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Redbud cauliflory:

The inside story

One of the most distinctive features of redbuds, *Cercis canadensis*, the 2013 VNPS Wildflower of the Year, is its production of flowers on mature trunks and major branches, a habit termed cauliflory. Redbud flowers also form on young, one-year old twigs; as explained below, twig- and trunk-borne flowers are parts of a single developmental continuum; twigs bearing flowers eventually becoming trunks and large branches that continue to bear flowers.

But before exploring the biological details of cauliflory, some attention to etymology is warranted. In the context of redbuds, the term cauliflory is derived in straightforward fashion from the Latin, "*caulis*" (stem) and "*flor-*" (flower). And while all flowers are borne on stems of one sort or another, botanical use of the term restricts cauliflory to those uncommon instances in which

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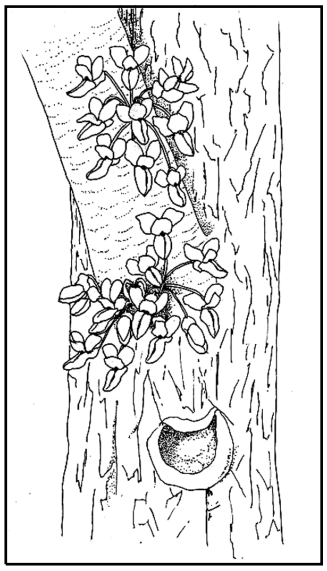

Cauliflorous flower clusters of eastern redbud. (Drawing by Nicky Staunton)

•Cauliflory

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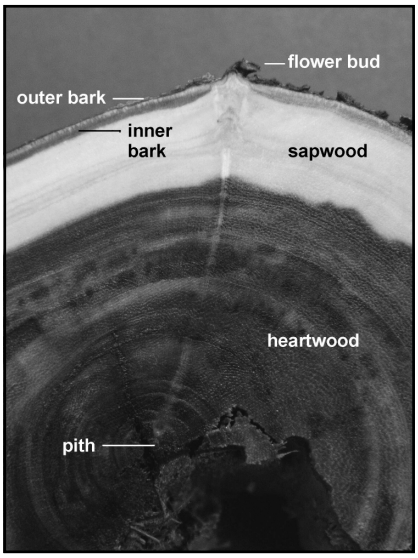
flowers develop on the sides of mature woody stems. Cauliflower, the vegetable, by this definition, is not cauliflorous! It seems that "*caulis*" also means "cabbage" and cauliflower the vegetable is, literally a massive glomeration of very early stage flower buds of plants closely related to cabbage; cauliflower buds form on the ends of succulent non-woody stems and thus do not qualify as cauliflorous as the term is usually applied in botany.

The vast majority of flowering plants produce flowers at or near the tips of relatively young actively growing stems. Commonly, flowers or inflorescences (flower clusters) form at the very ends of stems or from lateral buds located not far below the stem tip. Cauliflory, on the other hand, is decidedly uncommon, but it does occur in a small number of plant genera, mostly from the tropics. Perhaps the most familiar tropical cauliflorous plant is the chocolate tree (*Theobroma cacao*); the flowers are quite small, but the subsequent fruits, about six inches long, deeply ribbed and bright yellow, are decidedly eye-catching (and can be seen in a recent television ad). Redbuds constitute one of the few examples of cauliflory among temperate zone plants.

The developmental connection between redbud flowers produced on one-year old twigs and those found on mature trunks should be obvious to any careful observer. The first pertinent fact is that the alternate leaves of redbuds are borne in strict distichous phyllotaxy, which is to say that successive leaves are oriented 180 degrees apart from each other, alternately on opposite sides of the stem, leafy branchlets, thus, being more or less planar. Because redbud leaves occur along two lines (think right- and left-hand sides of the stem), flower clusters arising from lateral buds of one-year old twigs also occur in two lines—nothing unusual here, a great many plants produce flowers in the axils of one-year old twigs. If one carefully studies a flowering redbud tree, however, it will soon become evident that flowers on slightly older twigs continue the distichous pattern seen on the youngest twigs, as do the truly cauliflorous flowers of large branches and main trunks. The straightforward conclusion is that the pattern of flower production for any redbud stem must be initiated in its earliest growth stages, following the architecture established by distichous leaves and the flower buds that form in their axils.

To explain how principal trunks and main branches of redbud retain the capacity for flower formation requires microscopic examination, and such studies have been reported in a series of papers by Shirley Owens and Frank Ewers from Michigan State University (see literature cited). One key point is that redbuds make not one, but a series, of lateral buds in their leaf axils. As many as 10 first order lateral buds per node have been documented, and these occur in a linear series of descending size. The largest lateral buds have the potential to produce a flower cluster in the year subsequent to their initial formation; successively smaller buds occur below the largest one, with the smallest located closest to the leaf axil proper and likely to remain dormant for as long as five years before forming flowers (on what would then be a fairly substantial branch). In part, then, cauliflory in redbuds is a straightforward matter of the plants possessing multiple lateral buds capable of forming flowers over a number of years as that stem becomes incrementally thicker. But redbud stems much older than five years continue to produce flowers, which is the distinctive hallmark of cauliflory. It seems that the first order lateral buds, those that formed when the stem segment was very young, also have the ability over time to proliferate new second order buds. Thus, cauliflory can continue indefinitely from proliferating bud clusters that were initiated in primary growth.

Another way to conceptualize the developmental pattern of redbud cauliflory is to remember that lateral buds, in general, also have the capacity to make branch stems. In the usual case, the branch stem elongates rapidly and, over time, its basal region becomes engulfed as its parent stem increases in diameter, eventually forming a knot in the woody tissue of the parent stem.



Chop-saw dissection of an eastern redbud trunk showing the small knot-like trace left as one cauliflorus bud cluster has become engulfed by yearly increments of woody tissue. (Photo by John Hayden)

The cauliflorous bud clusters of redbud can be viewed as the tips of greatly foreshortened branches that grow so slowly that their tips barely protrude beyond the bark of their parent stems. And just like ordinary branches that form knots as their parent stems overgrow their bases, careful dissection of redbud trunks will reveal small knot-like tracks that extend from the central pith to surface bud clusters.

So that's the "how" of cauliflory. What about the "why?" "Why" questions are often difficult. In the case of redbuds, one is tempted to assert that because its closest relatives are tropical plants, and because most cauliflorous trees are tropical, cauliflory in *Cercis* is an ancestral trait that belies the tropical origin of now temperate zone redbuds. But that explanation only shifts the context of the question in time and space: so why did the tropical ancestors of redbuds develop the cauliflorous habit? Frankly, attempts to answer such questions tend to be speculative and most speculation revolves around the complexity of tropical forests and the intricacy of pollination interactions observed in tropical plants. Understory trees and shrubs in the tropics can't be expected to attract the same pollinators that service flowers in the canopy. Rather, understory trees and shrubs are more likely to be

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•Redbud

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pollinated by insects or other animals that live near the forest floor; cauliflory may thus be a means to provide easy access to flowers for these inhabitants of the lower strata of tropical forest. Returning to modern redbuds, one notes that bumblebees and carpenter bees are frequent pollinators, and these are insects that spend a great deal of their time relatively close to the ground. So, perhaps the "Why cauliflory?" explanation boils down to "it worked" for the tropical ancestors and it continues to work in its present temperate zone habitats. If it ain't broke, don't fix it!

W. John Hayden, VNPS Botany Chair

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