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A NOVEL METHODOLOGY FOR FERTILISATION STRATEGIES: EXAMPLE OF BORON UPTAKE AND ACCUMULATION IN *CAMELLIA OLEIFERA*

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Boron deficiency is widespread in *Camellia oleifera*, which is an economically important plant in China. However, little information is available on the uptake, translocation and accumulation of boron in *C. oleifera*. The translocation of boron in *C. oleifera* was investigated for the first time in this study. In order to study the dynamic changes in mineral nutrition within plants in-situ, we established biomass models of various *C. oleifera* components and performed a 13-month follow-up study on *C. oleifera* boron concentrations. The uptake of boron peaked from June till October, and boron mainly accumulated in the fruits and leaves. Boron translocation only occurred from other plant parts towards the fruits. A small amount of translocation occurred during fruit set in March and a larger rate occurred during fruit maturation period. Roots were the first structure to respond to boron uptake and translocation in *C. oleifera*. The results suggested that boron applications to *C. oleifera* plantation should be at least 258 mg tree^{-1} year^{-1} (637 g ha^{-1} year^{-1}), and they should be applied from early June till October. The method used here, which combines biomass models and nutrient concentrations, represents a nondestructive methodology that has potential for use in further in-situ studies of dynamic nutrient changes of whole plants as well as for research conducted over longer time periods.

Keywords: Micronutrient, boron concentration, boron deficiency, fertiliser, biomass

INTRODUCTION

Camellia oleifera is an economically important evergreen shrub/small tree in China. Approximately 4 million ha of *C. oleifera* plantations are distributed in southern China, making it the largest hectarage in the world, although a smaller distribution is observed in South-East Asia. Cultivation of *C. oleifera* is pivotal in alleviating conflicts over edible oil supply in China, and it increases the income of farmers and protects the environment. In commercial plant production, sufficient boron supply is important for increasing yield (Khayyat et al. 2007, Wójcik et al. 2008), fruit quality, crop storability (Wójcik et al. 2008) and stress tolerance (Cakmak & Römheld 1997). Boron deficiency causes a loss in apical dominance of trees and leads to lower quality sawn timber which reduces yield. Reproductive structures have higher requirement for boron than vegetative structures and the movement of boron to reproductive structures may be restricted in certain plants (Dell & Huang 1997). *Camellia oleifera* fruit crops are sensitive to boron deficiency, and low yields are widespread in areas where boron deficiency occurs. Boron fertiliser has varying effects depending on its quantity, method and application period. Thus, a better understanding of the uptake, translocation and accumulation of boron in *C. oleifera* is important for developing a sound fertilisation programme.

Boron was once assumed to be one of the most immobile plant nutrients. However, boron mobility has been demonstrated in certain plants such as canola (Stangoulis et al. 2001), sunflower (Matoh & Ochiai 2005) and white lupin (Huang et al. 2008). Boron mobility has been shown to increase with lower boron status in several species, including coffee (Leite et al. 2007) and olive trees (Liakopoulos et al. 2009). In the field, foliar boron concentrations remain stable in Scots pine during dormancy (Helmisaari 1990, 1992), and boron mobility from the leaves to the flowers and fruit has been demonstrated in apples, prunes, pears (Hanson 1991) and olive trees (Delgado et al. 1994). Boron was particularly mobile in tree species that use sorbitol as major carbohydrate such as *Malus* and *Pyrus* species (Brown & Hu 1996). However, boron mobility was not as closely related to the presence of polyols as expected, and it appears that, to some degree, remobilisation occurs in many plant species (Lehto et al. 2004b). There is considerable translocation of boron from mature to growing leaves in tea (*Camellia sinensis*) despite lacking polyol compounds (Hajiboland et al. 2013). The processes of translocation vary depending on the season. Shoot extension growth in boreal conifers occurs within a relatively short period, and the buds burst when both stomatal conductance and nutrient uptake are limited by low soil temperatures (Domisch et al. 2002). In Norway spruce, boron mobility has been observed from other parts towards new growth in spring (Lehto et al. 2004a).

Although the boron isotope tracer method is available, investigating mineral nutrition variations within plants in-situ in different periods remains difficult. Further studies on whole plants conducted over longer time periods are needed to assess the quantitative importance of boron mobility (Lehto et al. 2004a). For other nutrients, small number of tree samples (< 10 stems) have been used to determine the mineral nutrients required throughout the growth period which resulted in significant inter-tree variation (Hristovski et al. 2008, Cao et al. 2012a, b). To improve the experimental accuracy and enlarge the sample size without using destructive methods, a novel sampling method must be designed.

In this paper, two experiments were conducted: biomass models of various *C. oleifera* components were established and a 13-month follow-up study on year-round variation in boron concentrations in various *C. oleifera* plant parts was performed. Establishing the biomass models permitted in-situ investigations of the year-round variation in biomass. In addition to the year-round variation in boron concentration in various plant parts, we also determined the year-round variation in boron uptake and accumulation. The objectives of this study were to (1) introduce a novel nondestructive methodology for studying the dynamic changes in mineral nutrition within plants in-situ, (2) investigate the annual pattern in boron uptake, translocation and accumulation within *C. oleifera*, and (3) offer suggestions for the application of fertiliser to *C. oleifera*.

MATERIALS AND METHODS

Sampling site

Sampling sites were located in Pingyuan County, Guangdong Province, south China. The study was conducted in a 7-year-old plantation of *C. oleifera*, which was planted at a spacing of 2 m × 2 m. The plantation presented a survival rate of 95% and had a 6.12 ± 1.87 cm mean basal diameter (0.3 m above ground) and 2.83 ± 0.56 m mean tree height. Characteristics of the site and sampling times are listed in Table 1. The experimental flow is summarised in Figure 1.

Table 1 Climate, forest conditions, soil physical and chemical properties of the study region and phenology of *Camellia oleifera*

Site		
	Longitude	115° 43'–116° 07' E
	Latitude	24° 23'–24° 56' N
	Temperature	21.7 °C
	Rainfall	1637 mm
	Sunshine	1873 hours year^{-1}
	Frost-free	320 days year^{-1}
Stand		
	Age	7 years
	Area	200 ha^{2}
	Spacing	2 m × 2 m
	Survival	95 %
	Diameter	6.12 ± 1.87 cm
	Height	2.83 ± 0.56 m
Soil		
	Soil bulk density	1.4 g cm^{-3}
	Organic matter	2.2 mg kg^{-1}
	Available N	14.1 mg kg^{-1}
	Available P	3.3 mg kg^{-1}
	Available K	29.7 mg kg^{-1}
	Available B	0.16 mg kg^{-1}
Phenology		
	Dec–Feb	Dormancy
	Mar–May	Shooting and fruit set
	Jun–Jul	Vigorous growth
	Aug–Nov	Fruit maturation

Diameter and tree height are each presented as mean ± standard deviation

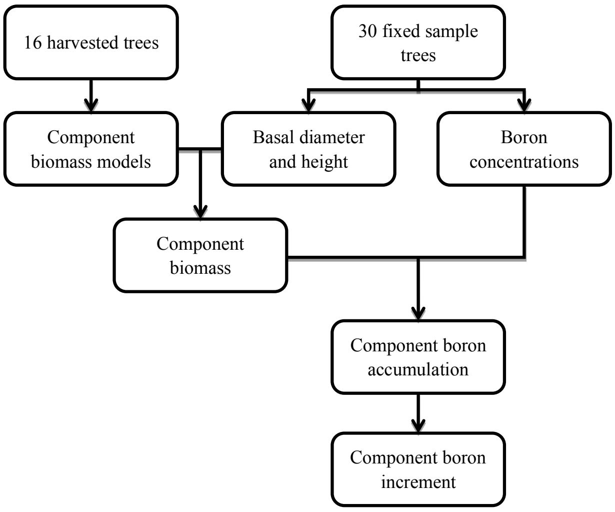


Figure 1 Experimental work flow for this study

Biomass models

Three 600 m^2 *C. oleifera* forest sample plots were selected for the measurements. In these plots, 16 trees planted along pathways designed in the south and west directions were selected for biomass investigation. Basal diameter and tree height of the 16 harvested trees were 6.48 ± 1.16 cm and 2.35 ± 0.42 m respectively. Aboveground vegetation was separated into trunks, branches and leaves. The underground parts (tap roots, roots and fine roots > 5 mm) were excavated for fresh weight measurements conducted in the field using scales with 50 kg capacity. After fresh weight measurement of the components, three 5-cm thick discs and approximately 1 kg of branch, leaf and root samples were collected randomly from all sides of the tree. Fresh weights of all samples were measured.

The samples of various components were oven dried at 65 °C to constant weight for 48 hours. The dried samples were weighed and biomass of various components of the 16 sampled trees was calculated. The relationships between biomass of the various components and tree measurement parameters were established to estimate the biomass of various tree components (Durkaya et al. 2013). Biomass models of the components were established (Table 2).

Table 2 Biomass models of various components of *Camellia oleifera*

Component	Regression equation	Correlation coefficient	p-value
Leaf	$W = 0.0617\ (D^2H)^{0.9017}$	0.88	< 0.01
Branch	$W = 0.1272\ (D^2H)^{0.6233}$	0.87	< 0.01
Trunk	$W = 0.0854\ (D^2H)^{0.8412}$	0.91	< 0.01
Root	$W = 0.2151\ (D^2H)^{0.6026}$	0.89	< 0.01

W = biomass, D = diameter (cm), H = height (m)

Boron concentrations

Due to the interlinked vascular system and similar function of the trunk and branches, we selected boron concentration of the branches as representative of the trunk because monthly trunk sampling for the boron concentration determination would have been destructive to the plants. We selected 30 *C. oleifera* trees along the south and west directions of the orchard as fixed sampling trees. In each tree, 20 leaves, 5 fruits and approximately 50 g of branches and roots (roots and fine roots) were collected from the east, west, south and north directions and stored in sealed bags. Bulk samples from the 30 trees were cleaned with distilled water, air dried and then oven dried at 65 °C to constant weight for 48 hours. Dried samples were grated and sieved to determine boron concentrations using the curcumin colorimetric method (Silverman & Trego 1953). The experiment was conducted in the middle of each month between December 2013 and December 2014 (Table 3). The formulae used in the study were:

(1) Component boron accumulation (mg) = component boron concentration (mg kg^{-1}) × component biomass (kg)

(2) Boron accumulation per tree (mg $tree^{-1}$) = Σ (component boron accumulation) (mg $tree^{-1}$)

(3) Boron accumulation per hectare (mg ha^{-1}) = boron accumulation per tree (mg $tree^{-1}$) × number of trees per hectare (trees ha^{-1})

(4) Number of trees per hectare (trees ha^{-1}) = 51 × 51 × 95% (spacing 2 m × 2 m and approximately 95% for the survival rate) ≈ 2471 (trees ha^{-1})

Statistical analysis

Mean values and standard deviations were calculated and analysed. Equations for calculations and graphs for plotting were generated using Microsoft Excel 2010 and a regression analysis was employed using the data processing software SPSS 17.0 (2008).

RESULTS

Biomass

The biomass of 16 sampled trees was 4.10 ± 1.79 kg for leaves, 2.27 ± 0.69 kg for branches, 4.22 ± 1.56 kg for trunk, 3.48 ± 1.10 kg for roots and 6.85 ± 1.83 kg for fruit. In addition to the fruits, correlations were observed between height, diameter and biomass of the leaves, branches, trunk and roots (Table 2).

Boron concentration

Annual patterns of boron concentrations in the leaves and branches and trunk were synchronous and could be roughly divided into three stages: stable (December–February), decreasing (March–May) and increasing (June–October) (Figure 2). Roots had slight inflection points, i.e. the values were stable in December–February, decreased in March–April, increased in May–August and decreased in September–November. For the fruit, the trend increased in March, decreased in April–May and increased in June–October.

Boron accumulation

Since biomass model for the fruit was not available in this study, its biomass can only be obtained after the harvest in October. Patterns of boron accumulation for the various components and the tree (excluding fruits) were stable from December till May and showed a small decline in March, a marked increase from June till October and a decline in November. Boron accumulation in the roots increased in May and decreased in September (Figure 3).

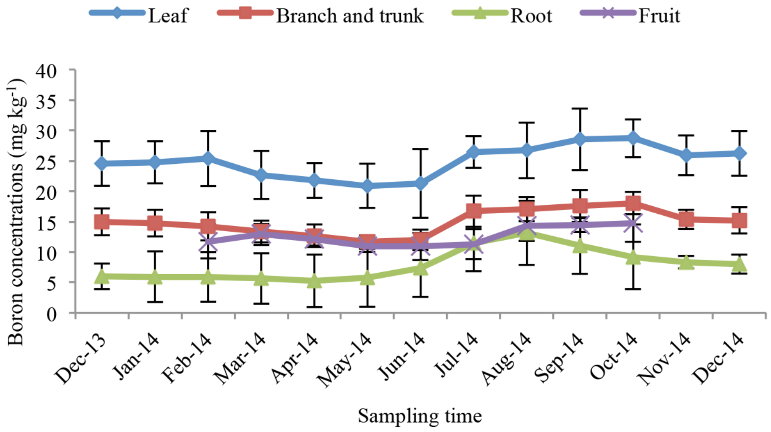


Figure 2 Annual patterns of the boron concentration in *Camellia oleifera* plant parts; fruiting period spans from February till October; values are means ± standard deviations

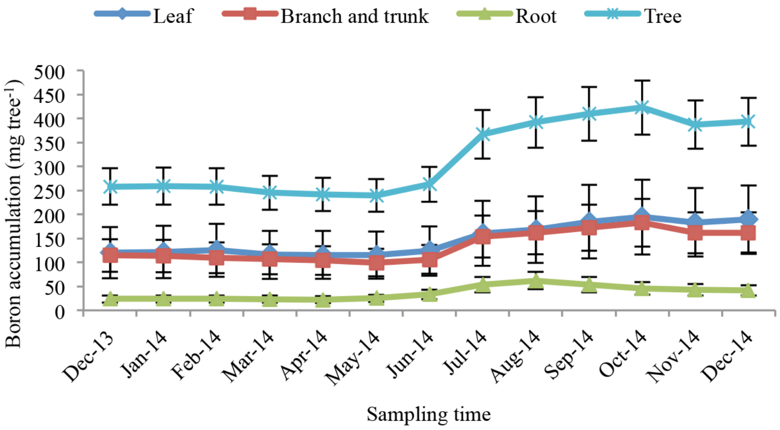


Figure 3 Annual patterns of boron accumulation in the *Camellia oleifera* plant parts and accumulation in the whole tree (excluding fruits); values are means ± standard deviations

Table 3 Year-round variation in basal diameter, height and boron of the 30 fixed sampling *Camellia oleifera* trees

Sampling time (Month-year)	Basal diameter (cm)	Height (m)	Biomass (kg tree^{-1})					B concentration (mg kg^{-1})				B accumulation (mg tree^{-1})			
			Leaf	Branch	Trunk	Root	Fruit	Leaf	Branch and trunk	Root	Fruit	Leaf	Branch and trunk	Root	Fruit
Dec-13	6.64 ± 1.19	2.88 ± 0.21	4.87 ± 2.13	2.60 ± 0.86	5.03 ± 2.27	3.99 ± 1.28	0	24.55 ± 3.65	14.97 ± 2.21	5.95 ± 2.12	0	119.81 ± 36.26	114.43 ± 29.65	23.77 ± 6.59	0
Jan-14	6.66 ± 1.23	2.89 ± 0.20	4.91 ± 2.19	2.62 ± 0.87	5.06 ± 2.30	4.00 ± 1.29	0	24.79 ± 3.48	14.75 ± 2.17	5.94 ± 4.19	0	121.74 ± 34.74	113.42 ± 31.21	23.80 ± 6.75	0
Feb-14	6.71 ± 1.13	2.90 ± 0.22	4.92 ± 2.17	2.62 ± 0.86	5.08 ± 2.27	4.01 ± 1.27	NA	25.38 ± 4.50	14.21 ± 2.29	5.92 ± 4.10	13.69 ± 2.80	125.04 ± 35.30	109.54 ± 20.64	23.78 ± 7.19	NA
Mar-14	6.78 ± 1.18	2.91 ± 0.23	5.10 ± 2.22	2.69 ± 0.88	5.25 ± 2.32	4.11 ± 1.29	NA	22.67 ± 3.95	13.38 ± 1.81	5.66 ± 4.15	12.90 ± 1.73	115.79 ± 37.51	106.31 ± 29.76	23.27 ± 5.47	NA
Apr-14	6.93 ± 1.16	2.94 ± 0.24	5.30 ± 2.28	2.76 ± 0.88	5.44 ± 2.37	4.22 ± 1.30	NA	21.79 ± 2.89	12.67 ± 1.86	5.25 ± 4.32	10.58 ± 1.01	115.61 ± 33.24	104.06 ± 28.54	22.16 ± 4.88	NA
May-14	7.03 ± 1.22	2.95 ± 0.18	5.52 ± 2.33	2.84 ± 0.90	5.65 ± 2.44	4.33 ± 1.33	NA	20.86 ± 3.63	11.68 ± 1.10	5.75 ± 4.76	9.90 ± 0.88	115.31 ± 33.43	99.33 ± 33.18	24.95 ± 6.64	NA
Jun-14	7.17 ± 1.21	2.98 ± 0.19	5.80 ± 2.43	2.94 ± 0.92	5.92 ± 2.49	4.48 ± 1.34	NA	21.29 ± 5.66	11.98 ± 1.65	7.38 ± 4.75	10.90 ± 2.23	123.66 ± 37.51	106.28 ± 30.87	33.10 ± 6.89	NA
Jul-14	7.33 ± 1.29	3.01 ± 0.21	6.06 ± 2.53	3.03 ± 0.94	6.16 ± 2.60	4.61 ± 1.38	NA	26.46 ± 2.60	16.70 ± 2.55	11.51 ± 4.71	11.29 ± 2.45	160.34 ± 46.49	153.60 ± 38.67	53.11 ± 15.34	NA
Aug-14	7.45 ± 1.26	3.03 ± 0.24	6.28 ± 2.58	3.10 ± 0.95	6.37 ± 2.63	4.72 ± 1.39	NA	26.73 ± 4.59	17.06 ± 2.04	13.18 ± 5.29	13.83 ± 2.48	167.92 ± 44.36	161.75 ± 39.96	62.29 ± 17.67	NA
Sep-14	7.56 ± 1.24	3.05 ± 0.23	6.48 ± 2.69	3.17 ± 0.97	6.57 ± 2.72	4.82 ± 1.42	NA	28.51 ± 5.06	17.62 ± 2.64	11.03 ± 4.66	13.84 ± 1.14	185.00 ± 53.65	171.77 ± 34.22	53.24 ± 14.87	NA
Oct-14	7.67 ± 1.27	3.08 ± 0.25	6.77 ± 2.92	3.27 ± 0.96	6.84 ± 2.74	4.97 ± 1.43	8.94 ± 3.36	28.72 ± 3.11	18.03 ± 1.86	9.18 ± 5.30	13.73 ± 3.04	194.62 ± 48.96	182.38 ± 39.20	45.61 ± 12.32	122.8 ± 25.32
Nov-14	7.73 ± 1.22	3.11 ± 0.20	7.07 ± 2.96	3.37 ± 0.97	7.12 ± 2.77	5.11 ± 1.42	0	25.90 ± 3.27	15.40 ± 1.58	8.34 ± 1.04	0	183.18 ± 50.34	161.62 ± 32.76	42.68 ± 10.76	0
Dec-14	7.79 ± 1.11	3.12 ± 0.21	7.21 ± 2.92	3.41 ± 0.95	7.25 ± 2.74	5.18 ± 1.42	0	26.23 ± 3.66	15.20 ± 2.19	8.04 ± 1.57	0	189.22 ± 47.26	162.23 ± 30.89	41.67 ± 9.89	0

The biomass of various components was obtained by the corresponding biomass models in Table 2, fruit biomass was obtained after the harvest in October; results are presented as means ± standard deviations, NA = not available

Monthly difference in boron accumulation

In October 2014, fruits of the 30 fixed sample trees were harvested and mean biomass of the fruits per tree was obtained (Table 3). By combining these data with the fruit boron concentration in October, we obtained the boron increment of the fruit (Table 4). The monthly difference in the boron accumulation was the difference between value of the particular month and that of the immediately preceding month. Differences in boron accumulation in the various plant parts are shown in Figure 4. Initially, the differences in boron accumulation in the tree remained small, i.e. from December till May. Its value declined slightly in March but had positive values from June till October. Negative values were observed again in November. The order of the differences in boron accumulation of the *C. oleifera* plant parts was: fruits > leaves > branches and trunk > roots. The fruits and leaves accounted for more than 70% of the total boron increase (Table 4).

DISCUSSION

Nondestructive sampling methodology

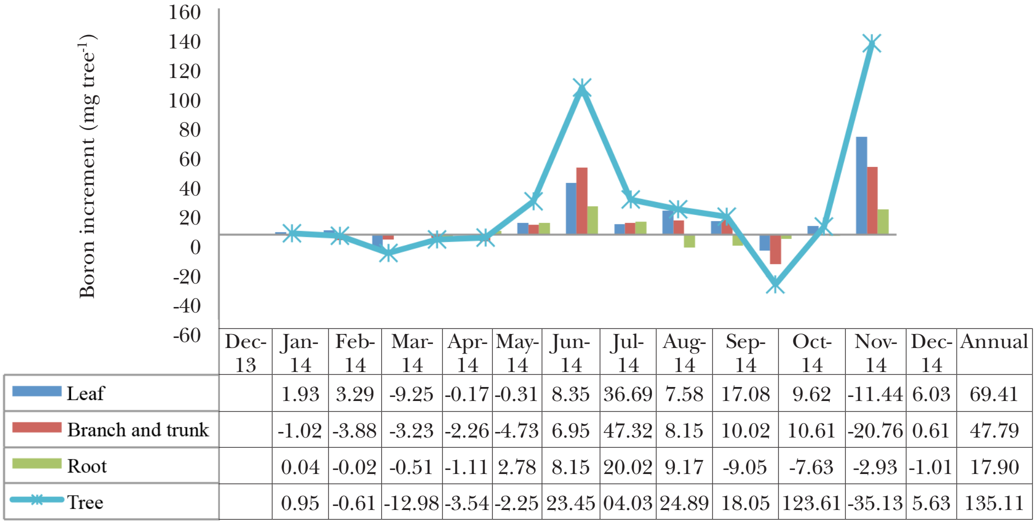
In this study, biomass models were applied to determine the *C. oleifera* component biomass for every month. We were able to trace the boron uptake and accumulation in various *C. oleifera* components. However, trunk sampling was difficult and was a limitation in this study. Despite this challenge, the biomass model is a potential nondestructive sampling methodology that can be used for further nutrient studies on whole plants and for research conducted over long time periods.

Boron uptake, translocation and accumulation

Accumulation and increment of boron in the tree were stable from December till May and showed a modest decline in March (Figures 3 and 4). Boron concentrations decreased from March till May in the leaves and branches, from

Table 4 Rate of boron accumulation in various components of *Camellia oleifera*

Boron accumulation	Component				
	Leaf	Branch and trunk	Root	Fruit	Total
Boron rate (mg tree^{-1} year^{-1})	69.4	47.8	17.9	122.8	257.9
Boron rate (g ha^{-1} year^{-1})	171.5	118.1	44.2	303.3	637.2
Proportion (%)	26.9	18.5	7.0	47.6	100.0



	Dec-13	Jan-14	Feb-14	Mar-14	Apr-14	May-14	Jun-14	Jul-14	Aug-14	Sep-14	Oct-14	Nov-14	Dec-14	Annual
🟦 Leaf		1.93	3.29	-9.25	-0.17	-0.31	8.35	36.69	7.58	17.08	9.62	-11.44	6.03	69.41
🟥 Branch and trunk		-1.02	-3.88	-3.23	-2.26	-4.73	6.95	47.32	8.15	10.02	10.61	-20.76	0.61	47.79
🟩 Root		0.04	-0.02	-0.51	-1.11	2.78	8.15	20.02	9.17	-9.05	-7.63	-2.93	-1.01	17.90
✱ Tree		0.95	-0.61	-12.98	-3.54	-2.25	23.45	04.03	24.89	18.05	123.61	-35.13	5.63	135.11

Figure 4 Patterns of monthly differences in the boron accumulation of the *Camellia oleifera* plant parts and whole tree (excluding fruits); a positive number denotes an increase and a negative number denotes a decrease in boron accumulation

March till April in the roots and from April till May in the fruit. This trend can be attributed to the increased biomass of the components in the shooting and fruit set periods. These findings indicated that little boron uptake occurred in *C. oleifera* from December till May. Similar results were obtained for foliar boron concentrations in Scots pine during dormancy (Helmisaari 1990, 1992). Nutrient uptake may be limited by low soil temperatures (Domisch et al. 2002).

The small decline of boron accumulation in March may be explained by the increased boron concentration in the fruits. Thus, boron could be translocated from leaves, branches and roots towards the fruits during the fruit set period in March, and this behaviour was also observed in olive trees during flowering (Delgado et al. 1994) and Norway spruce in spring (Lehto et al. 2004a). Limited boron uptake and modest boron translocation (10.5% of total boron accumulation in the fruits) towards the fruit occurred in *C. oleifera* during fruit set period in March (Figure 3).

Boron concentration and accumulation in *C. oleifera* components increased markedly from June till October because of the vigorous growth and fruit maturation period of the tree. Peak boron uptake was likely enhanced because of the higher soil temperature and the increased transpiration (Domisch et al. 2002). A similar uptake peak was also observed for phosphorus in *C. oleifera* (Cao et al. 2012a). In the roots, boron concentration inflection points occurred earlier (Figure 2) and there was increased accumulation in May (Figure 3) and decreased accumulation in September compared with the patterns of the leaves and branches. The earlier increase in the inflection point of boron in the roots in May is related to the root physiological function because root tips are the starting point of mineral nutrient uptake. The earlier decrease in the inflection point of boron in the roots in September could be attributed to boron translocation towards the fruits at the beginning of the fruit maturation period. In contrast, there were no inflections in other *C. oleifera* components until November. Thus, the root was the first structure to respond to changes in boron conditions in *C. oleifera*. This result was consistent with boron deficiency symptoms which occurred first in meristematic tissues of the roots (Dell & Huang 1997) as well as with reduction in number of root tips (Möttönen et al. 2001a, b) and root dry weight (Räisänen et al. 2007) in other plants.

Boron increment of the trunk, branches, leaves and tree (excluding fruits) was negative in November (Figure 4). This indicated a large increase in boron translocation (28.6% of total boron accumulation of the fruits) from other components towards the fruits during fruit maturation period in October, especially from the root. This result was also observed for potassium (Cao et al. 2012a) and manganese in *C. oleifera* (Cao et al. 2012b). About 20 to 35% of boron content in the new parts of orange trees come from plant reserves (Boaretto et al. 2008). In the field, when boron was sprayed once on the leaves, about 4% of the fruit boron was derived from the foliar fertiliser (Leite et al. 2007). The previously acquired boron in the shoot was recirculated to the root via the phloem before being transferred into the xylem in the root and transported via the xylem to the shoot. In addition, some previously acquired boron in the leaves may have been translocated into the rapidly growing inflorescence (Huang et al. 2008). Boron was particularly mobile in trees such as apples, prunes and pears which use sorbitol as major carbohydrate (Brown & Hu 1996). However, in tea (*Camellia sinensis*), considerable translocation of boron occur from mature to growing leaves despite lacking polyol compounds (Hajiboland et al. 2013). Since translocation of boron in *C. oleifera* was investigated for the first time in this study, results of C. *sinensis* could provide circumstantial evidence for the degree of boron mobility in *C. oleifera*. Boron mobility from the leaves to the flowers and fruits was also reported for olive trees (Delgado et al. 1994). As a woody oil species, boron translocation patterns of *C. oleifera* may be similar to those of olive trees. In coffee (Leite et al. 2007) and olive (Liakopoulos et al. 2009) trees, boron translocation increases with lower boron status.

Boron accumulated to a greater degree in the fruits and leaves compared with roots, branches and trunk (Table 4) because of the higher biomass increment in the former compared with the latter (Table 3). In addition, reproductive structures have higher requirement for boron than vegetative structures (Dell & Huang 1997, Wells et al. 2008).

Boron fertilisation

Concentration and accumulation of boron in *C. oleifera* components increased markedly between June and October, which is the time for highest boron uptake (Figure 4). Our study indicated that 258 mg $tree^{-1}$ $year^{-1}$ of boron and 2.3 g $tree^{-1}$ $year^{-1}$ of borax should be applied to 7-year-old *C. oleifera* stands, and these values are much less than those reported in production pilot studies which used 20 g $tree^{-1}$ $year^{-1}$ of borax for 5-year-old trees (Pan et al. 2003) and 4.5 g $tree^{-1}$ $year^{-1}$ for 10-year-old trees (Mei & Du 2014). These discrepancies could be related to the study conditions because studies conducted in the field are vulnerable to environmental impacts such as leaching, soil pH (Goldberg 1997), soil temperatures (Domisch et al. 2002) and soil moisture (Sutinen et al. 2006) which caused serious loss in boron fertiliser. The variations may have also resulted from differences in provenances and tree ages. Based on this study, we proposed that at least 258 mg $tree^{-1}$ $year^{-1}$ (637 g ha^{-1} $year^{-1}$) of boron be applied to *C. oleifera* orchards primarily from early June till October.

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