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Does the Nutritional Status of Reproductive Shoots of Olive Tree (cv. 'Kalamon') Differ from that of Vegetative Shoots during Inflorescence Development?

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ABSTRACT

During inflorescence development of olive trees, Fe, Zn, Mn, Cu, Ca, Mg, K and P contents of leaves, wood and bark of vegetative shoots (VS) and leaves, wood, bark and inflorescences of reproductive shoots (RS) were monitored. The level of K, P, and Cu of inflorescences remained rather stable during their development, whilst the time-course of inflorescence Zn, Fe, Mn, Mg, and Ca levels followed a concrete pattern. The revealed alterations in RS nutritional status were in close relation to this pattern. A decrease in K content characterised wood up to one week before full bloom. When inflorescences were characterised by a minimum content in Zn, Fe, Mn, Mg, and Ca, a general increase in P, Cu, Zn, Fe, Mn, Mg, and Ca content of bark and in Cu, and Zn content of wood took place, with a decrease in Zn content of leaves. At the beginning of the flower development period, Zn, Fe, Mn, Mg, and Ca contents of inflorescences kept increasing, and RS bark was characterised by increased Cu, Zn, and Fe and RS leaves by increased Cu, Zn, Fe, Mn, Mg, and Ca contents. One week before full bloom, inflorescences were characterised by restored maximum contents of Zn, Fe, Mn, Mg, and Ca and RS presented no changes in the nutrient contents of wood. Instead, RS were characterised by an increased Zn content in bark and in leaves, and decreased P and Zn contents. Only Zn content was found to be altered during the flower fertilization period, increased in bark and decreased in leaves.

Keywords: bark, leaves, *Olea europaea*, wood
Abbreviations: FB, full bloom; **FDP**, flower development period; **FFP**, flower fertilization period; **IEP**, inflorescence elongation period; **RS**, reproductive shoots; **VS**, vegetative shoots

INTRODUCTION

Olive (*Olea europaea* L.) tree is one of the most important crop plants grown in the Mediterranean region, an indeterminate evergreen fruit tree that bears fruit on 1-year-old shoots found on its outer periphery. Not all 1-year-old wood is reproductive and previous year olive shoots are differentiated into vegetative shoots (VS) and reproductive shoots (RS). Under normal conditions, flower bud differentiation in olive tree occurs in February and March and full bloom in May or June, about two months after flower bud burst. Inflorescence development could be distinguished into three developmental periods: a first one corresponding to the elongation of the inflorescence (inflorescence elongation period, IEP), a second one devoted to the development of flowers (flower development period, FDP) and the third one including full bloom and flower fertilization (flower fertilization period FFP). The boundary between FDP and FFP characterised full bloom (FB) (Bouranis *et al*. 2004).

Olive inflorescence development has attracted considerable attention. The inflorescence's emergence and flowering stages have been described, where it is stressed that phenological growth stages are specific for each species, however the timing when each stage is reached differs between cultivars or years (Sanz-Cortés *et al*. 2002). Flower bud formation is affected by many parameters, i.e. leaf area, growth regulators, nutrition, and environmental conditions (Weis *et al*. 1988; Cirik 1989; Lavee 1989). The effects of flower position in an inflorescence on its opening day, gender, and petal persistence has been studied in various cultivars (Seifi *et al*. 2008). The influence of olive tree nitrogen status on flower development and quality was studied in terms of flower number per inflorescence and pistil abortion, floral quality parameters, ovary growth and development, ovule development and ovule longevity (Fernández-Escobar *et al*. 2008).

Seasonal changes of mineral nutrients in olive leaves during the alterate-bearing cycle have been described by Fernádez-Escobar *et al*. (1999). These seasonal variations in leaf-nutrient concentration and leaf-nutrient content are necessary in order to understand the physiological aspects of olive nutrition, being also helpful in the interpretation of leaf analysis. Data for the nutritional status of olive tree leaves grown in the cultivation areas of olive in Africa where Mediterranean climate prevails, have been provided by El-Fouly *et al*. (2007). Fernández-Hernández *et al*. (2007) searched for possible correlations between the mineral composition of the olive leaves and the floral buds at different stages of development, in order to establish the use of flower analysis to determine the nutritional status of the olive orchards. Results showed a lack of significance on the correlation coefficients between leaf and floral analysis and it is concluded that floral analysis cannot be considered as an alternative to the foliar diagnosis in the olive. Ulger *et al*. (2004), studying the endogenous hormones, sugars and mineral nutrition levels during the induction, initiation and differentiation stage and their effects on flowers, they found that hormone levels were significantly different in on and off years and concluded that carbohydrates and mineral nutrients may not have a direct effect to induce flower initiation. The nutrient element fluctuations of olive tree flowers during their development have been studied in cv. 'Konservolia' (Bouranis *et al*. 1999). For cv. 'Kalamon', it has been reported that RS differed in several points compared with

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VS in terms of nitrogen metabolism, whilst water content was higher in bark of VS after IEP and in wood during the entire period (Bouranis *et al*. 2004).

Apart from nitrogen, does inflorescence development and anthesis affect the nutritional status of the carrying shoots, i.e. the RS? To address this question, we determined and compared the iron (Fe), zinc (Zn), manganese (Mn), copper (Cu), calcium (Ca), magnesium (Mn), potassium (K) and phosphorus (P) contents of leaves, wood and bark of RS with that of VS, in terms of the periods of inflorescence development and its nutritional dynamics.

MATERIALS AND METHODS

Plant material and growth conditions

Three 40-year-old highly-flowering olive trees (*Olea europaea* L. cv. 'Kalamon') of the olive orchard of the Agricultural University of Athens grafted on seedling stocks were selected and samples were taken weekly at 09:00 h from late March (just after axillary bud burst, when inflorescences were about 1 cm long) to mid-May (about 10 days after full bloom). An 11-15-15 NPK commercial fertilizer was applied at a rate of 2 kg per tree in January and ammonium nitrate in a rate of 1 kg per tree in March. Trees were irrigated weekly by means of a spray system. Soil chemical characteristics of the experimental orchard during olive inflorescence development and anthesis were as follows: pH 7.72, total $CaCO_3$ 21.7%, organic matter 2.78%, [N]=0.18%, and [K]=42 ppm. The prevailing climate conditions during olive inflorescence development and anthesis in March, April, and May were as follows: mean air temperature 16.0, 15.9, 20.8°C, mean relative humidity 65, 60, 51%, total radiation and PAR 13.65/5.95, 17.39/7.05, 21.68/8.50 MJ m^{-2}, evaporation 51.0, 55.6, 81.8 mm and precipitation 0.6, 50.5, 1.0 mm, respectively.

Hanging or horizontal abundantly flowering reproductive shoots (with 10 or more inflorescence-bearing nodes) and vigorous vegetative shoots from the medium or upper portion of the canopy were collected each sampling day (**Table 1**). The shoots were immediately placed in plastic bags and transferred to the nearby laboratory. Samples of leaves, bark and wood were taken from the one-year-old region of both shoot types. Inflorescence samples were collected from the same region of reproductive shoots. Three replicates per sample were separately analyzed. Fresh weight per sample was recorded, samples were oven-dried at 80°C, dry weight was recorded and the samples were ground to pass a 40-mesh screen using an analytical mill (IKA, model A10) prior to chemical analysis (Mills and Jones 1996).

Chemical analysis

Fe, Cu, Zn, Mn, K, Ca, Mg, and P were determined following a wet acid digestion procedure based on the combination of HNO_3 and 30% H_2O_2 (Mills and Jones 1996). Phosphorus quantitative analysis in the diluted digests was carried out colorimetrically by determining the absorption of the blue phosphomolybdate complex at 660 nm, using the ammonium molybdate and stannus chloride procedure (Peach and Tracey 1956). The concentrations of all other nutrients were determined in the diluted digests by atomic absorption spectrophotometry using a GBC Avanta spectrophotometer. For the determination of Ca and Mg, 1% (w/v) lanthanum chloride was added in the digests.

Table 1 Sampling days in terms of inflorescence development, relative to floral bud burst and full bloom. IEP: inflorescence elongation period, FDP: flower development period, and FFP: flower fertilization period.

	IEP				FDP			FFP	
Sampling dates	22/3	28/3	4/4	10/4	18/4	25/4	2/5	8/5	16/5
Days from bud burst	10	16	23	29	37	44	52	58	66
Weeks from bud burst	1.4	2.3	3.3	4.1	5.3	6.3	7.4	8.3	9.4
Days from full bloom	-48	-42	-35	-29	-21	-14	-6	0	8

Table 2 The relative change of nutrient content in the bark, wood and leaves of reproductive shoots (RS) within each stage of inflorescence development. The relative change refers to vegetative shoots and it was calculated only when the comparison of the mean values of the corresponding nutrient contents by means of t-test was found to be significant at p=0.05. "**-**" means no statistically significant difference. **b**: bark, **w**: wood, **l**: leaves. **DBFB**: days before full bloom.

DBFB	Relative change (%) of nutrient content in RS								
	Plant part	K	P	Cu	Zn	Fe	Mn	Mg	Ca
-48	b	-	62.2	204.2	845.5	85.2	68.7	92.3	51.6
	w	-22.8	-	-	372.7	-	-	-	-
	l	-	-	-	-	-	-	-	-
-42	b	-	52.7	540.0	591.7	113.4	91.7	53.3	61.9
	w	-20.0	-	172.4	758.3	-	-	-	-
	l	-	-	-	-43.4	-	-	-	-
-35	b	-	-	336.4	365.0	84.7	-	-	-
	w	-20.4	-	204.8	483.3	-	-	-	-
	l	-	-	-	-51.3	-	-	-	-
-29	b	-	-	81.4	84.0	123.9	-	-	-
	w	-24.7	-	-	-	-	-	-	-
	l	-	-	235.3	87.3	88.7	79.8	93.3	83.6
-21	b	-	-	40.4	-	45.8	-	-	-
	w	-30.6	-24.5	-	-	-	-	-	-
	l	-	-	122.6	-	-	-	-	-
-14	b	-	-	64.9	-	-	-	-	-
	w	-25.1	-18.0	-	-	-	-	-	-
	l	-	-29.9	-	-	-	-	-	-
-6	b	-	-	-	240.0	-	-	-	-
	w	-	-	-	-	-	-	-	-
	l	-	-41.8	-	-78.7	-	-	-	-
0	b	-	-	-	570.6	-	-	-	-
	w	-	-	-	-	-	-	-	-
	l	-	-	-	-45.8	-	-	-	-
8	b	-	-	-	769.2	-	-	-	-
	w	-	-	-	-	-	-	-	-
	l	-	-	-	-75.4	-	-	-	-

Statistical analysis

The significance of differences between means of RS and VS was evaluated using a *t*-test at p=0.05, and when significant the percent of the relative change was calculated (**Table 2**). A curve based on the calculation of the moving average of 2nd order was applied to the data of VS and RS to visualise the fluctuations during inflorescence development in each case (i.e., for each column the average between this column and the previous one was calculated; then, the averages were connected by a line).

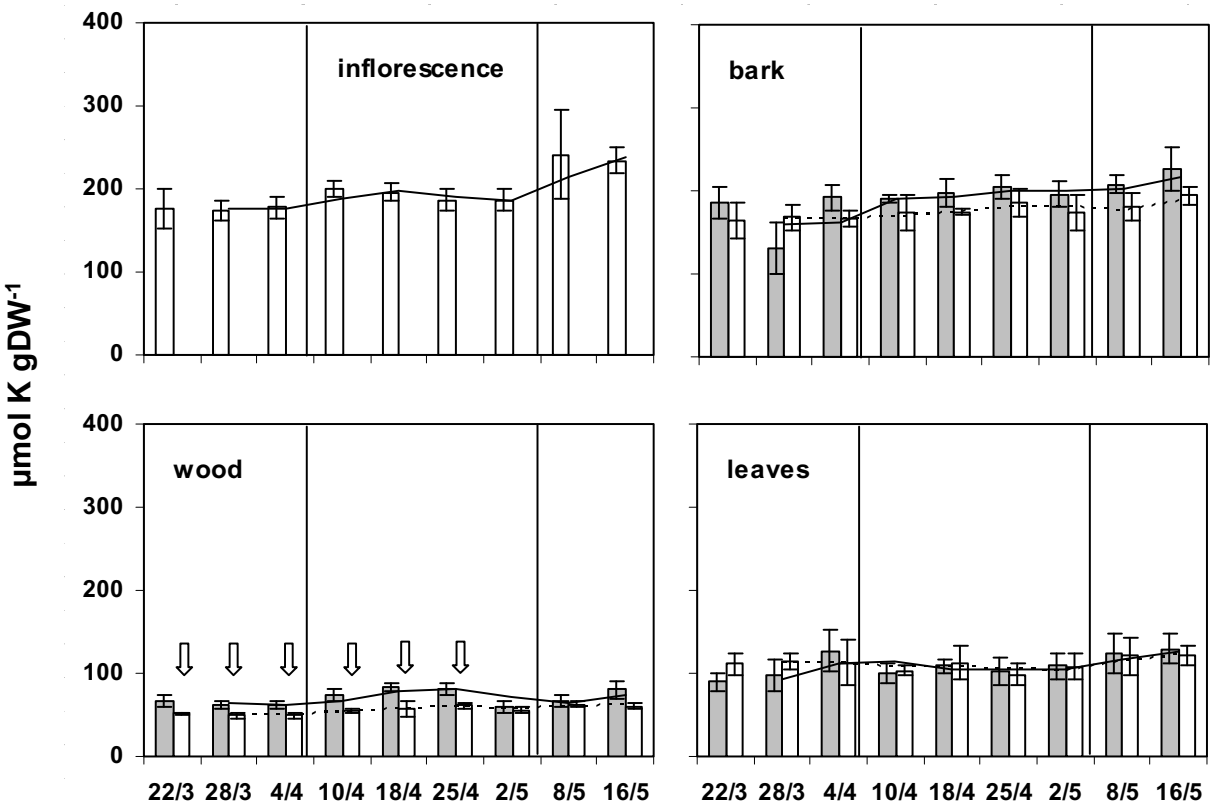

Fig. 1 Time-course of potassium content (on dry weight basis) of bark, wood, and leaves of reproductive (white columns) and vegetative (grey columns) shoots during inflorescence development, along with the fluctuations in the inflorescence K content. Bars indicate standard deviation. Arrows indicate statistically significant differences (p=0.05). The first 3 weeks were devoted to inflorescence elongation (IEP), the next 4 weeks to flower development (FDP) and the last 2 ones to flower fertilization (FFP) period.

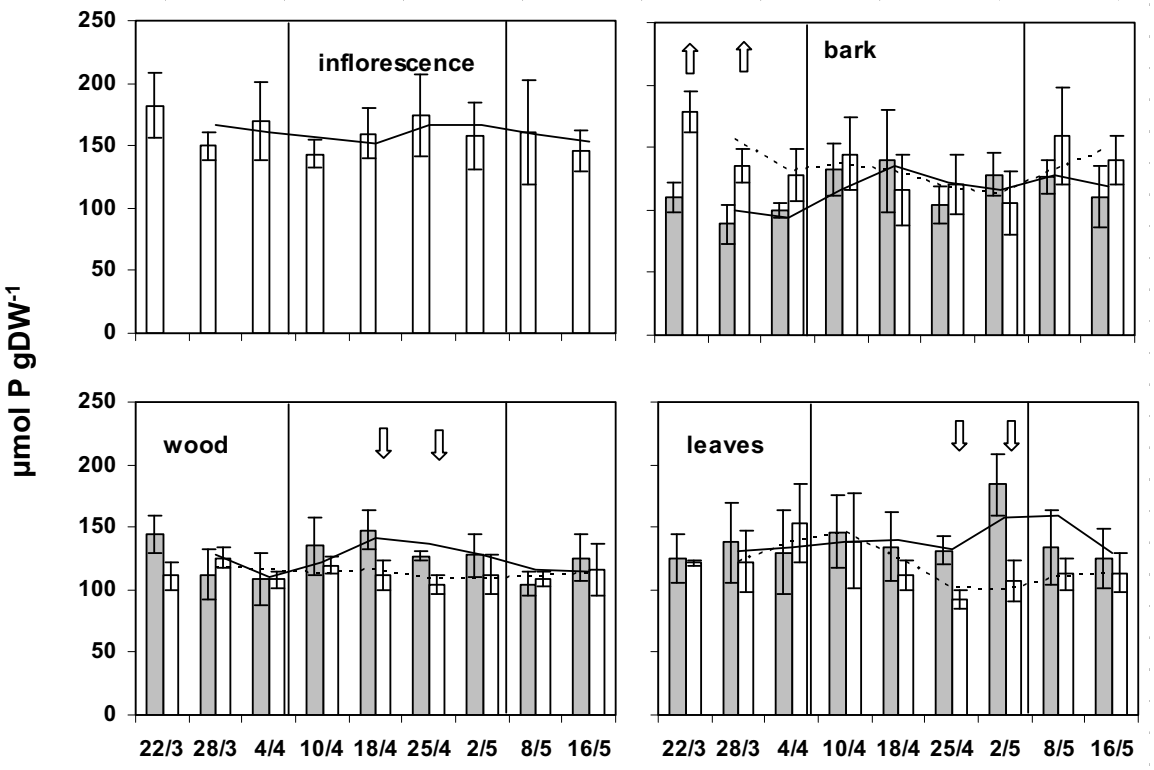

Fig. 2 Time-course of phosphorus content (on dry weight basis) of bark, wood, and leaves of reproductive (white columns) and vegetative (grey columns) shoots during inflorescence development, along with the fluctuations in the inflorescence P content. Bars indicate standard deviation. Arrows indicate statistically significant differences (p=0.05). The first 3 weeks were devoted to inflorescence elongation (IEP), the next 4 weeks to flower development (FDP) and the last 2 ones to flower fertilization (FFP) period.

RESULTS

Inflorescence development was monitored for 10 weeks and full bloom took place the 8th week after floral bud burst (**Table 1**). The first 3 weeks were devoted to inflorescence elongation, while the next 4 weeks to flower development. During inflorescence development, K fluctuated around 197 μmol gDW^{-1} in inflorescence, 192 and 176 μmol gDW^{-1} in the bark of VS and of RS, 70 and 55 μmol gDW^{-1} in the wood of VS and of RS, 109 and 111 μmol gDW^{-1} in the leaves of VS and of RS, respectively. Significant decreases were found in wood of RS during the first six weeks (**Fig. 1**). Phosphorus content fluctuated around 160 μmol gDW^{-1} in inflorescence, 116 and 136 μmol gDW^{-1} in the bark of VS and of RS, 126 and 113 μmol gDW^{-1} in the wood of VS of RS, 139 and 119 μmol gDW^{-1} in the leaves of VS and of

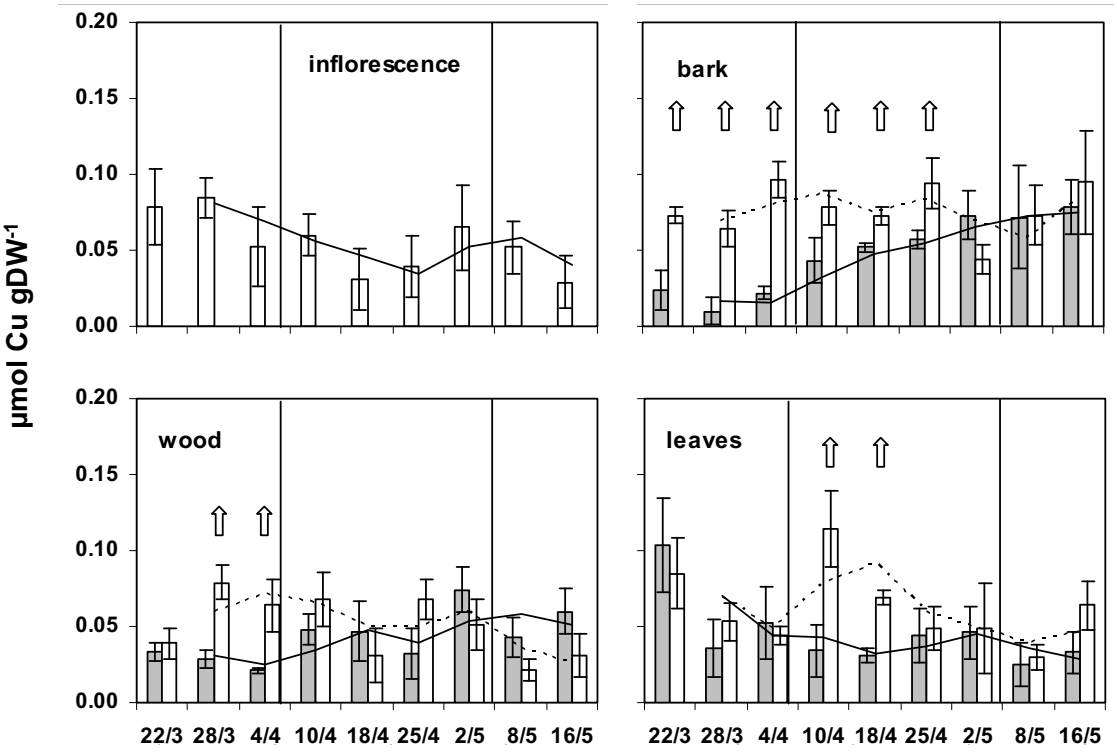

Fig. 3 Time-course of copper content of bark, wood, and leaves of reproductive (white columns) and vegetative (grey columns) shoots during inflorescence development, along with the fluctuations in the inflorescence Cu content. Bars indicate standard deviation. Arrows indicate statistically significant differences (p=0.05). The first 3 weeks were devoted to inflorescence elongation (IEP), the next 4 weeks to flower development (FDP) and the last 2 ones to flower fertilization (FFP) period.

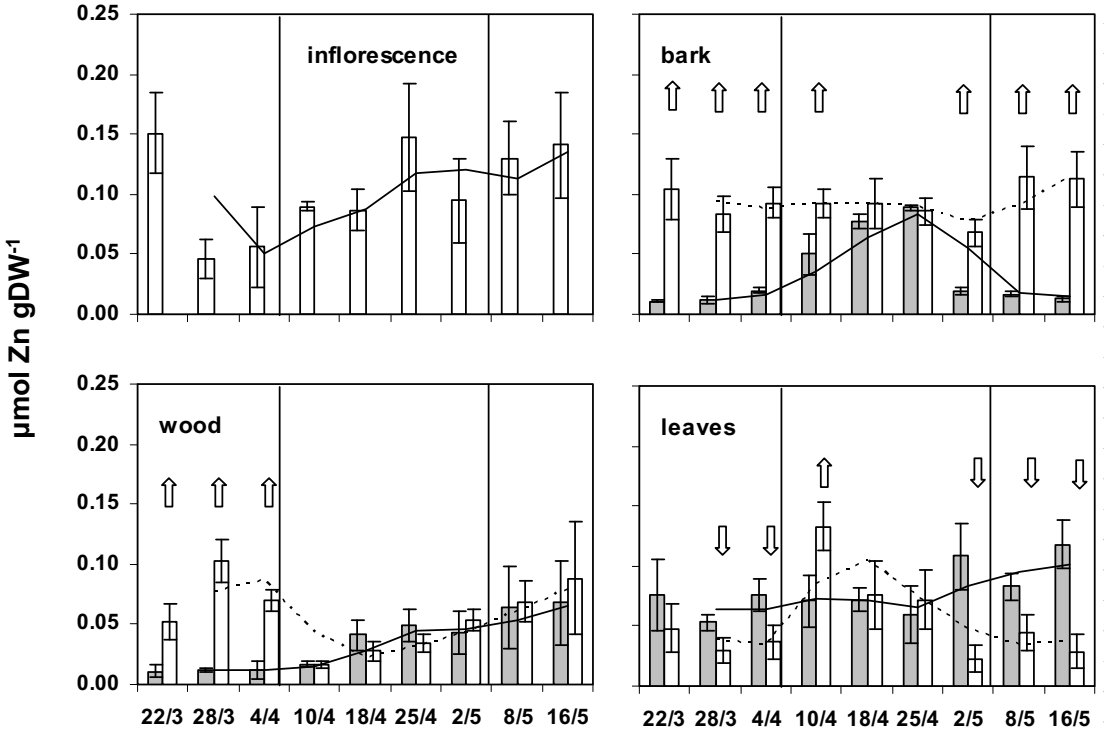

Fig. 4 Time-course of zinc content of bark, wood, and leaves of reproductive (white columns) and vegetative (grey columns) shoots during inflorescence development, along with the fluctuations in the inflorescence Zn content. Bars indicate standard deviation. Arrows indicate statistically significant differences (p=0.05). The first 3 weeks were devoted to inflorescence elongation (IEP), the next 4 weeks to flower development (FDP) and the last 2 ones to flower fertilization (FFP) period.

RS, respectively during inflorescence development. Significant increases of P content were found in the bark during the 1st and the 2nd week, and decreases the 5th and the 6th week in the wood, and the 6th and 7th week in the leaves (**Fig. 2**). Copper content fluctuated around 0.05 μmol gDW^{-1} in inflorescence, 0.05 and 0.08 μmol gDW^{-1} in the bark of VS and of RS, 0.04 and 0.05 μmol gDW^{-1} in the wood of VS and of RS, 0.05 and 0.06 μmol gDW^{-1} in the leaves of VS and of RS respectively during the inflorescence development. Statistically significant increases in Cu content of RS were detected in bark the first six weeks from bud burst, in wood the 2nd and 3rd week, and in leaves the 4th and 5th week. Therefore, when Cu level changed, only increases were found (**Fig. 3**).

Contrary to K, P, and Cu, the level of which remained rather stable during inflorescence development, the other examined nutrients, namely Zn, Fe, Mn, Mg, and Ca, presented a very similar pattern of fluctuations. The nutrient

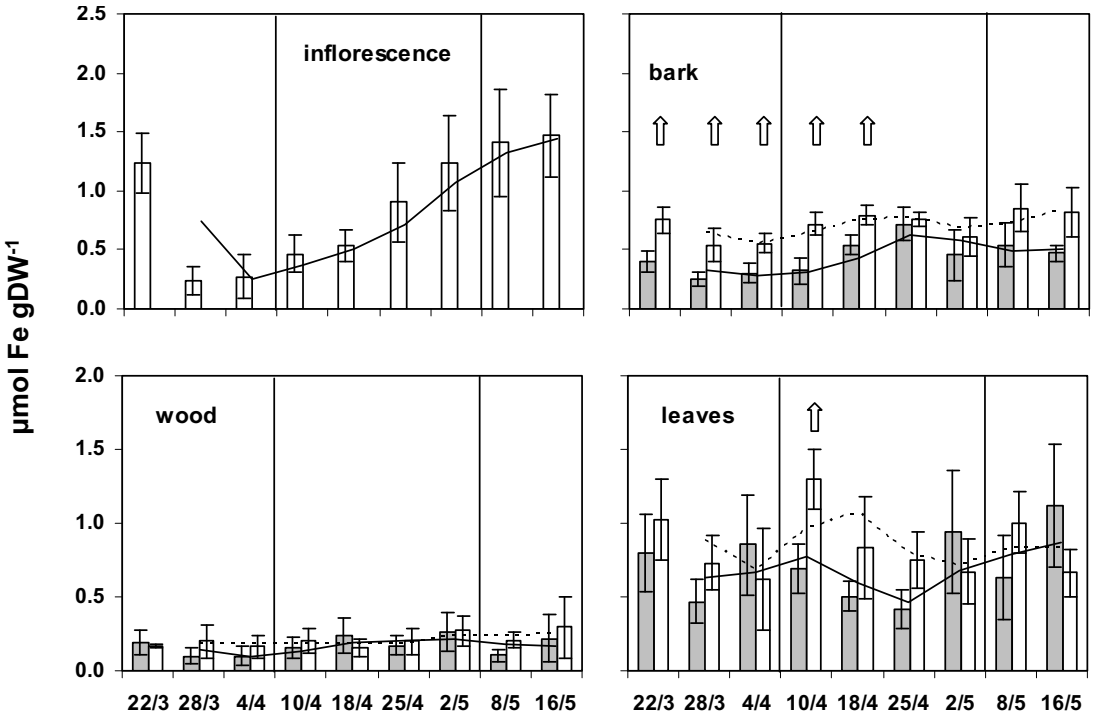

Fig. 5 Time-course of iron content of bark, wood, and leaves of reproductive (white columns) and vegetative (grey columns) shoots during inflorescence development, along with the fluctuations in the inflorescence Fe content. Bars indicate standard deviation. Arrows indicate statistically significant differences (p=0.05). The first 3 weeks were devoted to inflorescence elongation (IEP), the next 4 weeks to flower development (FDP) and the last 2 ones to flower fertilization (FFP) period.

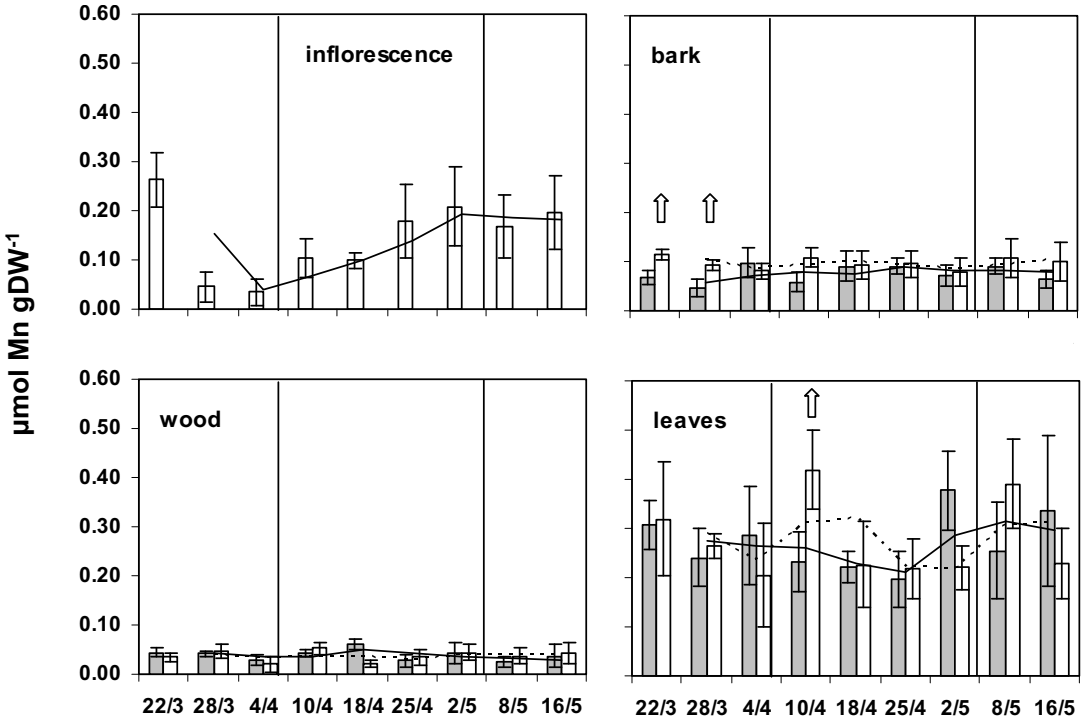

Fig. 6 Time-course of manganese content of bark, wood, and leaves of reproductive (white columns) and vegetative (grey columns) shoots during inflorescence development, along with the fluctuations in the inflorescence Mn content. Bars indicate standard deviation. Arrows indicate statistically significant differences (p=0.05). The first 3 weeks were devoted to inflorescence elongation (IEP), the next 4 weeks to flower development (FDP) and the last 2 ones to flower fertilization (FFP) period.

content was the highest at the 1st week (phase A), and the lowest one at the 2nd week, then increased progressively for the next 3 weeks (phase B) and stabilised from the 6th week onwards (phase C). The stabilised levels were comparable with that of the 1st week. Inflorescence development characterised by the following three mean values of Zn content: 0.15-0.07-0.13 µmol gDW^{-1} during phase A, B, and C respectively. In the other tissues Zn content fluctuated around 0.03 and 0.09 µmol gDW^{-1} in the bark of VS and of RS, 0.03 and 0.06 µmol gDW^{-1} in the wood of VS and of RS, 0.08 and 0.06 µmol gDW^{-1} in the leaves of VS and of RS respectively during the inflorescence development. Several significant differences characterised Zn content in the various tissues of RS during inflorescence development. The tissues that did not present significant differences were wood throughout FDP and FFP, and both bark and leaves in the mid FDP. When a difference appeared, bark and wood presented increases, whilst leaves decrease (**Fig. 4**).

With regard to Fe, inflorescence development characterised by the following three mean values of iron content: 1.24-0.38-1.26 µmol gDW^{-1} during phase A, B, and C, respectively. In the other tissues Fe content fluctuated around

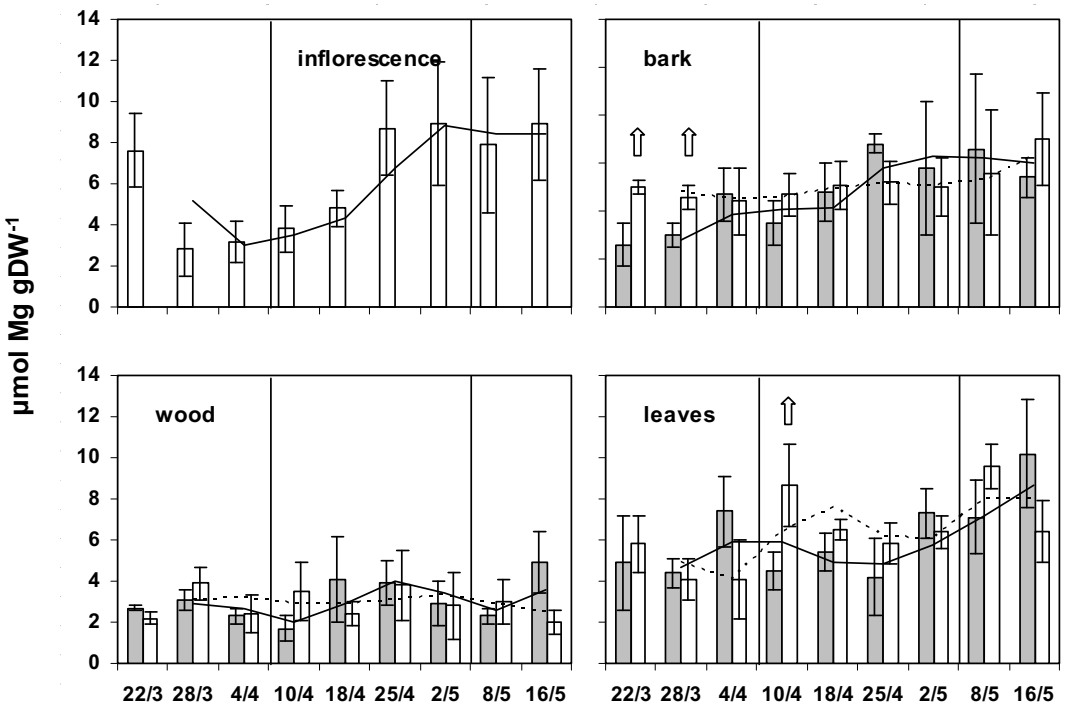

Fig. 7 Time-course of magnesium content of bark, wood, and leaves of reproductive (white columns) and vegetative (grey columns) shoots during inflorescence development, along with the fluctuations in the inflorescence Mg content. Bars indicate standard deviation. Arrows indicate statistically significant differences (p=0.05). The first 3 weeks were devoted to inflorescence elongation (IEP), the next 4 weeks to flower development (FDP) and the last 2 ones to flower fertilization (FFP) period.

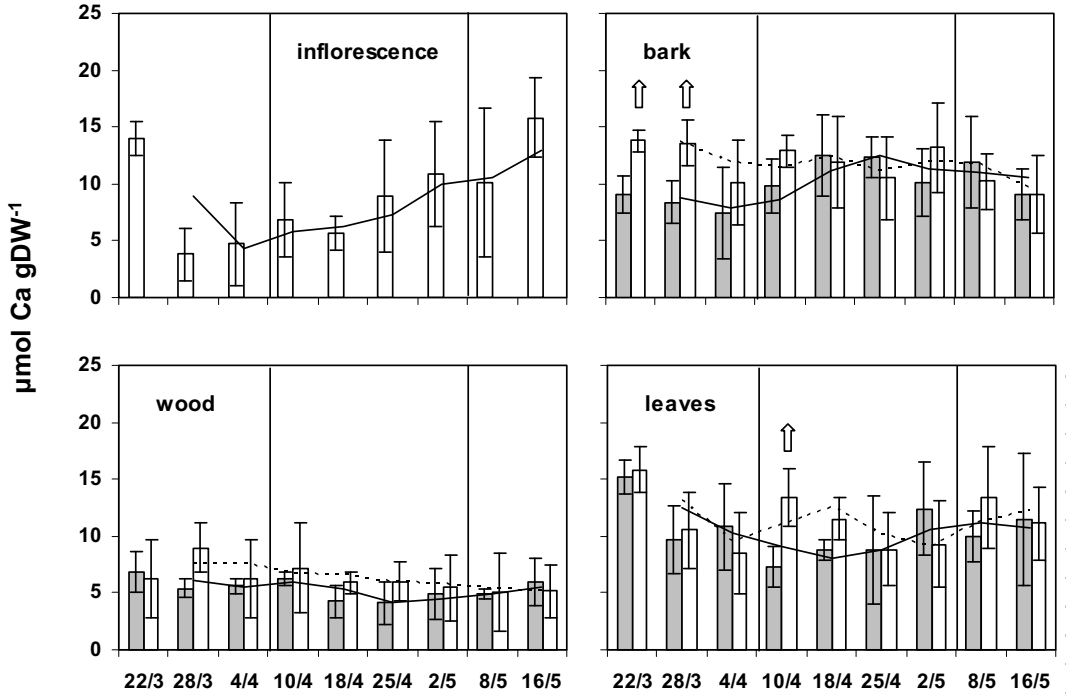

Fig. 8 Time-course of calcium content of bark, wood, and leaves of reproductive (white columns) and vegetative (grey columns) shoots during inflorescence development, along with the fluctuations in the inflorescence Ca content. Bars indicate standard deviation. Arrows indicate statistically significant differences (p=0.05). The first 3 weeks were devoted to inflorescence elongation (IEP), the next 4 weeks to flower development (FDP) and the last 2 ones to flower fertilization (FFP) period.

0.45 and 0.71 μmol gDW^{-1} in the bark of VS and of RS, 0.17 and 0.21 μmol gDW^{-1} in the wood of VS and of RS, 0.71 and 0.84 μmol gDW^{-1} in the leaves of VS and of RS respectively during the inflorescence development. Wood presented much lower Fe content compared with leaves and bark. Significant changes were located in the bark during IEP and half FDP, and in leaves in early FDP (**Fig. 5**). Manganese content during inflorescence development reached 0.26-0.07-0.19 μmol gDW^{-1} during phase A, B, and C respectively. In the other tissues Mn content fluctuated around 0.08 and 0.10 μmol gDW^{-1} in the bark of VS and of RS, 0.04 and 0.04 μmol gDW^{-1} in the wood of VS and of RS, 0.27 and 0.28 μmol gDW^{-1} in the leaves of VS and of RS respectively during the inflorescence development (**Fig. 6**).

The mean values of Mg content during inflorescence development were 7.6-3.6-8.6 μmol gDW^{-1} during phases A, B, and C, respectively. In the other tissues Mg content fluctuated around 4.8 and 5.2 μmol gDW^{-1} in the bark of VS and of RS, 3.1 and 2.9 μmol gDW^{-1} in the wood of VS and of RS, 6.2 and 6.4 μmol gDW^{-1} in the leaves of VS and of RS respectively during the inflorescence development (**Fig. 7**). With regard to Ca, inflorescence development characterised by the following three mean values of Ca content: 14-5.2-11.4 μmol gDW^{-1} during phases A, B, and C, respectively. In the other tissues Ca content fluctuated around 10.1 and 11.7 μmol gDW^{-1} in the bark of VS and of RS, 5.4 and 6.3 μmol gDW^{-1} in the wood of VS and of RS, 10.5 and 11.4 μmol gDW^{-1} in the leaves of VS and of RS respectively during the inflorescence development (**Fig. 8**). Mn, Mg, and Ca presented statistically significant increases in bark during the 1st and 2nd week, and in the leaves of RS during the 4th week.

DISCUSSION

Nutrient content dynamics during inflorescence development could be distinguished in two groups. The 1st group includes Cu, P and K, where a stable content was found throughout the period of inflorescence development. The 2nd group includes Zn, Fe, Mg, Ca and Mn, with the same pattern, briefly the highest nutrient content during the first week, the lowest one during the second week, followed by an increase up to the 5th week where it stabilised until the end of the inflorescence development period.

In this context and taking under consideration the quantitative approach of the described perturbations summarised in **Table 2**, the above results provide clear evidence that the inflorescence development affected the nutritional status of the reproductive shoots in a differential manner. Moreover, each stage of inflorescence development presented a differential effect on the nutritional status of RS. A strong influence was found for Zn and Cu contents in bark, wood and leaves, as well as Fe in bark of RS. Weak influence presented P in bark, wood and leaves, K in leaves, and Mg in bark of RS.

Analysing further the existing differences in the nutrition dynamics of each tissue, the following patterns were found: In the bark of RS K presented no differences. During FDP only Zn, Cu, and Fe changed level, while during FFD only Zn altered. In the wood of RS Fe, Mn, Mg, and Ca presented no differences. Differences during IEP presented Zn and Cu, during FDP only P whilst K in both IEP and FDP. No nutrient level altered in the wood of RS during FFP. In the leaves of RS the increase in the content of Cu, Zn, Fe, Mn, Mg, and Ca during the 4th week of inflorescence development was indeed a characteristic one, whilst 2 weeks before full bloom P content was significantly lower. Potassium in leaves presented no changes. In bark, increases only in nutrient levels were observed, whilst in wood and leaves decreases also took place. The picture that emerges could be marked by wood K content. A decrease in K content in the wood is characteristic during IEP and most of the FDP, while this is not the case one week before, during and after full bloom.

At day 16 from floral bud burst, inflorescence is characterised by a minimum content in Zn, Fe, Mn, Mg, and Ca. A general increase in P, Cu, Zn, Fe, Mn, Mg, and Ca content of bark and in Cu, and Zn content of wood took place, whilst a decrease in Zn content of leaves was observed. After day 16 and for the next four weeks the levels of these nutrients in inflorescence were found to increase steadily. In the transition from IEP to FDP at day 29, wood was characterised by decreased K, while bark by increased Cu, Zn, and Fe and leaves by increased Cu, Zn, Fe, Mn, Mg, and Ca contents. The increase in the content of these six elements is the definite characteristic of the transition to FDP. At day 52, inflorescence was characterised by restored maximum contents of Zn, Fe, Mn, Mg, and Ca. RS presented no changes in the nutrient contents of wood. Only Zn content found to be altered during FFP increased in bark and decreased in leaves.

Based on data published for the 'Konservolia' cultivar (Kitsaki *et al*. 1995; Kitsaki *et al*. 1999), the above highlighted developmental points seem to be in accordance with the peaks reported for respiration rate, ethylene production rate and ABA contents. In 'Konservolia', early in FDP respiration rate and ethylene production and ABA content were high. In contrast, one week before full bloom respiration rate and ethylene production were minimised, with high ABA content. It could be suggested that the characteristic nutrient fluctuations may be driven by this hormonal combination, or contribute to the physiological shift from the one period to the other.

We could hardly distinguish leaves collected from RS, based only on Zn content, despite of its perturbations during most of the period. Instead, RS could be distinguished from VS by means of the nutritional status of their bark, based on the conbined analysis of its Zn and Cu content.

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