Carbohydrate Assimilation, Translocation, and Utilization

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GROWER RECOMMENDATIONS

Tree growth and nut production are primarily a function of carbohydrates made available through photosynthesis. Photosynthesis occurs mainly in the leaves and is control by the amount of light, carbon dioxide, and water available to the leaves.

Photosynthesis in walnut increases proportionally to the amount of light reaching the leaves up to one-third of full sunlight. Nut production requires use of thinning and pruning practices that develop trees with large crowns with leaves exposed to light of moderate levels of sunlight for at least part of the day. Pruning is especially important on lateral bearing cultivars to allow light penetration to the fruiting spurs. Carbon dioxide, an essential ingredient for production of photosynthates, enters the leaves primarily through the stomata. Insufficient soil moisture during summer droughts results in reduced transpiration and closure of stomata. Excessive soil moisture can lead to unhealthy roots incapable of supplying sufficient water to the leaves for transpiration. Photosynthesis and respiration are biological processes that involve plant proteins or enzymes made up of carbon, nitrogen, oxygen, and various mineral nutrients. Different parts of a walnut tree have changing demands during the year for photosynthates for respiration, growth of new plant parts, and the developing nut crop. Depending on the cultivar, heavy crop loads may adversely affect the following year's crop by adversely affecting female flower initiation and reduced amounts of stored carbohydrates. Anthracnose, a common leaf spotting disease, utilizes carbohydrates that normally would be used by the tree for growth and nut production. Late summer fertilization in Missouri may enhance nut production by reducing severity of anthracnose or possibly altering the plant growth regulators involved in female flower initiation and development. The processes associated with nut production appear to be under strong genetic control; thus annual heavy nut production will require selection of walnut cultivars exhibiting multiple leaf layers to maximize photosynthate production, tendencies toward lateral bearing, good resistance to anthracnose, and efficient use of photosynthates for tree growth and nut production.

TECHNICAL INFORMATION SUPPORTING RECOMMENDATIONS

Many environmental factors and cultural practices can affect the ability of walnut trees to convert atmospheric carbon dioxide (CO2) via leaf photosynthesis into carbohydrates, the subsequent translocation or distribute these carbohydrates throughout the tree, and, finally, their utilization for respiration, growth, or nut production. Little research has been done on carbohydrate assimilation, translocation, and utilization in eastern black walnut; however, what we know about these processes appears similar to what has been found for other walnut and large mast producing species. Thus, when information was not available, research information obtained by other researchers was used on carbohydrate assimilation, translocation, and utilization within English walnut (Juglans regia L.) and pecan to develop the following picture for eastern black walnut. Figure 1 is a schematic

representation of the carbon cycle for eastern black walnut as adapted from the model for English walnut developed by DeJong and Ryugo (1985).

The carbon cycle begins with the conversion of carbon dioxide and water into carbohydrates CH ^{2} 2O)n and oxygen through a process called photosynthesis. Green pigments (chlorophylls) capture light energy from the sun and convert it into chemical energy. This chemical energy is used to drive the reduction of carbon dioxide into simple carbohydrates that eventually become sugars. The actual process consists of a complex series of chemical reactions. As depicted in Figure 1, the leaves take up carbon dioxide and produce sugars that become part of the photosynthate pool. Depending on the demands for energy within the plant, these photosynthates can be translocated to other plant parts or converted to starches and stored for future use. The sugars are broken down to produce the energy (growth respiration) needed to assimilate other sugar-derived chemicals into various cellular components or broken down to produce the energy needed to maintain living tissues (maintenance respiration).

The carbon dioxide used during photosynthesis comes from the air surrounding the leaves primarily through stomata located on the lower surface of the leaves. The size of the stomatal opening is regulated by two guard cells that are quite sensitive to various environmental factors. These stomatal openings are also important in controlling the transpiration rate or loss of water vapor from the leaves. If insufficient water is available to the leaves, the stomata close and cut off the supply of carbon dioxide needed for photosynthesis to occur.

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                                                  __Atmospheric carbon dioxide CO2)___
                                                                  /\                /\      /\
                                              | (Photosynthesis)  |                |       |
                                              |                   |                |       |
Photosynthate    <---------------\     |                   |                |       |
pool (CH20)                                \   |                   |                |       |
                                            \  \/                  |                |       |
   |  /\   |                          |-->Leaves-> |              |                |       |
   |   |   |                          |                |__Growth___|                |       |
   |   |   |                          |                |   respiration              |       |
   |   |   |                          |-->Trunk -->|                        |       |
   |   |   |                          |   Branches   |                            |       |
   |   |   |                          |                |_______ Maintenance _____|       |
   |   |   |----------------> |          |          respiration                |
   |   |        (Translocation)       |-->Roots -->|                            |
   |   |   |----------------> |          |_____________________        |
   |   |   |                          |                |            |                |       |
   |   |   |                          |-->Flower-->|              |                |       |
  \/   |   |                          |                |            \/               \/      |
Storage pools                          |                |      Diseases and     Litter and
|
  (starch)                             |--> Nuts --> |insects            prunings     |
                                              |                   |                |       |
                                              |                   \/               \/      |
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|------> Organic carbon losses ------> |

Figure 1. Carbon cycle for nut-producing eastern black walnut trees.

FACTORS INFLUENCING PHOTOSYNTHESIS, PHOTOSYNTHATE POOLS, AND RESPIRATION

Light intensity - Walnut leaves produce photosynthates proportional to the amount of sunlight striking the leaf surface. Their leaves can effectively utilize up to approximately one-third of full sunlight after which increases in light do not result in additional production of photosynthates. The same photosynthetic mechanisms are activated at light intensities of five percent of full sunlight. Eastern black walnut has relatively thin crowns, so most leaves are likely to be exposed to light levels within this range for at least part of the day as the sun moves across the sky. If walnut trees are not thinned or the canopies are allowed to become to dense, the inner portions of the tree crowns become so shaded the leaves cannot produce sufficient photosynthates for maintenance respiration and die. This is especially important in high-production nut orchards using cultivars with lateral bearing characteristics. These cultivars have leafy fruiting spurs on the inside of the tree crown along the main branches. On English walnut, if the leaves on these spurs receive insufficient sunlight, the spurs eventually die. It is unclear if lateral bearing cultivars of eastern black walnut will also produce crowns sufficiently dense to lead to death of fruiting spurs.

Temperature - Most plant processes, including photosynthesis and respiration, have a minimum temperature at which the process begins and an optimum temperature for maximum efficiency. Above this temperature, the processes slow until lethal temperatures are reached. For English walnut, photosynthesis has a broad optimum between 60 and 86 °F after which the rate of photosynthesis rapidly declines. High temperatures are also very likely to limit the rate of photosynthesis in eastern black walnut, especially when the stomata are closed in response to limited soil moisture. Photosynthesis and respiration probably show similar response patterns to increasing temperature, although optimum temperatures for respiration are probably higher than for photosynthesis.

Deficient water supply - Insufficient available soil moisture causes stresses that can lead to wilting and premature defoliation under extreme conditions. Under less extreme conditions, the stomata close to decrease the rate of transpiration. When this occurs, carbon dioxide can no longer enter into the leaves through the stomata and photosynthesis decreases. If nut orchards are not going to be irrigated, then soil depth and water holding capacity become very important during site selection for the nut orchard. The water held within the rooting zone determines if adequate soil moisture is available during dry spells. In the Central Hardwood region, droughts usually occur in late summer when there is a high demand for photosynthates to fill the developing nuts. Lack of adequate soil moisture in late summer can also affect the physiological condition of the tree and suppress the initiation of female flowers necessary for the following year's crop.

Excess water supply - On soils subject to flooding or with shallow restrictive layers, excess soil moisture can also be a problem. Excess soil moisture during the growing season leads to decreased oxygen in the soil and death of roots needed to absorb adequate soil water during periods of high transpiration. On soils with restrictive layers in the walnut rooting zone, soil water accumulates above the restrictive layer leading to a perched water table during the dormant season. Walnut roots within the perched water table die from a lack of oxygen. If these roots are not replaced during the

growing season, it results in a reduced capacity to absorb soil moisture during the following growing season followed by stomatal closure from moisture stress and subsequent decreases in the rate of photosynthesis.

Nutrient supply - Maintaining proper mineral nutrition will be important for maintaining high rates of photosynthesis. Plant nutrients play important roles in the mechanisms for light trapping and in the carbon conversions associated with photosynthesis. Nitrogen is an important component of the amino acids that make up the proteins or enzymes involved in both processes. Phosphorus is an essential element in the chemical processes associated with energy transfer. Elements like potassium, magnesium, manganese, and iron are important cofactors associated with the proteins or enzymes involved with photosynthesis. Other elements like boron are important for nut production in English walnut. Research has shown that late summer application of nitrogen in black walnut plantings will enhance nut production.

Carbon dioxide concentration - Although atmospheric changes in carbon dioxide within walnut canopies can range from 350 to 600 ppm, these amounts are still adequate to maintain high photosynthetic rates. In fact, high carbon dioxide concentrations have been shown to increase the growth of eastern black walnut seedlings. However, stomatal closure in response to high temperatures or insufficient soil water will lead to low carbon dioxide concentrations within leaves and reduced rates of photosynthesis.

Insects and diseases - Anthracnose, a common leaf spotting disease, can cause significant losses in photosynthates during disease development and premature defoliation of trees. Initial infections occur in the spring and increase rapidly during wet weather. Significant amounts of photosynthates are drawn to the developing infection centers before they become visible. Heavy infection usually leads to premature defoliation during the period of female flower initiation and kernel maturation. Some walnut cultivars show good resistance to the leaf spotting disease. Cultural practices that decrease overwintering spore populations or increase nitrogen availability during the growing season have also been shown to be effective. Insects that feed on foliage reduce the leaf area and can affect the supply of photosynthates to the tree for growth and nut production.

TRANSLOCATION AND UTILIZATION OF PHOTOSYNTHATES

The goal of orchard management is to maximize photosynthesis and partitioning of photosynthates into a harvestable nut crop with minimal losses to pests, disease, or excessive growth. Virtually anything that is done to manage the orchard will influence some aspect of the carbon economy. The translocation of carbohydrates from the photosynthate pool can be viewed as a series of conflicting demands made on a limited resource (Van Sambeek and Rink 1982).

Although leaves are normally thought of as a source of photosynthate it is important to recognize that they are important sinks for photosynthates during their initiation and development in the spring. The primary sources of photosynthates at this time are stored reserves or starch in the bark and roots. Late spring killing frosts are especially damaging because the walnut tree must initiate a second set of shoots from already depleted storage reserves. It is not until leaves attain about half their maximum size that the sink-source relationships are such that a leaf produces sufficient photosynthate to complete its development. When leaves reach two-thirds of their maximum size, they become net exporters of photosynthates.

In addition to leaf initiation and elongation, stored starch is also necessary for shoot elongation and development of male catkins and pistillate flowers. Flowers begin to appear about mid April in the south and progressively later until early June in the northern parts of the natural range of eastern black walnut. If the walnut trees produced a heavy crop of nuts the previous year, these starch reserves may only be adequate to develop weak pollen and pistillate flowers. When leaves initiated during bud burst reach full size, they become important sources of photosynthate for the developing nuts, additional shoot elongation, and initiation of next year's male catkins. A developing nut crop is a stronger sink for photosynthates than these other processes and can limit additional shoot and leaf initiation and elongation.

During May and June, the fertilized nuts go through a period of rapid expansion. At the same time, the trees are putting on rapid height and diameter growth. During July, photosynthate demands remain high as nuts go through a period of nut expansion and shell hardening for the next month. Summer droughts during these three months will reduce photosynthesis and availability of photosynthates to the developing nuts resulting in small nuts.

In August, the embryo grows into the nut cavity and absorbs the endosperm. During September, fats are deposited as the kernel develops and matures. This is also the period when walnut forms pistillate flower initials in the terminal buds. Because photosynthate sinks closest to the leaves tend to be the strongest, foliar leaf diseases like anthracnose can utilize a significant amount of the photosynthate produced. Insufficient photosynthates in the late summer and fall can result in shriveled kernels and development of weak pistillate flowers. Once the nuts are mature and until the leaves are lost to disease or a killing frost, photosynthates are translocated to storage tissues for utilization the following spring. The mature nuts usually drop a few days after the leaves fall in October.

Recent studies in southern Missouri have shown mid-August fertilization with chemical weed control can significantly enhance nut production the following year. Because late summer fertilization can delay dormancy, recommendations still need to be developed for the timing of fertilization in the northern part of the walnut range to prevent winter damage. Several explanations have been suggested as to why later summer fertilization increases nut production. Increased nitrogen within the branch tips may alter the plant growth regulators responsible for the fall initiation of female flowers with the dormant buds. It may be the added nitrogen suppresses foliar diseases so that leaves are retained for a longer period and increase the stored reserves. It is generally recognized that increasing the length of leaf retention following nut maturation will decrease the alternate bearing tendency. The choice of ground covers can also greatly influence the retention of leaves into the fall and the amount of stored reserves that are deposited in the bark and roots.

Some studies suggest photosynthetic efficiency, translocation, and nut production appears to be under strong genetic control. In one study, Hammons Products Company determined the individual tree production on more than 12,000 trees during a seven-year period. During this time, around 40 trees produced no nuts while three trees produced more than 300 pounds of nuts annually. In general the heavy bearing trees are not significantly smaller than adjacent trees that have produced few nuts. The heavy bearing trees have lateral bearing characteristics with numerous fruiting spurs. These spurs normally produce eight to ten leaves which may dramatically increase the total leaf area and the amount of photosynthates needed for high nut production.

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