When Oak Leaves Fail to Fall

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Introduction

Most leaves abscise (fall) from deciduous trees in autumn. But, at about the time of bud-break in the spring, many oaks, beeches, and other woody plants go through a second phase of leaf-fall. The desiccated leaves that persist on the tree through winter are called "marcescent" leaves, and this phenomenon of deciduous leaves persisting past the end of the growing season is called "marcescence" (rhymes badly with "farce essence," with emphasis on the second syllable). Ghostly white, hanging from the beeches; noisy, rattling in the black oaks; curled, chrysalis-like, rusty on the narrow branches of the musclewood—they fall periodically throughout the winter, but then suddenly the remainder of them abscise in spring. What happens?

It is probably easier to begin with the story of normal leaf abscission in the fall. By late spring, a zone of distinct cells forms near the base of the leaf's petiole (leaf-stalk). The cells in this region, which is called the abscission zone, weigh the amount of a hormone, auxin, flowing toward them from both directions. If the leaf can broadcast the auxin signal loudly enough to be detected above the chemical din coursing through the tree, the abscission zone remains in a state of arrested development and the leaf remains attached. But eventually the leaf's ability to feed the tree diminishes. Disease, drought, frost, or the shortening days of autumn finally weaken the leaf, reducing its production of auxin. In many species, this triggers cells within the abscission zone to secrete a digestive enzyme, cutting the leaf from the tree. In other species, the petiole will break through the thin walls of rapidly dividing separation layer cells. As the separation layer is ripening, a group of cells closer to the base of the petiole form a suberized, lignified protective layer. (Suberin and lignin are two waterproof, phenolic polymers that are particularly important in woody plants.) By the time the leaf falls from the tree, the protective layer has become a barrier against infection.

The story in marcescent leaves is less straightforward. Take, as an example, the population of black / Hill's oak (a putative hybrid, Quercus ellipsoidalis x Q. velutina, also known by the name Quercus x palaeolithicola) on the sandy moraine that runs through the University of Wisconsin-Madison Arboretum, studied in 1964 by Chester O. Marvin and Ray F. Evert but never published. In these plants, leaves in the bud are without a defined abscission layer. Within weeks or even days of bud-break, however, the abscission layer begins to differentiate. Then, near the end of the growing season, a few layers of cells at the far edge of the abscission zone begin to lignify (become filled with lignin, the brown, phenolic polymer found in wood and certain classes of plant cells, typically with a structural or protective function). Cells on the far side of this lignified layer die. In some cases, cells on the near side of the lignified layer may divide to form a separation layer, but the layer does not become functional. In other cases, no separation layer forms. This, in the oaks studied, appears to be the key difference between normal deciduous leaves and marcescent leaves. For at around this time, normal leaves on the tree fall, but the marcescent leaves persist on the branches through winter unless they are broken off by wind, snow, or other mechanical forces.

Then spring comes, and with it the opening of buds. Expanding buds may push the leaves off the branch, or the leaves may stay attached. In either case, cork cells filled with suberin, the phenolic polymer found in bark and roots, begin to form at the base of the petiole stump at about the time of bud expansion. Several layers of cork develop across the base of the petiole. Suddenly the outermost cork cells break. With that break, rather than through the actions of a typical abscission zone, the remaining marcescent leaves and petioles fall to the ground in spring, months after the normal deciduous leaves have fallen.

This same story holds for several other oak species (including scarlet oak, Quercus coccinea, and the Old World species Q. hispanica and Q. pedunculata). According to Seneca legend, oak trees hang onto their leaves in defiance of winter, and the pine trees stand in alliance with them. The tamaracks, however, drop their needles in resignation. Legend notwithstanding, the ecological causes and consequences of marcescence are not well understood. A study of Q. subpyrenaica in Spain revealed that leaves that receive more sunlight persist longer on the tree and consequently are likelier to become marcescent at the end of the growing season. A similar phenomenon may be seen in the Midwest, where leaves high in the canopy of a large black oak may be marcescent while the most shaded leaves fall normally. Marcescence, then, may reflect selection for increased photosynthetic potential over the lifetime of each leaf on a tree.

At the same time, marcescence in our climate seems a troublesome phenomenon as limbs covered with leaves in winter may be weighted down more heavily with snow than limbs from which leaves have fallen. Consequently, limbs with marcescent leaves may be at a greater risk of breakage. Close study of this phenomenon by naturalists with an eye for ecology may reveal a great deal not yet known about the correlates and possible causes and consequences of marcescence.

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