

GATHERING BENEATH TREES

Background and Context

Every now and then most of us have the wonderful experience of seeing something "ordinary" with fresh eyes. A minute ago it was just that bush on the corner but now it's a bush on fire with life. Or, perhaps, it was an ant crawling over your toe that normally you would have brushed away but which now suddenly holds your full attention. It is not that the bush or the ant changed; rather, you changed the way you saw them. In effect, you saw them more fully. Perhaps it could be this way with trees -- with a tree.

When it comes to thinking about other species, like red-tailed hawks or white oaks, we are easily able to see the differences between us and them, but less practiced, it seems, at discerning similarities and connections. For example, if I were to ask you to think about the ways that trees and humans are related, it is likely that your mind would first race to all the differences: We can walk and trees can't; we have a brain and trees don't; we can talk and trees can't, and so forth. Only with some prodding might you recall that humans have shared an intimate relationship with trees throughout our evolutionary history. Our primate ancestors lived in trees; our more recent ancestors built whole civilizations from trees; and today the forests of the world continue to regulate water flow, supply forest products, and ameliorate climate.

But there is much more to our relationship with trees, and plants in general, than utilitarianism. Indeed, we share a great deal in common with plants. Consider the likenesses:

- **Elemental composition.** There is no part of gross human anatomy that looks anything like a plant leaf and, yet, when we compare the ratios of nitrogen, carbon, phosphorus, etc. in leaves to these ratios in the human body, the two are remarkably similar. So it is that the greens on our plate offer us something quite close to what our bodies need.
- **Biochemistry/genetics.** Tree tissues, like our tissues, are composed of carbohydrates, fats and proteins. Plants use the same amino acid building blocks to construct proteins that we use. They employ very similar, sometimes identical, biochemical pathways for the synthesis and breakdown of compounds in their cells. And like humans, their cells contain a nucleus with DNA packaged in chromosomes. Also, just like us, they have an array of hormones that act as messengers, regulating cellular processes.
- **Sex.** It is not just humans and other animals that have sex; trees have sex too. Flowers are the genitalia of trees and plants in general. The minuscule pollen grain is analogous to the entire male reproductive tract. When pollen arrives to a flower (transported on the wind or carried by an insect pollinator), it extends a penis-like tube down into the flower's ovary. Then sperm descends this tube and fertilizes one of the "eggs" in the flower's ovary.
- **Population expansion.** Successful mating in humans and trees leads to the production of

offspring (seeds in the case of trees). Although trees are stationary during their adult lives, their seeds can be carried considerable distances by the wind or water or animals. So it is that trees, like humans, are effective at colonizing new territories.

- **Defenses.** Trees, like humans, have defenses to protect themselves. Indeed, without some sort of defense system, most plants would be eaten to death. A solution is to produce special chemicals to deter herbivores. Some of these plant compounds are familiar to us as drugs (caffeine, nicotine), poisons (cyanide) or insecticides (rotenone). Many of them simply taste bad; some interfere with digestion; others cause reproductive abnormalities, paralysis, or blindness. All send the message: "Stay away!"
- **Communication.** The investigation of plant defenses has revealed another remarkable similarity between trees and humans. Namely, that plants are able to communicate with each other.

"Talking" Trees

In the early 1980s, David Rhoades, an ecologist at Princeton, was studying tent caterpillars when he made an important observation: Tent caterpillars grew very slowly when they were fed leaves from intact willow trees that were growing in close proximity to heavily defoliated willows. Based on this, as well as other observations, Rhoades speculated that the defoliated willows were emitting some signal that induced the nearby, undamaged willows to produce substances in their leaves that would deter insect defoliators. It was as if the damaged trees were saying: "Hey neighbor, I am getting eaten. If you want to survive, you better make some toxins quick." Another ecologist, Jack Schultz, decided to test Rhoades' idea with a greenhouse experiment using three sets of sugar maple seedlings and two experimental chambers. Schultz placed the first two sets of maple seedlings in one chamber. One set was subjected to mild defoliation. Specifically, two of the 20 leaves of each maple seedling were torn in half; the second set of seedlings was left untouched, but was in the same air space as the defoliated seedlings. The third group of seedlings was also left untouched and placed in the second chamber with its own air supply.

After cutting the leaves in the first set of seedlings, Schultz went to the greenhouse every few hours and removed several seedlings from each of the three "treatment" groups to monitor changes in leaf chemistry. As expected, there were no changes in the leaf chemistry of the "control" seedlings placed in the separate chamber over the 72-hour experimental period. The story was different for the seedlings with the torn leaves. Chemical tests on the undamaged leaves of these seedlings revealed increases in compounds (e.g., tannins and phenols) that render leaves less palatable to insect defoliators. Most interesting of all, Schultz also detected significant increases in concentrations of phenolic compounds in the set of seedlings in the first chamber that was not harmed at all but which shared air space with the damaged set of seedlings.

Overall, this experiment revealed that sugar maple trees are somehow able to communicate, presumably using airborne chemical signals. The capacity to communicate in this way is thought to be beneficial to trees because it means that they don't have to expend a lot of energy making defense compounds when the danger of defoliation is low.

As we come to recognize the many commonalities between ourselves and trees, we slowly build the scaffolding for a relationship with the plant world. Suddenly a tree is much more than an isolated brown and green object sticking out of the ground. The air that moves in and out of the tree, the water coursing through its vessels, the sunlight penetrating its leaf chloroplasts, the insects fertilizing its flowers, and the mycorrhizal fungi shunting nutrients to its roots are all integral parts of the tree. The tree is not separate but part of a larger whole.

Check In:

Recall a memory of a tree in your past. Whether it was a tree in your back yard or a tree in a city park or even a tree that you have read about (for example, Shell Silverstein's *The Giving Tree*), each of us has a past experience with a tree. Think of this while we walk outside outside among the trees and when we have arrived, let's share.

Tree Identification

An Introduction to Dichotomous Keys

We begin with a brief introduction to dichotomous keys. A dichotomous key is a tool used by scientists to quickly and easily identify organisms in a way which is many times more efficient than a comparison of their appearance against every description in a field guide. Dichotomous keys consist of sets of paired statements, both beginning with the same word or phrase. Following each statement is a direction to another pair of statements until one eventually arrives at the name of the organism in question. Dichotomous keys can be developed to identify anything. As an example, this key differentiates various types of sports balls:

- 1. Ball spherical----- 2.
 - 1. Ball smaller than a fist----- 3.
 - 3. Ball dimpled----- GOLFBALL
 - 3. Ball not dimpled----- PING PONG BALL
 - 2. Ball bigger than a fist----- 4.
 - 4. Hexagonal pattern on the outside of ball ----- SOCCER BALL
 - 4. Hexagonal pattern not on outside of ball ----- BASKETBALL
- 1. Ball not spherical -----FOOTBALL

Keys change according to the items they are attempting to identify. How, for example, would the above key have to be modified to include a baseball?

A dichotomous tree key, then, takes advantage of differences such as: hard vs. soft wood (or deciduous vs. coniferous), alternate vs. opposite branching, simple vs. compound leaves,

smooth vs. toothed leaf outlines, etc. Your guide will help to brief you on the tree key that you will use today.

Instructions

1. The Identification Process: The campus of Penn State is itself an arboretum, having a robust variety and number of trees. This justly befits a land grant institution in a state named after its trees. Recall that Pennsylvania means "Penns Woods." Today we will walk through campus, tree to tree, to see the great wealth that we have here. As we arrive at a tree, (working in pairs or small groups) use your "tree key" to determine what/who stands so tall before you. Do not shout out your answer until everyone has had the chance to discover the name of the tree. Does anyone have anything to share about this tree? A story from their life? Knowledge from a book?

2. The Meat: Although we have named the tree, does this really tell us anything about it? It is true that ecologists have been able to create a dichotomous key to identify trees, but why have they been able to do this? That is, why is there a diversity of trees? Why does this tree have leaves and that one needles? Why does this one alternate and that one oppose its branches? Why is the bark here smooth; there, rough? Why this one tall and that one fat? We have identified this tree because, it is true, it has its own peculiar species identity. Yet, why is this species of tree a species—that is, why does it exist at all, what does it do, and why does it do the things it does the way it does them? Ask a question—or questions—and see how many answers you can find. Voice your answers even if you are unsure. This type of exercise mimics the first steps in the scientific process, where we make observations and attempt to answer questions we don't already have answers for. [Consider the Darwinian dictum regarding survival of the fittest: nature selects that most fit—that is, most appropriate—to the given condition(s)].

What do you see? And of that "what," **Why?** And of that "what," the further, **What**—that is, your "what" may be, "tree bud," but, really, what *is* a tree bud? **How? When?**

Check Out:

If you were a tree, which would you be?

OUT-OF-CLASS FIELD STUDY: TREES

Part 1: Communion

As you walk around campus begin to pay attention to the trees you pass. Notice the differences among them. Each is a unique individual. As you explore our campus trees, you will, no doubt, notice that you are attracted to some trees more than others. For example, maybe you are naturally attracted to things that are large and so you note that you are drawn to the big impressive trees on campus. Or maybe you notice that you are attracted to pines because there was a certain pine that you used to climb as a kid. Or maybe acorns and the squirrels gathering them catch your attention and you find yourself spending more time looking at oak trees.

At some point as you are walking and observing, give yourself permission to actually approach an individual tree that appeals to you and then proceed to spend at least 15 minutes with that particular tree.... looking at it as if you have never truly seen it before. Because you haven't! In other words, I am asking you to see this tree that you have chosen as a one-of-a-kind, utterly unique living being. Further, I am asking you to suspend judgment and to entertain the hypothesis that this tree actually has things to teach you, provided you can slow down enough to look and pay attention. . . **This means slowing down so that you can enter the realm of "tree time."** Five minutes won't do it; ten minutes isn't enough....give yourself 15 minutes at a minimum.

What might you do during those 15 minutes? Open all your senses to the tree—smell, taste, touch, hearing, sight. Get close to this tree you have chosen; feel the bark, pay attention to its texture. Examine the tree's leaves; notice anything interesting about them. If you start to feel uncomfortable just let that thought go. We human ones came from the trees! As humans, our intimacy with trees extends far back in time. Continue your encounter by observing the branches and the overall "body" of the tree. Take note of the tree's seeds. In addition to your five senses, open your sixth sense—**your heart sense**—to this tree you have chosen and consider: What teaching might this tree be offering you?

Conclude your visit with the tree by becoming aware of the fact that you are giving your breath to the tree and, at the same time, receiving your breath from the tree. To really allow this to sink in, take hold of a leaf, gently, and then bring your attention to your breathing. As you breathe out, carbon (as carbon dioxide) is passing from your body into the leaf that you are holding. Charged by the sun, this carbon leaving your body in your breath is being forged into sugars in the leaf's interior. Next pay attention to your in-breath. As you breathe in, the byproduct of the tree's solar forging, oxygen, is finding its way into your lungs and thence, via blood, to the trillions of cells of your body. Breathe in and then out with full consciousness of this exchange taking place. Now, slowly let go of the leaf and, as you do, hold your breath, signifying the breakage of your life bond with trees. Then touch the leaf and commence breathing again. After a time, cup your hands around this leaf without touching it and continue to breathe, giving your breath to and receiving breath from this leaf. Finally, open your arms to embrace the whole tree and breathe in and out, feeling your breath going out to the tree and the tree's "breath" entering your body. As you engage in this practice, you will be giving yourself the opportunity to develop a bodily sense of your participation in Earth's breathing. This is a vital exchange that connects you to the greater **cycles** of the planet. In fact, the evolution of earth's atmosphere is directly linked to the evolution of photosynthetic organisms. The ozone layer and the heightened levels of oxygen in our atmosphere derive from and are sustained by photosynthetic LIFE.

Finally, take your journal in hand and record your observations and discoveries during this encounter with your tree.

Part 2: Questions & Answers

Now that you have had some time with your tree, you may have some questions about your future together. Do you really know what you're getting into? Do you *really* know this tree? Because life isn't all tire swings and leaf piles ... begin an inquiry. Start asking questions.

1. Specifically, drawn from this experience with this one tree as well as from past experiences, write down thirty questions about this tree, in particular (and trees, in general).
2. From these thirty questions, formulate two solid, personally intriguing, and potentially researchable final questions.
3. Formulate two hypotheses for each of these two questions.
4. Research: what do other ecologists have to say? Briefly summarize the results of this research.

Here are a few questions to get you started. If you are particularly engaged by any question here, please feel free to pursue an answer:

- What are roots and what do they do?
- How do trees "breathe"?
- How do trees move water tens to hundreds of feet above the ground? Or do they?
- Why are tree leaves green? What is green?
- What are pine cones? nuts? acorns?
- Why do plants/trees have flowers?
- What is soil and what makes a good soil?
- Why does ringing a tree kill it?
- How fast is a photon moving and how does a leaf snag one?
- Why do leaves change color in the fall?
- How long do trees live and how can you tell their age?
- Do different trees have different smells? tastes, sounds? feels? Why?
- Why do trees branch? Why are branching patterns different?
- How much atmospheric CO₂ does an acre of forest sequester?
- Has this tree co-evolved with any other species?

Supplemental: Dichotomous Key for Some Trees on the PSU Campus

1. Leaves needlelike or scale-like		
2. Needles > 1 inch long, round in cross section, in bundles		
3. Needles in bundles of 5's	Eastern White Pine	<i>Pinus strobus</i>
3. Needles in bundles of 2's or 3's	Other Pines	
2. Needles < 1 inch long, flat and arranged along twigs		
3. Needles white beneath; tree is evergreen	Eastern Hemlock	<i>Tsuga canadensis</i>
3. Needles not white beneath; tree is deciduous		
4. Twigs alternately arranged along branchlets	Bald Cypress	<i>Taxodium distichum</i>
4. Twigs oppositely arranged along branchlets	Dawn Redwood	<i>Metasequoia glyptostroboides</i>
1. Leaves broad		
2. Leaves opposite or whorled		
3. Leaves simple		
4. Leaves with a single main vein, margins without lobes or teeth		
5. Leaves elliptic, < 5 inches long	Eastern Dogwood	<i>Cornus florida</i>
5. Leaves heart shaped, > 6 inches long	Northern Catalpa	<i>Catalpa speciosa</i>
4. Leaves with 3-7 main veins radiating from one point, margins lobed and maybe toothed	See Maples below	
3. Leave compound		
4. Leaves fan-compound		
5. 7 leaflets; end bud sticky	Horse Chestnut	<i>Aesculus hippocastanum</i>
5. 5 leaflets; end bud not sticky	Ohio Buckeye	<i>Aesculus glabra</i>
4. Leaves feather compound		
5. Leaflets are of different sizes and shapes	Box Elder	<i>Acer negundo</i>
5. Leaflets similar in size and shape	See Ash Trees below	
2. Leaves alternate		
3. Leaves simple		
4. Leaf margins entire: no teeth or lobes		
5. Leaf tipped with single bristle, dark green above and hairy beneath	Shingle Oak	<i>Quercus imbricaria</i>
5. Leaf heart shaped, with veins branching from base.	Eastern Redbud	<i>Cercis canadensis</i>
4. Leaf margin with lobes or teeth		
5. Leaf is either deeply or shallowly lobed or waved, but not toothed		
6. Leaf with 4 lobes, the main vein ending in a notch, and tip of leaf looks cut off	Tulip Poplar	<i>Liriodendron tulipifera</i>
6. Leaf with more than 4 lobes	See Oaks below	
5. Leaf may be lobed or not, but margin toothed or doubly toothed along all or most of its margin		
6. Leaf is lobed as well as saw toothed, and about as long as wide with 3 to 5 main veins	Go to 7.	
6. Leaf is not lobed	Go to 8	

7. Margins finely toothed, leaf with 5 main lobes and veins, star shaped and aromatic, leaf surface glossy	Sweet Gum	Liquidambar styraciflua
7. Margins coarsely toothed and jagged, leaf with 3 main lobes and veins, leaf surface dull	Sycamore	Platanus occidentalis
8. Teeth all about the same size (note that there are a number of trees that could be included here)	American Beech	Fagus grandifolia
8. The margin is doubly toothed, with small teeth between the larger ones		
9. Leaf base is lop-sided	American Elm	Ulmus americana
9. Leaf base symmetrical (Birches also would be included here)	American Hornbeam	Carpinus caroliniana
3. Leaves Compound		
4. Leaflet margins toothed or partly toothed, 11-21 leaflets all about the same size	Black Walnut	Juglans nigra
4. Leaflet margins not toothed at all		
5. Leaflets less than 1½ inches long, with both compound and doubly compound leaves present, large thorns sometimes present	Honey Locust	Gleditsia triacanthos
5. Leaflets 2 – 2½ inches long, leaves always doubly compound	Kentucky Coffee Tree	Gymnocladus dioica
Maples: Leaves opposite, fan-lobed		
1. Notches between lobes V-shaped		
2. Leaves distinctly 5-lobed, whitish beneath.	Silver Maple	Acer saccharinum
2. Leaves appear 3-lobed, the two basal lobed reduced or absent	Red Maple	Acer rubrum
1. Notches between lobes U-shaped		
2. Leaf stem with milky juice when broken	Norway Maple	Acer platanoides
2. Leaf stem without milky juice.	Sugar Maple	Acer saccharum
Ash Trees: Feather compound opposite leaves		
1. Twigs and leaf stalks hairy	Red Ash	Fraxinus pennsylvanica
1. Twigs and leaf stalks not hairy		
2. Leaflets whitish beneath	White Ash	Fraxinus americana
2. Leaflets green on both sides	Green Ash	Fraxinus pennsylvanica ssp. subinterrima
Oaks with lobed alternate leaves (the last two may be difficult to distinguish)		
1. Lobes are rounded	White Oak	Quercus alba
1. Lobes are bristle-pointed		
2. Leaf is not deeply lobed (less than half way to the midrib)	Northern Red Oak	Quercus rubra
2. Leaf is deeply lobed		
3. Leaf with 7 or more lobes, the lobes often enclosing an oval and broadening toward their tips; end bud somewhat hairy; acorn base bowl shaped	Scarlet Oak	Quercus coccinea
3. Leaf usually with fewer than 7 lobes, the space between them wedge shaped, and the lobes tapering toward their tips; end bud hairless; acorn base saucer shaped	Pin Oak	Quercus palustris

Supplemental: Background Information on Trees

Adapted from: Peter Thomas, Trees: Their Natural History, 2000.

Conifers

Back in the Silurian, over 400 million years ago, the first vascular plants (those with internal plumbing) appeared on the Earth. From these the first trees evolved in the early Devonian around 390 million years ago. Within 100 million years, the coal-producing swamps of the Carboniferous (360-290 million years ago) were dominated by lush forests. We would have recognized the tree ferns from today's forests but the others have long since disappeared leaving us just a few small relatives. In these forests the first primitive conifers appeared and by around 250 million years ago (the late Permian) trees such as cycads, ginkgos and monkey puzzles were recognizable: the sort of trees found fossilized in the petrified forests of Arizona. The pines were not far behind, probably evolving around 180-135 million years ago (Jurassic) to share the earth with the dinosaurs.

Hardwoods

Conifer domination was long and illustrious but the early hardwoods were diversifying during the early Cretaceous, around 120 million years ago. The hardwoods probably evolved from a now extinct conifer group that had insect-pollinated cones. During the Cretaceous period and into the early Tertiary (65-25 million years ago) the hardwoods underwent a massive expansion, displacing the conifers, undoubtedly helped by the warm humid global climate of the early Tertiary. By 95 million years ago a number of trees we would recognize today were around -- laurels, magnolias, planes, maples, oaks, and willows. By the time the dinosaurs were disappearing (65 million years ago) the hardwoods were dominating the world with the conifers exiled mostly into the high latitudes.

Living fossils

Most of the types of trees we see every day have been around for a very long time. Perhaps the most incredible are the growing number of rediscovered "living fossils:" trees known from fossil record and which were thought to have become extinct, and yet have been found hanging on in remote parts of the world. The "dawn redwood" (*Metasequoia glyptostroboides*) was 're-found' in China in 1945. It would have been familiar to the dinosaurs. We have (at least) one here on campus (near Fenske and Althouse labs). Knowing 1) that this tree type was found just 60 years ago, and determining 2) how old the one on campus is, 3) how long after it was first discovered did Penn State plant one for our on-campus arboretum here?

Tree Structure

A tree lives in basically the same way as any other plant. The leaves produce sugars, which are the fuel used to run the tree and to make the basic building blocks of cellulose and lignin

that form the bulk of the tree. The sugars are moved through the inner part of the bark (the phloem) to where they are needed around the rest of the tree. Sugars not required for immediate use are stored in the wood of the trunk, branches, and roots. The roots at the other end of the tree absorb water and minerals (such as nitrogen, phosphorous, and potassium) from the soil. The water and dissolved minerals are pulled up through the wood of the tree (the xylem, which is actually dead) to reach the leaves, the main users of water. The minerals are used with the sugars to build essential components of the tree, including the flowers and fruits needed to start the next generation.

Growth

Trees get bigger in two ways: 1) the buds scattered along the tree act as growing points for making existing branches longer or for making new branches. Once made, 2) the woody skeleton gets fatter by a thin layer of tissue (the cambium) beneath the bark, adding new bark and new wood. In temperate areas where growth stops over winter these new layers are seen as the familiar annual rings in the wood. Generally, the living portion of the tree is a thin skin (the cambium, or cambial tissue) over a long-dead skeleton, which nevertheless must be preserved from the attentions of fungal rot and animals.

Tree Leaves

Count / extent

The leaves are the main powerhouse of the tree. Combining carbon dioxide from the air with water taken from the soil they photosynthesize, using the sun's energy to produce sugars and oxygen. These sugars (usually exported from the leaf as sucrose, the sugar we buy in packets) are the real food of the tree. A large apple tree holds 50,000-100,000 leaves, a normal birch may average 200,000 leaves, and a mature oak can have 700,000 leaves. But a mature American elm may have 5 million leaves. With this many leaves, a mature beech can fix 2kg of carbon dioxide per hour, producing enough oxygen (as a byproduct) for ten people every year. Inside the leaf, the chlorophyll that captures the sun's energy is contained in tiny chloroplasts, which are concentrated in tightly packed cells of the upper part of the leaf where there is the most light. Beneath each square millimeter of leaf there are up to 400,000 chloroplasts, giving the total area exposed to light within a large deciduous tree of more than 350,000 square kilometers!

Leaf surface structure

The leaf needs to be waterproof to maintain a moist working environment inside and prevent the leaf from wilting. To this end leaves have a skin (epidermis) of tightly packed cells overlaid by a waxy cuticle, which has the property of resisting the passage of water without halting completely the movement of air. There is still a need for holes in this waterproof skin to allow effective exchange of gases. In trees, these holes or stomata (stoma, singular) are usually concentrated on the underside of the leaf away from direct heat of sunlight (especially in glossy, evergreen leaves) but occur on the upper surface (although in low density) in about 20% of tree species. Stomata can also be found on twigs and branches that have a green photosynthetic layer.

Sun and shade leaves

With a large number of leaves held by a tree it is almost inevitable that some will shade others. Part of the solution to this problem is that leaves of most trees can be divided into "sun" and "shade" leaves. Shade leaves are larger, thinner, with a thinner cuticle, darker green (more chlorophyll per unit mass), less lobed, with half to a quarter the density of stomata. They can work more efficiently at lower light levels than "sun" leaves but cannot handle the bright for long periods. However, "shade" leaves have a quicker response time in opening stomata and so can utilize the brief moving sunflecks that dapple the ground under the canopy. "Sun" leaves on the otherhand work better in bright light and if put into deep shade their higher respiration rates require more carbohydrate than they can produce, so they lose weight and eventually die. Each leaf develops according to the conditions under which it grows, so sun and shade leaves and their overall proportion on any particular tree depends entirely upon the location of the leaf and the growing conditions of the tree.

Gas exchange vs. water loss

The loss of water by a tree (called transpiration) can be prodigious -- up to 40-300 liters per day in a large deciduous tree. Although water loss is a side effect of having holes in the leaves for gas exchange, it does have its benefits. The flow of water up the tree is the main way of getting dissolved minerals taken up by the roots to where they are needed. Moreover, evaporation helps to keep leaves from overheating in hot sunshine. Because most of the water is lost through the stomata, this is an obvious place to control water movement. Most trees optimize the need for carbon dioxide uptake against needless water loss!! Stomata usually close when it is too cold or dark for photosynthesis or when the leaves are in danger of losing too much water and wilting. For example, on a bright day photosynthesis often shows a mid-day dip when sunlight is most extreme and the leaves are losing more water than they are supplied, so the stomata close to prevent wilting and damage. A nearby shrub in the shade may photosynthesize all day.

So delicate is the balance between gas movement and water loss that the density of stomata has been found to change in response to external conditions. Measurements from fossil leaves show that 140,000 years ago the dwarf willow had 40% more stomata than the 12,500 stomata/square cm found today. Reduction in density over time appears to be in response to increasing carbon dioxide concentrations -- fewer holes are needed to let in gas (and, thus, accidentally release water). This decrease has also been seen to happen over just a few decades by comparing herbarium specimens from the 1920s with the modern-day material. And a similar response has been seen over a much shorter time in response to carbon dioxide and temperature. Compared with leaves produced in the comparative coolness of spring, oak leaves growing in a warm late summer have 15% fewer stomata.

Boundary layer adjustment

In addition to stomatal water loss, some water is also lost directly through the cuticle of the leaf -- though this is likely only 5-10% of total water loss. In order to combat this, hairs,

such as the felted underside of some oak leaves, can help by reflecting light and by increasing the boundary layer (the stationary layer of air held over the surface of the leaf) making it harder for water to escape. (see more about very interesting boundary layer features on the photocopied attachment (pp.22-23).

Leaves for nutrient uptake, in addition to roots

Although the root system is the primary means of nutrient intake, nutrients can also be taken up through the leaf. Nitrogen compounds in all forms (gaseous, liquid, and particulate) have been seen to be taken up through the cuticle or stomata of trees. In Central European forests this absorption of nitrogen through leaves may contribute to 30% of the nitrogen demand of the trees.

Evergreen vs. deciduous

Why are some trees evergreen and some deciduous? Starting at the beginning, if there is no unfavorable period for growth during the year, as in the tropics, a plant will usually be evergreen: there is no reason to lose leaves that are still working. In climates with a period unfavorable for growth -- a winter or a hot dry summer -- deciduous trees have the upper hand. It is cheaper to grow relatively thin, unprotected leaves, which are disposed of during the inhospitable season, than to produce more robust leaves capable of surviving the off-season. In areas with even worse growing conditions, however, evergreen leaves will reappear. Firstly, this includes areas where the growing season is very short, as in northern and alpine areas. Evergreen leaves start photosynthesizing as soon as conditions allow and no time is wasted while a new set of leaves is grown. Secondly, evergreen leaves are found where nutrients are in short supply on poor soils or very wet soils where rooting is restricted. Here it is too expensive to grow new leaves each year and it is cheaper to pay the cost of producing more robust leaves that can survive the inhospitable period. Last of all, if the growing conditions become even more severe, such as in the far north and upper alpine areas, trees may again revert to being deciduous. Despite the problems of having to cope with a short growing season and few nutrients, the winter is so severe that being deciduous is still a cheaper strategy than trying to keep leaves alive over the winter.

Leaf color

Most leaves look green because photosynthesis is driven by blue and red light and it is the green that is left over to be reflected or passed through the leaf. But not all leaves are green -- a study in Panama found that one species of tree has leaves which only turn green as they mature. It turns-out that because tender young leaves are prone to being eaten, the trees do not put valuable chlorophyll into leaves until they are fully expanded and tough. Still, this is merely a response to peculiar conditions and is not the norm.

Autumn leaf color

As a leaf starts to die in autumn, the substances that can be reused, such as proteins and chlorophyll, are broken down and taken back into the tree. At the same time as leaves are systematically stripped of useful assets they are filled with unwanted things such as silicon,

chlorine, and heavy metals. The yellow pigments (carotenoids) normally found in a leaf but previously masked by the chlorophyll now show through. Red pigments (anthocyanins) mixed with the yellow in different proportions produce the oranges, reds, purples, and sometimes blues of autumn leaves. These red anthocyanins are commonly produced in great quantities in dying tissues from sugars that remain in the leaf. Thus red is usually the first color to show in a leaf, as it breaks down sugar and moves toward orange and yellow. And leaves with the most sugar -- such as sugar maple leaves -- are those with the most red. However, all this requires warmth and bright light during the day for the remaining chlorophyll to work, and cold nights to slow the transport of sugar out of the leaf. Which is why the sunny autumns of the eastern U.S. get splendidly colored maples, and the British, say, with their grey shores are left with a duller, browner autumn maple.

Review: Green – chlorophyll; Red (from sugars) – anthocyanin; Yellow/brown - carotenoids and xanthophylls; Brown - caused when all other pigments break down

Why have compound leaves? Imagine two trees, one of which has branches with ordinary leaves and the other has compound leaves the same overall size and shape as the first tree's branches. The tree with compound leaves finds two ready advantages: First, its compound leaves help to reduce water loss in arid seasons. Small twigs are the biggest source of water loss once leaves have fallen, so compound leaves (which reduce the twig points still connected to the living tree) are found in areas with severe dry summers. Second, cheap disposable branches may be useful in areas where rapid vertical growth is important. It is assumed that the structure of the compound branch, less woody than a standard branch, is less of a nutrient burden to construct. It can therefore direct more energy to height growth and save energy on tree "branches" that will only be used for a short time, anyhow (as they'll be too shaded, otherwise). Compound leaves are seen in many early-successional species that need to grow tall quickly to stay ahead of the competition, especially in tropical trees that invade gaps.

Supplemental: Notes on Trees

Taken from: Charles Fergus, "Trees of Pennsylvania and the Northeast," 2002.

White Pine (*Pinus strobus*)

The White Pine is the largest pine east of the Rocky Mountains. The seedling grows slowly at first, though, taking perhaps ten years before it is even 5 feet tall, even in full sunlight. After that, growth takes off, and trees can be 60 feet high and have a 2-foot trunk diameter in only thirty years. Averaging 16 inches of new growth per year, white pine can tower up to 200 or even 220 feet before it reaches its mature stature. Old-growth pines can have trunks 6 feet in diameter, although 3 to 4 feet is more common. Interestingly, the white pine has no taproot, instead it sends out 3 to 5 large lateral roots to keep it tolerably wind-firm.

The cutting of white pines, primarily as masts for ships of the British navy, began in 1654 in the Piscataqua River watershed, which currently separates coastal New Hampshire from Maine. Ships designed specifically to haul pine masts carried up to thirty trees at a time back to England. By 1691 the cutting of pine for the British navy and colonial use had reduced the numbers of easily accessible large pine enough to prompt the British Admiralty to pass a new law for the Massachusetts Bay Colony Charter. It mandated that all white pine twenty-four inches and larger in diameter be reserved for the navy.

Under the king's command, all such trees were blazed with the mark of a broad arrow. Three blows with an ax produced a symbol that probably looked more like a large turkey track than an actual arrow. Although the fine for cutting one of these large trees was one hundred pounds, the lack of enforcement did little to curb unauthorized cutting and use of these superb pines. By the early 1700s, all white pines were placed under the king's protection, yet indiscriminate cutting of the region's most majestic trees continued, reaching ever deeper into the river drainages of central New England. This prompted a Timothy Dwight to write in 1821, "There is reason to fear that this noblest of all vegetable productions will be unknown in proper size and splendor to future inhabitants of New England." This was prophetic, for not one of these huge white pines remains.

Sugar Maple (*Acer saccharum*)

Sugar Maples leaves, obviously, turn a vivid orange and brilliant red in autumn, and they form the primary colors of autumn in New England and elsewhere in the East. In the open they grow a short trunk and sprout stout erect branches that form a round-topped crown. In a wood setting, however, they grow a long, straight trunk and shallow crown, often self-pruning its lower branches for over half its overall height.

Syrup and sugar made from the sap were the only sweeteners available to the original human inhabitants of North America. Members of the Iroquois and Chippewa tribes collected the sap in vessels, then concentrated it by letting it freeze and removing the ice to get rid of excess water. They also boiled the sap in small batches by filling elm-bark containers and troughs hollowed into logs, and putting fire-heated rocks in with the sap to steam off the water. No other

type of sugar was locally available in the colonial era, and maple successfully competed in price with cane sugar until the second half of the nineteenth century.

Sugar Maple cannot tolerate polluted air; for city plantings, the imported Norway maple does better. Salt, used to melt the ice on paved roads, can kill sugar maples. Far more dangerous to the species as a whole is the ongoing problem of acid rain and snow, which ecologists term acid deposition. Across the northeastern United States and southern Canada, the health of sugar maples has declined markedly in the last half century, and acid deposition, caused by power plant and industrial emissions farther west, may be the culprit. The acid leaches out key elements from the soil, including magnesium, potassium, and phosphorus. It may kill or disable mycorrhizal fungi, microorganisms that mingle with the roots of trees and improve their ability to take in nutrients and water.

Red Maple (*Acer rubrum*)

Whatever the season, Red Maple shows its namesake color, vividly or with subtlety and restraint. In winter, the buds and twig tips are a rich wine red. As winter gives way to spring, the swelling buds form a red haze on the hilltops. Soon the flowers open, adding crimson to the faintly greening landscape. The leaves unfurl ruddily in April and May; when they assume their summer green, the leafstalks remain touched with red. And in autumn, the leaves become scarlet, some of the brightest foliage in the woods. Weather and soil moisture affect the colors' brilliance each year, and soil chemistry may have an impact: researchers suggest that the more acidic the soil, the deeper the red coloration. The scientists also believe that most of the trees turning orange are females, with the males displaying that particularly combustible red.

The wind, and perhaps a few wild, solitary bees, pollinate red maple flowers. Pollination is timed to take place before the emergence of leaves, which might shield the flowers from the wind and obstruct the successful transfer of pollen. Fertilized female flowers ripen into winged fruits, called keys or samaras, 1/2 to 1 inch long, attached in opposing pairs at the ends of the drooping stems.

White Oak (*Quercus alba*)

The pale bark gives the tree its name. It is made up of small, irregular scales or patches -- looking like ski-trails on a mountain -- that often are only loosely attached. On small branches the bark may be light green, reddish green, or almost silvery and not patchy.

Lacking a strong tannin defense -- as opposed to the Red Oak -- white oak acorns germinate quickly after they fall; before freezing weather, their first small roots have penetrated the soil, with the shoot remaining dormant until the following spring. Animals avidly search out these sweet-tasting nuts which, at about 6% protein and 65% carbohydrate, constitute a high-energy foodstuff. The Native Americans boiled the nuts to remove the water-soluble tannins, then ground them into a meal used in baking bread. Acorns from some white oaks are sweet enough to eat out of hand.

In Virginia, botanists monitored a single sixty-nine year-old white oak and found that it bore more than sixty thousand acorns in one year; the tree was 69 feet tall and had a 25-inch trunk diameter. Typical production for a mature forest-grown tree, however, is probably closer to 10 thousand acorns per year.

Because it risks decay, white oak has been used for log houses, barn frames, covered bridges, railroad ties, and fences. The pores are plugged with woody cells, preventing liquid seepage, unlike Red Oak which would give you a leaky cabin, bridge, or barrel.

Eastern Hemlock (*Tsuga canadensis*)

Pennsylvania is graced with many old-growth Hemlock stands, remnants of the original forest that covered much of the Northeast before Europeans arrived. Alan Seeger park, just outside of town, has a lovely trail which leads through a small stand of these giant remnants.

Seen from the side or above, hemlock foliage is a dark blue-green; seen from below, it looks silvery. The needs account for this bicolored aspect: they are a dark green on top and pale below. The pale aspect comes from a chalky white line on either side of the central rib. The white line is a series of stomates, openings that allow gas exchanges between the need and the atmosphere.

When scientists studied hemlocks in an old-growth stand at Heart's Content Scenic Area, in Warren County, they found sapling 2 to 3 inches in diameter at breast height that were two hundred years old! -- waiting in the shade beneath ancient, but ultimately mortal, giants. A tree with a diameter just over 10 inches was 359 years old; nearby dominant trees were the same age but stood much taller and were 24 to 35 inches in diameter. Most hemlocks live 150 to 200 years, however the oldest yet found was 988 years, having a diameter of 84 inches (that's 7 feet) and a height of 160 feet. In Cook Forest State Park in Clarion County there is a tree that is 125 feet tall at 193 inches around the diameter -- that's over 16 feet wide.

Horse Chestnut (*Aesculus hippocastanum*)

This is a non-native species originally from the Eurasian continent. It is said that horsemen in Turkey used the seeds to brew a remedy given to horses afflicted with coughing, a practice commemorated in both the common and Latin species name. Perhaps surprisingly, then, all parts of the plant are toxic to humans. Symptoms include depression, vomiting, weakness and stupor, and paralysis. The nuts, though quite pretty, have killed children who've eaten them.

Ohio Buckeye (*Aesculus glabra*)

The Ohio Buckeye is a native specie of our western counties, though it is not particularly common and the "likeliest places to see them are parks, campuses, and arboretum." Buckeyes have opposite, compound leaves whose large, toothed leaflets fan out from the tip of a long, single stem, resembling the spokes of a wheel or the outspread fingers of a hand. No other group of North American trees exhibits this arrangement.

Interestingly, Ohio Buckeye is also called "Fetid" or "Stinking" Buckeye, as the twigs and foliage, when broken or crushed, release a foul smell.

Over summer, fertilized flowers develop into fruits that consists of one to three large seeds housed in a rounded, leather, slightly spiny husk. These are the Buckeyes your students are playing with -- so dubbed because early settlers thought they resembled the eye of a deer: dark brown, gleaming, and possessing a large, pale scar of attachment suggesting an eye's iris. When they fall in September and October, squirrels carry them off and bury them.

The seeds contain a narcotic alkaloid which is poisonous to livestock, so many farmers have eradicated the tree from their property. The Native Americans were aware of this narcotic property and used the mashed seeds and branches to stun fish so they could be easily caught.

Green Ash (*Fraxinus pennsylvanica*)

There exist between 60 and 70 different species of ash trees across the Northern Hemisphere; sixteen in North America, and three in Pennsylvania. The most abundant (and also most valuable) is White Ash; Black Ash occurs statewide; Red Ash (also known as Green Ash ... and what we're looking at, here), is also widespread in the state.

Ash trees have strong links to legend and mythology. Germanic peoples believed that a giant ash, Yggdrasil, supported the universe. One of the tree's roots extended into the underworld, another into the land of the giants, and a third into the home of the gods; dew that dripped from the tree's leaves supposedly made flowers spring up all over the earth. To new world immigrants, a door framed with ash was a "Witch Door," which warded off evil spirits. Others placed ash in their boots and leggings, believing that no snake would ever cross such a barrier. If bitten, they treated the snakebite with preparations made from the buds and bark of ash.

Red Ash and Green Ash were once considered separate species (the former has hairy twigs; the latter doesn't) but now taxonomists merge the two under the generally accepted name of red ash. This hardy lowland tree grows to a maximum height of 75 feet in mostly wet habitats such as bottomland woods, stream banks, and moist fields.

Sweet-gum (*Liquidambar styraciflua*)

Sweet-gums grow mainly in the Southeast, where in the past loggers cut 140-foot tall sweet-gums, their trunks 4 to 5 feet thick, from the deep gumbo soils of the Mississippi River valley. In Pennsylvania, however, they tend to range between 20 to 50 feet in height, perhaps reaching up to 75 feet.

If its bark is breached, a sweet-gum will seal the wound with a thick sap that hardens and weathers to a sticky golden or brown gum. The tree's common name comes from this sweet smelling repair agent. The Latin name, *Liquidambar*, comes directly from Linnaeus, who described its aroma and the substance as resembling amber. Pioneers used the "liquid amber" as chewing gum and an antiseptic.

It is considered a relatively ancient species, geologically speaking, having emerged during the Cretaceous Period between 135 million and 65 million years before the present, a span during which dinosaurs disappeared and flowering plants began to develop.

Over the summer the fertilized female flowers develop into prickly brown balls -- "gum balls" -- 1 to 1.5 inches in diameter, laden with seed-bearing fruits. As do the seeds of maples, those of the sweet-gum have papery wings -- and the wind disperses them to a distance of up to 200 feet from the parent tree.

Ironwood (*Carpinus caroliniana*)

Also known as Hornbeam, connecting two old words: *horn*, meaning "hard" or "tough" and *beam*, cognate with the German *baum*, as in *tannenbaum*, meaning "tree." Thus, "hard tree." Which is why it's commonly known as Ironwood. Naturally, the wood is close-grained, hard, and heavy, at 45 pounds per cubic foot. Early settlers used it to make leak-proof bowls and dishes -- wrote William Wood of that era, "requires much paines in riving as is almost incredible."

The autumn foliage is scarlet and jack-o'-lantern orange, among the fieriest hues in the eastern woods. Its graceful three-pointed bract (the leaflike structure just below any flower, fruit, or stalk) functions like the blade on a maple samara (a maple "key"), giving the seed the buoyancy it needs to travel on the wind.