# The physiology of "stay-green" in sorghum

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## Abstract

Developing crops that use water more efficiently is one of the greatest challenges facing crop scientists today. In the face of diminishing water resources, the world is expected to consume twice as much food in the next 50 years as it has in the past 10,000 years. To meet this demand, world grain production will have to increase 40% by 2020. Crops such as sorghum and millet are specially adapted to semi-arid regions, and contain various mechanisms enabling these crops to escape and resist drought. Understanding the genetic, physiological, molecular and biochemical basis of such drought-resistance mechanisms is fundamental to the development of new strains that are better adapted to dry conditions. Keeping leaves alive longer is a fundamental strategy for increasing crop production, particularly under water-limited conditions. This paper reviews recent physiological studies into the stay-green drought resistance trait in sorghum, including an outline of future research proposed in collaboration with three American universities during the next 3-5 years. Recent studies in Australia have examined two sources of stay-green: B35 and KS19, derived from sorghum lines native to Ethiopia and Nigeria, respectively. Early in crop growth, stay-green hybrids partition more carbon and nitrogen to leaves compared with their senescent counterparts, resulting in higher specific leaf nitrogen (SLN). It is hypothesised that the higher SLN initiates a chain of responses, including enhanced radiation use efficiency (RUE) and transpiration efficiency (TE), which enable the plant to set a higher yield potential by anthesis. After anthesis, higher SLN delays the onset and reduces the rate of leaf senescence and this is associated with stay-green crops taking up more nitrogen from the soil compared with senescent crops. These processes lead to increased grain yield and lodging resistance in stay-green lines under post-anthesis drought.

## Key Words

*Sorghum bicolor,* drought resistance traits, stay-green, SLN

## Introduction

Combating drought in Australia's northern grain belt requires farmers to utilise a combination of genetic, agronomic and management solutions to optimise grain yield. Genetic solutions could include breeding for drought-resistance traits such as osmotic adjustment, leaf area retention (stay-green) or enhanced transpiration efficiency. Agronomic solutions could include varying sowing time, planting density, variety selection or fertiliser application. Planning rotations to conserve water is an example of a management solution to combat drought.

This paper focuses on genetic solutions to combating post-anthesis drought stress in grain sorghum, in particular, the stay-green trait. We provide an update on the physiological basis of stay-green in sorghum, and introduce a new gene discovery project involving the Department of Primary Industries, Queensland, and three American universities.

## What is Stay-Green?

Stay-green can be defined as extended foliar greenness during grain-filling under post-anthesis drought, and can be viewed as a consequence of the balance between N demand by the grain and N supply during grain filling (5). Nitrogen dynamics alone, however, do not fully account for leaf longevity. There is mounting evidence that enhanced transpiration efficiency is an important component of some types of stay-green (7). Two sources of stay-green will be discussed in this paper: B35 and KS19 , which are derived from sorghum lines native to Ethiopia and Nigeria, respectively.

**Nitrogen Dynamics and the Stay-Green Phenomenon**

From as early as 40 days after emergence, more nitrogen was allocated to the leaves of stay-green hybrids compared with their senescent counterparts, resulting in a higher specific leaf nitrogen (SLN) (2). It is hypothesised this higher SLN initiates a chain of responses, including enhanced radiation use efficiency (RUE) and transpiration efficiency (TE), which enable the plant to set a higher yield potential by anthesis, ultimately leading to higher grain yield and lodging resistance under post-anthesis drought. It is further hypothesised that after anthesis, higher SLN delays the onset and reduces the rate of leaf senescence, and that this is associated with increased nitrogen uptake from the soil compared with the senescent control. Interestingly, this response has been observed under both high and low N conditions.

Evidence to support this framework (Fig. 1) will be presented. Borrell and Hammer (2000) found that leaf N concentration at anthesis was an important determinant of both the onset and rate of leaf senescence during grain filling. Higher SLN was associated with thicker leaves in sorghum hybrids containing the B35, but not KS19, source of stay-green. The thicker and greener leaves exhibited by B35 hybrids may be due to changes in leaf morphology, resulting in differences in sink strengths of leaves for carbon and N.

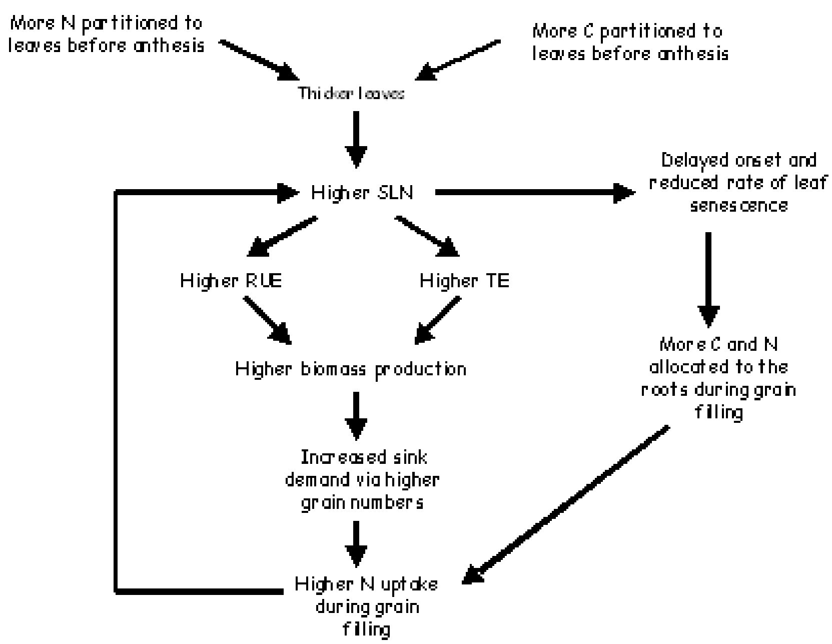


**Figure 1: Nitrogen dynamics and the stay-green phenomenon in grain sorghum.**

The concept of a minimum SLN level, below which leaves will senesce, was proposed by Borrell and Hammer (2000). They concluded that SLN in stay-green hybrids remained above the ‘threshold’ senescence level for longer than in senescent hybrids for at least three reasons: (i) the leaf N benchmark at anthesis was higher in stay-green than senescent hybrids; (ii) N uptake during grain filling was higher in stay-green than senescent hybrids; and (iii) the remobilisation of N from leaves of stay-green hybrids during grain filling was less compared with that of senescent hybrids. A field experiment under rain-out shelters at Hermitage Research Station in south-eastern Queensland (4) showed that a stay-green hybrid retained photosynthetic competence under severe post-anthesis drought for an additional 15 days compared with its senescent counterpart.

## What of Transpiration Efficiency?

Patterns of crop water use vary among hybrids with the B35 and KS19 sources of stay-green (7). A35/RQL36, a hybrid containing the B35 source of stay-green, was found to have higher TE than eight other hybrids examined. In this case, the higher TE was due to increased photosynthetic capacity (associated with higher SLN), rather than reduced stomatal conductance. More research is planned to determine the contribution of TE to the stay-green phenomenon.

## Stay-Green and Yield

Stay-green and yield were positively associated in a range of studies conducted in both Australia (4) and India (3), highlighting the value of retaining green leaf area under post-anthesis drought. Grain yield is the product of grain number and grain size. Grain number is generally the main determinant of differences in grain yield, and this has also been observed for sorghum, grown under post-anthesis drought stress in southern India (3). In wheat, grain number is a function of the spike weight around anthesis (8, 10), and similar results have been obtained for sorghum (van Oosterom and Hammer, unpublished data). Factors, related to the stay-green mechanisms of B35 and KS19, that can potentially increase the panicle growth rate around anthesis, and hence can have a positive effect on grain number, include increased LAI (3), increased SLN, as that increases RUE (11), and competition for assimilate from the stem (6, 9). Grain size is a secondary yield determinant and is often negatively associated with grain number, e.g. Bidinger et al. (2001) for a set of 93 pearl millet hybrids. Hence, grain size is independent of green leaf area at anthesis (3). However, the retention of photosynthetic capacity under water-limited conditions of stay-green hybrids ensures continued availability of new assimilates and is associated with increased N-uptake during grain filling (2), potentially improving grain size. This was illustrated in the recombinant inbred line study, where Borrell et al. (1999) found that grain size was correlated with relative rate of leaf senescence during grain filling such that reducing rate of leaf senescence from 3 to 1% loss of leaf area per day resulted in doubling grain size from about 15 to 30 mg. Thus stay-green can potentially increase grain yield by improving grain number and grain filling ability.

## Where to From Here?

An international project has been funded by the Grains Research and Development Corporation and the Department of Primary Industries, Queensland, to physiologically dissect four key stay-green quantitative trait loci in sorghum. Partners with DPI in this project are Texas A&M University (TAMU), Texas Tech University (TTU), and the University of Missouri. A set of near-isogenic lines varying in four genomic regions (*Stg1*, *Stg2*, *Stg3* and *Stg4*) derived from the B35 source of stay-green has recently been developed by scientists at TTU and TAMU, providing an opportunity to physiologically characterise sorghum lines with and without these genomic regions. Australian scientists will provide expertise in plant breeding and physiological characterisation (gene function), while US scientists will provide near-isogenic lines and expertise in fine mapping and map-based gene cloning. Outcomes will be the identification of candidate genes associated with each of the four genomic regions, ultimately leading to the cloning of these genes.

## Conclusion

The need to drought-proof cropping in the northern grain belt is a high priority of the Australian Sorghum Industry. Knowledge of gene function will assist plant breeders to “custom-make” drought resistant hybrids for specific water-limited environments.

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