), and may be difficult to interpret with respect to adaptation (Negus *et al.* 1992). Animal as well as plant taxonomy is vulnerable to errors when morphs with a common genetic basis are erroneously named as distinct taxa (Meyer 1987; Pigliucci *et al.* 1991).

Despite the relatively sudden interest in the subject shown by evolutionary biologists and ecologists in the past few years, several crucial aspects of phenotypic response remain poorly understood. Apart from evidence that average heterozygosity does not correlate with phenotypic plasticity (Macdonald & Chinnappa 1989; Counts 1993) and that norms of reaction can be changed under selection (Waddington 1959; Scheiner 1993 and references), little consensus exists as to the genetic basis of plasticity (Andersson & Shaw 1994). Clearly, little progress can be made in our understanding of the evolution of phenotypic response until the genetic basis of such response becomes less of a mystery. Indeed, despite a wealth of mathematical models for the evolution of plasticity, there are as yet remarkably few empirical data on critical parameters such as the distribution of environmental variability, the possible cost of plasticity, constraints on the mechanisms of plastic response, and its functional and fitness consequences (Scheiner 1993; Zhang & Lechowicz 1994).

To truly understand the process of evolutionary change, it is essential to study the relationships of organisms to their environments both on an evolutionary timescale and in terms of individual developmental and physiological response. A focus on individual phenotypic response will enlarge our view of developmental mechanisms, of genetic diversity, and of evolutionary diversification.



## ACKNOWLEDGEMENTS

The author wishes to thank the Royal Botanical Society of The Netherlands for the invitation to participate in the symposium. She also acknowledges with thanks the comments of Dr Cynthia Seiwert, Dr Fred Cohan, and Professor Konrad Bachmann on an earlier version of the manuscript.

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