Photosynthesis and Leaf Water, Carbohydrate, and Hormone Status during Rooting of Stem Cuttings of *Acer rubrum*

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Abstract. Leaf water status, carbohydrate levels, net photosynthesis, stomatal conductance, ABA, dihydrozeatin riboside (DHZR), and *trans*-zeatin riboside (ZR) levels were determined in a greenhouse during rooting of stem cuttings of *Acer rubrum* L. 'Red Sunset' taken on 3 Sept. 1987 and 28 May 1988. Leaf water status deteriorated before rooting and improved after root emergence. Leaf carbohydrate concentrations (glucose, sucrose, total soluble sugars, and total carbohydrates) increased until rooting and decreased after rooting, while changes in starch concentrations were trendless. ABA levels increased after insertion of cuttings into the rooting medium, but decreased before rooting. No correlation between timing of rooting and concentrations of the cytokinins ZR or DHZR was observed. Photosynthetic rates during rooting were higher for the Sept. 1987 cuttings and did not decrease to the compensation point as did those for May 1988 cuttings. Low photosynthetic rates and stomatal conductance of the cuttings during rooting were associated with water stress. The relationship between photosynthetic rates of such cuttings and cytokinin (CK) or ABA content was unclear. Chemical names used: [S-(Z,E)-5-(1-hydroxy-2,6,6-trimethyl-4-oxo-2-cyclohexen-1-yl)-3-methyl-2,4-pentadienoic acid (abscisic acid, ABA); 2-methyl-4-(1H-purin-6-ylamino)-2-buten-1-ol (zeatin, Z).

Many authors have noted that photosynthetic rates of leafy cuttings decrease after excision from stock plants and remain low until adventitious roots emerge (Cameron and Rook, 1974; Davis, 1988; Davis and Potter, 1981; Eliasson and Brunes, 1980; Negishi and Satoo, 1956; Okoro and Grace, 1976). This decrease in photosynthetic rates might be caused by water stress experienced by the cuttings and consequent stomatal closure (Loach, 1988; Machida et al., 1977; Negishi and Satoo, 1956). High ABA levels in water-stressed cuttings may affect photosynthetic rates by prompting stomatal closure or deleteriously affecting the photosynthetic apparatus of the mesophyll cells (Raschke and Hedrich, 1985). The decrease in photosynthetic rate after cuttings are taken may also be attributed to the absence of roots and root-produced cytokinins (Okoro and Grace, 1976). Cytokinin levels may regulate photosynthetic rates through effects on chlorophyll levels (McDavid et al., 1973), enzyme activity (Carmi, 1986), and stomatal conductance (Blackman and Davies, 1985). The photosynthetic rates of cuttings may be reduced before the development of roots due to the absence of sinks for photosynthates causing an accumulation of photosynthates, which, in turn, results in a suppression of photosynthesis (Loach and Gay, 1979).

Statements about potential regulators of photosynthesis in woody cuttings have been made with little correlative evidence.

Therefore, the purpose of this research was to examine correlations among leaf water status and leaf carbohydrate, CK, and ABA levels relative to photosynthetic rates of cuttings during rooting. Correlations between two factors do not necessarily indicate a cause and effect relationship. However, correlations between phenomena, particularly when corroborative data are considered, can indicate a potential relationship deserving more definitive study.

Photosynthate production during rooting may be important for rooting (Davis, 1988) and overwinter survival (Smalley et al., 1987) of cuttings. A correlative study of the factors that limit photosynthesis during rooting could suggest a method to limit the decrease in photosynthesis during rooting.

Materials and Methods

Cuttings. Single-node stem cuttings (5 cm long) were obtained from a 3-year-old containerized stock block of *Acer rubrum* 'Red Sunset' on 3 Sept. 1987 and 28 May 1988 (hereafter referred to as September and May, respectively). The leaves of the cuttings were those most recently matured and about equal in size. On both cutting dates, the shoots were elongating, but a physiological similarity between cuttings of the two dates is not implied. The basal 12 mm of the cuttings was dipped into a 50% ethanol solution of 5000 mg 1H-indole-3-butyric acid (IBA)/liter for 5 sec, and placed in 560-mm³ pots (7.5 cm square × 10 cm deep) containing a rooting medium of 2 perlite : 1

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Abbreviations: CK, cytokinins; LWP, leaf water potential.

peat (v/v). The greenhouse propagation bench was enclosed in a plastic tent and misted for 2 1/2 sec every 7 min from 8:00 AM to 8:00 PM. Day/night temperatures in the greenhouse were 30/18C for September cuttings and 33/22C for May cuttings.

Sampling. For each sampling date, four cuttings were randomly selected. The September cuttings were sampled on days 0, 3, 6, 9, 12, 15, 18, 21, 24, and 30; those for May on days 0, 2, 4, 7, 14, 21, 28, 35, 42, 49, and 56. For ABA analysis, interveinal leaf tissue was excised from a severed leaf, wrapped in aluminum foil, submerged in liquid nitrogen, and stored at -20C.

Leaf water relations. For the May cuttings, two disks (7-mm diameter) were removed from interveinal areas of the remaining leaf and placed in a C-52 hygrometer chamber (Wescor, Logan, Utah) for determination of LWP using a PR-55 psychrometer (Wescor). Similarly, two more disks were removed, wrapped in aluminum foil, submerged for 5 sec in liquid nitrogen, and stored at -2C for leaf osmotic potential measurement of a thawed disk. Turgor pressure was determined by subtracting osmotic potential from LWP.

Photosynthesis. The leaf was placed in an assimilation chamber (Armitage et al., 1983) for determining photosynthetic and transpiration rates and stomatal conductance. Photosynthetic photon flux (September: $170 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; May: $125 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and temperature (25 to 27C) were similar to intensities in the misting bed. The photosynthetic rate of a cutting in the mist bed could only be approximated because relative humidity (RH) in the assimilation chamber was 80%, whereas relative humidity approached 100% in the mist bed. Such high relative humidity in the assimilation chamber interfered with measurements of stomatal conductance and photosynthetic rates. Relative humidity was monitored with a RH-101 Omega humidity sensor (Omega Engineering, Stamford, Conn.) and adjusted with an anhydrous drying column. The photosynthetic rate of the cuttings was recorded before the lower humidity in the assimilation chamber stressed the cutting. The difference in CO_2 levels in the air entering ($340 \mu\text{l}\cdot\text{liter}^{-1}$, $1 \text{ liter}\cdot\text{min}^{-1}$) and leaving the assimilation chamber were measured to determine net photosynthetic rate (Long and Hallgren, 1985).

Transpiration and stomatal conductance. Measurement of the dewpoint (model 911 hygrometer, EG & G, Waltham, Mass.) of the air entering and leaving the leaf assimilation chamber was used to obtain the transpiration rate (Long and Hallgren, 1985). Stomatal conductances were calculated by dividing the transpiration rate by the absolute humidity deficit.

After photosynthetic measurement, leaf area was measured (LI-3000, LI-COR, Lincoln, Neb.), and the leaf was wrapped in aluminum foil and submerged in liquid nitrogen for CK and carbohydrate analysis.

Rooting. After the leaves had been removed, the percentage of cuttings with a root longer than 1 mm was determined.

Hormone quantification. Absciscic acid, ZR, and DHZR concentrations were determined according to the enzyme immunoassay EIA methodology developed by Wood (1988) using Phytodetek EIA kits (Idetek, San Bruno, Calif.). Lyophilized leaf tissue (100 mg) was extracted for 20 h in 10 ml of 80% methanol : 20% water. The extract was purified with reverse-phase Sep-Pac C-18 columns (Waters Assoc., Milford, Mass.). Serial dilution studies indicated that only ZR required further thin-layer chromatography purification on a silica gel F-254 plate.

Any reference to plant hormone concentrations implies quantities of hormone-like substances, as possible cross-reactivity with molecules similar to the plant growth regulators precludes

the unequivocal assumption that hormone levels determined via immunological techniques directly reflect antigen levels in samples (Wood, 1988). The use of radiolabeled internal standards revealed that the recovery rate was $93.8\% \pm 2\%$, $67.0\% \pm 1\%$, and $40.2\% \pm 1\%$ for ABA, DHZR, and ZR, respectively. Because radiolabeled DHZR and ZR were unavailable, their recovery rates were assumed to be similar to the recovery rates for dihydrozeatin (Wood, 1988).

Soluble sugars. Techniques elaborated by Beaudry et al. (1990) were used to analyze soluble sugars. The methanol : water extraction solution contained phenyl- β -D-glucopyranose (2.2 mg/10 ml) as an internal standard. After homogenization (Kinematica, Kriens-Luzern, Switzerland) and extraction, 100 μl of the extract was analyzed with a Hewlett Packard (Avondale, Pa.) 5890A gas chromatograph.

Starch. About 100 mg of freeze-dried leaf tissue was placed into a 50-ml centrifuge tube for starch analysis (Beaudry et al., 1990). Five milliliters of 80% methanol was added, and the mixture was homogenized for 30 sec. Five milliliters of 80% methanol was used to rinse the homogenizer. The homogenized mixture was heated for 2 h in a reciprocating hot water bath at 100C to gelatinize the starch and evaporate the methanol. The tubes were cooled to 55C, and 1 ml of a citrate buffer was added to maintain the pH between 4.5 and 5.0. Amyloglucosidase (3.75 units in 100 μl of citrate buffer) was added to hydrolyze the starch. After incubation for 48 h at 55C in a reciprocating water bath, 5 ml of an internal standard solution (1 mg of xylitol/5 ml) was added. The solution was gas chromatographed.

Data analyses. Correlations were developed using SAS correlation procedures (SAS Institute, 1985).

Results and Discussion

September and May rooting. Marked differences existed between the rooting rates for the two cutting dates; 12 days for 100% rooting of the September cuttings (Fig. 1A) vs. 56 days for 100% rooting of the May cuttings (Fig. 2A). However, directly comparing the results of two seasons is impermissible because differences in environmental conditions and in stock block carbohydrate reserve, nutrient, and physiological status confound the results (Hartmann and Kester, 1983). Rooting of the May cuttings appeared to decrease on day 42 because of the early rooting of one cutting on day 35 (Fig. 2A).

Leaf water relations during rooting. The LWP (Fig. 2B), turgor (Fig. 2B), and osmotic potential (Fig. 2C) of the May cuttings decreased after day 12 until rooting commenced. Near zero turgor on days 21 and 28 indicated that cuttings experienced water stress. After rooting commenced (day 35) (Fig. 2A), the newly formed roots alleviated the water stress, and the LWP, osmotic potential, and turgor increased. Other studies have demonstrated that LWP decreased after cuttings were inserted and increased after rooting (Davis and Potter, 1987; Loach, 1977).

Stomatal conductance, transpiration, and photosynthetic rates during rooting. The transpiration rates (Fig. 1B) and stomatal conductance (Fig. 1C) of the September cuttings decreased until day 18 and then increased, and those of the May cuttings (Fig. 2D and E) decreased after cuttings were inserted and remained near zero until rooting after day 42 (Fig. 2A). The evidence from this study and others (Gemma et al., 1979; Loach, 1988) indicated that stomata can remain open during rooting, but stomatal conductance is reduced until rooting occurs. In cuttings, such as those of May, stomatal conductance was severely lim-

Fig. 1. Percent rooting (A) and leaf transpiration (B), stomatal conductance (C), net photosynthesis (D), glucose (E), sucrose (E), soluble sugars (E), starch (F), total carbohydrates (F), abscisic acid (ABA) (G), dihydrozeatin riboside (DHZR) (H), and zeatin riboside (ZR) (I) levels during rooting of stem cuttings of *Acer rubrum* 'Red Sunset'. Cuttings taken 3 Sept. 1987. Values $\pm$ SE ($n = 4$).

ited until rooting. Gay and Loach (1977) and Loach and Gay (1979), who reported that stomata of cuttings remained closed before rooting, measured stomatal conductances after the cuttings had been removed from the propagation bed and subjected to 91% RH for 68 h, conditions that may have prompted stomatal closure.

During rooting, the photosynthetic rate of September cuttings never decreased to the compensation point (zero net photosynthesis) (Fig. 1D). However, within 9 days after insertion, the photosynthetic rate of May cuttings decreased to or slightly above the compensation point and remained at this level until significant rooting occurred after day 42 (Fig. 2 A and F). The photosynthetic rate returned to the initial level more rapidly in the September cuttings (Fig. 1D) that also rooted more rapidly than the May cuttings. Similarly, Machida et al. (1977) noted that the photosynthetic rate of four woody taxa returned to the initial level most rapidly in the cuttings that rooted most rapidly.

Stomatal conductance and the photosynthetic rate of the May cuttings were highly correlated ($r = 0.90$). Water stress of cuttings, as indicated by loss of turgor, could cause stomatal closure and subsequent reduction in stomatal conductance and the photosynthetic rate. Except for days 15 and 30, the changes in September photosynthetic rates also mirrored the changes in stomatal conductance (Fig. 1 C and D). Random variation may be responsible for the poor correlation on those days.

The photosynthetic rates of cuttings can decrease to near the compensation point until rooting, as in the May cuttings, or remain near the level when the cuttings were taken, as in the September cuttings. If abundant photosynthate production during rooting is important for rooting (Davis, 1988) or survival of the cutting (Smalley et al., 1987), then propagators may be able to alleviate these problems by selecting cutting material

from a stock block at a time when photosynthesis during rooting is probable.

The variations in the transpiration, conductance, and photosynthetic rates can be attributed to differences in date of rooting or differences in ambient misting bed conditions when the cuttings were sampled. Loach (1977) determined that variations in LWP in cuttings could be accounted for by the current day's radiation and the previous day's LWP or radiation. The LWP of the cuttings may affect assimilation, transpiration, and conductance rates because water stress, as indicated by lower LWP, can cause stomata to close. For the May cuttings, LWP was significantly ($P = 0.0001$) correlated with photosynthetic ($r = 0.56$), conductance ($r = 0.54$) and transpiration rates ($r = 0.59$).

A growth chamber study might have limited some of this variation, but a greenhouse study is the most realistic method for examining factors that limit photosynthesis under typical propagation conditions. Characteristics measured during a greenhouse study may respond at differing rates to changing environmental conditions in the propagation environment. If a response varies in parallel with photosynthesis, despite changing environmental conditions, it suggests that the factor regulates photosynthesis or is regulated by photosynthesis.

Leaf carbohydrate levels during rooting. Leaf glucose, sucrose, soluble sugars, and total carbohydrate levels increased after the cuttings were inserted and decreased within 1 week after rooting for the September (Fig. 1 E and F) and May cuttings (Fig. 2 G and H). No similar relationship between rooting and starch levels was observed (Figs. 1F and 2H). The leaf carbohydrate levels of the cuttings increased before rooting, presumably because no sink existed to which carbohydrates could be translocated. Potential sinks, such as roots or actively ex-

Fig. 2. Percent rooting (A) and LWP (B), turgor (B), osmotic potential (C), transpiration (D), stomatal conductance (E), net photosynthesis (F), glucose (G), sucrose (G), soluble sugar (G), starch (H), total carbohydrate (H), abscisic acid (ABA) (I), dihydrozeatin riboside (DHZR) (J), and zeatin riboside (ZR) (K) levels during rooting of stem cuttings of *Acer rubrum* 'Red Sunset'. Cuttings taken 28 May 1988. Values $\pm$ SE (n = 4).

panding buds, did not exist in these unrooted cuttings. The results concur with evidence from studies examining the total shoot (leaves plus stem) carbohydrate content (Hansen et al., 1978; Loach and Gay 1979).

Water relations and hormone levels during rooting. ABA accumulates in the leaves of water-stressed plants (Radin and Ackerson, 1982), and water stress occurs in cuttings under mist (Gemma et al., 1979; Grange and Loach, 1985; Loach, 1977). Therefore, ABA levels are expected to increase after cuttings are stuck and decrease after rooting occurs and water stress is alleviated. As expected, ABA levels of the September cuttings (Fig. 1G) increased after cuttings were taken and decreased after 100% rooting occurred on day 12 (Fig. 1A). The high mean levels of ABA on day 18 were caused by the high level of ABA in one cutting that had just begun to root and had one-fourteenth the number of roots and three to 20 times more ABA than the other three cuttings sampled (data not presented).

The ABA levels of the May cuttings (Fig. 2I) increased after the cuttings were stuck and decreased before rooting was observed on day 35. Thus, no relationship between rooting and ABA levels was exhibited over the entire rooting period. However, after rooting, ABA levels decreased to levels at the time

of excision. The ABA level in cotyledons of cuttings of tomato (*Lycopersicon esculentum* Mill.) also decreased before rooting (Maldiney et al., 1986).

Water stress can reduce the activity of CK in leaves (Hubick et al., 1988; Itai and Vaadia, 1971). No correlations between leaf water status (Fig. 2 B and C) and DHZR and ZR (Fig. 2 J and K) levels were observed for the May cuttings. A difference in CK measurement techniques between this study and others may explain the differing results, as other studies have used soybean [*Glycine max* (L.) Merr.] assays that measure CK glucosides; the immunoassay techniques we used did not measure CK glucosides. Glucosides of DHZR and ZR may have increased after rooting and alleviation of water stress in this study, but they were not measured because the available evidence indicated they are not biologically active forms of CK (Van Staden, 1976). The results of this study suggest that the activity of CK glucosides should be further investigated.

Some of the hormone concentrations (Figs. 1 G, H, and I and 2 I, J, and K) appear to be sine waves, which could be a cyclic artifact. An analytical artifact is unlikely because each hormone was extracted and analyzed on the same date with identical reagents.

Potential regulators of photosynthesis during rooting. Carbohydrate feedback inhibition appeared not to be an important factor regulating photosynthesis during rooting. A high starch to low photosynthetic rate correlation suggests feedback inhibition (Guinn and Mauney, 1980), but photosynthetic rates were not significantly correlated with starch levels in this study. Mauney et al. (1979) concluded that feedback inhibition is only demonstrable when starch levels are >10%, but the starch levels of the cuttings never rose above 3%.

When the results of both cutting dates are considered, no close relationship between hormone levels and photosynthetic rates is apparent. The inverse correlation between ABA levels and photosynthetic rates ($r = -0.46$) was higher than for any other characteristic measured for the September cuttings (Fig. 1); however, the ABA levels of the May cuttings (Fig. 2I) decreased before there was a corresponding increase in the photosynthetic rate.

Many other studies have demonstrated a strong correlation between rooting, CK levels, and photosynthetic rates (Carmi, 1986; Livne and Vaadia, 1965; McDavid et al., 1973). As discussed previously, no conclusion about the influence of CK on photosynthetic rates of rooting stem cuttings of *Acer rubrum* can be reached until the activity of CK glucosides in the leaves of the cuttings is ascertained.

Photosynthetic rates during rooting of the May cuttings were more highly correlated with LWP ($r = 0.55$, $P = 0.0001$) than with any other potential factor that might affect photosynthetic rates except sucrose and soluble sugar levels. Our results concur with evidence in the literature (Machida et al., 1977; Negishi and Satoo, 1956) that water stress limits photosynthetic rates of cuttings. However, the photosynthetic rates of the May cuttings (Fig. 2F) decreased for the first 9 days after insertion without any corresponding increase in water stress of the cuttings. This disparity highlights a frequent phenomenon in this study; an apparent close correlation between some variables and photosynthesis at certain times, but not throughout the rooting period. Biological and experimental variation and the interaction of several factors in regulating photosynthesis could have caused the resulting low correlation coefficients.

In summary, unlike previous studies, the data for September demonstrated that *A. rubrum* cuttings can maintain photosynthetic rates during rooting. Although this study did not support the hypothesis that decreasing CK levels limit photosynthesis of rooting cuttings, further elucidation of the biological activity of CK glucosides is warranted before making a definitive conclusion. This study suggests that the decrease in photosynthetic rate of cuttings after sticking and before rooting can be minimized through proper management of cuttings to limit water stress or, possibly, by selection of cutting date.

Literature Cited

- Armitage, A.M., H.M. Vines, Z.P. Tu, and C.C. Black. 1983. Water relations and net photosynthesis in hybrid geraniums. *J. Amer. Soc. Hort. Sci.* 108:310-314.
- Beaudry, R.M., R.F. Severson, C.C. Black, and S.J. Kays. 1990. Banana ripening: Implications of changes in glycolytic intermediate concentrations, glycolytic and gluconeogenic carbon flux, and fructose 2,6-bisphosphate concentration. *Plant Physiol.* 91:1436-1444.
- Blackman, P.G. and W.J. Davies. 1985. Root to shoot communication in maize plants of the effects of soil drying. *J. Expt. Bot.* 36:39-48.
- Cameron, R.J. and D.A. Rook. 1974. Rooting stem cuttings of radiata pine: Environmental and physiological aspects. *N.Z. J. For. Sci.* 4:291-298.
- Carmi, A. 1986. Effects of cytokinins and root pruning on photosynthesis and growth. *Photosynthetica* 20:1-8.
- Davis, T.D. 1988. Photosynthesis during adventitious rooting, p. 79-87. In: T.D. Davis, B.E. Haissig, and N. Sankhla (eds.). *Adventitious root formation in cuttings*. Dioscorides Press, Portland, Ore.
- Davis, T.D. and J.R. Potter. 1981. Current photosynthate as a limiting factor in adventitious root formation on leafy pea cuttings. *J. Amer. Soc. Hort. Sci.* 106:278-282.
- Davis, T.D. and J.R. Potter. 1987. Physiological response of rhododendron cuttings to different light levels during rooting. *J. Amer. Soc. Hort. Sci.* 112:256-259.
- Eliasson, L. and L. Brunes. 1980. Light effects on root formation in aspen and willow cuttings. *Physiol. Plantarum* 48:261-265.
- Gay, A.P. and K. Loach. 1977. Leaf conductance changes on leafy cuttings of *Cornus* and *Rhododendron*. *J. Hort. Sci.* 52:509-516.
- Gemma, H., H. Yamamoto, M. Ishida, and Y. Sobajima. 1979. Fundamental studies on propagation of peach (*Prunus persica* Sieb. et Zucc.) by stem cuttings. II. The characteristic of photosynthesis of softwood cuttings during mist propagation. *Scientific Rpt. Kyoto Prefectural Univ. Agr., Jpn. no.* 31:21-31.
- Grange, R.I. and K. Loach. 1985. The effect of light on the rooting of leafy cuttings. *Scientia Hort.* 27:105-111.
- Guinn, G. and J.R. Mauney. 1980. Analysis of CO₂ exchange assumptions: Feedback control, p. 1-16. In: J.D. Hesketh and J.W. Jones (eds.). *Predicting photosynthesis for ecosystem models*. vol. 2. CRC, Boca Raton, Fla.
- Hansen, J., L.-H. Strömquist, and A. Ericsson. 1978. Influence of the irradiance on carbohydrate content and rooting of cuttings of pine seedlings (*Pinus sylvestris* L.). *Plant Physiol.* 61:975-979.
- Hartmann, H.T. and D.E. Kester. 1983. *Plant propagation: Principles and practices*. 4th ed. Prentice-Hall, Englewood Cliffs, N.J.
- Hubick, K.T., J.S. Taylor, and D.M. Reid. 1988. The effect of drought on levels of abscisic acid, cytokinins, gibberellins and ethylene in aeroponically-grown sunflower plants. *Plant Growth Regulat.* 4:139-151.
- Itai, C. and Y. Vaadia. 1971. Cytokinin activity in water-stressed shoots. *Plant Physiol.* 47:87-90.
- Livne, A. and Y. Vaadia. 1965. Stimulation of transpiration rate in barley leaves by kinetin and gibberellic acid. *Physiol. Plant.* 658-663.
- Loach, K. 1977. Leaf water potential and the rooting of cuttings under mist and polythene. *Physiol. Plantarum* 40:191-197.
- Loach, K. 1988. Water relations and adventitious rooting, p. 102-116. In: T.D. Davis, B.E. Haissig, and N. Sankhla (eds.). *Adventitious root formation in cuttings*. Dioscorides Press, Portland, Ore.
- Loach, K. and A.P. Gay. 1979. The light requirement for propagating hardy ornamental species from leafy cuttings. *Scientia Hort.* 10:217-230.
- Long, S.P. and J.E. Hallgren. 1985. Measurement of CO₂ assimilation by plants in the field and the laboratory, p. 62-94. In: J. Coombs, D.O. Hall, S.P. Long, and J.M.O. Scurlock (eds.). *Techniques in bioproductivity and photosynthesis*. Pergamon Press, New York.
- Machida, H., A. Oishi, and T. Hosoi. 1977. Studies on photosynthesis in cuttings during propagation. I. Changes in the rate of apparent photosynthesis in the cuttings of several plants after planting. *J. Jpn. Soc. Hort. Sci.* 46:274-282.
- Maldiney, R., F. Pelé, G. Pilate, B. Sotta, L. Sossountzou, and E. Miginiac. 1986. Endogenous levels of abscisic acid, indole-3-acetic acid, zeatin and zeatin-riboside during the course of adventitious root formation in cuttings of *Craigella* and *Craigella* lateral suppressor tomatoes. *Physiol. Plantarum* 68:426-430.
- Mauney, J.R., G. Guinn, K.E. Fry, and J.D. Hesketh. 1979. Correlation of photosynthetic carbon dioxide uptake and carbohydrate accumulation in cotton, soybean, sunflower and sorghum. *Photosynthetica* 13:260-266.
- McDavid, C.R., G.R. Sagan, and C. Marshall. 1973. The effect of root pruning and 6-benzylaminopurine on the chlorophyll content, ¹⁴CO₂ fixation, and the shoot/leaf ratio in seedlings of *Pisum sativum* L. *New Phytol.* 72:465-470.

- Negishi, W.J. and T. Satoo. 1956. Photosynthesis, respiration and consumption of reserves of sugi (*Cryptomeria japonica*) cuttings. J. Jpn. For. Soc. 38:63-84.
- Okoro, O.O. and J. Grace. 1976. The physiology of rooting *Populus* cuttings. I. Carbohydrates and photosynthesis. *Physiol. Plantarum* 36:133-138.
- Radin J.W. and R.C. Ackerson. 1982. Does abscisic acid control stomatal closure during water stress? What's New in Plant Physiol. 13:9-12.
- Raschke, K. and R. Hedrich. 1985. Simultaneous and independent effects of abscisic acid on stomata and photosynthetic apparatus in whole leaves. *Planta* 163:105-118.
- SAS Institute. 1985. SAS user's guide: Statistics. 5th ed. SAS Institute, Inc. Cary, N.C.
- Smalley, T.J., M.A. Dirr, and G.G. Dull, 1987. Effect of extended photoperiod on budbreak, overwinter survival, and carbohydrate levels of *Acer rubrum* 'Ocotber Glory' rooted cuttings. J. Amer. Soc. Hort. Sci. 112:459-463.
- Van Staden, J. 1976. Occurrence of a cytokinin glucoside in the leaves and in honeydew of *Salix babylonica*. *Physiol. Plantarum* 36:225-228.
- Wood, B.W. 1988. Axillary shoot abscission in pecan and its relationship to growth regulators. J. Amer. Soc. Hort. Sci. 113:713-717.