



Foliar nutrient resorption in rubber trees (*Hevea brasiliensis*)

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(Manuscript Received: 09-01-12, Revised: 27-03-12, Accepted: 24-05-12)

Abstract

The extent of resorption of nutrients before senescence was determined in a rubber plantation which received nutrients at different ratios from establishment onwards. Rubber tree is a leaf exchanging species which defoliates before the onset of dry season, and refoiliates within 2-3 weeks, during the middle of dry season. The objective of the study was to quantify the extent of resorption of major nutrients and the influence of nutrient supply on nutrient resorption. Substantial part of the nutrients was resorbed before leaf fall, 52 to 66 percent N, 53 to 80 percent P and 48 to 88 percent K were resorbed depending on the rate of fertilizer application. Year to year variation in nutrient resorption was observed. Resorption proficiency and efficiency of K were significantly influenced by nutrient ratios, wider N:K ratios resulting in significantly higher resorption proficiency and efficiency. The study concludes that nutrient resorption is an important nutrient conservation mechanism of rubber trees and change in soil nutrient dynamics will influence the extent of resorption and thus litter quality.

Keywords: *Hevea brasiliensis*, nutrient ratio, resorption efficiency, proficiency, soil nutrient status

Introduction

Nutrient resorption, the process by which nutrients are translocated from senescing leaves prior to abscission, for storage in the plant tissues (Killingbeck, 1996), is an important mechanism of forest trees and many economically important trees for nutrient conservation. This mechanism reduces the loss of nutrients through litter and thus litter quality. Litter quality has lot of implications at the ecosystem level, it will influence the rate of litter turnover and nutrient cycling leading to a positive feedback between plant species dominance and nutrient availability (Aerts, 1999).

The factors influencing the nutrient resorption efficiency (percentage of a nutrient withdrawn from mature leaves before abscission) are still not clear. The most widely studied parameter is soil nutrient availability and though it has often been suggested that species from low nutrient habitats have higher nutrient resorption efficiencies than species from

habitats with high nutrient availability, it is still a subject of debate. Several authors have suggested that nutrient resorption efficiency is influenced by soil nutrient availability (Pugnaire and Chapin, 1993; Enoki and Kawaguchi, 1999; Toet and Aerts, 2003; Yuan *et al.*, 2005). Aerts (1996) suggested that high nutrient resorption efficiency is characteristic of all perennial growth forms and is not very responsive to changes in nutrient supply, and other authors have supported this observation (Del Arco *et al.*, 1991; Aerts and Chapin 2000). Some others have proposed soil moisture availability as an environmental factor controlling the nutrient resorption (Del Arco *et al.*, 1991; Pugnaire and Chapin, 1993; Killingbeck, 2004; Renteria and Jaramillo, 2005).

Resorption efficiencies reported in literature vary depending on species, management practices and environmental factors. Aerts (1996) reported that before leaves detach from plants, 50 percent of N and P in green leaves is resorbed and redirected

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towards growing parts of storage tissues. Toet and Aerts (2003) reported nitrogen resorption efficiency ranging from 40 to 80 percent and phosphorus resorption efficiency from 39 to 72 percent depending upon species.

Killingbeck (1996) suggested resorption proficiency (the minimum level to which a nutrient is reduced during senescence) to be more responsive to soil nutrient availability. Higher nutrient proficiency corresponds to lower level of nutrients in the senescing leaves and lower proficiency indicates higher level of nutrients in the senescing leaves. Resorption proficiency is directly related to the nutrient recycling through litter since it indicates the amount of nutrients that is available in the litter and thus litter quality. Soil nutrient availability influences nutrient proficiency (Aerts and Chapin 2000). Intrinsic species to species variation was also reported, woody evergreens have higher resorption proficiency than woody deciduous species (Killingbeck, 1996).

Rubber tree is a leaf exchanging species which defoliates before the onset of dry season, and refoiliates within 2 to 3 weeks, during the middle of dry season. Annual litter addition was estimated as 7.1 to 7.9 tonnes in South India (Jessy *et al.*, 2009). Murbach *et al.* (2003) studied the nutrient resorption in a rubber plantation in Brazil based on the calcium content in the green and senescing leaves, which does not exclude the error due to accumulation of calcium as the leaf gets older when calculations are made on mass basis.

In the present study, the resorption proficiencies and efficiencies of major nutrients were studied in a 16 year old rubber (clone RRII 105) plantation which received varying levels of nutrients from the year of establishment onwards in South India.

Materials and methods

Study site

The experiment was laid out at Kodumon estate, Adoor, Kerala, India in 1989 in RBD with three replications. The soil was Ustic kandohumults, high in organic carbon content (1.95 per cent) and low in available P (0.11 mg/100 g) and K (3.12 mg/100 g)

with a pH of 4.7. The treatments were selected combinations of three levels of nitrogen (30, 60 and 90 kg/ha/yr), two levels of phosphorus (30 and 60 kg/ha/yr), two levels of potassium (20 and 40 kg/ha/yr) and a control which received no fertilizers.

Polybag plants of clone RRII 105 were planted at a spacing of 4.9 m x 4.9 m in 1989. The gross plot size was 24 trees with a net plot size of eight trees. Urea, rock phosphate and muriate of potash were applied as the sources of N, P and K respectively in two equal splits during April-May and September-October every year. *Mucuna bracteata* was maintained as cover crop during the immature phase. All the cultural operations were carried out as per the recommendation of the Rubber Board.

Sample collection and analyses

Leaf samples were collected during 2005-06 and 2006-07. Period of leaf sample collection was decided based on an earlier study in the region (Abraham *et al.*, 1997). Four net trees (excluding the border trees) were tagged for leaf sample collection. Fully expanded mature leaves were collected during October to determine the maximum nutrient content. Fully senesced leaves were collected from the tagged trees by gently shaking the branches during January. The sampling time of senesced leaves varied during both years. During December 2005, the rains were received up to 11th of December. Leaf shedding was delayed and samples were collected on 19th of January 2006. During 2006, there were no rains after 26th November and leaf shedding was comparatively early. Senesced leaf samples were collected on 6th January 2007. The samples were dried in the oven at 70°C to constant weight and analysed for nutrients as per the methods described by Piper (1966). Nitrogen content was determined by Kjeldahl method (Kjeltec 2300, Foss Tecator, Sweden), phosphorus content by vanadomolybdate method using autoanalyzer (AA3- Brant Luebbe, Germany) and potassium content flame photometrically using autoanalyzer. Calcium and magnesium contents were determined using atomic absorption spectrophotometer (Avanta- GBC Scientific equipment Company Ltd. Australia).

Soil samples (0-30 cm) were collected during October and analyzed for pH (1:2.5 soil water ratio), organic carbon by Walkely and Black's method (Jackson, 1973) available phosphorus by chloromolybdic stannous chloride reduction method using Bray II extractant (Bray and Kurtz, 1945), available potassium using flame photometer (Morgan, 1941) and available calcium and magnesium by ammonium acetate extraction (Vogel, 1969) followed by subsequent determination by atomic absorption spectrophotometer.

Resorption calculation

Because of the possible underestimation of resorption efficiency (RE), if calculated on mass basis (Killingbeck, 1988; Toet and Aerts, 2003; Renteria and Jaramillo, 2005), we calculated RE based on area basis. To determine the leaf area, four leaves were collected separately from each plot and the leaf area was determined using a leaf area meter (LiCOR). The element concentration on mass basis was converted to area basis based on area per unit weight of the leaf. The resorption efficiency (%) was calculated as the content of green mature leaves (maximum content) minus that of senesced leaves divided by that of green mature leaves (Killingbeck and Costigan 1988).

$$Nur_{eff} = 1 - (Nu_{sen} / Nu_{green})$$

Where, Nur_{eff} - nutrient resorption efficiency

Nu_{sen} - nutrient content of senescing leaves (area basis)

Nu_{green} - nutrient content of green leaves (area basis)

The nutrient concentration in the senesced leaves was considered as a measure of resorption proficiency (Killingbeck, 1996), lower nutrient concentration in the senesced leaves indicate higher proficiency.

The different treatments were compared by ANOVA. The effect of nutrient supply ratios were compared by Duncan's multiple range test.

Results and discussion

Soil nutrient status

After 17 years of fertilizer application with graded levels of fertilizers, soil available P status

was significantly higher in all the P applied plots (Table 1). It ranged from 7.9 in the control to 197.8 mg/kg soil in the treatment which received $N_{60}P_{60}K_{40}$ indicating the possibility of reducing the dose of P fertilizer in plantations which received regular manuring previously. Soil organic carbon, available potassium, calcium and magnesium did not differ between treatments. Continuous fertilizer application significantly increased soil acidity also.

Table 1. Soil organic carbon, pH and available nutrient status 17 years after commencing the experiment

Treatment	pH	OC (%)	Available nutrients (mg/kg soil)			
			P	K	Ca	Mg
0:0:0	4.63	2.30	7.9	40.6	17.3	8.6
30:30:20	4.49	2.38	118.1	58.7	18.9	10.6
30:30:40	4.50	2.30	79.1	51.6	26.3	11.4
30:60:20	4.49	2.25	107.6	49.1	30.7	08.2
30:60:40	4.51	2.48	183.0	53.5	31.2	11.6
60:30:20	4.46	2.54	88.5	51.9	21.0	8.9
60:30:40	4.48	2.32	57.1	50.4	20.2	11.1
60:60:20	4.52	2.73	127.2	50.0	23.7	8.8
60:60:40	4.45	2.55	197.8	51.9	31.0	10.4
90:30:20	4.49	2.33	87.5	65.4	24.9	9.4
90:30:40	4.50	2.41	60.3	57.9	19.8	8.1
90:60:20	4.45	2.31	97.4	74.3	20.7	9.5
90:60:40	4.50	2.18	115.5	55.6	25.6	8.8
SE	0.03	0.15	18.1	8.9	4.7	1.4
CD	0.10	NS	52.7	NS	NS	NS

Nutrient concentration of green leaves

Foliar nitrogen concentration in the green leaves ranged from 29.9 mg g⁻¹ to 39.8 mg g⁻¹ during 2005 and from 36.4 to 41.1 mg g⁻¹ during 2006 and did not indicate any treatment effect in both years (Table 2). Concentration of P in green leaves also did not indicate any treatment effect during 2005, values ranged from 2.7 to 3.6 mg g⁻¹. During 2006, the P concentration in green leaves was significantly higher in the plots which received higher levels of P fertilizers. Foliar potassium concentration also did not indicate any significant treatment effect during 2005, values ranged from 6.9 mg g⁻¹ in the control to 10.9 mg g⁻¹ in the plot which received NPK at 60:30:40 kg ha⁻¹. During 2006, K concentration in the green leaves varied between treatments, but did not indicate any definite trend. Foliar Ca and Mg concentrations also did not indicate any treatment effect.

Direct correlation between nutrient supply or soil nutrient status and leaf nutrient concentration

Table 2. Nutrient concentration (mg g⁻¹) of green diagnostic leaves. The experiment was commenced during 1989 and leaf samples were collected during October 2005 and 2006

NPK (kg ha ⁻¹)	N		P		K		Ca	Mg
	2005	2006	2005	2006	2005	2006	2006	2006
0:0:0	33.9	37.9	2.7	3.5	6.9	7.77	7.67	2.77
30:30:20	39.8	39.4	3.2	3.5	9.4	10.77	10.17	2.50
30:30:40	33.4	37.4	2.7	3.3	10.5	8.70	9.87	2.67
30:60:20	33.1	39.2	3.3	4.1	8.9	7.67	11.70	3.17
30:60:40	33.7	36.4	3.0	4.6	9.3	9.50	10.87	2.93
60:30:20	32.0	39.6	3.1	3.8	7.9	9.0	8.13	2.80
60:30:40	36.4	39.0	3.0	3.4	10.9	9.77	8.10	2.87
60:60:20	34.4	39.3	3.4	4.1	7.5	8.80	8.90	2.57
60:60:40	32.2	38.4	3.6	4.0	9.7	10.07	11.77	2.97
90:30:20	34.3	38.8	3.2	3.1	8.9	7.33	10.43	2.63
90:30:40	33.3	37.1	3.3	3.4	8.7	7.83	10.73	2.63
90:60:20	32.0	41.1	3.6	3.6	9.8	7.17	9.37	2.80
90:60:40	29.9	39.1	3.6	4.4	8.2	9.13	10.73	3.00
SE	0.20	0.14	0.4	0.3	1.2	0.61	0.10	0.23
CD	NS	NS	NS	0.8	NS	1.77	NS	NS

is rarely reported in the various fertilizer trials conducted in different rubber growing countries (Shorrocks, 1960; Punnoose *et al.*, 1975; Kalam *et al.*, 1979; Pushpadas *et al.*, 1979; Jessy, 2004). In our study also, continued application of graded levels of nutrients influenced leaf P and K status during 2006 only. The leaf nutrient status in the control was comparable to that of treatments which received fertilizers and this might be due to the ability of rubber trees to maintain leaf nutrient status without depending on added fertilizers. Rubber is a forest tree which grows well in less fertile soils and its ability to acquire P from usually unavailable forms of P is well documented (Jessy, 2004).

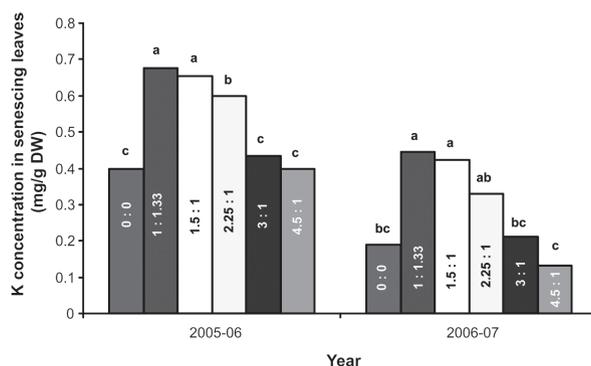
Nutrient resorption proficiency

Nitrogen concentration in the senesced leaves followed the same pattern as that of green leaves, no significant treatment effect was indicated in both years (Table 3). However, the absolute values of nitrogen concentration was considerably low in senesced leaves compared to green leaves, ranging from 17.4 to 21.6 mg g⁻¹ during 2006 and 19.0 to 25.8 mg g⁻¹ during 2007. P concentration in senesced leaves ranged from 1.1 to 2.1 mg g⁻¹ in 2006 and from 1.3 to 2.2 mg g⁻¹ in 2007. Proficiency of P was significantly ($p < 0.05$) influenced by nutrient supply, significantly higher proficiency (lower P concentration) was observed in the plots which

Table 3. Nutrient concentration (mg g⁻¹) of senescing leaves. The experiment was commenced during 1989 and senescing leaf samples were collected during January 2006 and 2007

NPK (kg ha ⁻¹)	N		P		K		Ca	Mg
	2006	2007	2006	2007	2006	2007	2007	2007
0:0:0	21.6	24.1	1.60	1.93	4.0	1.90	8.83	3.23
30:30:20	20.5	20.3	1.80	1.90	6.4	5.83	11.27	2.60
30:30:40	18.7	23.3	1.50	1.63	7.5	5.20	9.77	2.97
30:60:20	18.4	23.5	1.70	1.70	5.6	3.10	10.90	2.87
30:60:40	18.7	19.6	2.10	1.70	6.2	3.70	11.67	2.67
60:30:20	17.4	21.5	1.60	1.50	4.1	2.30	10.83	2.53
60:30:40	18.9	21.1	1.10	1.30	7.2	3.30	10.33	2.93
60:60:20	20.8	23.3	1.90	2.20	4.6	2.00	9.37	3.30
60:60:40	18.8	21.7	1.70	1.50	7.0	4.67	13.00	2.93
90:30:20	17.7	19.0	1.40	1.30	3.8	1.10	10.07	2.67
90:30:40	18.4	21.3	1.40	1.50	6.0	4.20	9.83	2.30
90:60:20	19.0	25.8	1.30	1.40	4.2	1.57	11.47	2.37
90:60:40	18.9	21.3	1.30	1.30	6.0	2.40	11.50	2.60
SE	1.2	1.5	0.1	0.2	0.7	0.58	1.08	0.31
CD	NS	NS	0.50	0.60	2.1	1.69	NS	NS

received higher levels of N without a corresponding higher level of P. Proficiency was higher in the treatments which received lower levels of P. The same trend was observed during both years. Interestingly, proficiency of P was comparatively lower in the control, indicating the lack of control of P application in the P concentration of senesced leaves. In the case of potassium also, rates of nutrient supply significantly ($p < 0.05$) influenced proficiency. Lowest K concentration in senesced leaves (highest proficiency) was observed in the N₉₀P₃₀K₂₀ in both years (3.8 and 1.1 mg g⁻¹). K proficiency was comparatively lower in the treatments which received higher levels of K or lower levels of N (Fig. 1).

**Fig. 1.** K resorption proficiency as influenced by N:K supply ratio in a mature rubber plantation. Different letters indicate significant difference ($p < 0.05$)

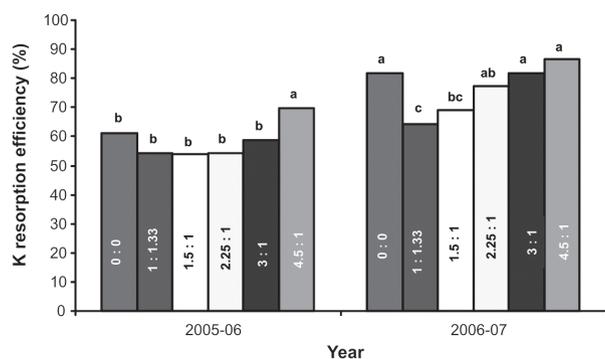


Fig. 2. K resorption efficiency as influenced by N:K supply ratio in a mature rubber plantation. Different letters indicate significant difference ($p < 0.05$)

The nutrient resorption proficiency (NRP), the level to which nutrients are reduced in the senescing leaves is directly influenced by nutrient availability (Aerts and Chapin, 2000). Other factors like source sink relations, timing of abscission, activation of resorption machinery and initial green leaf concentration also influence NRP (Killingbeck, 2004). In our study, the concentration of N, P and K in senescing leaves were considerably lower in the senescing leaves indicating withdrawal of these nutrients before leaf fall. Nitrogen resorption proficiency was not influenced by N fertilizer application. Unlike green leaf nutrient concentration, the P and K concentration in senescing leaves were significantly ($p < 0.05$) influenced by treatments. According to Killingbeck (1996), resorption of P is complete if litter concentration is less than 0.5 mg P per g dry weight in deciduous species and litter concentration above 1.2 mg P per g dry weight indicate incomplete resorption and according to this grouping, in *Hevea* resorption is incomplete. Toet and Aerts (2003) studied the effect of N fertilization on P resorption proficiency of six perennial species and observed that the effect is species specific. They suggested that the demand for P increased after N fertilization and the species with incomplete resorption could increase resorption proficiency leading to lower litter P concentration after N fertilization. However, in our study, the N/P ratios did not significantly influence P proficiency. In the control unfertilized plot also, the P proficiency was lower indicating that trees are not withdrawing P in higher amounts from the senescing leaves for meeting their requirement. The effect of nutrient supply ratios on nutrient concentration of senescing

leaves was significant in the case of K, proficiency was significantly higher when N/K ratio was wider (Fig. 1). This indicates the nutritional control over resorption proficiency in *Hevea* and this might be an adaptive strategy of trees to maintain balanced nutrient status within the trees. Calcium and magnesium are accreted to the senescing leaves as in many crops (Killingbeck, 2004) and in rubber also, there was no withdrawal of these nutrients before senescence.

Nutrient resorption efficiency

Nitrogen resorption efficiency (NRE) ranged from 52 to 66 percent, PRE from 53 to 80 percent and KRE from 48 to 88 percent (Table 4). Nutrient supply influenced resorption efficiencies and the effect of N/K ratio was significant in the case of KRE. Wider N/K ratio significantly enhanced KRE in fertilizer applied plots (Fig. 2). Higher resorption efficiency was observed during 2007 compared to 2006. In the case of calcium and magnesium, there was no resorption except in a very few treatments in the case of Mg.

Table 4. Nutrient resorption efficiency (%)

NPK (kg ha ⁻¹)	N (%)		P (%)		K (%)	
	2006	2007	2006	2007	2006	2007
0:0:0	57	57	57	57	61	82
30:30:20	52	64	53	59	52	59
30:30:40	54	56	56	62	60	55
30:60:20	56	60	57	71	60	71
30:60:40	59	66	53	73	48	74
60:30:20	55	57	60	63	59	80
60:30:40	59	59	70	80	49	74
60:60:20	58	55	58	66	59	84
60:60:40	58	58	61	73	52	72
90:30:20	59	61	58	78	70	88
90:30:40	60	61	60	71	58	74
90:60:20	65	55	59	64	69	85
90:60:40	56	60	53	75	51	80
SE	4.44	3.24	4.0	5.01	3.29	3.92
CD	NS	NS	NS	14.63	9.60	11.45

The resorption efficiencies of N and P observed in our study were in the higher range when compared with majority of the reported values in literature. A resorption efficiency of 22 percent in the case of N and 26 percent in the case of P was reported in a tropical dry forest in Mexico by Renteria and Jaramillo (2005). Based on a large literature survey, Aerts (1996) reported an average resorption efficiency of 50 per cent in the case of N

and P. The RE reported in a tropical dry forest in India (Lal *et al.*, 2001) is 58 percent for N and 50 percent for P. In a tropical dry forest in Venezuela, a higher RE of 65 percent (N) and 64 percent (P) was observed. In our study, RE was highest in the case of K. Very few studies on K resorption were reported so far. Milla *et al.* (2005) reported that resorption of K is less efficient than the resorption of N and P in Mediterranean woody plants. They suggested that K is retained in the leaves during most of the senescence phase to provide appropriate cell hydration to conduct senescence adequately, and after that, there is little time left to reabsorb K leading to high amounts of K remaining in litter. Murbach *et al.* (2003) also reported high resorption of K in *Hevea* in Brazil based on the calcium content of green and senescing leaves. This indicates that the hypothesis of Milla *et al.* (2005) is not applicable in rubber trees and the high efficiency of conservation of K by rubber trees. The significantly higher KRE and higher proficiency when the N/K supply ratio is wide further support this. However, potassium is leached easily from leaves (Killingbeck, 2004) and hence the observation of high KRE can be explained with caution only. In our study, nutrient supply was manipulated for a long period, and results might not be similar in different sites with inherent fertility differences.

Year to year variation in green leaf nutrient status, resorption efficiencies and proficiencies were observed and this might be due to variation in environmental parameters. Contrary to the reports that early abscission result in low resorption and late abscission in elevated resorption (Killingbeck, 2004). In the present study, RE was lower when senescence was delayed. This might be due to reduced soil moisture availability as the senescence occurred late in the season in 2006. Water stress has been reported to reduce resorption in other crops also (Del Arco *et al.*, 1991).

Rubber tree defoliates during the beginning of the summer in December - January and re-leaf after 2 to 3 weeks in the middle of summer when nutrient uptake is limited by soil moisture stress. The results indicated that a substantial portion of nutrients are resorbed by the trees before senescence and these resorbed nutrients might be

retranslocated and used for the rapid re-growth of foliage. Among the different nutrients, K is resorbed in the highest quantity. Proficiency and resorption efficiency of potassium are influenced by nitrogen supply rates.

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