

# Plant developmental responses to the environment: eco-devo insights

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Evolutionary ecology and developmental biology have converged on the key insight that phenotypic expression is powerfully conditioned by environmental information. Plant ecological development (eco-devo) aims to firstly, determine precisely how plants perceive and respond to the varying environmental conditions they encounter in the real world and secondly, understand the ecological and evolutionary consequences of environmentally mediated phenotypic outcomes. This full explanatory scope, from molecular interactions to natural populations and communities, is just now being realized for two adaptively important aspects of developmental response: shade avoidance and flood tolerance. These and other new findings point to the complex, interactive nature of both environmental cues and gene-regulatory networks, and confirm the importance of incorporating realistic environmental variation into studies of development.

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## Introduction

The emergent field of ecological developmental biology examines how organisms develop in response to environmental conditions that vary in nature [1–4]. Intense current interest in this integrative ‘eco-devo’ approach reflects the confluence of two scientific directions. First, ecological and evolutionary studies in the past 15 years have increasingly focused on individual developmental plasticity, defined as the capacity of a given genotype to produce different phenotypes in different environmental conditions. In plasticity studies, cloned or inbred replicates of a genotype are raised in a range of environmental states such as light or moisture levels, rather than a single controlled environment. Expanding experimental conditions in this way has

made clear that plants and other organisms possess an extraordinary capacity for modulating developmental outcomes in response to a host of environmental factors [5–8]. Remarkably, many of these developmental responses represent adaptive morphological, anatomical, allocational, and life-history adjustments to the functional demands of contrasting environments. For instance, when soil resources such as water or nutrients are limiting, plants produce relatively larger root systems with long, thin roots, maximizing uptake capacity; in reduced light, they alter biomass allocation and leaf structure and size to increase photosynthetic surface area despite light-limited total growth (Figure 1) [9]. Different species, and even populations or genotypes within species, have evolved to express distinctive response patterns, so these individual developmental repertoires are now understood to be a key aspect of adaptive diversity.

Over this same time period, increasingly sophisticated mechanistic studies have revealed how external and cellular environmental factors participate in the extraordinarily complex gene-regulatory networks that shape development [10–13]. This fundamental insight challenges the experimental convention of a ‘control’ environment, seen as a neutral developmental backdrop. Instead, plant and animal biologists are coming to recognize the environment as a source of specific, essential regulatory information. If we intend our findings to apply to the real world — in which environments are variable, multifaceted, and often stressful — it is necessary to study developmental processes and outcomes in realistic ranges of conditions that accurately recreate these regulatory elements.

Together, these converging insights have led to the cross-disciplinary ‘eco-devo’ research strategy, which aims to study development in environmental context by firstly, identifying the precise cues, perception, and transduction mechanisms through which environmental inputs inform development; and secondly, testing how the resulting phenotypes influence the ecological distribution and evolutionary trajectories of natural populations. In just the past few years, the full eco-devo picture from molecular regulatory mechanisms to adaptive consequences has been greatly advanced for two major aspects of plant developmental response: avoidance of neighbor shade, and tolerance of soil flooding. Here I present a brief overview of these two exciting research areas as eco-devo case studies. Both exemplify three key aspects of developmental responses to the environment: (i) the integration of

Figure 1



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Plastic developmental responses to environmental demands. Genetic replicates of the same inbred line of *Polygonum cespitosum* express dramatically different juvenile phenotypes in contrasting naturalistic greenhouse treatments. Left, plant grown in dry soil and full insolation produces multiple branches and reproductive axes, narrow (water-conserving) leaves with thick mesophyll and cuticle, and high biomass allocation to root tissue (maximizing access to soil moisture). Right, plant grown in moist soil and simulated canopy shade (79% reduction in photosynthetically active radiation with R:FR ratio filter-reduced to 0.70) expresses a less branched, upright habit with elongated internodes, large, broad leaves with thin mesophyll and cuticle, and high biomass allocation to leaf tissue, responses that maximize photosynthetic surface area despite lower total biomass. Photo credit: Tim Horgan-Kobelski.

multiple internal and external cues; (ii) the use of shared regulatory elements such as transcription factors, target proteins and hormones in diverse developmental cascades; and (iii) the role of physiological feedbacks to provide indirect environmental information. I then examine how these and other recent findings illuminate the complex nature of environmental cue-and-response systems in plants, noting in conclusion how research directions and design can be expanded in line with eco-devo goals.

### Shade avoidance: the influence of neighbors on plant development

Plants have evolved sophisticated systems for perceiving and responding developmentally to shading by neighbors so as to maintain access to photosynthetically active radiation (PAR). These systems use distinct facets of the shade environment as cues to initiate a well-studied suite of 'shade avoidance' responses, including rapid stem and petiole elongation, reduced branching, and more erect leaf angles. Even before a plant's shoot tissues

are actually shaded, they sense a reduced ratio of Red to Far-red wavelengths (R:FR ratio) in light reflected horizontally from adjacent leaves; as the canopy develops overhead they continue to receive this signal from FR-enriched transmitted light [14,15<sup>\*\*</sup>]. The specialized receptors for this spectral cue have long been identified as photo-convertible phytochromes [16,17], but only very recently have the details of this well-studied regulatory pathway become clear [18<sup>\*</sup>]. When converted to the active form, phytochromes are translocated to the nucleus where they bind to a group of phytochrome interacting (transcription) factors (PIFs), which regulate genes that mediate elongation [19]. This reversible phytochrome switch allows for remarkably fine-tuned developmental responses to light quality; stem elongation can begin to occur within minutes of the R:FR light cue [20]. Specialized chemical receptors also sense the reduction in light *quantity* that indicates shading by neighbors. Cryptochromes and phototropins are receptors for blue light, which is absorbed by vegetation and hence reduced in shade [18<sup>\*</sup>]. Phototropins also mediate the spatial

distribution of chloroplasts within mesophyll cells to maximize the light-harvesting capacity of leaves in low light [15\*\*].

These signaling pathways are only a part of an extraordinarily complex network of regulatory interactions and feedbacks. In addition to R:FR ratio, diurnal light/dark cycles regulate the transcription levels of certain PIF genes, such that internal circadian rhythms and external light conditions jointly mediate this response [21,22\*]. Stem and petiole elongation are also regulated by the DELLA family of growth-restraining proteins, which integrate several hormonal pathways initiated by both reduced light quantity and R:FR ratio: first, gibberellins (which increase in response to low light) promote elongation by degrading DELLAs; second, auxin biosynthesis is rapidly upregulated by reduced R:FR ratio via PIF and DELLA protein interactions; and third, ethylene, which also increases in response to low R:FR, affects both gibberellin function and DELLA protein stability [18\*,23]. In addition to their regulatory effects on DELLA, both ethylene and auxin appear to control other independent targets that influence elongation [23]. Lower PAR flux also reduces the excitation level of photosystem II, which influences the expression of genes involved in leaf morphology [15\*\*]. Reduced light intensity also alters the concentration of carbohydrates in plant tissues, which influences the expression of genes that influence shoot morphology as well as photosynthesis and carbon storage, both of which in turn influence subsequent growth [15\*\*].

Pierik and coworkers studied these signaling pathways in ecological context by testing the growth responses of mutant and transgenic *Arabidopsis* lines in dense stands [24\*]. They found that with natural neighbor shading, increased shoot elongation was accompanied by the breakdown of a specific DELLA protein, confirming that abundance of these proteins is regulated by plant density via R:FR ratio, blue light signals, and gibberellin. They also documented light-mediated degradation of DELLA proteins in response to specific elements of a density-generated canopy, using blue light absorbing filters, neutral shade cloth, and FR-emitting diodes to reduce blue light, total light, or R:FR ratio, respectively [23]. Through genetic and phenotypic manipulations of both model and naturally evolved taxa (reviewed in [25]), Schmitt and colleagues have confirmed that developmental responses to neighbor shade influence plant performance and selective change in real populations. Their greenhouse and field experiments show that the developmental plasticity to produce elongated phenotypes in neighbor shade and shorter, more branched phenotypes in open conditions is adaptive: that is, these alternative phenotypes enhance individual fitness in the environments that elicit them, and selec-

tion in open habitats strongly favors this sun/shade plasticity [26].

### Adaptive developmental responses to flooding

Owing to the low solubility and slow diffusion rate of gases in water, submerged plant tissues experience a metabolically critical shortage of oxygen as well as diminished capacity for photosynthetic gas exchange. This environmental challenge induces a suite of dramatic developmental and physiological adjustments in many wetland species, including the formation of cortical aerenchyma channels that permit oxygen to diffuse to flooded organs from shoot tissues in contact with air [27], and/or rapid elongation and vertical orientation of internodes and petioles to elevate leaves above water level [28,29].

Although these adaptive responses have long been recognized, it is still not known precisely how plants perceive flooding, or what molecular signaling events are involved. As in the case of neighbor shade, various coincident aspects of submergence could provide either direct or indirect cues: changes in ambient or tissue concentrations of oxygen and carbon dioxide (CO<sub>2</sub>), lower temperature, even reduced blue light intensity under water. Recent work by Voesenek and colleagues has revealed that build-up of the gaseous hormone ethylene in submerged tissues provides a likely cue for rapid shoot elongation, a response mediated by interactions between ethylene and the growth regulators abscisic acid, auxin, and gibberellin (possibly via a pathway that involves DELLA protein degradation) [30,29]. Their research also links naturally evolved differences in this signaling pathway to different degrees of flood tolerance in the field. In a comparative study of 22 herbaceous plants that occur on the Rhine river floodplain, species' differences in ethylene sensitivity resulted in characteristic shoot elongation responses that were associated with contrasting ecological distributions [31]. For instance, plants of *Ranunculus acris* (a species of upland, nonflooding sites), elongated petioles only 20% in response to submergence, while individuals of *R. scleratus* (a species found in sites that experience prolonged flooding) increased petiole length by 250% [31].

A critical insight from this body of work is that stem elongation responses to both flooding and neighbor shade are mediated in part by shared hormonal pathways, although they are initiated in each case by distinct environmental signals. Ethylene also appears to initiate a second transduction pathway that contributes to elongation by enhancing expression of expansin genes that affect cell-wall extensibility [32,33]. The mechanisms for other aspects of submergence response, such as aerenchyma formation and leaf structural changes that

enhance photosynthetic rates under water, are less well understood [29,34,35].

### The nature of environmental cue-and-response systems

Both case studies make clear the astonishing complexity of developmental systems as networks of interacting external and internal signaling elements leading to flexible, functionally integrated outcomes. These and other recent insights to the ways plants perceive and transduce environmental information suggest some intriguing directions for future research.

### Environmental cues

Plants have evolved to perceive whatever abiotic and/or biotic cues are consistently associated with alternative environments. Such cues can include any of the coincident aspects of an environmental state, sensed directly or indirectly (e.g. via effects on plant tissue status) as either immediate or predictive indicators of growth conditions. Evolution has evidently favored redundant cues (such as light quantity and quality effects of neighbors), which provide temporally and spatially robust environmental sampling to insure initiation of appropriate responses. This area is ripe for comparative studies, as differences among plant species in the nature or effectiveness of environmental perception mechanisms may be an important influence on patterns of phenotypic expression.

Plants receive environmental signals at the level of individual modules such as leaves, branches, or roots. Although certain responses may be expressed at this level, individuals must integrate distinct bits and types of environmental information to produce functionally coordinated phenotypes [36–38]. In some cases this can be achieved via a single sensor that integrates two immediate cues: for example, the actin cytoskeleton of root cap columella cells is sensitive to both gravity and touch, a mechanism that may explain the ability of roots to grow around soil obstacles while proceeding downward [39]. In other cases, one environmental factor can alter the transduction events of another factor or factors via shared hormonal or genetic components. Temperature has recently been shown to interact with R:FR photoreceptor effects on elongation and flowering time; since temperature also affects gibberellin synthesis, this hormone too may be involved in ‘crosstalk’ between light and temperature signals [40]. (Interestingly, a direct plant temperature sensor has yet to be identified.) In *Arabidopsis*, the *LEAFY* gene is one of several that integrate photoperiod and vernalization cues to determine transition to flowering [12]; atmospheric CO<sub>2</sub> concentration interacts with photoperiod cues as well through a yet unknown mechanism [41].

Some environmental cues are remarkably subtle: one recently discovered example is the volatile organic com-

pounds released by plants that have been attacked by herbivores [42]. These airborne signals induce neighboring plants to pre-emptively elevate their own defense-chemical production. Another new area of investigation is the ability of certain species to distinguish their own root systems from those of other individuals, leading to allocational and positional adjustments that minimize within-individual root competition [43,38]; the cues for this self-nonsel self recognition are not yet known.

### Response mechanisms

Among other shifts in research foci, eco-devo studies have generated renewed interest in plant hormones as coordinators of ecologically important responses to environmental conditions, often via complex molecular interactions [44,45]. Distinct environmental cues and initial transduction events can converge on shared hormonal pathways to elicit common responses, such as shoot elongation in response to both shading and submergence (see above), or similar biochemical induction and suppression effects of both herbivory and salinity stress [45]. Conversely, a given signal can activate divergent response pathways; for instance, in addition to its key role in shade perception, phytochrome also regulates defensive responses to herbivory via both direct and interactive effects on the jasmonate signaling pathway [15\*\*]. Phototropins not only sense blue light quantity to influence elongation, but also monitor its spatial distribution to guide the movements of stems and roots respectively toward and away from light gaps [46]. In addition to specialized receptors and phytohormones, response pathways utilize molecules that provide physiological feedbacks, such as sugars and amino acids, as well as osmotic signals [37]. Evolutionary changes at any point on these complex regulatory networks can alter phenotypic outcomes; as a result, even closely related species may express different developmental responses to a given environmental signal [47].

Developmental responses of plants to their environments can also include specific adaptive adjustments to offspring traits, a fascinating trans-generational aspect of individual plasticity that can enhance fitness when seedlings and parents encounter similar conditions. For instance, drought-stressed *Polygonum persicaria* plants produce seedling offspring with larger, more rapidly extending root systems [48], and the light environment experienced by *Campanulastrum americanum* plants influences offspring life-history to adaptively match alternative habitats in the field [49]. The mechanisms underlying these trans-generational responses are poorly understood, though they likely include changes to seed hormone composition [50]. Adaptive changes to gene expression in response to environmental signals can also be transmitted epigenetically to offspring [13]. For example, environmentally appropriate life-history responses of high-altitude plants to cold period are

mediated by flowering locus C (*FLC*) gene activity, which is controlled by DNA methylation [51].

### Conclusions and future directions: bringing realistic environments into development studies

The plant environment informs development in numerous specific ways: as cues to initiate particular responses, as multilayered regulatory influences on transduction pathways and gene expression, and as the ecological context that determines the functional success of developmental outcomes. This specificity holds a key implication for experimental design: instead of a neutral backdrop for studying developmental processes, the experimental environment shapes the results, so it is not possible to simply extrapolate from standard lab conditions to real-world habitats. This point is perhaps most dramatically made by studies showing that not only the activity but also the identity of genetic elements that contribute to trait expression can differ between artificial and natural conditions [52,53].

To understand how development works beyond the lab, research protocols must expand to include more, and more realistic, environmental conditions. Designing such experiments calls for knowledge of environmental variation in natural settings to identify the factors that initiate and modulate developmental responses [54]. In nature, these responses reflect the interactions of environmental factors with each other, so multifactorial studies of signaling pathways will be particularly useful [55]. It is challenging to include biotic factors such as competitors and mycorrhizal symbionts, but omitting them constrains our understanding of essential growth processes [38]; indeed these biotic interactors are evidently important sources of developmental cues. Together, these elements suggest a far richer environmental context for developmental studies.

Despite the exciting advances here discussed, it remains a surprisingly open question precisely how plants perceive a host of specific environmental signals, and how these signals are integrated via regulatory interactions to generate functional phenotypes. Studies of these cue-and-response systems also provide exceptional insights to the selective forces, genetic architecture and adaptive potential that have shaped plant diversity over evolutionary time, particularly when carried out on genotypes from natural populations and on ecologically or phylogenetically distinct taxa. Broadening our knowledge of plant developmental responses to the environment beyond the few well-studied cases is particularly crucial as we aim to understand and possibly prevent the phenotypic impacts of a host of anthropogenic changes on biological communities. Knowing the eco-devo response patterns for functional and reproductive traits in different conditions, and the genetic variation for those patterns, can provide key

insights to the potential for rapid range shifts and adaptive evolution in response to global climate change and other novel challenges, as well as the spread of invasive species across new habitats [3]. A research approach linking development with ecology could not come at a more crucially important moment in plant biology, or a more intellectually exciting one.

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