Indian Journal of Agriculture
and Allied Sciences
A Refereed Research Journal

ISSN 2395-1109
e-ISSN 2455-9709
Volume: 2, No.: 4, Year: 2016

www.mrfsw.org

Received: 24.10.2016, Accepted: 20.12.2016

PHENOTYPIC PLASTICITY IN PLANTS

M. Amaranatha Reddy[1*], C.V. Ramanarayana[2], G. Purna Dattha Reddy[3] and G. Chandramohan Reddy[4]

[1]Dept. of Genetics and Plant Breeding, College of Horticulture, Anantharajupeta, Dr. YSRHU, E-mail: amylarapu001@gmail.com, [2]Dept. of Plant Physiology, COH, KAU, Vellanikkara (KERALA), [3]Dept. of Vegetable science, College of Horticulture, Anantharajupeta, Dr. YSRHU and [4]Dept. of SPMA, College of Horticulture, Anantharajupeta, Dr. YSRHU, Corresponding Author: M. Amaranatha Reddy

Abstract: *Climate change is altering the availability of resources and the conditions that are crucial for plant performance. Plants respond to these changes by inducing shifts in phenotype. A single genotype can produce different phenotypes in different environments. This fundamental property of organisms is known as phenotypic plasticity.*

Based on the duration of the change both long term and short term plasticity have been reported. Abiotic factors such as light, temperature, water, salt stress, CO_2 *and biotic factors such as neighbouring plants and herbivory influences the phenotypic plasticity. Functional traits are those that help to describe the ecology of species. To asses plasticity in plants, a few easily quantifiable variables have been identified the plant functional traits. Functional types are widely used in global climate models to group species according to their function in the ecosystem or community. Evolution of adaptive plasticity requires that plastic genotypes have the highest global fitness averaged over the environments rather than the highest fitness in each environment separately.*

The plastic molecular responses to environmental signals can occur in many ways. An external stimulus must first be perceived at the cell surface by a receptor that then initiates a signaling cascade. The evolution of plasticity may be constrained by costs and limits of plasticity, and that as a consequence specialist genotypes or intermediately plastic ones may evolve instead of highly plastic generalist genotypes.

Keywords: *Phenotypic Plasticity, Food Security, Biodiversity and Climate Change*

1. Introduction: Climate change is altering the environments in which all organisms develop. Plant species can adjust to these novel conditions through phenotypic plasticity, adapt through natural selection or migrate to follow conditions to which they are adapted; these options are not mutually exclusive. For any given plant species or population, determining responses to environmental changes will require an understanding of the environmentally induced variation in the phenotype of individual plants. Once regarded as noise, phenotypic plasticity is now understood to be genetically controlled, heritable and of potential importance to species' evolution [1]. With mounting evidence from molecular and developmental biology, we are now at the threshold of gaining a sophisticated understanding of the mechanisms of plasticity, which will be crucial for predicting changes in species distributions, community composition and crop productivity under climate change [2, 3].

Some authors have argued that plastic responses to rapid climate change are less important than adaptation or shifts in the geographic range of distribution [4]. These studies argue that the failure to expand beyond current limits demonstrates that a species' adaptive potential has been largely exhausted, or argue that plasticity will be an unimportant factor because the cues that signaled the plastic responses in the first place might no longer be 'reliable' in changed climates [5]. However, as we show below, plastic changes in seed longevity, phenology, leaf lifespan and the temperature responses of metabolic processes are all well documented in response to elevated CO_2 and climate change factors.

There is general acceptance that high levels of genetic variation within natural populations improve the potential to withstand and adapt to novel biotic and abiotic environmental changes including the tolerance of climatic change. A portion of this genetic variation determines the ability of plants to sense changes in the environment and produce a plastic response. For example, genetic variation in genes encoding temperature sensors and transcription factors regulating vernalization could help plant populations adapt to changes in temperature. Plasticity, therefore, can both provide a buffer against rapid climate changes and assist rapid adaption. Thus, in the context of rapid climate change, phenotypic plasticity can be a crucial determinant of plant responses, both short- and long-term. Here, we provide a conceptual toolbox with definitions of the key theoretical elements and a synthesis of the current understanding of the molecular and genetic mechanisms underlying phenotypic plasticity, as relevant to climate change. We discuss how new developments in our under- standing of signaling cascades and epigenetics in particular hold promise for interdisciplinary approaches to understanding the evolution of plasticity and for predicting how plasticity will influence the responses of native plants and agricultural systems to climate change. We aim to provide background on the ecological and evolutionary literature on phenotypic plasticity and outline emerging techniques in molecular biology. By bringing these perspectives together, we hope to stimulate crucial cross disciplinary dialogues on the topic of plasticity and plant responses to climate change.

2. Phenotypic Plasticity: A single genotype can produce different phenotypes in different environments. This fundamental property of organisms is known as phenotypic plasticity [6]. A genotype will vary in its expression depending on the organism's external and internal environments. The phenotypic response pattern of a given genotype is its 'norm of reaction', a term coined by German geneticists at the start of the 20th century. Later researchers typically studied genotypes in a single, standardized laboratory environment, essentially measuring one phenotypic point along each genotype's norm. Norms of reaction can be determined by cloning the genotype and measuring phenotypic traits of interest on the genetically identical replicates in each of several controlled environments. (When cloning is not possible, inbreeding can provide reasonably uniform genetic replicates.) The range of experimental environments might include extreme or unrealistic treatments to investigate the limits of potential phenotypic expression, or might be based on environmental conditions encountered by the organism in nature to provide ecologically and evolutionarily relevant information. A genotype's norm of reaction for any specified trait can be depicted as a two-dimensional plot of its phenotypic values for that trait in each experimental environment (Fig.1). Such a plot makes explicit association of a given phenotype with the particular environment in which it is expressed (e.g. phenotype 1 and environment 1). Norms of reaction for a group of genotypes can be plotted together to show graphically the pattern of genotypic variance within and across environments.

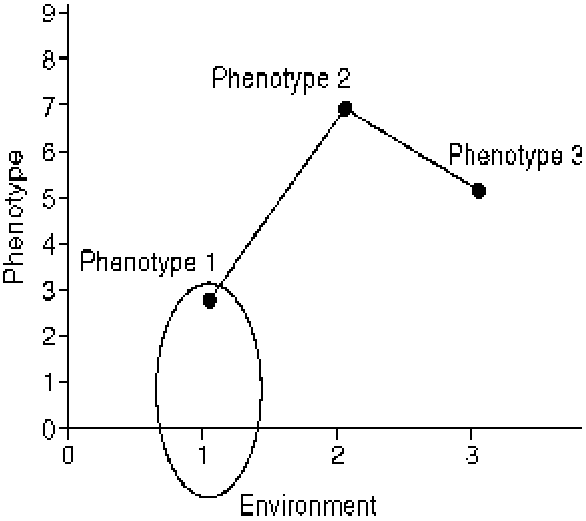
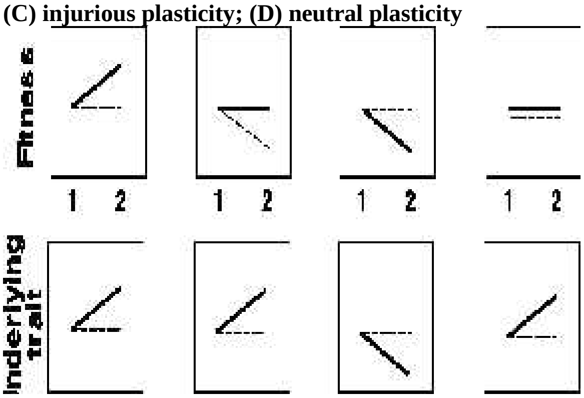


Fig: 1 The response pattern of a genotype under different environments

3. Types of Plasticity

3.1. Adaptive Plasticity with Increased Plasticity in Fitness: This type of adaptive plasticity might be involved in invasions of grassland by non-native grasses in North America. Comparisons between sets of native and non-native, invasive grasses from the same habitats suggest that the non-natives may often have relatively similar growth rates to those of the natives at low levels of water or nitrogen availability but have much higher growth rates than those of natives at high levels of resource availability [7]. It has been hypothesized that capacity for plasticity in general is an important factor in the invasiveness of non-native species [8] (Fig. 2A).

Fig. 2: Some types of phenotypic plasticity: (A) adaptive plasticity with increased plasticity in fitness; (B) adaptive plasticity with decreased plasticity in fitness; (C) injurious plasticity; (D) neutral plasticity



---Genotype more plastic for underlying trait
----Genotype less plastic for underlying trait

3.2. Adaptive Plasticity with Decreased Plasticity in Fitness: Increasing plasticity is an underlying trait which increase fitness in an environment in which fitness was formerly lower than in another environment, increasing mean fitness across environments while decreasing plasticity in fitness (Fig. 2B). This appears to be the case in two of the best-documented examples of adaptive plasticity in plants, shade-induced stem elongation and induced defense. Some plants respond to shading from other plants by growing longer stem internodes [9]. Increasing internodes length (plasticity in an underlying trait) helps these plants avoid limitation of photosynthesis due to shading by neighbors and thereby increase their seed production under crowded conditions (an environment where their fitness is relatively low). Many plants respond to damage by herbivores by accumulating chemicals or undergoing changes in form that deter subsequent herbivore. Plasticity in these underlying traits can help plants to accumulate more biomass and produce more seeds in the presence of herbivores [10].

3.3. Injurious Plasticity: Plasticity in an underlying trait that decreases mean fitness across environments is ‘injurious plasticity’ (Fig. 2C). Inability to compensate for environmental stress, such as inability to maintain high water potential and hence growth in an arid environment, is likely to be an example of this type of plasticity. Other examples could include changes in form imposed by physical forces or obstacles, such as 'flagging' of trees near timberline by ice abrasion or the formation of less extensive rhizome systems by plants grown in more compact soil [11].

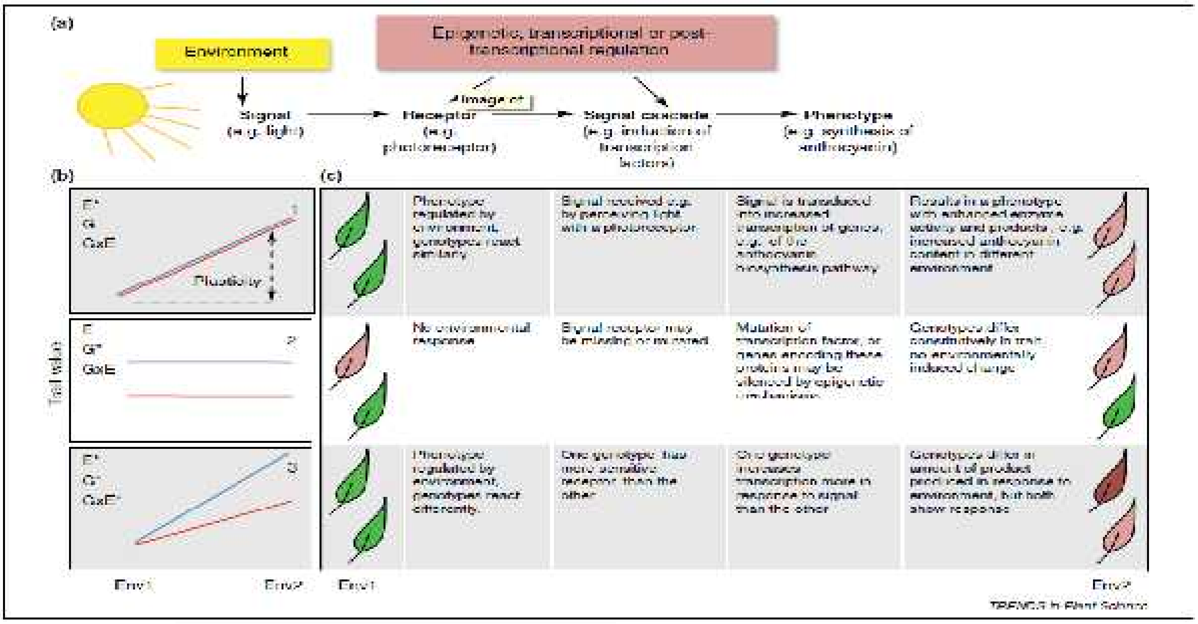
3.4. Neutral Plasticity: Plasticity in an underlying trait might have no effect on fitness and thus be 'neutral plasticity' (Fig.2D).

4. Factors Influencing Phenotypic Plasticity

4.1. Light: Anthocyanins are produced in leaves in response to excess light and temperature and osmotic extremes, and serve as a reversible plastic mechanism for the protection of photosynthetic machinery. Here, we use an anthocyanin example to illustrate (a) the points in the molecular machinery, which translate an environmental signal (excess light in this case) into a phenotype. (b) In the evolutionary and ecological literature, these responses are commonly presented as reaction norms. Here, the blue and red lines indicate the reaction norms of two different genotypes responding to a change from a low light environment (Env1) to a high light one (Env2). The extent of phenotypic change in response to a signal is its phenotypic plasticity. Asterisks in the panels denote whether there is a significant effect of environment (E) or genotype (G), and whether there is a significant genotype by environment interaction (G **x** E). (c) Likely examples of the mechanisms underlying the cases depicted in panels 1-3 are given separately for each point in the signal pathway. The leaves on the left and right represent the phenotypes in Env1 and Env2, respectively [12] (Fig.3).

4.2. Temperature: *Cassia pistula* is of immense symbolic and cultural significance to keralites as it signals seasonal change with agriculture calendar of the state. Usually the tree budding during peak summer season in the maliyalam month menam (mid march) and came to full bloom only madam (mid april). For the last few years the tree flowers ahead and by the time “vishu” arrives,the tree would shed their flowers. The early blooming of kanikonna signals climate change and is a plastic to the environmental conditions.

Fig: 3 Response of anthocyanin pigments to different environmental conditions



Phenotype regulated by environment, genotypes react similarly

Signal received e.g. by perceiving light with a photoreceptor

Signal is transduced into increased transcription of genes, e.g. of the anthocyanin biosynthesis pathway

Results in a phenotype with enhanced enzyme activity and products, e.g. increased anthocyanin content in different environment

No environmental response

Signal receptor may be missing or mutated

Mutation of transcription factor, or genes encoding these proteins may be silenced by epigenetic mechanisms

Genotypes differ constitutively in trait, no environmentally induced change

Phenotype regulated by environment, genotypes react differently.

One genotype has more sensitive receptor than the other

One genotype increases transcription more in response to signal than the other

Genotypes differ in amount of product produced in response to environment, but both show response

4.3. Water: Interactions between oaks and understory herbs vary depending on plastic responses of oaks to water. Oaks that are able to access the water table have high water potentials, few shallow roots, and facilitate understory herbs by adding litter and nutrients leached from foliage by rain. Oaks that cannot access the water table have low water potentials, many shallow roots, and compete with understory herbs. The native bunchgrass *Stipa pulchra* is much more common under shallow rooted oaks than under deep-rooted oaks [13].

4.4. Water Stress: *Mesembryanthemum crystallinum* is a prostrate succulent plant native Africa to, Western Asia and Europe. The plant is covered with large, glistening bladder cells or water vesicles, reflected in its common names of common ice plant, crystalline ice plant or ice plant. The bladder cells are enlarged epidermal cells. The main function of bladder is to reserve water.

Facultative CAM plants such as Mesembryanthemum crystallinum (ice plant) possess C_3 metabolism when unstressed but develop CAM under water or salt stress. When ice plants shift from C_3 metabolism to CAM, their stomata remain closed during the day and open at night. Recent studies have shown that the stomatal response of ice plants in the C_3 mode depends solely on the guard cell response to blue light. Recent evidence for a possible role of the xanthophylls, zeaxanthin in blue light photoreception of guard cells led to the question of whether changes in the regulation of the xanthophylls cycle in guard cells parallel the shift from diurnal to nocturnal stomatal opening associated with CAM induction. In the present study, light-dependent stomatal opening and the operation of the xanthophylls cycle were characterized in guard cells isolated from ice plants shifting from C_3 metabolism to CAM. Stomata in epidermis detached from leaves with C_3 metabolism opened in response to white light and blue light, but they did not open in response to red light. Guard cells from these leaves showed light-dependent conversion of violaxanthin to zeaxanthin. Induction of CAM by NaCl abolished both white light- and blue light-stimulated stomatal opening and light-dependent zeaxanthin formation. When guard cells isolated from leaves with CAM were treated with 100 mM ascorbate, pH 5.0 for 1 h in darkness, guard cell zeaxanthin content increased at rates equal to or higher than those stimulated by light in guard cells from leaves in the C_3 mode. The ascorbate effect indicates that chloroplasts in guard cells from leaves with CAM retain their competence to operate the xanthophyll cycle, but that zeaxanthin formation does not take place in the light. The data suggest that inhibition of light-dependent zeaxanthin formation in guard cells might be one of the regulatory steps mediating the shift from diurnal to nocturnal stomatal opening typical of plants with CAM.

4.5. Carbon Dioxide Content: CO_2 enrichment studies in *urena labata* were conducted in AICRP weed control in the College of Horticulture. CO_2 level in the chamber was increased from 300 ppm to 550 ppm by closing the chamber at 4 pm continuously during the growth period of the plant. The chamber was then opened by 9 am so that the CO_2 content in the chamber increased by respiration. The plant growth in the chamber showed higher growth and biomass production than the plants grown out side. The morphological plasticity of the plant to CO_2 enrichment was evident from the study.

4.6. Neighbouring Plants: Neighboring plants cause dramatic phenotypic responses in many plant species. For example, Rice et al. (1993) grew *Quercus douglasii* seedlings in three different plant communities. Morphological traits differed and water use efficiencies were higher for seedlings grown with annuals than for those grown with perennials. Soil water depletion was more rapid in annual plant communities, suggesting that plasticity in water use efficiency may have been adaptive, enhancing the competitive ability of oak seedlings. Clonal plants provide many examples of plastic responses to neighbors [14]. Turkington [15] found that the morphology of *Trifolium repens* responded plastically to the presence of different grass species. Moreover, the plastic response of *T. repens* clones to different grass species in the greenhouse depended on which species the clone had previously been associated with in the field. Furthermore, *T. repens* responded differently to the presence of root systems of three different grass species. Because grass shoots were removed in this study, the plastic responses of *T. repens* were not likely to have been caused through effects on aboveground resources.

4.7. Herbivores: Though there were several early reports of plant phenotypic plasticity in response to insect attack, the study of induced plant responses to herbivory became of general interest in plant-herbivore interactions in the 1970s [16]. In particular, studies of tomato plants' chemical responses to beetle grazing and thereduced growth of caterpillars on damaged compared to undamaged birch trees were responsible for popularizing the study of induced responses. The study of plant morphological responses to herbivory has a more recent history, with studies demonstrating induced plant production of thorns and trichomes. For the best-studied systems, those where insects chew the leaves of plants, there is a high level of evolutionary conservation in the hormonal regulation of induced plant responses. For example, responses including plant toxins, trichomes, volatiles, and extrafloral nectar are regulated by jasmonic acid.

5. Genetic Variation in Phenotypic Plasticity: Phenotypic plasticity in a trait can only evolve when there is sufficient genetic variation [17]. By now, hundreds of studies on genetic variation in plasticity, often measured as genotype by environment interactions in analysis of variance, have been published and allow general conclusions to be drawn. For example, although heritabilities of plasticity are generally lower than those of mean trait values [18], most studies show that there is genetic variation in plasticity. Such variation can be found even over spatial scales of only a few metres [19].

Despite the progress in methods to analyse multiple independent studies together (i.e. meta-analysis) the large number of studies on genotype-by-environment interactions has not yet been fully explored for general patterns. Relevant questions that could be answered by metaanalysis are whether genetic variation in phenotypic plasticity has been more strongly reduced by selection in sessile organisms than in free-moving organisms and in clonal than in nonclonal organisms, and whether it has been more strongly reduced for presumably adaptive plasticity than for non-adaptive plasticity.

Most studies on genotype-by-environment interactions used replicated genotypes or full-sib families and thus quantified broad-sense heritabilities of phenotypic plasticity [20]. Only a few used half-sib families to quantify narrow-sense heritabilities. Still fewer studies tested for narrow-sense heritabilities of phenotypic plasticity by studying realized evolutionary responses to selection on plasticity. Such studies are especially scarce for plants, as a consequence of their relatively long generation times.

Some studies selected indirectly for reduced plasticity (often called canalization) by crossing individuals that have high trait values in an environment that induces low trait values with individuals that have low trait values in an environment that induces high trait values [21]. Other studies selected indirectly for low or high plasticity as a correlated trait to selection on trait values in single environments. A line of *Plantago lanceolata* selected for long leaves under a low red-far red ratio of light mimicking shading by plants, and another line selected for short leaves under a high red-far red ratio were more plastic in leaf length than lines that had been selected in opposite directions in the respective light environments. This shows that phenotypic plasticity can evolve indirectly as a correlated response to selection on trait mean values. However, it does not necessarily imply that this mode of the evolution of plasticity is the most common one.

6. Natural Selection on Phenotypic Plasticity: Phenotypic plasticity of a trait is generally assumed to be under selection when one environment selects for a different trait value than does another environment. As a consequence, selection on phenotypic plasticity has generally been inferred from comparisons of selection on trait values in different environments [22, 23]. Most such studies were concerned with natural phenotypic variation and used selection gradient analysis, in which the fitness of individuals is regressed on the trait of interest separately for different environments [24]. Other studies were concerned with studying fitness effects of phenotypic variation induced by experimental manipulation [25] or of mutant and transgenic plants [26] in different environments. All these methods are powerful in determining whether a plastic response *per se* would be beneficial. However, they do not unequivocally prove that the plastic genotypes are selected for, rather than two groups of specialist genotypes.

Evolution of adaptive plasticity requires that plastic genotypes have the highest global fitness averaged over the environments [27] rather than the highest fitness in each environment separately. Given that genotypes differ in their plasticity, it might be better to use selection gradient analysis in which the global fitness of genotypes or seed families averaged over the environments is regressed on their plasticity values [28]. For two reasons, however, averaging of fitness over environments is a potential problem with this method. First, in nature the chance that a plant encounters one environment or another may differ. Therefore, fitness should be weighted by the frequency in which the species occurs in each environment. Second, the accuracy with which a genotype will produce a certain trait value and have corresponding fitness may differ between environments. Therefore, when the variance in fitness differs between environments, it might be better to use the geometric rather than the arithmetic mean of fitness over environments.

In conclusion, evidence for opposing selection forces in different environments suggests that there may be selection for phenotypic plasticity. Alternatively, however, it could indicate that different groups of specialist genotypes should evolve in different environments. To distinguish between these alternatives, it needs to be tested whether plastic genotypes have the highest global fitness across all environments. Of course, even if this is the case plasticity may not respond to selection, depending on the rate of migration between populations.

7. Natural genetic differentiation in phenotypic plasticity

In nature, adaptive phenotypic plasticity is likely to evolve in environments that are heterogeneous in space or time. Several studies compared the outcome of evolution in heterogeneous and homogeneous environments [29] of organisms with short generation times such as *Escherichia Coli* [30]. Most of these experimental studies showed that in heterogeneous environments generalists with high global fitness evolved. However, they did not reveal which underlying physiological or morphological traits had actually evolved a higher adaptive plasticity. Moreover, to our knowledge no such study has addressed plants.

A few studies tested whether plants from more heterogeneous natural environments exhibit higher adaptive plasticity than ones from more homogeneous environments. Donohue *et al.* [31] showed that plants of *Impatiens capensis* from an open habitat with a vertical shading gradient, where plastic internode elongation in response to density may position leaves in better light conditions, showed higher adaptive plasticity than plants from a woodland habitat, where internode elongation in response to density would hardly be effective because of the closed canopy. Weinig [32] compared plants of *Abutilon theophrastii* from cornfields, where plastic internode elongation should only be effective early in the season, with plants from weedy sites where plastic responses should be more effective later in the season. Indeed, early in plant life plasticity in internode length in response to shading was higher for plants from cornfields than for plants from weedy sites, whereas it was lower at later life stages. We compared the response to competition of genotypes of *Ranunculus reptans* microhabitats, which were competitively heterogeneous due to patches of competing grasses, with the response of genotypes from homogeneous microhabitats without competing grasses. Plasticity in traits that enable escape from competitors, such as specific internode length and vertical angle of stolons, turned out to be higher for genotypes from the heterogeneous microhabitat. Because these studies show that more plastic genotypes had evolved in more heterogeneous environments, they indicate that adaptive evolution of phenotypic plasticity is possible in nature, even at small spatial scales.

8. Genetic and Environmental Interactions Determine Plant Defences against Herbivores

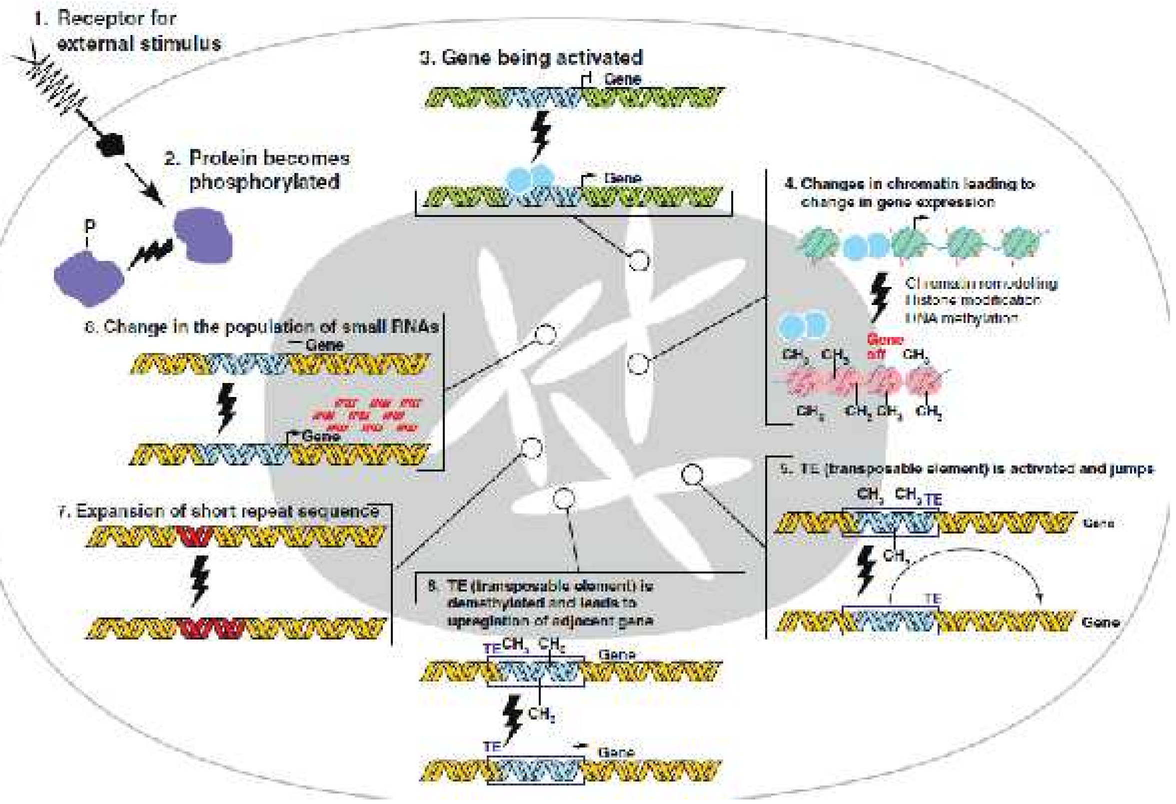
1. Plants express multiple defensive traits, but little is known about the genetic stability and phenotypic plasticity of these traits in nature. To investigate sources of variation and their potential ecological consequences for herbivores, we combined field observations of cyanogenic lima bean with laboratory experiments.
2. Field studies in South Mexico revealed a distinct variability of cyanogenic traits within and among wild lima bean populations. To differentiate among genetic variation and the impact of ambient conditions on plant phenotypes, we used seed-grown plants as well as clones propagated fromhigh- (HC) and low-cyanogenic (LC) wild type plants.
3. In growth chamber experiments, we cultivated plants under three intensities each of drought and salt stress, nutrient supply, and light availability. We consecutively quantified cyanogenesis and total phenolics as chemical defences, soluble proteins as measure of leaf quality, and leaf mass per area and tissue hydration as physical defence-associated traits.
4. Plant traits were genetically stable, as clones propagated from the HC- and LC-mother plants maintained their cyanogenic features and also showed constancy of other leaf parameters tested.
5. In contrast to genetically heterogeneous seed-grown plants, cyanogenesis and soluble protein concentration in clonal plants showed significant variation in response to reduced water supply, increased soil salinity, and fertilization. The other leaf traits, however, showed no significant phenotypic plasticity depending on treatment.
6. Among all traits analysed, genetic and phenotypic variation in cyanogenesis proved the best predictor of herbivore behaviour and development, as LC-plants were preferred by adult Mexican bean beetles and allowed for faster larval development.
7. Synthesis. We demonstrate that (i) functional analyses of plant responses to abiotic factors require methodical separation of genotypic variability and phenotypic plasticity, (ii) different abiotic parameters quantitatively affect the plants' chemical phenotype and that (iii) changes of plant phenotype can have strong impacts on natural herbivores. Our results suggest that genetic variability and phenotypic plasticity of plant anti-herbivore defences allow plant populations to rapidly respond to changing environmental conditions.

9. Environmental Influences on Aquatic Plants in Freshwater Ecosystems: An interesting biogeographic observation about aquatic plants is that their frequency of endemism is less than that of terrestrial plants. Even in ancient tropical habitats, there are relatively few endemic species of aquatic plants (i.e., compared with terrestrial plants). Many species of aquatic plants are widespread, occurring on more than one continent as a result of extensive dispersal by natural vectors (and more recently, by humans). Nevertheless, all species have particular ranges of environmental tolerance. Inhospitable environments for aquatic plants are characterized by some combination of dryness, a flow velocity >1 m/s, irradiance <2 % of that at the surface, high salinity >390 g/L, persistent ice cover >9 months (i.e., a short growing season), and growing-season temperature <3 ◦C at high latitude or altitude or >45 ◦C in thermal habitats. Although many aquatic plants can tolerate a wide range of conditions, others are narrower in their tolerance and are potentially useful as environmental indicators. As was suggested in various sections of this review, it is possible to identify various species of macrophytes that are sensitive to specific thresholds of environmental conditions, and are therefore potentially useful indicators of change. However, these tolerances are idiosyncratic, in that species that are sensitive to one environmental factor are not necessarily highly responsive to other ones.As such, the use of aquatic plants as indicators must rest on a foundation of the known tolerances of species, within an ecoregional context. The greatest dearth of relevant understanding concerns interacting factors, such as complexes of factors (i.e., chemical, physical, and biological) and their effects on indvidual species and communities.

10. Molecular Mechanism: The plastic molecular responses to environmental signals can occur in many ways. An external stimulus must first be perceived at the cell surface by a receptor that then initiates a signaling cascade. Responses to the environmental challenge (lightning bolts) can include the post-translational modifications of the components of signaling pathways. Alternatively, regulatory gene transcription can occur in many ways and in response to a broad range of stimuli. Epigenetic processes, including DNA methylation, histone modification and transposable element activation, can also alter gene expression and thereby mediate plasticity. Changes to the population of small RNAs can lead to post-transcriptional control (RNAi) as well as changes in chromatin modification. Lastly, the expansion of short repeat sequences can affect gene expression (Fig.4).

New developments in our understanding of signaling cascades and epigenetic in particular hold promise for understanding the evolution of plasticity in natural systems and for predicting how plasticity will influence the responses of native plants and agricultural systems to climate change. For example, mutant or gene expression studies are useful for discovering genes underlying specific responses techniques, such as quantitative trait loci and linkage disequilibrium mapping, have also been used to identify natural variants in plasticity genes. Plasticity genes might also evolve by the diversification of gene families in which the promoters of different family members perceive specific environmental cues. Once specific genes that lead to genetic variation in phenotypic plasticity have been isolated, one can employ molecular population genetic analyses of natural 'plasticity alleles' to infer the evolutionary histories of plastic phenotypes and the evolutionary forces that shape variation in these key loci. On a genome-wide scale, approaches to characterizing gene expression and epigenetic changes, including high-throughput sequencing, microarrays and proteomic approaches, offer the possibility to characterize patterns of plasticity at the scale of the genome rather than gene by gene. This discussion demonstrates how phenotypic responses to environmental signals can be correlated with molecular signals at single genes and across the entire genome. Further investigation to identify the genome architecture that confers the responsiveness of key traits to particular stimuli might enable the prediction of plastic responses to novel environments posed by climate change.

Fig: 4 Signalling cascade response to environmental signal



11. Plasticity in Plant Functional Traits: In recent years, ecologists have categorized species according to plant functional types and have also identified several continuous plant functional traits that vary in predictable ways along environmental gradients. Functional types are widely used in global climate models to group species according to their function in the ecosystem or community (e.g. C_3 or C_4 grasses, herbs, shrubs, deciduous trees, N-fixing legumes, etc.). Functional traits are those that help describe the ecology of species using a few, easily quantified variables (e.g. seed size, plant height, leaf lifespan, leaf mass per area, etc.). Functional traits are relevant to both global climate models and mechanistic models of plant distributions. Considering their probable importance, we advocate that plant functional traits should have priority for the investigation of (adaptive) phenotypic plasticity and identification of molecular and genetic mechanisms across species. Adaptive plasticity in functional traits is likely to assist rapid adaptation to new conditions. Thus, a natural question to ask is whether we can predict patterns of plasticity in functional traits based on the means of those traits themselves or based on other aspects of a species' ecology. Although many studies have compared patterns of phenotypic plasticity in small numbers of species of contrasting ecologies, little consensus has emerged. As such, this question might be best addressed using a meta-analysis approach [33] (Table.1).

Table:1 Plant functional traits that show predictable plasticity

Priority	Trait	Biological significance
A	Leaf mass per unit area (LMA, the inverse of SLA, specific leaf area)	An easily measured correlate of relative growth rate, photosynthetic capacity, leaf lifespan and leaf nitrogen content.
A	Stomata size, density	Stomata control water loss and uptake of CO_2.
A	Height at maturity	Indication of competitive position in a stand, relevant in herbaceous and woody species, harder to measure in long-lived species.
A	Flowering time, size at reproduction, phenology	Plasticity in these traits will determine the ability of many species to respond to a changing climate.
A	Seed size, number	Indicators of fitness; these can also be plastic in their own right.
B	Water use efficiency	Carbon gain as a function of water loss. Can be measured as an integrated measure using isotopes, but instantaneous measures are also of interest.
B	Leaf size, shape, thickness	Leaf form, as the site of photosynthesis, is crucial to growth and carbon balance.
B	Root-to-shoot ratio	The relative allocation of total plant mass to roots and shoots (i.e. leaves and stem)
B	Specific root length	Root length per unit mass, a belowground analog to SLA or LMA. Of interest from a global change perspective in particular as precipitation patterns shift.
B	Plant chemical defenses	Presence, absence and concentration of secondary metabolites employed in defense vary in many species depending on growth conditions and herbivore pressure.
B	Leaf pigmentation	Pigmentation changes (e.g. anthocyanin) is associated with the ability to protect the photosynthetic apparatus from excess light and could contribute to leaf longevity during senescence, as well as freezing-, drought- and osmotic-tolerance.

12. Constraints on the Evolution of Adaptive Phenotypic Plasticity in Plants: Theoretical studies indicate that the evolution of plasticity may be constrained by costs and limits of plasticity, and that as a consequence specialist genotypes or intermediately plastic ones may evolve instead of highly plastic generalist genotypes [34, 35]. So far, there have only been a few studies that empirically tested for costs and limits of plasticity. Even fewer of these studies addressed the nature of these costs and limits of plasticity, although this is absolutely essential for a better understanding of the evolution of phenotypic plasticity.

DeWitt *et al.* [36] distinguished five potential costs and four potential limits of plasticity. Newer insights question whether all of these costs and limits should be classified separately, suggesting that not all of them are relevant for phenotypic plasticity in plants, and suggesting that the list was not complete.

A cost of plasticity is the reduction in fitness of a genotype as a consequence of expressing a certain phenotype through plastic rather than fixed development. First, there may be costs of acquiring information about the environment by actively sampling it. Such costs, however, are likely to be more widely spread for free-moving organisms such as most animals, but not for sessile organisms such as plants. Second, there may be costs of maintenance of the sensory and regulatory machinery required for plastic responses. Third, production costs of structures through plastic development may be higher than the ones through fixed development. This, however, is an unlikely cost in modular organisms such as plants, in which there is no obvious reason why the production of, say, a new 10-cm long leaf through plastic development should be more expensive than the production of such a new leaf through fixed development. Such production costs may only exist when the timing of the production of new structures differs between plastic and non-plastic genotypes and takes place at a different developmental stage of the plant where costs may differ. Fourth, the capacity for plastic development may result in less stable development (i.e. developmental instability), which in turn may result in reduced fitness [37]. Fifth, there may be so-called genetic costs of plasticity caused by negative genetic correlations between phenotypic plasticity in a trait and fitness as a consequence of pleiotropy, or of linkage or epistasis involving genes relevant for variation in fitness and phenotypic plasticity. Because plasticity costs due to information acquisition, maintenance, production, and developmental instability will all become apparent as negative genetic correlations between plasticity and fitness, the fifth category of so called genetic costs should more narrowly be termed intrinsic genetic costs, to clearly distinguish them from negative genetic correlations brought about by the other mechanisms.

In addition to these potential costs of plasticity, DeWitt *et al*. distinguished four potential limits of plasticity. These limits differ from costs of plasticity in that there is a cost of the trait value expressed in a single environment as a consequence of plasticity rather than a cost of having the potential for plastic development *per se*.

First, when the information from an environmental cue is unreliable, a plastic response may result in a mal-adaptive phenotype. Although this is a limit and not a cost, it is often referred to as an ecological cost of plasticity [38]. A mal-adaptive phenotype may also be produced in response to an environmental cue if this cue is not specific to a particular environmental change and this may be ‘misunderstood’. For example, plants of *Ranunculus reptans* that occur in temporarily flooded habitats with different levels of interspecific competition elongate their internodes in response to shading. This elongation response is adaptive when shade is imposed by a naturally co-occurring. However, when it is imposed by the water column during inundation, it is maladaptive because plants under water cannot afford the higher respiration needed for longer internodes [39]. Second, plastic change requires time and during this time lag the phenotype of the organism is mal-adaptive. Third, it has been argued that because plastic genotypes have more developmental baggage to carry, they may not be able to produce trait values as extreme as non-plastic genotypes [40]. However, this so-called developmental-range limit has to be the consequence of maintenance or production costs of plasticity, and therefore is no separate limit of plasticity. Fourth, there may be the so-called epiphenotype problem in which a structure added to an organism as consequence of plastic development is weaker than one that is integrated during early development. This, however, is a rather specific limit that is only likely to apply to a few traits such as secondary spine development in zooplankton in the presence of predators.

In conclusion, the costs and limits of plasticity are most relevant for plants are genetic costs including maintenance and developmental instability costs, and plasticity history, environmental-reliability, and lag-time limits. The latter two have been studied most frequently, often by using phenotypic manipulation, and generally show that there are costs of expressing the wrong phenotype. Therefore, we now focus on empirical tests of the poorly studied costs of plasticity.

13. Conclusions: There is increasing evidence of the importance of plasticity in plants under climate change in both natural and agricultural systems. It has been to discuss the potential roles of plasticity in determining plant response to and effects of climate change in a way that is accessible and relevant to ecologists, physiologists and molecular biologists alike. Progress in this field is being very much dependent on multidisciplinary approaches and the application of emerging techniques.

References

1. Bradshaw, A. D. (2006). Unraveling phenotypic plasticity-why should we bother? *New Phytologist* 170, 644–648
2. VanKleunen, M. (2007). Selection on phenotypic plasticity of morphological traits in response to flooding and competition in the clonal shore plant Ranunculus reptans. *Journal of Evolution Biology*, 20, 2126–2137

3. Van Kleunen, M, Fischer, M. (2001). Adaptive evolution of plastic foraging responses in a clonal plant. *Ecology,* 82: 3309–3319.
4. Jump, A. S. and Penuelas, J. (2005). Running to stands till: adaptation and the response of plants to rapid climate change. *Ecological Letters,* 8, 1010– 1020.
5. Visser, M. E. (2008). Keeping up with a warming world; assessing the rate of adaptation to climate change. Proceedings Royal Society of Lond. B. *Biological Science 275,* 649–659
6. Sultan, S. E. and Spencer, H. G. (2002). Metapopulation structure favors plasticity over local adaptation. *American Naturalist,* 160: 271–283.
7. Claassen, V. P. and Marler, M. (1998). Annual and perennial grass growth on nitrogen-depleted decomposed granite. *Restoration Ecology*, 6, 175–180.
8. Willis, A. J., Memmott, J. and Forrester, R. I. (2000). Is there evidence for the post-invasion evolution of increased size among invasive plant species? *Ecological Letters,* 3, 275–283.
9. Dudley, S. A. and Schmitt, J. (1995). Genetic differentiation in morphological responses to simulated foliage shade between populations of *Impatiens capensis* from open and woodland sites. *Functional Ecology,* 9: 655–666.
10. Agrawal, A. A. (1998). Induced responses to herbivory and increased plant performance. *Science*, 279, 1201–1202.
11. Schmid, B. and Bazzaz, F. A. (1990). Plasticity in plant size and architecture in rhizome-derived vs. seed-derived Solidago and Aster. *Ecology*, 71, 523–535.
12. Nicotra, A. B. (1997). Patterns of genotypic variation and phenotypic plasticity of light response in two tropical *Piper* (Piperaceae) species. *American Journal of Botany,* 84:1542-1552
13. Callaway, R. M. (1990). Effects of soil water distribution on the lateral root development of three species of California oaks. *American Journal of Botany*, **77**:1469-1475.
14. Hutchings, M. J., and H. De Kroon. (1994). Foraging in plants: the role of morphological plasticity in resource acquisition. *Advances in Ecological Research,* 20:159-238.
15. Turkington, R. (1990). The influence of grass root systems on growth and form of *Trifolium repens. Canadian Journal of Botany,* 68:1034-1038.
16. Karban, R., and I. T. Baldwin. (1997). Induced responses to herbivory. University of Chicago Press, Chicago, Illinois, USA. 2: 123-126.
17. Via, S. (1987). Genetic constraints on the evolution of phenotypic plasticity. In: Loeschcke V, ed. *Genetic Constraints on Adaptive Evolution.* Berlin, Germany: Springer-Verlag, 47–71.
18. Scheiner, S. M. (1993). Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics,* 24: 35–68.
19. Stratton, D. A. (1994). Genotype-by-environment interactions for fitness of *Erigeron annuus* show fine-scale selective heterogeneity. *Evolution,* 48:1607–1618.
20. Hedges, L. V. and Olkin, I. (1985). *Statistical Methods for Meta-Analysis*. Orlando, USA: Academic Press, Inc. 356p.
21. Thompson, S. R. and Rook, S. K. (1988). Lack of a correlated response to canalizing selection in *Drosophila melanogaster*. *Journal of Heredity,* 79: 385–386.
22. Steinger, T. Roy, B. A., and Stanton, M. L. (2002). Evolution in stressful environments II: Adaptive value and costs of plasticity in response to low light in *Sinapsis arvensis*. *Journal of Evolutionary Biology*, 16: 313–323.
23. Huber, H., Kane, N. C., Heschel, M. S., von Wettberg, E. J., Banta, J. Leuck. A. and Schmitt, J. (2004). Frequency and microenvironmental pattern of selection on plastic shade-avoidance traits in a natural population of *Impatiens capensis*. *American Naturalist,* 163: 548–563.
24. Lande, R. and Arnold, S. J. (1983). The measurement of selection on correlated characters. *Evolution* 37, 1210–1226.
25. Schmitt, J., Dudley, S. A., and Pigliucci M. (1999). Manipulative approaches to testing adaptive plasticity: phytochrome-mediated shade-avoidance responses in plants. American Naturalist 154: 543–554.
26. Galen, C., Huddle, J., and Liscum, E. (2004). An experimental test of the adaptive evolution of phototropins: blue-light photoreceptor controlling phototropism in Arabidopsis thaliana. *Evolution*, 58: 515–523.
27. Releya, R. A. (2002). Costs of phenotypic plasticity. *American Naturalist,* 159: 272–282.
28. Stinchcombe, J. R., Dorn, L. A. and Schmitt J. (2004). Flowering time plasticity in *Arabidopsis thaliana*: a reanalysis of Westerman & Lawrence. *Journal of Evolutionary Biology,* 17: 197–207.
29. Kassen, R. (2002). The experimental evolution of specialists, generalists, and the maintenance of diversity. *Journal of Evolutionary Biology,* 15: 173–190.
30. Bennett, A. F., Lenski, R. E. and Mittler, J. E. (1992). Evolutionary adaptation to temperature. I. Fitness responses of *Escherichia coli* to changes in its thermal environment. *Evolution,* 46: 16–30.
31. Donohue, K., Hammond Pyle, E., Messiqua, D., Heschel, M. S. and Schmitt, J. (2003). Adaptive divergence in plasticity in natural populations of *Impatiens capensis* and its consequences for performance in novel habitats. *Evolution*, 55: 692–702.

32. Weinig, C. (2000). Plasticity versus canalization: population differences in the timing of shade-avoidance responses. *Evolution*, 54: 441–451.
33. Cornelissen, J. H. C. (2003). A hand book of protocols for standardized and easy measurement of plant functional traits worldwide. *Australian Journal of Botany,* 51, 335–380.
34. Tufto, J. (2000). The evolution of plasticity and non-plastic spatial and temporal adaptations in the presence of imperfect environmental cues. *American Naturalist,* 156: 121–130.
35. Ernande, B., Dieckmann, U. (2004). The evolution of phenotypic plasticity in spatially structured environments: implications of intraspecific competition, plasticity costs and environmental characteristics. *Journal of Evolutionary Biology*, 17: 613–628.
36. DeWitt T. J., Sih, A. and Wilson, D. S. (1998). Costs and limits of phenotypic plasticity. *Trends in Ecology and Evolution*, 13: 77–81.
37. Møller, A. P. (1999). Developmental stability is related to fitness. *American Naturalist*, 153: 556–560.
38. Cipollini, D., Purrington, C. B. and Bergelson, J. (2003). Costs of induced responses in plants. *Basic and Applied Ecology,* 4: 79–89.
39. Lenssen, J. P. M., van Kleunen, M., Fischer, M. and de Kroon, H. (2004). Local adaptation of the clonal plant *Ranunculus reptans* to flooding along a small-scale gradient. *Journal of Ecology*, 92: 696–706.
40. Wilson, D. S. and Yoshimura, J. 1994. On the coexistence of specialist and generalists. *American Naturalist*, 144: 692–707.