Several decades later, a new tobacco strain cropped up in the valleys of southern Maryland and reignited interest in the ways that plants see the world. These valleys have been home to some of America's greatest tobacco farms since the first settlers arrived at the end of the seventeenth century. Tobacco farmers, learning from the Native tribes such as the *Susquehannock*, who had grown tobacco for centuries, would plant their crop in the spring and harvest it in late summer. Some of the plants weren't harvested for their leaves and made flowers that provided the seed for the next year's crop.

In 1906, farmers began to notice a new strain of tobacco that never seemed to stop growing. It could reach fifteen feet in height, produce almost a hundred leaves, and would only stop growing when the frosts set in. On the surface, such a robust, ever-growing plant would seem a boon to tobacco farmers. But as is so often the case, this new strain, aptly named Maryland Mammoth, was like the two-faced Roman god Janus.

On the one hand, it never stopped growing; on the other, it rarely flowered, meaning farmers couldn't harvest seed for the next year's crop.

In 1918, Wightman W. Garner and Harry A. Allard, two scientists at the U.S. Department of Agriculture, set out to determine why Maryland Mammoth didn't know when to stop making leaves and start making flowers and seeds instead. They planted the *Maryland Mammoth* in pots and left one group outside in the fields. The other group was put in the field during the day but moved to a dark shed every afternoon. Simply limiting the amount of light the plants saw was enough to cause *Maryland Mammoth* to stop growing and start flowering. In other words, if *Maryland Mammoth* was exposed to the long days of summer, it would keep growing leaves. But if it experienced artificially shorter days, then it would flower.

This phenomenon, called **photoperiodism**, gave us the first strong evidence that plants measure how much light they take in. Other experiments over the years have revealed that many plants, just like the Mammoth, flower only if the day is short; they are referred to as "short-day" plants. Such short-day plants include chrysanthemums and soybeans. Some plants need a long day to flower; irises and barley are considered

"long-day" plants. This discovery meant that farmers could now manipulate flowering to fit their schedules by controlling the light that a plant sees.

It's not surprising that farmers in Florida soon figured out that they could grow *Maryland Mammoth* for many months (without the effects of frost encountered in Maryland) and that the plants would eventually flower in the fields in midwinter when the days were shortest.

## What a Difference a (Short) Day Makes

The concept of photoperiodism sparked a rush of activity among scientists who were brimming with follow-up questions:

Do plants measure the length of the day or the night? And what color of light are plants seeing?

Around the time of World War II, scientists discovered that they could manipulate when plants flowered simply by quickly turning the lights on and off in the middle of the night. They could take a short-day plant like the soybean and keep it from making flowers in short days if they turned on the lights for only a few minutes in the middle of the night.

On the other hand, the scientists could cause a long-day plant like the iris to make flowers even in the middle of the winter (during short days, when it shouldn't normally flower), if in the middle of the night they turned on the lights for just a few moments.

These experiments proved that what a plant measures is not the length of the day but the length of the continuous period of darkness.

Using this technique, flower farmers can keep chrysanthemums from flowering until just before Mother's Day, which is the optimal time to have them burst onto the spring flower scene. Chrysanthemum farmers have a problem since Mother's Day comes in the spring but the flowers normally blossom in the fall as the days get shorter.

Fortunately, chrysanthemums grown in greenhouses can be kept from flowering by turning on the lights for a few minutes at night throughout the

fall and winter. Then ... boom ... two weeks before Mother's Day, the farmers stop turning on the lights at night, and all the plants start to flower at once, ready for harvest and shipping.

These scientists were curious about the color of light that the plants saw. What they discovered was surprising: the plants, and it didn't matter which ones were tested, only responded to a flash of red during the night. Blue or green flashes during the night wouldn't influence when the plant flowered, but only a few seconds of red would. Plants were differentiating between colors: they were using blue light to know which direction to bend in and red light to measure the length of the night.

Then, in the early 1950s, Harry Borthwick and his colleagues in the USDA lab where Maryland Mammoth was first studied made the amazing discovery that far-red light—light that has wavelengths that are a bit longer than bright red and is most often seen, just barely, at dusk—could cancel the effect of the red light on plants. Let me spell this out more clearly: if you take irises, which normally don't flower in long nights, and give them a shot of red light in the middle of the night, they'll make flowers as bright and as beautiful as any iris in a nature preserve. But if you shine far-red light on them right after the pulse of red, it's as if they never saw the red light to begin with. They won't flower. If you then shine red light on them after the far-red, they will. Hit them again with far-red light, and they won't. And so on. We're also not talking about lots of light; a few seconds of either color is enough. It's like a light-activated switch: The red light turns on flowering; the far-red light turns it off. If you flip the switch back and forth fast enough, nothing happens. On a more philosophical level, we can say that the plant remembers the last color it saw.

By the time John F. Kennedy was elected president, Warren L. Butler and colleagues had demonstrated that a single photoreceptor in plants was responsible for both the red and the far-red effects. They called this receptor "phytochrome," meaning "plant color." In its simplest model, phytochrome is the light-activated switch. Red light activates phytochrome, turning it into a form primed to receive far-red light. Far-red light inactivates phytochrome, turning it into a form primed to receive red light. Ecologically, this makes a lot of sense. In nature, the last light any plant sees at the end of the day is far-red, and this signifies to the plant that it

should "turn off." In the morning, it sees red light and it wakes up. In this way a plant measures how long ago it last saw red light and adjusts its growth accordingly. Exactly which part of the plant sees the red and far-red light to regulate flowering?

We know from Darwin's studies of phototropism that the "eye" of a plant is in its tip while the response to the light occurs in the stem. So we might conclude, then, that the "eye" for photoperiodism is also in the tip of the plant. Surprisingly, this isn't the case. If in the middle of the night you shine a beam of light on different parts of the plant, you discover that it's sufficient to illuminate any single leaf in order to regulate flowering in the entire plant. On the other hand, if all the leaves are pruned, leaving only the stem and the apex, the plant is blind to any flashes of light, even if the entire plant is illuminated. If the phytochrome in a single leaf sees red light in the middle of the night, it's as if the entire plant were illuminated. Phytochrome in the leaves receives the light cues and initiates a mobile signal that propagates throughout the plant and induces flowering.