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Shade Avoidance Syndrome Ornamentals in Shadow Landscape

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Abstract

The greatest effect of shade on the ornamentals is a change in morphological characteristics, which changes their beauty. Ornamentals have strategies to survive in the shade term of dense flowers. By knowledge and breeding these strategies, we can increase the competitiveness of the ornamentals in shady conditions in landscapes. In this review, investigated the physiological mechanisms involved in R: FR, phytochromes and the phenotypic changes in ornamentals to avoid shade. The phytochrome signals play a protective role in low R: FR ratios. This is done primarily with phyB. The PhyA to act as an FR effective sensor in high radiation reactions. In shady conditions on the leaves, auxin accumulates and stimulates the expression of the cytokinin oxidase gene to break down cytokinins and inhibit leaf growth. ATHB2 and ATHB4 work in concert in the control of leaf development specifically in a low R/FR light environment. The PIFS main motives were in response to shadow avoidance, and with transcription factors Prevents branches from branching in shady conditions. As a result, the shadow resistanse ornamentals provides molecular and biochemical and morphological mechanisms to tolerate or prevent the shade of neighboring vegetation and increase the survives with preserving the beauty of flowers ornamentals in shadow landscape.

Introduction

Most landscape space in cities is located between buildings. Therefore, ornamental plants that are used in landscapes, they may have to grow in shady environments and at high densities. Shade not only affects the light received by plants, it also affects other small environmental conditions such as air and ground temperatures. Plants are divided into two categories in terms of the effect of shade on them: 1- Shade-resistant plants (Table 1), for example; the *Trichloris crinita*, *Capsicum chinense* and 2- Shade sensitive plants, for example, *Eustoma grandi-florum*, *Liatris spicata* [1-5]. The greatest effect of shade on the plant is a change in morphological characteristics, which changes their beauty [5]. Hou et al [6] investigated the effects of shading on plant growth, flower quality and photosynthetic capacity of *R. hybrid*, the results showed that shade not only delayed the initial flowering date, but also prolonged the flowering time.

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Table 1: The list almost shadow resistanse ornamentals which can be grown in shade landscapes [7].

Shade-resistant ornamentals	Deciduous or ever green	tree	shrub	Perennial herbs and	Ferns and vine
Basswood (*Tilia Americana*)	deciduous	*			
Yellow Birch (*Betula alleghaniensis*)	deciduous	*			
Hemlock (*Tsuga Canadensis*)	evergreen	*			
White Pine (*Picea glauca*)	evergreen	*			
American Hornbeam (*Carpinus caroliniana*)	deciduous		*		
Canada Plum (*Prunus nigra*)	deciduous		*		
Common Witchhazel (*Hamamelis virginiana*)	deciduous		*		
Eastern Wahoo (*Euonymus atropurpurea*)	deciduous		*		
Hop Hornbeam (*Ostrya virginiana*)	deciduous		*		
Nannyberry (*Viburnum lentago*)	deciduous		*		
Pagoda Dogwood (*Cornus alternifolia*)	deciduous		*		
Purpleosier Willow (*Salix purpurea*)	deciduous		*		
Speckled Alder (*Alnus rugosa*)	deciduous		*		
Eastern Redcedar (*Juniperus virginiana*)	evergreen		*		
Arrowwood Viburnum (*Viburnum dentatum*)	deciduous		*		
Flowering Raspberry (*Rubus odoratus*)	deciduous		*		
Gray Dogwood (*Cornus racemosa*)	deciduous		*		
Witherod (*Viburnum cassinoides*)	deciduous		*		
Hobblebush(*Viburnum alnifolium*)	deciduous		*		
Spicebush (*Lindera benzoin*)	deciduous		*		
Wayfaring Tree (*Viburnum lantana*)	deciduous		*		
Mountain Laurel (*Kalmia latifolia*)	evergreen		*		
Rhododendron (*Rhododendron sp*)	evergreen		*		
Baneberry, White and Red (*Actaea pachypoda*)				*	
Barrenwort (*Epimedium sp*)				*	
Barren Strawberry (*Waldsteinia sp*)				*	
Bloodroot (*Sanguinaria canadensis*)				*	
Blue Cohosh (*Caulophyllum thalictroides*)				*	
Bluebead-lily (*Clintonia borealis*)				*	
Bowman’s Root (*Gillenia trifoliate*)				*	
Bugbane (*Cimicifuga sp*)				*	
Bugloss (*Brunnera macrophylla*)				*	
Bunchberry (*Cornus canadensis*)				*	
Creeping Phlox (*Phlox stolonifera*)				*	
Foamflower (*Tiarella sp*)				*	
Forget-Me-Not (*Myosotis sp*)				*	
Hosta (*Hosta sp*)				*	
Indian Cucumber-roo (*Medeola virginiana*)				*	
Jack-in-the-Pulpit (*Arisaema triphyllum*)				*	
Jewelweed (*Impatiens capensis*)				*	
Lamiastrum (*Lamiastrum galeobdolon*)				*	
Ligularia (*Ligularia sp*)				*	
Lily of the Valley (*Convallaria majalis*)				*	
Lily-turf (*Liriope spicata*)				*	
Masterwort (*Astrantia major*)				*	
Pachysandra (*Pachysandra terminalis*)				*	

Periwinkle (*Vinca minor*)				*	
Solomon's Seal (*Polygonatum sp*)				*	
Wintergreen (*Gaultheria procumbens*)				*	
Christmas Fern (*Polystichum acrostichoides*)					*
English Ivy (*Hedera helix*)					*
Virginia Creeper (*Parthenocissus quinquefolia*)					*

Threat to plant survival provided by light limitation, cause the evolution is a strategy for tolerating or escaping the shade of neighboring plants [8]. Shade-resistant plants (Table 1) have morphological flexibility against light [9]. Many genetic and molecular and chemical studies have shown, that phytochromes, cryptochromes and UVR8 (UV-8 photoreceptor protein) monitor the changes in light intensity under shade and regulate the stability or activity of phytochcrome- interacting factors (PIF_S) [10]. UV-B light is strongly filtered by plant canopies, thus providing further information on plant density [11,12].

In the following, we will briefly review recent findings on molecular and biochemical mechanisms in R: FR ratios, phytochromes, changes in lateral branch growth, and leaves in response to SAS (shade evoidance syndrome). Research is also needed to understand the mechanisms created by shade on ornamental plants and the selection of shade-resistant varieties.

R: FR ratio on shade conditions

In addition to providing a key energy source for photosynthesis, light signals provide plants with important spatial and temporal information about their surrounding environmental [8]. In natural light environment, phytochrome exists in dynamic equilibrium of each being R and FR [8,12]. Plants detect such neighboring vegetation as a reduction in the red to far-red ratio (R:FR) of the incoming light [10,13]. This diagnosis is directly related to the properties of phytochromes and is often defined as follows:

$$R: FR = \frac{\text{photon irradiance between 660 and 670 nm}}{\text{photon irradiance between 725 and 735 nm}}$$

The low R/FR ratio signals of reflected light can provide early warning of the presence and proximity of neighbouring vegetation, enabling the initiation of adaptive development strategies [8,13]. The low R/FR ratio signal triggers a set of responses collectively know as the Shade Avoidance Syndrome (SAS), intended to reduce the degree of current or future shade from neighbors by over toping such competitors or inducing flowering [10]. These light signals provide a range of morphological changes in stem growth relative to products organs, which are generally symptoms of shade avoidance syndrome [13]. Martinez et al [10], said in a experiment, that the SAS response included an increase length of hypocotyl, that other responses at low R/FR is, include decreased leaf chlorophyll levels and increased end dominance. However if the reduce R/FR ratio signal persists and the plant is unable to overtop competing vegetation, flowering is aceelerated [8]. The usual phenotypic changes in the SAS can cited be attributed to changes in leaf hyponasty, an increase in hypocotyle and internode elongation and extended petioles. Also less branching, increased susceptibility to insect herbivory and decreased seed yeild, one of the side effects of the SAS [13].

Arabidopsis phyB mutants exhibit a constitutive shade-avoidance response even under normal high R: FR conditions, including elongation of hypocotyl, petioles and stem, accelerated flowering, and increased apical dominance, indicating that phyB negatively regulates SAS [14]. Very recent work has shown that prolonged shade results in an early exit from proliferation in the first pairs of Arabidopsis leaves, and that this process depends on the action of ATHB2 and ATHB4 [15]. The phyB, phyD, and phyE have all been implicated in the regulation of ATHB2 by changes in the ratio of R/FR light [16]. The HY5, on one hand, down regulates genes induced early by low R/FR light, and on the other hand, positively regulates photomorphogenesis-promoting genes under persistent shade [17]. Evidence exists that HY5 binds to PIF proteins [18,19]. FAR-RED elongated hypocotyl (FHY1) and its less abundant homolog FHY1-LIKE mediate FR responses by facilitating light-induced phyA nuclear translocation and by interacting with transcription factors [20,21]. Xie et al [22] suggested that EOD-FR treatment suppresses FHY3 and FAR1 is expressed at both the mRNA and protein levels.

In addition, the accumulation of PIF proteins rapidly increases in response to simulated shade. Moreover, multiple PIFs (PIF1, PIF3, PIF4, and PIF5) can directly bind to the G-box motifs present in the promoters of several *MIR156* genes and down regulate their expression [14]. Prolonged exposure to Low R/FR leads to the accumulation of HFR1/SICS1 and the formation of non-active heterodimers with PIF4 and PIF5 [23,24]. The negative regulators of shade avoidance controlled by PIF proteins is Long Hypocotyl in Far Red 1/Slender In Canopy Shade 1 (HFR1/SICS1), which is an a typical bHLH protein. HFR1/SICS1 is rapidly induced by FR-enriched light, and it has been demonstrated that it is recognized in vivo by PIF5 [23,24]. There are now extensive examples of other signaling pathways converging on the PIFs to regulate an increasing number of downstream processes, including developmental processes like stomatal index, carpel formation, and ovule fertilization [25,26].

Phytochrome changes in SAS

There are three types of phytochromes in plants, included pr-pr, pfr-pr and pr-pfr [27] (Figure 1).

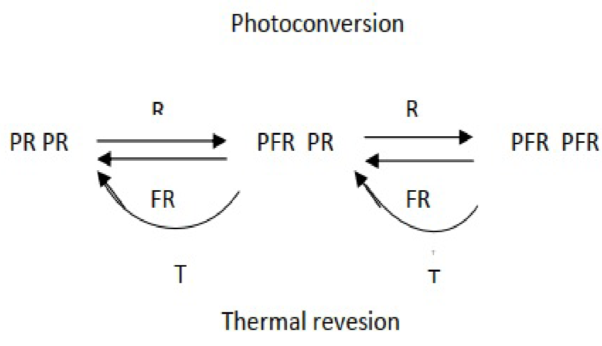

Figure 1: Types of phytochromes that can be converted to each other [27].

Light is one of the main factors determining the flowering and greening in compact ornamentals and shadow avoidance. The phytochrome pathways and signals play a protective role in low R: FR ratios in shade conditions [28]. R is absorbs light in the form of PR and FR have light absorption in the form of PFR. In the dark, phytochromes synthesize the PR-shape, after stimulation with R light, the PR-form becomes the active form of PFR and it can absorb FR and return to the form of PR. The active form of PFR is transferred to the nucleus and cause the responses [12]. Therefore, phytochromic responses depend on the proportion of PFR conofers [27]. Plant phytochromes are dimers. Each monomer contains 1150 amino acids, which is covalently connected to its chromophores, and forms a linear tetrapyrrole that called phytochromobilin [27]. Phytochrome apoproteins are found in plants by a small family of genes, that in Arabidopsis, they are encoded by five genes PhyA – PhyE. Also Kara [8] observed three Main types of phytochromes in angiosperms, that their apoproteins are encoded by PhyA, PhyB and PhyC genes. Martinez et al [10] were examined Arabidopsis seedling response and PhyA and PhyB contribution to understanding the decrease in R / FR ratio at three different levels, and their results showed that, Shadow avoidance syndrome is caused by PhyB disabling, which gradually has an antagonistic effect with PhyA. Recent progress showed that phytochromes could function as transcriptional regulators by interacting directly with numerous transcription factors on the promoters of target genes, conferring rapid responses to light signals. More importantly, phytochromes suppress the shade response by antagonizing a group of BHLH transcription factors termed PHYTOCHROME-INTERACTING FACTORS (PIFs). Shade induces the dephosphorylation and activation of PIF7 and also promotes the protein stability of other PIFs (PIF1/3/4/5) as the result of deactivation of phyB [29].

The SAS causes significant reductions in flowering, the *PHYA* gene (or its modified form) has been introduced into crop plants such as tobacco, tomato, potato, wheat, rice, and turfgrasses to enhance shade tolerance, and in some cases promising results have been achieved [29]. PhyA decomposes rapidly in PFR form and generates signals during conversion between PR and PFR as intermediaties. The PhyA unique features enable this receiver, to act as an FR effective sensor in high radiation reactions (HIR) [8,12,31-33].

PhyB-E phytochromes are relatively stable in PFR form. Among optically stable phytochromes, PhyB played a dominant role in regulating shadow avoidance responses [12]. In the shade condition, the Pfr form of phytochormes translocates into the nucleus to trigger genome-wide transcriptional changes and subsequent photo-responses. Shade reduces the Pfr:Pr ratio, and also the nuclear accumulation of phyB, leading to the accumulation of the E3 ligase CONSTITUTIVE PHOTOMORPHOGENIC1 (COP1) in the nucleus and enhanced 26S proteasome-mediated degradation of several transcription factors, including ELONGATED HYPOCOTYL5 (HY5), HY5-HOMOLOG (HYH), LONG HYPOCOTYL IN FAR-RED1 (HFR1), and LONG AFTER FAR-RED LIGHT1 (LAF1) [29]. The relatively low R/Fr response was performed primarily by PhyB which is called the shadow avoidance response [8,14]. At the nucleus, phytochromes directly bind to transcriptional cross-factors (PIFs), Which is the main subfamily of transcription factors involved in controlling plant growth and development [23]. Shi et al [28] in a study on maize stated that the $ZmphyA_1$, $ZmphyB_1$ and $ZmphyB_2$ and five genes of the PIF family are regulated by FR and they play an important role in responding to shadows.

Changes in lateral bud growth and elongation in SAS

physiological studies have suggested the existence of a cotyledon/leaf-originated mobile signal involved in phytochrome-mediated regulation of gene expression and stem elongation [30].

that the role of FHY3 in regulating branching might represent a separate function independent of its roles in regulating light signaling. Regardless, elucidating how the low R: FR intersects with these hormone signaling pathways to coordinately regulate lateral branching represents an interesting avenue for future research [30].

Reduction lateral bud growth is one of the most common changes in response to shade avoidance [28]. PhyD and PhyF activity with PhyB encourages shadow elongation, In contrast, PhyA decreases elongation in response to low (R/FR) optical induction [12]. Most PIF_S encourage growth. While seem PIF6 and PIL1/PIF2 to have opposite functions [12]. In vegetation in the shade, decreased R/FR leads to PhyB (pfr) becoming an inactive form of pr, Which is separated from PIF_S and come out of the nucleus and increases PIF_S stability [10].

In most cases, the interaction of PIFS with PhyB leads to PIFS phosphorylation, and their ubiquity leads to the rapid destruction of protozeiums 26s and as soon as phytochromes are inactivated in the shade, PIF3, PIF4 and PIF5 Protein levels rise rapidly [12]. So at a low R/FR ratio, a small PhyA pool were joined PIF4 of proteins together and protects them from destruction, and an overall increase in PIFS activity leads to an increase in the expression of genes involved in elongation. These include genes involved in the biosynthesis of gibberellins [10].

PIF1, PIF3, PIF4, PIF5 AND PIF7 are all directly involved in the response to shadow avoidance [12]. for example, The concentration of gibberellin may increase with long-term growth in the shade, therefore, it increases the destruction of the DELLA. The destruction of the DELLA has increased the stability of the PIFS and promotes long vegetative growth [10]. The types PIFS are involved in the expression of auxin biosynthesis, carrier genes, and signaling, which are the main stimuli for inducing hypocotyl elongation in the shade [13]. *SMALL AUXIN UP-REGULATED RNA* (*SAUR*) genes are the largest family of early auxin-response genes [34,35]. *SAUR9, 10, 19, 20, 22*, and *23* are rapidly induced by shade treatment, suggesting they might be involved in the shade avoidance response [36,37].

The perception of low R/FR in the shoot also results in a decrease in Lateral Root (LR) emergence, and it has been proposed that HY5 regulates this process by inhibiting the auxin efflux carrier PIN3 and the influx carrier LIKE-AUX1 3 (LAX3) auxin transporters, which act in concert in the process of LR emergence [38,39]. Also AS2/GH3.17 (GRETCHEN HAGEN3.17) catalyzes the conjugation of free IAA to inactive IAA-Glu (IAA-glutamate). Disruption of VAS2/GH3.17 resulted in accumulation of free IAA, thus enhancing shade-induced hypocotyl elongation [34,40].

In Arabidopsis, TCP (PCF, CYCLOIDFA, TEOSINTE BRANCHED 1) transcription factors BRC1 type are directly linked and transcription activates a group of HD-ZIP1 transcription factor genes which includes HB21, HB40, HB53. Therefore, it prevents the growth of lateral branches. It also appears that the genetic units involved in BRC1/TB1 ratio and HD-ZIP transcription factors in dicotyledons and monocots are stored as an evolutionary program, and prevents the branches from branching in the shade [28].

Changes in leaf growth in the shade

One of the most prominent phenotypes observed in dicotyledonous plants in low proportion R/FR is the rapid elongation of stems and leaves [8]. In shade-tolerant species such as alocasia, Compatibility was observed in photosynthetic structures that is includes thinner leaves, higher chlorophyll content, and lentil-shaped epidermal cells to focus light on mesophilic tissue [8]. Several proteins encoding proteins are involved in photosynthetic light reactions, ZMPSBA, ZMLHCB1, ZMPSBQ and ZMPSB28 that are regulated by Fr light [28]. In shady conditions on the leaves, auxin accumulates and stimulates the expression of the cytokinin oxidase gene to break down cytokinins and inhibit leaf growth [13]. Furthermore, evidence has been provided that ATHB2 and ATHB4 work in concert in the control of leaf development specifically in a low R/FR light environment, likely forming heterodimeric complexes as suggested by yeast two-hybrid assays [15,41]. The data provide novel insights on the molecular mechanisms underlying leaf development in shade. However, further work is needed to uncover the links between the ATHB2 and ATHB4 transcription factors and the known regulatory pathways involved in the control of leaf cell proliferation [41,42].

Conclusion

The greatest effect of shade on the plant is a change in morphological characteristics, which changes their beauty. We investigated briefly review recent findings on molecular and biochemical mechanisms in R: FR ratios, phytochromes, changes in lateral branch growth, and leaves in response to SAS (shade evoidance syndrome). The usual phenotypic changes in the SAS included be changes in leaf hyponasty, an increase in hypocotyle and internode elongation and extended petioles. Also less branching, increased susceptibility to insect herbivory and decreased seed yeild, one of the side effects of the SAS. It was found that the accumulation of PIF proteins rapidly increases in response to simulated shade. The types are involved in the expression of auxin biosynthesis, carrier genes, and signaling, which are the main stimuli for inducing hypocotyl elongation in the shade. Therefore, PIFS play an important role in selecting shade-resistant cultivars.

The PhyA to act as an FR effective sensor in high radiation reactions. But PhyB-E phytochromes are relatively stable in PFR form. Among optically stable phytochromes, PhyB play a dominant role in regulating shadow avoidance responses. Then Reduction lateral bud growth is one of the most common changes in response to shade avoidance. PhyD and PhyF activity with PhyB encourages shadow elongation, In contrast, PhyA decreases elongation in response to low (R/FR) optical induction.

In shady conditions on the leaves, auxin accumulates and stimulates the expression of the cytokinin oxidase gene to break down cytokinins and inhibit leaf growth. Numerous experiments have shown that ATHB2 and ATHB4 work in concert in the control of leaf development specifically in a low R/FR light environment. As a result, the plants provides molecular and biochemical mechanisms to tolerate or prevent the shade of neighboring vegetation and Preservation the beauty ornamental. By knowledge and breeding these strategies, we can increase the competitiveness of the ornamental in shady conditions in landscapes.

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