REVIEW

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The plant perceptron connects environment to development

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Plants cope with the environment in a variety of ways, and ecological analyses attempt to capture this through life-history strategies or trait-based categorization. These approaches are limited because they treat the trade-off mechanisms that underlie plant responses as a black box. Approaches that involve the molecular or physiological analysis of plant responses to the environment have elucidated intricate connections between developmental and environmental signals, but in only a few well-studied model species. By considering diversity in the plant response to the environment as the adaptation of an information-processing network, new directions can be found for the study of life-history strategies, trade-offs and evolution in plants.

Plants show a wide variety of growth forms and patterns of life events (life-history strategies), and they can grow in extreme conditions that include dry or water-saturated ground, warm or cold environments and resource-rich or resource-poor soils[1]. Despite these diverse circumstances, most plant species can be characterized by variations in only a few important trait characteristics, of which only certain combinations are well represented in nature[2,3]. Different species therefore seem to adapt to the environment by using combinations of a finite response 'tool kit' of mostly morphological adaptations. Physiological studies have provided considerable evidence that individual species of plant can adapt their growth and development to changes in the environment, as well as exhibit considerable plasticity in their functional response[4]. Unravelling how plants respond to the environment from the molecular level to the level of phenotype expression, and understanding how this shapes the evolution of life-history strategies, is a substantial challenge for molecular biologists and ecologists.

It is assumed that plant fitness depends on plasticity, which provides optimal trade-offs between the costs incurred by specific challenges such as resource capture, defence and the timing of reproduction[5]. Because plants have to exploit the environment from a relatively fixed position, the 'weighing up' of several conditions must steer decisions on how to invest available resources[6]. However, plasticity is not unlimited and various plants specialize their responses, which defines their ecological niche. The past two decades have yielded considerable progress in detailing molecular circuits that control plant responses to a wide range of environmental stimuli in model species. The quality and quantity of light, the availability of nutrients, drought or toxicity stresses, physical damage and pressure from pathogenic agents seem to serve as inputs for regulatory circuits that control numerous physiological and developmental responses[7,8]. Despite these advances in understanding, how plant responses define life-history strategies as a balancing act between plasticity and specialization at several levels, from molecular processes to community interactions, remains a principal scientific question.

Plant life-history strategies are studied by two contrasting approaches: building upwards from the molecular and physiological level to understand organ and whole-plant responses in a limited set of well-defined model species (for an example, see ref. 9); and deducing mechanisms from the ecology of species and their interactions in specific, multi-species environments (as demonstrated in ref. 10). These studies on plant responses by plant biologists and ecologists represent opposite ends of the spectrum; however, they are developing towards each other, given the increasing environmental complexity under which model systems are being studied[11] and the increasing detail in which information on traits can be processed in ecological studies[12]. The purpose of this Review is to explore advances in plant molecular and ecological approaches and to discuss future challenges that must be overcome to improve our understanding of species and community responses to altered global environmental conditions and to enable the tailored breeding of crop varieties that are better able to cope with stressful changes in the environment.

Growth and stress responses are two cornerstones of the overall plant response to the environment, and they are assumed to be involved in a trade-off: the ability to cope with stress comes at the expense of growth, and vice versa[13]. In the context of biotic stresses such as the presence of pathogenic species and herbivores, this classic concept considers plant species as either 'growers' or 'defenders', relating to the extent to which individual organisms may reconcile costly ecological strategies[14]. However, not all defences may necessarily be traded off against growth[15]. For example, it is established that species with a fugitive life-history strategy, such as *Arabidopsis thaliana*, may still possess elaborate stress and defence systems, which are well connected with growth signalling pathways[16–18]. It is not well understood how plants use such a developmentally wired defence system under various circumstances or whether the system wiring differs systematically in plant species that are predicted to stand and fight. Growth and stress responses also have to be considered with other trade-offs that play into the selection of response patterns. For example, the choice for precision or variability, or for plasticity or uniformity, in the response may be steered by the predictability of the environment, and the maintenance of resistance to pathogenic agents can be explained by community-wide interactions[4,19].

Here, we assess recent insights into plant life-history strategies and molecular pathways that integrate external signals and connect them to growth responses. Plants respond rapidly and reversibly to signals through the production of environmentally induced metabolites, which include osmolytes to cope with osmotic stress, antimicrobial agents and volatile compounds that attract enemies of herbivores and pathogenic species[20–22]. However, we will not elaborate on these biochemical responses here. Instead, we will explore how environmental stimuli

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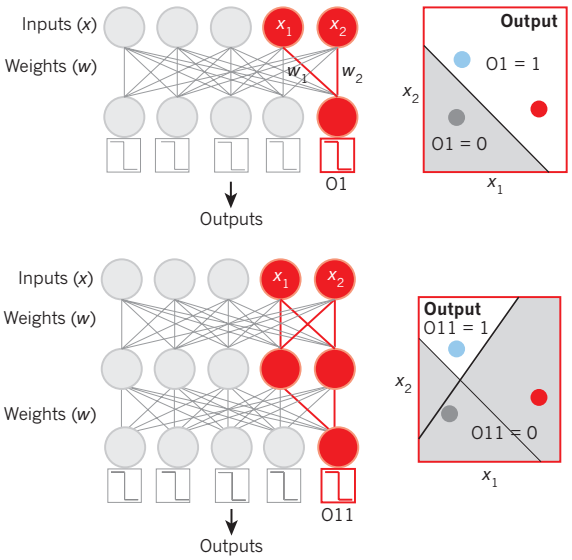
BOX 1

Information processing by perceptrons

In the field of machine learning, mathematical models of neurons as input-processing units have led to the concept of the perceptron (Box Fig., top), an information-processing system in which input values x_i are multiplied by adjustable weights w_i and fed into 'neurons' that produce an output on the basis of specific activation functions (rectangles) that are applied to the sum of the weighted inputs $w_i x_i$. A single-layer perceptron can learn, from a given set of examples, to perform a linear separation of inputs into output classes, such as the separation of the grey input combination from the red and blue input combinations (inset). Multilayer perceptrons (Box Fig., bottom) contain intermediate 'hidden' layers that enable successive separations, which permit nonlinear discrimination of the weighted inputs so that only the blue input combination leads to an output (inset). Extra layers add further linear separators, which facilitates the precise matching of selected inputs to a given output.

Analogous to perceptrons, protein molecules and gene promoters can form processing units (the neurons) that are connected through biochemical connections (edges). Together, these yield an information-processing network that selects appropriate outputs for combinations of inputs. Plant molecular responses to environmental challenges perform similarly to multilayer perceptrons in information processing, in the sense that several perception units operate in parallel and are 'weighted' appropriately at subsequent levels to define an output transcriptome. This enables the selection of alternative outputs on the basis of information from many different inputs. In this view, the 'logic' of an individual plant's life-history strategy is encoded in the connections and weights of this information-processing network, which translates combinations of environmental inputs into appropriate responses.

The plant multilayer perceptron analogy that is pursued in this Review, in which environmental inputs modulate nodes in a developmental network, bears a number of structural and functional features that differ from their electronic counterparts. First, biological networks are connected in more intricate ways and inputs are not processed synchronously. Second, intermediate layers are modified by environmental and developmental signals that operate over different time scales. Environmental inputs operate on the order of seconds to minutes, whereas developmental responses and feedbacks operate mostly on the order of hours to days. Third, lower nodes provide feedback to upper nodes. Interestingly, recurrent neural networks, especially those with a long-short term memory, encode feedback properties, which indicates that such networks may be more accurate analogies for biological information processing. Last, machine-learning algorithms learn by adjusting their output to the input, using back-propagating error-correction functions on the weights. Although feedback exists, there is no evidence to show that the molecular networks involved in the plant response to the environment learn by other mechanisms apart from the random adjustment of weights through mutation and selection that shapes their evolution.



influence developmental traits at the molecular level. We select examples that reveal an analogy between plants and a well-defined information-processing structure known as the perceptron. In our analogy, the plant is described as a multilayer perceptron. Environmental and developmental signals are defined as inputs that are processed in several steps through transfer functions that are divided into network layers to define outputs[23–26] (Box 1). The view that is emerging from such studies suggests that research in fresh directions is needed that offers an increased understanding of plant behaviour and trade-offs both in a natural context and in relation to important and worldwide agricultural and environmental changes.

Plant ecological strategies

Most classifications of plant ecological strategies are made on the basis of trade-offs[27–29]. Species of plants with an opportunistic and acquisitive life strategy focus more on reproduction and dispersal, whereas those with a more conservative approach to resource acquisition follow a stand-and-fight strategy[14,30,31]. Resource-use economy has therefore been an important property in the classification of plant ecological strategies[28,32,33]. Examples include the division of plant species into *r* (opportunistic species with high rate of reproduction) and into *K* (species that live close to their carrying capacity)[34], which generally corresponds with the early versus late occurrence of plant species during the colonization of bare land that is defined as succession[35]. The *r*–*K* concept, which is based strongly on trade-offs between plant ecological strategies that were observed in the field[34], can explain extreme strategies well but the many intermediary strategies less so[3].

Universal adaptive strategy theory[27] positions plants in triangles in which the corners represent extremes that are classified on the basis of competitor, stress tolerance and ruderal ability (CSR) strategies; the theory is therefore better able to handle intermediary strategies than the linear *r*–*K* continuum. Classifications made on the basis of CSR strategies are now being replaced by trait-based approaches, which provide more opportunities for the refinement of classifications because numerous traits can be quantified for individual species of plant[36]. However, a large number of traits are not always necessary for classification. For example, a global trait-based assessment of around 46,000 plant species showed that as few as six combinations of traits were sufficient to classify most species into relevant ecological types[3].

Modern trait-based approaches may reveal variations between and within species that cannot be accounted for by species-based approaches[37]. In *Arabidopsis*, variation in flowering time influences geographic range and niche occupancy, as well as the potential for colonizing new ranges[38]. The level of such trait variation in species can be as high as the level that occurs between species[37]. However, species of different phylogenetic origins can express the same traits, which explains why they compete for the same resources[39]. Despite substantial progress towards understanding plant strategies, trait-based approaches are still

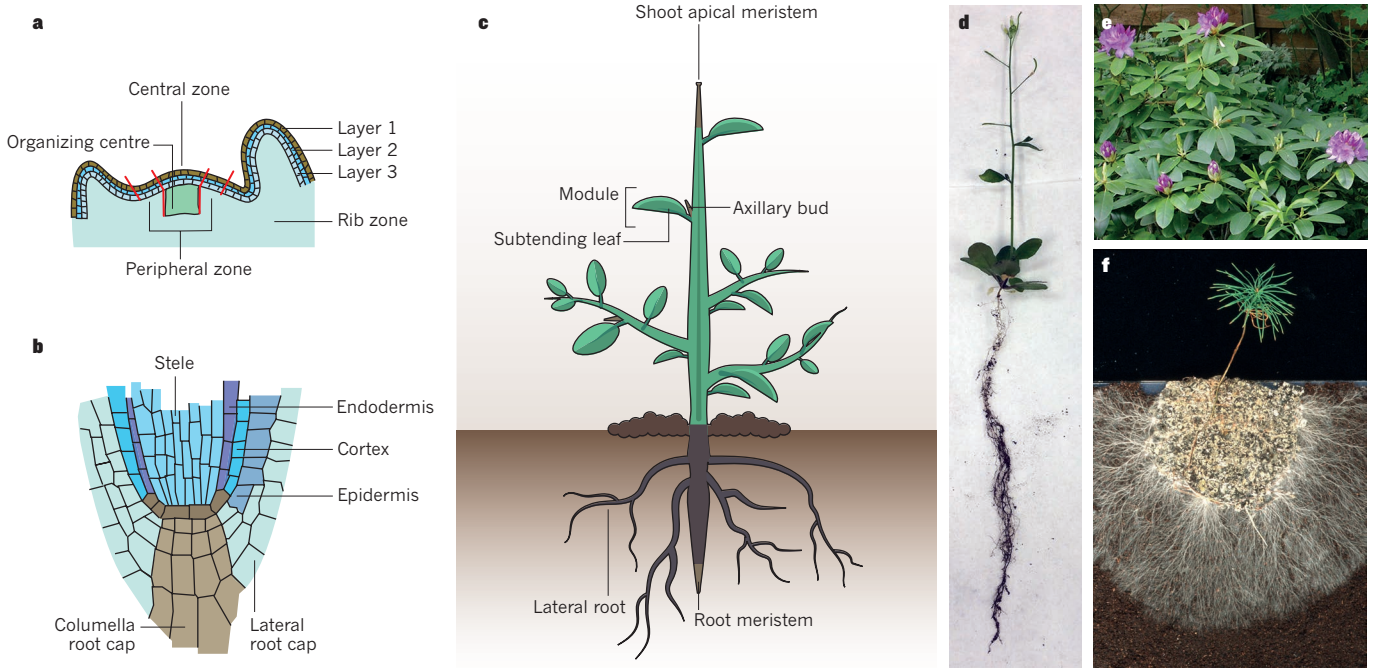


Figure 1 | Plant development and life-history strategies. **a**, **b**, The extension and modification of plant architecture from shoot (**a**) and root (**b**) meristem growth zones. Shoot zones and root cell types are indicated. **c**, Meristems form modules. Each shoot and root deposits new lateral meristems. In the shoot, these reside in the axillary buds. **d**, *Arabidopsis* annual flowering and sparse rooting. **e**, Perennial flowering of *Rhododendron* sp. **f**, The dense roots of a pine seedling with an associated network of ectomycorrhizae.

mostly based on aboveground plant properties, even though further advances could be made by including root traits into these classifications[40]. Moreover, current ecological trait-based approaches strongly depend on phenotypic and physiological characterizations of plant traits, and it is a separate challenge to link these to the characteristics of the biotic environment[41,42].

A considerable drawback of ecological models constructed on the basis of either traits or life-history strategies is that they consider the machinery that translates environmental challenges into functional (proximate) and evolutionary (ultimate) plant responses to be a black box. Natural selection acts on genetic variation that simultaneously influences fitness at several levels, from the efficiency of molecular networks to the traits that determine ecological strategies[43]. Therefore, of the molecular interactions that shape the phenotype of a particular plant , those that can be evolved need to be determined. Do trait linkages and major plant life-history strategies reflect constraints on the capacity of underlying networks to evolve? Progress towards answering this question is hampered by the relatively small number of wild plant species that have been studied at the molecular level. Combining trait-based approaches with molecular studies, in only a few selected species combinations, at first, should help to explain why certain trait combinations are more abundant in nature than others, as well as why particular traits have evolved in various plant phylogenetic groups. Conversely, ecological (trait-based) studies that unravel unexpected trait combinations in specific species can inspire molecular studies that aim to further understand constraints on and opportunities for optimizing plant responses to the environment.

Molecular networks that underlie growth responses

The basic body plan of flowering plants, in which interior vascular tissues are surrounded by layers of ground tissue and the external epidermis, is elaborated during embryogenesis. Zones of cell division called meristems are specified at the root and shoot poles, as well as in the vasculature. Cells with stem-cell-like properties maintain the meristems throughout the life of the plant, during which they produce organs and new lateral meristems. Much of the plasticity of plant development arises from the functional diversification of these shoot- and root-derived organs in response to environmental signals (Fig. 1). The rate of growth, direction of growth and the fate of the organs, as well as the number and position of the new meristems, determine growth and architecture[44]. Environmental inputs influence the positioning and growth of organs and the fates of new meristems and therefore create functionally appropriate differences in appearance between individual plants of the same species.

Work in model species such as *Arabidopsis* reveals that the intrinsic genetic program for the elaboration of plant architecture depends on the appropriate activation of transcription programs in space and time, which is achieved through tissue- and cell-specific transcription factors guided by signals with specific patterns of distribution. The often highly tissue-specific expression of the biosynthesis and perception machinery of these signals — the plant growth regulators — indicates that a genetically determined basic body plan that is set up in the embryo diversifies hormone-response pathways. Transcription factors and their mutual regulation by peptide signalling and the movement of proteins and microRNAs can form the pre-patterns for this diversification. Hormone pathways can also lead to self-organized pattern formation; well-studied examples of this include the spacing of the leaf and flower primordia and the specification of leaf shape[45,46]. In these cases, feedback loops in regulatory networks that control the distribution of hormones and transcription factors provide tuneable pattern-formation mechanisms through which environmental signals can operate to achieve developmental plasticity[47].

The growth and architecture of plants are strongly controlled by the indole-derived plant hormone auxin, which accumulates, and defines regions of growth by triggering a transcriptional response that is associated with the formation of meristems or organ primordia, in roots and shoots (Fig. 1a, b). Patterns of auxin accumulation are strongly influenced by transmembrane proteins that are capable of polar auxin transport, and so auxin can be positioned by collective cell-to-cell transport by many cells in a tissue rather than by a cell-autonomously defined centre[48,49]. Although polar auxin transport has an important role in integrating tissue-level information to regulate organ initiation and outgrowth, region-specific auxin biosynthetic enzymes also contribute to the stable positioning of auxin concentration maxima.

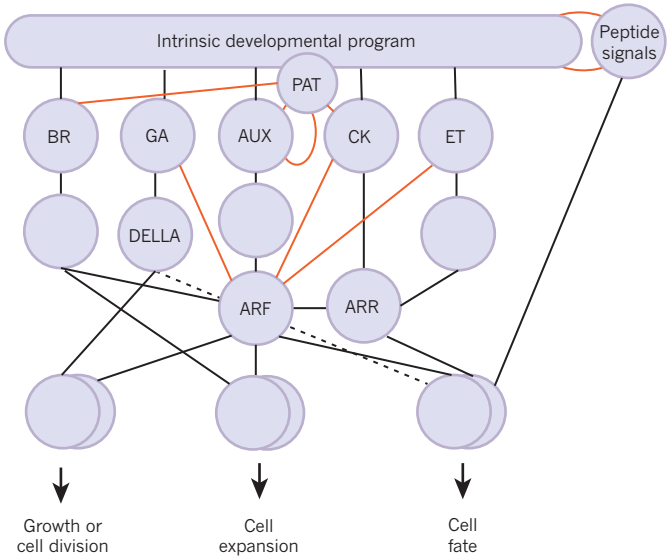


Figure 2 | Connectivity in plant growth-regulatory networks. The intrinsic developmental program in plants sets up spatially restricted domains of growth-factor signalling and their response systems (upper layer of the network). Polar auxin transport (PAT) is shown as an example process. Cross-talk between growth factors (brassinosteroids (BR), gibberellic acid (GA), auxin (AUX), cytokinins (CK) and ethylene (ET)) occurs through signal-transduction pathways, which form 'hidden' layers that integrate information by changing their activity in response to inputs. Ultimately, the hidden layers control transcription in the output layer (bottom row). Nodes in the output layer represent genes with promoters that integrate weighted inputs from the previous layer. A single output node in the drawing may represent several genes, the encoded proteins of which control a developmental process. Feedback between different information-processing nodes is indicated by red lines. ARF, auxin response factor; ARR, *Arabidopsis* response regulator.

Other small plant growth factors or hormones that can trigger cell-fate decisions or cell division, or increase rates of cell expansion, include cytokinins, brassinolides, strigolactones, gibberellic acid and the gas ethylene[50]. Deepening insights into the connections between signal-transduction components and the target genes of plant growth-factor signalling pathways in *Arabidopsis* support the idea that the distribution, production and signal transduction of all hormones are intimately connected to each other[51–53] (Fig. 2). These connections serve two separate and important roles: conferring local robustness on development or regulating plasticity. Auxin and cytokinin interactions make a considerable contribution to the robust definition of meristem boundaries and the specification of two vascular cell types[54–56]. Global plasticity of tissue architecture during shoot branching, however, involves the systemic movement of auxins and strigolactones that are synthesized in shoots and roots, as well as their interaction at the site of incipient lateral shoots (buds), to control the outgrowth of local modules[57,58] (Fig. 1c).

Similar to the conventionally recognized non-peptide plant hormones, small excreted peptides and their receptors play important parts in determining plant architecture and growth. These signalling pathways can also take on the two roles of conferring local developmental robustness or regulating plasticity. Several peptide pathways control cell proliferation and fate specification locally[59,60]. In these cases, the peptides and their adjacently expressed receptors help to define robust cell-fate choices[61–63]. Other peptides move over long distances from the root to be perceived by receptors in the shoot or as a response that influences specific developmental modules such as the lateral root primordia, which regulate root-system plasticity[62,64].

Plant growth regulators act mainly by changing the activity of transcription factors. A single-layer perceptron-like view of plant growth in which the inputs of hormones are weighted through the convergence of their downstream transcription factors on overlapping targets is at odds with largely non-overlapping early transcriptional responses[65]. Instead, numerous transcriptional effects of particular hormones on the levels of others have been reported, including those described in refs 66 and 67, which suggests a web of feedback on growth outputs that involve a few main nodes (Fig. 2). This feedback not only controls growth homeostasis, which confers robustness to developmental processes, but also coordinates the growth of plant modules by long-distance signalling and acts as an entry point for environmental signals that act on it.

Linking environment perception to the growth response

During their lifetime, plants must simultaneously deal with variable temperatures, light conditions and nutrient and water availability[68], as well as toxins and external networks of symbiotic, antagonistic and commensal biota[69]. These conditions influence the germination, establishment, growth, development and competitive and facilitative interactions of plants with their intraspecific or interspecific neighbours. The responses of plants to these environmental conditions are therefore often correlated to ecological traits. Plants measure and use such external inputs to considerably adjust their growth and architecture (Fig. 3). Light is one of the most important environmental factors, and in trait-based approaches, the light preferences of plants are related to traits such as leaf size, thickness and stem height.

All of the developmental signals we have discussed are connected to environmental signals, as shown by a growing body of work in model species. Photoreceptor proteins enable the discrimination of various parts of the light spectrum, from the far-red to ultraviolet B, which means that both the quality and quantity of light can influence growth and development[70,71]. The phytochrome photoreceptor family regulate light-dependent growth processes through the degradation of important hub proteins that connect the light input to the developmental output, which are known as phytochrome interacting factors. These factors interact directly with another signalling hub that is comprised of DELLA family transcription factors that mediate gibberellic acid signal transduction and control the transcription of auxin biosynthesis and signalling genes to influence plant architecture[72–74]. Photoreceptor proteins also connect the light input to directional growth responses (tropisms) through polar auxin transporters[75,76].

Plants measure the length of the day to control both flowering time, an essential trait for the optimization of pollination and seed production, and dormancy, which is the temporary cessation of growth for the protection of growing tissues in winter[77,78]. The circadian clock, a cyclical network of diurnally activated and repressed transcription factors that are entrained to daylight by photoreceptor signalling, plays an essential part in day-length measurement. A combination of mechanisms, including the external coincidence mechanism of light-dependent activation of transcription factors with diurnal expression dynamics, enables the circadian-clock time to be compared with the actual conditions of light[79]. Day-length measurement and the direct light-signalling-dependent activation of transcription factors form the basis of the main transcriptional switch that exploits developmental modularity by reprogramming specific meristems to form flowers instead of leaves[77,80]. In the examples we mention, light signalling is coupled to various intermediate signal-processing layers of the developmental network.

Extreme temperatures provoke programs of stress response, which have been well studied[81,82]. However, the ambient temperature also controls day-length-dependent flowering and growth, which is frequently quantified as an ecological trait. Prolonged exposure to the cold can preload repressive chromatin-modifying complexes onto the promoter of the gene that encodes the transcription factor Flowering locus c (FLC), which represses the floral reprogramming of meristems. FLC inhibits transcription factors that initiate the formation of floral organs and counteracts transcription factors that are induced in response to day length; cessation of a period of cold activates the spreading of repressive modifications at the *FLC* locus, which means that flowering is enabled only after the plant experiences prolonged cold[83]. The FLC floral reprogramming switch is conserved between annual and perennial plants (Fig. 1d, e), which indicates that similar environmental signal integrators

may operate in plants with diverse life-history strategies[84]. Light and temperature cues for flowering are therefore integrated in successive information-processing layers, in an analogy with multilayer perceptrons. Furthermore, in *Arabidopsis*, the ambient temperature has been shown to control growth processes through one of the phytochrome interacting factors[85–88]. As discussed previously, phytochrome interacting factors connect to auxin biosynthesis and the auxin response, which reveals how temperature and light information can be jointly weighted by the information-processing network and coupled to growth regulation[89].

The deprivation of nitrogen and phosphorus, which are often limiting resources in soils for plants, can lead to developmental adaptations in lateral root outgrowth and the rate of root growth (Fig. 1). Lateral roots elongate when nitrate is available after systemic deficiency but such elongation is halted in the absence of nitrate. Without nitrate, the main nitrogen sensor, which is a dual-affinity nitrate transporter, acts as an auxin pump that alters auxin distribution to inhibit growth[90]. Besides this local response to nitrogen, root growth under conditions of nitrogen limitation can be systemically controlled by root-borne mobile peptides that are perceived in the shoot[91]. A candidate phosphorus sensor inhibits a transcription factor that activates the phosphate-starvation response in a phosphorus-dependent manner, which is linked to an increase in auxin signalling and the promotion of lateral root initiation and emergence[92]. The transcriptional responses to combined nutrient starvation regimes indicates that complex interactions occur between various signals[93], which suggests that an elaborate decision-making mechanism to adapt growth and root architecture on the basis of potentially competing demands may exist. Furthermore, specialized cells in the root endodermis can modify cell differentiation to adapt to nutrient stresses, demonstrating that cells may have specialized roles in the nutrient response[94].

Salinity and drought are considerable environmental stresses that prompt the plant to modify its growth and architecture[22,95,96]. Although the molecular sensors that function upstream of the main stress-induced hormone abscisic acid remain largely unknown, stress-mediated changes in growth involve families of transcription factors that are associated with drought- and salinity-induced abscisic acid signalling[97]. Such signalling also affects gibberellic-acid-responsive DELLA transcription factors; it thereby controls root developmental responses that are under the control of gibberellic acid and auxin signalling by connecting to transcription-factor nodes[17,96,98].

As well as continually adapting their growth and reproduction to the prevailing abiotic environment, plants must cope with the presence of microorganisms, insects and other invertebrates, including (symbiotic) mutualists, commensals and enemies. Many plants can respond to nutrient limitation by increasing their root-to-shoot ratio or by producing root systems that have a larger capacity for uptake, such as cluster roots. However, they can also associate with microbes, including mycorrhizal fungi for the uptake of phosphorus, or nitrogen-fixing bacteria or actinorhizal symbionts that make atmospheric nitrogen available for plant growth. Plants recognize and defend against aversive biota through immune signalling networks, which regulate constitutive microbe-associated molecular pattern (MAMP)-triggered defences and induced effector-triggered immunity (see page 328; refs 99–101). MAMP-triggered defences involve the membrane-receptor-kinase-triggered recognition of MAMPs and effector-triggered immunity results from the receptor-recognized entry of pathogen effectors.

The responses to both MAMP-induced and effector-triggered immunity pathways involve plant hormonal signals such as jasmonic acid, salicylic acid, abscisic acid and ethylene, which initiate organ-specific defences but also influence growth. This cross-talk occurs at many levels: for example, it occurs between growth hormones and MAMP receptors at the plasma membrane[102]; between pathways for sensing the quality of light and biotic stress; and between growth- and defence-activated components of signal transduction[16,103–106]. Simultaneous alteration of jasmonic acid and photoreceptor signalling revealed uncoupling of the growth–defence trade-off, which strongly suggests that network wiring underlies trade-offs[18]. Jasmonic acid and salicylic acid pathways

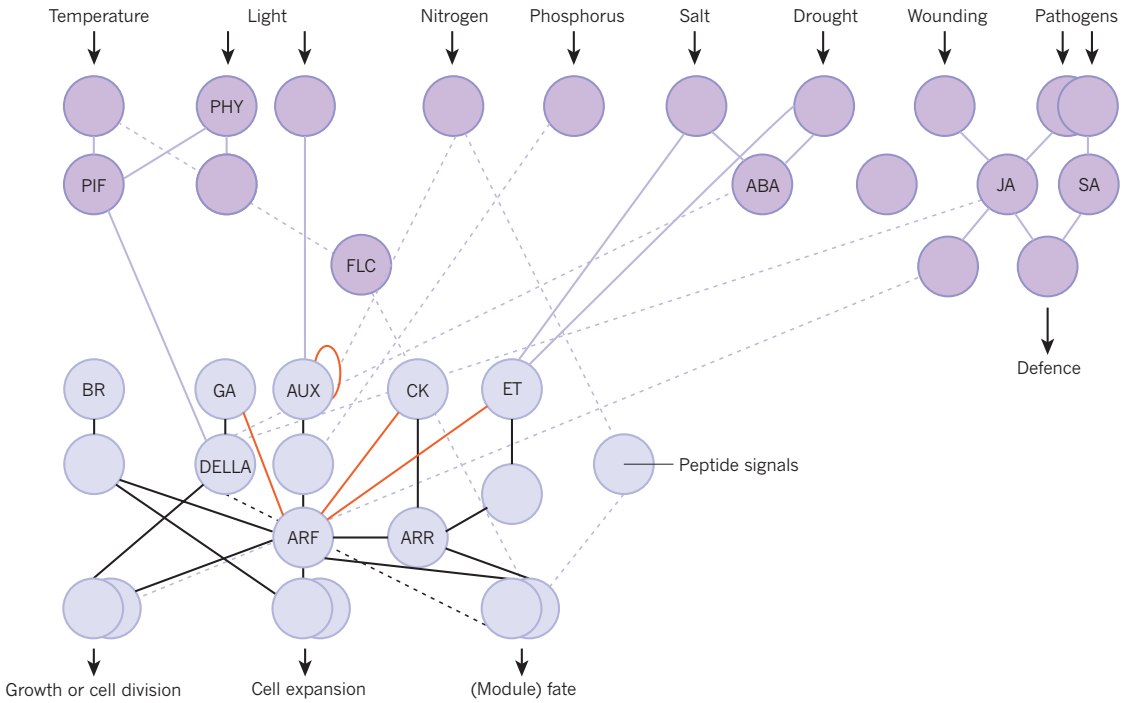


Figure 3 | Environmental control of growth networks. Environmental inputs interact with each other through converging signal-transduction pathways (top hidden layer, dark purple) and with the growth networks that are active in specific developmental contexts (purple solid and dashed edges and bottom hidden layers, lighter purple). This integration modulates activity of the growth network, which specifies various developmental outputs. In the perceptron view, environmental inputs change the weights of the growth network. (For clarity, not all known links are shown, and environmental responses through connections in the top hidden layer to outputs that represent stress-response genes are also not shown.) The two light nodes represent light of differing qualities and the pathogen nodes represent two types of pathogen. ABA, abscisic acid; JA, jasmonic acid; PIF, phytochrome interacting factor; PHY, phytochrome; SA, salicylic acid.

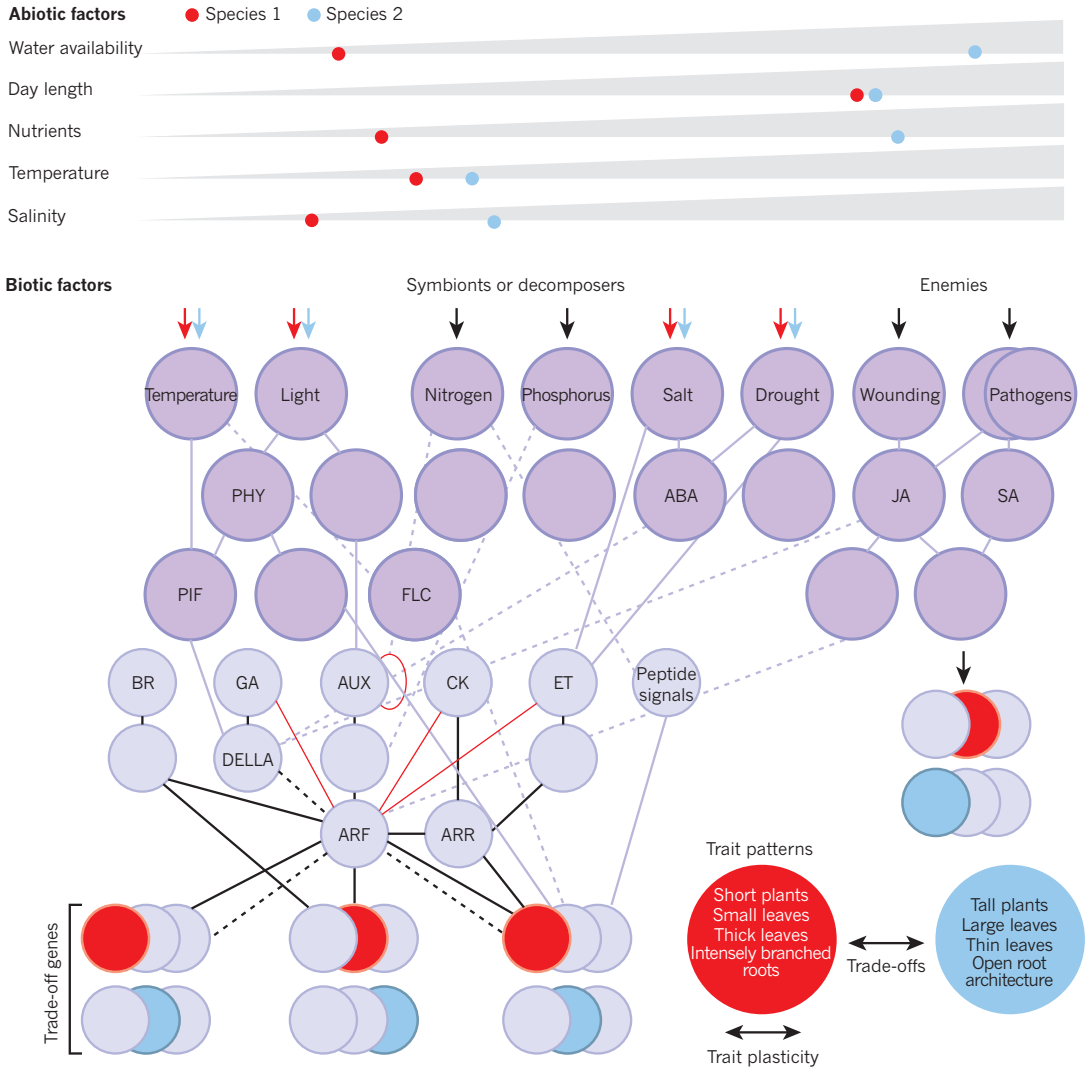


Figure 4 | Relating signal perception to plant traits. Two example species, species 1 (red) and species 2 (blue), are shown. Plants sense the abiotic environment and can influence growth networks in response. They also obtain direct and indirect information from the biotic environment, for example, through defence triggers and alterations in nutrient availability caused by symbionts and decomposers. All such inputs can lead to plant responses that involve growth or cell division, cell expansion, cell fate, stress or defence through outputs that lead to the upregulation of genes (red or blue nodes). Some of these genes may underlie trait patterns and trait plasticity. Trade-offs between trait patterns are determined by the wiring diagram of the perceptron. An increased knowledge of how growth and defence responses are influenced by the biotic and abiotic environment can reveal trade-offs between these two processes. Understanding how inputs influence the output in wiring diagrams that have evolved differently may help to define the limits of plasticity, as well as why certain trait patterns are underrepresented in nature or why certain traits can undergo rapid evolution.

provide inputs into auxin, brassinolide and gibberellic acid signalling and help to adapt the growth program of the plant to biotic stress. Conversely, growth hormones such as brassinolide can suppress immune signalling[107]. Such inputs and the mutual interactions between stress, growth and immune signals can vary substantially between species[108,109].

The list of established molecular connections between environmental stimuli and developmental processes is growing steadily, although current examples are restricted to a few well-studied species. Nevertheless, we suggest that a common theme is emerging — namely, that abiotic and biotic signals provoke fast biochemical responses but alter the growth of the plant through a network that operates over a longer timescale. To do so, these signals interact with specific nodes of the endogenous signalling circuit that orchestrates growth. The nodes can be intermediate-layer transcription factor hubs, but may also consist of proteins that influence the distribution and biosynthesis of growth hormones. The 'output' of these junctions of environmental and developmental signalling connects to transcription factors that regulate the 'actuators' of growth. These actuators include genes involved in cell division and cell expansion as well as those that trigger the initiation of primordia or change their fate. The signal-transduction network is wired to distinct developmental programs in specific modules in the plant such as the roots and shoots, and in various cell types[110]. As a result, a three-dimensional arrangement of developmental signalling networks in the plant interacts in a context-specific way with environmental inputs that include light in the shoot and nutrients in the root.

Zooming in on a cell with a particular wiring would reveal an information processing system in which specific environmental and developmental inputs are combined to produce a developmental output and to coordinate the plastic development of modules by long-range signalling, such as between the roots and the shoots. However, the plasticity of individual species of plant is bounded and can even be disadvantageous under certain circumstances[4]. It is unknown how information processing in plants relates to the evolution of the trait spectrum of wild plant species that are under natural selection.

From specific model systems to ecological interactions

As explored previously, current knowledge implies that plant trade-offs need to be considered as the fitness function of a multilayered decision-making structure that enables a certain plasticity in response to the environment. Compared to the *r–K* continuum, modern trait-based approaches are increasingly being used to account for multiple-variable environmental conditions under which plants are selected. The challenge will be to connect the observed traits to the internal molecular states that may occur in plants and how these are used to respond to the environment[29]. To achieve this, it will be necessary to obtain molecular information from plant species with life-history strategies other than those of the early successional types that are represented by most model species used in molecular biology[3]. A good example is provided by the comparison of flowering control between *Arabidopsis thaliana* and *Arabis alpina*[84], which has a perennial life-history strategy. Such approaches need to be extended further to include other plant families and life-history strategies, which will enable important open questions to be addressed, including how alternative plant life-history strategies operate at the molecular level and how plant information-processing circuits vary in nature (Fig. 4).

The original concept of trade-offs was based on the existence of linear scales from species that ranged from fast-growing, poorly defended plants to those that are slow-growing and well defended[14]. These trade-offs were considered to occur at large ecological gradients and for relatively simple defence strategies targeted at natural enemies that are based on costly chemicals that can be traded off with resources used for growth[31]. However, little is known about how these trade-offs are orchestrated at the molecular level[16]. Work in wild tobacco (*Nicotiana attenuata*) demonstrated that the expression of an important enzyme involved in photosynthesis is downregulated by the oral secretion of the caterpillar *Manduca sexta*. Plants in which the corresponding gene was silenced not only showed reduced growth, but also reduced jasmonic acid signalling and reduced levels of defence[111]. Although this points to a molecular-based mechanism of trade-off, another study in the same model system showed that jasmonic acid could reduce sugar concentrations in leaves, which led to reduced growth in the caterpillars[112]. Therefore, trade-off mechanisms seem to involve complex feedback that may influence growth–defence trade-offs in a manner that is independent of resource consideration.

As well as the work to clarify the molecular mechanisms that are involved in growth–defence trade-offs, progress has been made towards understanding interactions between plants and their biotic environment. Many studies have revealed interactions that can operate at the same time or at different times in different parts of the plant — for example, above and below the ground[113,114] — and that may or may not impose conflicts on internal decision making. Moreover, plant defence strategies that target natural enemies can act directly through defensive chemicals, resistance or tolerance, or indirectly through interactions with symbionts or the enemies of plant enemies. It is assumed that the induction of these defences on attack is less costly to plants than their constitutive production. However, it becomes more challenging to understand the advantages of induction when plants are challenged by several enemies[115] or when plant–enemy interactions are studied in relation to the species diversity of the surrounding communities[116]. Furthermore, symbioses, such as those with mycorrhizal fungi (Fig. 1f), nitrogen-fixing microbes or endophytes, not only provide plants with resources but can also interfere with plant defence responses[114,117]. Rapid growth may also reduce the robustness of plant systems to abiotic and biotic perturbations[4]. Understanding the fitness function of a given information-processing network will therefore require insights into the function of growth, abiotic signal-response and defence-network components, as well as the cross-talk between them, under a realistic variety of positive and negative interactions.

Towards the quantification of plasticity and trade-offs

A future challenge will be to study molecular networks and their activities under various conditions and combinations of abiotic stress and multitrophic biotic interactions (Fig. 4). This will enhance our knowledge of how plants integrate environmental inputs with developmental information to adjust growth and development with plasticity, under real-world conditions. Because many of the outputs of the plant perceptron can be quantified by transcriptomic approaches and refined to the levels of tissues or cells[118,119], it should become more straightforward to describe the outputs of combinations of environmental inputs with cellular resolution. However, it will still be a challenge to understand the behaviour of the 'hidden' layers that connect such inputs to the outputs. One approach that addresses this is to monitor quantitatively the activity of key integrators of signalling (such as DELLA proteins and phytochrome interacting factors) using carefully controlled variations of their environmental inputs, and to link the results to the activation of particular target genes. Activity sensors that are specific to hub proteins in hidden layers and the quantification of related outputs will help us to understand how internal plant networks respond to combinations of several environmental factors and how this information is weighted to lead to appropriate responses. These findings will reveal how trade-offs work at the level of individual plants, which should enable us to further understand the molecular basis of plant traits and plant-trait syndromes.

Molecular research on early successional wild-plant model species and crops that were derived from early successional wild plants[120] has provided us with a picture of an intricately connected signalling network. If pursued in isolation, the current model-species-based approach will leave many open questions about the interplay of molecular growth and abiotic or biotic stress-response networks in species with contrasting ecological strategies. It will therefore be necessary to perform molecular–ecological studies in new model species with contrasting ecological strategies, both in the laboratory and under ecologically realistic conditions (Fig. 4). A promising approach combines networks of gene expression with genome-wide association studies, which has been applied successfully in plants to study the microevolution of traits[121–124]. Such a 'systems genetics' approach reinforces the view that the activity of transcription factors is a network output of relevance to microevolution; this is because many quantitative trait loci coincide with transcription-factor binding sites or *trans*-acting transcriptional regulators[124]. Continual advances in sequencing and gene-editing technologies will make it more feasible to expand the number of model species available to researchers in highly comparable ecological settings, as standardized environmental input assays can be coupled with transcriptional-output assays to compare responses between species[125,126]. A challenging aspect will be to compare signal integrators in the hidden layers of species with contrasting life-history strategies, which probably requires the identification of relevant nodes as well as ways to measure their inputs and outputs. This knowledge may also help us to understand why phylogenetically distant plant taxa can show similar ecological responses, as well as how certain traits may have evolved independently in several plant families[3].

A joint molecular and ecological analysis of non-model species under relevant conditions of change will shed further light on the opportunities for and the limitations of plant responses and adaptations to new conditions. This may inform us about as-yet unexplained variation such as the noticeable differences in strategies for nutrient uptake by characteristic species of nutrient-poor soils[127]. Plant responses to rapid, global changes in climate and land use, and to their introduction by humans to exotic ranges (sometimes on different continents), indicate that evolutionary developments in relation to abiotic and biotic environmental conditions can take place at a high rate and may sometimes include only several generations[128–131]. Under such new environmental conditions, plant traits that are usually the subject of a trade-off, including resource acquisition or defence, may no longer be selected[130,132]. For example, most species of invasive exotic plants are of the resource-acquisition type; however, when they are introduced to a new environment that lacks their specialized natural enemies, such species may alter their performance and adaptation in comparison to the original range[133,134]. Yet in a new range, only some exotic plant species may evolve to become increasingly competitive[135]. The explanation and prediction of this limited potential remains a great challenge for invasion ecologists[131,136]. Linking a molecular view of the plant perceptron to trait-based approaches can enhance our understanding of the rise and fall of invaders[137]. More broadly, land-use and other global environmental changes are altering the network structure of the biotic environment of plants[69], although the abiotic environmental conditions can also move in other, unprecedented directions[138,139]. Knowledge about the basis of trade-offs and the limits of plasticity will enable us to assess the potential consequences of these changes. ■

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