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Characteristics of Trees Predisposed to Die

Stress causes distinctive changes in photosynthate allocation

R. H. Waring

Around the world, there is increasing interest in the question of why large groups of trees or whole forests suddenly die, sometimes without apparent changes in weather or other conditions (Kimura 1969, Mueller-Dombois 1983, Schutt and Cowling 1985, Wardle and Allen 1983). In general, trees die when they cannot acquire or mobilize sufficient resources to heal injuries or otherwise sustain life.

Because of their size, trees have large storage capacities and may accumulate considerable nutrients, carbohydrates, and water. These resources can often be mobilized during periods of stress, enabling a canopy or root system to continue to function or to be reestablished following destruction (McLaughlin et al. 1980, Pook 1984, Stone and Vasey 1968). Yet, tree physiologists usually can detect in stressed and injured trees abnormalities in resource allocation and in the rates of other processes. The extent of the abnormalities can indicate the probability that a tree will survive a stressful period.

Recently physiological studies have been initiated in areas where forest decline and death are widespread. These studies are demonstrating how different environmental stresses affect the major components of a tree's carbon budget. Before going to specific cases of trees in stressful environments, I present a normal tree's growth pattern. Once the normal pattern is characterized, departures from normality may be used as a measure of stress or of predisposition to die (Waring 1983, 1985).

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Normal tree growth patterns

Foresters have recognized that healthy trees usually have symmetric crowns distributed in a predictable manner along the stem. Moreover, wood growth is laid down along the bole in a predictable pattern, so the growth in volume can be predicted from the growth in stem diameter near the base of the stem. Ecologists, like foresters, use normality in form as a means of estimating from stem diameter, the growth and total biomass of branches and large-diameter roots (Whittaker and Woodwell 1968).

Trees, like other plants, show a strong seasonality in their production of shoots, stems, roots, storage reserves, and defensive compounds (Figure 1). For example, any stress that coincides with the completion of shoot expansion, has a greater effect than it would later in the season, when storage reserves have been rebuilt. The best time during the year to assess the general physiological status of trees appears to be the period just before the buds break. At this time carbohydrate and nutrient reserves in twigs, older foliage, stems, and large diameter roots are good indices of future growth potential, as well as of a tree's ability to recover from defoliation and some other stresses (Wargo 1972, Webb 1981).

Growth abnormalities, such as departures from typical bole taper, may be useful as additional indicators of stress (Schutt and Cowling 1985, Waring 1985). Low production of stem wood per unit of foliage has been associated with a tree's inability to accumulate reserves or to produce defensive compounds. Stem growth only occurs once the resource demands of foliage and root growth have been accommodated (Figure 2).

Shade-induced stress

As a tree grows, its crown normally expands and begins to shade other trees. In a forest, wood production per unit of foliage decreases as the total canopy leaf area increases (Figure 3). The rate of that decrease depends not only on competition among trees for light, but also on competition with understory plants for water and nutrients.

Once a forest reaches maximal canopy, some trees continue to develop more canopy while others lose their canopies and die. The surviving trees' requirements for photosynthate may

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R. H. Waring is a professor in the Forest Science Department at the College of Forestry, Oregon State University, Corvallis, 97331.

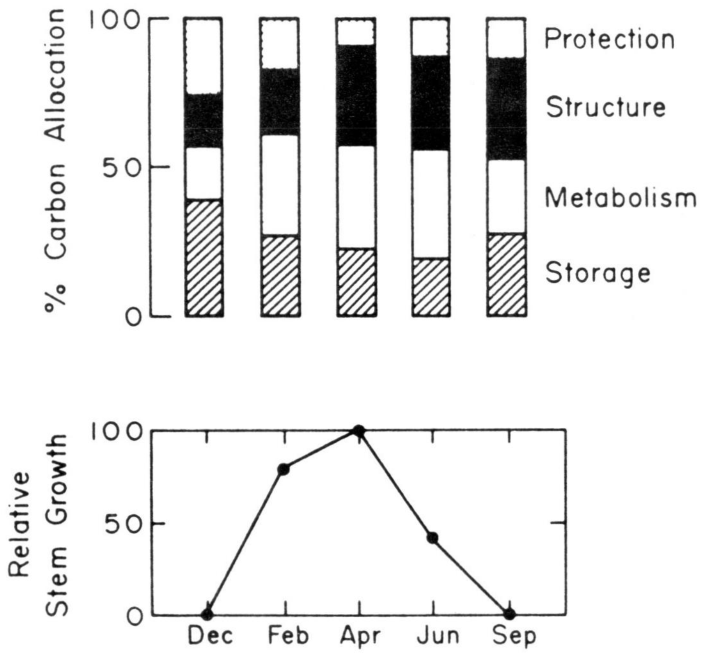

Figure 1. In seasons with conditions favorable for growth (labeled February, April, and June) the evergreen *Heteromeles arbutifolia* accumulates less storage reserves and defensive compounds than in seasons of low growth (December and September). After Mooney and Chu (1974).

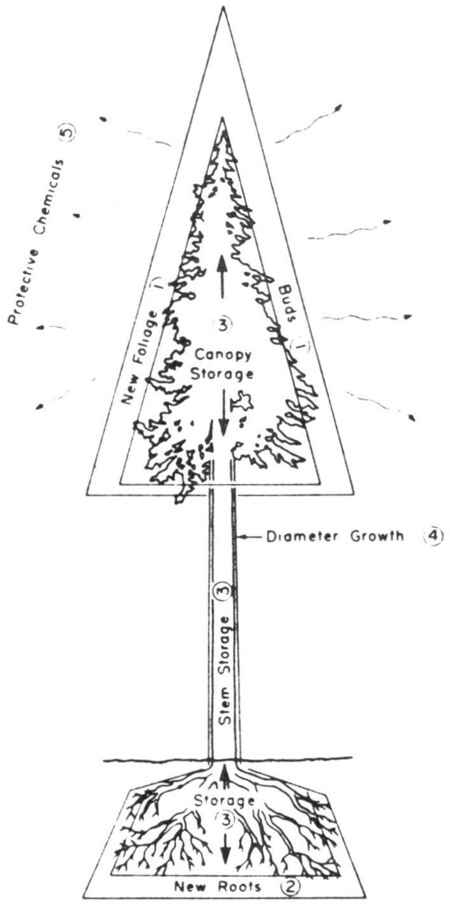

Figure 2. A postulated hierachy for normal carbon allocation in a tree. Photosynthetic tissue represented by buds and new foliage (1) and new roots (2) have high priority. If additional carbohydrates are available, they are likely to go into storage reserves (3), diameter growth (4), and defensive compounds (5). Trees do not produce reproductive organs annually, but once seed production is initiated it may deplete carbohydrate reserves and limit growth of other components. Under stress, allocation patterns can be expected to vary from this pattern. Redrawn from Waring and Pitman (1985).

increase more rapidly than their canopy can sustain, because as a tree grows in height the volume of living cells in conducting sapwood and associated tissues increases disproportionately to the increase in foliage. The maintenance cost of these additional living cells competes for a constant amount of photosynthate and thus 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 (Figure 4).

Because maintenance costs increase so dramatically with tree size, small saplings have a better chance of survival under a dense canopy than do larger, pole-sized individuals. Trees adapted to extreme shade often have umbrella-shaped crowns, thin leaves, little conducting tissue, very little taper in their stems from the base to the top, and greatly reduced root growth and seed production (Waring and Schlesinger 1985). New foliage is favored over other structures, and carbohydrate reserves are always low (Figure 5). Such suppressed trees have inefficient water transport and their shape makes them susceptible to damage by wind and snow. If light conditions suddenly improve, they do poorly in competition with more normally shaped trees.

Drought-induced stress

Periods of extended drought are not particularly harmful if trees have well-developed root systems and canopies that capture sufficient sunlight, so they can photosynthesize when conditions are suitable. Thus savana forests rarely die from drought (Griffin 1973). Because demands for shoot growth are immediately reduced, a slight drought that does not completely halt photosynthesis may actually increase carbohydrate reserves and the levels of defensive compounds (Bradford and Hsiao 1982, Wagner 1987). Sustained drought, however, halts photosynthesis, depletes carbohydrate reserves and defensive compounds, and eventually reduces the amount of canopy (Landsberg and Wylie 1983, Pook 1984).

Shallowly rooted trees growing in dense stands are usually susceptible to infrequent drought (Griffin 1973, Wambolt 1973). Thus, it is not surprising that in the boreal spruce forests of Norway, old, shallowly rooted trees growing with closed canopies suffered most from bark beetles following a series of drought years (Worrell 1983).

Forests subjected to chronic drought are characterized by trees with an abnormally large fraction of their carbon allocated to roots (Waring 1983). The leaves on such trees are usually smaller and thicker than those found on trees not subjected to drought. Because the canopy leaf-area is low on sites of chronic drought, wood production per unit of foliage often is comparable with that observed on sites subjected to less drought (Gholz 1982).

Stress by mechanical abrasion

Trees located on a seacoast, along gorges, or on ridges are often buffeted by high winds. Usually trees growing in such areas have asymmetrical canopies 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 Hampshire, synchronous death of trees periodically occurs (Reiners and Lang 1979, Sprugel 1976). Because the subalpine environment is harsh and the density of trees is high, wood production per unit of foliage is consistently low in forests of all ages (Marchand 1984). Marchand et al. (1986) and Foster (1987) have observed that, as the forests grow, air turbulence in the canopy increases. This situation causes rime ice accumulation and shearing of foliage during winter storms. Once canopy turbulence increases, the trees experience a substantial decline in foliage mass and prebudbreak foliage starch content. Compared with protected trees, those that are exposed show a dramatic increase in mechanical damage to roots and a two- to fivefold reduction in annual wood increment.

Stress through nutrient deficiencies or imbalance

Once a forest has developed, demand for nutrients can sometimes be greater than the supply returned to the soil by normal litterfall, root turnover, and decomposition. Sometimes a full canopy creates below it a microenvironment unfavorable for decomposition. In an extreme example, canopy closure may allow permafrost to form throughout the soil, restricting both decomposition rates and root growth (Van Cleve et al. 1981).

The symptoms of nutrient deficiency, as expressed in carbohydrate allocation, are similar to those observed for drought. This similarity is not surprising, because drought both

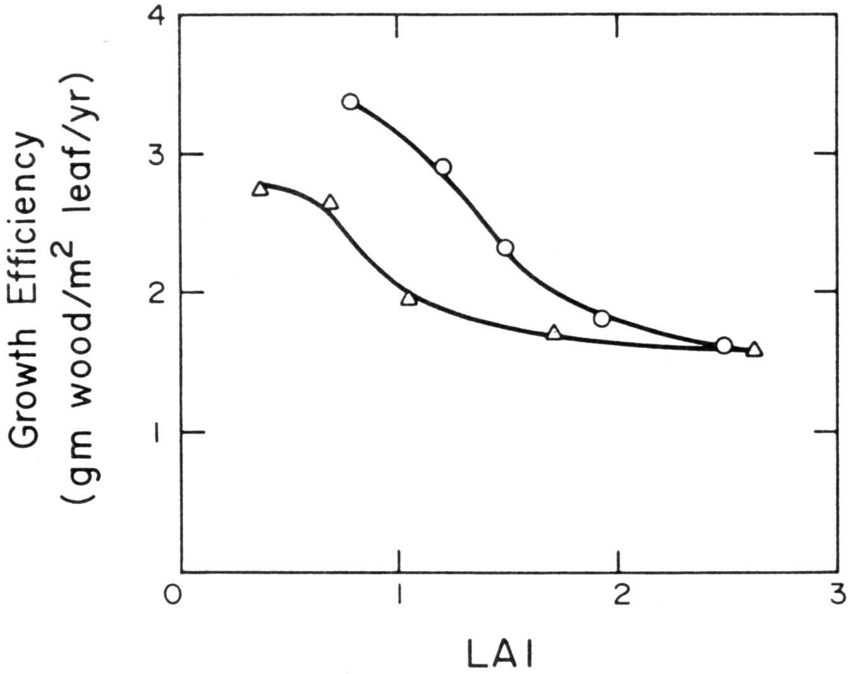

Figure 3. When shrub cover was removed (○) from beneath an arid-zone ponderosa pine forest, the growth efficiency of trees significantly increased over that observed with shrub cover present (△). However, as the total canopy leaf area (LAI) increased, efficiency of wood production decreased in both treatments, eventually reaching the same value when shading from the overstory pines excluded all ground cover. Calculated from Barrett (1970).

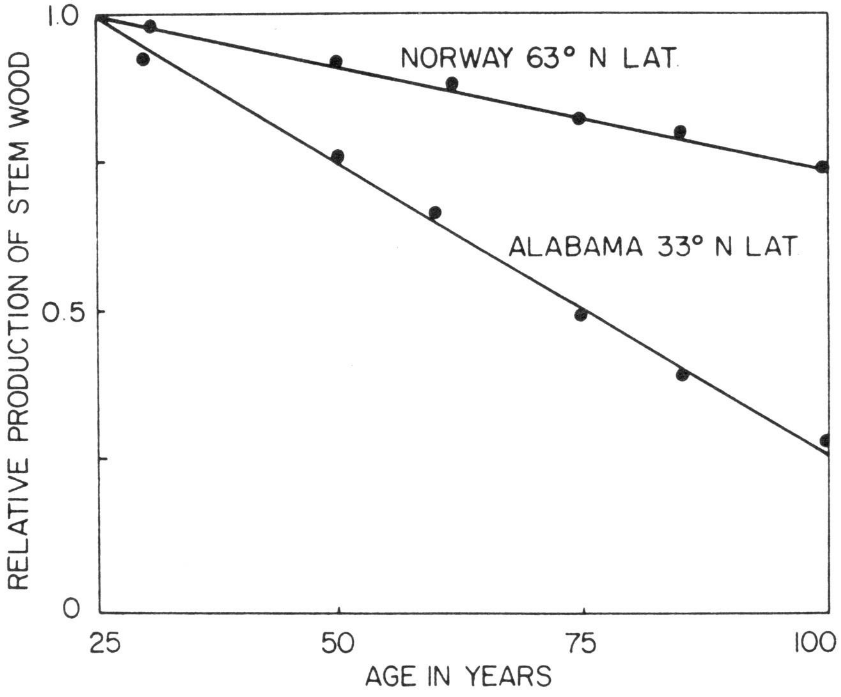

Figure 4. The rate at which stem wood production decreases as pine stands age depends on both the amount of respiring tissue in the sapwood and the temperature. In central Norway, where the annual mean temperature is approximately 5° C, production decreases by 20% over 75 years (from Waring and Schlesinger 1985). In contrast, longleaf pine growing in Alabama along the Gulf Coast, with a mean annual temperature of 18° C, decreases production by 70% over a comparable period (after Wahlenberg 1946). Site productivity is equal for these stands. At 100 years, both forests have the same estimated volume of sapwood, 170 m^3/ha.

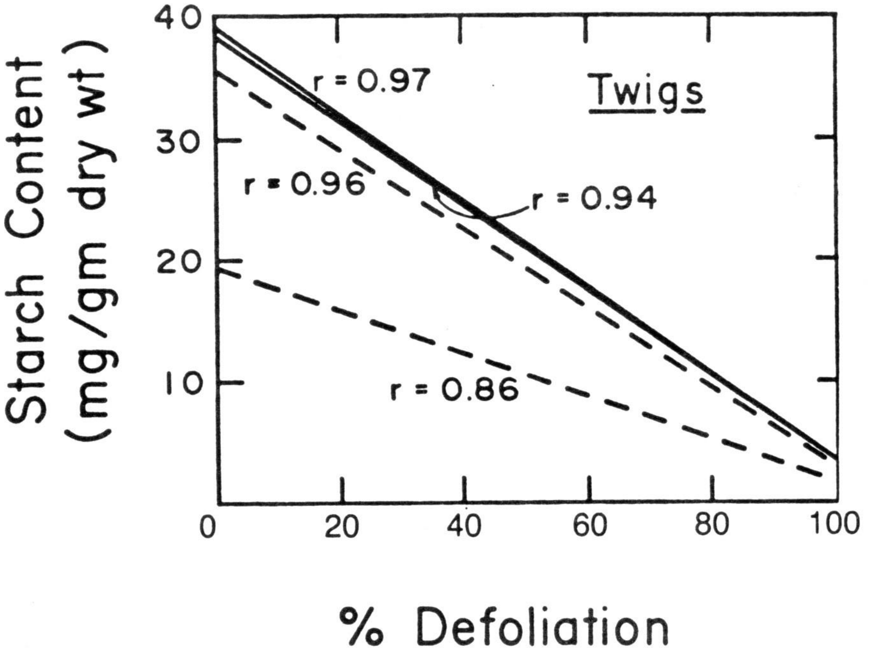

Figure 5. In a dense plantation of 70-year-old Douglas fir in New Zealand, starch concentrations in the twigs decreased linearly in relation to the amount of foliage removed by defoliating insects. The two dotted lines represent trees originally growing under the dense canopy of taller trees. The upper dotted line indicates a case where starch reserves could be increased substantially when overstory trees were removed. Solid lines indicate trees that were in a dominant position initially. Thinning the stand provided no measurable gain in starch reserves for these trees. After Cranswick (1979).

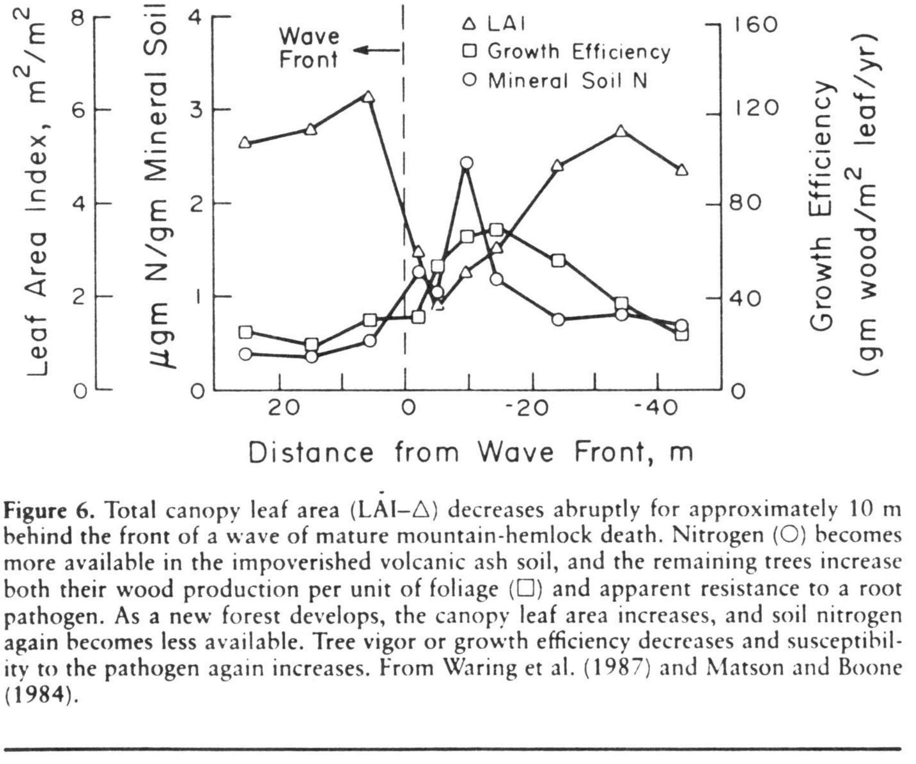

Figure 6. Total canopy leaf area (LAI–△) decreases abruptly for approximately 10 m behind the front of a wave of mature mountain-hemlock death. Nitrogen (○) becomes more available in the impoverished volcanic ash soil, and the remaining trees increase both their wood production per unit of foliage (□) and apparent resistance to a root pathogen. As a new forest develops, the canopy leaf area increases, and soil nitrogen again becomes less available. Tree vigor or growth efficiency decreases and susceptibility to the pathogen again increases. From Waring et al. (1987) and Matson and Boone (1984).

slows mineralization and forces roots to extract water from deeper soil horizons, where they obtain less nutrient. There is general agreement, at least for coniferous species, that soil nutrient deficiency leads to an increase in the proportion of carbohydrates allocated to growth of small roots (Axelsson 1981, Keyes and Grier 1981, Waring and Schlesinger 1985) and a reduction in foliage and stem growth. If the situation is chronic, tree vigor—expressed as wood growth per unit of foliage—may remain below normal, even though the canopy leaf area may be severely restricted. This situation is likely to lead to outbreaks of insects or disease.

For example, subalpine forests in the Pacific Northwest of the United States are found on nitrogen-deficient soils developed on volcanic ash deposited within the last 7000 years. These forests, dominated by mountain hemlock (*Tsuga mertensiana*), periodically die from infection of a root rot (McCauley and Cook 1980). After large trees die, younger ones become established and begin to grow without notable damage from root rot. But when the forest canopy reaches its maximum, decomposition and mineralization again slow, and wood growth per unit of foliage drops to a level associated with susceptibility to the root pathogen (Figure 6).

In controlled-environment studies, Matson and Waring (1984) demonstrated that sufficient additions of nutrients increased starch reserves, total nitrogen, and amino acids in mountain hemlock seedlings as compared with unfertilized seedlings. Susceptibility to root rot was reduced. On the other hand, fertilizing shaded seedlings caused these plants to become more susceptible to root rot. The photosynthate employed for metabolizing amino acids reduced the amount of photosynthate that might otherwise go toward defense against the pathogen (Figure 7).

An excess of some essential nutrients may cause relative deficiencies in other minerals, particularly if growth rates are increased (Ingestad 1979a,b). Entry et al. (1986) demonstrated in an experiment with western white pine seedlings (*Pinus monticola*) 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 (Zinke 1980) and in New England[1] and in conifers growing in the shade of nitrogen-

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[1] J. R. Foster, 1986. Unpublished manuscript. University of Wyoming, Laramie.

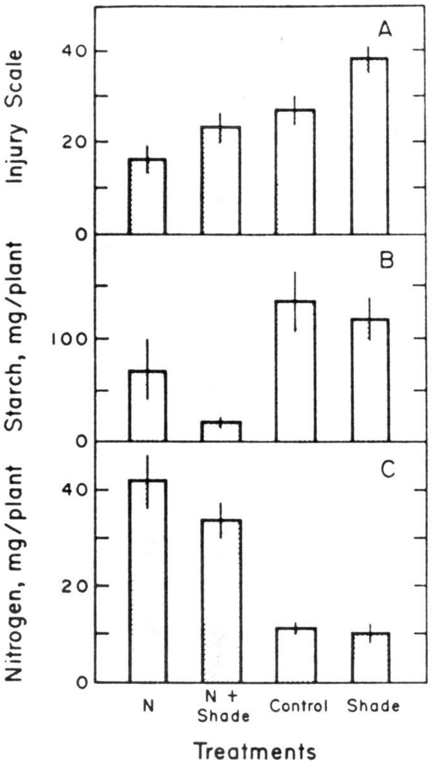

Figure 7. Mountain hemlock seedlings, maintained under controlled environments, were inoculated with a root-disease pathogen causing foliage discoloration and loss (**a**). Injury was greatest when seedlings were shaded so that photosynthesis was reduced by 40%, compared with unshaded conditions. Addition of nitrogen (N) decreased injury. The most resistant plants showed intermediate levels of carbohydrate reserves and high levels of nitrogen (**b** and **c**). After Matson and Waring (1984).

fixing deciduous trees (Waring 1985). It is not known whether these situations contribute to the forest decline associated with pathogens, but symptoms such as green-leaf fall, inverse patterns of bole growth, and reduced root production are suggestive (Schutt and Cowling 1985).

Conclusions

Trees experiencing stress exhibit a variety of responses that may help us diagnose the source and degree of stress and the probability of survival. Nearly any stress, if sustained, reduces the canopy, photosynthetic activity, and storage reserves throughout the tree. Shade, drought, mechanical abrasion, and nutrient imbalance cause distinctive alterations in how photosynthate is allocated along the bole and to the roots (Table 1). Successful attempts to ameliorate stresses should reestablish a more normal photosynthate distribution and lower the probability of death due to a variety of factors.

Table 1. Changes in carbon allocation patterns associated with various stresses (Waring and Schlesinger 1985).

Stress	Root growth	Stem taper	Foliage growth	Other
Shade	Reduced	Reduced		Umbrella-shaped crown
Drought	Increased	Increased	Reduced	Loss of older foliage
Mechanical		Increased		Asymmetrical shape of branches, bole, and large roots
Nutrient deficiency	Increased	Increased	Reduced	
Nutrient surplus	Decreased	Decreased	Increased	

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