**grassy tillers** promotes apical dominance in maize and responds to shade signals in the grasses


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**AUTHOR SUMMARY**

Unlike animals, which can relocate, plants must respond to unfavorable environmental changes by adjusting how they grow and develop. Many grasses, for example, sense when their environment is shaded and respond by repressing the growth of lateral branches. This response allows the plant to re-direct energy to the primary shoot, which grows taller and escapes the shade. Although researchers have investigated the genetic mechanisms that control branching and responses to light signals, little is known about how these mechanisms are integrated. In this study, we have identified a maize gene, *grassy tillers* (*gt1*), that inhibits lateral branching and responds to changes in shade within its environment. Interestingly, because *gt1* shows evidence of selection during the evolution of maize from its wild ancestor teosinte, the gene may have played an important role in the plant’s domestication.

Human selection has generated maize plants that produce very few basal lateral branches, known as tillers. Although tiller buds are initiated, the nascent branches ultimately arrest and fail to grow out, which results in the plant’s familiar dominant central stalk (Fig. P1A). The maize *gt1* mutant, in which the suppression of tiller bud growth is compromised, produces several tillers (Fig. P1B) as well as additional ear branches that are relatively elongated. Using a technique of progressive genetic mapping, we isolated the gene’s position and identified *gt1* as a class I homeodomain leucine zipper gene, a transcription factor likely involved in gene regulation. Little is known about gene function within this group of plant transcription factors, although previous studies have demonstrated that mutations in the closely related barley gene (*Hordeum vulgare*) six-rowed spike 1 (*Vrs1*) increase branching in the flowering stalk of cultivated barley (1). However, unlike barley *Vrs1*, which suppresses the growth of lateral buds in the flowering stalk, *gt1* suppresses buds that are initiated during vegetative growth. We examined *gt1* expression by RNA in situ hybridization and found that *gt1* transcripts were present in the leaves surrounding the lateral tiller buds (Fig. P1 C and D) but not in the bud meristem, which is composed of undifferentiated stem cells at the lateral bud apex that initiates bud leaves. We also examined the localization of GT1 protein by generating transgenic plants that expressed a GT1-yellow fluorescent protein (GT1-YFP) fusion. GT1-YFP was localized to the nucleus, as would be expected if GT1 is a transcription factor regulating gene expression. Interestingly, the GT1-YFP protein was detected in the lateral bud meristem in addition to the surrounding leaf primordia, suggesting that GT1 protein may move from its site of production in the leaves to the meristem, where it arrests meristem activity (Fig. P1E).

Next, we examined if *gt1* suppresses tiller growth in response to shade. Because photosynthetic pigments preferentially absorb light in the red spectrum, plants in shaded environments are sensitive to a reduced ratio of red to far-red light (R/FR), which is known to activate shade-responsive genes. We found that *gt1* expression was strongly induced by treatments with light in which the R/FR ratio was reduced. This induction requires the activity of the *phytochrome B* (**phyB**) photoreceptor, which perceives an increased R/FR ratio because plants lacking **phyB** are no longer able to activate **gt1** in response to shade. The maize gene *teosinte branched1* (**tb1**) also regulates tiller bud growth and lateral branching in maize (2). To test if *gt1* and **tb1** act through a common pathway, we examined the expression of each gene when the other gene is inactive. We found that *gt1* expression requires the activity of **tb1** but that **tb1** expression does not require *gt1*. As with **gt1**, shade signals have also been shown to induce **tb1** expression (3). Together, these results suggest that *gt1* and **tb1** belong to a common pathway in which *gt1* acts downstream of **tb1** to inhibit outgrowth of tiller buds in response to changes in light (Fig. P1F).

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The domestication of maize from its wild ancestor teosinte resulted in a striking modification of the plant’s architecture. In particular, like gt1 mutants, teosinte plants are highly branched and tillered, whereas branching in domesticated maize lines is strongly suppressed. These morphological differences are controlled by chromosomal regions that have been previously identified, including one to which gt1 maps (4). We therefore asked if gt1 might have been selected to suppress tiller growth during maize domestication. To examine this question, we sequenced gt1 from diverse lines of maize and teosinte and tested the sequences for selection. The tests revealed that gt1 was significantly selected during domestication, suggesting that modification of the gt1 locus at least partially accounts for the reduced tillering of cultivated maize.

In summary, we have identified gt1 as a key regulator of tiller repression that acts downstream of tb1 in maize and have provided evidence that gt1 expression is controlled by light signaling. We have also shown that gt1 was under selection during maize domestication. Tilling is an important agronomic trait in the grass family, and modifying tiller production has increased yield in diverse grasses, such as maize and rice. Understanding the molecular mechanisms that regulate tiller growth will not only provide insight into an important aspect of plant development but may provide a means to increase biomass production in emerging biofuel crops, such as switchgrass (Panicum virgatum).