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Plant culture: thirteen seasonal pieces

April – watching sap flow

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What force drives the opening of buds in the spring? It is an axiom of plant physiology that the negative water potential of the atmosphere pulls up water to the top of even the tallest tree: but through the leaves. What, then, unfurls the leaves? An event that might, to a naturalist, seem related is the rising of sap in the spring. Here I highlight some of the observations of WS Clark on the subject, and outline subsequent advances in our understanding of sap movement. I conclude that there is more than one mechanism behind sap flow; and that while rising sap may drive bud burst in some plants, it does not seem to in all, or even most of them. Knowledge of bud opening mechanisms seems surprisingly limited, given the resonance of the onset of spring for so many millions of our listening public. But then perhaps we don't do science for them? A research programme based on 'Spring Strains' by William Carlos Williams may be the answer.

While Gerard Manley Hopkins explored the inscape of bud burst in England (see 'March'), WS Clark, President of the Massachusetts Agricultural College, was co-ordinating a highly systematic survey of various 'phenomena of plant-life', with particular emphasis on the patterns and causes of sap flow in trees. The results were published in 1874–75. Where Hopkins found evidence of the divine hand in the lineaments of opening buds, Clark was concerned with the scientific explanations that careful, quantitative observation might furnish. While Hopkins provided a unique and lasting expression of wonder at the world, Clark laid the foundation for our understanding of the movement of sap (defined here as sugar-enriched xylem fluid). And both men, observing the movement of nature in spring, were interested in explanations for related phenomena.

Clark recorded the flow of sap from a range of trees. He observed that in grape (*Vitis aestivalis*) and birch (several *Betula* spp.), sapflow results from renewed activity of the roots in spring that leads to root pressure. The enormous pressure generated by one root of black birch (*Betula lenta*) was, at its maximum, enough to support a 26 m column of water. The function of this sap mobilization is presumably to drive leaf opening so that photosynthesis can begin. It also bleeds the hydraulic system of air, at least in grape, whose vessels are full of air during winter. Root pressure flow drives the air out of the system, in preparation for the transpirational flow of water that takes over once leaves become functional.

Clark also discovered that detached roots follow the same seasonal pattern as the rest of the plant. Thus: 'One of the main roots of the vine was uncovered and followed from the stem toward its extremities, a distance of four feet, where it was cut off. To the large end of this detached root, the remainder of which was left undisturbed in the soil as it grew, was firmly fastened a piece of stout rubber hose, which was connected by means of a stopcock to the lead pipe of a mercurial gauge. This was on May-day. The tissues of the root, which had not yet awakened from its winter sleep, at once began to absorb the water from the gauge, and the next day there appeared a suction equal to –4.53 feet of water. This continued, though gradually diminishing, till it reached zero, on the tenth of May. From this time the pressure still increased until, on the twenty-ninth of the month, it became sufficient to sustain a column of water 88.74 feet in height, which is more than twice as great as the maximum observed by Hales, and the greatest pressure ever produced by the sap of a plant so far as we know. It is an interesting fact that this maximum occurred on the warmest day in May, the mean temperature having been 71.7 degrees F. It is also noteworthy that, on the very day when the gauge first showed pressure, the vine which was tapped began to flow, though it was half a mile distant.'

In sugar maple (*Acer saccharum*), in contrast to birch and grape, Clark concluded that sap flow had no connection with root activity, but was, rather, associated with temperature fluctuations, and had its origin in the stem. This was supported by later research that confirmed that a 'good run' of sap was associated with freezing nights followed by sunny days. Later still, it was shown by Milburn and co-workers that the freeze–thaw cycle generates the stem pressure responsible for the flow of sap in maple and other *Acers*. This sap flow seems unrelated to spring bud opening.

Clark's work shows the importance of careful accumulation of data, recorded free of the prejudice that can arise from a strongly held hypothesis. Although it would be fascinating to know what Clark thought about photosynthesis and leaf function, it may be that his data are more interesting because these matters did not dominate his thinking. The observations on detached roots emphasise how root function is independent from, but closely related to shoot function.

But to come back to that deceptively simple question 'what drives bud opening in the spring?'. Clark's research suggests that movement of water by an osmotic mechanism (e.g. root pressure) can be significant. But this is not always the case. Thus, Clark states that, in contrast to birch and grape, "it is a well-established fact that the roots of most woody plants have not the power at any season to force water to any considerable height when separated from their stems". It's odd that, although we can guess what goes on in an opening bud, we don't really know.

Rising sap and bud burst epitomize the regeneration of life, as metaphors of the reproductive bloodrush to which the natural world succumbs after the long darkness of winter. Perhaps our research should take account of this,

because it is important to non-scientists. It gives a new, refreshing perspective on the questions we choose to ask and answer, as do William Carlos Williams' Cubist spring picture in words, and the painting it is said to conjure up, 'Tirol' by Franz Marc (Fig. 1).

SPRING STRAINS

In a tissue-thin monotone of blue-grey buds
crowded erect with desire against the sky
tense blue-grey twigs
slenderly anchoring them down, drawing
them in –

two blue-grey birds chasing
a third struggle in circles, angles,
swift convergings to a point that bursts
instantly!

Vibrant bowing limbs
pull downward, sucking in the sky
that bulges from behind, plastering itself
against them in packed rifts, rock blue
and dirty orange!

But –
(Hold hard, rigid jointed trees!)
the blinding and red-edged sun-blur –
creeping energy, concentrated
counterforce – welds sky, buds, trees,
rivets them in one puckering hold!
Sticks through! Pulls the whole
counter-pulling mass upward, to the right
locks even the opaque, not yet defined
ground in a terrific drag that is
loosening the very tap-roots!

On a tissue-thin monotone of blue-grey buds
two blue-grey birds, chasing a third,
at full cry! Now they are
flung outward and up – disappearing suddenly!

Fig. 1. 'Tirol' by Franz Marc (1914). (AKG London)

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