

Ironically, ABA is no longer thought to play a primary role in bud dormancy or leaf abscission, but it is very important in other functions. Unlike the growth-stimulating hormones we have studied so far—auxin, cytokinins, gibberellins, and brassinosteroids—ABA *slows* growth. ABA often antagonizes the actions of growth hormones, and the ratio of ABA to one or more growth hormones determines the final physiological outcome. We will consider here two of ABA's many effects: seed dormancy and drought tolerance.

**Seed Dormancy** Seed dormancy increases the likelihood that seeds will germinate only when there are sufficient amounts of light, temperature, and moisture for the seedlings to survive (see Chapter 38). What prevents seeds dispersed in autumn from germinating immediately, only to die in the winter? What mechanisms ensure that such seeds do not germinate until spring? For that matter, what prevents seeds from germinating in the dark, moist interior of the fruit? The answer to these questions is ABA. The levels of ABA may increase 100-fold during seed maturation. The high levels of ABA in maturing seeds inhibit germination and induce the production of certain proteins that help the seeds withstand the extreme dehydration that accompanies maturation.

Many types of dormant seeds germinate when ABA is removed or inactivated. The seeds of some desert plants break dormancy only when heavy rains wash ABA out of them. Other seeds require light or prolonged exposure to cold to inactivate ABA. Often, the ratio of ABA to gibberellins determines whether the seed remains dormant or germinates, and adding ABA to seeds that are primed to germinate makes them dormant again. Inactivated ABA or low levels of ABA can lead to precocious (early) germination (**Figure 39.12**). For example, a maize mutant with grains that germinate while still on the cob lacks a functional transcription factor required for ABA to induce expression of certain genes. Precocious germination of red mangrove seeds, due to low ABA levels, is actually an adaptation that helps the young seedlings to plant themselves in the soft mud below the parent tree.

**Drought Tolerance** ABA is the primary internal signaling molecule that enables plants to withstand drought. When a plant begins to wilt, ABA accumulates in leaves and causes stomata to close rapidly, reducing transpiration and preventing further water loss. By affecting second messengers such as calcium, ABA causes potassium channels in the plasma membrane of guard cells to open, leading to a massive loss of potassium ions from the cells. The accompanying osmotic loss of water reduces guard cell turgor and leads to closing of the stomatal pores (see Figure 36.17). In some cases, water shortage stresses the root system before the shoot system, and ABA transported from roots to leaves may function as an “early warning system.” Many mutants that are especially prone to wilting are deficient in ABA production.



◀ Red mangrove (*Rhizophora mangle*) seeds produce only low levels of ABA, and their seeds germinate while still on the tree. In this case, early germination is a useful adaptation. When released, the radicle of the dart-like seedling deeply penetrates the soft mudflats in which the mangroves grow.



▲ Precocious germination in this maize mutant is caused by lack of a functional transcription factor required for ABA action.

▲ **Figure 39.12** Precocious germination of wild-type mangrove and mutant maize seeds.

## Ethylene

During the 1800s, when coal gas was used as fuel for streetlights, leakage from gas pipes caused nearby trees to drop leaves prematurely. In 1901, the Russian scientist Dmitry Neljubow demonstrated that the gas **ethylene** was the active factor in the coal gas. The idea that ethylene is a plant hormone was not widely accepted, however, until the advent of gas chromatography simplified identification.

Plants produce ethylene in response to stresses such as drought, flooding, mechanical pressure, injury, and infection. Ethylene is also produced during fruit ripening and programmed cell death and in response to high concentrations of externally applied auxin. Indeed, many effects previously ascribed to auxin, such as inhibition of root elongation, may be due to auxin-induced ethylene production. We will focus here on four of ethylene's many effects: response to mechanical stress, senescence, leaf abscission, and fruit ripening.

**The Triple Response to Mechanical Stress** Imagine a pea seedling pushing upward through the soil, only to come up against a stone. As it pushes against the obstacle, the stress in its delicate tip induces the seedling to produce ethylene. The hormone then instigates a growth maneuver known as the **triple response** that enables the shoot to avoid the obstacle. The three