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University of California
Agriculture and Natural Resources
Making a Difference for California

Landscape Notes

Vol.23 No.3	November 2011

Why Trees die?

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(Excerpted from a presentation give at the Western Chapter International Society of Arboriculture in Santa Barbara, CA. October, 20, 2011.)

Trees grow, mature and die within a given lifespan that is regulated by their own genetics, the site on which they grow and by the sequence of events (either natural or anthropogenic) that befall them over their lifetime. Trees die for many reasons, but all trees are constrained by physiological processes that they must follow to grow, develop and survive. When the limits of physiological functioning are reached, trees stop growing, draw on stored reserves, and when these run out, they decline and die. Trees also die when pathogens kill them. Diseases can kill trees of any age, but tree death is also hastened when decay advances within a tree, and finally, tree declines bring about the death of many mature trees.

There is general agreement between various authors that trees die when they deplete all the energy reserves required to sustain respiration in their tissues (Manion, Kramer and Kozlowski, Shigo). Thus, it is important to understand the basic physiological processes that trees use to obtain and store energy. All energy for trees comes from the sun. Sunlight energy is captured by trees in the process called photosynthesis. The chemical equation is shown below.

-- $(6C0_2 + 24H_20 + \text{light} \rightarrow C_6H_{12}O_6 + 6O_2 + 18H_20)$

-- $3CO_2 + 6H_2O + \text{light} \rightarrow C_3H_6O_3 + 3O_2 + 3H_2O$

Although widely shown in texts that photosynthesis produces a six carbon sugar (equation in parenthesis), this is not actually the case. Photosynthesis produces a three (sometimes a four) carbon sugar that is rapidly converted to glucose or sucrose and then moved by the phloem to areas of necessity. Once sugar reaches its destination in the tree, it is enzymatically converted to starch and stored or it is stripped of its available electrons (oxidized) and energy is produced according to the following equation:

$$-- \quad C6H12O6 + 6O2 \rightarrow 6C02 + 6H20 + \text{Chem E} + \text{Heat}$$

This process is called respiration, it is the oxidation of glucose. Respiration is in some ways the opposite reaction to photosynthesis. During respiration carbon dioxide is released along with water, energy (for other chemical reactions) and heat. The loss of heat during respiration is unavoidable and means that not all the energy captured during photosynthesis can be used for tree life processes. Heat loss and other energy losses require the tree to be very efficient at continual production and storage of sugars.

Phloem moves sugars produced in leaves and stems via a source and sink model. The source is green parts of the tree, mostly leaves, and the sink is those areas of storage or rapid growth. As it turns out, trees have a hierarchy of where sugar will move. Sugar goes first to all cells that need respiration, this is to all the living cells of the tree for their maintenance, it is next allocated to cells that generate root tips, then to cells that grow shoots and finally to the vascular cambium for growth of wood and bark. Any remaining sugar not used in these growth processes is stored in the wood of stems and roots or fruit. Stored sugars are mobilized and used by respiring cells when leaves are not present (deciduous trees) or when the environment does not favor photosynthesis (cold winters). Even in cold climates, roots continue to respire using stored sugars to maintain their cells. As trees age, more and more sugar is needed to sustain larger and larger respiring root systems.

As trees increase in size and age, they go through various phases of growth. Early in their lives, trees grow at an accelerating rate. Young trees grow more cells each year and their size increases exponentially. As trees mature, their growth rates are constant, adding similar amounts of cells each year, steadily increasing their size. At the end of their lives, mature trees growth rates begin to decelerate—each year the tree produces fewer cells. Old trees sometimes enter declines where cells die faster than they are produced (Figure 1).

From a forestry perspective, old, large trees are considered decadent because they are losing energy faster than they are storing it (Merker and Hopper). Another trend in tree growth is that the total number of respiring cells continues to increase over time but the canopy of leaves becomes somewhat constant as a tree matures. Large trees develop a burden to maintain their ever increasing size and quantity of living cells both in the enlarged stem as well as the root system. This sets up a situation where the canopy cannot continue to feed sugar into growing points because most of it is used just to sustain respiration in all the living cells. First, primary growth then secondary growth slows or stops in the decadent or over mature tree.

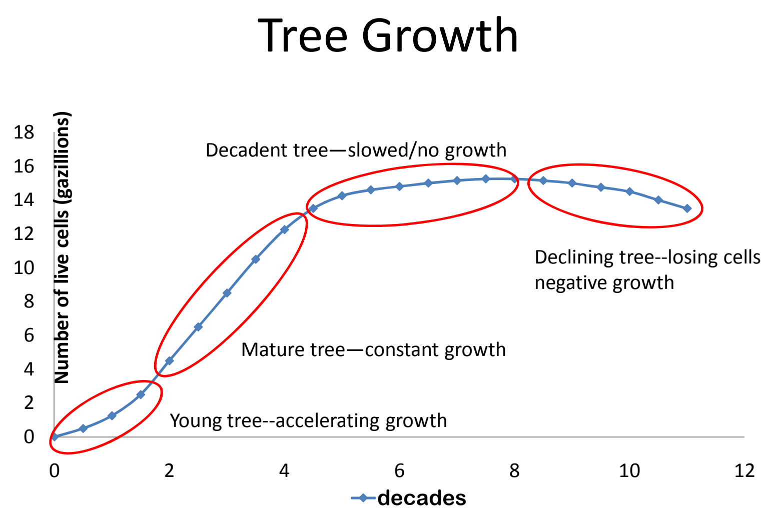

Figure 1 A hypothetical growth curve for trees

Since the vascular cambium is lower in the hierarchy of demand for sugar than root growth or shoot growth, tree rings easily show the vigor decline of older trees. Bark and wood cells decrease in size and quantity as sugar is allocated preferentially away from the vascular cambium—the annual rings shrink. Because less sugar is available as stored energy in older trees, they can't bounce back from harsh environmental factors (cold, heat, drought etc.), over pruning, construction injuries, insect attack or pathogen attack that all demand the vascular cambium to respond with wound tissues growth. Open wounds leave access for decay organisms and wood formed over old decay infested wood is less vigorous and abundant.

Decay in trees can eat both the dead heartwood (heartrot) and the living sapwood (saprot of trees).

Figure 2. The dark areas of this oak stem were stained with iodine and indicate stored starches, the light line around the heart rot is where decay fungi are eating away at stored reserves in the sapwood.

Since sapwood is often living and a major storage tissue, decay of the sapwood not only causes disease but severely hampers a tree by depriving it of its energy storage capabilities. In advanced stages, decay so destroys the support system of trees that they may fail or fall over, this is often the endpoint in a tree's lifetime and results in its death. Mature trees fall down and die. Heart rot fungi are not generally considered pathogenic but some of the Ganoderma fungi that cause heartrot can also move outward in the wood absorbing carbohydrate in older sapwood (Figure 2.). Saprotters are pathogens because they kill living cells, block water movement in the xylem and cause symptoms in the foliage. Wood decay organisms are also categorized as brown rot or white rot fungi. Brown rot fungi usually heartrotters only remove cellulose--the brown colored lignin remains giving the decay a brown color. The white rotters replace most of the wood with fungal mycelium decaying both lignin and cellulose and give a very white colored rot that is wet and fungal smelling. Ganoderma lucidium, Armillaria mellea and Oxyporus latemarginatus are all white rot fungi also sapwood decay fungi and also pathogenic to the trees they occur in. Decay fungi usually enter trees through wounds either in the root or shoot systems. As trees age, the likelihood that they are infected with one or more decay organisms increases. Also, as trees grow older, so do the infections inside them, increasing the likelihood that major amount of wood have been converted into fungal mycelium. In summary, decay fungi kill trees by removing their structural support so they break and fall, by removing the storage tissue in their wood, thus eliminating carbohydrate reserves and finally by plugging the xylem and preventing water from flowing to the canopy, thus reducing or killing the photosynthetic machinery of the tree which further prevents carbohydrate production.

Another reason trees die is because of attack from a virulent pathogen. Pathogens of trees attack all parts of the tree. The most deadly pathogens kill trees that are not adapted (genetically) to deal with the pathogen or are poorly adapted to grow in the location in which they are planted. Wilt, canker, and root rot diseases can all directly kill shade trees. Indeed, diseases like chestnut blight, Dutch elm disease, pitch canker, cypress canker, oak root fungus, sudden oak death, and Phytophthora root rot, have all killed millions of trees. In each case, the host tree did not have the genetic capability of preventing the disease from infecting or spreading within itself and killing it. Trees can and will die from incurable diseases, especially as new pathogens are moved around the world. Oak Wilt, Laurel Wilt, several Fusarium diseases, and Sudden Oak Death are on the move and threaten western states but mostly are not here yet. Sometimes a new insect can be the start of an upsurge of tree killing disease. The rapid spread of the glassy winged sharpshooter in California, resulted in various strains of the bacterium Xylella fastidiosa being injected into many kinds of trees that never experienced the races of bacteria that were typically isolated to a few hosts. As a result we have Olive, purple leaf plum and liquidambar trees dying over much of Southern California. The bacteria have been here all along, but the importation of a new vector with a wide host range caused the onset of these tree killing diseases.

Sometimes pathogens are adapted to live in conjunction with its host, but when multiple factors simultaneously occur, they can become deadly. When pathogens are only one part of a chain of events in the death of a tree it might be part of a larger process called a tree decline (Manion). Trees in decline are losing living cells over time (Figure 1.)—the tree cannot keep up with cell production to replace those that are dying. Tree declines were proposed by many authors, but Paul Manion elucidated the process as an interwoven set of events that lead to the death of the tree. Trees of any age can enter a decline, but mature trees typically decline as soon as their carbohydrate reserves are depleted. No one factor in a decline is responsible for tree death, but rather dependant on the others that are involved in the process. In Manion's concept declines are composed of three basic phases: 1 the predisposing factors; 2 Inciting factors and finally; 3 contributing factors. Predisposing factors are long term conditions, often abiotic conditions that weaken a tree. Salinity, drought, continued attack by foliage feeding insects can all be predisposing factors. Inciting factors are short term catastrophic events that further push the tree into decline. Overpruning, rootpruning, construction injury, compaction, herbicide injury, all could be inciting factors. Finally contributing factors are longer term factors that bring about the demise of the weakened trees. Oak root fungus, Phytophthora, bark boring insects are all contributing factors that can kill a tree and end the decline. Often, the various phases of a decline are necessary for the others, especially for the contributing factors to be able to infect/attack the weakened tree.

Detecting, diagnosing or understanding the stages of decline in a specimen tree requires knowledge of the tree's past history and the events that had befallen it. Often these can be assessed as old pruning wounds, construction activities, and use patterns around the tree which are easily observed. Past useage of fertilizers, herbicides or other pesticides and environmental toxicants are often difficult to track. Declines are often assessed by making an canopy assessments. Since root loss and sapwood loss both show up as leaf loss, and stunting of primary growth, canopy assessments are valuable for documenting tree declines. I like to call these, the "blue Sky test". On a clear summer day if you stand at the base of the tree and look up you will see some amount of blue sky, A mature tree that has not been recently pruned should have a closed canopy of healthy leaves. If you can see 50% blue sky the tree is likely in serious decline. Other measures of canopy health are shoot lengths, leaf retention and leaf size. All these measures are relative and some examination of healthy trees in the vicinity of the tree in question should be used as a baseline for canopy health assessments. Finally, I suggest documenting the canopy photographically so comparisons can be made year to year to determine the progress of recovery or decline.

Some authors (Merker and Hopper) attribute loss of open space around trees to their ultimate decline. Trees in natural systems drop leaves to the ground thus forming a natural mulch or litter under their canopy. Urban trees have reduced litterfall areas under their canopies and these trees are at greater risk for decline and a shortened life than trees in more open landscape circumstances.

How do we sustain or treat the aged and declining tree. As previously mentioned, carbohydrates are the key to growth of a tree. If there are no carbohydrates the tree stops growing. Sugars only come from leaves. So the first tenant in treating/maintaining the geriatric or declining tree is to stop pruning of anything with green leaves on it. Since pruning removes photosynthetic capacity it cuts down the ability of a tree to make and store energy. Mature trees with structural, hazard or storm damaged limbs may still require restorative pruning but if they are also in decline the damage and resulting pruning will often move these trees further down the decline spiral. It is important to know when to remove the tree. Assessment of the root system, starting with the root collar and moving outward to the fine root system is also essential in treating trees in decline. Roots starved for sugar are very susceptible to root rot organisms. Early detection and fungicidal treatment of incipient root rot can forestall the ultimate outcome of a tree decline. As root health increases, the canopy can respond by producing more leaves, which in turn will produced the sugars needed for roots. The decline will abate.

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