Seasonal dynamics of nutrients in leaves and xylem sap of coffee plants as related to different soil compartments

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Abstract

The northwestern province of Costa Rica is a marginal coffee growing area. At the onset of the rainy season low redox potentials probably induce the mobilization of soil Mn resulting in enhanced plant uptake of Mn. To test this hypothesis we monitored from April to the end of June 1995 the mobile Mn in the soil and nutrient and Mn concentrations in leaves and xylem sap of coffee plants. Every 2 weeks we took aggregate and bulk soil samples. The aggregates were mechanically separated into interior and exterior, air-dried and all soil samples were extracted with 1 M NH_4NO_3 . We also extracted the field moist soil with distilled water. In addition, the 3rd and the youngest pair of coffee leaves and xylem sap were sampled and analyzed. According to the results of leaf analyses the nutrient supply of the coffee plants in general seemed to be balanced. However, Mn concentrations of 223 mg kg^{-1} in the 3rd leaf pair at 18 April were above the optimum and the youngest leaves indicated Fe deficiency, but senescent leaves accumulated Fe and overcame the deficiency. Manganese concentrations in the xylem sap showed a pronounced maximum 2 weeks prior to a similar maximum of mobile Mn in the aggregate exterior. But in general the temporal variation of nutrient concentrations (especially Ca and Mg) in the plants are well correlated with the easily extractable nutrient concentrations in bulk soil. Probably due to its specific absorption and high rates of redistribution within the plant, K in the soil extracts did not correlate with plant concentrations. Element concentrations of youngest leaves could not be correlated with soil concentrations and are not considered to be an adequate tool for monitoring current nutrient uptake. Since plant element concentrations did not correlate with the aggregate interior, plants probably cannot use that nutrient source efficiently.

Introduction

The northwestern province of Costa Rica, Guanacaste, is a marginal coffee growing area. Guanacaste has a pronounced dry season from December to April (Janzen, 1991). The rainy season generally starts at the end of April with heavy rainstorms. The climatic conditions effect nutrient dynamics in the soil and plant growth. The soils of Guanacaste have high Mn contents (MAG, 1993) and since reduction processes at

the onset of the rainy season mobilize Mn, this element shows exceptional dynamics (Bundt et al., 1997).

The soils in this area generally have a high clay content and are well aggregated (MAG, 1993). Aggregation influences many physical, chemical and biological processes in soil (Augustin, 1992; Demuth and Hiltbold, 1993). Spatially differentiated rates of these processes result in small scale chemical heterogeneities (Horn, 1987, 1990; Wilcke, 1996).

Because of the strongly developed soil structure, only part of the soil body is accessible to plant roots. They tend not to penetrate the aggregates but to grow along their surface (Whiteley and Dexter, 1983). Since plant roots take up the nutrients from their immedi-

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ate adjacency (Claasen et al., 1981; Hendriks et al., 1981), the exterior of soil aggregates should contribute to plant nutrition, whereas nutrients in the interior are protected.

In standard analyses, the 3rd mature pair of leaves is sampled (Carvajal, 1984; Müller, 1966; Snoek, 1987). However, the element concentration of these leaves do not reflect the current nutrient uptake. Possibly, the youngest, still growing leaves may be a better parameter to monitor the current uptake (Hannam and Ohki, 1988; Loneragan, 1988). Dambrine et al. (1995) and Stark and Spitzner (1985), working on coniferous trees, found xylem sap adequate to characterize the nutrient uptake of plants.

The objectives of this study are (I) to assess the nutrient status of the studied coffee plants with emphasis on Mn, (II) to monitor the nutrient dynamics of xylem sap and leaves at the onset of the rainy season and (III) to evaluate the prognostic qualities of the aggregate fractions as compared to bulk soil with respect to the plant nutrient status.

Materials and methods

Study site

The study was conducted at the finca Loria, located at 600 m above sea level near Hojancha in the north-western province of Costa Rica, Guanacaste (Figure 1). Since 1989 the plot is covered with coffee (*Coffea arabica* L.) of the high yield variety Catuai. Between the coffee trees shade trees (*Cassia spp.* and *Inga spp.*) are planted at a distance of 5×5 m.

The mean annual temperature is 26°C and mean annual precipitation adds to 2500 mm, restricted to the months April–November.

The soil type is a *Typic Haplustalf* (Soil Survey Staff, 1994), whose eluvial horizon was probably eroded completely during the former use as pasture and groundcover-less coffee field. Some important properties are given in Table 1.

In May and August 250 kg ha^{-1} of the complete fertilizer 18-5-15-6-2 (N-P-K-Mg-B) are applied plus $250 \text{ kg ha}^{-1} \text{ NH}_4\text{NO}_3$ in November. Twice a year Cu, Zn and B are applied via atomization. The yield in 1993 was 53 Fa ha^{-1} (Fa = Fanega, 1 Fa = 45 kg coffee), in 1994 40 Fa ha^{-1} , which is about an average yield in Costa Rica. In general the coffee trees on the sampling plot seemed healthy. The flowering started

shortly before the first sampling date at 18 April 1995 and was finished completely at 16 May.

Sampling

The study started at 4 April 1995 and went through to 26 June. Soil samples were taken every 2 weeks from 18 April to 26 June. They consisted of aggregate and bulk soil samples and were taken in depths of 0–10 cm and 30–40 cm. The bulk soil was homogenized, sieved (2 mm) and air-dried.

The aggregates were separated manually into interior and exterior, using the method described by Kayser et al. (1994). This method combines rapid freezing with liquid N_2 and wet sieving. During the latter process the aggregate exterior disperses, falls through the sieve and is collected. After separation, aggregate interior and exterior were air-dried. Leaves were collected from randomly chosen trees and combined to 2 mixed samples. According to the standard procedure for coffee sampling (Carvajal, 1984; Snoek, 1987) we took the 3rd mature pair of leaves from the upper tree half from branches pointing into all directions. One sample consisted of 50 leaves, taken from 5 different trees. From the same plants we also took 50 young, still growing leaves. To remove dust and atomization residuals, all leaves were washed briefly with a mild detergent and rinsed with distilled water. The leaves were dried and ground to $<1 \text{ mm}$.

Xylem sap was collected using a pressure chamber (Scholander et al., 1965). At every sampling date we took 2 mixed samples, each containing ca. $300 \mu\text{L}$ xylem sap extracted from 1 branch each of 5 randomly chosen coffee trees. The xylem sap was extracted from 30 cm long branches, taken from the upper tree half and pointing in all directions. To prevent contamination with phloem sap, the bark was removed ca. 4 cm from the cut. The pressure on the chamber was increased slowly to 0.05 MPa above the plant water potential. At this pressure no contamination of xylem sap with cell fluids of ruptured cells takes place (Berger, 1988; Osonubi et al., 1988). The exuding xylem sap was collected with Pasteur pipettes and immediately frozen until analysis. We also measured the relative air humidity with a hair hygrometer.

Extractions and analyses

Two grams of the bulk soil and aggregate fractions were extracted by shaking end-over-end with 50 mL unbuffered $1 \text{ M NH}_4\text{NO}_3$ for 24 h (Zeien and Brümmer,

Figure 1. Location of the study site.

Table 1. Some properties of the studied soil

Hor.	Depth (cm)	Color	C _{org} (g kg ⁻¹)	pH		Structure ^a	Clay (%)	Sand (%)	Silt (%)	ECEC (mmol _c kg ⁻¹)	BS (%)	Mn _{tot} (mg kg ⁻¹)	Fe _{tot} (g kg ⁻¹)
				H ₂ O	KCl								
A1	0–11	7.5YR 4/6	39	4.8	4.0	Subangular blocky	76	4	19	123	93	1581	87.4
A2	11–35	5YR 3/4	37	5.7	4.5	Subangular to angular blocky	76	5	20	130	100	1620	87.5
2Bt	35–52	5YR 3/4	14	6.2	4.9	Angular blocky	80	3	17	111	100	1887	116.1

^aSoil survey division staff, 1993.

1989), to receive the Al, Ca, Fe, K, Mg, Mn, and Na fraction available to plants. Iron could not be measured in the NH₄NO₃ extract. Therefore, we extracted the easily reducible Fe fraction by shaking end-over-end with 50 mL 0.1 M NH₂OH–HCl + 1 M NH₄OAc at pH 6.0. After extraction we rinsed two times with 25 mL 1 M NH₄OAc (Zeien and Brümmer, 1989).

We additionally extracted the field moist bulk soil with distilled water at a soil to water ratio of 1 to 3. Each 200 mg of ground coffee leaves were digested with 2 mL HNO₃ (suprapur) at 170 °C for 4 h in a pressure chamber.

In all extracts we measured Al, Ca, Fe, K, Mg, Mn, and Na by atom absorption spectrometry (Varian AA 400). Elements in the xylem sap were measured by ICP (JY 70+). Total C and N were determined with the

C/N-Analyzer (Elementar Vario EL). The gravimetric water content was determined after drying subsamples at 105 °C.

Calculations and statistical analyses

All leaf concentrations are related to dry weight. Linear correlations were calculated using the least squares method (Hartung, 1989, p. 545). Calculations and statistical analysis were performed with STATISTICA for Windows 5.1 (Statsoft 1995). Due to the destructive sampling techniques we could not sample the same spots twice. Therefore, we assume that all samples are independent from each other.

Table 2. Leaf concentrations at 18 April 1995 and reference values for coffee (Carvajal, 1984; Snoek, 1987)

	N (g kg ⁻¹)	K (g kg ⁻¹)	Ca (g kg ⁻¹)	Mg (g kg ⁻¹)	Mn (mg kg ⁻¹)	Fe (mg kg ⁻¹)
3rd pair young leaves	25 29	22 19	13 10	4 4	223 172	215 53
High	>28	>27	>17	>3.5	>150	—
Medium	23–28	17–27	11–17	2–3.5	50–150	75–275
Low	2–2.3	10–17	8–11	1–2	25–50	<75

Results and discussion

Nutrient status of the coffee plants

To assess the nutrient status of the coffee trees at the start of the study, we show the nutrient concentrations of the leaves and comparative values from the literature for the 3rd pair of leaves in Table 2. The analysis of the 3rd pair of leaves show that the coffee plants were adequately supplied with nutrients. The concentrations of the major nutrients were in the optimum range. Mn only was well above that optimum. The young leaves showed high Mn concentrations as well, but could be slightly deficient in Fe as Müller (1966) quoted work describing Fe deficiency in youngest coffee leaves at a level of 67 mg kg⁻¹. Many of the young leaves showed chlorosis during growth, a typical symptom for Fe deficiency (Müller, 1966). These symptoms disappeared in the senescent leaves with increasing Fe accumulation. One reason for the low Fe concentrations in the young leaves could be a Fe–Mn antagonism (Carvajal, 1984; Mengel, 1984; Müller, 1966). Manganese induced Fe deficiency is caused by a disturbed Fe uptake and a competition or an imbalance on the cell level (Marschner, 1986).

Temporal dynamics of nutrient concentrations in the coffee plants

(a) 3rd pair of leaves

During the growing cycle the nutrient concentrations of the coffee leaves changed (Figure 2). The decrease of Ca, Fe, Mg, and Mn concentrations during the study are consistent with the results of other authors (Carvajal, 1984; Chinchilla, 1973; Müller, 1966).

Besides a decreasing nutrient uptake plus translocation within the plant, a 'dilution' due to an increase in leaf biomass is often discussed (Müller, 1966). However,

Figure 2. N, K, Ca, and Mg concentrations (a) as well as Mn and Fe concentrations (b) in the 3rd pair of leaves from 18 April to 26 June 1995.

we even found a decreasing 100-leaf-weight during the study. It decreased from 54 g at 18 April to 32 g at 12 June. The average was 40 g. Therefore, the decrease of any nutrient concentration in the coffee leaves was not caused by a 'dilution' due to higher leaf biomass.

Nitrogen normally shows a steep rise of the concentrations in leaves after the first rains and a slow decrease after the flowering. The rise is caused by a mineralization flush at the beginning of the rainy season (Birch, 1960) and by an improved uptake at the beginning of the new growth cycle (Carvajal, 1984).

To initiate new growth, only 10 mm of rain are necessary (Müller, 1966).

In contrast, the N concentrations of the coffee leaves in this study showed a slow but steady increase, even after the flowering was terminated. This indicates a high N supply during the whole study. Part of the rise may be explained by a concentrating effect brought about by the decreasing leaf mass. Mn and Fe showed a pronounced decrease after 3 May. Partly, this can be attributed to a decreased uptake (see concentrations in the xylem sap, Figure 5), partly it could be caused by the physiologically older age of the 3rd pair at 18 April and 3 May compared to the rest of the sampling dates. This phenomenon results from the regular growing pattern of coffee plants. In the rainy season *Coffea arabica* produces one new leaf pair every two weeks. This ensures that the sampled 3rd pairs always were of the same physiological age (Carvajal, 1984; Müller, 1966). In 1995 the rain started early. Two weeks before the beginning of the study it already rained ca. 30 mm (Coopepilangosta, pers. comm.). This means, that the 3rd leaf pair at 18 April and 3 May must have developed during the dry period, when growth is much slower if not totally restricted. Therefore, they were likely to be physiologically older and concentrations of elements that accumulate in mature leaves might be higher. Part of the decrease may also be caused by leaching from the leaves which we did not measure. As all sampled leaves had the same physiological age differences in the extent of leaching during the study period do not seem likely.

(b) Young leaves

In general, the young leaves showed similar nutrient dynamics as the 3rd leaf pair at the beginning of the rainy season (Figure 3). Manganese concentrations decreased sharply after the first sampling date. The high concentrations at 18 April 1995 are probably due to a high Mn uptake after a mineralization and reduction flush, initiated by the very first rains in 1995 at the beginning of April.

(c) Element concentrations in the xylem sap

We tried to reduce factors influencing the element concentrations in the xylem sap. These are (a) diurnal fluctuations (Berger, 1988; Stark and Spitzner, 1985), (b) the plant water potential (Berger, 1988; Osonubi et al., 1988), (c) the water content of the soil (Osonubi et al., 1988) and (d) the saturation deficit of the air (Berger, 1988).

Figure 3. N, K, Ca, and Mg concentrations (a) as well as Mn and Fe concentrations (b) in the young leaves from 18 April to 26 June 1995.

(a) We tried to overcome fluctuating element concentrations in the xylem sap in the course of the day by always sampling at dawn. This is also favorable, since the release of phloem sap into the xylem is smaller in the morning (Berger, 1988). Photosynthesis is at rest during the night and assimilates only rise to significant values with a few hours delay after daybreak.

(b) Osonubi et al. (1988), in contrast to Stark et al. (1989), found no dependence of element concentrations in the xylem sap on changes of the plant water potential between -0.2 and -1.2 MPa. During sampling the water potential of the coffee plants was -0.42 to -1.23 MPa, except for 3 May when the water potential was -0.05 MPa at a slight drizzle. We cannot exclude completely an influence of the water potential on the element concentrations in the xylem sap. However, we did not find a correlation either.

(c) Berger (1988) did not find a change of the element concentration in xylem sap after drying the soil slightly. In our study the gravimetric water content rose from 210 g kg⁻¹ to 540 g kg⁻¹ in the surface soil at 3 May. Then it changed only negligibly. Because of the minor changes in water content after 3 May, the element concentrations in the xylem sap could have

Figure 4. Correlation of the water content in the topsoil (a) and subsoil (b) with the plant water potential (each point represents one sampling date).

been influence by the soil water content at 18 April only.

However, there is a close negative correlation between soil water content and plant water potential (Figure 4). For the subsoil this correlation is significant ($r = -0.91$, $p < 0.05$), which means that the plants took up water from the depth 30–40 cm as well. We did not find any correlations between element concentrations in the subsoil extracts and the plants. Therefore, we focus on the topsoil, where the correlation between soil water content and plant water potential was slightly less pronounced ($r = -0.75$).

(d) According to Berger (1988), the element concentrations of the xylem sap increase as the saturation deficit of the air increases, when plants are shortly exposed to higher or lower water vapor pressures in controlled environment chambers. In the long run she could not find any changes at saturation deficits of 3–12 Pa kPa⁻¹. The water vapor deficit in our study ranged from 7 to 16 Pa kPa⁻¹. Again, we cannot rule out completely a slight influence on the element concentrations in the xylem sap.

We conclude, that the element concentrations in the xylem sap of the various sampling dates can be compared with each other. Figure 5 shows the temporal variations of element concentrations in the xylem sap.

Figure 5. Ca, Mg, and K concentrations (a) and Mn and Fe concentrations (b) in the xylem sap from 18 April to 26 June 1995.

Nitrogen was not measured since the emphasis was on metal ions.

Ca and Mg concentrations decreased after a maximum at the beginning of the study. In contrast to Ca and Mg, the K concentration did not decrease but fluctuated around 280 mg L⁻¹. K is an exception, because it is not only taken up passively but actively and selectively as well. It is also very mobile within the plant (Mengel, 1984).

Mn concentrations between 0.30 and 0.75 mg L⁻¹ were in the range measured by Osonubi et al. (1988) in *Picea abies* and by Stark et al. (1989) in *Pinus ponderosa* Laws. and *Pseudotsuga menziesii* (Mirb.) Franco from 0.1 to 4.4 mg L⁻¹. Comparative values for coffee do not exist. After a pronounced maximum at 3 May, the Mn concentrations in the xylem sap decreased. This can be caused by a lower supply in the root zone or by slower uptake rates (Aslander, 1958). In contrast, the Fe concentration in the xylem sap fluctuated but did not decrease. The higher Fe to Mn ratio in the xylem sap towards the end of the study may be attributed to the reduced impact of the Fe–Mn antagonism.

Correlations between the elements in the xylem sap

When comparing the element concentrations in the xylem sap with each other, one notices the strong cor-

Table 3. Coefficients of correlation of elements in the xylem sap ($n = 6$)

	Ca	Mg	K	Mn
Fe	-0.37	-0.09	-0.15	-0.38
Mn	0.98**	0.92*	0.11	
K	0.06	0.15		
Mg	0.87*			

* $p < 0.05$; ** $p < 0.01$.

Figure 6. Correlation of Mn (a, $r = 0.83^*$) and Ca (b, $r = 0.81$) concentrations in the xylem sap with the respective concentrations in the 3rd pair of leaves from 18 April to 26 June (each point represents one sampling date).

relation of Mn, Ca and Mg (Table 3). This points to similar uptake and transport rates of these mainly passively acquired nutrients. The Fe concentrations correlate only slightly negatively with Mn and Ca. K is acquired selectively and translocated easily within the plant. Its exceptional dynamics is reflected in low correlations with other elements.

Correlations between xylem sap and leaf concentrations

The temporal variation of the Mn and Ca concentrations in the xylem sap are closely related to the concen-

Figure 7. Concentrations of (a) plant available Mn (NH_4NO_3 extract) and (b) easily reducible Fe ($\text{NH}_2\text{OH-HCl}$ extract) in the bulk soil, aggregate interior, and aggregate exterior from 18 April to 26 June 1995.

trations of the 3rd leaf pair (Figure 6). In contrast, the temporal variations of elements in the young leaves do not correlate well with those in the xylem sap which might be explained by the role of phloem for the nutrient supply to youngest leaves.

Correlations between soil and plant cation concentrations

Manganese

When comparing the Mn concentrations in leaves and xylem sap to the concentrations of mobile Mn (i.e. Mn extracted with 1 M NH_4NO_3) in the soil (Figure 7a), one finds a rather close correlation between the 3rd pair of leaves and the bulk soil ($r = 0.72$). Probably due to the small data set, this correlation is not significant.

The mobile Mn in the aggregate exterior and xylem sap concentrations both show a pronounced maximum followed by a slow decline. However, the maximum in the aggregate exterior follows that in the xylem sap by 2 weeks, which generally renders a causal relationship unlikely.

Manganese concentrations in the aggregate interior exhibit the least close correlation with the plant compartments.

Figure 8. Plant available K concentrations (NH_4NO_3 extract) in bulk soil, aggregate interior, and aggregate exterior from 18 April to 26 June 1995.

Iron

Since the Fe concentrations in the coffee leaves decreased during the sampling period, probably due to their physiologically older age at the beginning of the rainy season, and since a clear temporal trend was missing in the xylem sap, no correlations of plant data could be found with the Fe concentrations in the soil compartments (Figure 7b). Only the trends in the xylem sap and in the bulk soil were similar. Missing relationships between the temporal trends in plants and soil compartments may be related with plant specific adaptation mechanisms for the acquisition and retranslocation of Fe (Mengel, 1984; Zhang et al., 1996).

Potassium

Similar to Fe, there are no correlations between K concentrations in the plants (Figures 2, 3 and 5) and in the soil compartments (Figure 8). This is according to the findings of Kazda and Weilgony (1988), who found no correlations between K concentrations in the xylem sap of *Picea abies* and in the soil solution.

Calcium and magnesium

The Ca and Mg concentrations in the water extract of field moist bulk soil (Figure 9) are well correlated with those in the xylem sap (Figures 10 and 11). This differs from the study of Kazda and Weilgony (1988), who did not find correlations between plants and soil solution neither for Ca nor for Mg.

Rating the quality of correlations between metal concentrations in the plant and in the soil compart-

Figure 9. Plant available Ca (a) and Mg (b) concentrations (NH_4NO_3 extract) in bulk soil, aggregate interior, and aggregate exterior from 18 April to 26 June 1995.

Figure 10. Correlation of Ca concentrations in the water extract with (a) the 3rd pair of leaves ($r = 0.86^*$) and (b) xylem sap ($r = 0.74$). Each point represents one sampling date.

Figure 11. Correlation of Mg concentrations in water extract with those in the xylem sap ($r = 0.87$). Each point represents one sampling date.

ments, one finds the sequence: bulk soil (water extract) > bulk soil (NH_4NO_3 extract) > aggregate exterior (NH_4NO_3 extract) > aggregate interior (NH_4NO_3 extract).

Conclusions

(I) The coffee plants of our experimental plot were well supplied with mineral nutrients. Mn concentrations were above the optimum range and surplus mobile Mn in the soil might have influenced Fe nutrition at the beginning of the rainy season. However, the Fe deficiency was only minor and could be overcome by the plants themselves.

(II) Because of the high fluctuations of element concentrations in the coffee leaves during the growing period, leaf analysis only informs about the nutritional status at the time of leaf sampling. With respect to a fertilizer recommendation one has to put emphasis on the right time in the course of the year for taking leaf samples. At the beginning of the rainy season coffee plants showed a pronounced peak of Mn concentrations in the xylem sap. It is questionable though, whether this short time maximum can harm the coffee plants. The young leaves showed nutrient imbalances, but their metal concentrations were not correlated with those in the xylem sap.

(III) Element concentrations in the xylem sap showed closest correlation with those in the water extract of field moist bulk soil. However, more data are needed to establish prognostic properties of the xylem sap. Next to metal concentrations in the water extract of field moist soil, those in the NH_4NO_3 extract of air-

dried bulk soil showed closest correlations with some plant element concentrations (Mn, Ca and Mg). In contrast, the aggregate interior showed no correlations with plant concentrations. In well aggregated soils, the non aggregated soil material between aggregates might be exceptionally important to plant nutrition.

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