

The Layered Look

Peter Del Tredici

The humble bunchberry yields startling insights into tree architecture

I shall never forget a walk in the woods I once took at the Harvard Forest in Petersham, Massachusetts, with Francis Hallé, the French botanist who pioneered the study of tree architecture. It was April 1975, and the forest floor was alive with wildflowers. Among them was *Cornus canadensis*, the bunchberry, which was just coming out. Dr. Hallé took one look at the little plant and said that it was like a flowering dogwood (*C. florida*) lying on its side, growing horizontally through the litter rather than vertically. It was a fanciful statement, containing more poetry than botany, I thought, yet something about it rang true.

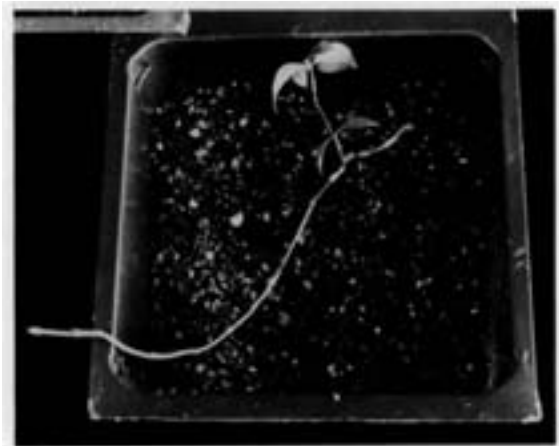
After years of thinking about Dr. Hallé's comment in only the vaguest of terms, I recently had the opportunity to look into it more critically when a group of bunchberry seeds I had collected near Mount Katahdin in Maine germinated in the Dana Greenhouses of the Arnold Arboretum (see the table, page 21). The little seedlings grew amazingly fast and after just a single season's growth were producing numerous underground stems. These rhizomes, as such underground stems are called, grew out either from the axils of the seed leaves — the cotyledons — or from the axils of the first few true leaves. Seedlings that did not produce rhizomes set large buds which grew out as rhizomes the following spring.

The fact that these bunchberry seedlings produced rhizomes in their first season came as a surprise to me because it is exactly the reverse of the behavior exhibited by most tree seedlings, which build a strong vertical stem by preventing the buds lower down on the trunk from growing

out during their first year. Clearly, *C. canadensis* lacks the strict apical control that most woody plants exhibit.

In the most well-developed year-old bunchberry seedlings, the tips of the rhizomes had turned up and formed new above-ground shoots, each with a characteristic whorl of leaves. At some variable point below this region of upturning, one or more new buds had formed in the axils of the rhizomes' bud scales; they were destined to continue horizontal growth through the forest litter when they grow out the following spring. What at first glance might appear to be a population of separate bunchberry plants, then, usually turns out to be a single individual.

While none of the bunchberry seedlings I grew reached flowering age, I found that mature



A *Cornus canadensis* seedling in its first season, showing rhizomes growing from the axils on the cotyledons. Photograph by Peter Del Tredici.

Germination of Bunchberry Seeds*

<i>Treatment</i>	<i>Germination %</i>
sow in greenhouse	0
3 months cold stratification	21
sow outdoors	4
1½ hr. sulfuric acid + 3 months cold stratification	18
1½ hr. sulfuric acid + sow outdoors	74

* The germination of *Cornus canadensis* seed collected wild on the Penobscot River, near Mount Katahdin, Maine Seeds (100 per treatment) were sown on September 14, 1982. Seedlings were counted on December 13, 1983. The soak in concentrated sulfuric acid was recommended by C. S. Schopmeyer in 1974.

specimens cultivated at the Arboretum usually, but not always, flowered on the upturned tips of these rhizomes, while buds closer to the base of the rhizome grew out, producing new rhizomes that would turn upward and flower the next spring. The plant thus produces a branch system built up by the activities of several different buds growing out in relays — each of which continues the line of growth in the horizontal direction after the previous bud turns up to produce a flower.

Before one can answer the question of whether this growth habit of *C. canadensis* is just a horizontal version of that of *C. florida*, as Dr. Hallé initially suggested, one needs to have a clear conception of how the latter species grows. First, flowering dogwood has a “layered” look in the arrangement of its branches, which Hal Borland



A *Cornus canadensis* seedling showing a well-developed cotyledonary crown. The arrow points to a relay bud that will grow out the following season. Photograph by Peter Del Tredici.



The earliest known illustration of *Cornus canadensis*, from the 1672 edition of *New England's Rarities, discovered*, with the following caption:

This plant I take for a variegated Herb Paris, True Love, or One Berry, or rather One Flower, which is milk white, and made up with four Leaves, with many black threads in the middle, upon every thread grows a Berry (when the Leaves of the Flower are fallen) as big as a white pease, of a light red colour when they are ripe, and clustering together in a round form as big as a Pullets Egg, which at a distance shews but as one Berry, very pleasant in taste, and not unwholesome. . . .

describes as "horizontal limbs that reach skyward at their tips and form a fine lace pattern." Among deciduous temperate zone trees, such layering is unusual. It occurs in the dogwood because the shoot that builds the central trunk is physiologically distinct from the shoots that build the lateral branches. The trunk is produced by the activity of a single meristem that grows vertically year

after year, while the lateral branches are produced by meristems growing horizontally in "relays." These relays originate in buds below the shoots that turned upward to produce flowers.

In reality, the distinction between the behavior of the terminal and the lateral shoots of flowering dogwood is not as clear-cut as I have described. In particular, the terminal shoot often seems to lose its vigor for no apparent reason and is replaced by one of the laterals. This usually occurs in the spring, when the young branches are beginning to grow out.

The growth habit of the bunchberry, of course, is entirely different from that of the flowering



Cornus florida winter silhouette. Drawing by Olga A. Smith, from *Tree Flowers of Forest, Park, and Street*, by Walter E. Rogers; courtesy of Dover Publications, Inc.

dogwood. Yet a curious similarity exists: the bunchberry plant resembles a lateral branch of flowering dogwood growing independent of a trunk. Dr. Hallé later discussed this in his book, *Tropical Trees and Forests*, written with R. A. A. Oldeman and P. B. Tomlinson. In it, he states that the architecture of herbs is derived from that of trees by a process he calls "fragmentation":

In *Cornus canadensis* the creeping, somewhat woody axis may be equated with one branch of a tree ancestor. The superficial similarity is enhanced by the development of foliage leaves in distinct rosettes along the horizontal axis in both forms. In such examples, if this interpretation is correct, there should be some evidence of the orthotropic [vertical] trunk in the epicotyledonary axis.

Having followed up Dr. Hallé's speculation with some solid observation of my own, I can now say that the only remnant of a trunk in *C. canadensis* is the vertical tip of the seedling shoot, which reaches a height of no more than two or three centimeters before the basal rhizomes grow out and compete with it. The fact that the rhizomes take root as they grow through the soil not only eliminates the need for a central trunk to distribute nutrients, but also the need for any centralized control over their growth pattern.

At this time, no one knows why bunchberry lacks apical control. There are two possibilities. The terminal bud may not produce the growth-inhibiting hormones that would keep the rhizomes from growing, or the rhizomes may be

insensitive to any inhibitory hormones the terminal bud might be producing. Regardless of which is true, apical control is at the heart of the differences in growth habit between *Cornus florida* and *Cornus canadensis*. Clearly, Dr. Hallé was right when he described the bunchberry as a flowering dogwood without a trunk.

Sources

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