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Root and Shoot Growth Patterns of Newly Rooted Woody Plants

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Additional index words. *Buxus sempervirens* × *Cupressocyparis leylandii*, *Euonymus kiautschovica* 'Sieboldiana', *Ligustrum ovalifolium*, *Prunus laurocerasus*, *Vitis labrusca* 'Concord', *Weigela florida*, ornamentals, propagation, root development

Abstract. Changes in primary root number (RN), root dry weight (RDW), and shoot dry weight (SDW) on newly rooted stem cuttings of 7 woody ornamental plants were evaluated over 18 or 24 weeks after either no root removal or root removal where remaining RN equalled 25%, 50%, or 100% of the average RN at transplanting. Regardless of root removal treatment or season (February, June, or July), increases in primary RN occurred after transplanting and preceded increases in RDW and SDW. RDW and SDW increased progressively and together after primary RN ceased increasing. Cuttings started in February attained maximum RN in 12 to 18 weeks after transplanting, whereas those started in June and July required 6 weeks. Results suggest that stem cuttings of woody plants have a minimum, species dependent, primary RN which must be attained before measurable shoot growth is initiated.

Rooted cuttings of woody plants are evaluated for future success on the quality and size of root system they produce (4, 6). Large numbers of roots on *Betula*, *Halesia*, *Malus*, *Prunus* and *Vitis* enhance transplant survival (2, 4) and shoot growth (16). Similarly, survival of bare root woody plants is facilitated by root development (8). Root removal studies indicate shoot growth to be related to root size: root reduction results in a decrease in shoot growth rate (7, 17, 18). Neither the aspect of root size (weight, volume, root number) nor the manner in which it mediates its influence is well understood.

Root modification of shoot growth has been attributed to control of nutrient and water uptake or to hormone synthesis (5, 15, 17). It is not clear whether reduced shoot growth following root pruning results from interference with nutrient or water uptake (3, 5, 7, 17). Resumption of shoot growth following cytokinin application to pruned roots (17, 18) indicates hormones may exert a regulatory influence. Control has been postulated to be localized in root tips since they are sites of high rates of nutrient and water uptake (2, 16, 17, 18) and of synthesis of cytokinins and gibberellins supplied to the shoot (5, 15, 17, 18).

Improved knowledge of the patterns of root change during

the establishment phase of newly rooted stem cuttings of woody plants would help clarify means by which growth is integrated between root and shoot. The present study monitored changes in root number, root dry weight, and shoot dry weight during the establishment of rooted shoot tip cuttings of several woody plants.

Materials and Methods

Softwood and hardwood shoot tip cuttings were propagated at the Univ. of Maryland greenhouses, College Park, Md. (38°58'N latitude). Rooting was facilitated by dipping the lower 2.5 cm of stems into commercial rooting powder containing 1H-indole-3-butanoic acid (IBA) and Thiram (15%). Cuttings were rooted in flats containing a mixture of 1 coarse perlite (#3): 1 Canadian sphagnum peat moss v/v under intermittent mist.

Once rooted (roots 2.5 cm or longer) cuttings were lifted, treated, and planted in containers in a 40% peat : 20% perlite : 20% vermiculite : 20% topsoil mix containing fritted trace elements (#503), and limed to pH 6.5. Plants were hardened-off under polypropylene shade cloth (53% transmittance) in the greenhouse for 2 weeks, given a fungicidal drench of Banrot (0.08%), and transferred to full sun in the greenhouse or outdoors.

Controlled release fertilizer (18N-2.6P-10K) at 5 g/liter of soil was provided within 2 weeks of initial transplanting. Plants were fertilized with 20N-8.7P-16.6K at 236 ppm N every 2 weeks after transplanting except at 4 weeks when applied at 470 ppm N.

Fourteen (Expt. 1) or 25 (Expt. 2 and 3) plants per treatment of each species were selected for evaluation at transplanting and

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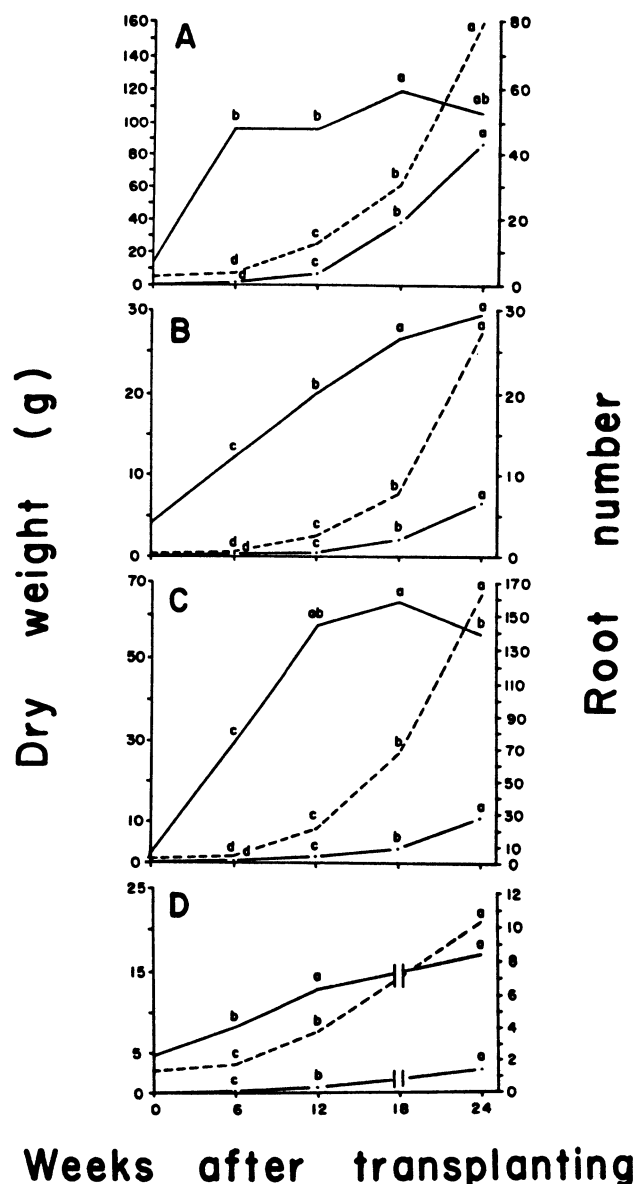


Fig. 1. Changes in dry weight of shoots (---) and roots (---), and root number (—) of rooted shoot tip cuttings of *Vitis labrusca* 'Concord' (A), *Ligustrum ovalifolium* (B), *Euonymus kiautschovica* 'Sieboldiana' (C), and \times *Cupressocyparis leylandii* (D), rooted in February. Mean separation among weeks by Duncan-Waller K-ratio *t* test, K ratio = 100.

every 6 weeks for 24 weeks (Expt. 1 and 2) or for 12 weeks (Expt. 3). After roots were washed, the number of primary roots 2.5 cm or longer was measured. Root and shoot dry weights were determined after oven-drying.

Data were analyzed after performing a $\log_e (x + 1)$ transformation (due to heterogeneity of variances) in Expt. 1 and 2 (20). Expt. 2 RN and Expt. 3 data were not transformed. Data presented have been retransformed. Mean comparisons were made by the Duncan-Waller K-ratio *t*-test. Correlations were calculated between RN, RDW, and SDW (Expt. 1 and 2). Regression analysis determined the relationship between original RN and final RN, RDW, and SDW (Expt. 3).

Expt. 1. Changes in root and shoot growth and the influence of artificial limitation of initial RN on plant growth were analyzed. Hardwood cuttings of *Vitis labrusca* L. 'Concord' (2

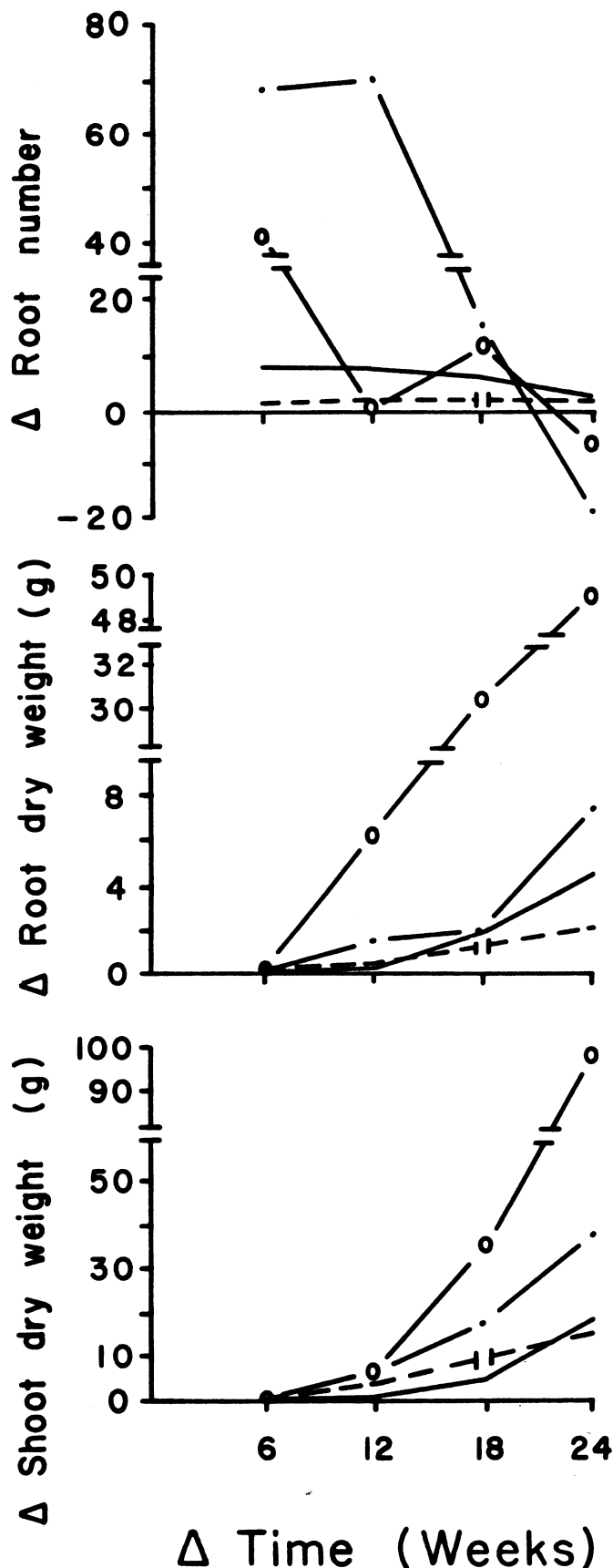


Fig. 2. Changes in growth at 6 week intervals from transplanting of *Vitis labrusca* 'Concord' (○—○), *Ligustrum ovalifolium* (—), *Euonymus kiautschovica* 'Sieboldiana' (---), and \times *Cupressocyparis leylandii* (---).

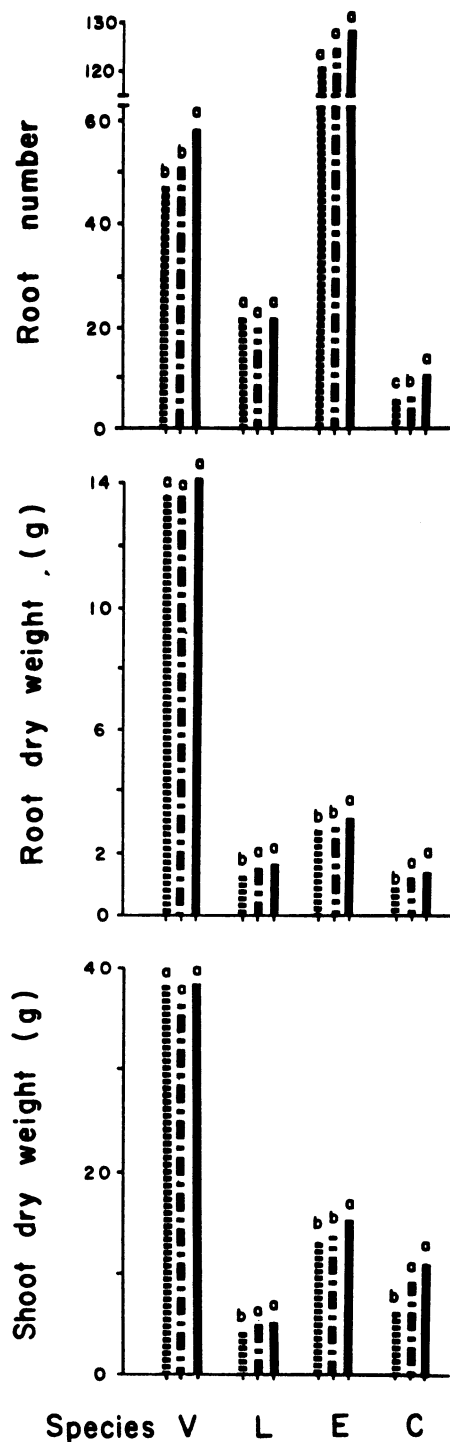


Fig. 3. Mean response to root removal to 100% of the mean root number (—), 50% of the mean (---), or 25% of the mean (····) root number of *Vitis labrusca* 'Concord' (V), *Ligustrum ovalifolium* (L), *Euonymus kiautschovica* 'Sieboldiana' (E), and *Cupressocyparis leylandii* (C). Values are means of combined observations of 6, 12, 18, and 24 weeks for each root number class. Mean separation by Duncan-Waller K-ratio *t* test, K ratio = 100.

nodes, 10–36 cm), *Ligustrum ovalifolium* Hassk. (18 cm), *Euonymus kiautschovica* Loes. 'Sieboldiana' (13 cm), and *Cupressocyparis leylandii* Dallim & A.B. Jacks (18 cm) were taken between 29 Jan. 1982 and 5 Feb. 1982. *Euonymus*,

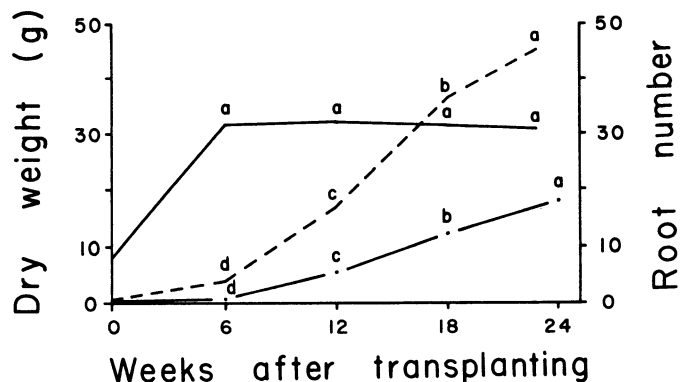


Fig. 4. Changes in dry weight of shoot (---) and roots (···) and root number (—) of rooted shoot tip cuttings of *Ligustrum ovalifolium*, propagated in June. Mean separation among weeks by Duncan-Waller K-ratio *t* test, K ratio = 100.

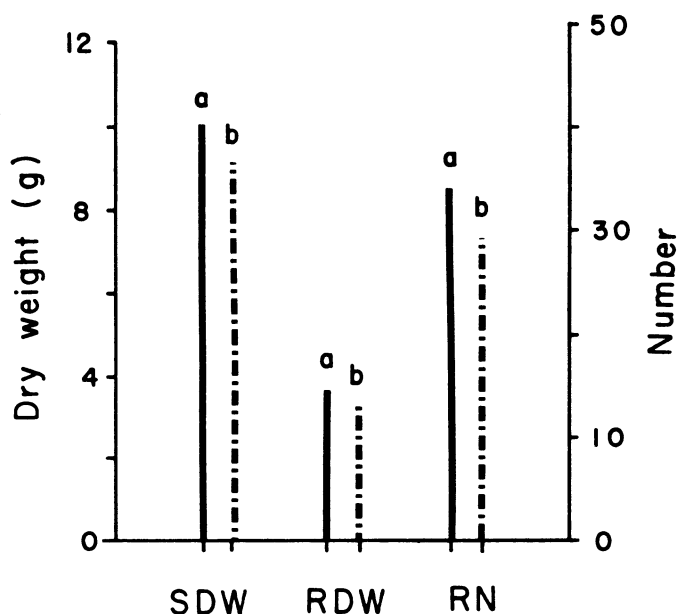


Fig. 5. Mean response over 24 weeks to no root removal (—) or to root removal to 25% of the mean (---) of *Ligustrum ovalifolium* propagated in June. Mean separation by Duncan-Waller K-ratio *t* test, K ratio = 100.

Cupressocyparis, and *Ligustrum* were wounded basally with 2 vertical cuts 2.5 cm long, treated with 0.4% IBA and rooted.

The average initial RN of 20 cuttings for each species was calculated after rooting. Roots were removed randomly at the point of origin so the number remaining per cutting equaled 25% (Low-L), 50% (Medium-M), or 100% (High-H) of the average RN and the following criteria were satisfied: 1) only primary roots 2.5 cm or longer were retained; 2) each cutting possessed at least M class RN; and 3) possession of more than M or H class RN was required for assignment to the M or H class, respectively. Average RN of *Vitis*, *Ligustrum*, *Euonymus*, *Cupressocyparis* were: 28, 8, 12, and 4, respectively.

Ligustrum and *Euonymus* were potted in 0.5 liter pots, *Cupressocyparis* in 0.8 liter pots and *Vitis* in 3.5 liter pots. After hardening-off, plants were placed in the greenhouse in a randomized complete block design with 14 replications. When roots filled containers, plants were transplanted (species, container size and date, respectively): *Vitis*—17 liter on 31 May, *Ligus-*

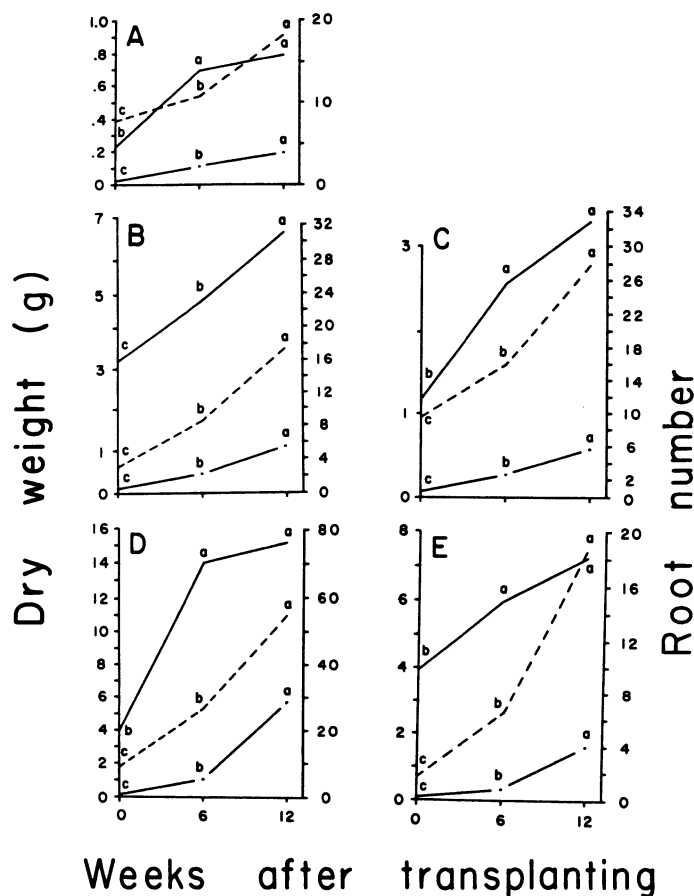


Fig. 6. Changes in dry weight of shoots (---) and roots (---), and root number (—) of *Buxus sempervirens* (A), *Ligustrum ovalifolium* (B), *Prunus laurocerasus* (C), *Vitis labrusca* 'Concord' (D) and *Weigela florida* (E), shoot tip cuttings propagated in July. Mean separation among weeks by Duncan-Waller K-ratio *t* test, K ratio = 100.

trum and *Euonymus*—2.4 liter on 3 June. Supplemental Osmocote (18N–2.6P–10K) at the rate of 4.9 g/liter soil was added at transplanting. Plants were moved outside on 15 May. Data were collected as described, except no data were available for *×Cupressocyparis* at week 18.

Expt. 2. The effects of root removal and the influence of original RN and season of propagation on subsequent growth were investigated. Softwood cuttings of *L. ovalifolium* 18 cm in length were propagated on 5 June 1982 as in Expt. 1, except plants were not wounded. On 2 July, rooted cuttings were divided into 2 treatments: (NP)—roots were counted but not removed; (P)—roots were removed to equal 25% of the average initial RN (average RN = 12) based on 20 randomly selected rooted cuttings.

After planting in 0.5 liter pots, plants were placed in the

greenhouse in a completely random design. They were moved outside on 21 July, and returned to the greenhouse on 8 Oct., under supplemental incandescent lighting ($4 \mu\text{mol s}^{-1} \text{m}^{-2}$) from 1700 to 2250 HR. Container sizes and transplanting dates were: 2.5 liter on 13 Aug., and 3.5 liter on 5 Nov.

Expt. 3. The influence of original RN and season on growth in additional species was analyzed. Between 29 June and 5 July 1982, softwood cuttings (species and lengths, respectively) were made of *Buxus sempervirens* L.—10 cm, *Prunus laurocerasus* L.—10 cm, *Ligustrum ovalifolium*—18 cm, *Vitis labrusca* 'Concord'—16–18 cm (2 nodes), and *Weigela florida* (Bunge) A.DC.—13 cm. *Buxus* and *Weigela* were rooted with 0.1% IBA. Other genera were propagated as in Expt. 1.

Once rooted, primary RN per cutting 2.5 cm or longer was counted, and plants were potted in 0.5 liter containers or in 2.4 liter containers (*Vitis*). Average initial RN, counting, and planting dates were: *Buxus*—7, 4 July; *Prunus*—15, 4 Aug.; *Ligustrum*—19, 5 Aug.; *Vitis*—25, 28 July; and *Weigela*—12, 3 Aug. Growing procedures of Expt. 1 were followed. Plants were placed in full sun in the greenhouse in a completely random design with 25 replications. Supplemental lighting, as described, was added from 8 to 28 Oct.

Results

Expt. 1. Since no interactions existed between root classes (L, M, H) and weeks after transplanting (6, 12, 18, or 24) for each species, main effect means are presented for RN, RDW, and SDW (Fig. 1). After transplanting, primary RN increased most rapidly the 1st 6 to 12 weeks, peaked between 12 and 18 weeks, and then declined or failed to increase further (Fig. 2). Development of primary RN preceded dry weight increases in roots and shoots. Differences in maximum primary RN existed among species.

Most rapid increases in RDW and SDW occurred between 18 and 24 weeks (Fig. 2). In all species, SDW was greater than RDW. Changes in RDW and SDW in the 1st 6 to 12 weeks were small but increased in parallel through week 24. RDW and SDW were correlated highly, but RN was correlated weakly with RDW and SDW (Table 1).

Root class differences (L, M, H) were small in all species (Fig. 3). RN, RDW, and SDW of H class plants were greater than or equal to those of the L or M class.

Expt. 2. Softwood cuttings of *Ligustrum* in NP and P classes showed no significant interactions with time; therefore, pooled average data are presented (Fig. 4). Maximum RN was attained within 6 weeks of initial transplanting. RDW and SDW increased most rapidly after RN peaked. RDW and SDW were highly correlated ($r = 0.978$, $P = 0.01$), but RN was correlated poorly with SDW and RDW ($r = -0.081$ and $r = -0.074$, $P = 0.01$, respectively). RDW was less than SDW. RN, RDW, and SDW in the P class were less than those in the NP class, but differences were small (Fig. 5).

Table 1. Simple correlation coefficients (*r*) between root number (RN), root dry weight (RDW), and shoot dry weight (SDW).

Species	RN × RDW	RN × SDW	RDW × SDW
<i>Vitis labrusca</i> 'Concord'	0.233* ^z	0.192*	0.974**
<i>Ligustrum ovalifolium</i>	0.574**	0.619**	0.985**
<i>Euonymus kiautschovica</i> 'Sieboldiana'	0.555**	0.596**	0.978**
<i>×Cupressocyparis leylandii</i>	0.473**	0.558**	0.936**

^zBased on transformed data: significant at the 5% (*) or 1% (**) level, respectively.

Expt. 3. RN increased rapidly in the 1st 6 weeks after transplanting (Fig. 6). RN of *Ligustrum* increased through 12 weeks whereas RN of *Buxus*, *Prunus*, *Vitis*, and *Weigela* did not change. Species differed in maximum RN, RDW, and SDW. RDW and SDW increased together, but accelerated after RN ceased increasing. RDW was less than SDW. Regression analysis showed a significant ($P = 0.01$) positive linear trend existed between original RN and final RN, but not between original RN and RDW or SDW (data not presented).

Discussion

Similar patterns of RN production and RDW and SDW accumulation were observed in all species. Primary RN increased following transplanting. The increase frequently was rapid (Expt. 2 and 3) and plateaued before major increases in RDW and SDW, despite differences in RN among species. This indicates primary root development, if not root initiation, occurs over a long time and appears to be a prerequisite for the establishment of integrated growth between roots and shoots. This behavior parallels responses of established woody plants, in which root development precedes shoot growth in plants initiating spring growth (10, 13) or exhibiting episodic shoot growth (10, 13, 14).

Root tips are sites of synthesis of gibberellin-like or cytokinin-like hormones (5, 15, 17, 18). Cytokinins have been implicated in control of shoot growth through regulation of cell division and elongation, leaf protein metabolism, and axillary shoot growth (15, 19). Roots also have been linked with promote effects on top growth. Ooyama (16) associated increased RN and subsequent growth in height. Well-rooted cuttings of *Vitis* produced a larger crop which fruited earlier than cuttings not well-rooted (23). Steinbeck (21) noted *Liriodendron* clones which produced larger initial root systems maintained substantial growth over a 4 year period. Similarly, reduction in cytokinin supply to the shoot after root removal or reduction in root size has been associated with shoot stunting (5, 12, 17, 18, 19). In *Prunus persica* (17, 18), reduced shoot growth followed root restriction or pruning and was a function of lowered root tip numbers. Cytokinin application to leaves overcame this reduction (17, 18). In our experiments, an increase in primary RN preceded shoot and root growth. Perhaps in rooted cuttings, a critical level of growth substance, regulated by the number of root tips, is required for shoot growth.

Mertens and Wright (14) proposed a theory that employs a source-sink concept to explain rhythmic growth of woody plants. As N is absorbed in roots, it reacts with carbohydrates to promote their development. Eventually, nutrient absorption exceeds root need, and surplus is transported to the shoot where it combines with carbohydrates to form protein and promote shoot growth. Since carbohydrates are used preferentially in the shoot, fewer are available to the roots resulting in reduced growth of roots and ultimately shoot growth. As shoot growth slows, carbohydrates become available for translocation to the root, and the cycle repeats. In newly established shoot tip cuttings of woody plants, the increase in primary RN may be associated with gradual translocation and accumulation of carbohydrates in roots, where they react with nutrients to enhance root development. When root needs are satisfied, nutrients are translocated to the shoot. Thus, shoot growth would follow an increase in RN.

A comparison of root removal treatments shows root and shoot growth were reduced, but by very small amounts. This reduction was expected and consistent with most commercial

practices and root pruning studies (3, 5, 7, 17, 18, 22). However, the reductions in root and shoot growth observed in our experiments were relatively insignificant when compared with the large increases observed over time. Andrews and Newman (1) suggested that root pruning, in species which root profusely, does not always reduce shoot growth. Three of 4 species examined in Expt. 1 possessed a vigorous rooting habit. Further confirmation of this hypothesis was observed in \times *Cupressocyparis*, which produced few roots and was stunted by severe root removal. Our plants were supplied adequately with water and minerals and did not function under stress conditions. It is possible that contrasts between classes would have increased had stresses been imposed (9).

In our experiments, each species produced a different maximum RN, but varied in time of achievement. Species started from softwood cuttings (Expt. 2 and 3) attained maximum RN in 6 weeks, whereas those started from hardwood cuttings (Expt. 1) required 12 to 18 weeks. The implication is that a minimum RN is required for onset of shoot growth, and season or cutting type affects time of achievement of this RN. Perhaps the delay in achieving growth or lack of vigor of many newly rooted woody plants (11) results from reduced or delayed development of sufficient RN or root tips. This hypothesis is supported by studies showing that RN is a valid index of success in transplanting and can affect future growth (4, 21). A regulatory role for RN suggests it may be possible to enhance shoot growth by promoting proliferation of roots. The use of maximum tolerable auxin concentrations at propagation and/or root pruning of newly rooted cuttings to promote additional root proliferation or reapplication of auxin to roots of rooted cuttings or bare root nursery stock could stimulate rapid shoot growth.

To clarify the role of RN in newly rooted stem cuttings of woody plants, future investigations should examine changes in cytokinin and gibberellin levels and in N and carbohydrate balances in roots and shoots of woody plant cuttings during establishment.

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Corrigendum

In the list of reviewers of manuscripts for volume 109 of the *Journal* [see *Journal* 109(6):903–904], the names of David R. Hershey and Dean R. Evert were omitted inadvertently.