



-Forest Environment- **Tree Physiology**

Adapted from the on-line Teachers Guide
<http://mff.dsisd.net>

MICHIGAN STATE
UNIVERSITY
EXTENSION

TREE PHYSIOLOGY

Quite a bit of time is spent on tree physiology, which is key to understanding many of our forest management practices, especially the concepts of shade tolerance and vegetation succession. Additionally, the topics of forest health, hydrologic cycle, and nutrient cycles are discussed.

This is a fairly long section for several reasons. One, it provides the basis for much of what is addressed later in terms of forest management. Two, it has many connections to the Michigan Curriculum standards, particularly in science. Three, there are a lot of neat activities and observations associated with the topic.

Concept List:

The Necessities of Life
Tree Parts
Photosynthesis and
Respiration
Chlorophyll
Tree Growth
Fall Color Change
Sunlight
Environmental Factors
Tree Regeneration
Strategies
Longevity
Winter Adaptations

Little Known or Interesting Factoids About Tree Physiology

- *Trees both produce AND consume oxygen.*
- *Young forests capture more carbon from the atmosphere than old forests.*
- *Old forests have more stored carbon in the biomass than young forests.*
- *The food that trees produce for themselves are sugars.*
- *The purpose of photosynthesis is to capture and store energy.*
- *Green light is the only part of the visible light spectrum that plants can't use.*
- *The timing of Autumn color change is largely controlled by lengthening nights.*
- *Conifers lose needles each fall, just the same as broad-leaf trees.*
- *Trees grow TWO rings each year, one in the spring and another during the summer.*
- *Swamp trees don't necessarily prefer swamps.*
- *Tree species have highly variable requirements for light, nutrients, and moisture.*
- *Oceans produce more oxygen and store more carbon than forests.*

Some Important Terms

- | | | |
|------------------|---------------------|------------------------|
| • Photosynthesis | • Carotenoid | • Producer |
| • Respiration | • Abscission Layer | • Consumer |
| • Oxygen | • Cambium | • Glucose |
| • Carbon Dioxide | • Meristem | • Shade Tolerance |
| • Trophic Level | • Annual Rings | • Crown |
| • Food Chain | • Spring/Summerwood | • Canopy |
| • Chlorophyll | • Cellulose | • Compartmentalization |
| • Anthocyanin | • Mycorrhizae | |

The Necessities of Life

The following is brief discussion of each of six key requirements for trees. More detail of some topics is found later in this guide.

1. **Sugars** supplied by photosynthesis. Air and water are chemically recombined to form glucose, which stores energy captured from the sun. Oxygen is a byproduct.

2. **Water** is required for most metabolic activities and serves as a vehicle to carry materials through a tree. A large tree may move as much as 50-100 gallons of water on a hot summer day.

3. **Nutrients.** It's not how much of a particular nutrient exists in the environment, it's a matter of how *available* the nutrient is to the tree. For example, the atmosphere is largely composed on nitrogen, but trees can only use nitrogen in forms that have been altered by soil bacteria and other organisms. The major chemical elements used by plants are: carbon, hydrogen, oxygen, phosphorus, potassium, nitrogen, sulfur, calcium, iron, and magnesium. You might be able to remember this by a jingle formed using the abbreviations for these elements: C H O P K N S Ca Fe Mg . . . "see hopkins café, might good."

4. **Hormones and enzymes.** These chemicals are critical in the controlling the timing and activity of physiological processes. They are usually produced in the roots or leaves. We don't often think of plants having "hormone" deficiencies, but they are critical to the survival of any organism, including trees.

5. **Mycorrhizae.** Pronounced "*my-core-HI-zee*", this a group of beneficial fungi associated with most tree roots. It represents an ecologically symbiotic relationship where the fungi receive food from the tree and the trees receive greatly enhanced nutrient and water absorption. Mycorrhizae will also protect tree roots from other invading fungi. There tends to be very specific species relationships between fungus and tree.

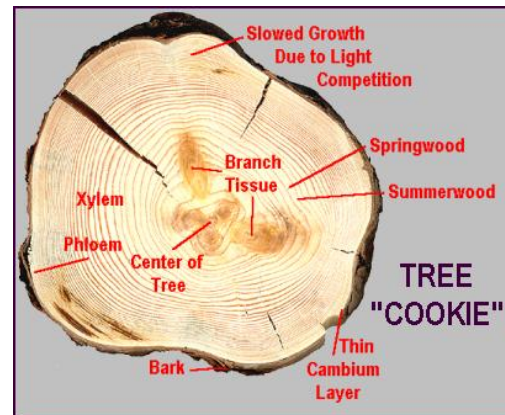
6. **Environmental factors.** A tree needs an appropriate mix of precipitation, temperature, sunlight, and soils in order to thrive. These factors need to occur at the right time. Each tree species has a different set of environmental requirements. Changing climate will lead to changing environmental factors, which can lead to changes in forest ecosystems.

Tree Parts

The parts and structure of a tree has obvious components and some not so obvious components.

What makes a tree a tree?

First, a tree has all the characteristics of green plants. Beyond that, a tree is a tall plant with woody tissue. It has the capability to "push" its crown (the primary location for photosynthesis) above other vegetation competing for light. Also, most people don't readily connect trees with having **flowers** but they do, although our conifers (pines, spruces, firs, etc.) don't have true flowers with petals. The reproductive structures of each species are particularly unique and are used more than any other structure to categorize trees. This categorization is called **taxonomy**. The tree identification chapter talks more about taxonomy.



Definition of a tree: A woody perennial plant, typically large and with a well-defined stem or stems carrying a more or less definite crown - **note**, sometimes defined as attaining a minimum diameter of 5 inches and minimum height of 15 feet at maturity with no branches within 3 feet of the ground.

-Society of American Foresters, 1998

A tree has a dilemma in terms of gathering its resources. It has a distinct light-gathering advantage of having its leaves high above other plants, but there is the problem of getting water and soil nutrients to the upper tissues. The microenvironment in the upper canopy is also rather hostile to sensitive tissues. At the other end of the tree, the roots are dependent upon materials produced way up in the crown. This problem, of course, is solved by the structure of the tree **trunk, or bole**, a most distinctive feature of trees.

Most of a tree trunk is dead woody tissue and serves only to support the weight of the crown. The very outside layers of the tree consists of bark. Underneath the bark is a **cork cambium** layer that generates new bark. Under the cork cambium lies a thin band of **phloem**, which is living tissue that transports materials from the crown to the roots. Under the phloem is another **vascular cambium zone** that produces both new phloem cells and new xylem cells. The wider band of **xylem**, or **sapwood**, transports water to the crown, but is not necessarily living. The innermost portion of the trunk is non-living **heartwood**, which is a repository for many waste products of the tree's living tissue. Only a thin band around the trunk, roughly a centimeter wide, is living tissue.

Each year, a tree grows a pair of **annual rings** (TWO rings each year!). In the spring, the usually wider and thinner-walled layer grows. It is called "**springwood**". In the summer, through about mid-July, a usually darker and thicker-walled layer is produced. It is called "**summerwood**". Annual rings are typical in temperate forest trees and tropical forest trees that have regular, annual dry seasons. In tropical humid rainforests, trees grow continually and do not have rings. The oldest portion of a tree is at the bottom and on the inside.

Parts List

Without going into a lot detail, important parts of a tree are:

Leaves	Broad-leaf or needles, the primary site of photosynthesis and the production of hormones and other chemicals
Twigs & Branches	Support structure for leaves, flowers, and fruits. Arrangement varies from species to species by growth strategy. Can sometimes have photosynthetic tissues. Two kinds of growth tissue, at the twig tips and cambium under the bark.
Crown	The upper region of the tree made up of leaves, twigs, branches, flowers, and fruits. Crowns of many trees are collectively called the "canopy".
Flowers	May have both female & male parts, or only one or the other. Some trees are either all female or all male (i.e. aspen). Flowers may have a full complement of flower parts, or may be missing certain elements. Conifers do not have petals and associated structures.
Fruits & Seeds	All trees have seeds. Most trees have seeds inside fruits. Most fruits are NOT edible, but many are, such as apples, cherries, nuts, etc.
Trunk or Bole	Most definitions of trees include a "single bole" concept, but many of our tree species sometimes occur with multiple stems. The main functions of a trunk are transport and support. The trunk has growth tissue called cambium.
Bark	A highly variable tree part. The main function is to protect the sensitive living tissues from weather and predation (by animals, insects, fungi, etc.)
Roots	Roots serve two main functions; collection of nutrients and water, and anchoring the tree. Roots also have growth tissue, bark, and wood. Like twigs and branches, roots have two kinds of growth tissue, at the root tips and cambium under the bark. Fine root hairs are where absorption occurs.

Photosynthesis and Respiration

All trees (most plants) both photosynthesize and respire. Photosynthesis is a process unique to green plants and produces sugars, which are "tree food." Animals only respire

and cannot produce their own food. That's why plants are called "**producers**" and animals are called "**consumers**."

Photosynthesis can be visualized in a couple ways.

- Sugars produced are analogous to a "solar battery." The sugar is a chemical way to store energy for future use (metabolism).
- Trees produce their own food. We call "tree food" sugar. These sugars are not usually of the chemical structure of refined sugar and don't usually taste sweet, but the basic organic components are similar.

The basic chemical formula for photosynthesis is:

Inputs: 6 carbons, 24 oxygens, 24 hydrogens

Outputs: 6 carbons, 24 oxygens, 24 hydrogens

Note: Inputs and outputs must balance in a chemical equation. In other words, what goes in, must come out!

Energy IN



Summary equation for photosynthesis

Energy is stored in the bonds of sugar molecules such as "**glucose**" and "**fructose**." Oxygen is a by-product of photosynthesis. The oxygen molecules produced by photosynthesis are not necessarily the same oxygen molecules the plants use for respiration.



Energy OUT



Summary equation for photosynthesis

These sugars are later broken apart and the released energy drives a variety of metabolic actions. The process of breaking down these sugars is called "**respiration**." It is the same process that animals (and people) use when they respire (not to be confused with "breathing"). So, either the plant uses its own store sugars, or some animal (or decomposer) consumes the plant, and uses the stored sugars. In either

case, the sugars are valued chemicals because they contain energy, as well as important elements (carbon, hydrogen, and oxygen).

Apply the Concept: *Crown size and photosynthesis*

*All the leaves and branches of a tree are collectively called the "**crown**." All the crowns of a forest are collectively called the "**canopy**." As forests age and trees grow, crowns begin to touch each other and the forest canopy closes. Most of the tree crowns will be unable to grow as rapidly as if they had free space to occupy. The photosynthetic capacity will be spread among a greater number of trees. That means less photosynthesis per tree, which translates into slower growth. Slow growth can be a contributor to tree stress, which can lead to tree health problems. Foresters understand how different forests grow in different ways. They can recognize a forest that is too crowded and prescribe a thinning, where some trees are removed so that others may grow better.*

In addition to channeling more growth onto a fewer number of trees, thinning the canopy can have a very positive impact on the understory. More light to the forest floor will stimulate the regeneration of trees and promote more vegetation in the understory layers of a forest. More vegetation in the understory creates more vertical structure, which often leads to greater species diversity in the forest.

Apply the Concept: *The "10% rule of thumb."*

*Plants are able to "fix" about 10% of the solar energy that reaches plant surfaces (usually less, however). "Fixing" means converting solar energy into chemical energy (sugars). Organisms that consume plants, are able to extract about 10% of the energy stored in the plant. Organisms that consume other consumers can extract only about 10% of the energy stored in their prey. These levels of energy consumption are called "**trophic levels**." Energy flow through an ecosystem (large or small) is a key life process. Threads of energy transfer are called "**food chains**." Food chains also include the transfer of chemicals other than sugar. Many nutrients, amino acids, and other compounds are digested and recombined by consumers along any particular food chain.*

What does a tree use its photosynthate for (glucose and fructose) in addition to energy storage and subsequent release?

- Cell walls are made of **cellulose** ($C_6H_{10}O_5$). Cellulose shows up in many plant parts in combination with other molecular elements. It is not only vital to the tree, but is also a very important material for people (wood, lumber, fuel, fibers, chemical extracts, energy, etc.).
- Production of **carbohydrates** such as sugars ($C_6H_{12}O_6$), starches ($C_6H_{10}O_5$), vegetable ivory (form of hemicellulose), pectins (for jellies, jams), gums (used in many products, including food products).

- Many **fats and oils** are common plant products (some of which come from trees). These are compounds of mostly carbon, hydrogen, and oxygen, but with lots more molecules of each.
- **Proteins** are formed when the C, N, O elements are combined with nitrogen, sulfur, and sometimes phosphorus. Certain proteins used by animals (and people) can only be obtained by ingesting plant products.
- There are numerous **secretions** produced by trees (and other plants) that are important to people, such as clove oil, cedar oil, resins, pitch, gums, balsam, camphor, natural rubber, pigments, drugs (legal and illegal), etc.

A note about energy allocation within trees. Energy is not a limitless resource for trees. A tree will typically move energy according to these priorities. As energy in the form of glucose becomes limited, a tree will begin to reduce resources spent beginning with the lowest priority. As you can see, a tree with a diminishing crown will become more vulnerable to insects and diseases rather quickly. That's one reason why foresters are so keen to maintain a vigorous growing environment.

1. Maintain respiration of all parts.
2. Produce fine roots and leaves.
3. Produce flowers and seed.
4. Extend branches and roots.
5. Store energy rich chemicals.
6. Add wood to stem, roots and branches.
7. Create anti-pest chemicals for defense.

Chlorophyll

Chlorophyll is the chemical compound where solar energy (light) is captured and photosynthesis happens. Chlorophyll is continuously produced and broken down during the growing season. The heart of the chlorophyll compound is a magnesium molecule. The magnesium molecule is bonded to many molecules of hydrogen, carbon, oxygen, and nitrogen.

C₅₅H₇₂O₅N₄Mg Chlorophyll "a", one of several forms of chlorophyll

There are different kinds of chlorophyll that absorb different colors in the light spectrum. The only color that is pretty much useless to plants is green, which is why plant tissues containing chlorophyll appear green. It's the color that is reflected back into the environment. The process of photosynthesis is very complicated and driven by a series of enzymes. Enzymes function within fairly narrow temperature windows. Within these temperature windows, heat accelerates photosynthesis to a certain point and cold slows it down. Outside the

Experiment Suggestion: Grow plants (beans, peas, fast-growing plants) in containers of different light. Transparent plastic wrap covering containers will filter light spectra. Compare growth rates of plants.

temperature window, photosynthetic activity drops off, most quickly with hot temperatures.

Tree Growth

So, photosynthesis produces all this glucose. . . what then? Essentially, the energy in glucose is used by trees (and most other living things) to drive metabolic processes that produce tissues and maintain life functions. Keep in mind that this whole thing called life is a big solar powered system!

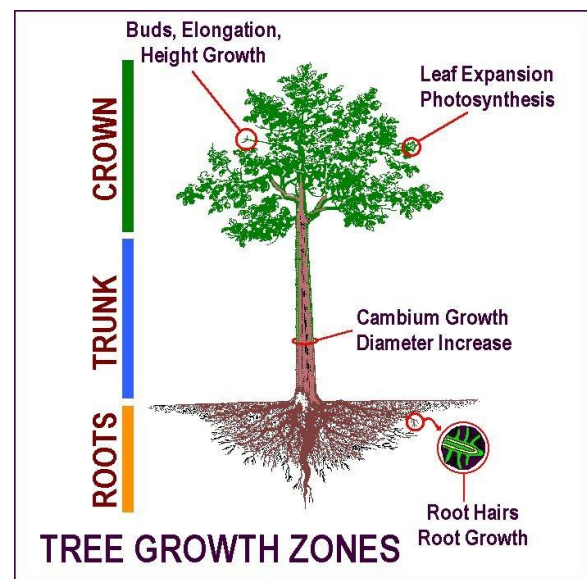
A tree will draw nutrients and minerals from the soil, break them down and put them back together to form compounds and chemicals that we recognize as a tree. The most common material made by a tree is "cellulose." Cellulose is a complex sugar that is the main component of wood and many other plant tissues. It's also an extremely useful material for lots of human uses, such as food products, paper, strengthener in plastics and concrete, clothing, and other things.

Wood is the answer to the tree challenge of pushing a crown as high as possible to obtain the best light-capturing position as possible, while maintaining a connection with water and nutrient supplies in the soil.

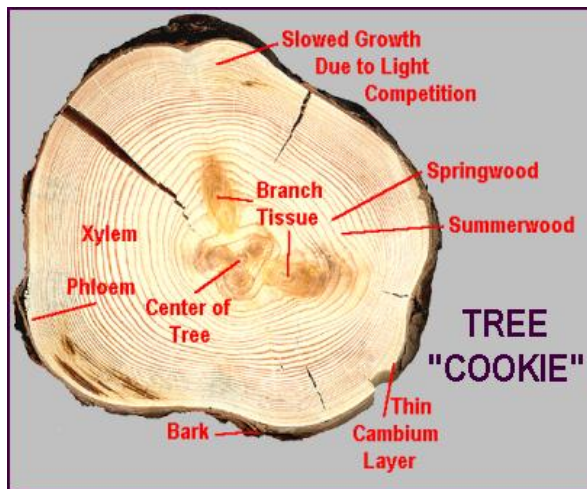
Where does a tree grow? In three places.

- At the twig tips (meristem).
- At the root tips (meristem).
- Around the outside of the trunk, branches, and roots (cambium).

One region of tissue expansion or tree growth is at the tips of both twigs and roots, called the "meristem." This is unspecialized tissue that can form wood, buds, or flowers. Each year, trees will lengthen twigs and roots, produce flowers and fruit, and grow new buds. The meristem and newly produced tissues are rich with nutrients and are often the target of attack by diseases, insects, and animals. Deer, for example, are Michigan's most significant browser. In areas of high populations, deer can destroy years of growth on small trees and entirely eliminate regeneration.



A tree with growth zones illustrated, branch meristem, root meristem, cambium.



Most of a tree trunk, branch, or root is dead wood. The living part is only a narrow band on the outside edge. This living layer is produced by thin bands of regenerating tissue called "cambium." Cambium produces new wood on the inside and new bark on the outside. The cambium grows only from the inside out, not up or down the length of a trunk, branch, or root. For awhile, the new wood and bark are living. The wood actively transports many materials up and down the tree and performs other functions. After the wood dies, it still serves as a transport route for several years. Eventually, even that

function is diminished and the wood serves primarily as structural support.

Each year the cambium produces TWO distinct rings of tissue. In the spring, a layer of thinner-walled cells are grown. In the summer, a layer of thicker-celled, sometimes larger cells are grown. The layers are called "springwood" and "summerwood," respectively. When counting the age of tree "cookie," either the springwood or summerwood rings can be counted, but don't count both (unless you divide your sum by two!). Most people count the typically narrower and darker summerwood. Tree such as oaks, ashes, and all the conifers produce fairly distinct rings which are easy to count. Other trees, such as aspens, red maple, and birch have less distinct rings. Foresters can count rings without cutting a tree down. A tool called an "increment borer" will extract a thin wood core from the tree, which can be used to age the tree.

Why do leaves change colors in the Autumn?

The short answer is that chlorophyll production drops-off as night length increases. The green part of the light spectrum is no longer reflected and other compounds, chemicals called "**anthocyanins**" (reds) and "**carotenoids**" (yellows), become the dominant pigments in the leaves. The longer answer involves discussions of changing day lengths and weather, and strategies dealing with nutrient loss with the dropping of leaves.

What is the story behind Autumn leaf fall?

The purpose of Autumn leaf fall is to prepare for **winter dormancy**. The cold temperatures prevent trees and

Project: Have kids collect different colored leaves in the fall. Categorize leaves by species and color. The same species may have many different colors, especially red maple. Also, have kids record the dates when trees at home, at school, or in another selected place begin to change color. Make notes by species and see if any patterns can be observed. It would be interesting to have a "sister" school in a different part of the state to compare color change with.

plants from functioning in at least three ways. Water would freeze in the plant tissues, causing cell rupture. Water in the upper soil layers often freezes, making absorption impossible. Lastly, the low temperatures are far outside the operating windows for the enzymes that control a tree's metabolic processes, such as photosynthesis and respiration. To avoid these environmental limitations, trees prepare for dormancy in the Autumn.

Trees drop leaves because they are too difficult to "winterize" (unlike most conifers that have strategies to maintain their green parts during the winter and needles have a much different structure than broad leaves). Or, in the case of conifers, the needles that have grown old after two to three years, no longer receive as much light, and are shed each Autumn. However, dropping tons of biomass per acre presents the problem of losing significant amounts of valuable nutrients. Much of the sugars and valuable nutrients are resorbed from the leaves, but the annual leaf drop still means the loss of a lot of good "stuff." In our north temperate climates, dropped leaves become part of the "organic layer" on the surface of the soil, to be recycled (in part) by decomposers.

There are two components influencing the Autumn color display, the **timing** and the **intensity**. The timing is usually controlled by lengthening nights and the intensity is strongly influenced by weather.

The most dependable seasonal environmental factor is the change in daylight, or more accurately, the lengthening dark period. Such things as rainfall or temperature might "fool" a tree into retaining leaves too long. For this reason, the timing of leaf-drop is regulated by the consistent movement of the Earth around the Sun. However, a late spring or extremely dry summer can postpone the response to lengthening nights by a week or two. Just "when" a tree begins to turn color varies from species to species, and geographically from north to south. In our northern forests, black ash is the first to change color. Tamarack (a needle-bearing tree) is the last.

The intensity or brilliance of the color change is influenced by weather conditions during the period of declining chlorophyll production. A series of sunny days and cool nights (above freezing) result in a more colorful display. The warm days increase production of both sugars and anthocyanin pigments. Sugars "stranded" in the leaf and greater concentrations of anthocyanins bring out the scarlets and reds, especially the deep purple of northern red oak. Carotenoids yield the yellow and golden colors but tend to remain at fairly constant concentrations regardless of weather.

So, how might weather affect the fall colors?

- Warm Autumn weather will generally reduce the color quality.
- Moist soils following a good growing season contribute to better displays.
- A few warm, sunny days and cool nights (at the right time) will increase brilliance.
- Droughts will usually result in poorer displays.

What causes the leaves to actually fall off?

Wind, most commonly. As nights lengthen, a layer of cells forms in the leaf stem near the twig, called the "**abscission layer**." Abscission means cutting or severing. This layer blocks transfer of materials to and from the leaf. The abscission layer also makes a weakened connection. Eventually, wind, rain, snow, or animals will knock the leaf from the twig.

Sunlight and Tolerance of Shade






It's commonly known that trees and plants need sunshine to live. However, not all trees need the same amounts of sunlight. Trees that require high amounts of sunlight are sensitive to shade. Foresters call this sensitivity "**shade tolerance**" or just "**tolerance**". The shade tolerance of some tree species will vary with age.

Tree species such as **aspen, cherry, paper birch, jack pine, and red pine** require lots of sun and are not tolerant of shade. That's part of the reason stands of these species tend to be all about the same age. Seeds of these species that germinate under a canopy of shade do not survive.

Other tree species are more tolerant of shade, such as **sugar maple, beech, balsam fir, hemlock, and cedar**. They can survive as seedlings or saplings under a fairly heavy canopy of shade for many years. When exposed to light, the small trees (not always young trees!) can quickly grow to take advantage of the new light regime.

There are a number of tree species that fall into the moderately tolerant category, such as **red oak, red maple, yellow birch, white ash, white pine, and white spruce**. They may be able to grow under the light canopy of an aspen or paper birch stand, but would not be very successful under the shade of a maple-beech-basswood stand.

Shade tolerance is key component of forest management systems.

Relative Sunlight Requirements For Representative Tree Species	
Paper Birch Tamarack Jack Pine	
Quaking Aspen Silver Maple Red Pine	
Red Maple Red Oak White Pine	
Yellow Birch Balsam Fir White Spruce	
Sugar Maple Basswood Cedar	

Other Environmental Factors

There are many environmental factors, both living and not living, that influence the growth of trees. This guide has already discussed some of them, such as light, nutrients, and temperature. Many of these factors interact with other. That's part of the reason why forest management can be complex. Tree adaptation to various environmental factors runs along gradients. Some tree species are more sensitive to a particular gradient than others.

Rainfall or Precipitation

Average annual rainfall varies across a wide geographical area. Some tree species can survive with less annual precipitation. As you move north and west, rainfall declines, and so do the number of tree species. More locally, *available* water may vary with microsites. The south sides of slopes will be drier, so will a sandy plain or areas with bedrock close to the surface.

Soil Variability

Scientists have identified over 475 soil types in Michigan. It stands to reason that different tree species have preferences for certain types of soil. Red pine and jack pine are well-known for their ability to grow well on sandier, poorer soils where most other trees grow poorly. Sugar maple and basswood prefer richer soils with lots of nutrients. Other species, such as bur oak and quaking aspen grow well on a wide variety of soils. This variability is largely related to the amount of available nutrients in a soil, the nutrient demand of a particular species, and a tree's ability to extract those nutrients.

Moisture

This is related to both rainfall and soils. The amount of *available* moisture varies during the year. High moisture levels during the dormant season will not help trees. Or usually hurt them. Saturated conditions from spring runoff or flooding does not hurt most trees because they are not actively growing. Some tree species are more tolerant of short periods of flooding during the growing season, such as bur oak or silver maple. Oddly enough, white cedar is quite sensitive to rapid changes in moisture, either wetter or drier. Northern swamp tree species grow on small, dry microsites. They don't usually grow in the water.

Biotic Factors

These are the living parts of an ecosystem that trees interact with. Other plants will impact forests. Insects and diseases play a major role in forests. Animals like white-tailed deer, porcupines, and squirrels also have prominent roles. Not all of these impacts are negative. Many are beneficial. Insects pollinate tree flowers. Soil animals loosen soil. Birds eat lots of insects. And of course, humans manage forests for a wide variety of reasons.

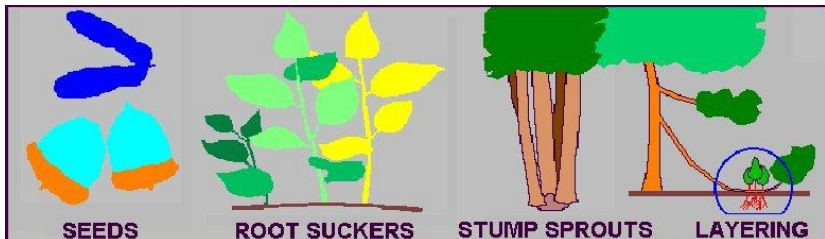
Mycorrhizae

Pronounced "*my-core-HI-zee*", these are beneficial fungi to trees. The fungi are associated with tree roots in a **symbiotic** relationship. That's where both partners benefit from each other. The mycorrhizae increase a tree's ability to absorb water and nutrients. The tree supplies the mycorrhizae with a share of photosynthate. Sometimes, species of mycorrhizae are only associated with a particular species of tree. The lack of proper mycorrhizae in the soil can prevent a tree from growing well, or maybe from surviving at all. It may be one of the factors that limit trees to a certain range. Scientists are learning more about these special fungi.

Tree Regeneration Strategies

There are four ways Michigan trees regenerate themselves.

- Seeds
- Root Suckers
- Stump Sprouts
- Vegetative Layering



All trees can reproduce by seeds. Each species has a unique set of requirements for seed production and germination. Seed dispersal strategies vary widely, from wind-driven seed to seeds carried by certain species of animals.

Sprouts and suckers are similar, in that dormant buds "come alive" to form new shoots of parent trees. Sprouts are shoots from stumps or the base of a tree. Suckers are shoots that originate from buds on the root systems. Often times, sprouts and suckers will not grow until the parent tree dies or becomes very sick. The buds are held in dormancy by hormones produced in the leaves. When these hormone levels drop below a certain point, the dormant buds will grow.

Vegetative layering is uncommon, occurring mostly in white cedar and Canada yew (which most would not consider a tree!). When branches or stems come in contact with the soil, cambium tissue sometimes form roots. In this way, former branches of a fallen cedar might become trunks of several "new" trees.

Tree Longevity

Trees do not live forever, therefore cannot be "preserved." A forest condition, or forest type might be preservable (if managed), but not individual trees. While people know that all living organisms eventually die, often times this is not taken into account when people consider forests.

Tree longevity varies from about 70 years to over 1000 years, depending upon the species. Most trees do not live past 50 years (or 10 years, for that matter), if you consider attrition from the time of germination. Short-lived species tend to be **successional "pioneers"**, or trees that first colonize an unforested site. Aspens, paper birch, cherries, jack pine are examples of short-lived tree species. They also tend to be intolerant of shade. Long-lived tree species tend to be more shade tolerant, occupy later stages of succession, and employ more "conservative" survival strategies. Sugar maple, basswood, beech, and white cedar are good examples.

Succession: The orderly and predictable series of vegetation type changes over time. Primary succession begins with bare soil, or nearly so. Secondary succession begins at some point earlier in the process than what was present before. Succession is a critical concept in developing *forest management systems*.

Note: "Succession" is further explained in another chapter in this guide and is one of the most important concepts in forest ecology.

Most Common Michigan Tree Species (by volume) and Their Expected Lifespans (in years)

Note: Maximum lifespans may exceed the ages listed.

Sugar Maple	200-300	Balsam Fir	70-100
Red Maple	125-150	White Oak	400-500
Quaking Aspen	60-90	Eastern Hemlock	400-500
Cedar	400-600	Jack Pine	80-100
Northern Red Oak	200-300	Yellow Birch	200-300
Red Pine	200-250	Black Cherry	150-200
Bigtooth Aspen	75-100	White Ash	unavailable
Basswood	125-175	American Beech	300-400
Paper Birch	70-100	White Spruce	150-200
White Pine	250-300	Black Spruce	200-250

Winter Adaptations of Trees

Trees must have adaptations to survive the cold and drying conditions of winter. Trees cannot change their location or behavior like animals can, so they must rely on physiological and structural adaptations.

The height advantage of trees becomes a liability in the winter, as tissues are exposed to the weather. There are four basic strategies that trees employ.

1. Either leaf drop or adaptations for leaf retention.
2. A physiological acclimatization process.
3. Resolution of water issues.
4. Methods of reducing mechanical damage.

Stomate: Small openings in leaves that permit the passage of air for respiration and photosynthesis. Leaves have the ability to open and close stomates.

Broadleaf trees (hardwoods) drop their leaves during the winter, avoiding the problems of maintaining foliage in cold and dry conditions. Conifers (softwoods) retain foliage and have special adaptations in order to do so (better stomate control and a waxy coating called cutin).

All trees go through an acclimatization process. Like leaf drop, the process is initiated by changes in photoperiod and is controlled by hormones and other chemicals. The process also exploits the physical properties of water.

Winter conditions make finding sources of liquid water and transporting water a challenge. Water loss is minimized in several ways. Water can be obtained from the ground, within the tree, or from the subnivean (under snow) micro-environment. Conifers have special cell adaptations to facilitate water transport whenever temperatures allow it.

Snow and ice accumulation can cause breakage, especially under windy conditions. Conifers have growth patterns that minimize the chances of damage occurring. Dramatic loss in vegetation from animal consumption increases pressure on woody tissues, especially foliage, buds, and bark. Browse damage can be significant in many regions of Michigan. Lastly, pollutants from highways, particularly road salts and exhaust, can damage trees, especially those more vulnerable to these chemicals.

A More Detailed Explanation of Winter Adaptations of Trees

Trees must have adaptations to survive the cold and drying conditions of winter. Trees cannot change their location or behavior like animals can, so they must rely on physiological and structural adaptations.

The height advantage of trees becomes a liability in the winter, as tissues are exposed to the weather. There are four basic strategies that trees employ.



1. Either leaf drop or adaptations for leaf retention.
2. A physiological acclimation process.
3. Resolution of water issues.
4. Methods of reducing mechanical damage.

Leaf Drop

Leaves are a major source of water loss and are difficult to protect from winter conditions. Most trees drop leaves in the autumn to avoid these problems. Conifers are the exception and will be looked at in the next section.

Annual leaf and flower expansion requires tremendous inputs of water and nutrients. Trees must produce and store a sufficient amount of reserves during the four to five month period when leaves are photosynthesizing. Buds are usually set by the end of July. Above-ground growth also ceases in late summer.

Physiological processes, including leaf drop, are stimulated largely by changes in photoperiod. The lengthening dark period changes the production rates of a number of chemicals and hormones. The most important is probably the increase in abscisic acid (AA). AA slows protein and RNA (ribonucleic acid) production. Both are keys parts of growth. AA also increases cell membrane permeability, which is important in the acclimation process.

Chemical breakdown of the green chlorophyll molecules reveal the pigmentation of the yellow and orange carotenes and xanthophylls. The scarlet colors are enhanced by hard frosts affecting residual sugars and anthocyanins.

Abscission layers between the leaf stem and the twig are formed. Cells along this line expand at different rates, and enzymes degrade tissue. As a result, a physical line of weakness develops. Scar tissue is formed over the attachment point that prevents water loss. Gravity and wind cause leaves to drop.

Not all trees lose their leaves at the same time. Black ash is usually the first to drop leaves. Some species will retain brown leaves well into the winter, especially oaks, ironwood, and beech. In May of each year, leaf growth can be tracked by species. Black ash and bigtooth aspen are among the last tree species to leaf-out.

Adaptations For Leaf Retention

In the north temperate forest, all broad-leafed trees lose their leaves. Each year conifers also drop leaves, similar to broad-leafed trees, they just don't shed them all. Most conifers retain needles for two to three years before shedding them. Although conifers require the resources to produce new needles each year, they gain a large measure of economy by using a set of needles for more than one year. The coniferous exception to this needle-retention strategy is the genus *Larix*, the tamaracks and larches.

Conifer needles have a thick, waxy coating of cutin that significantly reduces water loss. Needles also have much tighter stomatal closure. Stomata are the pores that

allow air and water to pass in and out of the needle. Lastly, tissues undergo an acclimation process, similar to other living tissues in trees.

Retaining needles allows trees to extend the length of the photosynthetic season. It also potentially allows trees to take advantage of winter thaws and, perhaps, even to permit slow rates of photosynthesis during cold weather. However, needle retention presents serious challenges in terms of water loss, water re-supply, and snow-loading.

Acclimation

Loosely analogous to animal hibernation, trees undergo changes that allow them to survive the cold, dry conditions of winter. This process occurs at the cellular level and exploits the physical properties of water.

All trees have a measurable “killing temperature”, the temperature where ice crystals form within cell structures resulting in cell death. Killing temperatures vary among different species, between populations of the same species, and even among different tissues. In some cases, killing temperatures are limiting factors for species ranges.

Tree Species With Northern Ranges Limited By Killing Temperatures	Tree Species With Killing Temperatures Below Average Low Temps	Tree Species With Adjustable Cold Tolerance
Northern Red Oak American Beech Black Cherry Sugar Maple Yellow Birch Musclewood White Ash Ironwood	Eastern Hemlock Northern White Cedar Black Spruce Balsam Fir Tamarack White Pine Jack Pine Red Pine Eastern Cottonwood Quaking Aspen Black Willow Paper Birch Basswood	White Pine White Ash Green Ash Red Maple
Source: Marchand (1996).		

Like leaf-drop, acclimation is prompted by changes in the photoperiod. Absciscic acid (AA), once again, plays a key role. Physiological changes include:

1. An increase in AA production.
2. Lipids (soluble fats) unsaturate.
3. Lipid concentration within cells increases.
4. Proteins de-polymerize.
5. Cell membrane permeability increases.

Solute concentrations within cells increase, slightly reducing the freezing point. Therefore, as temperatures drop, water outside cells freezes first. Freezing water releases small amounts of heat energy, which in turn, helps cell fluids remain unfrozen. Twig temperatures actually rise several degrees during this process. Water moves out of cells attracted to the ice crystals in the pore spaces. This process effectively reduces the freezing point of cell water to the killing temperature. Colder temperatures will begin to result in cell freezing and death.

Water Loss

Water is lost primarily from above-ground biomass. Bark and buds are fairly water-tight. Drastically lower levels of photosynthesis and respiration reduce water demand and subsequent loss. Conifers, however, have huge surface areas of living tissue in their needles. Any photosynthesis that might occur will increase water demand and risk of loss.

Water vapor moves from areas of high concentration to low concentration. Concentrations are usually higher inside needles, so the tendency is for water to be lost from foliage. Needles have advanced structures to present a barrier to water loss, but cannot eliminate it. In addition to tight stomatal closure and cutin, reduced air movement around needles will contribute to lower vapor gradients. Air “boundary layers” act like insulation. The dense foliage of conifers, especially stands of conifers, serves to mediate micro-environmental conditions somewhat. The fuzzy undersides of evergreen broad-leaf shrubs serve to increase this zone of “insulation”.

Oddly enough, warm, sunny days present the greatest water retention challenges for conifer foliage. Dark needle coloration readily absorbs heat and raises needle temperatures significantly above ambient air temperatures. Metabolic rates rise and internal vapor pressure increases. Despite thicker air boundary layers, the net effect is greater water loss.

Cloudy, windy days are actually better for conifers. Clouds block warming solar energy and wind readily removes heat from the needles, reducing the vapor pressure gradient.

Water Supply

Conifers have larger winter water demands than most broad-leaf trees (some hardwoods have photosynthetic bark and branches, which increases water demand). Without re-supply sources, trees would die from water loss. However, freezing temperatures and frozen water would make re-supply seem impossible.

There are three potential sources of water; 1) the soil, 2) internal tree reservoirs, and 3) subnivean (below snow) vapor absorption.

Soils are not always frozen. In fact, much of Michigan's soil remains unfrozen for all or part of the winter. The insulating effects of snow can result in ground thaws or prevent freezing in the first place. This means that liquid water is available. Transportation above-ground becomes an issue, discussed later.

The sapwood of trees and branches contains water. Oftentimes, this water is frozen and unavailable. However, differential warming (solar insolation) and winter thaws can melt the sapwood water, making it available for transport.

Lastly, conifer branches below snow-level might benefit from higher water vapor concentrations *outside* the foliage. Potentially, this absorbed water could be transported to other locations in the tree.

Water Transport

Given that liquid water sources exist during the winter, the problem of transport remains. Water cannot be moved while frozen, so temperatures along a transport line from source to sink must be near or above freezing.

Water is moved within a tree through the xylem, which consists of cells that make up long tubes, called tracheids. The strong cohesive properties of water permit continuous columns of water to be "pulled" through the tracheids. If a water column is broken, it is virtually impossible to restore the column.

When tracheid water freezes, two things potentially break the water column. Ice crystals stop the flow. More importantly, as ice forms, dissolved gases are expelled and form gaps in the column. Upon thawing, these air gaps remain, rendering the column unusable for water transport. Hardwood (broad-leaf) trees grow new xylem cells in the spring to re-establish the water transport system.

Conifers have some fascinating adaptations that overcome the problem of broken water columns.

Within the transport tubes, conifers have tiny "check valves" between each tracheid. Ice formation and volume expansion increase pressure within a water column causing the "float" within the check valve to seal the ends of each tracheid making up a tube. The float is called a "torus". The expelled gas is held under pressure within the tube by the incredibly strong tracheid walls. Measurements have demonstrated that the tracheids can hold pressure up to 900 psi. When the ice crystals melt, the gas is forced back into solution, pressure returns to normal, the tori migrate back to the middle of the check valve, and the water column is restored.

Water column restoration in conifers can occur multiple times during the winter during warm periods or when solar insolation is high. Foliar water stress caused by those warm, sunny winter days can be alleviated by restored water columns supplying water from any of the available water sources.

In addition to the clever adaptations of conifer xylem cells, there is evidence suggesting that water can also be diffused from cell to cell via the phloem, in both hardwoods and softwoods (conifers). Diffusion is slow but may be sufficient to meet the water demands of dormant hardwood species that appear to have no other winter water transport system. This may help explain why some hardwood species, such as paper birch, can survive winter conditions right up to the treeline.

Other Winter Season Challenges to Survival

Conifers have higher leaf densities than hardwoods. This means snow can quickly accumulate to the point of stem and branch breakage. Ice storms can be even more detrimental. To offset this snow-loading problem, conifers display alternative growth and branching patterns.

Conifers have a single leader or main stem (determinant growth), as opposed to the many leaders of hardwoods (indeterminant growth). The subsequent cone shape more effectively sheds snow. Conifer branches grow at more obtuse angles to the main stem. This allows branches to reach snow-shedding angles with less bending. Longer wood fibers also generally provide more flexibility.

Denser conifer foliage offers greater wind resistance, potentially leading to breakage, especially when foliage is loaded with snow and ice. Trees on the perimeter of conifer stands take the brunt of wind damage, but the dense foliage also protects those individuals internal to the stand. This factor creates typical stand shapes in mountainous terrain, but is not as pronounced in Michigan. However, Michigan conifers sometimes do display “flagging” in the direction away from prevailing winds. Tall white pine are particularly noteworthy in this regard.

Many conifer species become targets for animal browsing during the winter. Foliage contains some of the better sources of nutrients, although they are poor compared to summer food availability. In many parts of Michigan, high deer densities have eliminated the regeneration of most tree species (hardwoods and softwoods), along with other plant forms. High moose densities have had tremendous impacts on the vegetation of Isle Royale.

Porcupines, rabbits, and mice find sustenance in the living bark and phloem tissue of trees. If the bark is chewed all the way around the stem, the girdling will kill the tree beyond that point. Girdling is an especially severe problem in certain conifer plantations and young trees in old fields.

Many birds feed on the rich flower buds of trees. Ruffed grouse are particularly well-known for their affinity for the male flower buds of quaking aspen. However, flower bud browsing has seldom, if ever, resulted in significant damage. Plantations grown for fruit or seed production may be an exception.

The final winter challenge for trees is human-caused. Trees along major roads may eventually show signs of poisoning from road salts and vehicle exhaust. Some species are more resistant to these pollutants. The more vulnerable species include; white pine, red pine, hemlock, basswood, ironwood, sugar maple, and red maple.

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