

## Genomics and Biotechnology of Plant Adaptation to the Environment

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**The molecular basis of plant adaptation to the environment is one of the most complex areas of plant science and an understanding of this subject is critical to our ability to feed an increasing world population. Research on plant adaptation to the environment often involves two complementary approaches; top-down studies of well-adapted plants with the goal of identifying and describing the biochemical basis of adaptation and bottom-up targeted analysis of specific biochemical mechanisms with the goal of understanding how these mechanisms contribute to overall plant performance. This brief review will provide examples of both of these approaches by describing the study of sorghum's adaptation to dry environments and the role of a blue light responsive chloroplast promoter that helps protect plants against damage by high irradiance.**

**Key words:** *sorghum, blue light responsive promoters, high irradiance.*

The world's population will reach 9 billion over the next 20-40 years placing tremendous pressure on the earth's ability to provide food and fiber.<sup>1,2)</sup> To meet this demand, plant productivity will need to increase 2~3-fold on land currently used for agricultural production, otherwise, large areas of wildlife habitat will need to be converted to agricultural production. Plant productivity is related to the biological carrying capacity of the earth and is limited primarily by the environment, nutrients, and amount of arable land. Therefore, an understanding of the constraints on plant productivity and the basis of plant adaptation to the environment are critical to our ability to provide sufficient food and fiber for the world's population.

The theoretical limit to crop yield is determined primarily by the ability of plants to collect and use available light energy, the biochemical efficiency of carbon fixation, metabolism, and other growth processes, the duration of growing seasons, and the availability of nutrients. Record crop yields indicate that the genetic potential of most crop plants is 75~90% of the theoretical maximum. In other words, under optimal conditions, today's crop plants have excellent genetic potential and are extremely efficient in photosynthesis, growth, and development.

Surprisingly, average yields of nearly all-major crops in the U.S. are only 25~33% of record yields (USDA records).<sup>3)</sup> Approximately 10~20% of the loss of potential yield in U.S. agriculture, which is under intensive management, can be attributed to diseases and insects. Over 50% of the yield

reduction is due to unfavorable environments, lack of adaptation of crops to the environment, and nutrient deficiency. The large loss of yield due to environmental constraints suggests that current genotypes designed for use across large geographic areas are not ideally suited to all microenvironments within these regions of production. Taken together, this information indicates that genetic improvement of crop adaptation to the environment and nutrient acquisition represent important opportunities to increase crop productivity and satisfy future demand for food.

Exploration of the genetic and biological basis of plant adaptation to the environment is one of the most challenging areas of plant science research.<sup>3,8)</sup> This topic is complex because there are a large number of environmental factors that impact plant growth and development and because these factors occur in numerous combinations, with different intensity and their impact varies depending on the stage of plant development. Moreover, specific plants have adapted to different environments over long periods of time. Therefore, a deep understanding of this question requires in depth analysis of different plant species, their responses to a full range of environmental constraints, as well as knowledge of plant evolution, diversity, and biochemical responses to stress.

There are currently two major approaches being used to investigate the biological basis of plant adaptation to the environment. The first is a top-down approach that starts with the identification of plants that are well adapted to specific environmental niches. The genetic and biochemical features of these well-adapted plants are then investigated using genetic, physiological, biochemical and other methods

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**Abbreviations:** EST, expressed sequence tag; SSR, simple sequence repeat.

to discover the basis of adaptation. A major challenge in these studies is to develop technologies that have sufficient resolution to unravel the molecular basis of a complex well-adapted genotype. Recent advances in our understanding of whole genomes and the development of associated microarray technology will make top-down studies much more informative in the near future.<sup>9-14</sup> The second approach focuses on the analysis of specific biochemical or physiological mechanisms without immediate regard to their role in plant adaptation. The analysis of inducible gene expression and protein accumulation under stress provides one example of this approach.<sup>15</sup> The long-term goal of this approach is to reconstruct complex whole plant adaptive responses from a detailed understanding of specific adaptive mechanisms. Clearly, these two approaches are complementary and a combination of the two will allow a full understanding of plant adaptation to the environment as well as improvement of plant productivity in adverse environments.

### **Sorghum: A Model for Germplasm/Genome-based Investigation of Plant Adaptation**

Plants have numerous mechanisms that enable them to grow and reproduce successfully in diverse environmental niches.<sup>3-6,16,17</sup> For example, some ephemeral plants escape environmental stress by rapidly completing their life cycle following intermittent rainfall. Plants such as cacti avoid stress through slow growth and water storage. In contrast, the resurrection plant and lichens are desiccation tolerant, allowing them to occupy niches subject to rapid drying and wetting.<sup>15</sup> While all of these adaptations are interesting, some are more relevant to plant survival, whereas others contribute to plant productivity in agricultural systems that are subject to adverse environments. For this reason and others, our group has focused research on sorghum, a drought tolerant cereal that is used extensively in agriculture in the semi-arid tropics.

Sorghum originated in Ethiopia, but spread throughout Africa, and later to parts of India, China, Australia, South America, and the U.S. making it the 5th most important cereal grown worldwide.<sup>18</sup> Consistent with its center of adaptation, sorghum has a basic set of features that help it grow in hot dry environments including C4 photosynthesis, thick leaf wax, and deep roots to maintain a water supply. The plant also has inducible responses that allow continued growth under sub optimal conditions (osmotic adjustment, stay green), and mechanisms that provide tolerance of environmental extremes (i.e., quiescence). Sorghum has also been studied because of its disease resistance (downy mildew, head smut, grain mold, anthracnose, etc.), insect tolerance (i.e., green bug, midge, root worm), striga resistance, acid soil resistance, aluminum tolerance, heat tolerance, and genetic variation in flowering time, height, and other agronomic traits.<sup>18-24</sup>

The sorghum germplasm collection is large and includes over 40,000 accessions obtained from numerous adverse environments worldwide. The collection is extremely diverse making it an ideal source of gene variants that contribute to adaptation to the environment.<sup>25-28</sup> For example, analysis of 150 diverse sorghum accessions with SSR markers revealed between 5 and 23 variants with each marker analyzed.<sup>27</sup> Moreover, most sorghum genotypes are diploid, increasing the probability that genetic variation will impact plant phenotype. In addition, sorghum has a small genome (750 Mbp) relative to most other cultivated grasses with the exception of rice (~400 Mbp)<sup>29</sup> making it an excellent target for genome-wide analysis.

Over the past decade, sorghum researchers have created and screened sorghum populations for traits related to this plant's adaptation to the environment. To facilitate the mapping and isolation of relevant genes, detailed genetic maps of the sorghum genome have been constructed.<sup>30,31</sup> More recently, AFLP technology was combined with fingerprinting approaches to accelerate the construction of an integrated genetic and physical map of the sorghum genome.<sup>32</sup> This biological resource will enable rapid progress towards gene identification once trait loci are mapped in segregating populations. Other resources including an EST collection and gene maps are rapidly being established laying the groundwork for analysis of genome wide gene expression using microarray technology. These advances in technology and our understanding of the structure of the sorghum genome should accelerate the top-down analysis of well-adapted sorghum genotypes and the genes and alleles that contribute to sorghum's unusual adaptation to the environment. Once discovered, these genes could be moved to other species and used to enhance crop stress tolerance and adaptation on a wider scale thereby increasing agricultural productivity.

### **Blue Light Responsive Promoters and Plant Tolerance to High Irradiance**

Plants are designed to absorb light energy, to drive charge separation, electron transport, ATP synthesis and to generate reducing power for photosynthesis. To carry out this task, plants growing in the shade develop large chlorophyll antennae beds whereas plants grown in high light have reduced antennae. The ability to adjust the size of the antennae bed associated with each reaction center is one of many mechanisms plants use to adjust the amount of absorbed light energy to the capacity of their photosystems and downstream need for ATP and reducing power. Adaptation to varying light conditions is one of the most fundamental and important responses in plants because absorption of excess energy can cause photoxidation of the photosynthetic machinery, rapid bleaching and plant death. Not surprisingly, plants have numerous mechanisms allowing them to adjust to varying light conditions and to

tolerate periods of high irradiance.<sup>33,34)</sup>

Over ten years ago, a comparison of dark grown and light grown barley plants showed that light induced the accumulated an extra transcript encoding the chloroplast gene psbD.<sup>35)</sup> This gene encodes D2, one of the two PSII reaction center chlorophyll-binding proteins that mediate charge separation. Other studies showed that the PSII reaction center proteins are damaged when plants are exposed to high light and that plants have a complex repair system that removes and replaces damaged subunits.<sup>36,37)</sup> This suggested that the light-induced accumulation of psbD transcripts was part of this repair system.<sup>38)</sup>

A series of studies focused on the mechanism of light induction and the psbD promoter helped clarify the role and importance of this response. Early studies showed that light-induced accumulation of the psbD transcripts was due primarily to select activation of transcription.<sup>39)</sup> Analysis of promoter sequences in different plants showed that the psbD light responsive promoter was conserved in dicots, grasses, and black pine but not liverworts.<sup>40)</sup> This suggested that the promoter was initially selected for use in organisms carrying out oxygenic photosynthesis, especially those exposed to high irradiance. Analysis of the architecture of the psbD light responsive promoter showed that the promoter contained a TATA element and an upstream activating domain unlike typical -10/-35 promoters found in bacteria and plastids.<sup>41,42)</sup> Analysis of protein binding to the promoter revealed the involvement of ADP-dependent phosphorylation in gene regulation.<sup>43)</sup>

The physiological role of this promoter was revealed in part by analyzing the photobiology of gene activation. These studies showed the involvement of blue and red light photoreceptors in signal transduction.<sup>38)</sup> Analysis of mutants further refined the environmental parameters of induction confirming the need for both blue and red light and the involvement of phytochrome A in gene induction.<sup>44)</sup> These studies further substantiated the view that the special blue light promoter associated with psbD helps ensure that a sufficient supply of psbD transcripts is available in plants grown in high light. Moreover, this promoter is regulated by circadian cycling and during plant development.<sup>44,45)</sup> The detailed understanding of the biochemistry of this promoter now makes it possible to understand how plants benefit from this specific biochemical response. This provides an excellent example of a bottom-up approach to understanding plant adaptation to the environment. Genome scale analysis and the investigation of plants adapted to high light conditions will no doubt further expand our knowledge of the biological and ecological impact of this mechanism.

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