Assimilation and Translocation Patterns of Carbon-14 in the Shoot of Fruiting Pecan Trees, *Carya illinoensis* Koch\(^1,2\)

Joel T. Davis\(^3\) and Darrell Sparks

*University of Georgia, Athens*

Abstract. Assimilation and movement of \(^{14}\text{C}\) followed 3 patterns in the shoot and 1-year-old branch of pecan. During pattern I (bud break and leaf expansion stages), photosynthates were assimilated but not translocated from the leaves. Patterns II and III were characterized by bidirectional and basipetal translocation, respectively. When a leaf matured, initial translocation from the leaf was basipetal to other parts of the tree and acropetal to immature leaves and pistillate flowers. Bidirectional translocation from the leaf shifted to basipetal once distal leaves began to export photosynthates. Successively, as distal leaves matured, this pattern was repeated until all leaves were exporting photosynthates. Through the fruit-enlargement and shell-hardening stages, bidirectional and basipetal translocation occurred from the lower and upper leaves, respectively. As the kernel developed, the sink capacity of the fruit intensified and translocation from the more basal leaves again became bidirectional. After fruit maturity, translocation of photosynthates was basipetal from all leaves. Relationship of translocation pattern to the irregular fruiting habit of the pecan is proposed.

Irregular fruiting, often referred to as biennial or alternate bearing, is common in the pecan. The nature of fruit growth and correlative data suggest that irregular bearing is closely related to the carbohydrate content of the tree. Approximately 85% of the dry wt of the pecan fruit (shuck, shell, and kernel) accumulates during the last half of its 6-month growth period (31). Most of the growth (dry wt) of the shuck (involucre) and shell (ovary wall) precedes the growth of the kernel (seed coat, embryo, and endosperm) (10, 31). When shuck and shell growth are nearly completed, the kernel enters the exponential growth phase. Of the 3 fruit parts, the kernel appears to produce the greatest sink for carbohydrates. The mature kernel contains about 70% oil, most of which accumulates during the last 6 weeks preceding fruit maturity. Calculations of others (31) indicate that only 5% of the oil is formed from carbohydrates endogenous to the fruit before oil production begins. Since the kernel constitutes about 40 to 60% of the total dry wt of the mature nut (shell and kernel) (34), kernel growth represents a substantial accumulation of carbohydrates in a short period. The sink effect of kernel development is especially critical since it occurs during the latter part of the growing season (within the interval from ca mid-August to late October, depending on the cultivar). This permits only a short time before frost during which photosynthates are diverted from fruit growth to carbohydrate accumulation which are utilized as substrates during next season’s growth. The large amount of, and rapid rate of carbohydrate accumulation in the fruit during late season, when coupled with an inadequate leaf area per fruit, is correlated with suppressed kernel growth during the current season (3, 25), as well as suppressed pistillate flower production (3, 25, 30), fruit set (25, 30), and shoot growth (25) the following season. The suppressive effects of kernel development may be further compounded by premature leaf abscission that often occurs before or near the time of fruit maturity, which further suppresses fruiting the next season (13, 30). The importance of leaf area to kernel development and its subsequent relationship to alternate bearing is further evidenced by the fact that alternate bearing is accentuated by decreasing the leaf area (25, 30) and alleviated by increasing it (3, 30) just prior to the rapid rate of kernel development. The exhaustive nature of kernel development is ultimately reflected in depletion of starch reserves in the shoot (7) and in suppressed carbohydrate accumulation in roots (27, 28). These relationships suggest that fruit growth can suppress photosynthesis substrates to the point that flower formation and fruit set are limited the following season. Carbohydrates are of paramount importance in pecan growth and fruiting. Knowledge of \(^{14}\text{CO}_2\) assimilation and subsequent photosynthesis movement from bud break until natural leaf fall is prerequisite to understanding pecan growth and fruiting. Experiments were initiated with \(^{14}\text{CO}_2\) to examine translocation patterns of photosynthates in the shoots (current season’s elongation), leaves, fruit, and 1-year-old branches (previous season’s elongation) of pecan. The translocation patterns were delineated by treating entire shoots and single leaves with \(^{14}\text{CO}_2\) and then studying the

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3.\(^{3}\)Present address: Cave Spring, GA.

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relationships of the subsequent autoradiographs to leaf, shoot, and fruit development.

Materials and Methods
A stock solution of radioactive carbonate was prepared by dissolving 21.28 mg of C-labeled BaCO₃ (sp. act. 47.9 μCi/mM) and 85 g of Na₂CO₃ in 425 ml of water. Calculations from data of others (9,33) indicated that about 1 ml of stock solution per 10 g of fresh tissue per hr would be sufficient to produce adequate autoradiographs. The stock solution was reaeted with 1.0 N H₃PO₄ (1:5, v/v) in a generator to produce 14CO₂.

The 14CO₂ generator was as used by others (4,9) and consisted of a 500 ml Erlenmeyer flask and a 3-hole rubber stopper through which a funnel and 2 Tygon tubes, inlet and exit, were inserted. A closed system was produced when the funnel, used to deliver the carbonate and acid, was covered with the reaction solution. The ends of the 2 tubes were connected to a treatment chamber. One of the tubes was interposed with a 2-way hand aspirator. The aspirator was pumped intermittently (100 times) during treatment to circulate the 14CO₂ from the generator through the treatment chamber and out the other tube back into the generator.

The treatment chamber for shoots and individual leaves was a transparent plastic bag which varied in size with the plant part treated. The 2 tubes from the 14CO₂ generator were attached with modeling clay to the base of the plant portion to be treated. The plastic bag was placed over the plant part and the open end was sealed by depressing it into the modeling clay and tying it with a fine wire.

The most prominent shoot on a 1-year-old branch was treated to determine when photosynthate export was begun basipetally from the shoot to other parts of the tree. Treatments were begun at bud break, April 1, and continued until after a translocation pattern was established, May 5. In addition, single leaves on either the lower or upper portion of individual shoots were treated to determine the direction of photosynthate translocation during leaf and fruit development. Leaves, usually 8-10 per shoot, were numbered from the proximal to the distal end. Treatment of leaves was begun as soon as mechanically possible, April 10 and May 19 for the lower and upper leaves, respectively. After pistillate flower anthesis, treatment was limited to leaves on shoots bearing pistillate flowers or fruit.

The treatment period was 1 hr (10:00 AM - 11:00 AM) in full sunlight after which the leaves were re-exposed to the ambient atmosphere. The shoot and supporting 1-year-old branch were cut from the tree 8 hr after treatment, dissected, and glued in sequence onto white construction paper. Initially, entire shoots were mounted for autoradiographing, but as shoots grew, only representative structures were mounted. Cross sections of the shoot were taken at leaf nodes and placed with the base of the corresponding rachis and the basal portions of the first pair and terminal leaflets of that leaf. Later in the season the only leaf parts mounted were the base of the rachis and the basal portion of the terminal leaflet. Representative sections of the 1-year-old branch and the fruit were included where appropriate. The mounted specimens were dried at 60°C for 12 hr and then exposed to DuPont Cronex II safety X-ray film for 1 week. In the mounts, the third leaf is representative of leaves treated on the lower portion of the shoot and the sixth through ninth leaves are indicative of leaves treated on the upper portion of the shoot. The treatments were replicated 1 to 3 times. Replication was decreased as the number of leaves on a given date was increased. Reduction in replication was necessary because of time required for dissecting and mounting.

The elongation of the prominent shoot on the 1-year-old branch and of the third leaf from the base of the shoot was followed by measuring their lengths at weekly intervals from bud break until elongation ceased. Thirty shoots and leaves on each of 4 trees were measured each date. Kernel growth was measured by sampling 50 fruits at weekly intervals from July 29 until after maturity. The kernels were removed and dried at 60°C. Calculations from data of others (10) indicate a close relationship between oil and dry wt accumulation in the developing pecan kernel. The correlation coefficient (r) is near unity (r = 0.982); hence, kernel dry wt was used as an indicator of oil accumulation. Trees of cv. Stuart approximately 50 years old and bearing a commercial set of fruit were used.

Results
Assimilation of 14CO₂ began with bud break (Table 1). During the 3 weeks after bud break, photosynthates were assimilated in the elongating shoots and leaves (Table 1 and Fig. 1-3), but the assimilates were not exported from those organs. When the leaf began to export photosynthates, they were translocated bidirectionally acropetally to younger leaves and developing pistillate inflorescence and basipetally to the 1-year-old branch, the catkins (stamine inflorescences), and presumably to other parts of the tree (Fig. 4, 5). Comparison of the leaf which received translocated carbon-14 (Fig. 4) with those that assimilated 14CO₂ (Fig. 5) suggest that more photosynthate was assimilated in the immature leaf than was translocated to it from a mature leaf. The third leaf was about fully expanded (Fig. 6) at the time photosynthates were exported from it (Fig. 4). Shoot elongation was ceasing.

Table 1. Treatment dates and corresponding characteristic developmental stages of shoots, leaves, catkins, pistillate flowers, and fruits with notations on assimilation and translocation of carbon-14 by leaves of 'Stuart' pecan.

<table>
<thead>
<tr>
<th>Treatment date</th>
<th>Developmental stage</th>
<th>Lower X leaves</th>
<th>Upper W leaves</th>
<th>Response²</th>
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<tr>
<td>4-1</td>
<td>Advanced bud break</td>
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<td>4-6</td>
<td>Rapid leaf, shoot, and catkin elongation</td>
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<td>4-7</td>
<td>Rapid leaf, shoot, and catkin elongation</td>
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<td>4-10</td>
<td>Rapid leaf, shoot, and catkin elongation</td>
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<td>4-15</td>
<td>Leaf, shoot, and catkin elongation</td>
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<td>4-21</td>
<td>Catkin elongation ceasing, pistillate anthesis</td>
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<td>4-28</td>
<td>Leaf and shoot elongation ceasing</td>
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<td>AB¹</td>
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<td>5-5</td>
<td>Antner daiscience</td>
<td>B</td>
<td>AB¹</td>
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<td>Catkin abscission</td>
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<td>5-19</td>
<td>Fruit set</td>
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<td>Initial fruit growth</td>
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<td>AB¹</td>
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<td>6-16</td>
<td>Initial fruit growth</td>
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<td>AB¹</td>
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<td>Rapid fruit enlargement</td>
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<td>AB¹</td>
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<td>Rapid fruit enlargement</td>
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<td>AB¹</td>
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<td>7-22</td>
<td>Rapid fruit enlargement</td>
<td>B</td>
<td>AB¹</td>
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<td>Shell hardening</td>
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<td>AB¹</td>
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<td>Shell hardening ceasing and initial kernel growth</td>
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<td>AB¹</td>
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<td>8-26</td>
<td>Shell hardening ceasing and initial kernel growth</td>
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<td>9-8</td>
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<td>10-6</td>
<td>Fruit maturity</td>
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²P : photosynthesis occurring, no translocation; A, acropetal translocation; B, basipetal translocation.

³Entire shoot was treated.

Fig. 1-3. Assimilation of $^{14}$CO$_2$ by breaking buds, developing shoots, and the third leaf of 'Stuart' pecan. a, mounted specimens; b, autoradiographs. Fig. 1. The 3 apical buds were treated April 7. Fig. 2. Two developing shoots and catkins treated April 10. Fig. 3. Third leaf treated April 10. Developing leaves assimilated $^{14}$CO$_2$ as they broke the bud, but photosynthates were not exported from them. Catkins also assimilated $^{14}$CO$_2$ (see reference 4).
Fig. 4-5. Movement of assimilated $^{14}$CO$_2$ from the third leaf and from the shoot of 'Stuart' pecan. Specimens treated April 28. a, mounted specimens; b, autoradiographs. Fig. 4. Third leaf treated. Fig. 5. Shoot but not catkins exposed to $^{14}$CO$_2$. The acropetal movement from the third leaf was to a younger leaf and to a specific portion of the developing cluster of pistillate flowers. Carbon-14 was predominantly translocated into the younger leaflets of that leaf. Basipetal movement from the source leaf was to a specific catkin and presumably to other parts of the plant. Basipetal translocation from the third leaf bypassed proximal leaves.
Photosynthates were transported from a source leaf to rapidly maturing leaves older than that of the exporting leaf (Fig. 4, 7, 8, 9, 10, 11, 12, 14, 15, 16, 17). From any exporting leaf, a portion of the photosynthates was always translocated basipetally (Fig. 4, 7, 8, 9, 10, 11, 12, 14, 15, 16, 17).

Discussion

Assimilation and translocation of photosynthates from the pecan leaf are summarized in a schematic diagram showing the direction of translocation from approximate leaf positions and with developmental stages of growth (Fig. 18). Three patterns are indicated. The patterns overlap due to a) differential development along the shoot axis and b) the varying sink intensity of the fruit. During pattern I, bud break through the leaf expansion stage, assimilation occurs but photosynthates are not translocated from the leaves. The leaves during this stage are partially self-supporting as suggested by autonomous assimilation of $^{14}$C$_2$O$_2$, and as has been shown for sugar beet (17). An immature leaf also receives photosynthates produced by an exporting leaf, but the C assimilated by the immature leaf is apparently greater than that transported to it from a single mature leaf. Hence, an immature leaf is partially self-supporting and is dependent to some degree on substrates from older leaves. However, early growth of the shoot, leaves, and flowers appear to be also dependent upon substrates mobilized from reserves stored the previous season. This is suggested by the short period of rapid shoot elongation and leaf expansion and the fact that shoot growth (6, 8) and pistillate flower production (6, 8, 15) during the current season increase with the magnitude of the previous season’s growth. Such can also be inferred from carbohydrate analyses of pecan (27, 28) and other deciduous trees (12, 21, 24). Furthermore, since photosynthates are not transported basipetally from the shoot during early growth, growth that may occur elsewhere within the tree is obviously from mobilized substrates stored the previous season.

When a leaf matures (i.e., begins to export photosynthates), initial translocation from the leaf is bidirectional (Fig. 18, pattern II). Bidirectional translocation continues from the leaf until a distal leaf matures. Then translocation from the lower leaf is basipetal (Fig. 18, pattern III). This pattern is repeated as distal leaves mature successively until all leaves are exporting photosynthates. During early ontogeny of the shoot, a high proportion of the leaves export photosynthates bidirectionally (Fig. 18) suggesting that for a brief period the shoot apex (immature leaves and pistillate flowers) is a strong sink for current season’s photosynthates. Leaf removal studies (26) also suggest that the pistillate flowers are a strong sink at this stage. As the fruit grows, the proportion of leaves exporting photosynthates bidirectionally decreases to a minimum during fruit enlargement; basipetal and radial kernel development translocation from the more basal leaves again becomes bidirectional. This shift suggests a photosynthetic stress due to kernel development. Apparently alternate bearing is closely related to this stress since alternate bearing is alleviated by increasing (3) and accentuated (25) by decreasing the leaf area per fruit prior to rapid kernel development and after rapid shell development. The stress of kernel development is greater than shell development (Fig. 18). This differential stress is often reflected when trees have a heavy fruit set but poorly developed kernels. In such cases (14), return bloom often is not appreciably suppressed. After fruit maturity, translocation of photosynthates from all leaves is basipetal. During this stage, substrates depleted by an inadequate leaf to fruit ratio can be partially replenished as can be inferred from basipetal translocation per se (Fig. 18), from efficiency studies of pecan leaves (19), carbohydrate analyses (7, 27), and defoliation studies (13, 30). These relationships suggest that once a pecan tree reaches the fruiting condition, the magnitude of pistillate flower production and subsequent fruit set is a function of the relative degree of acropetal vs. basipetal translocation that occurs during fruit development in the previous year and the length of the period that the leaves remain functional after fruit maturity. During a low-yielding or nonfruiting year, and after all leaves on a shoot have matured, pattern III or basipetal translocation would be predominant. Conditions would be...
Fig. 7, 8. Movement of assimilated $^{14}$CO$_2$ from the sixth and the third leaf treated May 19 on a 'Stuart' pecan shoot. a, mounted specimens; b, autoradiographs. Fig. 7. Sixth leaf treated. Fig. 8. Third leaf treated. Acropetal movement from the sixth leaf was to an immature leaf and to a specific area of the developing cluster of fruit as well as basipetally. Photosynthates assimilated by the third leaf were translocated basipetally to other parts of the plant. Basipetal translocation from both the sixth and third leaf bypassed all proximal leaves.
Fig. 9, 10. Movement of assimilated $^{14}$C CO$_2$ from the apical and the third leaf treated July 15 on a 'Stuart' pecan shoot. a, mounted specimens; b, autoradiographs. Fig. 9. Apical leaf treated. Fig. 10. Third leaf treated. Photosynthates from the apical leaf were translocated to the developing fruit, but only to a specific area of the cluster. Photosynthates assimilated by the third leaf were translocated basipetally. Photosynthates translocated basipetally from both leaves bypassed all proximal leaves.
Fig. 11, 12. Movement of assimilated $^{14}$CO$_2$ from the sixth and the third leaf treated August 22 on a 'Stuart' pecan shoot. a, mounted specimens; b, autoradiographs. Fig. 11. Sixth leaf treated. Fig. 12. Third leaf treated. During kernel development photosynthates were transported acropetally from both leaves to specific areas of the fruit cluster. Within the fruit, transport was to the shuck (involucr) and kernel but not to the shell which had hardened by this date. Basipetal translocation from both leaves bypassed all proximal leaves. Acropetal transport of photosynthates from the treated leaves to the fruit bypassed all distal leaves.
optimum for accumulation of photosynthate reserves (27) and
the low-yielding or nonfruiting year would be expected to be
followed by a heavy fruit set (14, 29). A proposed relationship
of alternate bearing to carbohydrate reserves does not preclude
a hormonal concept for alternate bearing as suggested for apple
(2, 5, 11). In the apple, seed formation apparently inhibits
flower initiation to a greater degree than nutritional
competition by developing fruits (2). In some apple cultivars,
this is essentially an “all or none” effect (2, 5). If a similar
mechanism is operative in the pecan, it is not as dominant as in
the apple since seed production does not necessarily prevent
flower initiation and differentiation the following season (15).

The characteristics of photosynthesize movement from a single
pecan leaf; i.e., the effect of leaf development on time to initial
export, the bidirectional translocation from the newly exporting
leaf, the importing effect of the immature leaves and other
meristematic tissues, the apparent specific transport from the
source to the sink, and the lack of transport of photosynthates
between mature leaves are similar to those functions in
herbaceous plants (1, 16, 17, 23, 32). Generally, these
characteristics are also similar to those of woody plants (9, 20,
22). However, basipetal translocation which always occurred
from the exporting leaf of the pecan is at variance with results
on grape (9, 22), apple (20), and cottonwood (18). In these
plants, the first assimilates exported by the leaf were exported
acropetally to the growing shoot tip. Acropetal translocation
from the newly exporting grape leaf reportedly did not last
more than 1 or 2 days (9) which might suggest that treatment
timing was inadequate to observe only acropetal translocation in
the pecan.

Fig. 13. Dry wt of the kernel from the ‘Stuart’ pecan fruit as a function
of time.
Fig. 14, 15. Movement of assimilated $^{14}$CO$_2$ from the apical and the third leaf treated September 22 on a 'Stuart' pecan shoot. a, mounted specimens; b, autoradiographs. Fig. 14. Apical leaf treated. Fig. 15. Third leaf treated. After kernel development only the shuck received photosynthates from the apical leaf and none from the third leaf. Acropetal translocation did not occur from the third leaf. Basipetal translocation from both leaves bypassed all proximal leaves.
Fig. 16, 17. Movement of assimilated $^{14}$CO$_2$ from the apical and the third leaf treated October 6 on a 'Stuart' pecan shoot. a, mounted specimens; b, autoradiographs. Fig. 16. Apical leaf treated. Fig. 17. Third leaf treated. At fruit maturity photosynthates from leaves were translocated basipetally and bypassed all proximal leaves. However, acropetal movement occurred from the apical leaf to a distal bud.
Directions of Translocation

<table>
<thead>
<tr>
<th>Stages of Development</th>
<th>Leaf Position</th>
<th>Shoots Develop</th>
<th>Pollination</th>
<th>Fruits Develop</th>
<th>Fruits Enlarge</th>
<th>Shells Harden</th>
<th>Kernels Develop</th>
<th>Fruits Mature</th>
<th>Leaves Fall</th>
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Fig. 18. Proposed direction of translocation of photosynthates in the 'Stuart' pecan leaf from their approximate positions on the shoot numbered from the base, with the changing stages of physiological development. Pattern I – assimilation, but no export. Pattern II – bidirectional translocation. Pattern III – basipetal translocation.

Literature Cited
