

# A new vision for plant productivity

Peter H. Quail

Plants live on light. It is not surprising, therefore, that they have evolved an elaborate photosensory system to monitor the availability and quality of this ultimate source of energy in their environment. Similarly, because higher plants are immobilized for life following germination, it is not surprising that the strategies available to them for responding to fluctuations in the light environment are confined to changes in growth and/or development. Moving to a sunnier location is not an option. Unfortunately for agricultural productivity, the nature of plants' response to perceived competition for light is to channel energy into stem extension growth at the expense of harvestable components such as leaves, storage tissue, and reproductive tissue.

However, on pp. 995–998 of this issue, Harry Smith and colleagues<sup>1</sup> describe a promising biotechnological solution to this problem. They report field studies on plants in which this agriculturally undesirable response to competition has been disrupted through reverse genetic perturbation of the photosensory system.

The report is the culmination of a sustained research effort by Smith's group to understand the environmental factors controlling plant architecture and the distribution of assimilated resources within the developing plant<sup>2,3</sup>. Physiologists and farmers alike have long known that many plants, including crop plants, respond to crowding by growing taller. Whereas this response has potential competitive advantage in an ecological sense, in an agricultural setting in which dense monoculture crop stands are the rule, the reduced allocation of assimilates to nonstem tissue has the potential to limit yields below those achievable in the absence of this response.

In the early 1970s, Smith and colleagues set out to identify the environmental signals that induce this response, to determine which receptors perceive and transduce these signals, and to clarify whether this information might be exploited to abrogate production, perception, or transduction of these signals to redirect assimilates from stem growth into harvestable components.

It was soon established that the major sig-

nal for this response—christened the “shade-avoidance response”—is the ratio of red to far-red photons reaching the plant<sup>4</sup>. This ratio is markedly altered by reflection from, or filtration through, neighboring vegetation as a result of strong absorbance of red, but not far-red, photons by the chlorophyll present. Thus, light enriched in far-red photons signals the proximity of competing neighbors<sup>5</sup>.

Further investigations by Smith's group made it clear that the phytochrome photore-

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ceptor system was responsible for perception of this signal<sup>6,7</sup>. The phytochrome molecule has two forms: a red light absorbing Pr form and a far-red light absorbing Pfr form, which are indefinitely photointerconvertible.

At photoequilibrium, the ratio of the two forms of the molecule is a direct function of the ratio of red to far-red light, thereby providing the plant with an exquisite sensor of this parameter of the light environment—a primitive form of color vision<sup>4</sup>.

The more recent discovery that higher plants contain a small family of phytochromes [prototypically five in *Arabidopsis*, designated phytochrome A (phyA) through to phytochrome E (phyE)<sup>8</sup>], provided the opportunity to explore and manipulate the roles of the individual family members in the shade-avoidance response. Evidence from studies with *Arabidopsis* mutants showed that phyA and phyB exert mutually antagonistic effects on stem extension growth in response to far-red light enrichment<sup>7</sup>. These studies revealed that shade avoidance is initially suppressed by the high levels of phyA present in seedlings newly emergent from darkness, but that this suppression is rapidly relieved as the amount of phyA quickly declines to ineffective levels because of its intrinsic light lability.

Such results would predict that artificial maintenance of phyA at high levels in light-grown plants might sustain suppression of the shade-avoidance response<sup>8,9</sup>. Smith and colleagues showed in controlled environment chamber experiments that this is indeed the case<sup>10</sup>. Overexpression of transgene encoded phyA in transformed tobacco plants caused complete suppression of the

shade-avoidance response to light artificially enriched in the far-red region.

In this issue, Smith's group shows that phyA overexpression in transgenic tobacco effectively disrupts the capacity of field-grown plants to respond to natural far-red-enriched light signals generated by reflection of radiation from neighboring vegetation. Consequently, as plant density is increased, the increasing diversion of biomass from leaf to stem tissue experienced by wild-type plants is significantly reduced in the transgenic overexpressors, with an accompanying increase in harvest index. These results provide a gratifying substantiation of Smith's earlier prediction that the fundamental understanding of the light signals and photosensory system responsible for shade avoidance gained through physiological and photobiological studies could be coupled to the more recent advances in the molecular genetics of the phytochromes to provide a novel biotechnological approach to improving crop plant productivity<sup>8,9</sup>.

Extension of this approach to other crop plants has far-reaching potential for agricultural productivity. Because the majority of crops used in modern agriculture are shade avoiders<sup>8</sup>, they should theoretically be amenable to improvement using this technology. The possibilities of enhanced grain weight and increased tuber size in root crops without the need for increased fertilizer use are obvious examples where even modest effects could be of significant economic benefit. In addition, crop yield reduction due to shade avoidance induced by even small weed populations<sup>9</sup> may be avoidable by engineering “color blindness” into plants instead of applying excessive herbicide treatments. The combination of the economic and environmental benefits of this strategy is certain to appeal to farmers and biotechnology companies. Furthermore, the prospect of enhanced yield without the need for expensive agrochemicals or changes to agricultural practices provides an attractive avenue for improving crops such as rice that are central to food production in developing countries.

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