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SHORT COMMUNICATION

Influence of the irradiance on phenols content and rooting of *Ilex paraguariensis* cuttings collected from adult plants

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Abstract The influence of irradiance on phenolics contents and rooting of *Ilex paraguariensis* cuttings was studied. Results of the first experiment with stock plants under controlled-irradiance conditions show that when the irradiance level increased from 1.5 to 100 % PPFD, the oxidation of cuttings raised from 19 ± 11 to 88 ± 4 % ($r^2 = 0.64$). At the same time, a strong correlation was observed between total phenolics content and irradiance ($r^2 = 0.7$). In consequence, adventitious rooting diminished from 67 ± 5 to 3 ± 3 % under full radiation ($r^2 = 0.7$). In the second experiment with stock plants subjected to field conditions, the results showed that the rooting process is strongly affected by the genotype ($P < 0.0001$), while the statistical analysis did not show a correlation between rooting and age of the donor plant. Season had a variable effect and depends on genotype. Although we did not find correlations between the rooting ability and the canopy structure of the stock plants, the position of the branches in the mother plant affected rooting and depended on season in addition to genotype. Concomitantly, the levels of soluble phenolics compounds were higher from leaves subjected to high-irradiance conditions than samples collected from inner canopy; which was coincident with the pattern of cuttings oxidation. In conclusion, our results provide evidences which support the hypothesis that the physiological status of the stock plant at the time that cuttings are excised is of utmost importance for the subsequent rooting of *I. paraguariensis* cuttings. The influence on soluble phenolics content of different irradiances given to the stock plants negatively affect the rooting process since the product of its oxidation cause the browning and death of the cuttings.

Keywords *Ilex paraguariensis* · Stock plant · Adventitious rooting · Soluble phenolics content

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Introduction

Ilex paraguariensis St. Hil. is the most cultivated specie of the genus *Ilex* in America due to its economical relevance. Its leaves and shoots are used to prepare a traditional infusion named mate which has several health benefits. The establishment of a useful method for vegetative propagation of mature trees is difficult due to the reduced rooting capacity of softwood cuttings. However, it is not known whether the characteristics of cuttings are associated with genetic differences in rooting ability or simply an expression of growth and the condition of plant since the material for cuttings is normally sourced from established stock plants exposed to seasonal changes and subjected to a variety of environmental stresses which influence the growth and ability to provide cutting material that forms adventitious roots (Kibbler et al. 2004). Rooting success has often been correlated with the temperature of the stock plant environment prior to take cuttings. However, increased rooting may not be only the result of high temperature per se since it should be influence by the

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physiological state of the plant (Husen and Pal 2007). In fact, it is well known that plants adjust the level of free endogenous hormones and a variety of metabolites such as soluble sugars (Rosa et al. 2009), phenols (Edreva et al. 2008), and flavonoids (Treutter 2006) to reduce the negative impact of the adverse situation. Environmental influence may act through the variation in the level of auxin and certain phenols which affect the sensitivity to the rooting stimulus exert by the auxin (Faivre-Rampant et al. 2002). Numerous reports confirm the activity of *ortho*-dihydroxy phenols as a rooting co-factor or synergist. For example, *p*-coumaric, caffeic and chlorogenic acids enhanced rooting when supplied alone and increased the effect of auxin applications (Jarvis 1986). Furthermore, our previous result demonstrates that flavonoids promote rooting in *I. paraguariensis* cuttings (Tarrago et al. 2004). We found that quercetin promoted the formation of adventitious roots and improved the distribution of roots around the cutting without impacting the number of roots per rooted cutting. In contrast, the additions of naringenin or rutin to the culture medium inhibited the in vitro rooting of *Ilex dumosa* micro-shoots (Luna et al. 2003). Concomitantly, many plants naturally synthesize mono or polyphenolic compounds in response to either biotic or abiotic stresses which negatively affect the morphogenetic process (Vermerris and Nicholson 2008).

The aim of this study was to determine whether *I. paraguariensis* rooting correlates with the phenological status of the mother plant, the sunlight conditions, the total soluble phenols content, and the variation of chlorogenic acid, dicaffeoylquinic acids, caffeic acid, and rutin in the leaves at the time of cutting collections.

Materials and methods

Experiments

The first experiment aimed to determine whether irradiance on the stock plants correlates with rooting. Cuttings were obtained from stock plants of SI-49 clone grown in 4 L pots filled with lateritic red soil and subjected to different sunlight irradiances by covering the roof, eastern and western sides of iron-framed boxes with different layers of shading nets. Each box contained 12 pots and the light treatments (boxes) were repeated three times. The environmental conditions registered throughout the 120-day-experiment were as follows: average temperature 26.8 °C (ranging from 21.2 to 32.7 °C), average RH 65 % (ranging from 42 to 89 %). Only running tap water was added to the pots to keep the soil moisture at field capacity. This experiment was carried out in summer and cuttings were collected at the end of the second flash of growth.

Based on experiment 1, the second experiment was achieved to evaluate whether season and canopy structure of the field stock plants have an effect on the rooting process. Cuttings were collected from 15 mature plants localized in Gdor. Virasoro, Argentina (28°02′S, 55°54′W). The site is characterized by a mean annual rainfall of 1,800 mm, distributed mainly during spring and autumn; mean year temperature of 22 °C while frosts are scarce. The soil is described as Ultisol. Shoots (35 to 40-cm long) were harvested from the central and peripheral structure of each plant (inner and outer canopy) at the end of each seasonal flash of growth from 14 to 78-year-old plant grown at different densities.

Treatment of cuttings and growing conditions

Procedures for the collection and handling of cutting material are described in Tarrago et al. (2004). Softwood cuttings (10 to 12-cm long, 3 to 5-mm diameter) consisted of six to nine nodes in which the uppermost mature leaf was cut in half and retained while the lower six to eight leaves were removed. For rooting, cuttings were dipped in an aqueous solution of quercetin 500 µM (60 min) followed by a treatment of 4 min in 4,000 ppm of IBA ethanolic solution (50 %) and set into trays containing perlite plus 0.5 g of controlled release micro-fertilize (Osmocote®, 18-5-9). They were grown for 6–8 weeks in a growth chamber providing a day/night air temperature of 25–27/20–22 °C and substrate temperature of 22–25 °C. Relative humidity was maintained at 90 % during the first 7 days by a fog device and then decreased gradually until 70 %. Photoperiod of 12 h was kept throughout the rooting period using 20 % sunlight radiation (150–180 µmol m^{-2} s^{-1}, PAR) plus 100 µmol m^{-2} s^{-1} using eight cool-white fluorescent lamps (40 W) set at 1.8 m over the cuttings and outside the growth chamber.

Analysis of phenolic compounds

Total polyphenol determination

Hundred and twenty-five milligram of frozen powder from mature leaves was suspended in 500 µl methanol and incubated at room temperature (10 min). After centrifugation at 2,500*g* (10 min), 400 µl supernatant was collected. The pellet was re-extracted under the same conditions and 400 µl supernatant was removed and pooled with the first supernatant. Afterward, the extract was ten times concentrated by evaporation at 45 °C. To estimate the amount of phenolics, the methanolic extracts were diluted 1:40 with water and the Folin-Ciocalteu reagent diluted 8 times with distilled water (200 µl) and Na_2CO_3 20 % (650 µl) were added to the samples. Tubes were

incubated in darkness at room temperature for 120 min. Absorbance was measured at 765 nm. Results were expressed in gallic acid equivalent per milligram of leaf samples.

High performance liquid chromatography

The quantification of caffeoyl derivatives was carried out using validated HPLC external standard methods. A reverse phase IB-SIL RP 18 (5 µm, 250 × 4.6 mm I.D) Phenomenex column and a gradient consisting of solvent A: water: acetic acid (98:2); solvent B: methanol: acetic acid (98:2) was used. A gradient range from 15 % B to 40 % B in 30 min; 40 % B to 7 5% B in 10 min, and 75 % B to 85 % B in 5 min was employed. Flow rate was set at 1.2 ml/min. Identification and quantification were carried out by simultaneous analysis of retention times and detection with an UV detector and a photodiode-array detector at 325 nm for caffeoyl derivatives and 254 nm for routine.

Statistical analysis

Each treatment consisted of 24 cuttings and the experiments were repeated three times. Data were analyzed with ANOVA and regression modules. For analyses of correlations and lineal regression between PPFD values, replicates were individually considered.

Results and discussion

Table 1 shows the results obtained from potted SI-49 plants subjected to different sunlight conditions. Oxidation of cuttings raised from 19 ± 11 to 88 ± 4 % when the irradiance level increased from 1.5 to 100 % PPFD ($r^2 = 0.64$). Likewise, a strong correlation was observed between total phenols content and irradiance ($r^2 = 0.7$). Adventitious rooting diminished from 67 ± 5 to 3 ± 3 % under full radiation ($r^2 = 0.7$). Furthermore, the number of roots per rooted cutting was negatively affected by the incident radiation.

The rooting ability of cuttings taken from stock plants subjected to field conditions is shown in Table 2. The genotype strongly affected this morphogenetic process ($P < 0.0001$). Statistical analysis did not show a positive relationship between rooting and age of the donor plant. Season had a variable effect and depends on genotype. In most cases, rooting was greater in spring and summer than autumn ($P < 0.0001$) with the exception of V-8. Although we did not find correlations between the rooting ability and the canopy structure of the stock plants when the density varied from 1,000 to 5,600 plants per ha, the position of the branches in the mother plant affected rooting and depended on season in addition to genotype. In fact, rooting of varieties A-5 and V-11 (78 and 17-year-old, respectively) was higher in spring and the best result was obtained when the explants were collected from inner canopy. Otherwise, summer had a positive effect on the rooting process from V-1, V-12, and V-16 with a further interaction between canopy position and genotype. Although, V-1 and V-12 was the same age and belonged to the same orchard with an equal density, the obtained results were disparities respect to the position of the explants.

In general, the levels of soluble phenolics compounds were higher from leaves subjected to high irradiance conditions than samples collected from inner canopy and the pattern of oxidation show a similar performance, except for A-4, A-8, A-10, and V-5, in which, the results should not be explained only by the total phenolics content. In addition, the endogenous content of some diphenols (chlorogenic acid, dicaffeoylquinic acids) and flavonoids (caffeic acid, rutin) extracted from leaves of different varieties indicated that its whole concentration (Table 3) is not linked with the rooting ability exhibit by the genotype and its variation should be associated with the radiation level

Table 1 Influence of PAR irradiance (PPFD) on the leaf soluble phenolics content, oxidation, and rooting of cuttings obtained from stock plants grown in pots

	PPFD (%)				Linear regression (r^2–F)
	1.5	3	15	100	
Leaf soluble phenolics (ppm eq. gallic acid g-1 FW)	28,222 ± 4,821	19,524 ± 4,085	25,557 ± 3,586	47,797 ± 3,871	0.7–22.8
Oxidation and death of cuttings (%)	24 ± 3.4	19 ± 11.1	67 ± 4.1	88 ± 4.3	0.6–17.6
Rooting (%)	67 ± 4.8	63 ± 8.9	25 ± 0.4	3 ± 3	0.7–22.0
Roots per rooted cutting	10.1 ± 2.0	6.7 ± 1.3	5.3 ± 2.0	0.3 ± 0.3	0.6–14.5

Each value is shown as the mean ± SEM

Table 2 Effect of branch position, season, genotype and their interactions on leaf soluble phenolics content, oxidation, and rooting response of *Ilex paraguariensis* softwood cuttings taken from the field

Cultivar and age (years)	Orchard stands (plants/ha)	Canopy structure	Branch position	Soluble phenolics ppm eq. gallic ac g^{-1} FW	Oxidation of cuttings (%)	Rooting (%)		
						Spring	Summer	Autumn
A-4 (78)	1,250	Open	Interior	31,054 ± 1,586	25 ± 1.2*	24 ± 10.3	53 ± 1.4	17 ± 2.9
			Periphery	65,857 ± 401***	10 ± 5.2	12 ± 6.9	45 ± 2.6	22 ± 1.9
A-5 (78)	1,250	Open	Interior	23,466 ± 13,816	31 ± 6.6	75 ± 6.9*	15 ± 2.1**	26 ± 4.9
			Periphery	28,272 ± 3,950	30 ± 3.3	24 ± 2.6	55 ± 3.4	5 ± 5.0
A-6 (78)	1,000	Open	Interior	30,779 ± 255	2 ± 2.0	11 ± 0.7	25 ± 1.8*	11 ± 5.5
			Periphery	57,000 ± 9,026*	67 ± 2.9***	10 ± 5.2	15 ± 0.4	10 ± 5.2
A-7 (78)	1,000	Open	Interior	23,546 ± 2,881	28 ± 4.1	3 ± 3.0	0	0
			Periphery	55,391 ± 10,384*	49 ± 8.9*	25 ± 5.5	16 ± 1.2**	10 ± 5.2
A-8 (78)	1,000	Open	Interior	16,576 ± 9,120	70 ± 8.9*	16 ± 5.3	5 ± 2.5	37 ± 6.5
			Periphery	34,062 ± 1,067	30 ± 2.0	36 ± 3.2*	56 ± 4.0**	37 ± 6.5
A-10 (78)	1,000	Open	Interior	27,917 ± 5,169	48 ± 2.8***	12 ± 2.6	12 ± 2.1	0
			Periphery	34,228 ± 2,117	14 ± 1.4	1 ± 1.0	13 ± 1.6	0
V-1 (30)	1,250	Open	Interior	24,493 ± 5,117	41 ± 6.9	35 ± 2.9*	21 ± 3.3	16 ± 0.8
			Periphery	36,745 ± 2,566	40 ± 5.8	29 ± 2.1	52 ± 13.6	11 ± 5.5
V-2 (30)	1,250	Open	Interior	22,516 ± 3,754	92 ± 8.3	28 ± 2.8	8 ± 8.0	11 ± 5.5
			Periphery	34,399 ± 4,340	100	25	0	8 ± 8.0
V-12 (30)	1,250	Open	Interior	24,263 ± 2,474	0	36 ± 7.3*	65 ± 0.8**	7 ± 7.0
			Periphery	27,285 ± 2,783	22 ± 6.9	12 ± 3.2	3 ± 3.0	0
V-4 (25)	2,222	Open	Interior	30,182 ± 642	10 ± 2.1	56 ± 1.4	72 ± 3.9	53 ± 7.0
			Periphery	36,015 ± 1,455*	14 ± 7.5	49 ± 7.2	53 ± 1.5	30 ± 1.6
V-5 (27)	3,300	Middle	Interior	27,322 ± 1,744	64 ± 5.7	25 ± 1.3*	8 ± 3.9	6 ± 2.9
			Periphery	55,634 ± 3,758**	0	11 ± 3.3	32 ± 5.1	0
V-6 (18)	3,300	Middle	Interior	30,309 ± 7,984	47 ± 4.6	20 ± 2**	7 ± 1.9	0
			Periphery	51,533 ± 3,604	50 ± 4.1	0	0	0
V-11 (17)	3,300	Middle	Interior	24,025 ± 3,346	7 ± 3.7	89 ± 5**	7 ± 3.5*	16 ± 0.8
			Periphery	35,046 ± 1,892*	18 ± 5.1	44 ± 4.3	27 ± 1.2	10 ± 5.2
V-16 (17)	3,300	Middle	Interior	21,836 ± 1,634	0	30 ± 3**	88 ± 6.5*	0
			Periphery	35,683 ± 1,992**	25 ± 5.4	0	36 ± 7.2	0
V-17 (17)	3,300	Middle	Interior	30,972 ± 2,513	30 ± 3.7	32 ± 6.1*	26 ± 1.2	20 ± 12.4
			Periphery	32,508 ± 5,415	25 ± 9.1	3 ± 3.0	25 ± 5.7	26 ± 4.9
SI-49 (14)	5,600	Close	Interior	12,834 ± 764	33 ± 9.5	NT	70 ± 1.6	NT
			Periphery	25,418 ± 683***	29 ± 6.4	NT	54 ± 4.2	NT

For leaf soluble phenolics determination, samples were collected from internal and peripheral branches at the end of the second flash of growth (summer). Each value is shown as the mean ± SEM

NT not tested

*, **, and *** reflects significant difference between branch position at $P < 0.05$, $P < 0.01$, and $P < 0.001$ level, respectively

determined by the position of the branches in the donor plant.

Our results indicate that the variation in rooting ability was the result of genotypic difference and physiological state of the stock plants. Adventitious root formation is a culmination of the complex but specific response of some genomic domain(s) of competent cells elicited by the diverse effects of the external/internal environment (Ansari and Singh 2008). However, the genetic control and associated molecular mechanisms underlying adventitious rooting are still largely unknown (Han et al. 2009). Haissig and Riemenschneider (1988) arbitrarily categorized four genetic effects responsible for the process as direct, correlated, uncorrelated, and regulatory. The first effect refers to the genomic domain(s) carrying information for the process. The remaining three effects are peripheral and indirectly regulate the process via interactions with the first, e.g., expression of other genomic domain(s) responsible for synthesis and supply of metabolites and/or specific regulatory molecules. Even if genotypic differences in

Table 3 Effect of genotype, canopy structure, branch position and their interactions on the phenolics content of *Ilex paraguariensis* leaves at the end of the second flash of growth

Cultivar	Branch position	CHLA	3,4-CQA	3,5-CQA	4,5-CQA	CAA	RUT
V-6	Interior	49.5 ± 0.4	19.0 ± 0.1	36.3 ± 0.4	50.3 ± 0.8	0.73 ± 0.03	27.3 ± 0.2
	Periphery	51.0 ± 0.4	20.4 ± 0.1	56.9 ± 0.6*	59.6 ± 0.6*	0.49 ± 0.01*	43.4 ± 0.5*
V-16	Interior	52.0 ± 0.3	19.2 ± 0.1	40.7 ± 0.2	47.7 ± 0.5	0.53 ± 0.001	30.0 ± 0.2
	Periphery	43.1 ± 0.3*	17.3 ± 0.1	62.5 ± 0.4*	55.0 ± 0.3*	0.44 ± 0.004*	44.7 ± 0.4*
SI-49	Interior	38.6 ± 0.2	28.0 ± 0.3	54.3 ± 0.3	65.5 ± 0.6	0.72 ± 0.005	39.4 ± 0.4
	Periphery	47.8 ± 0.3*	17.9 ± 0.1*	47.7 ± 0.5*	44.2 ± 0.3*	0.43 ± 0.004*	62.5 ± 0.4*

Data are expressed as mg g^{-1} of lyophilized dry weight**.** The mean values are obtained from four samples ($n = 4$)

CHLA chlorogenic acid, *3,4-CQA* 3,4-dicaffeoylquinic acid, *3,5-CQA* 3,5-dicaffeoylquinic acid, *4,5-CQA* 4,5-dicaffeoylquinic acid, *CAA* caffeic acid, *RUT* rutin

* Significant difference between branch position at $P < 0.05$ (t tests)

utilization of hormones and metabolism of proteins and soluble carbohydrates available in the cutting likely contributed to variable response (Husen 2008), genotype *x* environment interactions are thought to have a major role in governing rooting response (Zalesny et al. 2005). In this study, the difficulty of separating environmental effects from genetic differences was overcame by comparing cuttings of a unique genotype grown in pots and subjected to different irradiance conditions. Percent rooting was negatively influenced by irradiance which probably determines a higher temperature and lower relative humid conditions at the level of the canopy. Furthermore, light or the exclusion of light can be a major factor that influences the physiological and anatomical status of the stock plant and the subsequent adventitious root formation of cuttings collected from these plants (Pijut et al. 2011). In addition, other factors like wounding, pathogens, symbiotic bacteria, and development regulate the activity of enzymes that control secondary metabolites biosynthesis such as phenols and its derivate compounds which play a major role in the adaptation of plants to the changing environment and in overcoming stress constraints (Edreva et al. 2008). Chemically, phenols are extremely heterogeneous substances and may range from simple monomers to very large polymers which may combine with proteins, either reversibly by hydrogen bonding or irreversibly by oxidation, holding backs the enzyme activity (Croteau et al. 2000). Our result clearly showed a high correlation between irradiance and leaf soluble phenolic content which promote the declination and death of cuttings.

Considering that *I. paraguariensis* plants every year have three periods of rapid shoot elongation, which alternate with periods of little or no growth (flashing) wherein is subjected to different environmental stresses such as high temperature and water deficit (Sansberro et al. 2004), we analyzed whether season and canopy structure of the field stock plants affect the survival and rooting of cuttings. The results of our experiments confirmed that the level of soluble phenolic content was higher from leaves exposed to full sunlight radiation than those collected from the central zone of the plant subjected to a more suitable condition; however, the leaf phenolics content not always show a correlation with the browning of the cuttings which may be explained at the base of the chemical heterogeneity of phenolic structure that could be a stimulator or inhibitor factor of adventitious rooting (Faivre-Rampant et al. 2002). Phenolic biosynthesis is positively affected by the environment (Ghasemzadeh and Ghasemzadeh 2011). It has been demonstrated that mainly light and thermal stress induces the production of flavonoids and phenylpropanoids compounds in chloroplast and cytoplasm through phenylalanine pathway, which is considered by most authors to be one of the main lines of cell acclimation against stress in plants (Rivero et al. 2001). Coumaric acid and caffeic acid are derived from cinnamic acid and lead to secondary metabolites such as flavonoids and phenolic acids. In the later step, chlorogenic acid is synthesized from caffeic acid and promotes the formation of dicaffeoylquinic acids (Moglia et al. 2008). In some way, the variation of phenolics content observed in our experiments should be explained based on its biosynthetic pathway as a clear response of the genotype to the environment. For example, while caffeic acid content decreased from 17 to 40 % in external leaves subjected to stress, the level of chlorogenic acid and its dicaffeoylquinic derived compounds varied according with the genotype. Expectedly, chlorogenic acid content increased in SI-49 clone by 40 % while the level of dicaffeoylquinic acids decreased from 12 to 36 %. This fact should be related with the mechanism of tolerance to drought performed by this genotype (data not shown), since Rivero et al. (2001) have reported the specific involvement of chlorogenic acid in stress responses. The results of current study suggest the ability of different shade level forced by the branch position in altering or modifying both the concentration and profiling of phenolics and flavonoids compounds in *I. paraguariensis* leaves. In summary, our

results provide evidences which support the hypothesis that the physiological status of the stock plant at the time that cuttings are excised is of utmost importance for the subsequent rooting of *I. paraguariensis* cuttings. The influence on total soluble phenolics content of different irradiances given to the stock plants negatively affects the rooting process since the product of its oxidation cause the browning and death of the cuttings, therefore, further physiological/biochemical studies are still needed in this specie to understand the detailed mechanism of this morphogenetic process.

Author contributions J. Tarrago and R. Fillip performed the experiments. L. Mroginski and P. Sansberro designed and instructed the research work. P. Sansberro wrote the manuscript.

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References

Ansari SA, Singh S (2008) Genetic difference in adventitious rhizogenesis in *Albizia procera* Benth. with IBA treatment. J For Res 13:79–82. doi:10.1007/s10310-007-0045-5

Croteau R, Kutchan T, Lewis N (2000) Natural products (secondary metabolites). In: Jones R, Buchanan B, Gruissem W (eds) Biochemistry and molecular biology of plants. American Society of Plant Biologists, Rockville, pp 1250–1318

Edreva A, Velikova V, Tsonev T, Dagnon S, Gürel A, Akta L, Gesheva E (2008) Stress-protective role of secondary metabolites: diversity of functions and mechanisms. Gen Appl Plant Physiol 34:7–78

Faivre-Rampant O, Charpentier J, Kevers C, Dommes J, van Onckelen H, Jay-Allemand C, Gaspar T (2002) Cuttings of the non-rooting *rac* tobacco mutant over accumulate phenolic compounds. Funct Plant Biol 29:63–71. doi:10.1071/PP01016

Ghasemzadeh A, Ghasemzadeh N (2011) Effects of shading on synthesis and accumulation of polyphenolic compounds in ginger (*Zingiber officinale* Roscoe) varieties. J Med Plants Res 5:2435–2442

Haissig BE, Riemenschneider DE (1988) Genetic effects on adventitious rooting. In: Davis TD, Haissig BE, Sankhla N (eds) Adventitious root formation by cuttings. Dioscorides Press, Portland, pp 47–60

Han H, Zhang S, Sun X (2009) Review on the molecular mechanism of plants rooting modulated by auxin. Afr J Biotechnol 8:348–353

Husen A (2008) Clonal propagation of *Dalbergia sissoo* Roxb. and associated metabolic changes during adventitious root primordium development. New Forest 36:13–27. doi:10.1007/s11056-007-9079-y

Husen A, Pal M (2007) Effect of branch position and auxin treatment on clonal propagation of *Tectona grandis* Linn. F. New For 34:223–233. doi:10.1007/s11056-007-9050-y

Jarvis B (1986) Endogenous control of adventitious rooting in non-woody cuttings. In: Jackson MB (ed) New root formation in plant and cuttings. Martinus Nijhoff Publishers, Dordrecht, pp 191–222

Kibbler H, Johnston ME, Williams RR (2004) Adventitious root formation in cuttings of *Backhousia citriodora* F. Muell. 1. Plant genotype, juvenility and characteristics of cuttings. Sci Hortic 102:133–143

Luna C, Sansberro P, Mroginski L, Tarrago J (2003) Micropropagation of *Ilex dumosa* (Aquifoliaceae) in a tissue culture system. BioCell 27:205–212

Moglia A, Lanteri S, Comino C, Acquadro A, De Vos R, Beekwilder J (2008) Stress-induced biosynthesis of dicaffeoylquinic acids in Globe Artichoke. J Agric Food Chem 56:8641–8649. doi:10.1021/jf801653w

Pijut P, Woeste K, Michler C (2011) Promotion of adventitious root formation of difficult-to-root hardwood tree species. In: Janick J (ed) Horticultural Reviews, vol 38. Whiley-Blackwell, USA, pp 213–251

Rivero RM, Ruiz JM, García PC, López-Lefebre LR, Sánchez E, Romero L (2001) Resistance to cold and heat stress: accumulation of phenolic compounds in tomato and watermelon plants. Plant Sci 160:315–321

Rosa M, Prado C, Podazza G, Interdonato R, González J, Hilal M, Prado F (2009) Soluble sugars-metabolism, sensing and abiotic stress. Plant Signal Behav 4:388–393

Sansberro P, Mroginski L, Bottini R (2004) Foliar sprays with ABA promote growth of *Ilex paraguariensis* by alleviating diurnal water stress. Plant Growth Regul 42:105–111

Tarrago J, Sansberro P, Filip R, López P, González A, Luna C, Mroginski L (2004) Effect of leaf retention and flavonoids on rooting of *Ilex paraguariensis* cuttings. Sci Hortic 103:479–488. doi:10.1016/j.scientia.2004.07.004

Treutter D (2006) Significance of flavonoids in plant resistance: a review. Environ Chem Lett 4:147–157. doi:10.1007/s10311-006-0068-8

Vermerris W, Nicholson R (2008) The role of phenols in plant defense. In: Vermerris W, Nicholson R (eds) Phenolic compound biochemistry. Springer, New York, pp 211–234

Zalesny R Jr, Riemenschneider DE, Hall RB (2005) Early rooting of dormant hardwood cuttings of *Populus*: analysis of quantitative genetics and genotype *x* environment interactions. Can J For Res 35:918–929. doi:10.1139/X05-018