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## Stability of the annual shoot diameter in Persian walnut: a case study of different morphotypes and years

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**Abstract** The basal diameter of the annual shoot (1YD) affects vegetative growth and fruiting of the walnut trees. In order to determine interdependency between the 1YD and the older parent wood, 64 walnut genotypes belonging to four different branching and fruiting habits (morphotypes M-I, M-II, M-III and M-IV) were investigated. Year-to-year stability of 1YD was tested with the architectural analysis of a 3-year-old fruiting branch and its constituents (a 3-year-old bearer + corresponding 2-year-old + annual shoots) during 3 successive years. Based on Pearson's correlation coefficients and the multiple regression analysis of 12 quantitative traits, 12 models (four morphotype in 3 successive years) of 1YD were formed. They were compared with the standard model which was calculated on the basis of 1-year measurements of 1Y with no respect to the branching and fruiting type and comprises three quantitative traits, i.e. basal diameter of a 2-year-old parent shoot (2YD), the length of 2Y shoot (2YL), and the length of annual shoot (1YL). In a single year, the 1YD was influenced by two–five parameters. Five out of 12 models agreed with the standard model: in the lateral fruiting genotypes (M-IV), 1YD was always under the influence of the 2Y diameter, and the 1Y length. In addition, the number of nodes of the 2Y parent shoot had an important influence on 1Y diameter. In the terminal bearers (M-I), the impact of 2YD on the 1YD slightly increased with the tree age, and some other parameters, like 1Ynumber and 1Ynodes, which became to be important for 1YD. In the intermediate genotypes with

mezotonic ramification (M-II), the number of vegetative buds per 1Y and angles of 1Y had significant effects on 1YD. In the intermediate bearers with acrotonic ramification (M-III), one to four other parameters were included into the model each year beside the 1Y number. Since the traits of a 2-year-old parent shoot have a great influence on the 1YD, the information from the year  $N$  can be used for the prediction of the annual shoot development in the year  $N + 1$ . Such a prediction is more reliable in M-I and M-IV than in M-II and M-III. When we deal with the intermediate fruiting cultivars, 1Y number has to be considered in prediction of 1Y diameter beside 2YD and 1YL.

**Keywords** *Juglans regia* L. · Radial growth · Fruiting branch · Regression models

### Introduction

Different organization levels, i.e. a metamer, growth unit, annual shoot, axis and branching system contribute to the edification of the observed form of the mature tree. The annual shoot is a useful tool for the explanation of dynamics and architecture of temperate species (Barthélémy and Caraglio 1991; Costes 1993). The growth of the annual shoot is the result of two complementary components, organogenesis and extension (Champagnat et al. 1986). Extension of shoot length, also known as primary growth, is followed by a diameter growth (i.e. secondary or radial growth) that increases shoot girth. Secondary growth originates in a lateral sheath of rapidly dividing cells called the vascular cambium which is responsible for the development of xylem and phloem (Ramos et al. 1998). The annual shoot in walnut could be formed in one or more events of organogenesis and elongation, and could thus be monocyclic, bicyclic or even polycyclic (Barthélémy et al. 1995; Sabatier et al. 1995). A part of the annual shoot consists of leaves that are preformed in a winter bud. This is called a preformed shoot. A part of the shoot consists of leaves whose differentiation and extension occurs

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simultaneously after the extension of preformation and is called a neoformed shoot (Caraglio and Barthélémy 1997).

In Persian walnut (*Juglans regia* L.), annual shoots were explored from different aspects by many authors like Mauget (1976), Barthélémy et al. (1995), Ducouso et al. (1995), Sabatier et al. (1995, 1998), Sabatier and Barthelemy (2001a) (see Solar and Štampar 2002). It is common for all of them that they investigated annual shoots from the qualitative point of view.

Only a few authors focused on the quantitative exploration of annual shoots connected to the quantity and quality of walnut fruits. Lauri et al. (2001) found out that at least two factors are involved in fruit weight variability: the length of preformed subtending axes of the bearing annual shoot and the number of fruits developed from the inflorescence. Sabatier and Barthélémy (2001b) showed that the formation of new shoots depends on the number and dimensions of the buds and their position along the parent shoot. The authors mentioned above were not concerned neither with the relationship between the quantitative traits (length and diameter) of the parent shoot nor with the number, dimensions and type of new shoots. This is the object of our study. The diameter of annual bearing shoots is one of the most important factors that influence the size and weight of fruits as well as kernel percentage. This is why we examined the annual shoots that were a constitutive part of the 3-year-old fruiting branches. Based on the quantitative description of 2-year-old parent shoots and corresponding 1-year-old shoots, we elaborated the statistical model of annual shoot diameter.

According to De Reffye et al. (1995), branch diameter of the base of growth unit is reported to be useful to describe the geometric aspect of the quantitative measurements. A long time ago, it was introduced into the tree architecture models as a prediction instrument (Kurth 1999). The oldest description dates back to Leonardo da Vinci (Leonardo rule). He postulated a preservation law for cross sectional area (Dzierzon 2003): all the branches of trees at every stage of their height, united together, are equal to the thickness of their trunk below them (Hallé et al. 1978). This theory was the basis of the pipe stem model of trees developed by Shinozaki et al. (1964a, b). He proposed that a given unit of leaf area is supplied with water from a constant quantity of conducting pipes. Showing a strong relationship between conducting tissues (the 'pipes' running from roots to branch tips) and tissues that receive water and nutrition in the crown (Peper et al. 2001), the pipe stem model determines the relative thickness growth of the woody part (Pertunen et al. 1998) and provides the basis for equations predicting leaf area from diameter-at-breast-height of the stem and sapwood area (Peper et al. 2001). This relationship has been used in a number of recent models, often associated with the root:shoot functional balance equation (Berninger and Nikinmaa 1997; Mäkelä 1986; Valentine 1985).

Models that treat only structural parameters are positioned at the bottom left corner of the model triangle presented by Kurth (1994). They do not have any process information (Dzierzon 2003). An example is Kellomäki and Kurtio (1991) who implemented an empirical dy-

namic crown model for Scot pines (*Pinus sylvestris* L.). It describes the behaviour of individual shooting. Its input consists of structural parameters like the length of growth units, the angle of branching, etc.

In our model, some other structural parameters of annual shoots like angle, number of nodes, number of buds and flowers were taken into account beside diameter and length. The general model is related to genotypes sampled irrespective of their fruiting habit and branching behaviour. As reported by Lauri et al. (2001), the quality and quantity of walnut fruits are also related to the branching and fruiting behaviour of the tree. Additionally, the largeness and homogeneity of the fruits varies from year to year as a consequence of different exogenous factors which may also be involved in the determination of the final diameter and length of branches (Sabatier and Barthélémy 2001b). So, in the research, we were trying to define the impact of a certain genotype and the age of the tree on the morphology and activity of annual shoots. For that reason, we analysed the basal diameter of annual shoots on trees with different branching patterns and fruiting habit, during the period of 3 successive years.

The aims of the study are: (1) to set up mutual dependency of annual shoot diameter and other structural components inside the 3-year-old fruiting branch and elaborate a general statistical model of annual shoot diameter; (2) to elaborate the statistical models of annual shoot diameter for genotypes with different branching and fruiting behaviour, and (3) to examine the stability of annual shoot diameter of each branching pattern and fruiting habit during the period of 3 successive years.

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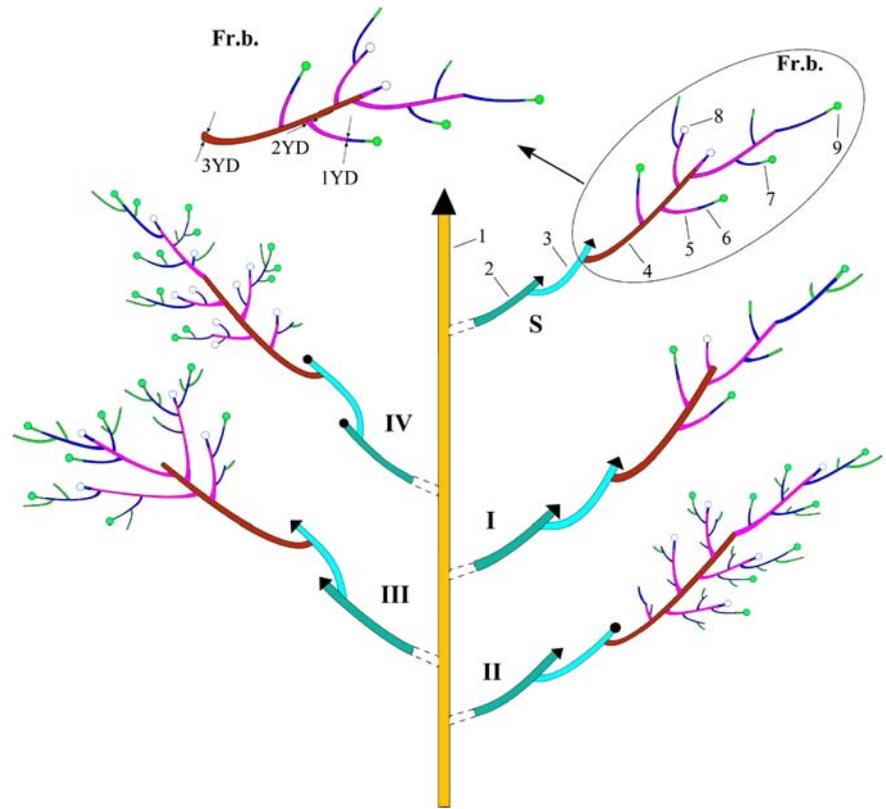
## Material and methods

### Study site and plant material

The experiment was performed in the walnut production orchard in Bistrica ob Sotli (SE Slovenia). This is the largest Slovenian population of randomly selected seedlings (more than 800 trees) grown on their own roots. They developed from healthy seeds of various trees of unknown origin. Due to a high degree of heterozygosity we assume that each tree represents one genotype. One-year old plants were planted in the period 1988–1992. The growth of the trees has been natural without pruning, fertilization, irrigation, pest and disease protection and other agrotechnical measures.

During the period 1993–1999, an architectural analysis of walnut seedlings was performed. Great phenotypic variability among the trees was discovered with regard to both vegetative traits (tree vigour, growth habit, branching density, tree height and trunk diameter, branch angles) and generative traits (duration of the juvenile period, fruiting type, appearance of male inflorescences) (Solar et al. 2001, 2002). During the year 1998, four most typical and frequent branching and fruiting types in the whole population were detected (Solar and Štampar, 2003). They were referred to as morphotypes and labelled from M-I to M-IV (Fig. 1). In the recent study, a 3-year-old fruiting branch was chosen

**Fig. 1** Scheme of 3-year-old fruiting branches (Fr.b.) that belong to four morphotypes (M-I, M-II, M-III and M-IV) and standard. *Legend:* 1, trunk (1st order axis); 2, primary branch (2nd order axis); 3, secondary branch (3rd order axis); 4, 3-year-old-parent branch (3Y) in the observed structure unit; 5, 2-year-old-shoot (2Y); 6, annual shoot (1Y); 7, current-year shoot; 8, fruit in the previous year; 9, fruit in the current year. With the *arrows*, the measuring points of the shoot diameters are pointed in fruiting branches (Fr.b.). Only one out of four fruiting behaviour represented by morphotypes I–IV is present on the same genotype involved into the research



for a very detailed quantitative analysis. The topology of the fruiting branch deals with the physical connections between its components (Godin and Caraglio 1998) which are, in our case, the 3-year-old parent shoot (3Y) + all the corresponding 2-year-old (2Y) and annual (1Y) shoots.

#### Shoot sampling and data records

In autumn 1998, we chose 25 trees per morphotype. In each tree, five fruiting branches, symmetrically distributed in the middle of the canopy (with regard to its height) and well exposed, were selected. We marked them with adhesive labels. On the axes, the successive years were labelled with different colours. In the first year of observations (1998/1999), the length of 3-year-old wood was measured. At the same time, we counted the total number of 2Y on the 3-year-old parent shoots and the total number of 1Y on the 2-year-old parent shoots. For both, 2Y and 1Y, the basal diameter, the length, and the angles were measured. We also counted the number of nodes on 2Y and 1Y. For annual shoots, the number of vegetative and flowering buds, and the number of female flowers per inflorescence were counted in the spring, at the beginning of the flowering. All other parameters were measured during winter dormancy.

The diameter of the shoots was measured with a caliper, as close to the base of the shoots as possible, in millimetre. The length of shoots was determined with a fabric tape measure, from the base to the top, in centimetre. The angles of shoots were measured with a goniometer where lower values (in degrees) represented more erect shoots.

The angle of 1Y was represented by the value ( $^{\circ}$ ) measured between 1Y and 2Y, and the angle of 2Y shoots was represented by the value ( $^{\circ}$ ) measured between 2Y and 3-year-old parent shoots. The nodes were counted from the base of the shoots towards the tip—from the first to the last still distinguishable node.

The data obtained through these measurements were used for the implementation of the general (standard) model of annual shoot diameter with no respect to the fruiting behaviour of the trees.

To test the impact of fruiting habit and age of the tree on the annual shoot basal diameter we repeated the same observations in the following 2 years. For this purpose, the number of trees per morphotype as well as the number of fruiting branches per tree was reduced. Randomly, we chose 14 trees per morphotype. Two fruiting branches per tree (28 fruiting branches per morphotype) were selected.

#### Time dynamics and extent of the measurements

Observations of uneven-aged wood inside the 500 fruiting branches (four morphotypes  $\times$  25 trees per morphotype  $\times$  five fruiting branches per tree) aimed at the implementation of general model of annual shoot basal diameter started in early spring 1998/1999 (year 1). 500 3-year-old parent shoots, 816 2-year-old and 2.647 annual daughter shoots were measured. In the same year, four models referred to different fruiting behaviour were created for randomly selected groups of 14 trees per morphotype. The same 14 trees were included in the observations in the next 2 years. During the winter dormancy 1999/2000 (year 2) and

2000/2001 (year 3), all 3-year-old parent shoots and 2-year-old (2Y) and annual (1Y) daughter shoots were observed. The same parameters as in the year 1 were measured. In total, 112 3-year-old shoots, 1,372 2-year-old shoots and 4,452 corresponded annual shoots were analysed in all morphotypes during 3 years to show the impact of fruiting habit and the year on the basal diameter of annual shoots in walnut.

#### Data analysis and modelling of annual shoot diameter

The data was analysed with the programme Statistica for Windows (StatSoft 2001). The phenotypic correlation coefficients (Pearson's correlation coefficients) were calculated based on mean values of several measurements of the traits with normal distribution. The traits which statistically significantly correlated with the diameter of annual shoot were included in the general (standard) statistical model. This was done by means of the multiple regression analysis. The effects of the morphotypes and different years on annual shoot diameter were evaluated with multifactor ANOVA. The hypothesis that the annual shoot diameter depends on the branching and fruiting habit and year (tree age), was tested by means of the comparison of each of the 12 models (four morphotypes in 3 years) with standard model of annual shoot diameter. A threshold below, for which the variables are not included in the individual model, is defined by  $R^2 \geq 0.60$ . The regression coefficients ( $B$ ) of variables that formed the models represent the weight of these variables. They are also used as the range of variations of each included variable against 1Y diameter for four morphotypes. For the comparison of the relative contribution of each independent variable from a certain model in the prediction of the dependent 1Y diameter the standardized regression coefficients ( $\beta$ ) are used. They are directly comparable to one another, with the largest coefficient indicating which independent variable has the greatest influence on the 1Y diameter.

## Results

### Annual shoot development

#### *Variation of annual shoot diameter according to branch age and morphotype*

A year-to-year variation in 1Y diameter of each morphotype was high and also statistically significant. In all morphotypes except M-II, the 1Y was the largest in the first year and the lowest in the third year of the experiment (Table 1). The largest 1Y (10.4 mm) were on M-IV in the first year, the smallest one (7.6 mm) were on the same morphotype in the third year. In a 3-year average, M-IV had the largest 1Y diameter (9.3 mm) compared to M-I, M-II and M-III where it was 8.9, 8.5 and 8.7 mm.

Standard basal diameter measured for 2,647 annual shoots irrespective to the fruiting behaviour and the age

**Table 1** 1Y diameter (mean  $\pm$  SE and 3-year average) of four walnut morphotypes (I–IV) in 3 years (1–3), and mean basal diameter of standard 1Y irrespective to the fruiting habit to the trees

Morphotype	Year	Diameter of 1Y (mm)
I	1	9.86 $\pm$ 0.23 bc*
	2	9.21 $\pm$ 0.39 b
	3	7.67 $\pm$ 0.31 a
	Average	8.91 A*
II	1	7.85 $\pm$ 0.13 a
	2	9.41 $\pm$ 0.29 b
	3	8.31 $\pm$ 0.19 a
	Average	8.52 A
III	1	8.67 $\pm$ 0.20 ab
	2	9.22 $\pm$ 0.35 c
	3	8.20 $\pm$ 0.25 a
	Average	8.70 A
IV	1	10.42 $\pm$ 0.20 bc
	2	9.85 $\pm$ 0.23 b
	3	7.63 $\pm$ 0.21 a
	Average	9.30 B
Average	1	9.20 1*
I–IV	2	9.42 1
	3	7.95 2
Standard 1Y		8.68 A

A\*, bc\*, 1\*—Means, marked with the same letter do not differ statistically significantly according to the Duncan multiple-range test  $p \leq 0.05$ . A\*—differences among means of 1Y diameter for different morphotypes; bc\*—differences among means of 1Y diameter for different years inside the same morphotype; 1\*—differences among means of 1Y diameter for all morphotypes in the same year

of the tree was similar to the values of M-I, M-II, and M-III, and statistically significantly thinner than M-IV. It ranged from 3 to 22 mm (Fig. 2). 30% of the 1Y measured between 7 and 8 mm, a quarter of 1Y were less than 7 mm, and one-third measured between 9 and 12 mm. Approximately, 10% of the shoots were thicker than 12 mm.

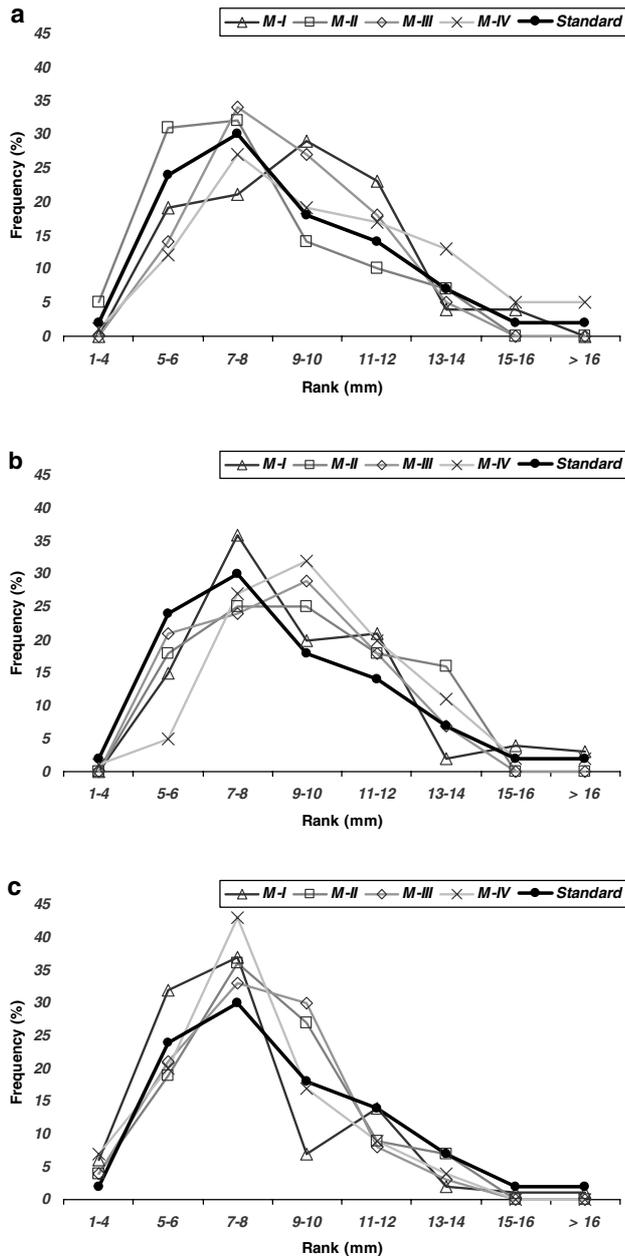
When compared the diameter of the annual shoots that belong to different fruiting habit we saw that the distribution of the diameter ranks were changing during the years in all the morphotypes, but it remained normal in all cases (Fig. 2).

### Model of the basal diameter of annual shoots

#### *Standard model*

Standard model was elaborated on the basis of Pearson's correlation coefficients of the phenotypic data (Table 2) and a multiple regression analysis of those parameters which are closely connected to the annual shoot diameter. According to Eq. (1), three quantitative traits of 3-year-old fruiting branch constituents were included into the model of annual shoot basal diameter.

$$\begin{aligned} 1Y \text{ diameter} = & 3.404 - 0.0897 \times 2Y \text{ length} + 0.6321 \\ & \times 2Y \text{ diameter} + 0.0649 \times 1Y \text{ length} \quad (1) \end{aligned}$$



**Fig. 2** Distribution of the basal diameter ranks of annual shoots in four walnut morphotypes (M-I, M-II, M-III and M-IV) in the year 1999 **a**, 2000 **b** and 2001 **c** in comparison to the distribution of the diameter ranks of standard annual shoots (*Standard*)

$R^2 = 0.664$ ;  $R = 0.815$ ; St. Error of Estimation = 0.842; Mean absolute error = 0.647, Durbin–Watson statistic = 1.71.

1Y diameter is positively correlated with the diameter of the corresponding 2Y (2YD) and with the length of annual shoot (1YL), and negatively correlated with the length of parent 2Y shoot (2YL).

The length of the 3-year-old parent wood which is the base for a 3-year-old bearing branch does not statistically significantly influence the diameter of annual wood.

### Individual models referring to four fruiting behaviours

Parameter coefficients of linear regression models for different morphotypes in 3 successive years are shown in Table 3. All individual models fit to the threshold that was defined, and for which the variables were not included. All of them explain at least 60% of variability ( $R^2 \geq 0.60$ ).

As could be seen from 12 individual models, the annual shoot diameter depends on two to five parameters. The 1Y diameter is most often under the influence of basal diameter of the parent 2Y shoot, and the length of corresponded 1Y shoots. In six models, the number of 1Y also has an important impact on 1Y diameter.

In morphotype I, the basal diameter of 1Y depends on the thickness of the 2-Y parent shoot in all 3 years (Table 3). In the first and second year, the 1Y length also significantly affected 1Y diameter. The angles of 1Y were included in the 1Y diameter model in the year 2, too. In the year 3, 1Y number and 1Y nodes were involved in the model in addition to 2Y diameter.

For the morphotype II, the 1Y diameter was statistically significantly dependent on the length of 1Y in all 3 years (Table 3). In the year 1, the angles of 1Y and the number of vegetative buds per 1Y also significantly affected 1Y diameter. 1Y angles also had strong impact in the year 2, while in the year 3, the number of 1Y shoots and the number of their nodes were included in the model beside 1Y length.

In morphotype III, the 1Y diameter was in negative correlation with the number of 1Y during the whole experimental period (Table 3). In the year 1, four other variables, i.e. 2Y length, 2Y angles, 2Y diameter and 1Y nodes created the model of 1Y diameter. In the year 2, 1Y length significantly affected 1Y diameter, while in the year 3, in addition to the 1Y number, 2Y diameter influenced the 1Y diameter.

In morphotype IV, the 2Y diameter and the 1Y length had a statistically significant influence on the 1Y diameter in all 3 years (Table 3). In the first year also 1Y angles were included in the model. In the third year, 1Y diameter depended on 2Y length, 2Y nodes and 1Y number beside 2Y diameter and 1Y length.

### Comparison of individual models with the standard model of annual shoot diameter

We can see that five individual models agree with the standard model, if we compare the standard model, which comprises three quantitative traits, with the 12 individual models of 1Y diameter. As the main variables that affect 1Y diameter, they comprise both the 2Y diameter and the 1Y length (Table 3). Two models out of five belong to the morphotype I (years 1 and 2), and the other tree models belong to the morphotype IV (years 1, 2, 3). The 1YD model for M-IV/year 3 also includes the length of 2Y shoot like the standard model. In the morphotype II only 1Y length influences 1Y diameter, while 2Y diameter is not included in the 1YD model at all. The greatest differences between the comparative model and individual ones are found in the

**Table 2** Pearson's correlation coefficients among 14 traits of fruit bearing wood

	1YD	3YL	2YN	2YL	2YD	2YNo	2YA	1YN	1YL	1YNo	1YA	1YVB	1YFB
1YFLO	0,52*	-0,21*	-0,19	-0,21*	0,22*	0,09	0,11	-0,30*	0,11	0,35*	-0,20	-0,23*	0,63*
1YFB	0,38*	-0,07	-0,08	-0,10	0,19	0,06	0,13	-0,21*	0,14	0,27*	-0,06	0,07	
1YVB	0,004	0,25*	0,15	-0,003	-0,17	-0,11	-0,05	0,025	0,32*	0,36*	-0,10		
1YA	-0,07	0,17	0,11	0,17	0,14	0,08	0,38*	0,57*	0,20*	0,14			
1YNo	0,56*	-0,001	-0,07	0,05	0,33*	0,28*	0,24*	-0,02	0,63*				
1YL	0,54*	0,15	-0,03	-0,19	0,13	-0,16	0,24*	0,02					
1YN	-0,36*	0,25*	0,21*	0,37*	0,03	0,15	0,15						
2YA	0,009	0,27*	0,52*	0,06	-0,24*	0,004							
2YNo	-0,007	-0,37*	-0,28*	0,70*	0,55*								
2YD	0,49*	-0,35*	-0,52*	0,40*									
2YL	-0,32*	-0,20*	-0,13										
2YN	-0,28*	0,59*											
3YL	-0,15												

1YD—diameter of 1Y, 3YL—length of 3Yparent branch, 2YN—number of 2Y, 2YL—length of 2Y, 2YD—diameter of 2Y, 2YNo—number of nodes of 2Y, 2YA—angles of 2Y, 1YN—number of 1Y, 1YL—length of 1Y, 1YNo—number of nodes on 1Y, 1YA—angles of 1Y, 1YVB—number of vegetative buds per 1Y, 1YFB—number of flower buds per 1Y, 1YFLO—number of female flowers per 1Y

\* $p < 0.05$

case of the morphotype III. Here, in all 3 years, only the number of 1Y is involved in the 1YD model. Two individual models of M-IV comprise 2Y diameter, whereas the 1Y length is only once included in the model. In the first year of the experiment, 1Y diameter in M-III is also influenced by 2Y length like the standard.

*Contribution of independent variables in the prediction of the 1Y diameter*

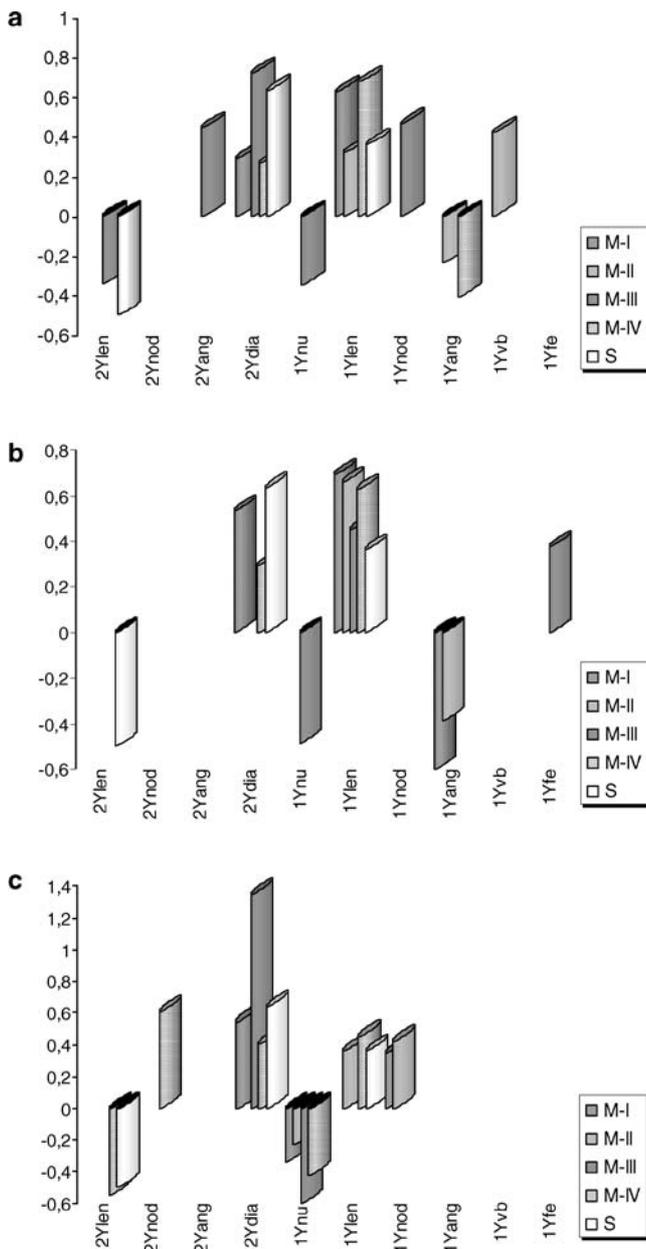
The regression coefficients of different independent variables which create 1Y diameter models represent their weight, and can also be used as the range of variations of variables from the models against 1Y diameter. Based

on the regression coefficients we can predict an impact of a certain independent variable on the 1Y diameter in its further development. In general, we can predict that annual shoots will be of a larger diameter if inserted onto the thick 2-year-old bearers. If the 2Y diameter increases by 1 mm, the 1Y inserted on these 2Y will be thicker by 0.2 mm and up to 0.7 mm. In the case of terminal and lateral fruiting genotypes as well as intermediate bearers with mezotonic ramification, 1Y diameter is expected to be dependent on 1Y length. The relationship is positive, which means that the basal diameter of 1Y increases by 0.5–1.3 mm, if 1Y elongates by 10 cm. In mezotonic intermediate bearing trees, the angles of 1YD also affect their basal diameter: when the angle of 1Y shoot grown on the 2Y parent shoot increases by 10%, the 1Y diameter becomes thicker by

**Table 3** Parameter coefficients of linear regression models of annal shoot diameter for four morphotypes in 3 years in comparison to the coefficients of standard model (ST)

Type	Year	Parameter coefficients										$R^2$	
		A	2Y			1Y				Veget. buds (no)	Female flowers (no)		
			Length (cm)	Nodes (no)	Angles (°)	Diameter (mm)	Number	Length (cm)	Nodes (no)				Angles (°)
I	1	5.13			0.215			0.099					0.60
	2	5.53			0.251			0.109		-0.055			0.73
	3	2.37			0.399		-0.929		0.347				0.61
II	1	6.57						0.057		-0.036	0.412		0.65
	2	9.40						0.123		-0.058			0.70
	3	5.14					-0.434	0.054	0.389				0.60
III	1	-1.39	-0.04	0.076	0.561		-0.226		0.306				0.62
	2	8.48					-0.672	0.105				0.927	0.79
	3	2.85			0.712		-1.59						0.72
IV	1	7.75			0.212			0.129		-0.07			0.70
	2	5.13			0.215			0.099					0.60
	3	4.45	-0.07	0.219	0.251		-0.739	0.067					0.66
ST		3.40	-0.09		0.632			0.065					0.66

ST—standard model for unselected branching and fruiting habit



**Fig. 3** Standardized regression coefficients of linear regression models of annual shoot diameter for four morphotypes (M-I, M-II, M-III and M-IV) in the year 1999 **a**, 2000 **b**, and 2001 **c** in comparison to the coefficients of standard model (S). *Legend:* 2Ylen—length of 2Y, 2Ynod—number of nodes on 2Y, 2Yang—angle of 2Y, 2Ydia—diameter of 2Y, 1Ynu—number of 1Y, 1Ylen—length of 1Y, 1Ynod—number of nodes on 1Y, 1Yang—angle of 1Y, 1Yvb—number of vegetative buds on 1Y, 1Yfe—number of flowers per inflorescence on 1Y

0.4–0.6 mm. When we want to predict annual shoot development in intermediate bearers with acrotonic ramification, the interdependency between the number of 1Y shoots and their basal diameter has to be taken into account: when the number of 1Y on parent 2Y decreased by 1, the 1Y diameter increased by 0.2 mm up to 1.6 mm (Table 3).

The size of various regression coefficients cannot be compared to each other since different variables are measured on different scales. We cannot directly tell which inde-

pendent variable has the most effect on 1Y diameter. For this reason we use standardized regression coefficients ( $\beta$ ) which are directly compared to one another. The independent variable with the largest coefficient has the greatest influence on the dependent 1Y diameter.

Standardized regression coefficients for standard and four morphotypes in 3 years are shown in Fig. 3. In the standard model, basal diameter of 2Y parent shoot at most contributes to the 1Y diameter ( $\beta = 0.636$ ). It is followed by negative impact of the 2Y length ( $\beta = -0.497$ ), and by positive contribution of 1Y length ( $\beta = 0.364$ ).

In single morphotypes, the relationship between the contributions of different traits of 2Y and 1Y shoots to the 1Y diameter is rather different than in standard. 2Y diameter has the greatest influence on 1Y diameter in M-I/year 3 (Fig. 3), and in M-III/years 1 and 3. In five cases (M-I/year 1 and 2; M-II/year 2; M-IV/year 1 and 2), the 1Y length has the greatest impact on the 1Y diameter. In the combination M-II/year 1, the number of vegetative buds per 1Y shoot is the most important trait that affects the 1Y diameter. In M-III/year 2, the number of 1Y shoots and their length almost equally contribute to the 1Y diameter, and only in the case M-IV/year 3, the number of 2Y nodes is the most influential variable (Fig. 3).

## Discussion

With the architectural analysis of the fruiting branch over the period of 3 years we described the development of annual shoots in common walnut. According to Forshey and Elfving (1989) the shoots are the most conspicuous and readily accessible fraction of the tree's vegetative growth. Because they are large enough to subsume the most important physiological processes, the shoots are convenient subunits for the modelling of growth (Lescourret et al. 1998).

In our study, we elaborated a morphological model of annual shoot diameter in walnut, based on the structure of 3-year-old fruiting branches. In the first part of the investigation, basal diameter of annual shoots from a large number of walnut genotypes irrespective of the fruiting and branching behaviour was analysed. Great variability in shoot diameter was ascertained. On average, the shoots were 8.7 mm wide and they were distributed into eight diameter ranks of 2 mm. Great phenotypic variability is due to the origin of the researched trees. All individuals are ownrooted seedlings. They developed from randomly selected seeds, originating from unknown indigenous genotypes from Slovene villages. Due to a high level of heterozygosity, each tree represented a unique genotype which strongly affects fruiting behaviour of the tree and, consequently, morphometric traits of the shoots. Our results revealed a genetically determined plan of the annual shoots development, which is, according to Seleznyova et al. (2003), one of the primary aims of the architectural analysis in general.

A significant inter-year variations in 1Y diameter has already been proved in Slovene terminal fruiting cultivar Elit, too. Here, 1Y diameter decreased from 10.4 mm in the first year, to 8.5 mm in the second year, and, finally,

to 7.5 mm in the third year of investigation (Solar et al. 2005).

Similar to our results, a great variability was proved by many authors when taking into consideration basic architectural traits like tree vigour and growth habit in different local populations as well as in hybrids (Aleta and Ninot 1997; Botu et al. 2001; Kuden et al. 1997; Germain 1997b; Germain et al. 1997; Lansari et al. 2001; Solar et al. 2001, 2002; Zeneli et al. 2005), while the quantitative description of annual shoots in walnut was reported only by Ducouso et al. (1995), Lauri et al. (2001) and Sabatier et al. (1998). The first authors dealt with the length and nodes distribution in annual shoots whereas the last ones investigated the current year shoots and their impact to the fruit weight variability.

Since the growth and fruiting capacity in walnut depend on fruit bearing and branching patterns (McGranahan and Leslie 1991; Germain 1997a, b; Solar and Štampar 2003; Solar et al. 2003, 2004), and vegetative growth is controlled at three levels: genetic potential, internal regulation, and environmental stimulation (Ramos et al. 1998), in the second part of the study we concentrated to the trees with different fruiting behaviour. Annual shoots from the trees which belong to four different branching and fruiting habits, represented as morphotypes I, II, III and IV were analysed in details in 3 successive years. We realised that basal diameter of annual shoots varied in relation to the branching and fruiting patterns and to the age of the tree. The trees with lateral fruiting habit had the thickest annual shoot. In such shoots the cambial activity is more intense than in thin shoots and it increases both the physical strength and the conducting capacities of large shoots (Puntieri et al. 2000). It can be expected that they are able to support a heavy fruit load and allow a good nutrient and water supply to the fruit, thus favouring higher fruit quality (Génard and Bruchou 1992). Indeed, lateral fruiting cultivars can bear even three times more flowering buds per shoot than terminal bearers (Solar et al. 2004). But, on the other hand, in lateral bearers the fruit size decreases and fruit heterogeneity increases from year to year (Lauri et al. 2001) as a consequence of decreasing the vegetative growth of fruiting shoots (Hasey et al. 1998).

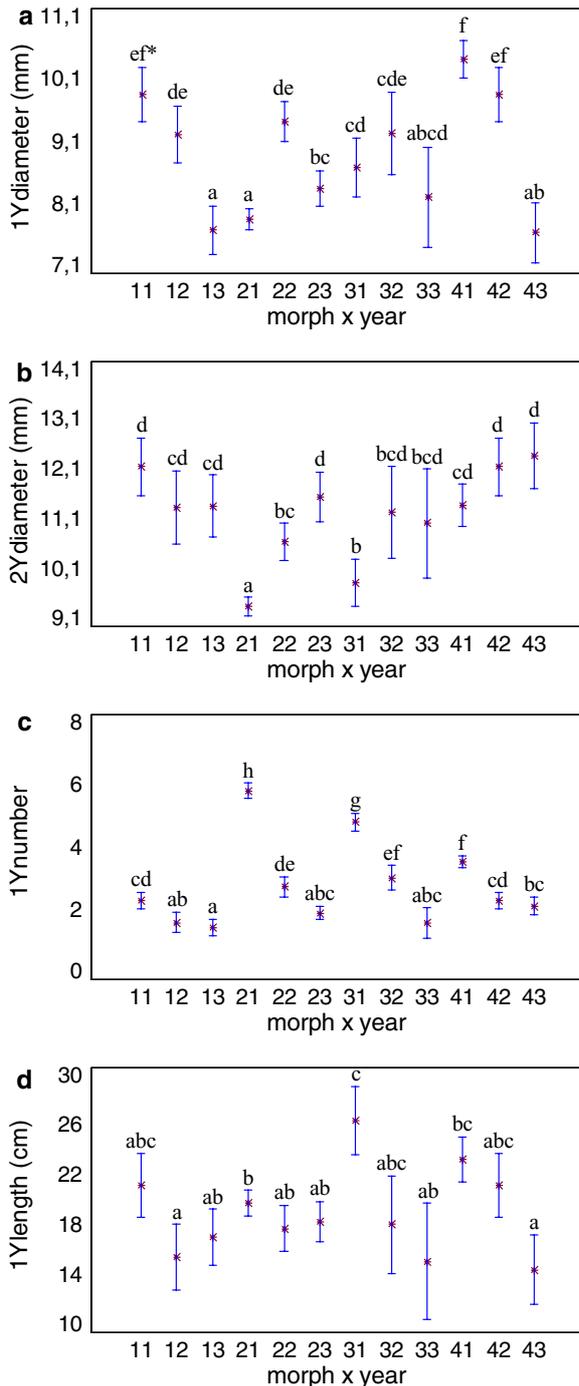
A tendency of decreasing of shoot vigour was proved in our research, too. In three out of four morphotypes annual shoots were the thinnest in the third year of the experiment. This phenomenon could indicate the ageing of parent meristems or the variation of physiological age of the parent meristems. According to Barthélémy (2003), the short axes are typical features of physiologically-aged structures. Short annual shoots that we observed in the year 3, were highly differentiated, but they had short growth units and may be considered as 'physiologically old' and are expected to have a short lifetime. When such situation appears in commercial walnut production, frequent pruning, mainly heading cuts are required to achieve good vegetative growth of the shoots and maximum yield (McGranahan and Leslie 1991; Lampinen et al. 2004; Olson et al. 2004). The reduction of vegetative growth with tree age is a very

common feature in trees, and has been found in some fruit species. Costes et al. (2003) reported a rapid decrease in the mean length of annual shoots in apple trees during the successive growth over 6 years. In apricot, diminishing of primary growth of annual shoots is more expressed than those of secondary growth (Fournier et al. 2004). In both cases, it depends on the cultivar and the location.

As we researched in previous work (Solar and Štampar 2003), in lateral fruiting genotypes (M-IV) beside the annual shoots also the 2-year-old parent shoots are thicker than in the other morphotypes. Thick 1Y shoots inserted on thick 2Y parent shoot showed a close relationship between the development of the 1Y shoot population and the radial growth of older (2Y) shoots, what was also reported by Suzuki (2003). He postulated that the early growth of young shoots of deciduous trees depends on stored resources in older stems. According to LeDizes et al. (1997) the volume of the mother branch is one of the factors that determine a final size of a new shoot. This is in agreement with Grossman and DeJong (1994) who say that the actual growth rate of organs reflects the pattern of available resources. During further development, in the production of flowers and in maturation of fruits, the shoots are found to be carbon-autonomous units (Hasegawa et al. 2003). In walnut tree, branch autonomy is nearly total in summer while in winter, the branch autonomy is more questionable (Lacointe et al. 2001). As reported the same authors, during the winter time when phloem is considered not functional, the xylem pathway is involved into the carbohydrate movements.

Positive relatedness between the size of parent shoot and the size and some structural parameters like the length of daughter shoots was also reported for Scot pines (*Pinus sylvestris* L.) by Kellomäki and Kurttio (1991), and *Nothofagus antartica* shrubs by Puntieri et al. (2002).

Relationships between the characteristics of different morphological units that compose a fruiting branch in common walnut were the objective of the third part of our study. Modelling of the annual shoot diameter in the seedling population without respect to fruiting and branching behaviour shows that the 1Y diameter is most often under the influence of basal diameter of the parent 2Y shoot, the length of 2Y, and the length of 1Y. With regard to these three parameters some of the individual regression models of 1Y diameter for four morphotypes that reflect four different fruiting and branching behaviours in 3 successive years agree with the comparative model. In all morphotypes, we determined inter-annual variations in the basal diameter of annual shoots (Fig. 4a). In the terminal (M-I) and lateral (M-IV) bearers, the variations were caused more or less by the same parameters (Table 3). 2Y diameter had an important influence on 1Y diameter in both morphotypes during the whole experimental period. In the M-I, 2YD slightly decreased, while in M-IV, it slightly increased from the first to the third year (Fig. 4b). In both morphotypes the inter-year variability was non significant and 2YD was always included in the 1Y diameter models. On the contrary, in the intermediate fruit bearers (M-II and M-III), more parameters affected the 1Y diameter (Table 3). 2Y diameter is not



**Fig. 4** Means and 95% LSD interval for 1Y diameter **a**, 2Y diameter **b**, 1Y number **c** and 1Y length **d** for four morphotypes in 3 years (morphotype  $\times$  year interaction). Legend: 11 — morphotype 1/year 1, ... 43 — morphotype 4/year 3. ef\* - Means, marked with the same letter do not differ statistically significantly according to the Duncan multiple-range test  $p \leq 0.05$

included in individual 1YD models of M-II (all 3 years) and M-III (year 2). ANOVA of morphotype  $\times$  year interaction shows that 2YD is not included in the 1YD model when it is extremely small. In M-II/year 1 combination, the 2YD is statistically significantly smaller than in all other combinations (Fig. 4b). Similar exception can be observed

in the case of 1Y number. When it was significantly higher (M-II/year 1) than in all other combinations (Fig. 4c), it did not affect the 1Y diameter in M-II. When 1Y length had the highest value among all cases (Fig. 4d), it was also not included in the 1Y diameter model (M-III/year 1).

Since the shoots are the basic units for the most important horticultural interventions (Lescouret et al. 1998), the knowledge on the interdependency between the annual shoot diameter and other morphometric traits of fruiting branch constituents is important from a technological point of view. Once we have learnt that the basal diameter depends on a lower number of factors it is easier for us to balance the growth of the basal diameter with certain technological measures. For instance, if the shoot diameter depends greatly on the shoot length, it is possible to encourage the vegetative growth with mineral nutrition and water supply. Or, when a close relationship between the shoot diameter and the number of shoots is obvious, an appropriate pruning (shorter or longer) can enable suitable branching.

In the further research on the trees of all four morphotypes we intend to employ certain agrotechnical measures and to evaluate their impact on the growth and development of shoots and the distribution of flowers and fruits within the shoots.

As reported by Hatta et al. (1999), the ‘branching principles’ governing the architecture of many species. As it has been forecasted by Lauri et al. (1995, 1997) for apple trees, we also expect that the thorough analysis of the fruiting branch structure as well as its physiological response to different environmental and agrotechnical impacts can benefit to the optimisation of the training methods. This will also enable us to learn more about the structure and functioning of a fruiting branch in walnut and establish the correlation between the growth and structure. Consequently, a dynamic interpretation of the tree structure can be done without a long-term observation (Tomlinson 1984), which is of great importance when studying walnut trees with respect to its longevity.

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