Secondary Plant Compounds of Quaking Aspen (*Populus tremuloides)*: A Review

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NRE 437 Graduate Student Requirement

The Trembling Aspen (*Populus tremuloides)* is one of the most widely distributed trees in North America (Barnes 2004). It can be found from northern Alaska all the way down to Mexico. In the western United States, the aspen lives in higher elevations, primarily between 6500 and 10000 feet, in high plateau and alpine habitats. Michigan is in the southern limit of the aspen's range, and it is more common in the northern part of the state.

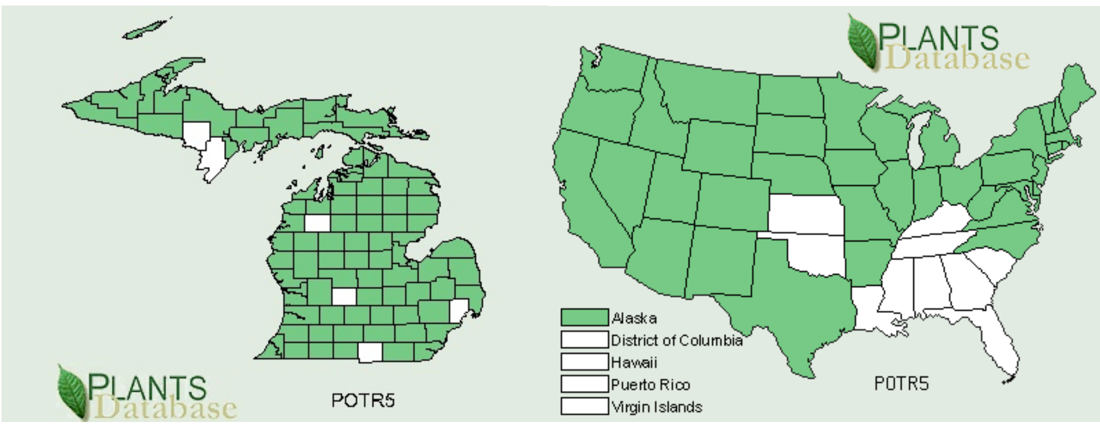

Figure 1 The distribution of *Populus tremuloides* within the stat of Michigan, county by county, and the distribution within the United States. (USDA Plants Database, *Populus tremuloides)*

Quaking aspen generally form pure stands or in mixed stands with bigtooth aspen (*Populus grandidentata),* but it is not uncommon to find it with scrub oaks and sagebrush at lower elevations or as a prostrate form at lower elevations (Perala 1990). It is shade intolerant, tolerant of disturbance and is quickly replaced in succession by shade tolerant species. The leaves that drop in the fall decay relatively quickly and produce a characteristic "aspen soil" with a generally high pH (Perala 1990). Aspen prefer moist soil and stream banks where water is nearby (Guennel 1995). Aspen tend to grow on soils that have supported clones for many years prior (Barnes 2004). The trembling aspen can also form hybrids, some of which include *Populus ×heimburger,* a hybrid with *Populus* *alba,* the European white poplar, and *Populus ×smithi,* a hybrid with *Populus grandidentata.* Both of these hybrids occur in the state of Michigan as well as other parts of the United States (Barnes 2004).

The quaking aspen is capable of both sexual and asexual reproduction forming clonal groups. Seedlings establish with great difficulty; once this takes place they start to reproduce via root sprouts. Reproduction via root sprouts produces genetically identical individuals, the group as a whole is termed a genet. Each distinct individual in the genet is called a ramet. Most root sprouts develop within 10 meters of the stem from roots that are 2-10 centimeters from the surface (Perala 1990). This can take place as soon as one year after initial sprouting. The root sprouts may grow up to 2 meters or more in the first year (Barnes 2004). Once a root sprout appears, surrounding growth is suppressed by the production of auxin in the leaf tissue and transported to the roots (Shepperd and Smith 1993). Auxin transport is cut off when an overstory stem dies, is cut, or browsed (Shepperd and Smith 1993), allowing the root sprouts to start growing again.

Sexual reproduction takes place from March to April in the east, including Michigan, and from May to June in the west, areas including the Rocky Mountains (Perala 1990) before the leaves are fully expanded. This allows maximum pollen dispersal because the canopy is not obstructed by the leaves. The trembling aspen is dioecious, with male and female flowers appearing on separate trees, and it is wind pollinated. The heat sum for aspen in order to trigger flowering is represented by a temperature above 12°C for about 6 days (Perala 1990). Female trees generally flower and leaf out before male trees do (Perala 1990); this is one of the ways that the aspen prevent inbreeding.

Aspens do well in areas of disturbance and are among the first trees to colonize a site after a disturbance such as fire. The current practice of fire suppression has lead to a decline in the aspen populations (Rogers 2007). Fires would sweep through an area clearing out dead and diseased trees and leaving the landscape clear for the aspen to grow. With a lack of natural fire, which promotes sprouting and regeneration, aspen are slowly being replaced by other species and are on a decline (Barnes 2004). Controlled burns in certain areas have lead to some regeneration (Shepperd and Smith 1993), but not on the scale that is needed. Aspen can also quickly reestablish themselves after such disturbances as avalanches, landslides, tree felling, and pathogens (Shepperd and Smith 1993). These disturbances mimic the effects of fire and can lead to re-growth of healthy stands. These activities, however, may also lead to higher disease rates from infection of logging-related wounds on the remaining trees (Shepperd and Smith 1993).

Aspen have been used by early pioneers and Native Americans as remedies for many different things. The bark was used as a fever remedy and for scurvy (Stubbendieck, Hatch et al. 1997). It also contains salicin, which is similar to the active ingredient in aspirin and is one of the compounds that will be discussed in detail later (Stubbendieck, Hatch et al. 1997). A substance similar to turpentine was extracted and used internally as an expectorant and externally as a counterirritant (Stubbendieck, Hatch et al. 1997). In the spring the pulpy inner bark was used as a sweet treat for children (Kershaw 2000). The bitter leaf buds and young catkins can also be eaten and used as a source rich in vitamin C (Kershaw 2000). Aspen bark also has a white powder on its surface that contains yeast and can be used in baking.

The quaking aspen is an important fiber source that is mainly used for paper pulp, flake board and many other composite products (Perala 1990). It can also be used for paneling, furniture, flooring, animal bedding, tongue depressors, playground structures and ice cream sticks (Perala 1990). Aspen does not splinter, making the tree ideal for wood products, but the wood is prone to warping and decay (Kershaw 2000). Even though aspens are attractive and fast growing, they are seldom used as landscaping trees because they are susceptible to many diseases and their propensity to produce root sprouts almost anywhere (Kershaw 2000).

The sum of all the chemical reactions that take place with in an organism represent its metabolism. Most of the time when we think of metabolism in plants we think of photosynthesis and respiration, the products of which are commonly called primary metabolites. The principal primary metabolites are: lipids, proteins and carbohydrates. Many plants, however, produce molecules that have no role in growth and development, these are called secondary metabolites (Hopkins 2004). They generally occur in low quantities and are commonly restricted to certain families, genera and even species. Aspen contain some of the most well know secondary metabolites. They include condensed tannins, phenolic glycosides, including salicin, salicortin, tremuloidin, and tremulacin, and coniferyl benzoate (Erwin, Turner et al. 2001). All of these compounds are phenolic products of the shikimic acid pathway.

The shikimic acid pathway links metabolism of carbohydrates to biosynthesis of aromatic amino acids, including phenylalanine, tyrosine, and tryptophan (Hopkins 2004). In a sequence of seven metabolic steps, phosphoenolpyruvate erythrose 4-phosphate are converted to chorismate, which is the precursor of the aromatic amino acids and many aromatic secondary metabolites (Herrmann and Weaver 1999). One of the pathway intermediates is shikimic acid, which has given its name to this whole sequence of reactions. This shikimic acid pathway can be found in bacteria, fungi, and plants, but not in animals (Hopkins 2004). The common herbicide, glyphosphate, (available commercially as Roundup) kills plants by blocking a step in this pathway (Herrmann and Weaver 1999).

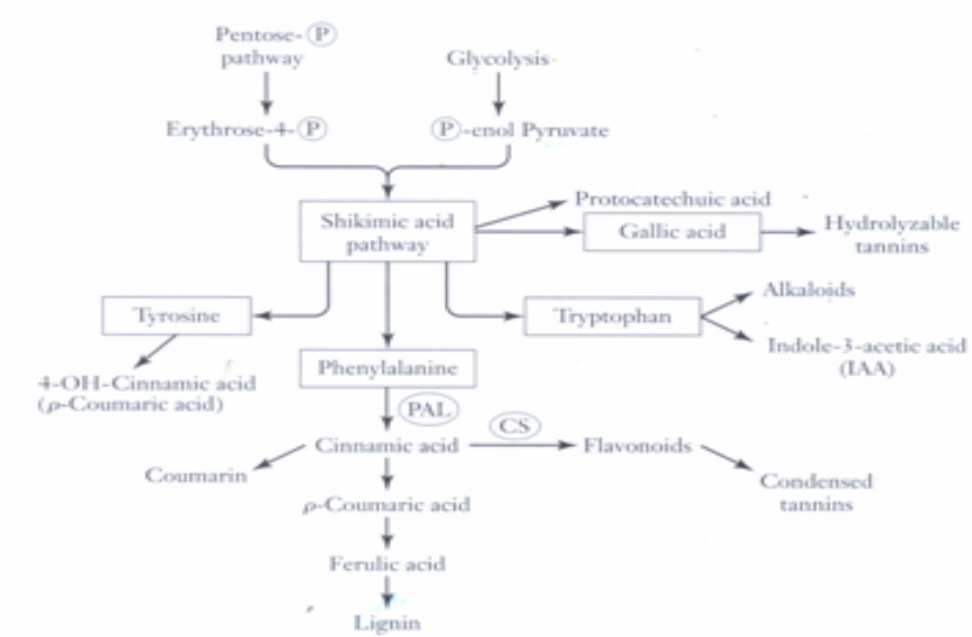

Figure 2The Shikimic acid pathway plays a vital role in the production of secondary metabolites of *Populus trenuloides (Hopkins 2004)*

Tannins and phenolic glycoside compounds are found in the leaves, stem and root tissue of plants, while coniferyl benzoate is found in flower buds (Erwin, Turner et al. 2001). It has been often hypothesized that these provide a significant role in protection from herbivores, either mammalian or insect. Aspen provide food for browsing mammals such as hare, beaver, deer, elk, and moose. These trees are also victim to regular insect outbreaks - such as forest tent caterpillars, gypsy moths, and large aspen tortrix - as well as fungal and bacterial pathogens. Because of this constant onslaught, juvenile sprouts typically express high levels of chemical defenses (Erwin, Turner et al. 2001; Lindroth, Donaldson et al. 2007). As the trees grow beyond the reach of mammalian herbivores, the levels of chemical defenses typically decline (Lindroth, Donaldson et al. 2007). Levels of tannins and phenolic glycosides tend to differ between young plants and older ones, with high levels of phenolic glycosides and low tannin levels in young ramets and the reverse in mature trees (Donaldson, Stevens et al. 2006).

Elk, *Cervus elaphus,* are common in the intermountain west and in the northern part of Michigan. Aspen saplings are a particular favorite of elk and it is often thought that they are part of the reason for the aspen's decline (Bailey, Schweitzer et al. 2007). Elk feed on shoots of mature aspen mostly in winter, as mature aspen are largely found in their winter ranges (Erwin, Turner et al. 2001). Elk also eat the leaves and shoots of the aspen seedlings that grow extensively throughout their summer range (Erwin, Turner et al. 2001). To help defend themselves against the elk, quaking aspen increase the concentrations of phenolic glycosides in their tissues. It has been shown that concentrations of certain phenolic glycosides, such as tremulacin and salicortin, in unbrowsed saplings were 5-7% greater after one year and 8-13% greater after four years compared to the initial concentrations before herbivory took place (Bailey, Schweitzer et al. 2007).

Ruffed grouse (*Bonasa umbellus*) feed on aspen staminate flower buds and catkins in the spring. The trees on which the grouse feed on, however, depend on the concentration of coniferyl benzoate contained within the tissues (Guglielmo and Karasov 1995). The grouse often locate the trees in the area that have the lowest concentrations of coniferyl benzoate and continue feeding on them throughout the winter (Guglielmo and

Karasov 1995). Coniferyl benzoate is toxic like the other secondary plant compounds, and has several physiologic effects upon the grouse, including inhibition of protein digestion, toxic effects, and antiestrogenic effects (Jakubas and Gullion 1990)

While much is known about the phenolic glycosides, very little research has been done on the effectiveness of tannins as defense compounds in aspen. Tannins are found in many plants, not just aspen. In general tannins inhibit herbivore digestion by binding to consumed plant proteins and making them more difficult for animals to digest and by interfering with protein absorption and digestive enzymes (Hopkins 2004). There are several categories of tannins that are found in plants, but condensed tannins are the form commonly found in aspen. Condensed tannins are polymers of flavonoid units linked by strong carbon-carbon bonds (Hopkins 2004). These bonds are not subject to hydrolysis but can be oxidized by strong acids to release anthocyanidins (Hopkins 2004). The tannins in aspen are thought to serve as protection against bacterial and fungal pathogens, viruses, and as inhibitors of photodamage (Stevens and Lindroth 2005).

Aspens are a very desirable tree in many respects. They have many uses, including everything from Popsicle sticks to playground equipment to the paper industry. Aspen in the United States are on decline, however, for various reasons, some of which include the suppression of fires that the aspen need to regenerate, and the overpopulations of elk that feed on new saplings. The trembling aspen are known for their chemical compounds that are used for defense against herbivory, which include phenolic glycosides, tannins, and coniferyl benzoate. Aspen are probably best known for their salicin, a phenolic glycoside, which is similar to the active ingredient in aspirin. Phenolic glycoside levels are influenced by herbivory by mammals and insects as well as age of the individual. Hopefully, with some new management practices, the aspen will be a tree that will be around for a very long time.

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