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CHARACTERISTICS OF TREES PREDISPOSED TO DIE

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ABSTRACT

A tree dies when it is unable to mobilize sufficient resources internally, or obtain additional resources through leaves and roots to sustain life or heal injuries. Although stress of any kind affects the availability of water, nutrients, and photosynthate, we can judge a tree´s probability of dying by assessing:(1) reduction in photosynthesis, (2) adjustments in maintenance costs, and (3) diversions of photosynthate away from expected growth patterns. Examples are provided for trees subjected to drought, mechanical abrasion, and nutrient stress.

INTRODUCTION

Around the world, there is increasing interest as to why large groups of trees or whole forests may suddenly die, sometimes without apparent changes in weather or other conditions. Tree physiologists that study stressed or injured trees usually find some degree of abnormalities in the rates of various processes and in the way that resources are allocated. The extent of abnormalities indicates the probability that a tree will sustain life or die.

In a general sense, stressed or injured trees alter their carbon balance in three ways: (1) by reducing photosynthesis, (2) by adjusting maintenance costs, or (3) by diverting photosynthate away from expected patterns of allocation. These changes in carbon balance usually are associated with concomitant changes in nutrition and water balance. The relative importance of water and nutrition, as we shall see, is reflected in the way that the carbon balance is adjusted in stressed plants.

Recently, in areas where forest decline and death are widespread, some preliminary physiological studies have been initiated. In reviewing these studies we learn how different kinds of environmental stresses affect the three major components of the carbon budget. Before going to specific cases, however, I shall first review typical tree response.

TYPICAL TREE RESPONSE

Foresters have recognized normal healthy trees exhibit a certain percentage of living foliage distributed in a symmetrical manner around and along part of the bole. They have characterized the distribution of wood growth along the bole so that measurements made at the base can be used to estimate growth throughout the length. Ecologists have expanded these kinds of relationships to estimate growth and total biomass of branches and large diameter roots (ref. 1). Maximum canopy leaf area has been estimated from correlations with the cross-sectional area of sapwood (ref. 2).

Trees, particularly temperate species, show a seasonal phasing in the production of shoots, stems, roots, storage reserves, and defensive compounds (ref. 3). During the elongation of new shoots, the production of other materials is greatly limited, and in the case of storage reserves, depleted. Therefore, any abnormal event that causes defoliation, be it drought, frost, or herbivory has its maximum impact at the time of shoot expansion when reserves are minimal.

In forest stands, small trees growing in the shade of larger ones may be particularly susceptible to drought and defoliation because their reserves are less than normal (ref. 4) and their root systems are also restricted in relation to their size (ref. 5, ref. 6). Large trees, on the other hand, have their canopies more exposed to frost damage, ice or snow breakage, and atmospheric pollutants.

To assess the general physiological status of a tree´s carbon balance, it is desirable to compare at common relative growth rates. For this reason comparisons are often made when growth processes have slowed or reached a minimum. Thus, just before buds break carbohydrate and nütrient reserves in twigs, older foliage, stem, and large diameter roots may be good indices of future growth and the ability of a tree to recover from defoliation (ref. 7, ref. 8).

Any reduction in net photosynthesis by the canopy may be determined by comparing changes in wood production by individual branches (ref. 9). To sustain photosynthesis, trees growing on infertile soils allocate a larger proportion of photosynthate to root growth than do those growing on more fertile substrates (ref. 4, ref. 10).

A tree´s inability to accumulate reserves or produce defensive compounds is associated with a low production of stem wood per unit of foliage. Stem growth is a component less critical to tree survival than foliage and root growth, thus its sensitivity to changes in the relative availability of resources (ref 11).

As a tree grows, its crown expands and begins to shade other trees. In a forest, wood production per unit of foliage therefore decreases as the total canopy leaf area increases. Once a forest reaches maximum canopy, some trees continue to develop more canopy while others lose theirs and die. The requirements of surviving trees for photosynthate may increase more rapidly than their canopy can sustain because the volume of living cells in conducting sapwood and associated tissues continues to increase as a tree grows in height. The maintenance cost of these additional living cells causes a drain on reserves and further reduces stem wood production per unit of foliage. The reduction in growth rates is particularly rapid in warm environments because respiration increases exponentially with temperature (ref. 4).

Departures from typically observed bole taper and other growth abnormalities may be useful as additional indicators of stress (ref. 12, ref.13). With some idea of what is normal, we may now look at structural and other physiological characteristics associated with dying trees in differing environments.

DROUGHT-INDUCED DEATH

Periods of extended drought are not particularly harmful if trees have well developed root systems and canopies are adequately exposed to photosynthesize when conditions are suitable. Thus savana type forests rarely die from drought (ref. 14). A slight drought that does not completely halt photosynthesis may actually increase carbohydrate reserves and the levels of defensive compounds because demands for shoot growth are immediately reduced. Sustained drought, however, halts photosynthesis, depletes reserves and defensive compounds, and eventually reduces the amount of canopy (ref. 15, ref. 16).

It is shallowly rooted trees growing in dense stands that are usually most susceptible to drought (ref. 14, ref. 17). Thus in the boreal spruce forests of Norway, old, shallowly rooted trees, growing with closed canopies suffered most from bark beetles following a series of droughty years (ref. 18).

If the density of trees in spruce stands is reduced, more light and more water are available to survivors. Trees provided with such an improved environment showed higher stem wood growth rates and could better resist a lethal fungus carried by bark beetles (ref.19). Trees with more exposed canopies had a larger surplus of photosynthate to contribute to defense reactions (ref. 20).

DEATH BY MECHANICAL ABRASION

Trees located on a sea coast, along gorges, or on high ridges are often buffeted by high winds. Usually trees growing in such areas have a tailored canopy shaped by the prevailing wind. They are short in stature and exhibit strong bole taper. In cases where heavy snows or ice accumulate, the combination of mechanical forces may threaten survival as trees grow in height and are subjected to increasing damage.

In dense forests of balsam fir (Abies balsamea) in the White Mountains of New Hamsphire (USA), synchronous death of trees periodically occur (ref. 21). The subalpine environment is harsh, and the density of trees such that wood production per unit of foliage is consistently low throughout the sequence from young to older forests (ref.22). As these forests grow, air turbulence in the canopy increases, favoring the accumulations of rime ice and shearing of foliage during winter storms (ref. 22, ref. 23). As a result, an increasing proportion of new foliage is removed from canopies as stand development proceeds towards dieback and death (ref. 24).

Following an experiment where trees were artificially exposed to increasing turbulence by selectively removing adjacent trees, a substantial decline in foliage mass and pre-budbreak foliage starch content was observed over a two year period (ref. 23). Increased exposure also resulted in a dramatic increase in root damage relative to control trees. Breakage of roots associated with extreme movement of tree boles was followed by secondary infection of roots, further weakening trees to mechanical stress. Loss of active foliage and roots was accompanied by a 2-to 5-fold reduction in annual wood increment among dieback zone trees (ref.23, ref.24).

DEATH THROUGH NUTRIENT DEFICIENCIES OR IMBALANCES

There are situations where nutrients are so limiting that once a forest has developed, demand for nutrients are more than what is returned through normal litterfall, root turnover, and decomposition. At other times, young or very old soils are sufficiently impoverished in some essential nutrient that existing trees are prone to repeated attack from insects or diseases. A case in point is a subalpine forest in the Pacific Northwest (U.S.A.) that grows on nitrogen deficient soils developed on volcanic ash deposited within the last 7000 years. These forests, dominated by mountain hemlock (*Tsuga mertensiana*), die periodically from infection of a root rot (ref.25). After large trees die, younger ones are reestablished and continue to grow without major damage from root rot until the forest canopy reaches maximum development; then rates of decomposition and wood production per unit of foliage again slow and the cycle is repeated (ref.26).

Fertilizing at only 50 kg N per ha per year increased the nitrogen content of foliage, and presumedly also the photosynthetic activity (ref.27). Wood production per unit of foliage by small trees situated in gaps, or in the open, also increased over that of unfertilized samplings (R.H. Waring, unpublished). In controlled environment studies, Matson and Waring (ref.28) demonstrated that starch reserves, total nitrogen, and amino acids were significantly increased when mountain hemlock seedlings were provided with sufficient light and nutrients. Susceptibility to root rot was reduced. On the other hand, fertilization in the absence of increasing light caused trees to become more susceptible to root rot, probably because protein synthesis and maintenance require large amounts of photosynthate that might otherwise go toward defense against the pathogen.

An excess of essential nutrients may also cause relative defiiencies in other minerals, particularly if growth rates are increased (ref.29, ref.30). Entry et al. (ref.31) demonstrated in an experiment with western white pine seedlings (*Pinus monti-*

cola) that imbalanced nutrition increased susceptibility of plants to injury by Amellaria root rot.

Imbalanced nutrition has been reported in conifers along air pollutant gradients in California (ref.32) and in the New England States (ref.33), and in association with nitrogen-fixing deciduous trees (ref.12). Whether these situations are contributing to forest decline associated with attack by pathogens is not known but symptoms such as green-leaf fall, abnormal bole growth, and reduced root production are highly suggestive (ref.13).

SUMMARY

Trees experiencing abnormal stress generally exhibit a variety of biochemical and structural responses that may help us in diagnosing the kind of stress and the probability of tree survival. Many types of stresses reduce the canopy and its photosynthetic activity. Drought, mechancial abrasion, and nutrient imbalances cause distinctive alterations in how photosynthate is allocated along the bole and to the roots. To amerliorate different kinds of stress, different treatments are required. Success should result in reestablishing a more typical pattern in which photosynthate is distributed within a tree.

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