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LEAF AREA AND FOLIAR WEIGHT TO SAPWOOD CROSS SECTIONAL AREA MODELS FOR *QUERCUS FRAINETTO* (TEN.) IN GREECE

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Abstract

The relationships between leaf area and foliar weight with four stem dimensions (sapwood area, total stem cross-sectional area, current sapwood area, and dbh) were studied in four different stem sections such as stump height (0.3 m), breast height (1.3 m), mid bole length and base of live crown, in the most important oak species in Greece, the Hungarian oak (*Quercus frainetto* Ten.). Twenty three trees were destructively sampled in the university forest Taxiarchis, Chalkidiki. Simple and multiple linear regression was used for model development. In all tested models total stem cross-sectional area was consistently the most accurate estimator for leaf area and foliar weight exhibiting R^2 = 0.859 and R^2 = 0.879 respectively. Current sapwood area was the next more accurate estimator (R^2 = 0.726 and R^2 = 0.762) followed by sapwood area (R^2 = 0.767 and R^2 = 0.843). The addition of more variables such as crown length, tree age and crown ratio improved slightly the accuracy in the multiple linear models. Both leaf area and foliar weight were best described as a linear function of current sapwood area and tree age R^2 = 0.861 and 0.846 respectively followed by sapwood area and crown length (R^2=0.808 and 0.829). These relationships were getting weaker as we move from stump height to upper stem sections. The results show that the whole sapwood area than the most recent two growth rings may be active in water conduction for Hungarian oak in the Mediterranean.

Key words: pipe model theory, foliar weight, crown classes, *Quercus frainetto*

INTRODUCTION

Hydraulic architecture tries to connect the plant architecture with its physiological processes (Zimmermann, 1983). According to this mechanism, the trees are consisted of a set of pipes through which the water flows and it is determined by natural processes (Tyree, Ewers, 1991). The environmental and physiological factors that influence the plants hydraulic architecture have not yet been fully understood, but previous studies have provided some useful understanding for its interpretation (Mencuccini, Bonosi, 2001).

Based on hydraulic architecture, a lot of allometric regression models among plants' different parts (trunk, roots, leaves) were developed aiming at the analysis of the functional relationship between conductor system and the foliar or photosynthetic biomass of the plants (McDowell et al., 2002; Wright et al., 2006).

One of the first allometric models on trunk sapwood and leaf area of the whole tree was published by Huber (1928) known as 'Huber value' and defined as the xylems cross sectional area of the stem or branch divided by the tree's total leaf area or the foliar dry weight. Many efforts have been made to calibrate models that involve plant leaf area, which estimation was and still is difficult and primary objective, and because the plant leaf area is directly linked to photosynthesis and transpiration it is considered an important key variable for estimating plant productivity (Lehnebach et al., 2018). Having the indirect estimation of tree crown biomass in mind, Shinozaki et al. (1964 a, b) proposed a concept of empirical rules for interpreting the relationship between the foliage and the conductive tissue of the plant. The pipe model theory, as it was named, suggests that a given unit of leaf area is associated with a constant amount of downward continuation of pipes that supply the leaves with water. Implicitly it is assumed that if the sapwood area and the leaf to sapwood area (A_L:A_S) ratio are known then the leaf area of the tree can be estimated (Waring et al., 1982). After the formulation of the pipe model theory by Shinozaki et al. (1964 a, b), several studies, based on this theory, have developed methodologies and allometric models of indirect estimations of leaf area and foliar biomass (Whitehead, 1978; Kaufmann, Troendle, 1981; Waring et al., 1982; Mazzoleni, Schirone, 1990).

According to pipe model theory, the plant development processes are affected by its form, the pipe model theory has been confirmed and applied in many studies conducted to understand the shape of the plant and the distribution of resources and architecture with reference to branching structure (Chiba, 1990, 1991). Other researchers used pipe model to estimate the ratio between sapwood and leaf area (A_L:A_S), or to assess leaf area and leaf biomass (Snell, Brown, 1978; Kaufmann, Tröndle, 1981; Mazzoleni, Schirone, 1990). Pipe model was also used to describe the way the water is transported within the plant and how it is stored in the stem (Ewers, Zimmermann, 1984a, b; Mäkelä, 1986). Many biomass distribution models also based its interpretation on pipe model theory (Chiba, 1998; Mencuccini, Bonosi, 2001). The measurement of leaf area and biomass, the tree growth verification through biomechanics are some of the areas that this model has proven useful (Ewers, Zimmermann, 1984 a, b). This ratio can be used as balance index between transpiration processes and water supply through the stem and as main component of the allocation of biomass and the leaves hydraulic architecture (Martinez-Vilalta et al., 2007).

Its validity is confirmed by the study of Tadaki, Shidey (1960). According to this, there is a proportional relationship between the active functional woody structures at a certain height (z) and the amount of the leaves they support. The pipes that make up the trunk and branches of a tree are renewed each year, but their quantities are controlled and determined by the supporting unit leaves they served. Vanninen et al. (1996) found that the dependence of leaf biomass on tree age, height and sapwood at the base of live crown is explained by the pipe model theory.

The linear relationship of foliar biomass above a certain height on the trunk and the sapwood area at this height was doubted by many authors who supported a nonlinear

relationship: Kershaw, Maguire (2000); Thompson (1989); Kantola, Mäkelä (2004) and the A_L:A_S ratio is directly connected with the tree dimensions and the stand growth conditions (Smith, 1988). Discrepancies were also reported by other researchers who found that the A_L:A_S ratio tends to decrease nonlinearly along the trunk (Mencuccini, Grace, 1995, 1996; McDowell et al., 2002) and in certain cases, to increase with the size and age of the trees (Phillips et al., 2003 a, b) or under drought conditions. The influence of factors such as the site, climate, species, tree size, stand density and tree social rank within the stand on A_L:A_S ratio was reported by a number of studies (Whitehead, 1978; Thompson, 1989; Coyea, Margolis, 1992; McDowell et al., 2002; Berniger et al., 2005; Schneider et al., 2008).

The scope of the present study was to evaluate the relationship among sapwood area, current sapwood area, total stem cross sectional area to leaf area and foliar dry weight weight for Hungarian oak in Greece and to calibrate linear models at four height sections along the tree stem such as stump height, breast height, middle of tree bole and height of live crown as predictor variables for leaf area and foliar dry weight.

MATERIAL AND METHODS

Study area

The study was conducted at Taxiarchis - Vrastama experimental forest, which is located on the central Holomontas mountain series of Chalkidiki peninsula, approximately 70 km southeast of the city of Thessaloniki (40° 25' N and 23° 31' E) and occupies 5800 ha. It consists of deciduous oaks and beech natural stands in upper elevations and evergreen broadleaved (marquis) vegetation in lower elevations. Conifers do not exist naturally in Holomontas mountain, black pine (*Pinus nigra* L.) in upper elevations and brutia (*Pinus brutia* Ten.) pine in lower elevations were planted in openings by the Forest Service and firs primarily Greek fir (*Abies cephalonica* L.) and hybrid fir (*Abies borisii regis* Mat.) and to a lesser extent Douglas-fir (*Pseudotsuga menziesii* (Mirb) Franco) were planted in agricultural private land by farmers for Christmas trees complete the tree species composition. Taxiarchis - Vrastama experimental forest is managed on a sustainable basis after a 10-year thinning cycle that removes 5% of the oak standing volume. The mean tree density is 1260 (±994) trees ha^{-1}; the mean diameter and height are 15 cm and 16 m, respectively (UFAMF, 2013). The region is characterized by a transitional Mediterranean to continental climate with a mean annual temperature of 11.3°C (37 years observations). The annual precipitation reaches 777 mm, of which 265 mm fall from May to September. Bioclimatically, the region belongs to the sub-Mediterranean bioclimate with biologically dry days 0–27 while the Emberger's ombrothermic quotient Q_2 equals 72mm $°C^{-2}$, setting the region in the Emberger's classification of wet bioclimate with harsh winters (Mavromatis, 1980). Geologically, the forest's bedrock consists of mica schist mixed with talc schist rocks with soil texture from sandy-clay to clay. The soil type in the oak stands is acid brown forest soil derived from the mica schist erosion (Matis, Alifragis, 1983). The vegetation composition at the

higher altitudes, where the study area is located is dominated by Hungarian oak (*Quercus frainetto* Ten.) coppice stands under conversion into high forest and covers about 44% of the forested area.

Methodology

Field measurements. Twenty three oak trees were destructively sampled during the summers of 2013 and 2014. The diameter at stump height ($D_{0.3}$ in cm) and at breast height ($D_{1.3}$ in cm) was measured before the tree felling. The sampled trees were cut at the stump height (0.30 m), and, after felling, total tree height (*H* in m), diameter at 50% of bole length ($D_{0.5}$ in cm) and diameter at the base of live crown were recorded. Subsequently, the crown was separated into three parts (upper, middle and lower) and thirty leaves from each part were randomly collected. The collected leaves were put in re-sealable plastic bags and in portable ice refrigerator for avoiding shrinkage until their transportation to the laboratory. After the leaves collection, the branches were removed from the stem, and fresh biomass was determined in the field using a crane scale. For trees up to 15 cm of diameter the whole crown was transferred to the laboratory, and for trees with more than 15 cm of diameter subsamples from lower, middle and upper part of each branch of the crown were taken for the determination of fresh and oven-dried biomass ratios. For more details on the tree measuring protocol see Zianis et al. (2016). Each one of the 23 stems was divided into six sections after felling, including stump height (0.3 m), breast height (1.3 m), mid bole length and height to the base of live crown, and fresh biomass of each section was measured in the field. From each section, a stem disk 7 cm wide was removed, weighed, taken to the laboratory, and oven dried at 80°C until a constant weight was reached to determine the fresh/oven-dried biomass ratio.

Laboratory measurements. The whole foliage from tree crowns with diameter up to 15 cm was separated from branches, and oven-dried at 80°C dry weight was determined. For the crown subsamples of trees with more than 15 cm of diameter the leaves were removed from twigs and branches to determine the foliage/branch biomass ratio. The fresh biomass was measured with an electronic scale and was subsequently oven dried at 80°C until a constant weight was reached. Fresh/oven-dried biomass ratios of twigs, branches, and foliage were applied to estimate the total crown dry biomass. The leaves from each crown part that were taken for leaf area and weight estimation were weighted one by one in a two decimal placed precision balance (PGW6002e, 6000* 0.01g). Afterwards, the leaves were scanned by a digital scanner (HP G4010) with 300 dpi resolution. The leaf area (*LA* in mm^{-2}) was determined analyzing the digital leaf scans in the freeware software Lafore (Lehsten, 2005). Subsequently, the leaves were placed in paper bags for drying in the oven (DAF-135, R. Espinar, S.L.) at 80°C until a constant weight was reached, usually in the next 48 h. After drying the leaves were weighted again for determination of the leaf dry matter.

Leaf dry matter content was calculated as the ratio of dry to fresh leaf weight (mg g^{-1}) and applied to the total fresh leaf weight of the crown for calculating the total tree foliar dry weight. The total leaf area (LA) was calculated by multiplying the 90 leaves leaf area times the ratio of total tree foliar dry weight to 90 leaves dry weight.

The 7 cm wide stem disks, before the oven drying were scanned by a digital scanner (HP G4010) with 600 dpi resolution. The sapwood area (*SAPA* in cm^{-2}), current sapwood area (*CSA* in cm^{-2}), defined as the early wood portion of the current growing season plus the entire growth ring of the previous season (Rogers, Hinckley, 1979; Meadows, Hodges, 2002) and the total stem cross sectional area (*STA* in cm^{-2}) were determined analyzing the digital stem disks scans in the freeware software Imagej (Schneider et. al., 2012). The specific leaf area was calculated by dividing the area of the fresh leaf by the dry weight (mm^2 mg^{-1}). Raw data are available from the authors on request.

Statistical analysis. Analysis of variance and the non-parametric test of Kruskal Wallis were used for testing the differences among crown parts regarding *SAPA*, *CSA* and *STA*, specific leaf area as well as the leaf area to sapwood area ratio. The Dunnett's C test for unequal variances was used to identify the homogenous groups of observations.

Simple and multiple linear regressions were used for the calibration of the linear model $y=\boldsymbol{b}X+\boldsymbol{\varepsilon}$ through the R lm function (R core team, 2018) where Y stands for LA and total foliar weight (*FW*) and X stands for *SAPA*, *CSA*, *STA*, $D_{1.3}$. Additional variables such as tree age (*Age*), tree height (*HT*), crown length (*CrlEN*) and the ratio of crown length to total tree height or crown ratio (*Cr*) were added in the model in an effort to improve the goodness of fit. The standard error of the estimate, coefficient of determination and Akaike information Criterion (AIC) were used for determining the models goodness of fit.

RESULTS

The analysis of 23 sampled Hungarian oak trees showed that the trees had a mean height of 14.98 m, mean age 47.5 years, breast height diameter 18.8 cm. The descriptive statistics of all measured variables are presented in the Table 1.

For the verification of the constancy of *SAPA*, CSA and STA along the tree stem such as stump height (0.3 m), breast height (1.3), mid bole length and height to the base of live crown we used Analysis of variance. As it can be seen in Table 2 there are statistically significant differences for all independent variables *SAPA*, *CSA* and *STA*. Hence we reject the null hypothesis that the *SAPA* remains constant among the different stem heights. The nonparametric Kruskal Wallis test also confirms the differences in the sapwood area (SAPA: Chi-Square: 73.30, df: 5 Sig: < 0.001), (CSA: Chi-Square: 65.84, df: 5 Sig: < 0.001) and (STA: Chi-Square: 73.05, df: 5 Sig: < 0.001).

Dunnett's C multiple comparison test distinguished two homogenous subgroups for SAPA, one subgroup for stump, breast height and mid stem and another one for the base of live crown and other two sections above the base of live crown (not shown in the analysis). For CSA the test revealed one subgroup for stump, breast height, mid bole length and base of live crown and a second subgroup for the two sections above the base of live crown. For STA Dunnett's C multiple comparison test revealed one subgroup for stump, breast height, mid bole and a second subgroup for the crown base and the two sections above the base of live crown.

Table 1. Dendrometric attributes of sampled trees

Parameter	Descriptive statistics (n=23)			
	Mean	**Min**	**Max**	**S.D.**
Age (years)	47.52	14	73	19.08
Stump diameter (cm)	22.42	12.4	42	7.07
DBH (cm)	18.79	9.8	35.5	6.20
Tree height (m)	14.98	8.2	22.6	3.99
Height to live crown (m)	8.40	3.25	14.8	2.68
Height to mid stem (m)	4.16	1.7	7.4	1.34
Total LA (m^2)	60.87	18.42	169.77	45.58
Total foliar dry weight (kg)	5.98	1.5	17.2	4.52
Stump SAPA (cm^{-2})	153.05	49.08	474.0	99.71
Stump CSA (cm^{-2})	16.75	6.45	62.51	12.3
Stump STA (cm^{-2})	322.49	75.92	1073.64	245.30
Breast height SAPA (cm^{-2})	112.75	37.39	298.26	58.53
Breast height CSA (cm^{-2})	12.29	5.56	36.62	6.97
Breast height STA (cm^{-2})	247.53	54.77	768.46	176.70
Mid bole length SAPA (cm^{-2})	91.94	36.27	212.02	40.85
Mid bole length CSA (cm^{-2})	10.75	5.68	30.62	5.24
Mid bole length STA (cm^{-2})	189.19	47.99	543.72	129.67
Live crown SAPA (cm^{-2})	74.99	26.37	175.09	32.97
Live crown CSA (cm^{-2})	10.08	4.54	28.46	5.01
Live crown STA (cm^{-2})	125.53	28.30	429.36	96.12

S.D: = Standard deviation

Table 2. Analysis of variance of sapwood areas in stem height sections

Variable		Sum of squares	d.f. ‡	Mean square	F‡‡	Sig.***
SAPA	Between groups	238573.75	5	47714.75	15.28	<0,001
	Within groups	358929.01	115	3121.12		
	Total	597502.76	120			
CSA	Between groups	2187.17	5	437.43	8.92	<0.001
	Within groups	5635.07	115	49.001		
	Total	7822.24	120			
STA	Between groups	1331951.45	5	266390.29	11.81	<0.001
	Within groups	2592913.36	115	22547.07		
	Total	3924864.81	120			

‡ d.f: degrees of freedom. ‡‡F: F distribution criterion. ***Sig<0.001 level of acceptance or rejection of the null hypothesis.

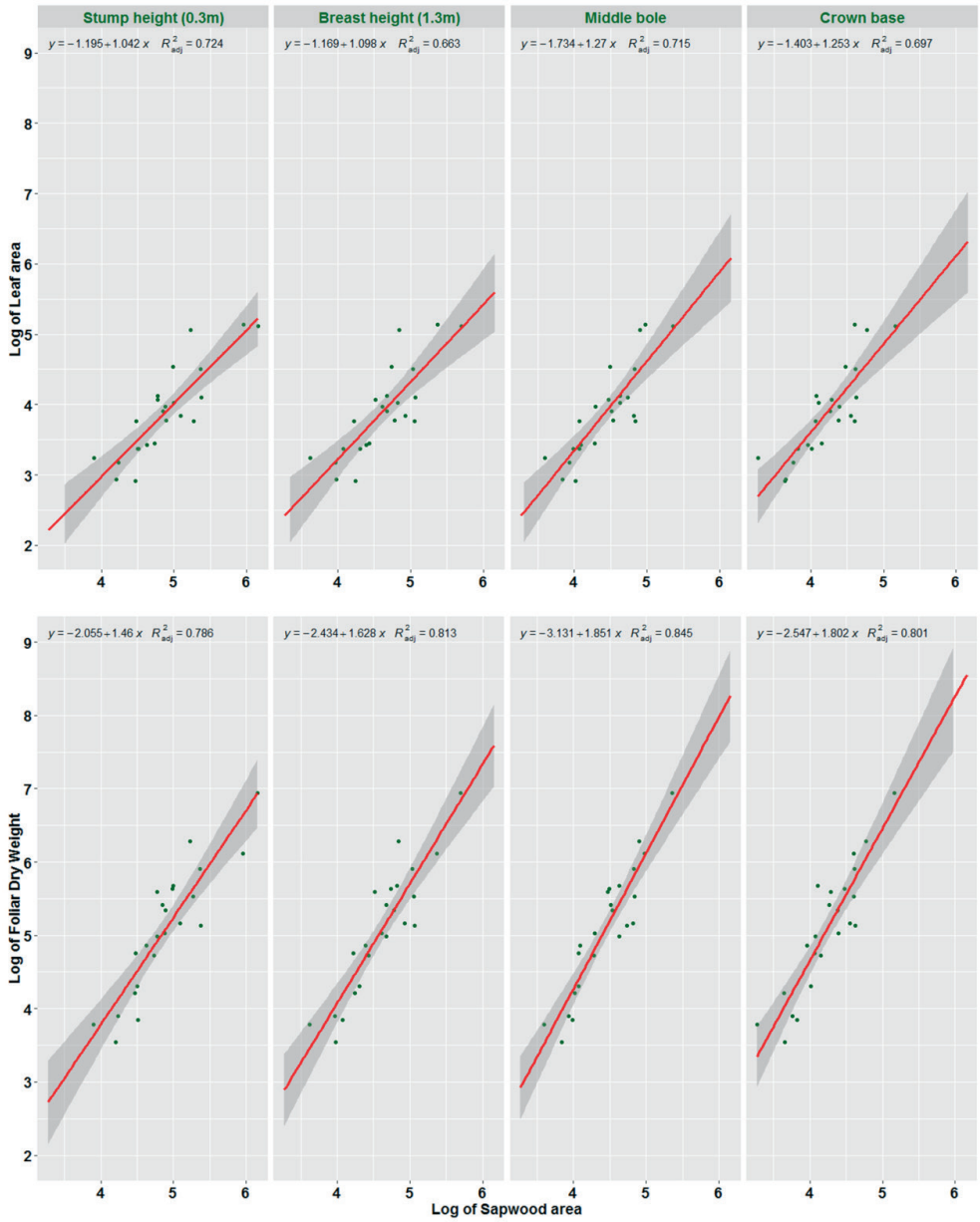

Fig. 1. Simple linear regression analyses of the logarithm of leaf area (LA), and foliar dry weight (FW), with the logarithm of sapwood area (SAPA) for Hungarian oak

Prediction of leaf area and foliar weight. Simple linear regression of the logarithmic model y=a+bx revealed that *STA* was the most accurate estimator of leaf area and foliar weight (Fig. 3) for Hungarian oak at the stump height section. *CSA* was also very good estimator for foliar weight and leaf area showing R^2 values of 0.70 and 0.77 respectively (Fig. 2) followed closely by the total sapwood area (Fig. 1). At

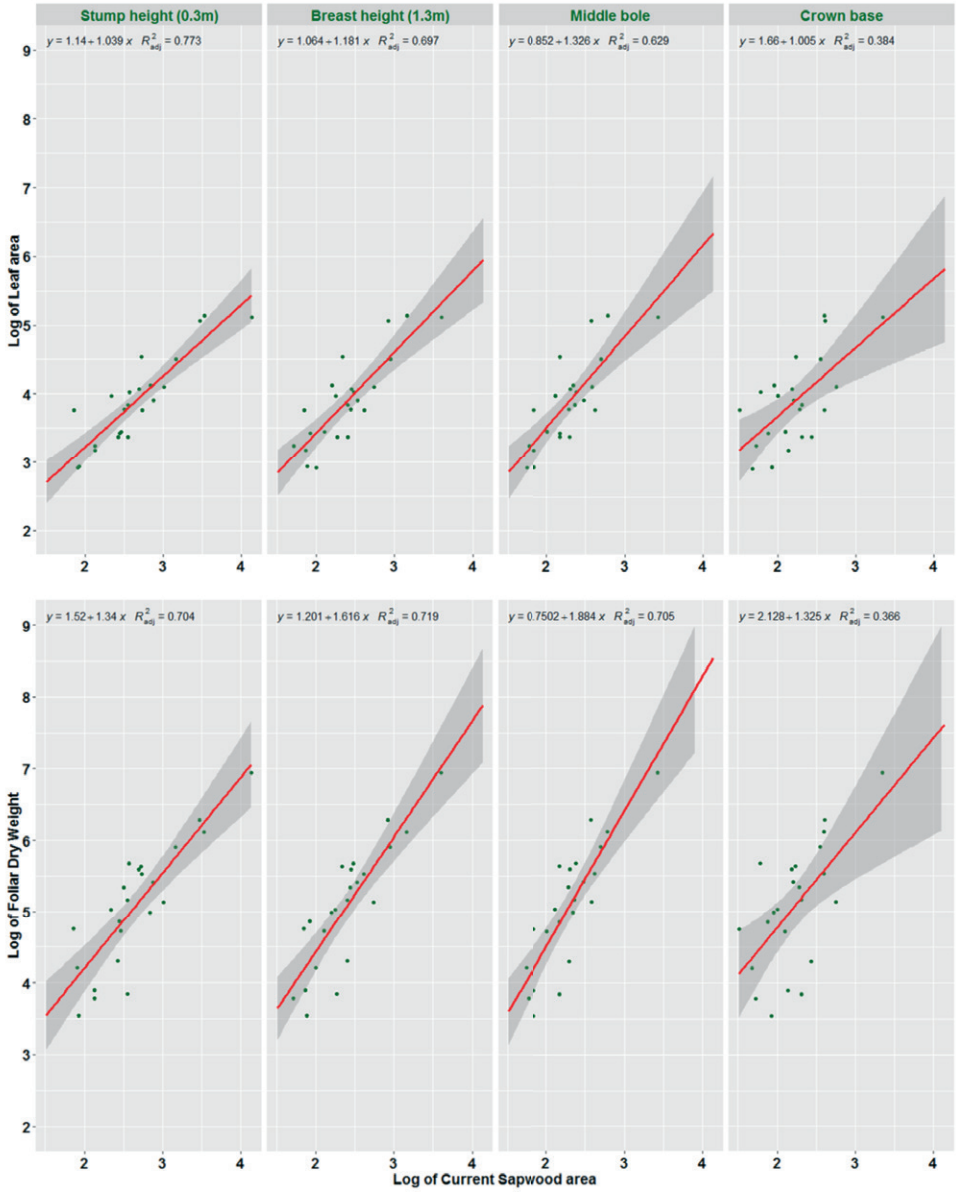

Fig. 2. Simple linear regression analyses of the logarithm of leaf area (LA), and foliar dry weight (FW), with the logarithm of Current sapwood area (CSA) for Hungarian oak

the breast height section, the same trend is observed with slightly lower coefficients of determination. Total cross sectional area is the best estimator (Fig. 3) and *CSA* still appears better estimator (Fig. 2) than total *SAPA* (Fig. 1). At the middle bole length, the same trend is observed with slightly lower coefficients of determination for total *CSA*, but the total *SAPA* appears a better estimator (Fig. 1) than the *CSA* with quite smaller R^2 (Fig. 2). Finally, at the base of live crown section the same trend is observed, the first

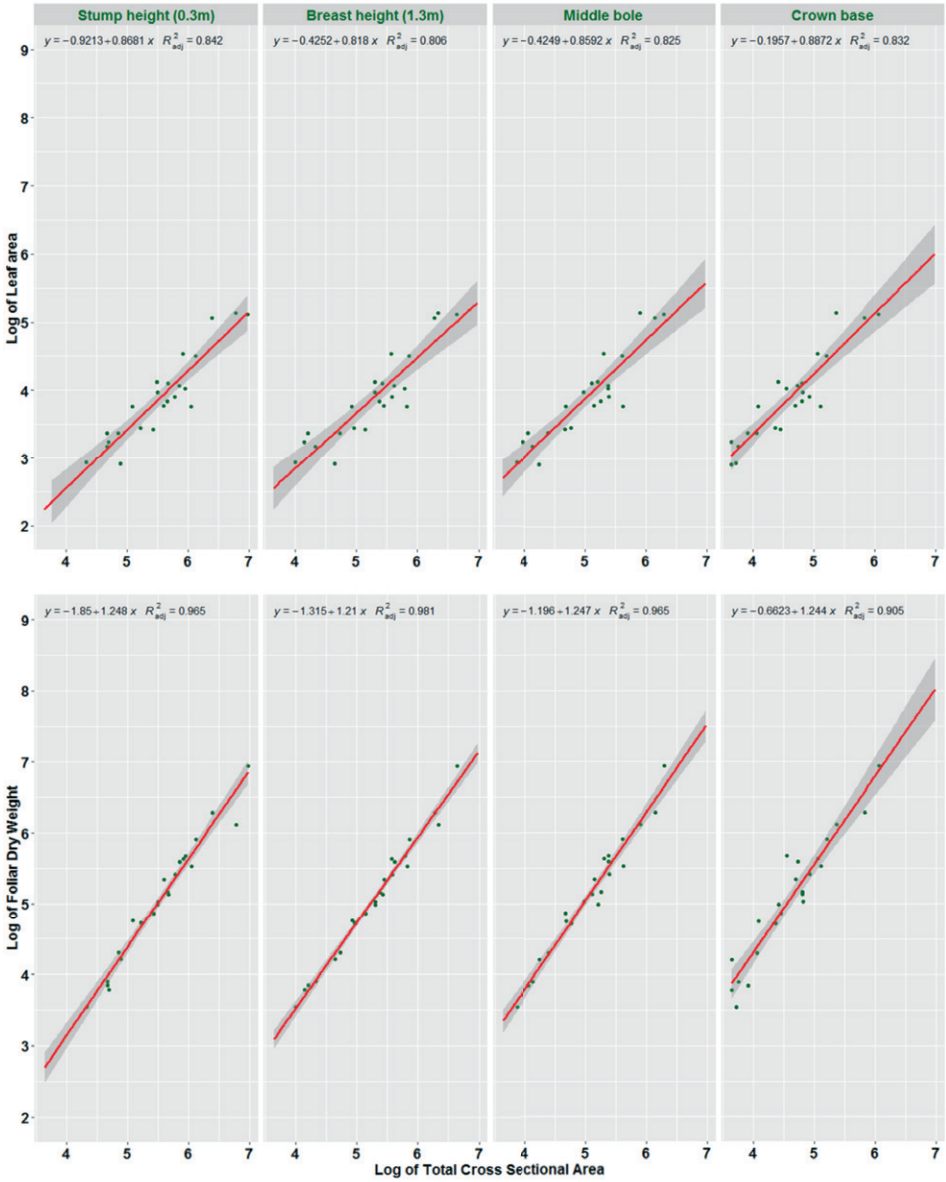

Fig. 3. Simple linear regression analyses of the logarithm of leaf area (LA), and foliar dry weight (FW), with the logarithm of total Stem cross sectional Area (STA) for Hungarian oak

and best estimator is the total *CSA* (Fig. 3) followed by the total *SAPA* (Fig. 1) but with constantly decreasing coefficients of determination. The *CSA* appears to be the worst estimator for total *LA* and foliar weight where it's R^2 = 0.384 and 0.366 respectively, explaining less than 50% of the recorded variation (Fig. 2).

The multiple linear regression model $\boldsymbol{X}$=a + b_1X + b_2Age + b_3HT + b_4CrLEN + b_5LCR was used to determine the significance of including additional independent

Table 3. Simple linear regression analyses in stem cross sections

	Y	X‡	a	b	SE‡‡	R^2
Stump height (0.3 m)	*LA*, m^2	DBH	-2.045	1.937	0.276	0.817
		STA	-0.921	0.868	0.256	0.842
		SAPA	-1.195	1.042	0.339	0.724
		CSA	1.139	1.039	0.308	0.773
	FW	DBH	-3.581	2.822	0.167	0.963
		STA	-1.849	1.248	0.164	0.965
		SAPA	-2.055	1.459	0.402	0.786
		CSA	1.520	1.340	0.473	0.704
Breast height (1.3 m)	LA	DBH	-1.172	1.757	0.2976	0.787
		STA	-0.425	0.818	0.284	0.806
		SAPA	-1.169	1.098	0.374	0.663
		CSA	1.064	1.181	0.355	0.697
	FW	DBH	--2.526	2.636	0.099	0.987
		STA	-1.315	1.209	0.119	0.860
		SAPA	-2.433	1.627	0.376	0.813
		CSA	1.201	1.615	0.407	0.719
Mid bole length	*LA*	DBH	-1.123	1.810	0.263	0.833
		STA	-0.424	0.859	0.269	0.825
		SAPA	-1.734	1.27	0.344	0.715
		CSA	0.852	1.326	0.393	0.629
	FW	DBH	-2.179	2.616	0.159	0.966
		STA	-1.196	1.247	0.162	0.965
		SAPA	-3.131	1.851	0.342	0.845
		CSA	0.750	1.884	0.472	0.705
Live crown base	*LA*	DBH	-0.631	1.746	0.274	0.819
		STA	-0.1957	0.887	0.264	0.832
		SAPA	-1.403	1.252	0.355	0.697
		CSA	1.659	1.005	0.506	0.384
	FW	DBH	-1.276	2.449	0.286	0.892
		STA	-0.662	1.244	0.268	0.905
		SAPA	-2.546	1.802	0.387	0.801
		CSA	-2.128	1.325	0.692	0.366

‡The model formula is log y= log a+bx. DBH in cm, ‡‡ Standard error of estimate in m^2 for LA and in Kg for FW.

variables such as age, tree height, crown length and crown ratio to predict the *LA* and foliar weight of the Hungarian oak. The analysis revealed that total cross sectional area and DBH were again the more accurate estimators for *LA* and *FW*. In all cases, except the total stem cross sectional area, the addition of at least one of the four independent variables improved the accuracy of the linear model in predicting leaf area and *FW* (Table 4). The only case where the total STA model improved with multiple regression was for *FW* at the breast height section, the addition of total tree height (HT) improved the R^2 from 0.86 to 0.89 which is considered slight improvement. In some cases, the use of

Table 4. Multiple linear regression analyses of leaf area (*LA)*, in m^2 and foliar weight (FW), in Kg on BDH, sapwood area (*SAPA*) Current sapwood area (*CSA*) and total stem cross sectional (*STA*) area for Hungarian oak in the different stem cross sections

	Y	X‡	a	b_1	b_2	b_3	b_4	b_5	SE‡‡‡	R^2
Stump height (0.3 m)	Leaf area (*LA*)	DBH	-129,84	5,68	n.s.	n.s. ‡‡	n.s.	142,12	19,45	0,834
		STA	5,362	0,17	n.s.	n.s.	n.s.	n.s.	17,54	0,859
		SAPA	-44,62	0,26	n.s.	n.s.	10,0	n.s.	20,92	0,808
		CSA	-87,43	2,37	0,97	n.s.	n.s.	139,84	18,27	0,861
	Foliar Weight (*FW*)	DBH	-4,888	0,75	n.s.	-0,39	n.s.	n.s.	1,96	0,824
		STA	0,417	0,02	n.s.	n.s.	n.s.	n.s.	1,60	0,879
		SAPA	3,390	0,03	n.s.	n.s.	0,70	n.s.	1,95	0,829
		CSA	-1,569	0,29	0,06	n.s.	n.s.	n.s.	1,85	0,846
breast height (1.3 m)	Leaf area (*LA*)	DBH	-128,56	6,39	n.s.	n.s.	n.s.	155,34	19,85	0,828
		STA	1,768	0,24	n.s.	n.s.	n.s.	n.s.	17,69	0,806
		SAPA	-55,64	0,36	n.s.	n.s.	11,55	n.s.	24,11	0,746
		CSA	-103,29	3,95	0,99	n.s.	n.s.	153,99	20,47	0,826
	Foliar Weight (*FW*)	DBH	-3,31	0,92	n.s.	-0,54	n.s.	n.s.	1,97	0,827
		STA	3,18	0,03	n.s.	-0,29	n.s.	n.s.	1,60	0,885
		SAPA	-4,62	0,05	n.s.	n.s.	0,84	n.s.	2,35	0,753
		CSA	-0,99	0,57	n.s.	n.s.	n.s.	n.s.	2,23	0,766
mid bole length	Leaf area (*LA*)	DBH	-112,52	7,17	n.s.	n.s.	n.s.	118,66	19,88	0,827
		STA	-0,016	0,32	n.s.	n.s.	n.s.	n.s.	18,74	0,839
		SAPA	-56,97	0,57	n.s.	n.s.	9,99	n.s.	24,21	0,744
		CSA	-60,61	3,31	n.s.	n.s.	13,07	n.s.	25,59	0,714
	Foliar Weight (*FW*)	DBH	-5,99	0,71	n.s.	n.s.	n.s.	n.s.	2,170	0,778
		STA	0,02	0,03	n.s.	n.s.	n.s.	n.s.	1,960	0,819
		SAPA	-2,56	0,09	n.s.	n.s.	n.s.	n.s.	2,494	0,707
		CSA	-5,22	0,42	n.s.	n.s.	1,01	n.s.	2,56	0,706
live crown base	Leaf area (*LA*)	DBH	-50,67	7,89	n.s.	n.s.	n.s.	n.s.	20,49	0,807
		STA	7,31	0,43	n.s.	n.s.	n.s.	n.s.	20,41	0,809
		SAPA	-22,97	1,12	n.s.	n.s.	n.s.	n.s.	27,46	0,654
		CSA	-69,80	n.s.	n.s.	n.s.	19,89	n.s.	27,82	0,644
	Foliar Weight (*FW*)	DBH	-4,89	0,77	n.s.	n.s.	n.s.	n.s.	2,14	0,784
		STA	0,73	0,04	n.s.	n.s.	n.s.	n.s.	2,10	0,791
		SAPA	-2,47	0,11	n.s.	n.s.	n.s.	n.s.	2,61	0,678
		CSA	-5,71	0,34	n.s.	n.s.	1,25	n.s.	2,72	0,669

‡The model formula is $Y= a+b_1X+ b_2 Age+b_3HT +b_4 CrlEN +b_5Cr$. Age in years, total height HT in m, crown length CrlEN in m, crown ratio Cr expressed as proportion. ‡‡ non-significant variable, not included in the model. ‡‡‡ Standard error of estimate in m^2 for LA and in Kg for FW.

multiple regression greatly improved the accuracy of the linear model. For example, the addition of crown length to the simple model using *CSA* to predict total *LA* and *FW* greatly improved the accuracy of the model, the R^2 increased from 0.38 to 0.64 and from 0.36 to 0.67 respectively at the base of the live crown section. The addition of crown length also improved substantially the accuracy of the model using total *SAPA* to predict *LA* at the stump height section, the R^2 increased from 0.66 to 0.75.

The addition of crown ratio as independent variable to the linear model using CSA to predict total LA also improved the accuracy of the model, the R^2 increased from 0.70 to 0.83 at the breast height section (Table 4). In general, multiple linear regression increased substantially the R^2s and decreased the mean standard errors of the estimates in models using sapwood and CSA as independent variables to predict both LA and FW and had zero or small effects on total CSA and DBH as independent variables.

It is worth to mention that in both linear regressions there is a decrease in the coefficients of determination and an increase in the mean error of estimate as we moved from the stump height to that of the base of live crown. All the tested models gave more accurate predictions when the independent variables were taken from the stump height rather than breast or other heights.

DISCUSSION

One property that is close associated with the pipe model theory is the constancy of the ratio of LA to conductive SAPA within a tree (Lehnebach et. al., 2018). This rule is expected to be valid in any point of the tree branching structure. A_L:A_S ratio can predict increasing SAPA from tree top downwards following the increase in leaf biomass or area towards the base of live crown and thus constant SAPA between crown and tree base. Our results showed that at the crown base it is different from the one at the middle of the bole, breast and stump height. This finding opposes the constancy property of pipe model theory except for stump and breast height sections where the slopes of the models are slightly, but significantly ($P < 0.01$), larger than unity 1.042, 1.098 respectively denoting close, near-isometric relationship between LA~SA which is close to the pipe model (Fig. 1). Despite the significant differences found in CSA in the different stem sections one homogeneous group from stem base towards crown base was distinguished by Dunnett's C multiple comparison test denoting a constancy in the CSA to LA. The model slopes for LA and CSA cut sections are slightly, but significantly ($P < 0.01$), larger than unity 1.039, 1.181, 1.326 and 1.005 respectively indicating, except for middle bole section, close, near-isometric relationship between LA~SA relationship which is close to the pipe model (Fig. 2). This is not the case for FW where the model slopes are much higher that unity indicating a rather allometric than isometric relationship. Lehnebach et al. (2018) in their extensive review on the pipe model theory cite many studies that found increases of SAPA from the base of live crown to breast height for both conifers and broadleaves.

Regarding the modeling of LA and FW our results showed that using multiple regression the CSA and total STA are the best estimators rather than total SAPA at the

stump height section. These findings oppose the key property of pipe model theory and suggest that the heartwood part of the xylem must also have a more active role in conducting water form roots to leaves in Hungarian oak than other broadleaf species of temperate forests. In the other, higher sections up to base of live crown, the total STA remains the best estimator compared to other independent variables. Studies on conifer species suggest that the pipe model theory can be applied for predicting the amount and distribution of LA (Waring et al., 1982). In contrast to the study of Rogers, Hinckley (1979) who found the CSA as the best estimator for LA for white and black oaks of Missouri, Meadows, Hodges (2002) found that the total SAPA rather than the CSA is the most accurate estimator of LA and FW for bottom land cherry-bark oak and green ash, attributing this to the fact that the white and black oak grow in moderately cool climates with high soil water availability and low transpiration demands while the bottomland species grow in warmer climate with higher soil moisture and transpiration demands and thus the trees need to contact very large amount of water in the growing period. White (1993) found that CSA was the most accurate estimator of FW for *Q. rubra* because tyloseis and embolism have closed the vessels of the older sapwood and the flow of water is realized only by the recently formed sapwood. This finding is supported by other studies in which vessels of larger diameters are more vulnerable to embolization phenomena than smaller ones, so water conduct is occurred by the last rings of the sapwood (Cochard, Tyree, 1990; Salisbury, Ross, 1992). Gajardo-Caviedes et al. (2005) studied the A_L:A_S ratio for the species *Nothofagus dombeyi* and found that the CSA was the worst estimator for the prediction of LA while the best estimator was the total SAPA. This might happen either because no embolisms occur in this particular species or the embolized vessels somehow return to their normal function due to root pressure effects before the appearance of new foliage in early spring. Nikinmaa (1992), studying the development and structure of Scots pine wood, found that the transformation of sapwood to heartwood is not proportional to the ageing of the foliage. The formation of the heartwood has often been associated with ageing phenomena, but there are indications that suggest a higher correlation with the tree crown dynamics and thus with the function of the tree. The length and width of the tree crowns as accurate estimators of foliar biomass are reported by Cienciala et al. (2006). Regression models have shown a statistically significant correlation of the sapwood volume and area with the biometric attributes of the trees such as the DBH, total tree height and the length and width of the crown. Nylinder (1961) found that the percentage of heartwood for Scots pine is decreased by increasing the length of the crown as well as by increasing the width of the last ten annual rings. According to Sellin (1993), the dominant spruce trees appear to have a larger SAPA than the suppressed as well as in the trees with high growth rates.

Generally, we can say that the LA and FW in the Hungarian oak is better determined by the total CSA at the stump height rather than the breast height. The pipe theory model does not seem to be confirmed taking into account the SAPA as the only water conductor. The total stem cross sectional area (STA) is probably somehow active in transporting water from the roots through the trunk. Further research is needed on this topic taking into consideration the particular Mediterranean climatic conditions where this species grows.

CONCLUSIONS

From the present study the following conclusions can be drawn:

The total sapwood and total cross sectional area do not remain constant from the base of the live crown downwards to stem base of the Hungarian oak and do not confirm the main property of the pipe model theory;

There is strong relationship of the leaf area and foliar weight with the sapwood area, current sapwood area and total cross sectional area. This relationship has its strongest value at the stump height and it is progressively weakens upwards to base of the live crown;

Total xylem's cross sectional area is the most accurate estimator of the leaf area and foliar weight.

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