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Growth dynamics and reproductive activity of annual shoots in the walnut cultivar 'Elit'

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ABSTRACT

An architectural analysis of a fruiting branch in the Slovenian variety 'Elit' was conducted during three successive years. The fruit bearing branch was constructed of a three-year-old parent shoot plus all corresponding two-year-old shoots and annual shoots (1Y). The construction of the bearing branch during the time caused a statistically significant increase in the number of annual shoots. The basal diameter and the length of 1Y significantly depended on a year whereas their angles did not. In spite of decreasing length of 1Y, the number of vegetative buds per shoot increased from the first to the third year of observations. The number of nodes was closely correlated with the length of the shoots. Activity points on the 1Y were most often on the apical two or three nodes, what was expressed by a marked acrotony. The number of active points varied as the tree matured. The ratio fruit bearing 1Y / total 1Y was 0.47 in year 1; 0.18 in year 2; 0.74 in year 3. It points to the slightly alternance. As the tree grew the number of flowering buds per 1Y as well as the number of female flowers per 1Y increased. The results of the three-year-long research show some growth and development rules in the walnut cultivar 'Elit', however, they do not allow a reliable prediction of the following activities. We assume that this will be possible after another three-year-long analysis, with the help of the Hidden Mark Model.

Key words: *Juglans regia* L., tree architecture, fruiting branch, vegetative growth, bearing potential, shoots

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IZVLEČEK

DINAMIKA RASTI IN RODNOSTI ENOLETNIH POGANJKOV OREHA SORTE 'ELIT'

Da bi proučili dinamiko rasti in rodnosti enoletnih poganjkov pri slovenski sorti oreha 'Elit', smo v treh zaporednih letih izvedli arhitektonsko analizo rodne veje, zgrajene iz triletnega nosilnega poganjka in vseh pripadajočih dveletnih in enoletnih poganjkov (1Y). Z izgradnjo rodne veje se je iz leta v leto statistično značilno povečevalo število 1Y. Leto je značilno vplivalo na bazalno debelino in dolžino 1Y, na njihove kote pa ne. Čeprav se je dolžina 1Y zmanjševala od prvega do tretjega leta opazovanj, je število vegetativnih brstov na 1Y naraščalo. Število nodijev je bilo v vseh letih v tesni zvezi z dolžino poganjkov. Aktivna mesta na 1Y so bila najpogosteje na zadnjih dveh ali treh nodijih, kar se odraža v izraziti akrotoni razrasti. Število aktivnih mest se je povečevalo s starostjo drevesa. Razmerje skupni 1Y/rodni 1Y je bilo v prvem letu 0.47, v drugem letu 0.18, v tretjem letu pa 0.74 in nakazuje rahlo izmenično rodnost. Z leti sta naraščali število rodnih brstov in število ženskih cvetov na 1Y. Triletni rezultati nakazujejo nekatere zakonitosti v rasti in razvoju oreha sorte 'Elit', ne dopuščajo pa še zanesljivega napovedovanja nadaljnje aktivnosti. Ocenjujemo, da bo s pomočjo Markove verige to mogoče po opravljenih analizah v naslednjem triletnem ciklusu.

Ključne besede: *Juglans regia* L., arhitektura dreves, rodna veja, rast, rodni potencial, poganjki

1 INTRODUCTION

The goal of each fruit production is a high and regular crop. In walnut, the crop depends on a cultivar and its characteristic fruit bearing type, agrotechnical measures and environmental factors. Irrespective of the fruiting type which can be terminal, intermediate and lateral (Germain, 1990, 1992), the walnuts are always developed on annual shoots. Flowering shoots can be monocyclic, bicyclic or even tricyclic (Mauget, 1976; Barthélémy et al., 1995; Sabatier et al., 1995; Ducouso et al., 1995; Sabatier and Barthélémy, 2001a). Monocyclic shoots are formed by the first growth flush in spring. They are usually completely preformed in winter buds. Bicyclic and tricyclic annual shoots grow from spring buds which are formed in the same year (Rivals, 1965; Sabatier et al., 1995). On the adult tree, monocyclic shoots are usually flowering, while the bicyclic and tricyclic shoots are mostly vegetative (Barthélémy et al., 1995).

Since the size and weight of nuts as well as kernel weight and kernel percentage are related to dimensions of fruiting annual shoots, in previous work we analysed the annual shoots in detail (Solar and Štampar, 2003; Solar et al., 2003a, b). Then, we concentrated on the shoot diameter which is, according to Sinoquet (1997), an important element of shoot morphology beside its length and the number of leaves. In a 3-year-old fruiting branch, composed of a 3-year-old parent shoot with corresponding 2-year-old and annual shoots, the annual shoot diameter is positively correlated with the diameter of the corresponding 2-year-old shoot, with the length of annual shoot and with the number of flowering buds per annual shoot. It is in negative correlation with the length of 2-year-old shoot and with the number of annual shoots per 2-year-old shoot (Solar et al., 2004). Fruiting and branching behaviour as well as the year and their interaction significantly influenced the annual shoot diameter. However, the highest influence on the annual shoot diameter is caused by the diameter of a 2-year-old parent shoot (Solar, unpublished data).

In present work, quantitative and qualitative characterization of annual shoots in Slovene variety 'Elit' was conducted in order to establish their growth dynamics and reproductive activities during the period of three years.

2 MATERIALS AND METHODS

Slovenian terminal fruit bearing cultivar 'Elit' was included into the trial. At the beginning of the experiment, the trees were seven years old. Planting density in the orchard was 9 m x 7 m (158 trees/ha). The trees were trained as a gobelet. They were minimally pruned till the fourth year after planting while the following growth was free, without any pruning. The investigated structural unit was a 3-year-old fruiting branch (Figure 1) inserted on the 4th order axis constructed from a 3-year-old wood + all corresponding 2-year-old shoots and annual shoots (1Y). 8 trees per 2 fruiting branches (Σ 16 fruiting branches) were observed. 172 annual shoots were measured in the year 2001, 246 in the year 2002, and 487 in the year 2003.

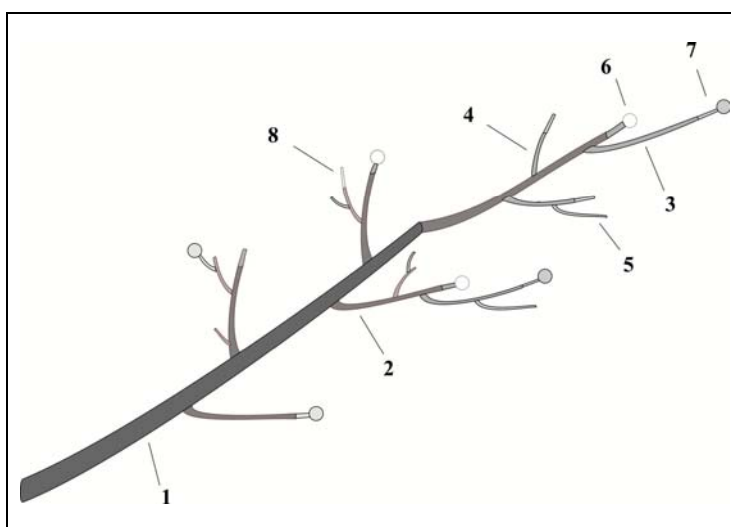


Figure 1. Scheme of a 3-year-old fruiting branch in the terminal fruiting cultivar 'Elit'.

Legend: **1** – 3-year-old parent branch, **2** – 2-year-old parent shoot, **3** – annual shoot, flowering (F1Y), **4** – annual shoot, vegetative (V1Y), **5** – current year shoot, **6** – fruit in the previous year, **7** – fruit in the current year, **8** – annual shoot with dead apex.

In the frame of quantitative analysis we counted the number of all shoots on the bearing branch. We measured the length, basal diameter, and angles of all axes. The number of nodes and the number of buds (vegetative and flowering), flowers, fruits and leaves per annual shoots were counted as well. A shoot length was measured in cm, from the base to the top, using a fabric tape measure. The nodes were counted from the base of shoots towards the top – from the first to the last still distinguishable node. The angles of shoots were determined using a special goniometer where lower values (in degrees) represented more erect shoots. The angle of the annual shoot was represented by the value ($^{\circ}$) measured between the annual shoot and a 2-year-old bearer. A shoot diameter was measured in mm at its base with a caliper. All parameters, except buds and flowers, were measured during winter dormancy.

The flowering shoots were determined according to the presence of flowering buds that could be in the terminal, subterminal or lateral position. Based on the presence or absence of flowering buds along the axis, the degree of persistence of the apical meristem and length of the axis, annual shoots were classified into 3 types (Figure 2). Meristem potential of each shoot type was determined in relation to the section along the 1Y where branching occurred.

Each type of annual shoot was presented by a sequence of different axillary structures with symbols: 0, 1, 2, 3, 4, 5 or 6 (see legend in Figure 2).

The data was analyzed with the programme Statistica for Windows (StatSoft, 2001). The effects of different years on annual shoot traits were evaluated with multifactor ANOVA, and the Duncan multiple-range test at $p \leq 0.05$.

3 RESULTS AND DISCUSSION

3.1 Quantitative characterization of annual shoots in a 3-year-old fruiting branch

The construction of the bearing branch during the time causes a statistically significant increase in the number of 1Y. It was constructed of 9.7 1Y in the first year, followed by 17.6 in the second year and 25.2 in the third year (Table 1). The basal diameter and the length of 1Y significantly depend on a year whereas their angles do not. A significant year-to-year variation in 1Y diameter was also determined when studying a stability of annual shoot diameter in Slovene walnut seedling population where the genotypes belong to different branching and fruiting behaviour (Solar et al., 2005). The length of 1Y decreases from the first to the third year of observations. This is in agreement with the results by Costes et al. (2001, 2003) who report a rapid decreasing in the mean length of annual shoots in apple tree during the six observed years. A decreasing length of the shoots could be due to extreme drought that reduced vegetative growth during the years 2002 and 2003. Another explanation could be the physiological age of the shoots. According to Barthélémy (2003), such shoots are considered as 'physiologically old'. They have short growth units, bear flowers and are expected to have a short lifetime.

Table 1. Morphometric traits of annual shoots in a 3-year-old fruiting branch in the cultivar 'Elit'.

Trait	Annual shoots (1Y)		
	2001	2002	2003
1Y length (cm)	22.1 a*	18.9 a	14.4 b
1Y basal diameter (mm)	10.4 a	8.5 b	7.5 a
1Y angle (°)	39.3 a	31.9 a	38.9 a
Σ 1Y per fruiting branch	9.7 a	17.6 b	25.2 c
Σ flowering 1Y per fruiting branch	4.6 a	3.2 a	18.7 b
Σ vegetative 1Y per fruiting branch	5.1 a	14.4 b	6.5 a
Flowering 1Y : Σ of 1Y	0.47 a	0.18 b	0.74 c
Vegetative buds (number / 1Y)	1.25 a	1.95 b	2.14 b
Flowering buds (number / flowering 1Y)	0.55 a	0.46 a	1.18 b
Female flowers (number / flowering 1Y)	0.75 a	0.76 a	1.86 b
Leaves (number / 1Y)	2.1 a	3.9 b	3.3 b

a*Means, marked with the same letter do not differ statistically significantly according to the Duncan multiple-range test $p \leq 0,05$.

In spite of decreasing length of 1Y, the number of vegetative buds per shoot increased from 1.25 in the year 2001 to 2.14 in the year 2003 (Table 1). The number of nodes

was closely correlated with the length of the shoots. The same relationship was proved also in walnut seedling population (Solar et al., 2003a).

The ratio fruit bearing 1Y / total 1Y is: 0.47 in year 1; 0.18 in year 2; 0.74 in year 3 (Table 1). It points to alternate bearing. As the tree grows the number of flowering buds increases on 1Y as well as the number of female flowers on 1Y. There was an antagonism between vegetative growth and flowering. The phenomenon was reported many times. Several authors point out that all factors which reduce vegetative growth, e.g. defoliation or training branches horizontally, promote flowering (Krekule, 1979), Lloyd and Firth (1990), Lauri et al. (1996). In our case, both developmental patterns were negatively correlated. Good crop in the year 2003 was a result of a high number of flowering buds and flowers per shoot that was shorter and thinner compared to the other two years. By contrast, the peach tree develops larger number of flowers only when the fruiting shoots are more vigorous (Fournier et al., 1998). Considering the extremely dry weather in June and July of 2002, the drought induced stress could be responsible for good differentiation in the walnut cv. 'Elit' during the summer 2002 and high number of flowering buds per 1Y as well as high number of female flowers per fruiting 1Y in 2003.

3.2 Qualitative description of annual shoots in a 3-year-old fruiting branch

3.2.1 Number of nodes distribution

Flowering annual shoots (F1Y) differed from the vegetative ones (V1Y) regarding the distribution of the nodes along the shoot axes (Figure 3). In particular, a great year-to-year variability was noticed. In the first year 62 % of F1Y had less than 11 nodes. In the second year almost a half of F1Y were longer and had between 11 and 20 nodes. In vegetative shoots the number of node intervals were distributed more equally: 69 % (year 1) and 61 % (year 2) belong to the first rank with 1-10 nodes; 19 and 28 % of V1Y had between 11 and 20 nodes. In both F1Y and V1Y the percentage of the longest shoots with more than 21 nodes was quite the same in both years. In the year 3 only one third of V1Y were short with 1 – 10 nodes (Figure 3). 66 % of V1Y belong to the second rank with 11-20 nodes. In the F1Y the distribution was quite opposite: 60 % of them were short (1-10 nodes) and only 40 % of them were longer (11-20 nodes). In the third year, neither vegetative nor flowering 1Y were long enough to be arranged in the rank with more than 21 nodes.

When considering the three-year average, it is evident, that the nature of the annual shoot does not affect the number of nodes distribution greatly. There was 54.8 % of V1Y and 53.4 % of F1Y with 1-10 nodes. 37.6 % of V1Y and 38.3 % of F1Y had between 11 and 20 nodes while only 7.6 % of V1Y and 8.3 % of F1Y belong to the rank above 21 nodes. Till now, the distribution of the nodes and internodes, respectively, was investigated by Ducouso et al. (1995). They realised that in an equal morphological type (monocyclic, bicyclic, threecyclic) of annual shoots the internodes were distributed according to an equal pattern irrespective of the fruiting type.

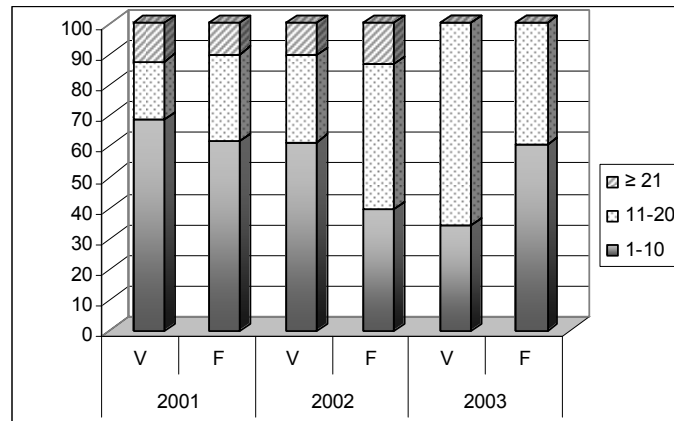


Figure 3. Frequencies of vegetative (V) and flowering (F) annual shoots with different ranks of node number in three years.

3.2 Branching pattern

Meristem potential depends on the type of the annual shoot (Figures 4a,b,c). Activity points on the 1Y were most often on the distal two or three nodes, what is expressed by a markedly acrotonic branching pattern. This is in accordance with the findings by Ducouso et al. (1995) who report that monocyclic annual shoots usually develop lateral shoots on the first, the second or the third node under the terminal flowering bud.

In all three years the vegetative annual shoots were most frequently branched on the distal part of the axes (Figure 4a). In between 25 and 30 % of V1Y the active nodes were on the medial part of the axis and less than 15 % of V1Y developed lateral shoots on basal part. In flowering 1Y the active nodes were also distributed mainly in distal part of the shoot axis (Figure 4b). Between 58 % (year 2) and 87 % (year 3) of F1Y were branched on their distal part. Basal nodes were active only in 2 % of flowering 1Y (year 3), 5 % of F1Y (year 1) and 15 % of F1Y (year 2).

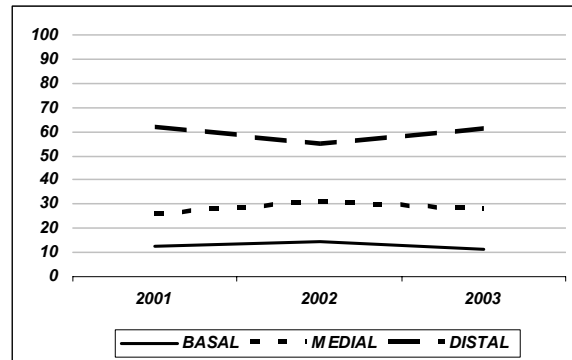
When the apex is dead, mesotony and also bazitony are expressed more frequently (Figure 4c). Between 33 % and 76 % of the shoots with dead apex developed lateral shoots in basal part. Medial part of those shoots was branched in 6 % (year 3) to 48 % (year 2), while the distal nodes were active in less than 20 % of the shoots.

The branching probability of different nodes of annual shoots was investigated by Sabatier and Barthélémy (2001b). With regard to the observed variation in size and content of axillary buds according to the position, they distinguished three successive zones on a parent shoot: the apical, medial and basal zone. In general, vegetative and flowering annual shoots are branched more or less uniformly. Sympodial branching occurs most frequently, whether the terminal bud is flowering or vegetative or the apical meristem is dead.

The sympodial development that appears in the adult stage of walnut tree was also reported by Barthélémy et al. (1995) and Sabatier and Barthélémy (2001a). In the shoots with dead apex lateral branching depends on the number of destructed buds from the apical part towards the basal part of the shoot.

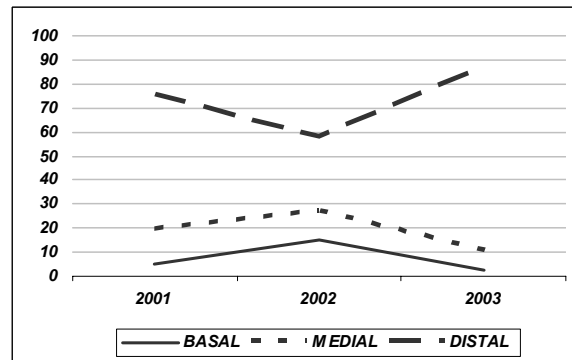
Types of axillary production	Sequence of events
	5
	0
	1
	0
	0
	2
	0
	0
	0
	0
	0
	0
	0
	0

Vegetative annual shoot (a)



	3
	0
	2
	0
	0
	2
	0
	0
	0
	0
	0
	0
	0
	0

Flowering annual shoot (b)



	6
	6
	6
	6
	0
	0
	1
	0
	0
	2
	0
	0
	0
	0

Annual shoot with dead apex (c)

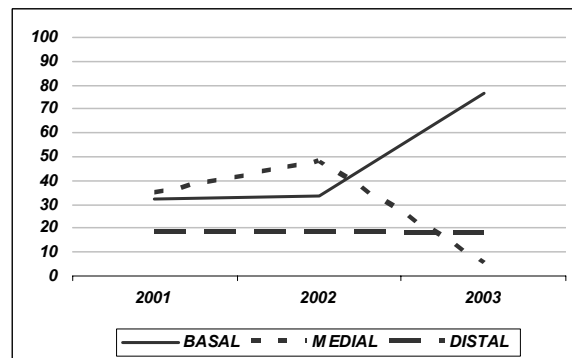


Figure 2. Types of axillary production and sequences of events in three types of annual shoot in cv. 'Elit' (0 – latent bud, 1 – long vegetative current year shoot, 2 – short vegetative current year shoot, 3 – long flowering current year shoot with nut, 5 – vegetative bud, 6 – dead distal part of the shoot).

Figure 4. Frequency distribution of active nodes in three sections (basal, medial, distal) on the axis of vegetative (a) and flowering (b) annual shoots, and annual shoots with dead apex (c) in the cultivar 'Elit' in three successive years.

Similar succession of monopodial branching (juvenile tree) and sympodial one (adult tree) was noticed also in apple. According to Seleznyova et al (2003), in the early stages of development, the vegetative structure of a young apple tree is primarily constructed of monopodial shoots, as most buds are vegetative. As the apple tree matures, the proportion of floral buds increases, resulting in a higher proportion of sympodial shoots. Sympodial branching is the most usual branching type also in fruiting apricot tree where the sympodium occurs when lateral shoots extend after the death of the meristem leading to axis edification (Costes, 1993; 1999).

The number of active points increased from 1.8 in the first year to 2.1 in the second year. In the third year there were only 1,2 active points per shoot. Lower vegetative activity of the annual shoots could be explained by more intensive reproductive activity. In the year 3 it was reflected in higher number of flowering 1Y per fruiting branch, and also in higher number of flowering buds and female flowers per shoot (Table 1).

3.3 Stability of terminal fruiting habit

Table 1 shows that in the year 2003 the number of flowering buds per fruiting shoot was higher than 1.0. It means that not only terminal buds but also subterminal or some of the lateral buds developed into fruits. An exact analysis of the nature of the sprouting buds shows that in at least 9 % of observed annual shoots, more than one flowering bud per shoot was determined (Figure 5). In the first year 91 % of the shoots bore nuts in the terminal position. In the second year there were only 62 % of the terminal bearing shoots, and in the third year the terminal fruit set increased again to 79 % of the shoots. Axillary fruit production was strongly expressed in the year 2002 when one third of the annual shoots bore nuts in the axillary position. In other two years there were between 8 and 15 % of axillary fruiting shoots. Subterminal fruit set was the least expressed in all years of the investigation.

It is evident that terminal fruiting behaviour in the cultivar 'Elit' is not so strict and in some years, and under certain environmental conditions it can alter towards the lateral fruiting habit.

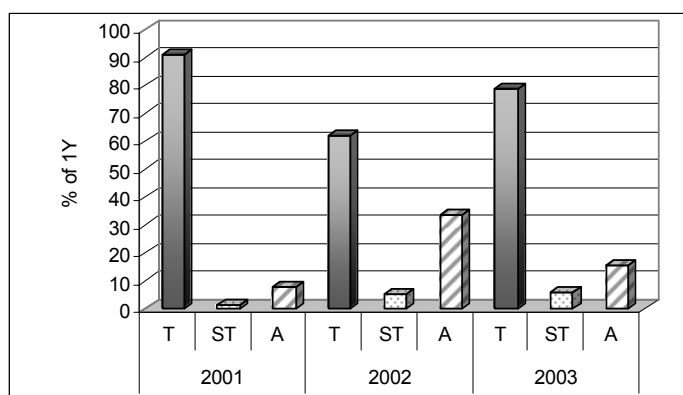


Figure 5. The frequencies of annual shoots with flowering bud in terminal (T), subterminal (ST) and axillary position (A) in 2001, 2002, and 2003.

4 CONCLUSIONS

The results of the three-year-long research show some growth and development rules in the walnut cultivar 'Elit'. At the observed age of the tree the annual shoots had mainly the reproductive and maintenance function regarding their vegetative and reproductive ability. In two out of three years not so good balance between growth and fruit production was noticed. Such relationship between growth and fruiting is not desired in commercial walnut production since it claims to the fruit growers to prune the trees very frequently and strongly to obtain regular crop. However, our results do not allow a reliable prediction of the following activities inside the fruiting branch, and consequently in the frame of the whole tree. We assume that this will be possible after another three-year-long analysis, when the impact of physiological age of the annual shoots as well as the impact of environmental conditions are expected to be clearly explained. The Hidden Mark Model will be used for the prediction of further development based on the long-term research.

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