

# Leaf chemistry of woody species in the Brazilian cerrado and seasonal forest: response to soil and taxonomy and effects on decomposition rates

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Received: 8 April 2016 / Accepted: 9 September 2016 / Published online: 16 September 2016  
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**Abstract** The Brazilian cerrado occurs interspersed with the semi-deciduous seasonal forest, and soil fertility is considered as the main determinant of the abrupt transitions between both vegetation types. We aimed to study patterns across chemical traits of green leaves in 121 cerrado and seasonal forest woody species from southeastern Brazil, their response to soil nutrient status, and their effects on decomposition rates. We compared leaf traits of both cerrado and forest species and constructed multilevel models to account for partitioning of variance in each trait. We calculated the community-weighted mean of each trait to assess their response to soil nutrient status and their effects on decomposition rates of standard plant material. Most of the traits were significantly correlated among themselves, with cerrado species having lower nutrient concentrations than the seasonal forest. Taxonomy accounted for 52 % of the total variance in leaf traits, whereas vegetation type accounted for 19 %. All leaf traits but leaf manganese and aluminium concentrations were significantly related to soil properties. Decomposition rates were affected indirectly by soil features through its effects on leaf traits. Contrary to the expected, the higher the leaf

nitrogen concentration in the surrounding litter, the lower the decomposition rate. Even with a large effect of taxonomy on leaf nutrient-related traits, soil exerted an important role on the chemical traits. Strategies of both cerrado and seasonal forest species were carried out through multi-element control of soil on leaf nutrient composition. The effect of such different strategies on functioning was, however, less prominent.

**Keywords** Decomposition · Leaf chemistry · Nutrient availability · Savanna · Tea bag index · Tropical forest

## Introduction

The occurrence of savannas and forests adjacent to each other is a common phenomenon in tropical regions around the world (Warman et al. 2013). Apart from the climate (Archibold 1995), several factors have been proposed to explain these abrupt transitions, such as fire regimes, hydrology, herbivory, and soil fertility (Murphy and Bowman 2012). In Brazil, the Central Plateau is covered by the cerrado vegetation, whose physiognomies go from grassland, through savannas, to tropical forest, in a gradient of soil fertility (Coutinho 1990). Very often, the cerrado vegetation occurs interspersed with the semi-deciduous seasonal forest (Coutinho 1990). The cerrado

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Communicated by William E. Rogers.

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persists even when it could be replaced by the seasonal forest, considering only the climate. Even if fire and water stress contribute to the cerrado occurrence and its physiognomic gradient, soil fertility is considered as the main determinant of such abrupt transitions (Goodland and Pollard 1973; Coutinho 1990). Whereas the cerrado is usually found on nutrient-poor, aluminium-rich, and sandy soils, the seasonal forest usually occurs on nutrient-rich, aluminium-poor, clayey soils, mainly derived from sandstones or volcanic rocks (Ruggiero et al. 2002; Durigan and Ratter 2006).

Soil is the biggest reservoir and provider of several chemical elements that sustain plant communities (Epstein and Bloom 2005). Soil nutrient availability determines plant growth rate, carbon allocation strategies, leaf nutritional content, and other key traits related to plant development (Wardle et al. 2004). Plants, in turn, regulate the vertical nutrient availability in soil through biogeochemical cycling via litterfall or direct leaching from leaves and uplifting demand (Wardle et al. 2004). According to the “nutrient uplifting theory” (Jobbágy and Jackson 2001), the nutrients plants depend on the most are found in the upper soil layers in a continuous plant–soil feedback.

Besides being important for biogeochemical cycling, plant chemical traits drive physiological processes and actively regulate community functioning, affecting species interaction with competitors, consumers, and decomposers (Reich 2005; Han et al. 2011; Zhang et al. 2012). Although great importance has been given to soil nitrogen and phosphorus (Reich 2005; Han et al. 2005), other elements are also critical for plant physiology. For instance, leaf potassium, calcium, and magnesium have been pointed out as important determinants of one axis of plant specialization, correlated to rapid growth (Grime 1977; Wright et al. 2005). Lower concentrations of these elements in foliar tissue, in turn, tend to be associated to an opposite specialization, towards nutrient retention under unproductive conditions, with low palatability, high toughness, and long-lived leaves (Craine 2009).

Similar to macronutrients, micronutrients, such as manganese, zinc, iron, copper, and boron, are essential for plant functioning (Hänsch and Mendel 2009). They are mainly involved in protein synthesis, photosynthesis, cell structure, and enzymatic activity, affecting metabolism regulation, cell protection, growth, and

reproduction (Hänsch and Mendel 2009; Zhang et al. 2012). Micronutrients may also affect community functioning, limiting litterfall, decomposition, and productivity (Kaspari et al. 2008; Powers and Salute 2011). For example, manganese acts on enzymatic activation and phosphorus uptake; zinc plays an important role in protein and enzyme syntheses; iron is important for protein synthesis and for respiration; copper acts on both photosynthesis and respiration, regulating carbon and nitrogen metabolism; and boron is important for protein synthesis, sugar transport, and nitrogen fixation (Hänsch and Mendel 2009; Lambers et al. 2014). Not only do micronutrients regulate plant metabolism and functioning (Hänsch and Mendel 2009), but they also influence litter decomposition rates by regulating the decomposer metabolism (Powers and Salute 2011).

The need to consider the effect and response of multiple elements in plant communities has been gaining recognition in terrestrial plant ecology (Asner and Martin 2011; Townsend et al. 2011; Han et al. 2011; He et al. 2016; Zhao et al. 2016). However, up to now, few studies in the cerrado and the semi-deciduous seasonal forest have considered leaf chemical elements other than nitrogen or phosphorus (Viani et al. 2014; Vourlitis et al. 2014). In fact, micronutrients have hardly been taken into account in these two vegetation types (Viani et al. 2014). Due to its high richness, high degree of endemism, and conservation status, the cerrado is among the world’s hotspot for biodiversity conservation (Myers et al. 2000). The few remaining cerrado areas, most of them surrounded by an agricultural matrix, are susceptible to nutrient enrichment caused by a run-off from agricultural land (Lambers et al. 2013; Hunke et al. 2015). Consequently, their floristic composition can be altered, and shifts in cerrado forest transition can occur with changes in nutrient availability (Miatto et al. 2016). Understanding how plastic in their chemical traits and how tightly related with community functioning cerrado and forest species are may help us to predict whether the cerrado will be replaced by the seasonal forest in a future scenario of eutrophication.

We aimed to study patterns in chemical traits of green leaves in both cerrado and seasonal forest woody species, in their response to soil nutrient status, and in their effects on decomposition rates. More specifically, we aimed (1) to compare leaf chemical traits in cerrado and forest species; (2) to partition the

variation in leaf properties into taxonomic, plot-environmental, and residual components; (3) to test to what extent soil features influence leaf properties in the cerrado and in the seasonal forest; and (4) to test the direct and indirect effects of community-level leaf nutrient concentration on litter decomposition rates, also considering the influence of soil features. We expected that (1) cerrado species would have lower nutrient content and higher aluminium content as a consequence of the nutrient status of their soils (Ruggiero et al. 2002); (2a) nutrients that are required in highest concentrations, such as nitrogen and phosphorus, would be less sensitive to vegetation type and soil nutrient-status, following the “stability of limiting nutrient” theory (Han et al. 2011); (2b) both vegetation type and taxonomy would influence leaf nutrient concentrations (Fyllas et al. 2009; Zhang et al. 2012); (3) leaf traits would respond to soil nutrient status in both vegetation types (Fyllas et al. 2009); and (4) soil features and leaf nutrient concentration would predict, directly and indirectly, decomposition rates (Bakker et al. 2011).

## Methods

We carried out this study in the Vaçununga State Park, Santa Rita do Passa Quatro municipality, São Paulo state, southeastern Brazil (21°41'00"–21°41'21"S and 47°34'37"–47°39'39"W). The park is at 590–740 m above sea level. Regional climate is classified as Cwa, with wet summers and dry winters (Köppen 1931). Annual rainfall lies around 1500 mm, concentrated from November to April, and mean annual temperature is 21.5 °C. The park encompasses 2071 ha, of which 1192 ha are covered by cerrado and 578 ha are covered by seasonal forest (Ruggiero et al. 2002). Soils are mainly Neosols and Latosols, according to the Brazilian classification system (Embrapa 2012), or Entisols and Oxisols, according to the USDA classification system (Soil Survey Staff 2014).

We established 100 25 m<sup>2</sup> plots across all the areas that were accessible to researchers. We placed the plots using a random stratified sampling (Krebs 1998; Sutherland 2006), taking into account the proportion covered by each vegetation type. Thus, we placed 68 plots in the cerrado and 32 plots in the seasonal forest. In each plot, we sampled all the individuals belonging to the woody component, defined as those woody

individuals with stem diameter at the soil level equal to or higher than 3 cm (SMA 1997). We identified the individuals to species level, comparing the collected material to vouchers lodged at the Botanical Institute of São Paulo herbarium or using identification keys based on vegetative characters (Batalha et al. 1998; Batalha and Mantovani 1999). We randomly selected 5–10 individuals of each species to be sampled, as recommended for measurements of most plant functional traits (Pérez-Harguindeguy et al. 2013). For species with less than five individuals, we made an additional effort, looking for other individuals close to the plots and trying to reach five individuals per species. From the 121 species we sampled for nutrient analyses, 60 occurred exclusively in the cerrado, 55 occurred exclusively in the seasonal forest, and six occurred in both vegetation types.

In the wet season, from October 2013 to April 2014, we collected five green leaves from the selected individuals. We placed the leaves in plastic bags, put them in a thermal box, with bottled iced water inside, and took them to the laboratory. We sent dried samples of 2 g each to the Luiz de Queiroz College of Agriculture, at the University of São Paulo, where nitrogen, phosphorus, potassium, calcium, magnesium, sulphur, boron, copper, manganese, iron, and aluminium concentrations were determined. In the beginning of the preceding dry season, from May 2013 to June 2013, we collected the available senesced leaves by flicking the branch or twig from two to seven individuals per species. As with the green leaves, we took the samples to the laboratory, dried them and sent them to the Luiz de Queiroz College of Agriculture, for nitrogen determination.

In each plot, we collected a composite soil sample to 5 cm deep by mixing four subsamples taken from the corners of the plot and one taken in the centre. We sent them to the Luiz de Queiroz College of Agriculture, for determination of pH, organic matter, total nitrogen, available phosphorus, exchangeable potassium, exchangeable calcium, exchangeable magnesium, exchangeable aluminium, sum of bases, base saturation, aluminium saturation, cation exchange capacity, and sand, silt, and clay content (see Miatto et al. 2016 for more details on soil analyses).

To obtain the decomposition rate in each plot, we used standard plant material—tea. We calculated the Tea Bag Index using green and rooibos tea bags and following a pertinent protocol (Keuskamp et al. 2013).

In January 2014, we buried two bags of the Lipton green tea and two bags of the Lipton rooibos tea per plot. Prior to burial, we measured the initial mass of each tea bag and subtracted the mass of an empty bag, assumed as a standard mass, to determine the initial mass of the tea (Keuskamp et al. 2013). After 3 months, we dug up the tea bags, removed adhered soil particles, and dried them in a stove for 48 h at 70 °C. Then, we removed the label and left the string, weighed the bag, and subtracted the mass of an empty bag without the label to determine the mass after incubation. After having the initial and final mass of each bag, we calculated the decomposition rate ( $k$ ), using a modified version of the classical decomposition equation of Wieder and Lang (1982):  $W(t) = ae^{-kt} + (1 - a)$ , in which  $W(t)$  was the mass of the substrate after incubation time  $t$ ,  $a$  was the labile, and  $1 - a$  was the recalcitrant fraction of the litter. This modified equation assumes that “during a short field incubations, mass loss of the recalcitrant fraction is negligible” (Keuskamp et al. 2013).

The tea bag method does not require a time series for the estimation of the decomposition rate ( $k$ ) and the recalcitrant fraction of the litter ( $a$ ). Instead, by using two types of litter with different decomposition rates, it enables the estimation the decomposition rate from rooibos tea at a single point in time (Keuskamp et al. 2013). Considering that part of the labile compounds stabilizes and become recalcitrant due to environmental factors, this method relates the actual decomposable fraction ( $a$ ) measured in the field to the hydrolyzable and chemically labile fraction ( $H$ ) obtained from a series of chemical analyses (Keuskamp et al. 2013), so that any deviation from these measures is attributed to the environmental conditions (Keuskamp et al. 2013). Hence, to solve the modified equation cited above, the following two equations were solved first:

$S = 1 - a_g/H_g$ , in which  $S$  was the stabilization factor or the inhibiting effect of the environment,  $a_g$  was the decomposable fraction and  $H_g$  was the hydrolyzable fraction of the green tea.

$a_r = H_r(1 - S)$ , in which  $a_r$  was the decomposable fraction and  $H_r$  was hydrolyzable fraction of the rooibos tea.

After measuring specific leaf area and obtaining the chemical results for all samples, we calculated average values of each leaf trait per species and log-transformed the data to reach normality. First, we applied

Pearson analyses to test whether leaf traits were correlated to each other. Then, we tested for differences in leaf traits between cerrado and forest species with a  $t$  test. To account for partitioning of variance in each leaf trait, we applied a multilevel model as proposed by Fyllas et al. (2009):

$T = \mu + v + f/g/s + \varepsilon$ , in which  $\mu$  was the mean value for trait  $T$ ,  $v$  was the vegetation type effect,  $f/g/s$  represented the taxonomic hierarchy effect in the data, since each individual belonged to a species  $s$  that belonged to a genus  $g$  that belonged to a family  $f$ , and  $\varepsilon$  was the residual effect, which represented both within species variability and measurement error. For each trait, we had a multilevel model. To test the significance of each component for each model, we constructed new models without a given component (family, genus, species, or vegetation type) and compared these models with the complete one using an analysis of variance and a likelihood ratio test.

To obtain the community-weighted mean for each trait, we calculated mean trait values of each species present in the community weighted by its relative abundance, which, in our case, was given in number of individuals (Garnier et al. 2004). In addition, to summarize the dimensions of the leaf trait matrix, we conducted a principal component analysis with the leaf trait data, standardizing the traits by their ranges. Then, we used species scores of the first axis to calculate a community-weighted “general leaf trait”. To account for the influence of soil fertility on leaf components, we conducted a principal component analysis with soil data, excluding variables that were strongly correlated to others (Pearson’s  $r > |0.70|$ ). We then used the first two principal components as a measure of soil fertility (Miatto et al. 2016). We did analyses of covariance, using the community-weighted mean of each trait as response variable and the first two principal components of soil data and vegetation type as explanatory variables. Similarly, we also did a covariance analysis using the community-weighted general leaf trait as response variable and the first two principal components of soil data and vegetation type as explanatory variables.

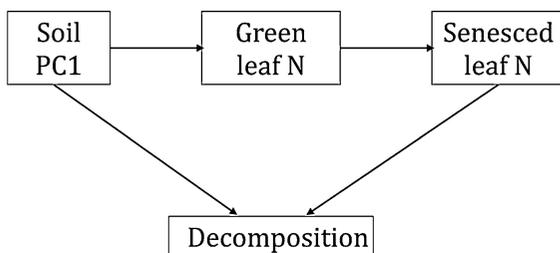
To test whether cerrado and seasonal forest leaf nutrient content would affect decomposition, along with soil features, we did a path analysis. We postulated a mediated model in which soil directly affected litter decomposition rates and indirectly affected decomposition rates by affecting leaf nutrient

content. In this model, green leaf nutrient content indirectly affected litter decomposition rates through its effect on litter nutrient quality, as follows (Fig. 1).

We considered soil attributes and litter quality as surrogates for the “chemical environmental conditions” for the tea decomposition rate. We expected that, to some degree, the variation in the decomposition rates of the tea bags in both cerrado and seasonal forest would be attributed to the environmental conditions created by soil and leaf qualities, which also affect decomposers activities. We used the first axis of soil PCA as a descriptor of soil quality. To avoid collinearity, we used green leaf nitrogen as a descriptor of leaf nutrient content, since it was correlated to almost all leaf nutrients (Table 1). Consequently, we used senesced leaf nitrogen as a descriptor of senesced leaf nutritional quality. We carried out the analyses in the R environment (R Core Team 2015), using the lme4 (Bates et al. 2014), vegan (Oksanen et al. 2013), FD (Laliberté and Legendre 2010), Hmisc (Harrell Jr and Dupont 2014), and lavaan (Rosseel 2012) packages.

## Results

Most of the leaf traits were weakly but significantly correlated among themselves (Table 1). The only strong correlation was between magnesium and calcium ( $R = 0.76$ ). Aluminium was weakly but significantly correlated only with zinc ( $R = 0.18$ ) and iron ( $R = -0.19$ ). Manganese was not correlated with any other trait (Table 1). Most of the traits values—nitrogen, phosphorus, potassium, calcium, magnesium, boron, copper, zinc, and iron—were lower in the cerrado than in the seasonal forest (Table 2). Manganese, sulphur, and



**Fig. 1** A priori causal model relating soil properties and nutrient content in green and senesced leaves to decomposition rates in cerrado and in seasonal forest. Solid arrows indicate positive relationships

aluminium concentrations did not differ between the two vegetation types (Table 2).

According to the multilevel model fitted for each leaf trait, vegetation type accounted for an average of only 19 % of the total variance in leaf traits, whereas the taxonomic component—from family to species—accounted for an average of 52 %. The residual effect, which represents the proportion of variance attributed to intraspecific variability or any other systematic font of error during trait measurement, accounted for an average of 28 % of the total variance. Vegetation type accounted for a significant proportion of the variance for nitrogen, potassium, calcium, magnesium, boron, zinc, and iron (27 % on average, Fig. 2). Family accounted for a significant proportion of the variance for phosphorus, potassium, and calcium (24 % on average, Fig. 2). Genus, for nitrogen (29 %, Fig. 2) and species, for copper (36 %, Fig. 2). Sulphur, aluminium, and manganese had no significant component of variance (Fig. 2).

The first axis of the principal component analysis carried out with leaf traits explained 34.4 % of the variation and was related to all traits, except aluminium (Fig. 3). The second axis of the principal component analysis explained 13.6 % of the variation in leaf traits and was mostly correlated to aluminium concentration (Fig. 3).

Soil ordination was divided in two axes of fertility. The first one, explaining 48 % of the variation, was related to clay content, pH, cation exchange capacity, organic matter, and sum of bases, being considered a general index of soil fertility (Miatto et al. 2016). The second one, explaining 18 % of the variation, was positively related to total nitrogen and aluminium and negatively related to available phosphorus (Miatto et al. 2016). All leaf traits but manganese and aluminium were significantly related to the first axis of the principal component analysis carried out with soil data and to vegetation type (Table 3). Conversely, only copper was significantly related to the second axis of the principal component analysis carried out with soil data (Table 3).

Decomposition rates ranged from 0.004 to 0.043  $\text{g g}^{-1} \text{d}^{-1}$  in the cerrado and from 0.003 to 0.045  $\text{g g}^{-1} \text{d}^{-1}$  in the seasonal forest. As a matter of curiosity, the decomposition rates calculated based on litter bags in a gradient of cerrado averaged 0.0006  $\text{g g}^{-1} \text{d}^{-1}$  ( $k = 0.02 \text{ g g}^{-1} \text{mo}^{-1}$ ; Silva 2013), whereas in the *cerradão* (cerrado tall woodland

**Table 1** Pearson's correlations among leaf nutrients in cerrado and seasonal forest woody species

Trait	SLA	N	P	K	Ca	Mg	S	B	Cu	Mn	Zn	Fe
N	<b>0.54</b>											
P	<b>0.41</b>	<b>0.62</b>										
K	<b>0.59</b>	<b>0.57</b>	<b>0.63</b>									
Ca	<b>0.43</b>	<b>0.25</b>	<b>0.35</b>	<b>0.59</b>								
Mg	<b>0.52</b>	<b>0.38</b>	<b>0.49</b>	<b>0.67</b>	<b>0.76</b>							
S	<b>0.32</b>	<b>0.46</b>	<b>0.45</b>	<b>0.44</b>	<b>0.22</b>	<b>0.26</b>						
B	<b>0.31</b>	<b>0.23</b>	<b>0.33</b>	<b>0.35</b>	<b>0.45</b>	<b>0.37</b>	<b>0.29</b>					
Cu	<b>0.35</b>	<b>0.32</b>	<b>0.55</b>	<b>0.37</b>	<b>0.19</b>	<b>0.32</b>	<b>0.44</b>	<b>0.34</b>				
Mn	0.07	0.06	0.06	−0.02	0	0.03	0.06	0	0.01			
Zn	<b>0.45</b>	<b>0.45</b>	<b>0.52</b>	<b>0.57</b>	<b>0.42</b>	<b>0.46</b>	<b>0.38</b>	<b>0.42</b>	<b>0.51</b>	0.12		
Fe	−0.02	0.04	<b>0.19</b>	0.03	<b>0.33</b>	<b>0.19</b>	0.16	<b>0.3</b>	<b>0.25</b>	0.1	0.15	
Al	0.02	0.04	0.09	0.12	−0.01	0.07	−0.09	−0.02	0.09	0.04	<b>0.18</b>	<b>−0.19</b>

Significant values ( $P < 0.05$ ) are in bold

**Table 2** Mean, standard deviation (SD), and ranges of each leaf trait for cerrado and seasonal forest woody species

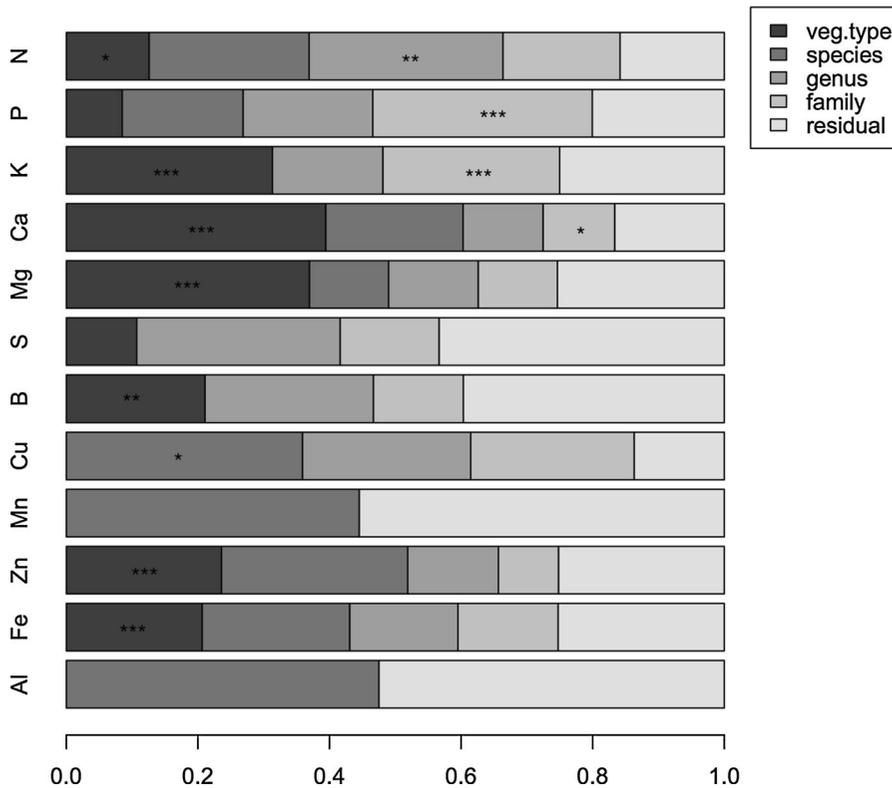
Trait (g kg <sup>−1</sup> )	Cerrado		Forest	
	Mean ± SD	Range	Mean ± SD	Range
N	<b>21.52 ± 7.63</b>	<b>10.78–43.62</b>	<b>26.29 ± 5.84</b>	<b>11.93–57.89</b>
P	<b>1.00 ± 0.38</b>	<b>0.45–2.19</b>	<b>1.25 ± 0.44</b>	<b>0.44–2.53</b>
K	<b>5.24 ± 3.27</b>	<b>1.53–16.32</b>	<b>10.83 ± 6.29</b>	<b>3.06–34.42</b>
Ca	<b>3.56 ± 1.48</b>	<b>0.92–8.47</b>	<b>8.78 ± 3.99</b>	<b>1.94–22.37</b>
Mg	<b>1.43 ± 0.51</b>	<b>0.60–2.8</b>	<b>2.72 ± 1.8</b>	<b>1.20–5.40</b>
S	1.29 ± 0.48	0.41–2.33	1.64 ± 1.50	0.59–9.90
B	<b>36.05 ± 19.88</b>	<b>10.01–157.82</b>	<b>49.79 ± 19.70</b>	<b>6.64–88.49</b>
Cu	<b>8.40 ± 5.31</b>	<b>2.50–40.50</b>	<b>11.99 ± 9.89</b>	<b>1.50–53.95</b>
Mn	174.80 ± 63.42	5.50–313.00	175.32 ± 78.97	8.00–331.00
Zn	<b>16.45 ± 5.85</b>	<b>6.90–32.66</b>	<b>23.94 ± 10.46</b>	<b>5.50–50.75</b>
Fe	<b>123.68 ± 65.90</b>	<b>47.25–359.50</b>	<b>186.5 ± 102.87</b>	<b>20.00–491.00</b>
Al	102.43 ± 42.95	7.00–181.67	101.96 ± 48.27	19.00–203.00

Significant differences between the two vegetation types ( $P < 0.05$ ) are in bold

physiognomy), they averaged  $0.00142 \text{ g g}^{-1} \text{ d}^{-1}$  ( $k = 0.52 \text{ g g}^{-1} \text{ year}^{-1}$ ; Valenti et al. 2008), and for globally distributed terrestrial plants, they averaged  $0.0082 \text{ g g}^{-1} \text{ d}^{-1}$  ( $k = 0.3 \text{ g g}^{-1} \text{ year}^{-1}$ ; Zhang et al. 2008).

The model we postulated to predict the decomposition rates was not plausible ( $P = 0$ ) but some of its paths were significant: soil features affected leaf nitrogen concentration in green leaves ( $R^2 = 0.29$ ,  $P = 0$ , Fig. 4); leaf nitrogen concentration in green leaves affected leaf nitrogen concentration in the senesced leaves ( $R^2 = 0.58$ ,  $P = 0$ , Fig. 4); and both

soil features and leaf nitrogen affected decomposition rates, considering the indirect paths ( $R^2 = 0.14$ ,  $P = 0.04$ , Fig. 4). The indirect effects given by paths *a* and *b* were significant ( $P = 0$  in both cases, Fig. 4) but the direct effect given by path *c* was not ( $P = 0.21$ , Fig. 4). The total effect was, thus, significant ( $P = 0$ , Fig. 4). Instead of having a positive effect on decomposition rates, litter nutrient content, given by nitrogen concentration in senesced leaves, exerted a negative effect on it (Figs. 4, 5). Besides, decomposition rates varied more as a function of litter nutrient content in the cerrado than in the seasonal forest (Fig. 5).



**Fig. 2** Partitioning of the total variance for each leaf trait into taxonomic (family/genus/species), environmental (vegetation type), and error (residual) components. All nutrient

concentrations are given in  $\text{g kg}^{-1}$ . Significance of each variance component was tested with a likelihood ratio test. Significance codes: \*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P < 0.05$

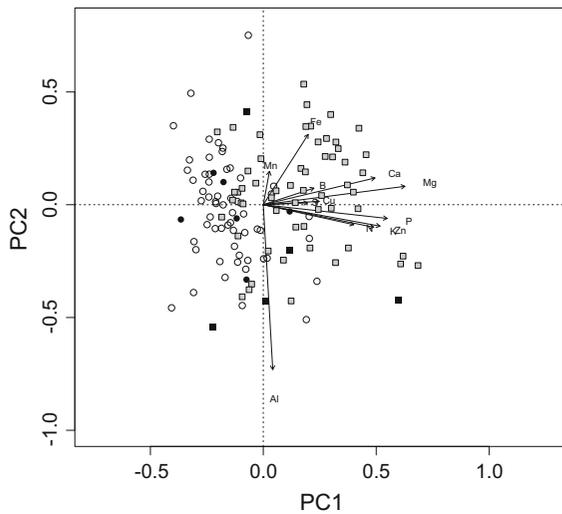
**Discussion**

Except for aluminium and manganese, leaf chemical traits were positively related to each other. Plants have basically the same requirements for nutrients devoted to growth and survival (Westoby et al. 2002). Besides, the assimilation and use of multiple elements are not independent (Zhao et al. 2016). Not only are leaf nutrients usually correlated among themselves, but they also tend to be correlated to other traits, such as leaf longevity, leaf palatability, and photosynthetic rate (Grime 1977). All these traits together form one main axis of plant variation, describing the capacity of a species to benefit from advantageous growth opportunities, so that plants in more productive conditions have higher leaf nutrient concentrations associated with rapid growth (Grime 1977).

As we expected, cerrado and seasonal forest species differed in almost all traits, with cerrado species having lower nitrogen, phosphorus, potassium, calcium, magnesium, boron, copper, and iron concentrations. Nitrogen

and phosphorus concentrations in green and senesced leaves are tightly correlated to specific leaf area and other structural traits, with cerrado species being at one extreme of the leaf economic spectrum, showing a conservative strategy, and forest species being at the other extreme, showing an acquisitive strategy (Miatto et al. 2016). Although nutrients other than nitrogen and phosphorus do not describe properly the leaf economic spectrum (Wright et al. 2005), our results indicated that the distinct strategies of cerrado and forest species have an effect over leaf nutrients concentrations in general. This is likely due to the construction costs and trade-offs involved in each strategy. Hence, while the slow growth and conservative strategy that prevail in the cerrado is associated with low specific leaf area and nutrient concentrations, the fast growth and acquisitive strategy that prevail in the seasonal forest is associated with high specific leaf area and nutrient concentrations.

Although cerrado and forest species were separated along the first principal component of leaf traits, there was not a distinction between both vegetation types in



**Fig. 3** Ordination diagram for the leaf trait matrix of the woody species in the Vaçununga State Park (21°36–47'S and 47°34–41'W). White circles represent cerrado species, gray squares represent forest species, black circles represent species common to both cerrado and seasonal forest occurring in cerrado, and black squares represent species common to both cerrado and seasonal forest occurring in the forest

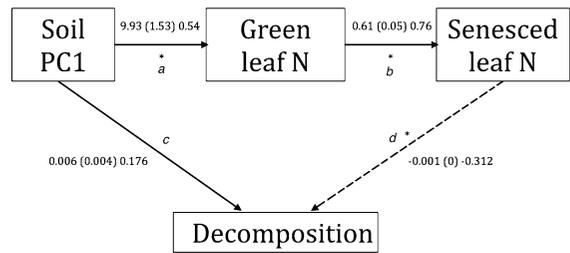
**Table 3** *P* values of the analyses of covariance between leaf trait community-weighted means as response variables and the first two principal components carried out with soil data and vegetation type as explanatory variables

Trait	Soil PC1	Soil PC2	Vegetation type	$R_{adj}^2$
N (g kg <sup>-1</sup> )	<b>&lt;0.001</b>	0.945	<b>&lt;0.001</b>	<b>0.572</b>
P (g kg <sup>-1</sup> )	<b>&lt;0.001</b>	0.361	<b>&lt;0.001</b>	<b>0.724</b>
K (g kg <sup>-1</sup> )	<b>&lt;0.001</b>	0.524	<b>&lt;0.001</b>	<b>0.740</b>
Ca (g kg <sup>-1</sup> )	<b>&lt;0.001</b>	0.082	<b>&lt;0.001</b>	<b>0.859</b>
Mg (g kg <sup>-1</sup> )	<b>&lt;0.001</b>	0.475	<b>&lt;0.001</b>	<b>0.850</b>
S (g kg <sup>-1</sup> )	<b>0.052</b>	0.949	<b>&lt;0.001</b>	<b>0.139</b>
B (g kg <sup>-1</sup> )	<b>&lt;0.001</b>	0.43	<b>&lt;0.001</b>	<b>0.711</b>
Cu (g kg <sup>-1</sup> )	<b>&lt;0.001</b>	<b>0.003</b>	<b>&lt;0.001</b>	<b>0.539</b>
Mn (g kg <sup>-1</sup> )	0.909	0.228	<b>0.015</b>	0.045
Zn (g kg <sup>-1</sup> )	<b>&lt;0.001</b>	0.517	<b>&lt;0.001</b>	<b>0.720</b>
Fe (g kg <sup>-1</sup> )	<b>&lt;0.001</b>	0.741	<b>&lt;0.001</b>	<b>0.554</b>
Al (g kg <sup>-1</sup> )	0.8448	0.659	0.4306	<b>0.834</b>
Leaf-PC1	<b>&lt;0.001</b>	0.092	<b>&lt;0.001</b>	<b>0.901</b>

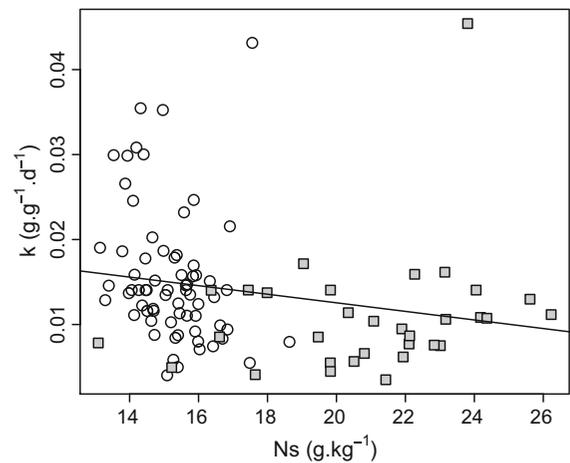
Leaf PC1 first principal component carried out with leaf trait data

Significant values (*P* < 0.05) are in bold

the second axis. Manganese was not useful in separating cerrado from forest species, probably due to its important enzymatic role and its role in phosphorus



**Fig. 4** Path analysis diagram of the relationships among soil features, leaf nutrient content, and tea decomposition rates in cerrado and seasonal forest. Solid arrows indicate positive paths; dashed arrow indicates negative path; asterisk indicates significant paths (*P* < 0.05). Values are estimate, standard error (between parentheses), and total standard. They represent, respectively, the nature and size of the relationship, the accuracy of predictions, and the standardized estimates on the variance of the variables



**Fig. 5** Decomposition rate (*k*) in relation to nitrogen concentration in senesced leaves in 100 plots in the Vaçununga State Park (21°36–47'S and 47°34–41'W). White circles represent cerrado plots and gray squares represent forest plots

uptake (Lambers et al. 2014), given that both cerrado and forest soils are equally deficient in phosphorus (Miatto et al. 2016). Aluminium was also not useful in distinguishing cerrado and forest species. Even though cerrado soils have higher aluminium concentrations, the capacity of accumulating aluminium is restricted to some families, being less expressive in the southern portion of the Cerrado domain than in other portions (Haridassan 1982; Souza et al. 2015). In addition, both the cerrado and the seasonal forest communities we studied presented some aluminium accumulators, especially among the members of *Melastomataceae* family (for a complete list of species and families found in both vegetation types, see Miatto et al. 2016).

Taxonomy exerted a strong role in leaf elemental composition, but not all traits had their variances significantly explained by taxonomy. When a taxonomic level influenced a given trait, other taxonomic levels did not: for example, genera accounted for leaf nitrogen concentration but not family or species; family accounted for leaf phosphorus concentration, but not genera or species. Similar patterns have been found for other floras (Broadley et al. 2004; Watanabe et al. 2007; Han et al. 2011; Zhang et al. 2012; Metali et al. 2015). Plant taxa may differ in their nutritional requirements and nutrient uptake capabilities (Han et al. 2011; Xing et al. 2015). The partitioning of the variation at different taxonomic levels could be then a result of differential controls over chemical trait variation, which, in turn, would be related to their differential roles in plant functioning. Additionally, it could also be a consequence of different selective forces over time (Asner et al. 2012). Both the differential control over chemical traits due to plant functional regulation and the effect of selective forces support the different axes of leaf elemental composition we found in this study and somehow found by other researches (Garten 1976, 1978; Watanabe et al. 2007; Zhang et al. 2012).

Even though taxonomy considerably explained the variation in leaf elemental composition of both cerrado and seasonal forest, it cannot be totally isolated from environmental factors (Westoby et al. 1995). As a whole, environment accounted for a smaller percentage of explanation, but its effect on each leaf chemical trait was more pronounced, except for nitrogen and phosphorus. Leaf nitrogen and phosphorus were notably much less influenced by vegetation type than by taxonomy when compared to the other elements, which is supported by the “stability of limiting elements” (Han et al. 2011), a theory that states that, for nutrients needed in higher concentrations in leaves and often limiting, plants should have lower sensitivity along environmental gradients. Low nitrogen and phosphorus concentrations in plant tissue should be constrained by stoichiometry requirements, as it would cause suboptimal growth. Similarly, high concentrations would also be unlikely, because an increased availability in nitrogen and phosphorus would lead to higher growth rates, with a consequent dilution of these nutrients in plant tissues (Han et al. 2011).

Almost all leaf nutrients were related to the first axis of the soil ordination, reinforcing the

environmental influence on leaf elemental composition. Soil drives plant functional traits through multiple nutrient controls on leaf traits and strengthens the importance of both cerrado and seasonal forest floras in redistributing nutrients from the soil (Jobbágy and Jackson 2004; Paiva et al. 2015). Likely, the significant effects of vegetation type on leaf nutrient concentration partitioning were due to the contrasting soil environments between cerrado and seasonal forest. Viani et al. (2014), however, did not find many differences in leaf nutrient concentrations and responsiveness to soil nutrient status between *cerradão*, the tall and closed woodland physiognomy of cerrado (Coutinho 1978), and seasonal forest. While they suggest that *cerradão* and seasonal forest have balanced nutrient acquisition and growth strategies despite less fertile soils in the former, we suggest the contrary when considering cerrado *sensu stricto*, a savanna physiognomy of the cerrado (Coutinho 1978): that there are considerable differences in nutrient use and growth strategies. These contrasting patterns found for soil–plant relationships in spatially close cerrado-forest transitions also suggest a need for additional broad-range studies.

Soil did not exert a direct effect on decomposition rates, only contributing indirectly, through its effects on green and senesced leaves nutrient concentrations. In fact, there is a tendency for leaf litter quality and climate to be more important for decomposition rates than soil features itself (Hector et al. 2000; Hättenschwiler et al. 2011), even though the effect of soil may sometimes prevail (Delgado-Baquerizo et al. 2015).

The importance of macro- and micronutrients for litter decomposition has been experimentally demonstrated (Kaspari et al. 2008; Powers and Salute 2011). Besides the effect of direct fertilization, it is also recognized that fresh leaf and litter leaf nutrients can be crucial for litter decomposition rates (Cornwell et al. 2008; Bakker et al. 2011). Sometimes, the effect of a single element can be even a stronger predictor of decomposition rates than the effect of multiple elements, especially for nitrogen (Bakker et al. 2011). We expected green and senesced leaf nitrogen would create favorable conditions for the decomposers activities. Conversely, the relationships between leaf nutrients in the surrounding litter and decomposition rates were opposite from the expected, and the decomposition rates varied more as a function

of the surrounding litter nutrient concentration in the cerrado than in the seasonal forest. This higher variation in the decomposition rates among cerrado plots in comparison to seasonal forest ones could even have strengthened the negative relationship between leaf nutrients in the surrounding litter and decomposition rates.

One possible explanation for the higher variation in the decomposition rates in cerrado is that the cerrado microorganisms and mesofauna, probably used to low-nutrient and tough leaves, were more plastic and more active in decomposing the teas than the forest ones. For instance, at least for soil isotopes, feeding preference can be determined by litter leaf toughness, irrespective of the prevailing or native litter type (Soma and Saitô 1983; Catalán et al. 2008; Quadros et al. 2014). Alternatively, the high spatial and temporal variability in canopy cover and understory light in cerrado (Lemos-Filho et al. 2010) might have created a more diversified environment for litter decomposition in terms of light and temperature, favoring the high range of decomposition rates in comparison to the more homogeneous canopy cover across the forest plots. As a matter of fact, light and temperature may enhance the microorganisms activity directly and indirectly, via leaf photodegradation with degradation of litter lignin or through its effects on soil organic matter (King et al. 2012; Bakker and Allison 2015; Austin et al. 2016). Besides, the effect of fresh leaf nutrients in creating microhabitats may not always be linear to the decomposer diversity and to decomposition rates due to the complexity and niche complementarity among decomposers (Hättenschwiler et al. 2011).

Although taxonomy accounted for a large part of the variation in leaf nutrient-related traits, our results showed that soil exerts an important role on the traits and strategies of both cerrado and seasonal forest woody species and that this is carried out through multi-elemental soil control. Nevertheless, the effect of such different strategies on functioning is less prominent, at least when accounting only for their indirect effects on decomposition rates. Our results reinforced that soil nutrient status and plant–soil feedbacks are crucial for the maintenance of the alternate stable states of cerrado and seasonal forest vegetation. Consequently, the cerrado vegetation may be impacted or even replaced by the seasonal forest, since it is susceptible to eutrophication (Hunke et al.

2015), even though we were not able to predict the magnitude of functioning change through the actual decomposition rates.

**Acknowledgments** The authors thank the São Paulo Research Foundation (Fapesp, grant 2012/18295-4) and the Coordination for the Improvement of Higher Education Personnel (Capes, grant BEX 12105/13-9) for the scholarships granted to RCM; the National Council for Scientific and Technological Development, for financial support and scholarship granted to MAB (CNPq, grant 305912/2013-5); the São Paulo Forestry Institute, for the research permit; the Vaçununga State Park staff, for logistical assistance; M Groppo and WM Mantovani, for help with species identification; GH Carvalho, for suggesting the tea bag method; the Tea Bag Team, for help with the decomposition rate calculation; N Abe, ALS Albino, AL Braga, E Carmargo, KR Coelho, P Dodonov, JR Freitas, CS Gonçalves, R. Grazziano, DT Gregolin, LA Joaquim, MB Leite, WB Nascimento, LV Nóbrega, BA Severian, and CB Zanelli, for help with field work; and MC Scalon for revising a previous version of this manuscript.

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