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# Vegetative axillary bud dormancy induced by shade and defoliation signals in the grasses

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**Vegetative axillary bud dormancy and outgrowth is regulated by several hormonal and environmental signals. In perennials, the dormancy induced by hormonal and environmental signals has been categorized as eco-, endo- or para-dormancy. Over the past several decades para-dormancy has primarily been investigated in eudicot annuals. Recently, we initiated a study using the monoculm phyB mutant (*phyB-1*) and the freely branching near isogenic wild type (WT) sorghum (*Sorghum bicolor*) to identify molecular mechanisms and signaling pathways regulating dormancy and outgrowth of axillary buds in the grasses. In a paper published in the January 2010 issue of *Plant Cell and Environment*, we reported the role of branching genes in the inhibition of bud outgrowth by phyB, shade and defoliation signals. Here we present a model that depicts the molecular mechanisms and pathways regulating axillary bud dormancy induced by shade and defoliation signals in the grasses.**

**Key words:** axillary bud, dormancy, shade, phytochrome, defoliation, shoot branching, teosinte branched1, MAX2, cell cycle, sorghum

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The dormancy and outgrowth of axillary buds is regulated by several plant hormones such as auxin, cytokinins, abscisic acid and strigolactones, and by environmental factors such as light quality, quantity and duration as well as water, temperature and nutrient status.[1-3] Since the fate of an axillary bud is regulated by such diverse hormonal and environmental signals and their interactions, the type of dormancy induced varies. In perennials, three types of bud dormancy have been identified.[4,5] Dormancy mediated by factors within the bud is known as endo-dormancy; while dormancy induced by factors within the plant but outside the bud is called para-dormancy or correlative inhibition; the best known example being apical dominance. Dormancy induced due to unfavorable environmental conditions is known as eco-dormancy. Although there is an in-depth knowledge about para-dormancy in annuals,[6] few studies have been conducted on eco-dormancy. Similarly, studies of endo-dormancy have largely been restricted to low-temperature mediated growth-cessation of axillary buds of perennial plants.[7,8] To understand the regulation of dormancy and outgrowth of axillary buds in monocots, we initiated a study on the molecular mechanisms inhibiting bud outgrowth by shade and defoliation signals in sorghum. Our results published in the January 2010 issue of *Plant, Cell & Environment* indicate that different types of dormancy may be induced in axillary buds of annual grasses by various signals and there may be overlapping and independent molecular mechanisms mediating induction of axillary bud dormancy.

## phyB Deficiency, Shade and Defoliation may Induce Different Types of Dormancy

The type of dormancy induced by hormonal and environmental signals has not been investigated in annuals. Our studies on the inhibition of bud outgrowth by shade and defoliation in sorghum showed that unlike shade, defoliation inhibits bud outgrowth immediately. Since defoliation causes a complete and irreversible change in the developmental status of a plant, an immediate response was anticipated. On the other hand, shade signals such as

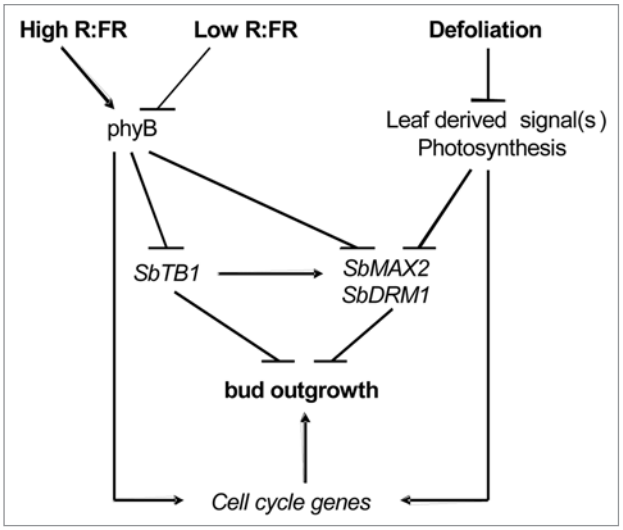


**Figure 1.** Model of the regulation of axillary bud dormancy and outgrowth by shade and defoliation signals.

far red light reflected from neighboring plants may vary in intensity and duration throughout the day, and response to such signals may cycle between transition states of growth and dormancy of axillary buds before commitment to dormancy is established. This may be explained by the reversible nature of the photoreceptor phytochrome B (phyB) that mediates the response to shade.[9,10] phyB is activated by red (R) light and inactivated by far red (FR) light, and response to shade depends on the proportion of active and inactive phyB pools (R:FR). Active phyB mediates the normal growth and development of a plant. When phyB is inactivated by shade signals, the plant initiates shade avoidance responses including increased plant height, inhibition of branching and early flowering to cope with the shade that could be detrimental to its survival.[11] Since shade signals may vary in intensity and/or duration, dormancy induced by such signals could lead to different types of dormancy. In fact, in hybrid aspen, a four-week short day treatment induces an eco-dormancy of cambial cells, while a six-week short day treatment induces an endo-dormancy.[12] In sorghum, the expression level of cell cycle-related genes was dramatically downregulated in axillary buds of WT repressed by shade but not in axillary buds of *phyB-1* mutants repressed by phyB deficiency. Together these results suggest that, as in perennials, different types of dormancy may be induced in annuals by hormonal or developmental and environmental signals, and the type of dormancy induced by environmental signals may depend on the intensity and duration of the signal.

## Inhibition of Bud Outgrowth in Annuals by Different Signals may be Integrated Through Diverse Molecular Mechanisms within the Bud

The immediate inhibition of sorghum axillary bud outgrowth by defoliation compared to shade suggests induction of different types of dormancy by those signals. This has been further revealed by the expression analysis of several branching and cell cycle-related genes in axillary buds. Branching related genes in annuals that specifically act within or close to a bud to repress its outgrowth include the *TEOSINTE BRANCHED1* (*TB1*) and *MOREAXILLARYGROWTH*(*MAX2*).[13-15] Inhibition of bud outgrowth by shade in sorghum was shown to be associated with increased expression of the sorghum *TB1* (*SbTB1*) gene suggesting phyB controls the fate of a bud by transcriptional regulation of *SbTB1*.[11,16] Interestingly, *SbTB1* expression level was not associated with the inhibition of bud outgrowth by defoliation indicating response integration within a bud through different mechanisms. However, the expression level of *SbMAX2* was upregulated to a comparable level by phyB deficiency, shade and defoliation suggesting a possible common mechanism of transcriptional regulation of *SbMAX2* by those signals. The results suggest variations in the molecular mechanisms mediating response to inhibitory shade and defoliation signals possibly leading to different types or degrees of dormancy.

## Signaling Pathways Regulating Bud Dormancy in the Grasses

The model in **Figure 1** summarizes the induction of bud dormancy in sorghum by shade through phyB, and defoliation through leaf-derived signals. phyB mediates the fate of a bud by controlling the expression level of *SbTB1*. However, since the inhibition of bud outgrowth by phyB deficiency is associated with changes in *SbTB1* but not cell cycle-related genes, shade signals in the WT may also repress bud outgrowth by a TB1 independent pathway through transcriptional regulation of cell cycle-related genes. Inhibition of bud outgrowth by phyB deficiency, shade and defoliation was also associated with increased expression of the *SbMAX2* and *SbDRM1* genes. The *MAX2* gene may play a role in either the perception or signal transduction of strigolactones.[15] In addition it also functions in light signaling and senescence.[17,18] Whether the role of MAX2 in the regulation of branching by shade or defoliation is a component of strigolactone signal transduction or signals other than strigolactones such as light or senescence needs further investigation. *DRM1* was identified as one of the genes associated with dormancy in axillary buds.[19] Its function has not been discovered, however, it has been used as a dormancy marker in several species. It appears both SbMAX2 and SbDRM1 act downstream of the branching inhibition signaling pathways. This model will serve as a guide toward establishing the hormonal and environmental signaling pathways regulating the fate of a bud in annual grasses.

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