FALLING LEAVES

ABSCISSION
by Fredrick T. Addicott
original line drawings
by Alice B. Addicott
University of California Press
376 pages; $39.50

Georgia O'Keeffe, **Pattern of Leaves,** ***1924***

No one who lives near maples, sycamores, oaks, or birches needs to be reminded that leaf fall, or abscission (the process by which plants let go of leaves, flowers, fruits, or twigs), is a dramatic physiological event. As every leaf raker knows, abscission is a precisely regulated process occurring at almost the same time in all members of each species of deciduous trees.

This timed reaction of the tree to the changing seasons serves a useful physiological function, since the bulk of the tree's nutrients are stored in its foliage. Thus, if frost injured the tender leaves while they were still on the tree, the tree would lose minerals and other nutrients when the leaves were shed. Before this can happen, the leaves export to the rest of the tree almost all of their foodstuffs, until they are little more than bare and dangling cellulose skeletons.

When the leaf begins its grand export, it stops producing chlorophyll and other compounds. Soon, pigments that have been hidden all summer by the vivid green of the chlorophyll—yellow xanthophyll and orange or red carotene—begin to show through; and as the chlorophyll slowly disappears, xanthophyll and carotene bring on the first harlequin colors of autumn. Later, chemical reactions in the leaf produce such other compounds as anthocyanins, which are scarlet, purple, or blue. These, blending with the xanthophyll and carotene, yield the full palette of autumn colors. When these gaudy leaves fall, the pageant is complete, but the trees themselves have lost little, having withdrawn almost everything of value from the leaf.

In most temperate zones, the onset of winter is heralded by the shortening of days, which triggers abscission. In arid regions, such as the southwestern desert of the United States, damage to the leaves by desiccation or wilting may be the physiological trigger. But not all abscission is seasonal. Some plants shed their leaves during floods; others abscise in response to mineral deficiency, atmospheric pollution, or insect attack. Whatever the behavior pattern, it is genetically programmed to be elicited by one of a group of hormones that govern abscission in green plants. One such hormone, abscisic acid (ABA), was discovered by Fredrick T. Addicott and his associates at the University of California at Davis, in the 1960s. They observed that in the cotton plant a certain growth-inhibitory substance always accumulates as the cotton bolls grow old and approach abscission. Successive rounds of isolation, assay, and purification led to the final isolation of the pure compound.

Meanwhile, by one of those coincidences with which the history of science abounds, another team of botanists, led by Philip Wareing, of the University College of Wales, in Aberystwyth, was studying a related phenomenon, bud dormancy in woody plants. This phenomenon, also induced by the shortening of days as the seasons progress, converts the succulent, tender, growing bud to a somewhat desiccated, dormant structure, insulated from the cold by cottony hairs and protected by an overlapping series of varnish-coated scales. This process, too, is accompanied by a buildup of a growth inhibitor in the bud.

Trying to find out what induces buds to change from active growth to dormancy, Wareing's team isolated and purified the active substance. As it happened, Wareing and Addicott finished in a virtual dead heat in their efforts to characterize these substances, which turned out to be identical. One week's publication priority by the Addicott group led to the name abscisic acid; otherwise the substance might have been called *dormin,* since Wareing knew it for its role in causing actively growing buds to enter a dormant state.

How convincing is the case that ABA actually controls abscission? Addicott addresses the question in the course of his excellent monograph, *Abscission,* which is a survey of all aspects of the process, from the descriptive, anatomical, and ecological to the biochemical, genetic, pathological,

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and evolutionary. Though it is designed to be read by those with some sophistication in botanical science, parts of it may be perused with profit by lay readers with some background in general biology and chemistry (and, perhaps, with piles of leaves on their lawns).

Addicott provides an appendix of almost four pages of references to support his view that ABA causes abscission; some of the evidence he cites is merely correlational, showing that abscission occurs when ABA levels are high; other evidence is more direct, demonstrating that abscission can be induced artificially if ABA is applied to plants' leaves. Yet not all plant physiologists are convinced, for in many instances the cause of abscission seems more closely related to ethylene, yet another plant hormone. There are still many botanists who believe that ABA's role is more closely linked to dormancy, or other affairs of the plant, than to abscission. If that is true, then ABA is a misnomer. Addicott's treatment of the controversy seems somewhat less than dispassionate; the same might be said about his very brief mention of ABA's role in dormancy—but that, after all, was not his subject.

As Addicott explains, it is generally agreed that all abscising leaves, flowers, fruits, or twigs form a special group of cells called the abscission zone. In this zone lies a special abscission layer whose cell walls, composed mainly of cellulose, are easily digested by enzymes produced in response to hormonal messages. When these cells become sufficiently weakened by enzymatic digestion, the weight of the abscising organ causes it to fall from the plant. The scar this creates may then be covered over by a protective secretion, or cell layer.

This apparently simple sequence of events is governed by a complex interweaving of external signals, including photoperiod, temperature, injury, and pathological agents; and internal biochemistry, mainly involving the plant hormones auxin, ethylene, and, of course, abscisic acid. In general, when enough auxin moves down to the stem from the leaf blade, abscission tends *not* to occur, although massive external application of ethylene or abscisic acid may still trigger it. As a leaf ages, its auxin production declines and its natural abscission may then be accelerated by a buildup of abscisic acid or a sudden burst of ethylene production. In all cases, abscission is preceded by a synthesis of cellulase and other cell wall–digesting enzymes. The system is immensely complicated and not well understood at the molecular level; consider only that auxin traveling down the stem toward the leaf *favors* abscission, while auxin coming from the leaf toward the stem *retards* abscission.

Addicott has lived with this subject for almost forty years and has amassed a wealth of information, both fundamental and trivial, about it. The field has its own special jargon, and he explains the meanings of such terms as *marcescent* (withering without falling off), *cladoptosis* (the annual dropping of twigs or branches), *disseminule* (a seed or spore), *peridiole* (the spore container in certain fungi), and *phyllomorph* (a leaflike perennial plant structure arising from a basal growth zone, as in the ornamental, *streptocarpus*). Addicott also instructs the reader in the secrets of how the bird's nest fungus disseminates its spores by rain—for having defined abscission as "the separation of cells, tissues and organs from the remainder of the plant body," he has given himself broad latitude in this book. He even includes in his consideration the shedding of some bark and the separation of cells of an algal filament, since, he says, "The evolution of abscission began when two cells separated for the very first time."

I find this perspective unhelpful, for Addicott has not adequately treated many phenomena that according to his unusually broad definition of abscission should be relevant. Surely, it is more useful to think of abscission in its narrower and more traditional sense, as the plant's shedding of its parts in an orderly way. That subject Addicott *has* described in a generally comprehensible manner in this book.

There are several pertinent topics whose absence puzzles me, however. The massive mobilization and transport of mineral nutrients and some organic materials from the leaf to the rest of the plant before abscission, ensuring that when the leaf falls not too much stored nutrient leaves the tree, is obviously an important physiological process linked to abscission. Yet it is not considered at all. Also, in considering defoliants that promote abscission, Addicott mentions the military advantages said to have accrued from their use in the tropics (such as Agent Orange in Vietnam) without mentioning the disadvantages— the ecological and health problems probably raised by the presence of dioxin contaminants in the chemical used as a defoliant. One ought to mention the bad along with the good.

On the whole, though, *Abscission* is authoritative, comprehensive, and clearly written. Addicott should be able to enjoy his retirement with great satisfaction now that this job is done. And by the way, the ABA under many of the book's lovely line drawings represents not abscisic acid but Alice B. Addicott, the author's wife and artistic collaborator. They must have had a good time doing this book together.

—Arthur W. Galston