

Spotlight

Phytochrome Responses: Think Globally, Act Locally

Carlos L. Ballaré^{1,2,*,@}

Localized responses to changes in the red to far-red ratio (R:FR) allow plants to efficiently forage for light in patchy canopies, and to fine-tune physiological activities to the local light environment. Recent studies are elucidating the molecular mechanisms that mediate localized responses to R:FR and the functional implications of these responses.

Phytochrome B (phyB) is a key photoreceptor protein that plants use to detect the proximity of other plants. Green leaves absorb R light, while reflecting and transmitting FR radiation. R light activates phyB, generating Pfr, the active form of the photoreceptor, whereas FR photoconverts Pfr back to the inactive form (Pr). By sensing changes in the R:FR ratio, plants can perceive shading by other plants and gauge the proximity of potential competitors. Perception of low R:FR triggers shade avoidance responses, which include the acceleration of stem and petiole elongation and phototropic orientation toward areas of high R:FR [1].

The precise site of R:FR perception has puzzled plant physiologists for years. Early studies using plants of goosefoot (*Chenopodium polyspermum*) demonstrated that internode elongation can be promoted by FR delivered to the internode itself or to the leaves situated just above and below the responding internode [2]. In more recent years, many of the mechanistic advances in the field of photomorphogenesis have used recently de-etiolated seedlings as a model system, where the aerial part is formed by just the apex, a pair of embryonic leaves (the cotyledons) and the hypocotyl. Using

this seedling model, the picture that has emerged is that the stem (hypocotyl) elongation response to low R:FR ratios is systemically controlled by light perceived by the cotyledons, not by the stem itself [3,4]. This seedling model has been useful in efforts to identify mechanistic connections between phyB, phytochrome-interacting factors (PIFs), and the downstream growth processes mediated by hormones, particularly auxin and brassinosteroids [5–7]. However, extrapolation of the physiological results obtained with this seedling model might lead to a biased perception of the mechanism of phyB-mediated shade avoidance responses at the whole-plant level, exaggerating the importance of interorgan signaling in the orchestration of these responses.

Local Hyponastic Response

Two recent papers [8,9] address shade avoidance responses to localized FR treatments in Arabidopsis plants at the rosette stage, which are structurally more complex than tiny seedlings. Both studies measured the upward leaf movement (hyponasty) caused by supplemental FR radiation. Leaf hyponasty is a classical shade avoidance response because it allows the plant to push leaf blades into well-illuminated areas of the canopy. The hyponastic movement depends on differential growth rates between the abaxial and adaxial sides of the petiole. How and where the light signal is perceived to initiate hyponastic responses was not known. Both studies found that low R:FR ratios delivered to a single leaf of the rosette caused a strong angular response that was restricted to the irradiated leaf. Therefore, the hyponastic response was clearly local, because other leaves of the rosette were not affected by the FR treatment. Furthermore, light-induced changes in auxin signaling within the shoot, which are required for leaf reorientation (see below), were also restricted to the leaf exposed to low R:FR conditions [8,9]. This autonomous leaf behavior intuitively makes sense, because different leaves of the same rosette can experience different light environments in a patchy canopy.

How Is the Local Hyponastic Response Generated?

Interestingly, FR treatment of a small area of the leaf tip is sufficient to elicit a strong hyponastic response, which is equivalent to the response elicited by illuminating the whole leaf with FR. By contrast, FR delivered to the petiole, which is the part of the leaf that bends to generate upward leaf movement, results in increased petiole elongation, but fails to elicit a hyponastic response [8,9]. Therefore, the local response, which is restricted to the treated leaf, requires ‘long-distance’ signaling within the responding leaf. Further characterization of the response [8,9], using an elegant array of transcriptomic, imaging, genetic, and pharmacological approaches, demonstrated that this hyponastic response is mediated by auxin synthesized in the blade and transported to the petiole. In fact, inactivation of phyB in the leaf tip activates the PIF/YUC regulon, leading to increased auxin biosynthesis. Auxin is transported to the petiole through a mechanism that requires the activities of PIN proteins PIN3, 4, and 7, and this transport leads to a concentration of auxin activity in the abaxial side of the responding petiole, which triggers the upward bending response [8,9]. From simulations based on a 3D model of plant and plant canopy architecture, Pantazopoulou *et al.* [9] concluded that neighbor sensing at the leaf tip is adaptive. This sensing allows the leaf to respond to competition signals perceived by the part of the organ that is most likely to be the first to interact with neighbors, and avoids unproductive responses activated by self shading at the petiole base.

The Advantages of Being Modular

Higher plants are modular organisms comprising interconnected repeated units or modules. Within the aerial part of the plant, organ-specific responses to local R:FR signals (Figure 1) can be important to maximize light capture and whole-plant fitness. For example, the fact that the internodes of plants with vertical

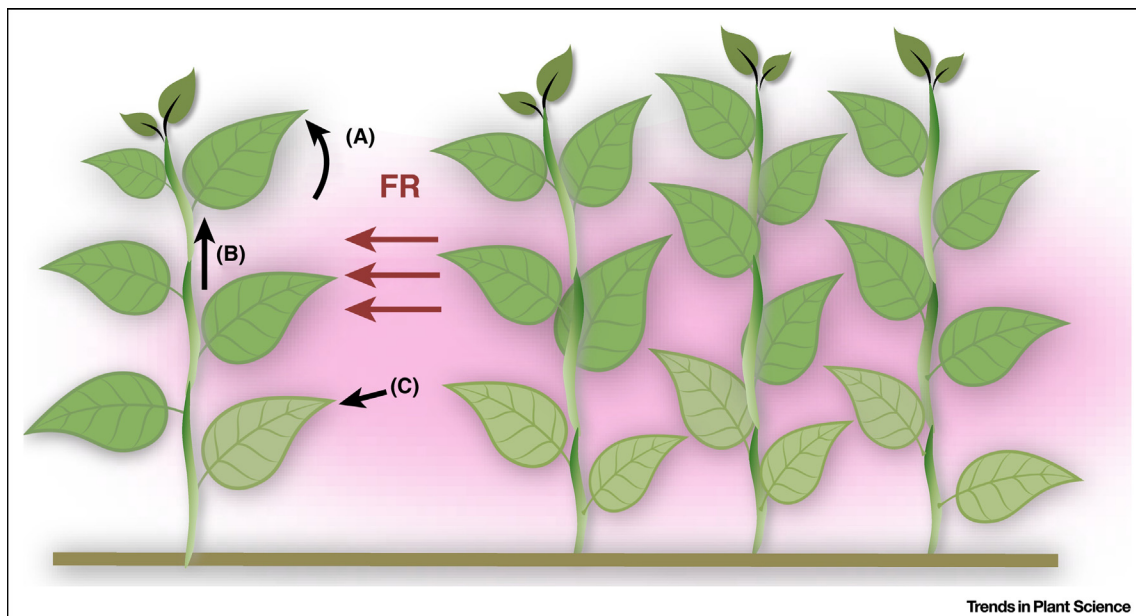


Figure 1. Neighbor Detection and Local Responses of Plant Organs to Changes in the Red:Far Red (R:FR) Ratios. Local responses to low R:FR ratios, such as those illustrated in the figure, allow plants to shape their architecture to optimize light interception, and to retain those leaves that are important for whole-plant photosynthesis. (A) Local hyponastic responses; (B) internode elongation responses triggered by stem-perceived FR radiation; and (C) local induction of leaf senescence and suppression of defense responses in leaves exposed to low R:FR ratios.

stems can autonomously detect and respond to lateral FR allows the plant to efficiently use FR radiation coming from the sides of the plant as an early signal of competition. This light is enriched in FR reflected from neighboring plants, and perception of reflected FR by individual internodes triggers rapid shade avoidance responses, even if the leaves (the principal light-harvesting organs) are still in the sun and not exposed to competition cues [10]. Similarly, FR can locally suppress defense responses to herbivory in individual branches [11] and locally activate leaf senescence [12]. These observations suggest that higher plants have evolved an organizational pattern that allows them to sacrifice those modules that experience low R:FR ratios and are unlikely to be valuable for the fitness of the plant as a whole.

Concluding Remarks

Plants have a reputation for not allocating resources to 'subprime' functional units. Each leaf is responsible for its own carbon budget, because mature leaves do not import photoassimilates from other leaves

even if they become shaded or carbon starved. As such, it makes sense that each leaf has the sensory systems and transduction elements to ensure its proper positioning for optimal light capture. This is what allows plants as a whole to efficiently forage for light in complex environments, and crop canopies to maximize light interception. The mechanism described for the control of leaf hyponastic responses [8,9] demonstrates that rosette plants have evolved a clever system to concentrate light sensing in the outermost tip of the leaf and to relay the information to the leaf base, where precise adjustments in the elongation of petiole cells can be effected to optimize the positioning of the light-harvesting parenchyma.

Systemic responses are likely to be adaptive in those cases where the information perceived by one part of the plant is spatially representative and relevant for the whole organism, such as information on daylength or the risk of herbivory. Long-distance signals, including sugars, hormones, and other small molecules that

move through the vasculature, as well as electric and hydraulic signals and volatile compounds, have an important role in interorgan communication and activation of systemic responses. By contrast, given the heterogeneity of the light environment in most plant canopies, the R:FR ratio perceived by a given leaf has little informative value on the risk of shading for other parts of the plant body. Therefore, local responses to R:FR are likely to have more adaptive value than systemic responses in heterogeneous light environments. The routes, direction, and boundaries of auxin transport are emerging as important elements in the mechanisms that determine the spatial extension of growth responses to light signals perceived by phyB.

Acknowledgments

Work in my laboratory is supported by CONICET and grants from UBACyT and FONCyT. I thank Amy Austin for helpful comments on the manuscript.

¹IFEVA, Consejo Nacional de Investigaciones Científicas y Técnicas – Universidad de Buenos Aires, Avenida San Martín 4453, C1417DSE, Buenos Aires, Argentina
²IIIB-INTECH, Universidad Nacional de San Martín, B1650HMP Buenos Aires, Argentina
 ©Twitter: @BallareCL

*Correspondence: ballare@ifeva.edu.ar (C.L. Ballaré).
<http://dx.doi.org/10.1016/j.tplants.2017.09.004>

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Spotlight

Pearl Millet Genome: Lessons from a Tough Crop

Marilyne Debieu,^{1,2}
Ghislain Kanfany,^{2,3} and
Laurent Laplaze^{1,2,4,*}

Pearl millet is an important cereal for food security in the arid regions of Africa and India. The recently published genome of this tough cereal crop has shed new light on its history and adaptation to

dry, hot climates and paves the way for much-needed genomic-based breeding efforts.

The world's human population is expected to reach 9.1 billion by 2050. Given that most models predict that climate change will have a negative impact on agricultural yields, particularly in Africa [1], new breeding strategies and adaptive agronomical practices are needed to face the future increase in food demand resulting from this expanding population.

Pearl millet (*Pennisetum glaucum* L.) is the sixth cereal in terms of world production and has a central role in food security in arid areas of sub-Saharan Africa and India with limited agronomic potential where other crops would fail. In these areas, it is the staple crop for an estimated 90 million small farmers because it represents a cheap source of essential micronutrients (such as iron and zinc) and proteins, as well as an important source of fodder for cattle and other animals. Nevertheless, pearl millet yields are low and it is considered to be an orphan crop because it lags well behind other cereals in terms of associated research and genetic improvement.

Pearl millet is a C4 crop that was domesticated approximately 4500 years ago in West Africa and it is well adapted to biotic and abiotic stresses. Moreover, some wild pearl millet strains can survive in extreme environments (up to the limit of the Sahara desert) and, therefore, represent an interesting resource for allele mining. Thus, pearl millet is an interesting biological model to understand the adaptation of cereals to dry, hot climates.

As part of an international effort to increase genetic gain in pearl millet, Varshney *et al.* [2] sequenced and analyzed the genome of a reference genotype. The good-quality genome sequence of the reference line revealed interesting features. First, the 1.79-GB pearl millet

genome is characterized by a high GC content (47.9%). Increased GC content has been associated with desiccation tolerance in monocots [3], suggesting that this genome characteristic contributes to the adaptation of pearl millet to dry environments. Moreover, 80% of the genome comprises repetitive elements, a proportion similar to that in the maize (*Zea mays*) genome (>85%) but higher than in other cereals, such as sorghum (~61%), foxtail millet (~46%), or rice (~42%). Transposable elements (TEs) can induce mutations and have been proposed to confer a higher adaptive potential to their host. In maize, TEs contribute to the activation of genes in response to abiotic stresses [4]. TE insertions can generate genetic and epigenetic variation favored by natural and artificial selection and, thus, contribute to adaptation and domestication. From an evolutionary perspective, the mating system may have an important role in governing TE evolution, as predicted by theoretical models. The genomes of the highly allogamous crops pearl millet and maize are TE rich. In such species, outcrossing and recombination may compensate for deleterious mutations resulting from TE insertions and allow the spread of repetitive elements throughout the species, increasing the genomic TE content. By contrast, species such as foxtail millet and rice, whose genomes comprise less than 50% TE, are autogamous crops. In such crops, purifying selection may contribute to the elimination of TE (Figure 1B). Experimental validations are needed to confirm those hypotheses among diploid plant species.

By combining transcriptome data and bioinformatics analyses, Varshney *et al.* [2] predicted that the pearl millet genome contains 38 579 genes. Interestingly, comparison of gene families with other cereal genomes revealed a strong enrichment in gene families involved in cutin, suberin, and wax biosynthesis. The cuticle is known to be important in protecting plants from excessive water loss [5] and