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Vegetation structure: Fine scale relationships with soil in a cerrado site

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ABSTRACT

There is a lack of understanding on factors influencing the occurrence of high species heterogeneity at fine scale in the Brazilian cerrado. Soil is a major determinant of vegetation in the Brazilian cerrado and an important candidate to influence species distribution at fine scales, since soil features vary at very small distances, whereas many environmental variables are relatively homogeneous at such scale. We tested plant–soil relationships at fine scales in a cerrado site. We placed 100 contiguous 25 m² plots, where we identified all woody individuals and measured several soil features. We did partial redundancy analysis, controlling for spatial autocorrelation, to test for relationships between soil features and floristic composition. We also did multiple regressions or spatial autoregressive models to test for relationships between soil features and: (1) the abundance of the five most common species, (2) total abundance, (3) richness, (4) evenness, and (5) diversity. We found weak relationships between soil and floristic composition, richness, and total abundance, which, coupled with also weak relationship found in another study with plant available water, indicate there is no major environmental variable influencing vegetation at fine scales, but several of them interacting. Organic matter was positively related with the abundance of *Myrsine umbellata* and was negatively related to evenness. Although a causal relationship cannot be inferred with certainty, the dominance of *Myrsine umbellata* seems to be related to a positive feedback with soil.

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Introduction

The Brazilian cerrado is the richest savanna in the world, with about 7000 plant species, of which about 1500 are shrubs or trees (Castro et al., 1999). Due to its high species richness, high degree of endemism, and present conservation status, the cerrado is one of the biodiversity hotspots in the world (Myers et al., 2000). High species turnover can be found at very small distances in cerrado, and there is a great number of species even in small areas (Carvalho and Martins, 2009; Silva and Batalha, 2009). However, there is a lack of studies about the determinants of this heterogeneity at fine scales (Ferreira et al., 2009).

Together with fire and climatic seasonality, soil is a main determinant of changes in plant species and vegetation structure in the Brazilian cerrado, whose physiognomic variation is considered by some authors (for example, Goodland and Pollard, 1973) to be a fertility gradient. The cerrado tends to occur on well-drained, acid, and nutrient-poor soils, with high levels of exchangeable aluminum, and, at increased water availability or soil fertility, it tends to be replaced by forest (Goodland and Ferri, 1979; Oliveira-Filho and Ratter, 2002). The cerrado productivity gradient is related to higher

availability of bases in the soil (Goodland and Ferri, 1979), whereas the sclerophyllous features of the cerrado vegetation are attributed to direct and indirect effects of high aluminum contents and low nutrient availability (Arens, 1958, 1963; Goodland and Ferri, 1979; Sarmiento, 1984). Aluminum is also related to changes in species richness between cerrado physiognomies (Carvalho and Martins, 2009).

Although many studies found relationships between soil conditions and plant species composition when moving from cerrado to other vegetation types (Amorim and Batalha, 2007; Ruggiero et al., 2002), the relationship between soil conditions and the occurrence of different cerrado physiognomies is controversial, since some studies did not find it (Amorim and Batalha, 2007; Marimon and Haridasan, 2005; Ruggiero et al., 2002), whereas others did (Carvalho and Martins, 2009; Goodland and Pollard, 1973). However, there is a lack of studies in cerrado about the determinants of vegetation at fine scales (Ferreira et al., 2009). Since in the cerrado many woody species can be found in relatively small areas (Oliveira-Filho and Ratter, 2002), fine scale studies may allow to understand what drives cerrado plant responses to the environment. As long as changes in soil features can be found at distances as small as 1 m (Souza and Martins, 2004), soil is an important candidate to exert fine scale effects upon the cerrado vegetation, because, at such a fine scale, other factors like climate and fire frequency, are more homogeneous.

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We assumed soil to be an important environmental filter at fine scale in cerrado plant communities. Thus, we expected floristic composition to change with fertility, reflecting, to some extent, success in exploiting resources and competing with other species (Magurran, 2004). Therefore we looked for relationships between soil and vegetation at fine scale in a cerrado site, trying to answer the following questions: (1) Is floristic composition related to soil features? (2) Are total abundance, richness, evenness, and diversity related to soil features? Moreover, species not only respond to soil, but also influence it as well (Ruggiero et al., 2002; Silva et al., 2008; Sparovek and Camargo, 1997). Additionally, we expected that, on nutrient-rich soils, where competition may be lower (Bertness and Callaway, 1994; MacArthur, 1972), total abundance, richness, evenness, and diversity would be higher.

Material and methods

We studied a cerrado woodland site at Federal University of São Carlos, southeastern Brazil (approximately 21°58'05.3"S, 47°52'10.1"W). The area is on dystrophic Oxisols, 850 m asl, under mesothermic, subtropical climate, with wet summers and dry winters (Cwa; Köppen, 1931). Mean annual temperature and precipitation lie around 21.3 °C and 1315 mm, respectively.

We placed a grid of 100 5 m × 5 m contiguous plots and sampled all individuals of the woody component (stem diameter at soil level ≥ 3 cm; SMA, 1997). We identified them to species level using identification keys based on vegetative characters (Batalha and Mantovani, 1999; Mantovani et al., 1985). We used the program 'Plantminer' (Carvalho et al., 2010) to correct species names, to find author names of all species, and to include them into families according to the latest phylogenetic classification.

We collected soil samples from soil surface (0–5 cm deep), the most correlated with cerrado vegetation structure (Amorim and Batalha, 2006; Ruggiero et al., 2002). In each plot, we collected a composite sample, mixing five sub-samples, four in the corners of each plot and one in the center. They were analysed at the University of São Paulo, according to prescriptions and protocols by Embrapa (1997), Silva (1999), and Raij et al. (1987). We determined pH, organic matter, available phosphorus, total nitrogen, and exchangeable K⁺, Ca²⁺, Mg²⁺, and Al³⁺. We calculated sum of bases, cation exchange capacity, base saturation, and aluminum saturation. We also determined sand, silt, and clay proportions.

Soil pH was determined in CaCl₂ solution, using 10 ml of soil in 25 ml of solution. CaCl₂ was used to avoid salt and oxides influences. Organic matter was determined by organic carbon oxidation with potassium dichromate and subsequent potassium dichromate titration with ammonium ferrous sulfate, using 0.5 g of soil and 10 ml of potassium dichromate solution. A correction factor (1.33) was used to compensate partial carbon oxidation. Available phosphorus was determined by spectrophotometry after anion exchange resin extraction, using 2.5 cm³ of soil. Total nitrogen was determined by digestion with H₂SO₄, followed by distillation with NaOH, using from 0.5 to 1 g of soil, 1 g of H₂SO₄, and 15 ml of NaOH. The cations K⁺, Ca²⁺, Mg²⁺, and Al³⁺ were extracted with 1 M KCl, using 10 cm³ of soil and 100 ml of solution. Then, potassium, calcium, and magnesium were determined by an EDTA complexometry. Aluminum was determined by NaOH titration. Sum of bases was calculated as the sum of potassium, calcium, and magnesium. Cation exchange capacity was calculated as sum of bases plus H⁺ and Al³⁺ concentrations. Base saturation was calculated as a percentage of total cation exchange capacity. Aluminum saturation was calculated as a percentage of sum of bases and Al³⁺. We quantified soil sand, silt, and clay proportions using the Boyoucos method: first, soil particles were settled using a dispersant, suspension was separated from the sediment, and clay content was calculated by suspension density

using a densimeter; then, the sediment was sieved to separate the sand, which was weighted. Silt proportion was calculated by the difference.

When necessary, we transformed variables to achieve normality. We calculated correlograms using Moran index (Moran, 1950) as a spatial autocorrelation index. Subsequently, we used only those soil variables that had the range of variation between positive and negative autocorrelation at distances smaller than 25 m, since, in this case, soil features would have enough variability to influence plant species distribution. Although the greatest distance between pairs of plots was higher than 50 m, beyond 25 m the results for spatial autocorrelation tests were not reliable due to the small number of pairs of plots.

To avoid collinearity, we tested for correlations among soil variables and, when the coefficient of correlation was higher than 0.7, we excluded one of the soil features in the subsequent analysis. We preferred more synthetic variables – that are the ones calculated from others or correlated with as many unused variables as possible. We standardized soil variables to zero mean and unit variance. To answer the first question, we did a partial redundancy analysis (Jongman et al., 1995), using the vegetation and soil matrices, and using the spatial coordinates to control for spatial autocorrelation. We also selected the five most common species and did stepwise multiple regressions with soil features as explanatory variables. When we found significant relationships in the multiple regressions, we tested the residuals for spatial autocorrelation with Moran's index, since spatial dependence could cause type I error (Dormann et al., 2007). As long as residuals were normally distributed, we used the autoregressive model to account for spatial autocorrelation (Dormann et al., 2007). To answer the second question, we counted the numbers of individuals (abundance) and species (richness) per plot and calculated evenness (Pielou, 1975) and Shannon's diversity (Shannon and Weaver, 1949). Using them as response variables, we also did multiple regressions or autoregressive models. We selected the best stepwise model, using the Akaike Information Criteria (AIC). In the cases in which it was necessary to correct spatial dependence, we tested the residuals of autoregressive models for autocorrelation, to check whether the analyses were capable of removing spatial dependence from the data. We did all analyses in R (R Development Core Team, 2009), using the vegan (Oksanen et al., 2009) and spdep (Bivand et al., 2009) packages.

Results

We sampled 2062 individuals, belonging to 61 species and 27 families. The five commonest species were *Myrsine umbellata* Mart. (567 individuals), *Vochysia tucanorum* Mart. (168 individuals), *Myrcia guianensis* (Aubl.) DC. (131 individuals), *Miconia albicans* (Sw.) Triana (125 individuals), and *Piptocarpha rotundifolia* (Less.) Baker (103 individuals). The richest families were Fabaceae (with eight species), Myrtaceae (with six species), Malpighiaceae and Melastomataceae (with four species each), and Annonaceae, Erythroxylaceae, and Rubiaceae (with three species each), summing 50% of all species sampled.

Soil was, on average, dystrophic (P = 5 mmol_c/kg, K⁺ = 1 mmol_c/kg, Mg²⁺ = 2 mmol_c/kg, Ca²⁺ = 3 mmol_c/kg), acidic (pH < 4), and with high concentration of Al³⁺ (17 mmol_c/kg) (Appendix A). The soil features that showed a complete range of variation at the scale of our study were organic matter, calcium, aluminum, sum of bases, aluminum saturation, cation exchange capacity, and H + Al. Many of these variables were correlated with each other (Table 1) and, thus, for statistical analyses, we used only organic matter, sum of bases, and aluminum saturation, which were not correlated with each other ($r < 0.7$), and are related to

Table 1

Pearson's correlation for soil variables varying within the scale of our study. OM (organic matter; g/kg); Ca²⁺ (mg/kg); Al³⁺ (mmolc/kg); SB (sum of bases; mmolc/kg); m (aluminum saturation; %); CEC (cation exchange capacity; mmolc/kg); H+Al (mg/kg). Data were collected in a cerrado site at São Carlos, Brazil (approximately, 21°58'05.3"S, 47°52'10.1"W).

	OM	Ca ²⁺	Al ³⁺	SB	m	CEC	H+Al
OM	1.00	–	–	–	–	–	–
Ca ²⁺	0.30	1.00	–	–	–	–	–
Al ³⁺	0.66	–0.16	1.00	–	–	–	–
SB	0.42	0.94	–0.09	1.00	–	–	–
m	0.03	–0.82	0.61	–0.83	1.00	–	–
CEC	0.82	0.12	0.74	0.23	0.23	1.00	–
H+Al	0.78	0.01	0.77	0.12	0.34	0.99	1.00

many others. Organic matter is related to the availability of macro- and micronutrients (Salisbury and Ross, 1991) and to better soil physical properties (Motta et al., 2002); sum of bases is related to the availability of magnesium, potassium, and calcium (see "Methods"); and aluminum seems to be important generally in determining the distribution of the cerrado vegetation (Arens, 1963; Carvalho and Martins, 2009; Goodland and Pollard, 1973; Ruggiero et al., 2002). All community descriptors presented large ranges of variation, but Shannon's diversity presented the smallest range (Appendix A).

The first axis of the redundancy analysis explained 12.86% ($p=0.005$) of the variation in floristic composition and was more related to organic matter and exchangeable aluminum, whereas the second axis explained only 0.02% and was not significant (Fig. 1). The most common species, *Myrsine umbellata*, showed a significant relationship with soil, but only with organic matter ($Rho=0.63$; $p<0.001$; Table 2). The other four commonest species showed no relationship with soil features. Total abundance was weakly, but in a significant way, positively related to organic matter ($R^2=0.16$; $p<0.001$). Species richness was also weakly correlated with sum of bases ($R^2=0.11$; $p=0.002$). Evenness was negatively related with organic matter ($Rho=0.59$, $p<0.001$). We found no relationship between diversity and soil features (Table 2). The use of autoregressive models to correct spatial autocorrelation was efficient, since we found no significant autocorrelation in the residuals of the autoregressive regression model. Moreover, after correcting for spatial autocorrelation, the explanatory power of soil variables increased (Table 2).

Table 2

Regression analyses using the abundance of the five commonest species, total abundance, richness, evenness, and diversity as response variables and soil features as explanatory variables. Best model selected according to the Akaike Information Criterion. Soil features were: OM (organic matter; g/kg); Al³⁺ (mmolc/kg); SB (sum of bases; mmolc/kg). Data collected in a cerrado site at São Carlos, Brazil (approximately, 21°58'05.3"S, 47°52'10.1"W).

	Best stepwise model	R ² ^a	Moran's ssd ^b	Rho ^c	Moran's ssd ^d	OM ^e	Al ³⁺ ^e	SB ^e
<i>Myrsine umbellata</i>	OM, SB	0.22 ^{***}	5.54 ^{***}	0.63 ^{***}	–0.16 ^{ns}	4.4 ^{***}	–	–1.18 ^{ns}
<i>Vochysia tucanorum</i>	OM, Al ³⁺ , SB	0.01 ^{ns}	–	–	–	0.23 ^{ns}	–0.23 ^{ns}	0.46 ^{ns}
<i>Myrcia guianensis</i>	OM, Al ³⁺ , SB	0.03 ^{ns}	–	–	–	0.81 ^{ns}	0.07 ^{ns}	–1.19
<i>Miconia albicans</i>	OM, Al ³⁺ , SB	0.01 ^{ns}	–	–	–	0.19 ^{ns}	–0.26 ^{ns}	0.28 ^{ns}
<i>Piptocarpha rotundifolia</i>	SB	0.01 ^{ns}	–	–	–	–	0.23 ^{ns}	–
Total abundance	OM	0.16 ^{***}	1.57 ^{ns}	–	–	4.4 ^{***}	–	–
Richness	Al ³⁺ , SB	0.11 ^{**}	–0.17 ^{ns}	–	–	–	1.71 ^{ns}	3.16 ^{**}
Pielou's evenness	OM, SB	0.13 ^{***}	5.12 ^{***}	0.59 ^{***}	0.19 ^{ns}	–3.22 ^{***}	–	0.50 ^{ns}
Diversity	OM, SB	0.06 [*]	3.26 ^{***}	0.42 [*]	–0.11 ^{ns}	0.22 ^{ns}	–	0.14 ^{ns}

^a Coefficient of multiple regression (linear regression when there is one variable in the model).

^b Moran's statistic standard deviate before correcting for spatial dependence.

^c Rho statistic for autoregressive models.

^d Moran's statistic standard deviate after correcting for spatial dependence.

^e t statistic for each variable include in the model; ns: not significant.

* $p<0.05$.

** $p<0.01$.

*** $p<0.001$; p-values refer to the regression analysis.

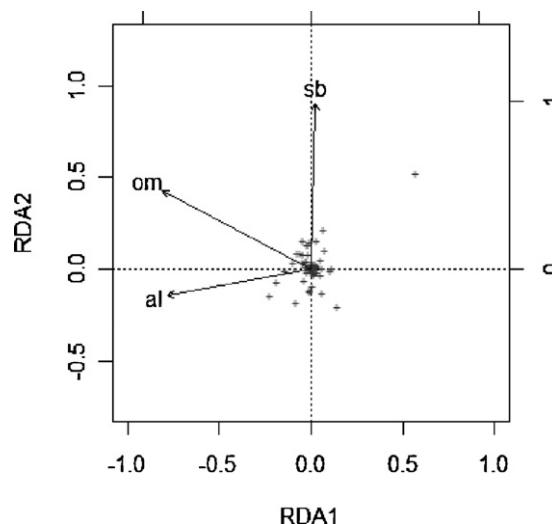


Fig. 1. Redundancy analysis biplot using floristic composition and soil features. Soil features: om = Organic matter (g/kg); al = Al³⁺ (mmolc/kg); sb = sum of bases; mmolc/kg). The crosses represent species. First axis was significant, more related to OM and Al³⁺, and explained 12% of the variation. Second axis was not significant. Data collected in a cerrado site at São Carlos, Brazil (approximately, 21°58'05.3"S, 47°52'10.1"W).

Discussion

Albeit significant, we found low explanatory power for floristic composition, richness, and total abundance in relation to soil features at fine scale. However, in contrast to some other studies carried out at larger scales, which found no relationship between vegetation and soil in cerrado (Amorim and Batalha, 2007; Marimon and Haridasan, 2005; Ruggiero et al., 2002), our results indicated that soil does have an influence, to some extent, on the distribution of woody species at fine scales. Ferreira et al. (2009) also found low, but significant, relationships of floristic composition and total abundance with plant available water at fine scale. In this sense, plant available water, together with soil features, could explain an important proportion of plant distribution at fine scales in cerrado sites.

It is worth considering that the low relationships found between floristic composition and soil features could be either related to stochastic events influencing the distribution of plants and soil or

be determined by dispersal and recruitment limitations, which is common in species-rich communities (Hubbell, 2001, 2005). Moreover, past events, such as fires (Silva and Batalha, 2008) or herbivory (Coley et al., 1985), could also influence the patterns of species and soil features distribution in the community. However, analyses as those used here generally remove the effect of spatial patterns generated by unconsidered variables (Fortin and Dale, 2005) and, thus, soil indeed seems to exert some influence in cerrado floristic composition at fine scales.

Evenness and abundance of *Myrsine umbellata* were related to the availability of organic matter. Organic matter is related to high soil fertility, since its negatively charged surfaces retain nutrients and some organic molecules can chelate micronutrients, making them available for plant roots (Salisbury and Ross, 1991). Moreover, organic matter provides clay aggregation stability, which allows water and air to move through the soil and allows roots to penetrate with little resistance (Motta et al., 2002). Organic matter may be even more important than clay in providing nutrients for plants in cerrado communities (Goodland and Ferri, 1979). This could be seen as an indication of soil preferences of *Myrsine umbellata*, which could be unable to grow on low fertility sites. Given that changes in organic matter in surface soil are likely to be caused by the vegetation itself (Ruggiero et al., 2002; Silva et al., 2008; Sparovek and Camargo, 1997), we could also postulate that this species is capable of incrementing the content of organic matter in cerrado soils. If these changes in soil organic matter help to increase its fitness, a mechanism of positive feedback (Kulmatisky et al., 2008) may explain the dominance of this species. Nevertheless, we cannot infer whether the dominance of *Myrsine umbellata* is the cause or the consequence of the high content of organic matter found in the soil. Studying the mechanism behind this relationship could help to understand how successional processes occur in cerrado. For example, it was proposed that, under fertile soils and in the absence of fire, the colonisation of cerrado by nearby species, typically occurring in forest formations, is likely to happen (Oliveira-Filho and Ratter, 2002; Silva et al., 2008). Since *Myrsine umbellata* also occurs in forest formations (Funch and Funch, 2002; Martins et al., 2004; Oliverira-Filho and Fontes, 2000), studying this mechanism could provide insights to discuss the idea of expansion of forest over cerrado (Silva et al., 2008).

Evenness was also related to organic matter, but since *Myrsine umbellata* was by far the most abundant species at the community, with more than twice the abundance of the second most abundant species, this relationship was probably influenced by this species. However, since the dominance of other species may be also influencing evenness, it can be supposed that in richer soils there is a tendency of greater dominance at fine scales. Maybe other species could also present positive feedbacks at fine scales.

Richness showed a weak positive relationship with sum of bases. This could be related to weak environmental filtering in nutrient-poor soils. More resources in nutrient-rich soils will allow the coexistence of more species. However, the low explanatory power of the correlations indicated that soil was not the major factor limiting the coexistence of species at fine scales. Since cerrado species have evolved in nutrient-poor soils, they generally should be adapted to subsist upon low levels of nutrients, and the distribution of species may be more related to dispersal and recruitment limitations – or stochastic (Hubbell, 2001, 2005). We did not find any relationship between richness and exchangeable aluminum, contrary to Carvalho and Martins (2009), who compared different cerrado physiognomies. Maybe, at the fine scale, variations in aluminum are not be wide enough to influence plants, especially because cerrado species are adapted growing on soil with high levels of this element (Sarmiento, 1984). Richness and evenness were related to different non-correlated soil features, and these two community descriptors are characterizing diversity. May be that the lack of relationship between diversity and soil features reflects different spatial distribution patterns of the sum of bases (positively related with richness) and of organic matter (positively related with evenness) that might cancel out each other.

In conclusion, although soil was not a main factor causing variations in floristic composition, richness, or total abundance, there was a low but significant relationship between soil and these descriptors. Soil seems to influence, to some extent, the occurrence of species in the community, but other factors such as water availability or dispersal and recruitment limitations, and also stochastic events, should be considered when an interpretation or even prediction is attempted for plant species turnover at fine scales in cerrado sites.

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Appendix A.

See Table A1.

Table A1 (Continued)

Quadrat	Total abundance	Richness	Evenness	Diversity	pH	OM	N	P	K ⁺	Ca ²⁺	Mg ²⁺	Al ³⁺	H+Al	SB	CEC	V	m	Sand	Silt	Clay
77	10	8	0.97	2.03	3.7	35	1708	2	0.9	2	2	12	60	4.9	64.9	8	71	69	3	28
78	6	5	0.97	1.56	3.8	30	1652	2	0.7	1	1	11	52	2.7	54.7	5	80	69	3	28
79	17	9	0.91	2.00	3.7	38	1428	2	0.9	2	2	14	73	4.9	77.9	6	74	68	4	28
80	21	9	0.89	1.95	3.7	33	1870	2	1.0	2	2	15	44	5.0	49.0	10	75	67	2	31
81	10	8	0.97	2.03	3.8	36	1960	3	1.0	2	2	14	72	5.0	77.0	6	74	70	2	28
82	26	9	0.82	1.80	3.6	49	1904	4	1.1	2	2	19	93	5.1	98.1	5	79	72	3	25
83	26	9	0.71	1.57	3.5	47	1670	4	1.0	2	2	22	88	5.0	93.0	5	81	68	4	28
84	16	9	0.90	1.98	3.5	47	2010	4	1.2	2	2	26	100	5.2	105.2	5	83	68	4	28
85	25	9	0.83	1.83	3.6	47	1680	4	1.0	2	2	19	88	5.0	93.0	5	79	70	2	28
86	24	7	0.62	1.21	3.6	33	1875	3	1.1	2	2	17	73	5.1	78.1	7	77	67	3	30
87	24	12	0.85	2.12	3.5	46	1860	3	1.1	2	2	21	95	5.1	100.1	5	80	66	4	30
88	18	8	0.90	1.88	3.6	42	1950	4	1.1	1	1	20	85	3.1	88.1	4	87	68	4	28
89	14	9	0.96	2.11	3.6	36	1710	4	0.9	2	2	19	74	4.9	78.9	6	79	69	6	25
90	29	7	0.83	1.62	3.6	41	1510	4	1.1	2	2	17	81	5.1	86.1	6	77	68	4	28
91	18	10	0.90	2.06	3.7	39	1704	4	0.9	2	2	18	82	4.9	86.9	6	79	68	4	28
92	23	12	0.84	2.09	3.5	50	1655	4	0.8	2	2	20	91	4.8	95.8	5	81	68	4	28
93	32	10	0.69	1.58	3.3	65	2600	5	1.2	2	2	29	124	5.2	129.2	4	85	69	6	25
94	39	9	0.49	1.08	3.4	57	2190	4	1.5	3	3	24	101	7.5	108.5	7	76	68	4	28
95	22	9	0.80	1.77	3.5	55	2240	5	1.4	4	4	25	106	9.4	115.4	8	73	69	6	25
96	36	10	0.77	1.76	3.6	46	2352	3	1.2	3	3	18	90	7.2	97.2	7	71	67	3	30
97	22	9	0.73	1.61	3.5	46	2110	4	1.6	3	2	19	97	6.6	103.6	6	74	67	3	30
98	22	9	0.92	2.02	3.7	40	1764	4	1.0	3	2	18	81	6.0	87.0	7	75	69	3	28
99	13	7	0.84	1.63	3.6	40	1792	3	0.9	3	1	16	80	4.9	84.9	6	77	69	3	28
100	33	12	0.82	2.04	3.7	39	1486	3	0.9	3	1	16	72	4.9	76.9	6	77	69	3	28
Mean	20.62	9.66	0.87	1.96	4	43	1740	5	1	3	2	17	80	7	87	8	72	68	3	28

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