Integrating the Role of Stressors Through Carbohydrate Dynamics

Philip M. Wargo[1]

Popular Summary

Introduction

Stress Definition

Biological stress is defined as any environmental factor (stressors) capable of inducing a potentially injurious strain in living organisms (Levitt 1972). Organisms respond to these stresses physiologically or developmentally, and depending on the duration and severity of the stress, may or may not be injured. Injury may occur directly from the stress, or indirectly when a stress reduces the capacity of organisms to resist additional or associated stresses. Injury occurs when the stress creates strain that exceeds the ability of organisms to resist the stress either by avoiding or tolerating it.

Stressor/Host/Pathogen Interactions: Decline Disease

Because trees are long-lived perennial-growing plants, they are exposed to numerous biotic and abiotic stressors (agents that cause stress) during their life time. The longevity of trees is testimony to their capacity to resist stress and their resilience to recover from injury when stressed beyond their capacity to resist. However, sometimes stress results in the premature death of a portion or all of a tree.

Decline diseases of forest trees are excellent examples of this deleterious stressor/host interaction and result in excessive and pre-mature mortality of canopy trees. Manion (1991) proposes that trees are predisposed by relatively static factors to inciting stressors that induce attack and colonization by contributing biotic factors which ultimately result in tree mortality. Houston (1992) proposed a similar but simpler model in which trees are predisposed by stressors to secondary pathogens (insects and disease organisms) that colonize and kill stress-weakened trees. The decline syndrome of dieback and progressive deterioration of the crown and eventual mortality illustrates the direct effects of stress and injury (dieback), and the indirect effects wherein the tree becomes susceptible and vulnerable to other stressors, i.e. secondary pathogens that cause additional and sometimes fatal injurious strain.

The effects of stress depend on the tree's genetic capacity (vigor) to resist the stress, the health or vitality of the tree when stressed, and the severity (e.g. % defoliation, millibars of moisture tension), duration or frequency (e.g. successive years of defoliation, length of drought), timing (when in the growing or dormant season), interacting or concert stressors (e.g. defoliation and drought, winter injury and drought), and the presence and aggressiveness of opportunistic pathogens (Wargo 1977, 1978, 1981a; Wargo and Auclair 1999).

These relationships are illustrated in Figure 1. Depending on their health or vitality class - here depicted as crown condition - trees in good, fair, or poor condition respond differently to different levels of stress (S1 < S2 < S3). The time relationship shows that trees change in health status more or less rapidly depending on the severity of the stress, and also that some trees can recover, the time of recovery dependent on initial tree health, and severity of stress. Also the figure illustrates that there is a threshold range where stress reduces the capacity of the tree to defend itself against secondary pathogenic organisms, and trees succumb to their attack and die. Interactions of health, stress level, and time are also illustrated in this threshold relationship.

Carbon Allocation

The threshold level of vulnerability of trees to attack by opportunistic secondary pathogens is a function of the abundance and aggressiveness of the secondary organism and the abundance of carbon allocated, or available to be allocated to defense in the case of organism attack, whether it be inhibitory compounds in tissues attacked by fungi or rapid growth to resist physical damage from insect infestations.

Source-sink Relationships

A simple model of carbohydrate allocation is given in Physiology of Woody Plants (Kramer and Kozlowski 1979):

income = carbohydrates manufactured by photosynthesis (source)

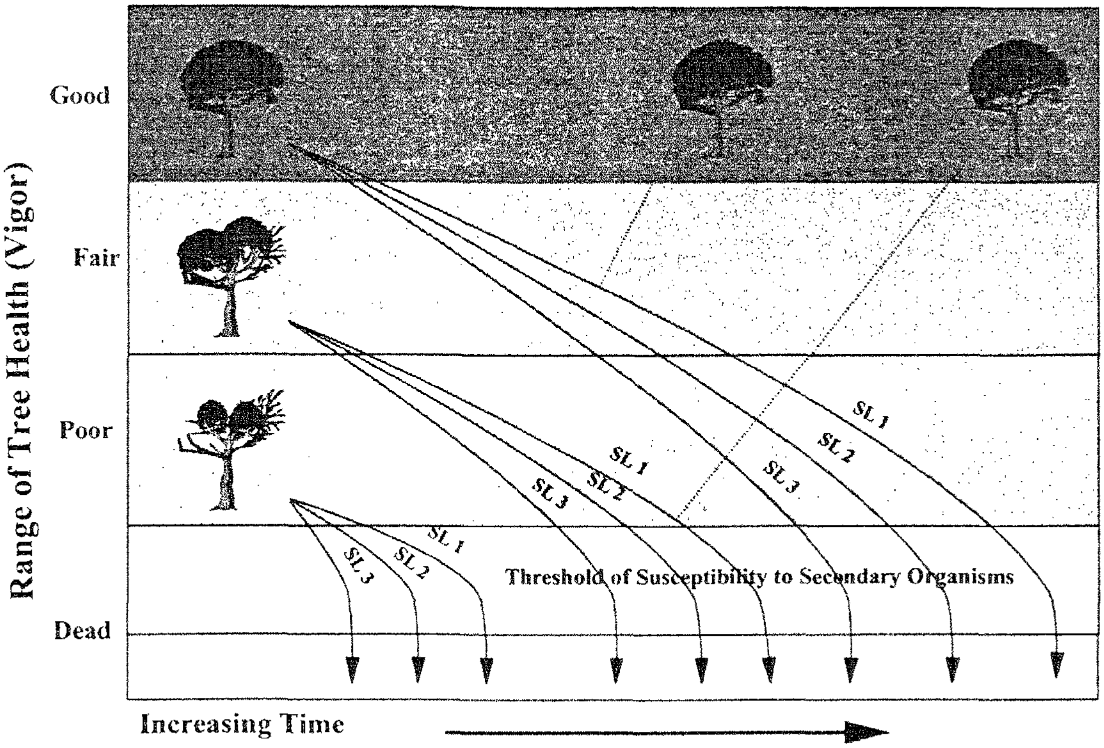
expenditures = carbohydrates used in assimilation and respiration (sinks)

balance = carbohydrates accumulated (sinks)

Although a simple model, it nicely illustrates the major uses of carbohydrates in forest trees and indicates where and how stressors can influence carbon allocation. Stressors can affect the carbon budget by directly affecting the source and reducing photosynthesis and carbohydrate production. Defoliating insects, fungi, and frost and drought can cause reductions in photosynthesis. Other stressors can affect the sinks for carbon allocation by accelerating the use of carbohydrates in assimilation or in increased respiration or both. Drought for example can result in an increase in fine root production which increases the amount of carbon needed for production and growth of the root system (Sharp and Davies 1979; Turner 1986). Reduced calcium in the

---

[1] Principal Plant Pathologist and Project Leader, Northeastern Research Station, USDA Forest Service, 51 Mill Pond Road, Hamden, CT



Interaction of Stress (SL1, SL2, SL3), Tree Condition, Secondary Organisms, and Time in the Decline and Death of Trees

Figure 1.—An illustration of the relationships and interactions of tree health, stress severity (levels S1 < S2 < S3), secondary organisms, and time in the dieback, decline, recovery, or death of trees.

foliage because of aluminum-induced calcium depletion or reduced uptake can increase dark period respiration and increase the carbohydrates used in respiration (McLaughlin et al. 1991).

Both the direct effects of stressors on photosynthesis and carbohydrate production and the increased use of carbon for assimilation and respiration can have effects on the third part of the budget, carbohydrate accumulation. Stresses such as defoliation can result in reduced carbohydrate storage by reducing the total amount of photosynthate available for storage, and by triggering the conversion of stored carbohydrate to assimilitable or respirable soluble carbohydrates during the stress period. The effects would depend on the severity, frequency, and timing of the stress event.

Stressors In Northeastern Forests

Lists of abiotic and biotic environmental factors, that can act as primary stressors in northeastern forests are found in Houston (1987), Manion (1991), and Millers et al (1989). Drought and defoliation are listed as the most common stressors, but sucking insects, such as the beech scale and hemlock woolly adelgid, and defoliation from late spring frosts or fungal pathogens are also prevalent. The most recent and widespread ice storm in the Northeast in January of 1998 has emphasized that ice injury also is a common stressor in our northeastern forests.

Stressors will continue to play a large role in forest health issues in northeastern forests partly because this region has experienced more change in climate, air chemistry, land use, site alterations and other human impacts than any other region in the United States (Wargo and Auclair, in press) and partly because more non-indigenous pests have been introduced and have become established in northeastern forests (Mattson et al. 1993; Liebhold et al. 1995). These "exotic" pests have caused significant damage (mortality) and have resulted in large changes in forest composition, structure, and function throughout the Northeast.

Measuring the Effects of Stressors

Carbohydrate Dynamics and Defoliation

Carbohydrate content, especially reserves stored as starch, has been used as a monitor or indicator of the effects of stressors on hosts, especially the effects of defoliating insects. In work on sugar maple, *Acer saccharum* Marsh. (Parker and Houston 1971; Wargo 1971, 1972; Wargo et al. 1972) starch content of the roots was an excellent indicator of tree response to defoliation. In stands of sugar maple defoliated by the saddled prominent, *Heterocampa guttivita* (Webr.) starch content of the roots not only reflected the severity of defoliation, but also the frequency (Wargo et al. 1972).

Artificial defoliation experiments on sugar maple saplings illucidated the timing and magnitude of change in carbohydrate levels in response to normal seasonal cycles and to defoliation (Wargo 1971, 1972). These studies indicated that changes caused by defoliation were far greater than those occurring because of normal seasonal change in production and use of carbohydrates. These studies also showed that the effects of defoliation depended on when in the growing season trees were defoliated. Effects depended mainly on whether the trees refoliated in response to defoliation and the length of the remaining growing season after refoliation. However, there was a strong interaction with carbohydrate status (starch) at the time of defoliation. Trees with low starch reserves were more likely to die than those with higher reserves, which in general increased as the season progressed. Starch reserves were also important to how these saplings responded to wounding. Wound areas were larger on defoliated trees and were highly and negatively correlated with starch content of the trees (Wargo 1977).

In field studies from 1972 to 1975 on mature oaks, (*Quercus alba* L., *Q. coccinea* Muench, *Q. prinus* L., *Q. rubra* L., and *Q. velutina* Lamarck) defoliated by the gypsy moth, *Lymantria dispar* L., starch content of the roots not only showed the effects of defoliation levels measured in 1972-75 but also revealed that trees had been defoliated prior to 1972 (Wargo 1981c). Although this defoliation was not severe enough to be recorded in earlier years, it still had a significant physiological consequence on the trees. Starch content in these trees was monitored after defoliation ceased and had not recovered to predefoliation levels even after two years of no or very low defoliation (Wargo 1981c).

Starch content in roots of oaks also indicated their vulnerability to mortality associated with defoliation (Wargo 1981c). Trees in the red or white oak groups were assigned a risk of mortality based on root starch content and then monitored for two years after a single heavy defoliation. Mortality was consistently higher in the low starch-high risk trees in both oak groups. Starch was a better indicator of risk of mortality than crown condition.

This relationship of low starch to high risk of mortality was demonstrated experimentally (Wargo 1981b). In these studies, starch content in maple and oak saplings at the time of defoliation determined their response to defoliation. Trees with lower initial starch contents died first after 1 or 2 years of defoliation, while trees with higher initial contents after 3 years of defoliation died later, and trees with still higher starch levels survived the ordeal entirely.

Starch and soluble carbohydrate status in the root system has also been related to crown dieback, rate of crown deterioration and growth loss, in declining mature sugar maple in Canada (Renaud and Muaffette 1991).

Consequences of Altered Carbohydrate Dynamics

Corresponding to decreases in starch content as a result of stress, are substantial increases in reducing sugars, especially in the root system. These increases can be four to five times higher than in unstressed trees at the same time of year and also than the normal seasonal high that occurs in spring when carbohydrates are mobilized for growth (Wargo 1971, 1972). Coupled with changes in nitrogen metabolism, these carbohydrate levels are important to opportunistic organisms, particularly species of *Armillaria.*which can attack and kill stressed trees (Wargo and Houston 1974). Reducing sugars, especially glucose, not only stimulates the growth of this fungus, but also enables it to grow in the presence of inhibitory phenols such as gallic acid (Wargo 1972, 1980, 1981d).

Winter starch reserves in roots of white oak were related to susceptibility and vulnerability to attack by the twolined chestnut borer, *Agrilus bilineatus* (Weber) (Dunn et al. 1987). White oaks with low starch reserves attracted more beetles than moderate or high starch trees. And only trees that had extremely low root starch were heavily attacked by the beetle and subsequently died.

Even susceptibility to aggressive primary pathogens have relationships with carbohydrate dynamics. Time of highest susceptibility of American elm, Ulmus americana L. to colonization by Ophiostoma ulmi (Ceratocystis), the Dutch elm disease fungus, is during leaf expansion when starch reserves in the growth rings were lowest (Shigo et al. 1986). In addition, infected trees stored less starch than healthy trees making them even more vulnerable to death after additional infections.

Carbohydrate Status in Declining Sugar Maple - Allegheny Plateau

Carbohydrate status of healthy and declining sugar maple on the Allegheny Plateau in northcentral Pennsylvania were assessed in a series of lime fertilizaiton treatment plots established in 1985 (Auchmoody 1985, Long et al. 1997). Samples were collected in autumn 1997 after leaf drop. Second order woody roots were collected from each of three sugar maples trees within each treatment plot within each block. Approximately 45 cm of root 1 to 2.5 cm in diameter was collected for a series of carbohydrate and phenol analyses. Roots were frozen on dry ice in the field and placed in freezers upon return to the laboratory. A small portion (2 to 3 cm long) was cut from a section of harvested root and used for a visual determination of starch content in the roots of each tree (Wargo 1975, 1978).

Root pieces were thawed quickly in tap water, washed, and trimmed for sectioning and staining as described by Wargo (1975). Root sections were then rated for starch content as very high, high, moderate, low or none based on the density

Table 1.—Visual ratings for starch content in roots of sugar maple trees in a series of lime-treated plots on the Susquehannock State Forest on the Allegheny Plateau in northcentral Pennsylvania

	Blocks[a]				
Treatments[b]	BD1	BD2	CS3	CS4	Average
Control	3.0	3.3	2.7	3.3	3.1
Control Fence	4.7	4.3	4.0	4.3	4.3
Herbicide	2.7	4.3	3.3	3.7	3.5
Herbicide Fence	3.3	4.0	4.7	3.7	3.9
	3.4	4.0	3.7	3.7	3.7
Limed	4.0	4.3	4.7	4.7	4.4
Limed Fence	4.0	4.7	5.0	3.7	4.3
Limed Herbicide	4.3	4.0	4.7	4.7	4.4
Lime Herbicide Fence	3.7	4.0	5.0	4.0	4.2
	4.0	4.2	4.8	4.3	4.3

[a] Blocks were located in 2 sections of the Susquehannock State Forest, Pennsylvania, Black Diamond Road (BD and BD2) and Cherry Springs (CS3 and CS4).

[b] Treatments were arranged in a split-plot design with deer fencing (fence, no fence) as the whole-plot treatment and four sub-plots treatments (herbicide, dolomitic lime, herbicide + dolomitic lime, and no herbicide or lime) within each whole plot (Auchmoody 1985, Long et al. 1997).

[c] Starch rating scale: 1=none, 2=low, 3=moderate, 4=high, 5=very high.

Table 2.—Starch ratings and vigor class of sugar maple trees in the lime treated series of plots in northcentral Pennsylvania

	Vigor of living trees[1]				
Starch ratings	1	2	3	4	Total
Very high	20	2	10	5	37
High	17	3	7	4	31
Moderate	8	0	8	4	20
Low	1	0	0	7	8
None	0	0	0	0	0
Total	46	5	25	20	96

[1] Mader-Thompson System (Mader and Thompson 1969)

of purple-black staining in the ray and xylem parenchyma. A descending numerical value of 5 for very high to 1 for none was assigned each rating and an average for each treatment was determined.

Preliminary results indicated that on average all limed treated plots had high starch contents (Table 1). Lowest starch levels were in untreated control plots. Cherry trees were sampled in only the fenced portion of block CS4. Three trees were sampled per plot. All cherry trees were rated very high or high. The average starch content for cherry was 5.0 for control plot, 4.3 for the herbicide plot, 4.3 for the limed plot and 4.7 for the limed herbicide plot.

Most trees rated as low in starch were in vigor class 4 or greater (vigor 1=healthy, 2=light decline, 3=moderate declin 4=severe decline, 5=dead; Mader and Thompson 1969); however not all poor vigor trees had low starch contents (Table 2). Seven of the 8 low starch trees were from unlimec plots and all were in class 4 vigor.

Conclusions

Carbohydrate status, especially storage carbohydrates primarily starch, integrates the effects of stress on trees vitality and largely determine their ultimate response to stress. Energy reserves are necessary for mobilization to support respiration and assimilation prior to new leaf production at the beginning of the growing season. They are also necessary to support these processes during times of stress. Inadequate carbohydrate reserves predisposes trees to injury from the stress itself but also and especially from opportunistic organisms that are ubiquitous in the environment and depend on stress weakened trees as energy sources.

Literature Cited

Auchmoody, L.R. 1985. **Effects of lime, fencing, and herbicide on establishment and growth of regeneration of problem sites.** Study Plan 4110-FS-NE-1152-141. USDA Forest Service, Northeastern For. Exp. Stn., Warren, PA.

Dunn, J.P.; Kimmerer, T.W.; Potter, D.A. 1987. **Winter starch reserves of white oak as a predictor of attack by the twolined chestnut borer, *Agrilus bilineatus* (Weber) (Coleoptera: Buprestidae).** Oecologia 74:352-355.

Houston, D.R. 1987. **Forest tree declines of past and present: current understanding.** Can. J. Plant Path.: 349-360.

Houston, D.R. 1992. **A host-stress-saprogen model for forest dieback-decline diseases.** In: Forest decline concepts. Manion, PD, Lachance D (eds). APS Press, St. Paul, MN. p 3-25.

Kramer, P.J.; Kozlowski, T.T. 1979. **Physiology of woody plants.** Academic Press, Inc.

Levitt, J. 1972. **Responses of plants to environmental stresses.** Academic Press Inc., N.Y.

Liebhold, A.M.; MacDonald, W.L.; Bergdahl, D.; Mastro,V.C. 1995. **Invasion by exotic forest pests: a threat to forest ecosystems.** For. Sci. Monograph 30. Supplement to For. Sci. 41(2).

Long, R.P.; Horsley, S.B.; Lilja, P.R. 1997. **Impact of forest liming on growth and crown vigor of sugar maple and associated hardwoods.** Can. J. For. Res. 27:1560-1573.

Manion, P.D. 1991. **Tree disease concepts.** 2nd ed. Prentice Hall Inc., Englewood Cliffs, NJ. 409 p.

Mattson, W.J.; Niemela, P.; Millers, I.; Inguanzo, Y. 1995. **Immigrant phytophagous insects on woody plants in the United States and Canada: an annotated list.** USDA For. Serv. Gen. Tech. Rep. NC-167.

McLaughlin, S.G.; Andersen, C.P.; Hanson, P.J.; Tjoelker, M.G.; Roy, W.K. 1991. **Increased dark respiration and calcium deficiency of red spruce in relation to acidic deposition at high elevation southern Appalachian Mountain sites.** Can. J. For. Res. 21:1234-1244.

Millers, I.; Shriner, D.S.; Rizzo, D. 1989. **History of hardwood decline in the eastern United States.** USDA For. Serv., Tech. Rep. NE-126. 75 p.

Parker, J.; Houston, D.R. 1971. **Effects of repeated defoliation on root and root collar extractives of sugar maple trees.** For. Sci. 17:91-95.

Renaud, J.-P.; Mauffette, Y. 1991. **The relationships of crown dieback with carbohydrate content and growth of sugar maple (*Acer saccharum*).** Can. J. For. Res. 21:1111-1118.

Sharp, R.E.; Davies, W.L. 1979. **Solute regulation and growth by roots and shoots of water-stressed maize plants.** Planta 147:43-49.

Shigo, A.L.; Gregory, G.F.; Campana, R.J.; Dudzik, K.R.; Zimel, D.M. 1986. **Patterns of starch reserves in healthy and diseased American elms.** Can. J. For. Res. 16:204-210.

Turner, N.C. 1986. **Adaptation to water deficits: A changing perspective.** Aust. J. Plant Physiol. 13:175-190.

Wargo, P.M. 1971. **Seasonal changes in carbohydrate levels in roots of sugar maple.** USDA Forest Service Res. Pap. NE-213.

Wargo, P.M. 1972. **Defoliation-induced chemical changes in sugar maple roots stimulate growth of *Armillaria mellea*.** Phytopath. 62:1278-1283.

Wargo, P.M. 1977. ***Armillariella mellea* and *Agrilus bilineatus* and mortality of defoliated oak trees.** For. Sci. 23:485-492.

Wargo, P.M. 1977. **Wound closure in sugar maple: adverse effects of defoliation.** Can. J. For. Res. 7:410-414.

Wargo, P.M. 1978. **Defoliation by the gypsy moth—how it hurts your tree.** U.S. Dep. Agric. Home Garden Bull. 223. 15 p.

Wargo, P.M. 1980. **Interaction of ethanol, glucose, phenolics and isolate of *Armillaria mellea*.** (Abstr.) Phytopath. 70:470.

Wargo, P.M. 1981a. **Defoliation and secondary-action organism attack: with emphasis on *Armillaria mellea*.** J. Arbor. 7:64-69.

Wargo, P.M. 1981b. **Defoliation, dieback and mortality.** In: The gypsy moth: research toward integrated pest management. Doane, C.C., McManus M.L. (eds). Tech. Bull. 1584, Washington, DC: US Dept. of Agric., Animal and Plant Health Inspection Service. p 240-248.

Wargo, P.M. 1981c. **Measuring response of trees to defoliation stress.** In: The gypsy moth: research toward integrated pest management. Doane, C.C., McManus M.L. (eds). Tech. Bull. 1584, Washington, DC: US Dept. of Agric., Animal and Plant Health Inspection Service. p 248-267.

Wargo, P.M. 1981d. ***In vitro* response to gallic acid of aggressive and non-aggressive "isolates" of *Armillaria mellea.*** (Abstr.) Phytopath. 71:565.

Wargo, P.M.; Auclair, A.N.D. in press. **Forest declines in response to environmental change in the northeastern United States.**

Wargo, P.M.; Houston, D.R. 1974. **Infection of defoliated sugar maple trees by *Armillaria mellea.*** Phytopath. 64:817-822.

Wargo, P.M.; Parker, J.; Houston, D.R. 1972. **Starch content in roots of defoliated sugar maple.** For. Sci. 18:203-204.

* * *