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The answer to “Why do trees die?” follows a reverse chronological sequence. Trees die because **respiration** terminates. Respiration terminates because **carbohydrate production** ceases and stored carbohydrates are depleted. Carbohydrate production ceases because **photosynthesis** discontinues. Photosynthesis discontinues because the **factors** necessary for photosynthesis are interrupted or obstructed. Those factors include: sunlight, water, nutrients, temperature, CO<sub>2</sub> and O<sub>2</sub>. Factors for photosynthesis are interrupted because of human activities or environmental changes. Many are summarized here.

To understand why or how trees die, we must first understand the processes by which they live. Broadly, these processes can be categorized under **physiology**, which is the branch of science dealing with the functions of living organisms and their parts. Major physiological processes in trees include photosynthesis, respiration and translocation.

The process of **photosynthesis** combines carbon dioxide with water in the presence of the sun’s energy to produce simple sugars (known as carbohydrates) and oxygen. This chemical reaction for photosynthesis occurs in leaves and can be written as:



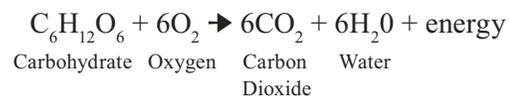
Photosynthesis is the most essential and basic physiological process, inasmuch as tree growth is dependent upon successful conversion of the sun’s energy into carbohydrates. Kramer and Kozlowski (1960) make the following observations about carbohydrates:

- they are the substances by which all other organic compounds are synthesized,

- they are the chief building blocks of cell walls,
- they form the starting point for synthesis of fats and proteins,
- they are oxidized in respiration, and
- any amount still remaining after all these processes accumulates as stored food reserves.

Carbohydrates are transported from the leaves to the stem and roots via phloem cells for use in respiration and other physiological processes, including growth. Excess carbohydrates not used in growth and respiration are stored in roots, buds, stems and cambium.

**Respiration** is the oxidization of carbohydrates to provide energy to keep cells alive and to fuel growth. Respiration essentially works in reverse order of photosynthesis, whereby the synthesized carbohydrates react with oxygen to produce carbon dioxide, water and energy; e.g., food is oxidized and energy is released. The chemical reaction for respiration can be written as:



Unlike photosynthesis, which is seasonal in most climates, at least some respiration occurs at all times (even during the dormant season). This is why the production of carbohydrates through photosynthesis must exceed the oxidation of carbohydrates through respiration. Without a surplus of carbohydrates, tree vigor declines and eventually death occurs. As trees age, the demand for carbohydrates increases, because the volume of respiring tissue increases while the amount of leaf surface area (photosynthesizing surface) remains fairly constant. Less carbohydrate is made available for

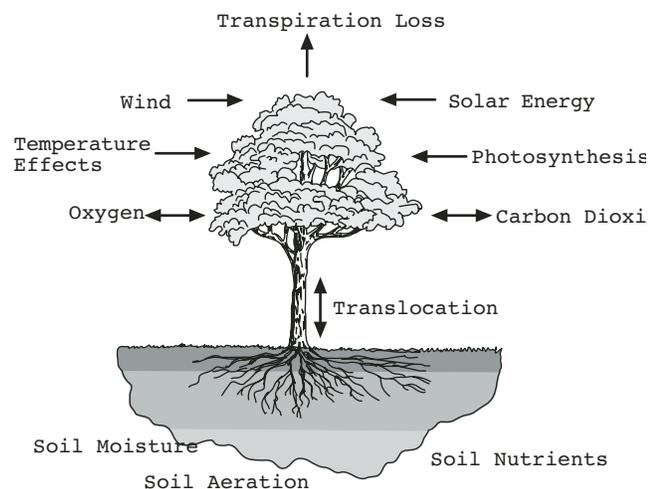
root and stem elongation because more is demanded for life-sustaining respiration. Perhaps this is why younger trees, having a higher ratio of photosynthetic surface to respiring tissue, grow more rapidly than older, decadent trees (Kramer and Kozlowski 1960).

**Translocation**, the third major physiological process, allows photosynthesis and respiration to function properly. Without the “piping” system of translocation, moisture and nutrients would not reach the leaves, leaves would not produce carbohydrates, carbohydrates would not be transported to organs and respiration would cease.

Through translocation, trees allocate carbohydrates to support five different physiological processes. Oliver and Larson (1996) identify these processes, placed in priority order for allocation of carbohydrates, as:

- Maintenance of living tissue (respiration),
- Production of fine roots,
- Flower and seed production,
- Primary growth (elongation of branches and roots), and
- Secondary/diameter growth (growth of xylem – the water-conducting cells).

When a tree is healthy and rapidly growing, each of these five processes is fueled by ample supplies of carbohydrates. Because secondary growth is the last to receive carbohydrates, wide annual growth rings of the lower trunk indicate that the needs of the other four processes are first being met and that excesses are being used for diameter growth. At such point, life for a tree is *plush*. If, however, annual growth rings



Factors affecting physiological processes in plants.

(secondary growth) begin to show a narrowing, this is a first indication that tree vigor is declining and that subsequent reductions in primary growth could also soon occur. As decline continues, carbohydrate allocations are gradually pulled up the physiological processes ladder. For instance, if a tree must allocate carbohydrates to either branch and root expansion, or seed and flower production, it will choose the latter; likewise, production of fine roots comes before seeds and flowers; lastly, respiration is a higher priority than fine root production. This reversal or *recall* of carbohydrates continues until there are essentially none left, at which point mortality occurs.

Tree mortality is not always a gradual, energy-consuming process. In *A New Tree Biology*, Shigo (1990) indicates that tree mortality can also occur rapidly through mechanical disruption. Examples include:

- severing cambium – disrupts translocation;
- compacting soil – reduces availability of water and nutrients, resulting in poor aeration (oxygen content) in the soil needed for root respiration;
- damage to or loss of larger limbs – reduces photosynthesis and carbohydrate production; if respiration rate does not decline proportionately, mortality results.

A tree growing in a suitable climate and on suitable soils will continue increasing in size until one or more factors for growth are no longer available (Oliver and Larson, 1996). More often than not, environmental factors work concurrently or sequentially to weaken trees, predisposing them to other insect, mite and disease agents, in turn leading to mortality. Wenger (1984) suggests a number of environmental factors that affect tree physiological processes. They are listed in Table 1, along with an interpretation of how each factor might affect the processes.

So why do trees die? Their death follows a reverse chronological sequence. Trees die because **respiration** terminates. Respiration terminates because **carbohydrate production** ceases and stored carbohydrates are exhausted. Carbohydrate production ceases because **photosynthesis** discontinues. Photosynthesis discontinues because the **factors** necessary for photosynthesis are interrupted or obstructed. Factors for photosynthesis are interrupted because of human activities or environmental changes.

**Table 1. Environmental factors and human activities that influence tree physiological processes.**

Factor	Subfactor	Effect on Physiological Process
1. Low site quality	a. Excessive drainage	Prohibits absorption of sufficient moisture necessary for production and distribution of carbohydrates
	b. Poor drainage	Creates a wet anaerobic condition, i.e., O <sub>2</sub> is not available for root respiration
	c. Thin or compacted soil	Challenges root penetration; both nutrients and moisture become difficult to absorb; reduces photosynthetic rate
	d. Excessive sun exposure	Transpiration increases, causing stomates (leaf pores) to close; reduces carbohydrate production while respiration continues
	e. Nutrient deficiencies	Decreases chlorophyll formation necessary for photosynthesis; sufficient carbohydrates are not produced to sustain respiration
	f. Abnormal soil pH	Affects absorption of nutrients, which in turn has the same effect as nutrient deficiency
2. Species planted off-site		Makes species less capable of performing normal physiological processes. Ex. – Trees adapted to wet conditions do not do well on dry ridges <i>or</i> trees adapted to dry conditions are outgrown on floodplain sites
3. Changes in habitat		a.k.a. disturbances alter wind, sunlight, temperature and water table conditions, all affecting photosynthesis, respiration and transpiration rates. Ex. – lightning or wind breakage removing too much of crown, new structures such as buildings and pavement alter the environment
4. Competition from adjacent vegetation		Reduction of resource allocation. Available carbohydrates are redistributed from secondary growth to more essential needs because of reduced photosynthesis; water translocation becomes inadequate and predisposes trees to insect attacks.
5. Weather influences	a. Prolonged drought	see excessive drainage
	b. Excessive rains	see poor drainage
	c. Sunscald	see excessive sun exposure
	d. Winter injury	Dries or damages foliage and twigs, causing carbohydrate demands to focus on restoration rather than growth
6. Human activities	a. Soil compaction	Creates drought-like conditions; reduces carbohydrate production; exposes and damages roots, leading to fungal entry blocking translocation; reduces nutrient absorption, lowering photosynthesis rate
	b. Air pollution	Inhibits proper balance of CO <sub>2</sub> , reducing photosynthesis
	c. Salt leaching along roadsides	Draws water away from roots so less is available for replacement upon transpiration; foliage desiccates and dies; photosynthesis ceases
	d. Improper herbicide use	Clogs leaf stomates and interferes with inward diffusion of CO <sub>2</sub> ; transpiration is reduced, causing temperature increases in leaves; photosynthesis becomes uneven

## References

Kramer, Paul J. and Theodore T. Kozlowski. 1960. Physiology of Trees. McGraw-Hill Book Company. New York.

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Shigo, Alex L. 1990. A New Tree Biology. Shigo and Trees Associates. Durham, New Hampshire.

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Gradual decline from the top of a mature red oak tree.



Paving completely around this ash tree has completely altered the tree's rooting environment and will influence the health of the tree.



Decline of sweetgum. The tree has grown larger than the limited rooting environment can support. The result is dying back from the top.

Photos by Wayne Clatterbuck

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