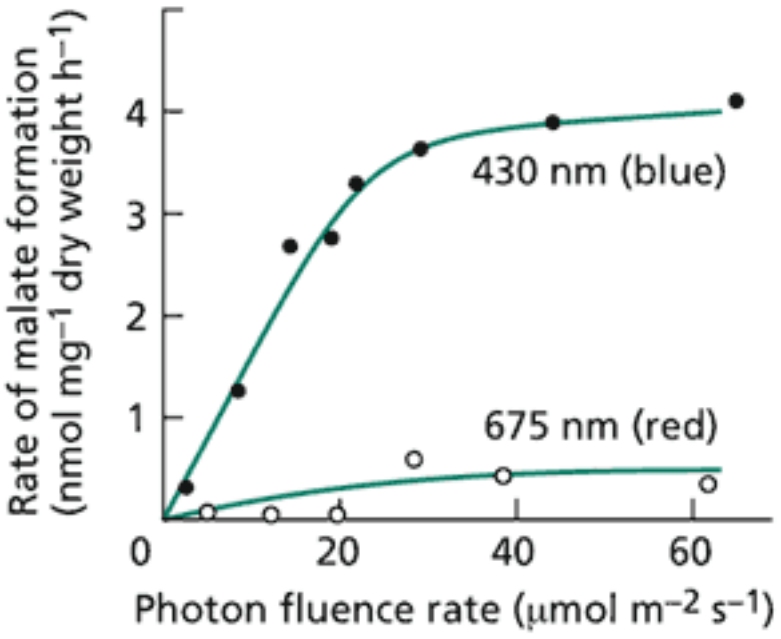
Topic 18.2

Guard Cell Osmoregulation and a Blue Light-Activated Metabolic Switch

Studies on photosynthetic algae, such as *Chlorella,* have shown that irradiation by blue light increases respiratory rates of dark-grown cells, with an action spectrum that is typical of specific blue-light responses (Kamiya and Miyachi 1974). These changes in respiratory rates are associated with a drastic shift in metabolism, which can also be observed in experiments using blue and red light.

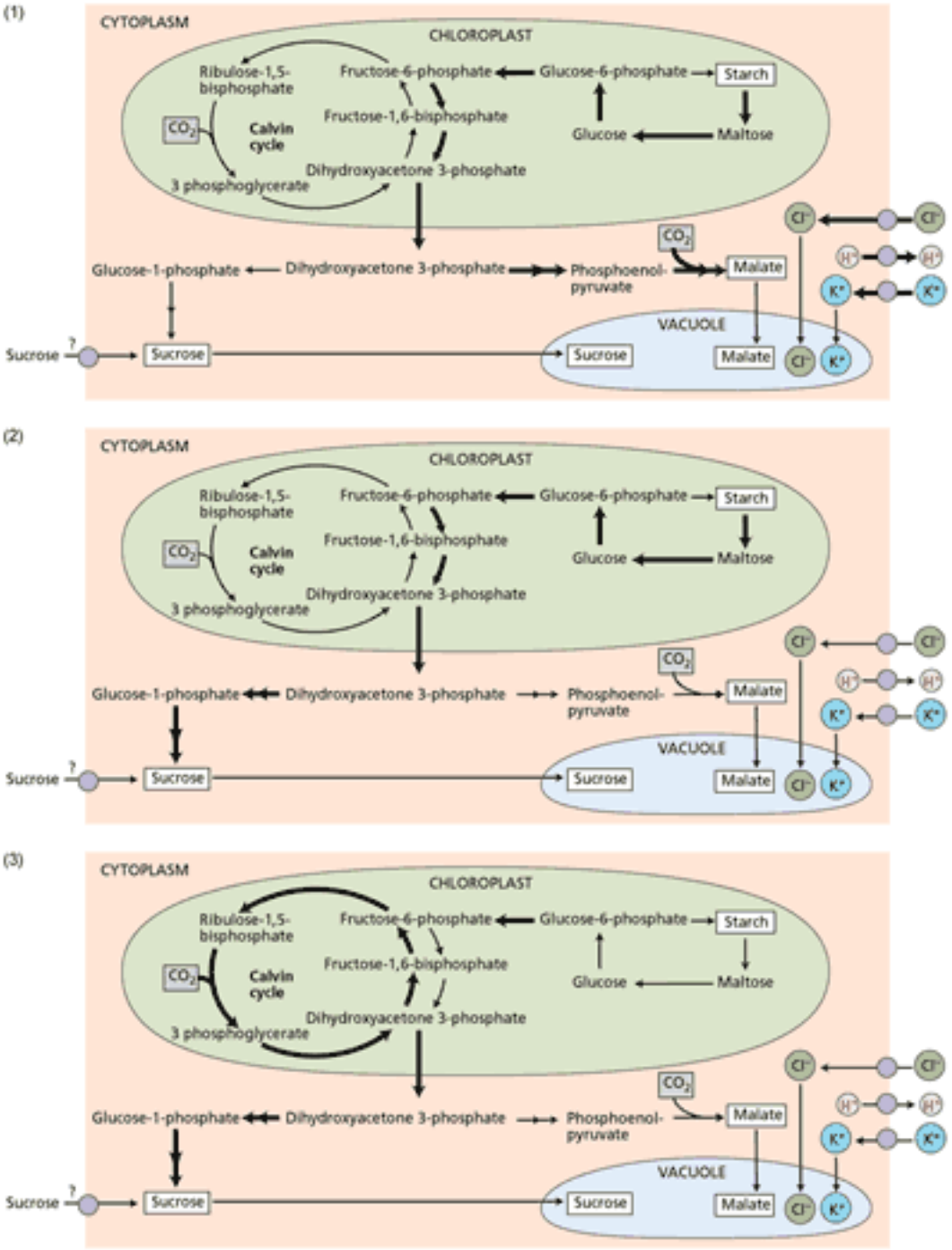
Red light stimulates photosynthetic carbon fixation in these algae, and the fixed carbon is incorporated into glucose and sucrose. The metabolic shift is observed when low photon fluxes of blue light are added to the red-light treatment; glucose and sucrose are no longer synthesized, and the fixed carbon is used in the biosynthesis of organic acids, amino acids, and proteins.

Blue light is also a powerful regulator of guard cell metabolism. Guard cells irradiated with red light accumulate sucrose (Talbott and Zeiger 1998); if low photon fluxes of blue light are added to the red-light irradiation, sucrose stops accumulating, and guard cells accumulate K^+ and malate^{2-} (Web Figure 18.2.A). Thus, the blue light–stimulated shift to the synthesis of the organic acid malate in guard cells parallels the shift to the synthesis of organic acids and amino acids in photosynthetic algae.



Web Figure 18.2.A Blue light stimulates malate synthesis in guard cells. Under red light, guard cells synthesize mostly glucose and sucrose; this metabolic pathway is deactivated by blue light, and metabolism switches to starch degradation and malate biosynthesis. (From Ogawa et al. 1978.) **(Click image to enlarge.)**

The experimental use of blue and red light has been useful for investigations of osmoregulatory pathways associated with stomatal movements (Web Figure 18.2.B). The rapid activation of proton pumping by blue light discussed in textbook Chapter 18 generates a proton gradient at the guard cell plasma membrane that drives potassium and chloride uptake (see Web Figure 18.2.B, part 1). Blue light also stimulates starch hydrolysis and malate biosynthesis. Prolonged incubations of guard cells in detached epidermis under low fluence rates of blue light result in large stomatal apertures accompanied by extensive starch hydrolysis (Tallman and Zeiger 1988).



Web Figure 18.2.B Three distinct osmoregulatory pathways in guard cells. The dark arrows identify the major metabolic steps of each pathway that lead to the accumulation of osmotically active solutes in the guard cells. (1) Potassium and its counterions. Potassium and chloride are taken up in secondary transport processes driven by a proton gradient; malate is formed from the hydrolysis of starch. (2) Accumulation of sucrose from starch hydrolysis. (3) Accumulation of sucrose from photosynthetic carbon fixation. The possible uptake of apoplastic sucrose is also indicated. (From Talbott and Zeiger 1998.) **(Click image to enlarge.)**

Guard cells also show a sucrose-dependent osmoregulatory phase (see textbook Figure 18.14) (Talbott and Zeiger 1998). Sucrose can originate from starch hydrolysis (see Web Figure 18.2.B, part 2). On the other hand, guard cells from detached epidermis irradiated with red light under ambient CO_2 concentrations operate a third metabolic pathway, showing no detectable

potassium uptake or starch hydrolysis (see Web Figure 18.2.B, part 3) (Tallman and Zeiger 1988). In these conditions, guard cells slowly accumulate sucrose, and this sucrose accumulation is blocked by DCMU (dichlorophenyldimethylurea), an inhibitor of photosynthetic electron transport (Poffenroth et al. 1992; Talbott and Zeiger 1993). A recent study of guard cell osmoregulation under red light illumination and CO_2-free air showed that under these conditions, in which photosynthesis is inhibited by the absence of CO_2, red light activates the potassium-dependent pathway (see Web Figure 18.2.B, part 1) (Olsen et al. 2002). These studies underscore the remarkable metabolic flexibility of guard cells.

A study of the effects of calcium and abscisic acid (ABA; see textbook Chapter 23) on stomatal apertures under red and blue light found that increasing calcium or ABA concentrations inhibited blue light–stimulated stomatal opening in a concentration-dependent fashion, but had no effect on red light–stimulated opening (Parvathi and Raghavendra 1997). These contrasting responses to blue and red light can be explained by the effect of the treatments on guard cell osmoregulation. ABA and high calcium concentrations have been shown to inhibit proton pumping and potassium uptake (see textbook Chapter 23), which are central to blue light–stimulated stomatal opening. Red light, on the other hand, stimulates guard cell photosynthesis and sucrose accumulation, and this osmoregulatory pathway appears to be insensitive to ABA and calcium.

Unlike visual systems, the color information in the blue light and red light treatments does not appear to have functional significance for photosynthetic organisms. Rather, their dramatic experimental effects appear to be a result of a differential stimulation of carotenoids and chlorophylls that are selectively excited by blue light applied under a saturating background of red light, or by red light alone, respectively.

Under solar radiation, regulatory pathways activated by the excitation of these pigments are used by the chloroplast to sense key features in their environment and to control their metabolism