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Cavitation May Explain Winter Damage to Rangeland Vegetation

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As spring advanced across the landscape of Central Oregon last May, people began to notice browning western juniper trees interspersed among apparently healthy green trees. Some of the affected trees died entirely, while others lost individual braches. The cause of this widespread juniper die back was most likely a short period of sub-zero temperatures in late October of 2002. Freeze damage to the unfortunate trees was not visually apparent until the foliage dried up and turned brown the following spring. So, what exactly happened? When we talk about "freeze damage" to plants, most people think that the plant tissues simply freeze and die. The reality of winter damage to plants, however, is a bit more complicated and a lot more interesting than that.

Experience with ornamental junipers planted in the relatively harsh winter areas of the northern US Midwestern states and Canadian prairie provinces is that most winter foliage damage is the result of drying rather than freezing. Although the subzero weather of October 2002 was unusual for Oregon, our high deserts and mountains experience subfreezing temperatures periodically throughout most winters. Long lived plants, such as western juniper, will experience several of these atypically cold periods during their 100+ year life time. So, our evergreen plants have developed very effective ways to avoid actual freezing of their over wintering tissues. When cells freeze, water is drawn out of the cell sap to form ice crystals. These crystals can mechanically puncture cell membranes, allowing the cell contents to spill out as the cell later thaws. This produces that dark wet look to previously frozen plant foliage that I like to think of as the "black lettuce syndrome". We see this look frequently on frost damaged herbaceous plants, but it is rarely seen in juniper, pine, fir, or other conifer foliage. Direct cell death from freezing can be readily avoided by simply increasing the amount of material dissolved in cell sap or by suppressing the formation of large ice crystals during freezing. Reducing the water content of the cell or dissolving more material in the cell sap will lower the cell's freezing point. Plants do this during the fall when they are "hardening off". Plants that have stored food for later use in the form of starch often convert it back to water soluble sugars that enter the sap, providing a form of natural anti-freeze. This is why root vegetables, such as turnips, carrots, and parsnips taste sweeter in the fall, after they have experienced a cold event.

Winter can be a surprisingly stressful time for evergreen plants. Although air temperatures may be low, leaf temperatures may be relatively warm on bright sunny winter days. The combination of warm leaves, relatively dry air, and cold or frozen soils makes it very difficult for plants to replace water as fast as it evaporates from their foliage. Water moving up tall plants is not pumped up from the roots, it is pulled up from the foliage. Water has a cohesive property that allows it to stick to itself. As water evaporates from the leaf surface, it is replaced from the water column that extends back through the branches, down the stem, and to the roots. This column is constructed by stacking a series of individual long but narrow xylem cells that have pores in their ends and sides. The cells are gathered together into bundles that form the equivalent of our veins and arteries. The chain effect of each exiting water molecule pulling the next one up to replace it, places tension on the water column. When water evaporates faster than it can be replaced, the tension on the water column will cause it to stretch, much like stretching a rubber band. Just as a rubber band becomes thinner when stretched, the diameter of large trees often decreases during stressful periods because of this xylem water tension. The cohesion force of water is surprisingly strong. Its ability to tolerate tension is similar to that of steel wire. However, it is not without its limits. When hot dry weather coincides with low soil moisture availability, xylem tension may exceed the breaking point. The xylem water column then snaps, and a vapor bubble (an embolism) containing air and water vapor splits the water column. This event is called cavitation. Since liquid water can not pass through the embolism, no water can move upward from below. However, the water above the embolism will be drawn up to support tissue for as long as it lasts. When this water is exhausted, the dependent tissue dries up and dies. A single embolism is not much of a problem because water can move around the blocked xylem cell through the side pores and back into the upward chain of cells above it. However, the inefficiency of using this indirect path increases the stress on adjacent cells and can cause them to fail as well, forming a “cascade of cavitation”. Since plants are organized with individual branches drawing their water primarily from identifiable portions of the xylem system below them, the chain reaction of xylem failure may be limited to the cells predominately supplying a single branch. This produces the dead strips of bark and dead branches commonly seem on old knarled juniper trees. Where dead wood starts is the probable point of cavitation. When a major portion of the xylem column cavitates, the entire top of the plant dies, but healthy branches may continue to grow below the point of failure. I have seen fairly large healthy trees that formed when a single surviving Douglas-fir branch has turned up to serve as a new top.

Cavitation occurs more easily if the xylem column is partially obstructed by air bubbles. These so called “seed bubbles” are most often formed by being sucked over from failed vapor-filled cells into adjacent functioning water-filled cells under high xylem tensions. This is thought to be a main contributor to cascading cavitation during summer drought stress. Freezing is a major contributor to winter cavitation. Water contained in the xylem typically has less dissolved material, and is more readily frozen than is cell sap. Mature xylem cells are generally considered to be non-living tissue, so freezing will not kill them. However, as xylem water freezes, any dissolved air will be forced out, forming seed bubbles for cavitation. The water column then breaks during thawing. Winter cavitation is fairly common in hardwoods such as beech, birch, and willows. Repeated freeze-thaw cycles are believed to increase susceptibility of the xylem to cavitation in the near future.

The impacts of cavitation on plant growth and development strongly reflect when cavitation happens and if the water column can be readily restored. When the water column snaps during a period of high moisture demand, little time is available for repair before down-stream tissue dies. I have seen conifer trees die so quickly during extreme heat events that the needles dry green and remain in the tree. The dead trees look freeze dried. Luckily, plants have several ways of overcoming xylem failure. Some plants can generate considerable “root pressure” from soil water being actively packed into root xylem from moist soil by a vigorous root system. This is the force that drives sap out of sugar maples so that it can be collected during spring sap rise. Some hardwoods are believed to be able to tolerate considerable winter cavitation by using root pressure to compress and redissolve xylem bubbles the following spring. Unfortunately, our western conifers have fairly low root pressure, as evidenced by lack of cut stumps “bleeding” water in the spring. Observations of failed xylem cells being refilled with water even though the vessels are under tension, suggests that repair is possible even for plants with little or no root pressure. However, the exact mechanism for this repair is poorly understood at present. Unrepairable xylem area can be simply replaced with new tissue during spring or other periods of rapid plant growth.

Plant physiologists used to view cavitation as a form of system failure. However, we are now coming to realize that cavitation and its reversal are common events for many plants. For example, afternoon cavitation in ash, maple, and spruce trees with repair during the evening and early morning may occur almost daily under the right conditions. The processes of cavitation and repair are part of a dynamic interaction that links plants with their environment. Although we most frequently think of cavitation in terms of stem or foliage die back, roots also cavitate. In fact, roots tend to be more prone to cavitation than are plant tops. It has been speculated that cavitation may actually benefit plants by providing the equivalent of an electrical circuit breaker that separates a high demanding section from the rest of the plant during particularly stressful periods. This allows the rest of the plant to function while the out-of-balance portion is either repaired or shed. The susceptibility of roots to cavitation has been interpreted as a useful way to temporarily separate the top of plants from dry soil that may otherwise tend to draw moisture back out of the top through the roots. Some people have gone as far as suggesting that desert plants may actually provide weak sections of the xylem column that then serve as prepositioned breaking points for cavitation so that expendable twigs or limbs may be sacrificed in an orderly manner during drought.

As Yogi Berea said “you can see a lot by looking”. As we have learned to look for evidence of cavitation, we have seen it everywhere. It is particularly dramatic in stressful environments such as our subalpine, arid, and semi-arid landscapes. It is manifest in the knarled knobcone pines of the Siskiyous, in the living sculpture of our ancient high desert junipers, and in the irregular crowns of old sagebrush plants. Cavitation has contributed much to the character of our wildland vegetation.