

Photosynthetic Rates of Ilex crenata Thunb.

'Helleri' during Propagation

by

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(ABSTRACT)

A series of experiments was conducted to determine the effect of light, auxin, carbohydrate levels, mineral nutrients and rooting on the net photosynthetic (Pn) rate of unrooted Ilex crenata Thunb. 'Helleri' cuttings. Optimal photosynthetic activity occurred at PAR levels of about 600 micro-Einsteins  $m^{-2} sec^{-1}$ . The emergence of roots increased the Pn rate. High plant carbohydrate levels were correlated to lower Pn rates while higher Pn rates were correlated to lower CHO levels. These relationships may be indicative of source-sink interactions on the Pn rate of Helleri holly cuttings. An exogenous basal application of indolebutyric acid (IBA) contributed to an increase in cutting Pn, as was the case with the addition of mineral nutrients.

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## INTRODUCTION

The propagation of woody ornamentals is a key operation in most commercial nurseries, since its success can ultimately affect the entire production schedule. Practices such as the application of a rooting hormone, the maintenance of shade to control temperature and intermittent misting are commonly utilized propagation techniques. Net photosynthesis ( $P_n$ ) is not a priority consideration, even though it may contribute significantly to the success of propagation. Experiments were conducted to study the rate of  $P_n$ , of Ilex crenata Thunb. 'Helleri', during propagation as affected by rooting, rooting hormone, fertilization and carbohydrate levels.

## LITERATURE REVIEW

Over the years, there has been much speculation as to the role of photosynthesis in the rooting of cuttings. More specifically, researchers have tried to resolve whether or not photosynthates produced after the cutting is excised from the stock plant are utilized in the initiation and emergence of new roots. If these photosynthates do not significantly contribute to the rooting process, then it follows that the cutting must rely on stored photosynthates. During the propagation of Cryptomeria japonica, Struve suggested that new photosynthate did not contribute significantly to the plant's total carbohydrate pool (42).

Since light is required for photosynthesis, some studies have concentrated on the effect of different light levels on rooting. One such study, by Hansen et al. (19), concluded that photosynthetically active radiation (PAR) levels are more beneficial for the stock plants than the cuttings of Pinus sylvestris. This conclusion was based upon the observation that the carbohydrate pool of the cuttings was enhanced more by higher PAR levels while still attached to the stock plant than when removed and put in the propagation bed. Consequently, it would seem that stored carbohydrates are of more importance to the rooting process.

While it is true that light may contribute to a greater accumulation of carbohydrates in the stock plant, the Pn of the cuttings may still be of importance to the rooting process (16,46). Eliasson (14), demonstrated that the number of roots which developed was directly related to the PAR level received by the cuttings. After placement in total darkness, no roots emerged, solidifying the conclusion that a decrease in cutting Pn adversely affected subsequent rooting. Davis and Potter (12) demonstrated similar results, with P. sativum, reporting a reduction in Pn to cause a corresponding reduction in the carbohydrate level in conjunction with decreased rooting. Results and conclusions similar to the two previous studies were reached, using excised cotyledons of Sinapsis alba (27).

The concept of whether plant growth determines to some extent the Pn rate, has received continued attention over the years. Since carbohydrate utilization is essential for plant growth, it has been proposed that the rate of utilization directly affects the Pn rate (10,43,47). When first proposing this theory in 1868, Boussingault (8) hypothesized that the accumulation of assimilates could directly effect a reduction in the Pn rate of an illuminated leaf. Over one-hundred years later, the wording of this theory has not been significantly altered.

Should high levels of photosynthates act to suppress the Pn rate, it follows that increasing the latter is possible by reducing the assimilate level. Assimilates are utilized in areas of growth and development, often referred to as "sinks". These sinks remove carbohydrates from the plant's carbohydrate pool, which is replenished by the photosynthesizing areas of the plant. The term "source" has been applied to these areas, which are composed mainly of the leaves. The concept of a source-sink relationship has arisen in an attempt to justify and support Boussingault's original theory. Basically, the concept states that if there is a sink present on the plant, the rate of Pn remains un-suppressed. There is competition between sinks for the assimilates produced by photosynthesis and some sinks will be "stronger" than others. In other words, specific sinks will be able to control a larger percentage of the total amount of assimilate produced. Using rooted cuttings of Populus tremula with reduced leaf areas (15), Eliasson found that there was normal, progressive root growth as long as there was no shoot growth. Decreased root growth was observed shortly after the initiation of shoot growth and root growth did not increase until the leaf area had expanded. This study illustrated that source-sink interactions are present in cuttings and are not restricted to larger, more structurally

complex plants. When considering cuttings, one usually thinks of both the rooted and unrooted condition. In terms of assimilates, the cuttings should have ample assimilate reserves, provided that the stock plant was not nutritionally deficient or otherwise stressed. There are then several observations which should be made regarding unrooted cuttings. First, assuming the cutting is leafy, there is a source of photosynthate. Secondly, it should have a carry-over supply of assimilates from the stock plant. Thirdly, until roots or shoots emerge, there is the absence of a sink. The presence of these conditions could result in an accumulation of carbohydrates. Then according to Boussingault's hypothesis, the Pn rate may be suppressed.

It has been shown that the translocation of photosynthetic products to the roots of young pine seedlings is greatly affected by the extent of root development (38). Root removal from Phaseolus vulgaris plants increased the amount of soluble sugars present in the entire plant (17). A substantial reduction in Pn rate was also observed in root pruned plants of P. vulgaris (11). Following the excision of 70-80% of the roots, the Pn rate followed a continued decline with the greatest reduction occurring six days after excision. These studies show that the excision of roots can effect an increase in the soluble sugar level and a decrease

in the Pn rate. Okoro and Grace (34) demonstrated that both phenomena can occur at the same time in one plant. Using unrooted hardwood cuttings of Populus sp., they discovered high carbohydrate levels associated with decreased Pn, until subsequent development of callus, roots or shoots.

Many other studies have demonstrated a relationship between source and sink, and its effect on the rate of photosynthesis. In Sorghum saccharatum it was found that the Pn rate peaked during times of active root or tiller growth (25,26). Similar results have been obtained using potato, spinach, sugar beet and spinach beet (22,23,24,33,44). One of the better illustrations was done utilizing sugar beet and spinach beet (44). Both are varieties of Beta vulgaris but the sugar beet root has a higher capacity for storage of assimilates. Although containing high levels of assimilates, the sugar beet leaves maintain a high Pn rate as compared to the spinach beet. If spinach beet leaves are grafted to sugar beet roots, their Pn rate increases, while a reciprocal graft between sugar beet leaves and spinach beet roots causes a reduction in Pn. It would appear that the Pn rate of photosynthesizing areas of the plant may be dependent, to some extent, on the ability of the sink(s) to accept photosynthates. However, in two other separate cases, studies conducted with sunflower, soybean and barley have

shown that this may not always be the case. In all instances, large amounts of assimilates have been allowed to accumulate in the plant without a significant decrease in the Pn rate (30,36).

Growth regulators also influence the photosynthetic process. These compounds have been used for years in the area of plant propagation, particularly to enhance rooting. The auxin compounds utilized include indoleacetic acid (IAA), indolebutyric acid (IBA) and naphthaleneacetic acid (NAA). An application of an auxin to the basal end of the cutting significantly increases the initiation and subsequent number of roots (20,40,41). This effect, in itself, may serve as a sink and possibly increase the Pn rate. In addition to the increase in sink size, auxin application has been shown to increase the accumulation of sugars at the basal end of the cutting, primarily attributed to an increased mobilization of assimilates from the source to the basal end of the cutting (2,3,9). Thus, the combination of greater sink strength and enhanced mobilization of assimilates could have a significant effect on the Pn rate, compared to a cutting which was not treated with an auxin.

The influence of mineral nutrition on photosynthesis has been studied in some detail. The rate of Pn declines in the absence of optimal quantities of all the macro and near-

ly all the macro elements (29), yet the extent of the rate drop depends on the element in deficit. An inhibition of the photochemical activities within the chloroplast has been cited as one of the major reasons for this reduction (35). Of course, all of the mineral elements do not exert an equal influence on the Pn rate. A deficiency in one of the primary plant nutrients appears to cause a greater reduction in the Pn rate than in one of the secondary or micro elements (7). Nitrogen deficiency causes the greatest reduction in Pn rate mainly by increasing mesophyll and stomatal resistance (37). Studies have repeatedly demonstrated this phenomenon in a wide variety of species (13,28,32). The fact that nitrogen and other mineral nutrients are essential to photosynthesis emphasises the need for optimal stock plant nutrition prior to propagation. This is especially important since subsequent cuttings will not absorb a significant amount of nutrients until roots are present (6). Blazich and Wright (4) have shown that there is no mobilization of nutrients from the upper to the lower areas of the cutting during the period of root initiation. Therefore, it is conceivable that the nutrients which are stored in the upper regions of the cutting would be adequate for the photosynthetic process. In light of this, it would seem advantageous to have a source of mineral nutrition available to

the cuttings as soon as roots begin to emerge. Especially since mobilization of nutrients begins to occur as soon as roots are present (5).

## MATERIALS AND METHODS

Expt.1. This experiment was conducted to determine the level of photosynthetically active radiation (PAR) required for light saturation in 'Helleri' holly cuttings. Rooted cuttings which had been kept in the greenhouse for six weeks, under full light, and fertilized at regular intervals were transplanted into 6 cm. (200 cm<sup>3</sup>) pots filled with a medium consisting of 1 peat:1 perlite:1 Weblite (Webster Brick Company, Roanoke, Va., 24012)(v/v/v). Plants were grown, from 12 April- 15 April 1982, in a greenhouse environment. During this time, a nutrient solution was applied daily consisting of 75 ppm N, from a 15N:3P:6K fertilizer, micronutrients according to Hoagland and Arnon (21), and Fe at 5 ppm as NaFeEDTA.

On 16 April 1982, Pn of five cuttings, at various levels of irradiance was determined with an infrared gas analyzer, according to Halfacre et al. (18). Cuttings were enclosed in a 400 cm<sup>3</sup> plastic chamber and exposed to 50-900 micro E m<sup>-2</sup> s<sup>-1</sup> radiation supplied by four 500 watt reflector flood lamps. Irradiance level was regulated by the insertion of wire mesh screens between the light source and the chamber. Infrared radiation emitted from the lamps was filtered out by an 18 cm deep flowing water bath placed 2 cm

below the lamps. The temperature within the chamber was maintained at  $25^{\circ} \pm 2^{\circ}\text{C}$  and air flow rate was regulated to 1 liter  $\text{min}^{-1}$ . Total leaf area determinations, for each cutting, were made by multiplying the length x width product of each leaf by a conversion factor of 0.88. This factor was determined by correlating the actual leaf areas to the length x width product of several leaves, in a manner similar to that of Ackley et al. (1)

Expt. 2. This experiment was conducted to determine the effect of the auxin (IBA), nutrients and the rooting process on Pn of 'Helleri' holly cuttings. Unrooted cuttings were received from a nursery on 24 September 1982, cut to uniform lengths of 12 cm and defoliated on the lower 4 cm. One-half of the cuttings were treated with 5000 ppm IBA in 50% ethanol as a five second dip. All cuttings were inserted into individual pots as described in Expt. 1., and placed in the greenhouse under 47% shade cloth. The cuttings were intermittently misted by a Solartrol (General Scientific Equipment Co., Hamden, Conn.) solar controlled system, for six weeks. When roots were visible on 50% of the cuttings in the total group, the complete nutrient solution as described in Expt. 1., was applied to one-half of the IBA treated and untreated cuttings at three day intervals. A randomized complete block design with three replicates, four treatments

(0, 0 + N, IBA, and IBA + N) and 36 cuttings per treatment was utilized. An additional twenty cuttings were dried and used to determine the initial nitrogen content.

The Pn rate for each cutting was determined weekly in the same fashion as in Expt. 1. The cuttings for all treatments were harvested, dried at 70°C, ground through a 20 mesh screen and analyzed for total N using a modified micro-Kjeldahl procedure.

Expt. 3, conducted from 12 March 1983 to 20 April 1983, served to investigate the effects of source-sink interactions on the Pn rate of cuttings. For this experiment, the source was defined as the leaves present on the cuttings at the time of insertion into the medium. Newly developing roots and shoots were regarded as the sinks.

Cuttings were handled in the same fashion as in both previous experiments. Half of the cuttings were treated with IBA and, within each of these two groups other treatments were imposed: 1) removal of roots 2) removal of shoots 3) removal of roots and shoots 4) roots and shoots intact. Shoots and roots were removed at three day intervals by either manually rubbing off newly emerged roots or excising new shoots with a scalpel. The eight treatments were arranged in a randomized complete block with four replicates and 40 cuttings per treatment. The Pn rate of 20 randomly

selected cuttings from each treatment, was determined on day 40. Unlike the previous two experiments, however, Pn rate was expressed on a per plant rather than leaf area basis. This was due to the presence of leafy axillary shoots on cuttings within some of the treatments. Rate determinations were made, on twenty cuttings, with and without the shoots intact. In this way, the percent of the total Pn rate attributable to the axillary shoots was determined and subsequently subtracted to obtain the Pn rate of the original leaves.

A composite of six cuttings per treatment per rep was utilized for carbohydrate analysis. The original leaves of these cuttings were dried at 70°C, ground through a 20 mesh screen and analyzed for total sugar and starch content. Ground leaf material was extracted with 80% ethanol for three hours using a micro-Sohxlet apparatus. The liquid extract was boiled for twenty minutes with 0.02N H<sub>2</sub>SO<sub>4</sub> to hydrolyze the sucrose. It was then filtered and analyzed for total sugars using Nelson's method (31). For starch determination the tissue, from which soluble sugars had been extracted, was boiled for twenty minutes in distilled water to gelatinize the starch. An amylase enzyme preparation (39) and 0.20N acetic acid-sodium acetate buffer (pH 4.9) were then added to each sample. Samples were incubated for 12

hrs. at 37°C (39), filtered, and Nelson's method was used to determine the total starch content.

## RESULTS AND DISCUSSION

Expt. 1. As can be seen in the mean light response curve in Figure 1, Pn ceased to increase at PAR levels above 600 micro-Einsteins. Figure 1 illustrates the average response of five cuttings. Although the value of 600 micro-Einsteins should not be regarded as an absolute value it is still quite useful. For instance, in early summer cuttings may be stuck in a glasshouse, under shade. In early June, on a clear day, the PAR level is approximately 750 micro-Einsteins. This would indicate that the cuttings would be able to achieve maximum photosynthesis in terms of light requirements. However, it is possible that excessive shade may be detrimental. While it is important to provide shade to reduce temperature, we should take into consideration the restrictions placed on photosynthesis. The significance of this latter point has been exemplified by the work of Eliasson (14) and Davis and Potter (12).

Expt.2. Roots were first observed on the cuttings treated with IBA on the 21st day after insertion into the medium. Roots were first observed on a few 0-IBA cuttings on the 30th day; however, the majority of these untreated cuttings did not root by day 42, the conclusion of the experiment. Those treatments designated for supplemental nu-

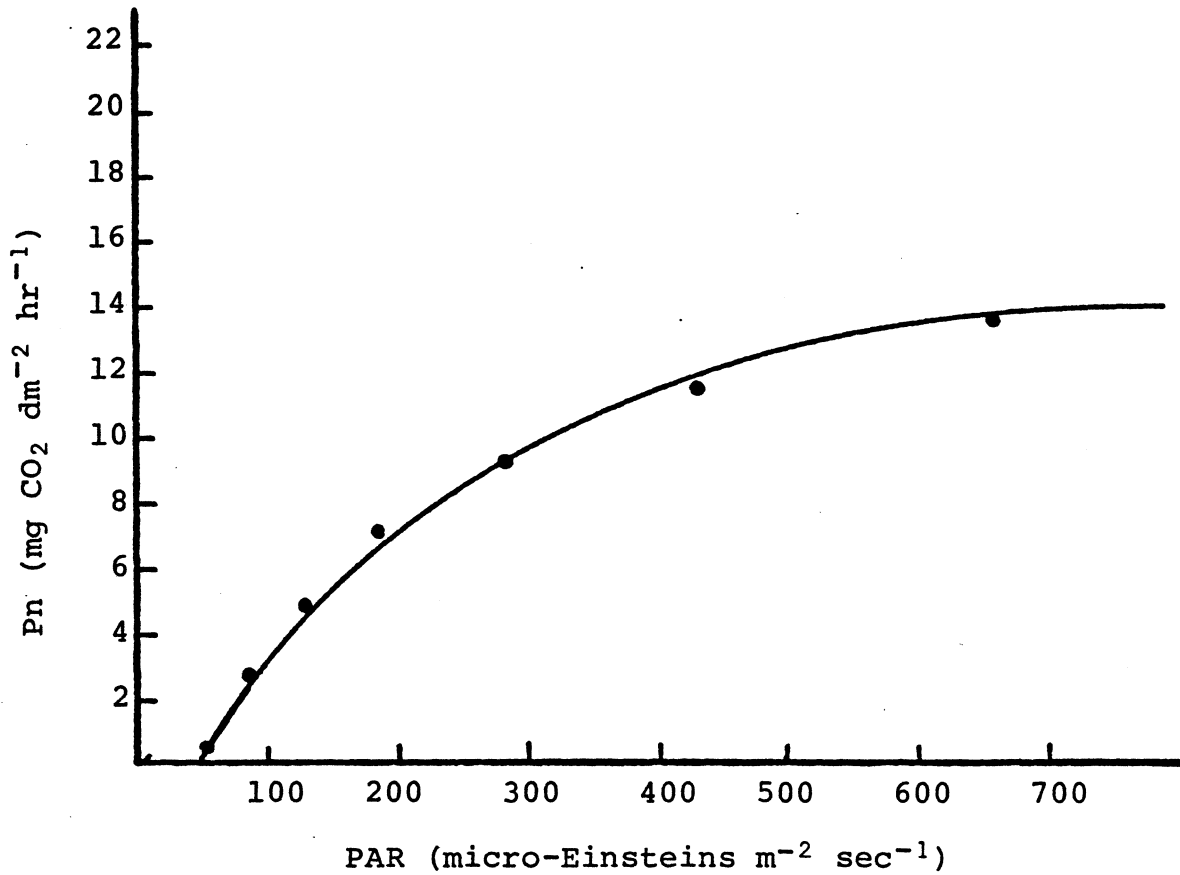
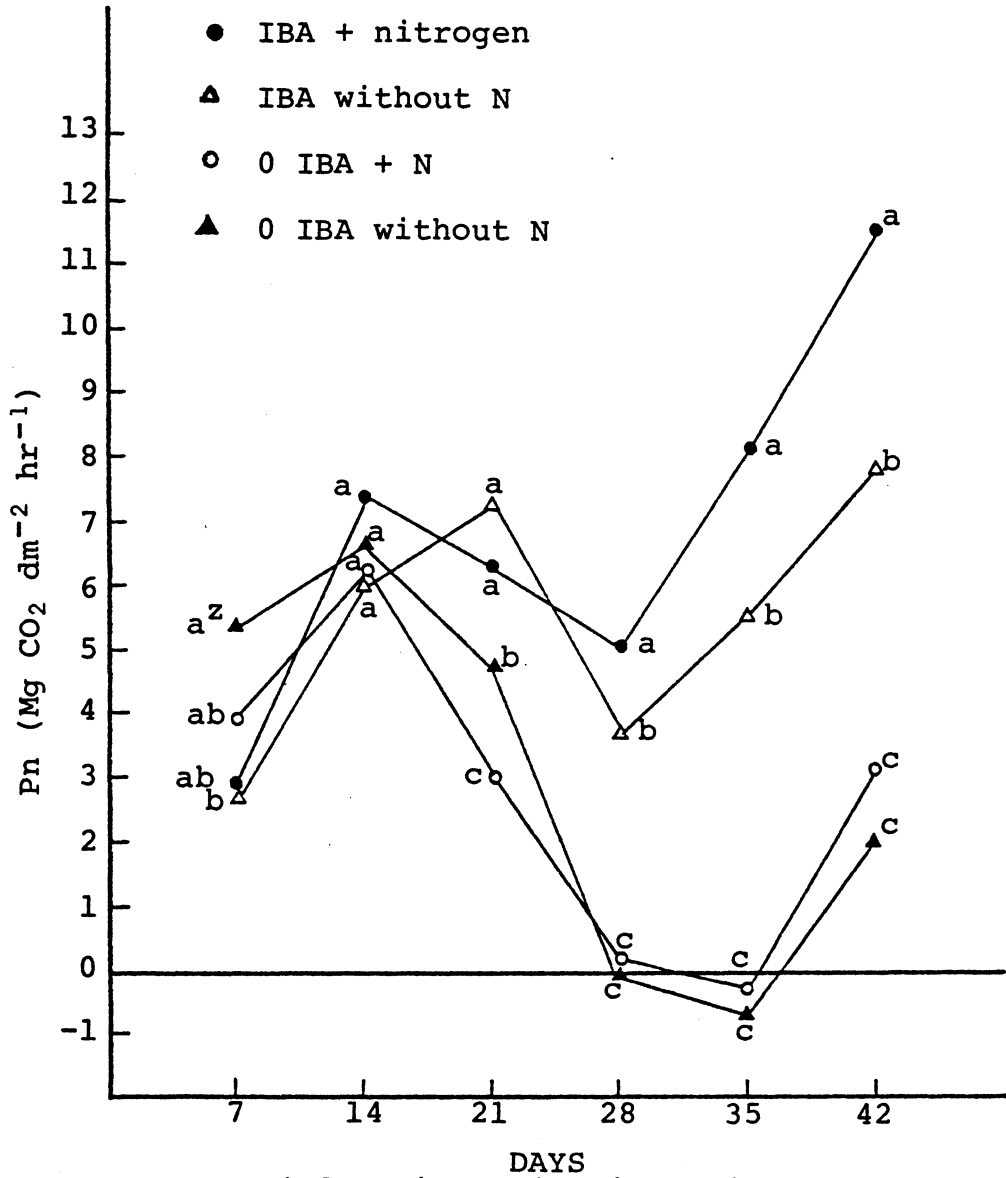


Figure 1. Mean photosynthetic response of 'Helleri' holly cuttings to various levels of irradiance.

trition began to receive the complete nutrient solution on the 24th day.

Figure 2 illustrates the progression of the Pn rate, for all treatments. Differences in the rates up until day 21 were minimal, especially at day 14 when there were no significant differences among treatments. Starting at the 21st day, cuttings treated with IBA exhibited higher Pn rates than untreated cuttings.

It is doubtful that the IBA was directly responsible for elevated Pn rates since the small amount applied would have been already metabolized by the cutting. The major difference between the treated and untreated cutting groups was the presence of a large number of roots on the IBA treated cuttings compared to virtually no roots on those lacking IBA. Differences in Pn rate between IBA and 0-IBA treatments were observed as of day 21 when roots were observed on the IBA treated cuttings. The rate of Pn for IBA treated cuttings never dropped as low as the 0-IBA cuttings and over time the differences in Pn rate became greater. No single explanation can likely account for these results, yet the presence or absence of roots on the cutting is an important consideration. Many studies linking root development to photosynthesis were previously discussed. Some explained the differences using the theory of source-sink



<sup>z</sup>Mean separation within days by Duncan's Multiple Range Test, 5% level.

Figure 2. Pn rates of 'Helleri' holly cuttings over time as influenced by IBA and nitrogen.

interactions, in that as soon as roots were present, a sink became available (10,11,16,22,24,25,33,34,43) thereby stimulating the Pn rate to increase. This explanation is pertinent to our results, as shown in Fig. 2. It was evident that the Pn rate increased upon rooting but decreased to levels of zero or less until roots were initiated. The possible effect of IBA was to stimulate a larger sink in less time and aid in the maintainance of higher Pn rates compared to the untreated cuttings. These results are in concurrence with those of two previously done experiments (data not shown).

Another aspect of the experiment was that of nutrition. Its effect on the IBA treated cuttings was noticeable as early as day 28, when only two applications of nutrient solution had been made (Fig.2). Those cuttings receiving the solution exhibited a higher Pn rate which increased over time. In the absence of IBA there was no response to the added nutrients, most likely because the absence of roots prevented nutrient uptake (6). The higher Pn rates achieved with the addition of nutrients on the IBA treated cuttings are supported by other studies where added nutrients increased the Pn rate (7,28,29,32,35). Further, it was shown that the % N contained in fertilized IBA treated cuttings was higher than for other treatments, due to absorption fol-

lowing rooting (Table 1). For the other treatments, % N was lower because of a growth dilution effect.

Expt. 3. In Expt.2, the Pn rate of the individual cuttings started to increase with the emergence of new roots. Since such roots can be regarded as a sink, then perhaps a source-sink relationship exists in 'Helleri' holly cuttings. This final experiment was established to further investigate this possibility.

Regardless of IBA treatment, when both roots and shoots, or either of the two, were allowed to develop, then the Pn rate was higher compared to cuttings where both were removed. The degree to which roots or shoots influenced Pn was dependent on the IBA treatment. The development of roots, without IBA, contributed to a higher Pn rate than when only shoots were allowed to develop. However, within the IBA treatment, shoot development appears to have exerted a greater influence. In fact, the highest Pn rate, for IBA treated cuttings, was attributed to the treatment where only the shoots were allowed to develop.

This difference between treatments can be explained if one considers the stage of development of each sink. For the 0-IBA treatment, the initial shoot flush had stopped and the plants were in a phase of secondary root development. Thus it is possible that the roots were a more active sink than

TABLE 1

Influence of nitrogen on 'Helleri'  
holly cuttings during propagation.

Treatment	Percent N
Initial	1.53a
IBA + N	1.47a
0 IBA, No N	1.15b
0 IBA, + N	1.07b
IBA, No N	1.06b

the shoots. However, with the IBA treatments, the shoots were in a phase of elongation and expanding leaves, with minimal root growth. Therefore, the shoots appeared to be a more active sink and probably contributed to a higher Pn rate than roots. However, the actual mean Pn rate for that treatment, where only shoots were present, may be inflated. It has been shown that the auxin produced in actively growing axillary shoots can effect a substantial increase in the Pn rate of the adjacent leaf (45). Nevertheless, it is probable that, despite this possible effect, the Pn rate of that treatment would be greater than that of the "roots only" treatment.

The cyclic type of growth and development, discussed here, is not uncommon to 'Helleri' holly. It has been shown that root elongation precedes shoot elongation by 2-3 weeks. Cuttings of the same physiological state were used in this experiment, yet, by the end of the study they were in different phases of growth. In the early days of the experiment, it was observed that shoot growth was progressing at a faster rate than root growth, on those cuttings not treated with IBA. For those cuttings which were treated, minimal shoot growth occurred until a substantial number of roots were present. Therefore, it would appear that the application of IBA initially created an active root sink at the expense of

shoot growth. However, with the 0-IBA treatment, shoot elongation and growth was able to occur sooner. This would then account for the switch in sink dominance for the different levels of IBA treatment.

The presence of a source-sink interaction was indicated by the occurrence of higher carbohydrates in cuttings with lower Pn rates (Table 2). A correlation coefficient of 0.73 was determined to exist between Pn rate and carbohydrate level. There was however an exception to this correlation. When axillary shoots alone were allowed to develop on IBA treated cuttings there was a high Pn rate and a high carbohydrate level. This would further support the explanation that the high Pn rate was due to an interaction of the shoot-auxin effect with the source-sink relationship. Also, in the 0-IBA treatment, the fact that roots had a greater effect on Pn is in line with the theory because carbohydrate levels were lower than when only shoots were present.

TABLE 2

Mean Pn rates and carbohydrate levels for Expt. 3 and accompanying ANOVA table.

Treatment	Pn rate	CHO level
0 IBA/Roots/Shoots	0.95 mg CO <sub>2</sub> cttg <sup>-1</sup> hr <sup>-1</sup>	12.51 mg/200 mg sample
0 IBA/No roots/No shoots	0.06	20.76
0 IBA/Shoots	0.09	14.55
0 IBA/Roots	0.50	13.92
IBA/Roots/Shoots	0.65	11.21
IBA/No roots/No shoots	0.16	17.30
IBA/Shoots	0.74	14.18
IBA/Roots	0.38	11.84

ANOVA Table

<u>SOURCE</u>	<u>DF</u>	<u>SS</u>	<u>F Value</u>	<u>SS</u>	<u>F Value</u>
Level of IBA	1	0.51	14.25* <sup>z</sup>	26.04	6.64*
Roots	1	5.96	163.60*	149.86	38.21*
Shoots	1	5.21	143.07*	64.72	16.50*
IBA x Roots	1	4.16	114.33*	0.09	0.02
IBA x Shoots	1	0.13	3.65	7.45	1.90
Roots x Shoots	1	0.00	0.04	26.55	6.77*
IBA x Roots x Shoots	1	0.89	24.45	2.65	0.68

<sup>z</sup> PR > F Test of hypothesis, significant at the 1% level.

## CONCLUSION

The emergence of roots and/or shoots contributed to an increase in the Pn rate of unrooted 'Helleri' holly cuttings. This increase could be attributed to an increased demand for photosynthate and a corresponding decrease in the carbohydrate levels of the leaves. It is therefore possible that a source-sink relationship exists for 'Helleri' holly cuttings. In three out of four instances, the use of IBA contributed to higher Pn rates. This may be due, in part, to decreases time to rooting and increased root number which may serve to increase sink size. Pn rate was also increased by the addition of mineral nutrients to the medium as soon as roots were present on the cuttings.

## REFERENCES

1. Ackley, W.B., P.C. Crandall and T.S. Russell. 1958. The use of linear measurements in estimating leaf areas. *Proceedings of the American Society for Horticultural Science*. 72:326-330.
2. Altman, A. and P.F. Wareing. 1975. The effect of IAA on sugar accumulation and basipetal transport of  $C^{14}$ -labelled assimilates in relation to root formation in Phaseolus vulgaris cuttings. *Physiol. Plant*. 33:32-38.
3. Bidwell, R.G.S., W.B. Turner and I.A. Tamas. 1969. The effects of auxin on photosynthesis and respiration---IN: Wightman, F.(ed.); *Biochemistry and Physiology of Plant Growth Substances*. 361-366.
4. Blazich, F.A. and R.D. Wright. 1979. Non-mobilization of nutrients during rooting of *Ilex crenata* Thunb. 'Convexa' stem cuttings. *Hort Science*. 14:242.
5. Blazich, F.A. and R.D. Wright. 1983. Mineral nutrient status of 'Convexa' holly cuttings during intermittent mist propagation. *J. Amer. Soc. Hort. Sci.* 108:(in press).
6. Booze, J.N. 1982. The influence of fertilization on Ilex crenata Thunb. 'Helleri' during propagation. Masters Thesis: Virginia Polytechnic Institute and State University, Blacksburg, Virginia, 24061.
7. Bottrill, D.E., J.V. Possingham and P.E. Kriedemann. 1970. The effect of nutrient deficiencies on photosynthesis and respiration in spinach. Plant and Soil 32:424-439.
8. Boussingault, J.B. 1868. *Agronomie, chimie, agricole et physiologie*. 2nd. ed. Mallet Bachelier, Paris, 1860-1874. pp. 236-212. (original not seen).
9. Breen, P.J. and T. Muraoka. 1973. Effect of indole-butyric acid on cuttings of 'Marianna 2624' plum. *J. Amer. Soc. Hort. Sci.* 98:436-439.
10. Burt, R.L. 1964. Carbohydrate utilization as a factor in plant growth. *Aust. J. Biol. Sci.* 17:867-877.

11. Carmi, A. and D. Koller. 1977. Effects of the roots on the rate of photosynthesis in primary leaves of bean (Phaseolus vulgaris L.). *Photosynthetica*. 12: 178-184.
12. 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.
13. DeJong, T.M. 1982. Leaf nitrogen content and CO<sub>2</sub> assimilation capacity in peach. *J. Amer. Soc. Hort. Sci.* 107:955-959.
14. Eliasson, L. 1978. Effects of nutrients and light on growth and root formation in Pisum sativum cuttings. *Physiol. Plant.* 43:13-18.
15. Eliasson, L. 1971. Adverse effect of shoot growth on root growth in rooted cuttings of aspen. *Physiol. Plant.* 25:268-272.
16. Eliasson, L. 1968. Dependence of root growth on photosynthesis in Populus tremula. *Physiol. Plant.* 21:806-810.
17. Ghobrial, G.I. 1983. Effects of root pruning on translocation of photosynthates in Phaseolus vulgaris. *J. Exp. Bot.* 34:20-26.
18. Halfacre, R.G., J.A. Barden and H.A. Rollins, Jr. 1968. Effects of Alar on morphology, chlorophyll content and net CO<sub>2</sub> assimilation rate of young apple leaves. *Proc. Amer. Soc. Hort. Sci.* 93:40-52.
19. Hansen, J., L. Stromquist and A. Ericsson. 1978. Influence of the irradiance on carbohydrate content and rooting of cuttings of pine seedlings (Pinus sylvestris L.). *Plant Physiology*. 61:975-979.
20. Hartmann, H.T. and D.E. Kester. 1975. *Plant Propagation: Principles and Practices*. Third Edition. Prentice-Hall, N.J.. pp. 88-89.
21. Hoagland, D.R. and D.I. Arnon. 1950. The water culture method for growing plants without soil. *Calif. Agr. Expt. Sta. Circ.* 347.
22. Humphries, E.C. and S.A.W. French. 1969. Photosynthesis in sugar beet depends on root growth. *Planta*. 88:87-90.

23. Humphries, E.C. and G.N. Thorne. 1964. The effect of root formation on photosynthesis of detached leaves. *Ann. Bot.* 28:391-400.
24. Humphries, E.C. 1963. Dependence of net assimilation rate on root growth of isolated leaves. *Ann. Bot.* 27:175-183.
25. Jesko, T. 1972. Removal of all nodal roots initiating the extension growth in Sorghum saccharatum (L.). *Photosynthetica*. 5(3):233-240.
26. Jesko, T., K. Heinrichova and A. Lukacovic. 1971. Increase in photosynthetic activity during the formation of the first node roots and first tiller in Sorghum saccharatum L. Moench. *Photosynthetica*. 5:233-240.
27. Lovell, P. and K. Moore. 1969. The effects of light and cotyledon age on growth and root formation in excised cotyledons of Sinapsis alba L.. *Planta*. 85:3511-358.
28. Lugg, D.G. and T.R. Sinclair. 1981. Seasonal changes in photosynthesis of field-grown soybean leaflets, 2. relation to nitrogen content. *Photosynthetica*. 15:138-144.
29. Natr, L. 1972. Influence of mineral nutrients on photosynthesis of higher plants. *Photosynthetica*. 6:80-89.
30. Natr, L. 1967. Time-course of photosynthesis and maximum figures for the accumulation of assimilates in barley leaf segments. *Photosynthetica*. 1:29-36.
31. Nelson, N. 1944. Photometric adaptation of the Somogyi method for the detection of glucose. *J. Biol. Chem.* 153:375-380.
32. Nghia, P.T.N., L. Natr, and S. Fialova. 1982. Changes in photosynthetic rate of spring barley induced by the removal of nitrogen or phosphorous deficiency. *Photosynthetica*. 15:216-220.
33. Nosberger, J. and E.C. Humphries. 1965. The influence of removing tubers on dry-matter production and net assimilation rate of potato plants. *Ann. Bot.* 26:579-588.
34. Okoro, O.O. and J. Grace. 1976. The physiology of rooting Populus cuttings; I. Carbohydrates and photosynthesis. *Physiol. Plant.* 36:133-138.

35. Possingham, J.V. 1970. Some effects of mineral nutrient deficiencies on the chloroplasts of higher plants. Proceedings of the 6th International Colloquium on Plant Analysis and Fertilizer Problems (ISHS), Tel Aviv, pp. 155-165.
36. Potter, J.R. and P.J. Breen. 1980. Maintenance of high photosynthetic rates during the accumulation of high leaf starch levels in sunflower and soybean. *Plant Physiology*. 66:538-541.
37. Ryle, G.J.A. and J.D. Hesketh. 1969. Carbon dioxide uptake in nitrogen deficient plants. *Crop Science*. 9:451-454.
38. Shiroya, T., G.R. Lister, V. Slankis, G. Krotkov and C.D. Nelson. 1962. Translocation of the products of photosynthesis to roots of pine seedlings. *Canadian J. of Bot.* 40:1125-1135.
39. Smith. 1969. Removing and analyzing total non-structural carbohydrates from plant tissue. Wisconsin Agric. Exp. Sta. Res. Report 41. 1969.
40. Smith, D.R. and T.A. Thorpe. 1975. Root initiation in cuttings of Pinus radiata seedlings; II. Growth regulator interactions. *J. Expt. Bot.* 26:193-202.
41. Stromquist, L. and J. Hansen. 1980. Effects of auxin and irradiance on the rooting of cuttings of Pinus sylvestris. *Physiol. Plant.* 49:346-350.
42. Struve, D.K. 1981. The relationship between carbohydrates, nitrogen and the rooting of stem cuttings. *The Plant Propagator*. 27(2):6-7.
43. Sweet, G.B. and P.F. Wareing. 1966. Role of plant growth in regulating photosynthesis. *Nature*. 210:77-79.
44. Thorne, G.N. and A.F. Evans. 1964. Influence of tops and roots on net assimilation rate of sugar beet and spinach beet and grafts between them. *Ann. Bot.* 28:499-508.
45. Turner, W.B. and R.G.S. Bidwell. 1965. Rates of photosynthesis in attached and detached bean leaves and the effect of spraying with indoleacetic acid solution. *Plant Physiol.* 40:446-451.

46. vanOverbeek, J., S.A. Gordon and L.E. Gregory. 1946. An analysis of the function of the leaf in the process of root formation in cuttings. *Amer. J. Bot.* 33:100-107.
47. Warlaw, I.F. 1968. The control and pattern of movement of carbohydrates in the plant. Botanical Review. 34:79-105.

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