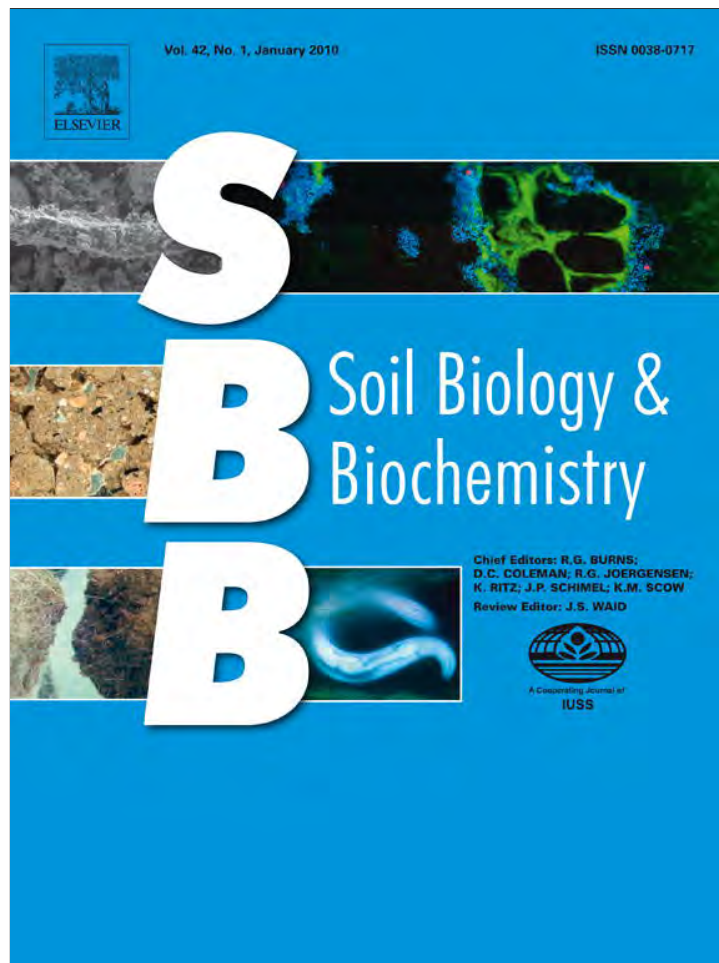


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Review

Three decades of soil microbial biomass studies in Brazilian ecosystems: Lessons learned about soil quality and indications for improving sustainability

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ABSTRACT

Soil microbial biomass plays important roles in nutrient cycling, plant–pathogen suppression, decomposition of residues and degradation of pollutants; therefore, it is often regarded as a good indicator of soil quality. We reviewed more than a hundred studies in which microbial biomass-C (MB-C), microbial quotient (MB-C/TSOC, total soil organic carbon) and metabolic quotient ($q\text{CO}_2$) were evaluated with the objective of understanding MB-C responses to various soil-management practices in Brazilian ecosystems. These practices included tillage systems, crop rotations, pastures, organic farming, inputs of industrial residues and urban sewage sludge, applications of agrochemicals and burning. With a meta-analysis of 233 data points, we confirmed the benefits of no-tillage in preserving MB-C and reducing $q\text{CO}_2$ in comparison to conventional tillage. A large number of studies described increases in MB-C and MB-C/TSOC due to permanent organic farming, also benefits from crop rotations particularly with several species involved, whereas application of agrochemicals and burning severely disturbed soil microbial communities. The MB-C decreased in overgrazed pastures, but increased in pastures rotated with well-managed crops. Responses of MB-C, MB-C/TSOC and $q\text{CO}_2$ to amendment with organic industrial residues varied with residue type, dose applied and soil texture. In conclusion, MB-C and related parameters were, indeed, useful indicators of soil quality in various Brazilian ecosystems. However, direct relationships between MB-C and nutrient-cycling dynamics, microbial diversity and functionality are still unclear. Further studies are needed to develop strategies to maximize beneficial effects of microbial communities on soil fertility and crop productivity.

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1. Introduction

Soil microbial biomass-C (MB-C) is the living portion of soil organic matter, constituted by archaea, bacteria and eukaryotes, excluding roots and animals smaller than $5 \times 10^3 \mu\text{m}^3$ (e.g. Jenkinson and Ladd, 1981). Fungi, bacteria and archaea represent 75–98%, protists 1–6%, and meso- and macro-fauna (microarthropods, macroarthropods, enchytraeids and earthworms) only a minor fraction of total living biomass in soil (Beare, 1997). The MB-C has been correlated with several functional microorganisms, such as ammonifiers and nitrifiers (Andrade et al., 1995), microbial diversity (Nogueira et al., 2006), legume-nodulating bacterial populations (Pereira et al., 2007) and enzyme activities in the soil (Matsuoka et al., 2003; Mendes et al., 2003; Balota et al., 2004b). Furthermore, the MB-C could be related to diverse soil processes, including decomposition of organic residues, nutrient cycling, solubilization of

nutrients (particularly phosphates), degradation of xenobiotic compounds and pollutants, soil structuring, organic matter storage, and biological control and suppression of plant pathogens; and for that reason, it has often been indicated as an important component for maintaining soil quality and plant productivity (Nogueira et al., 2006; Roscoe et al., 2006).

Three decades after publication of the first method for MB-C evaluation (Jenkinson and Powlson, 1976), several studies have been made on MB-C in ecosystems in Brazil, most of which are published in national journals and proceedings in Portuguese. The purpose of this paper is to review many of these studies identifying patterns in MB-C responses to various land uses in Brazilian ecosystems, emphasizing gaps in knowledge to inspire future research.

2. Methods for evaluation of MB-C

Prior to three decades ago, MB-C could be estimated only by microscopic observations by trained personnel with sophisticated equipment. Then Jenkinson and Powlson (1976) described the fumigation–incubation approach (FI), a much less subjective method to evaluate MB-C, based on fumigation, re-inoculation with

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live microbial biomass, incubation under controlled conditions, and measurement of differences of CO₂ fluxes between fumigated and non-fumigated soils. Later, Vance et al. (1987) proposed the fumigation–extraction method (FE), a modification to extract contents of MB-C with chemicals, immediately after fumigation.

Initially, Jenkinson and Powlson (1976) assumed that 50% of MB-C is effectively mineralized during an incubation period of 10 days, resulting in a coefficient for conversion of $K_C = 0.50$. Later, Jenkinson and Ladd (1981) proposed $K_C = 0.45$ assuming a bacterial to fungal biomass of 1:3, which could be applied to different soils without serious error, and since then, this value has been widely accepted. Values of K_C could be slightly different under tropical conditions, and indeed, Sampaio et al. (1986) incubated known amounts of microbes in several Brazilian soils and concluded that a $K_C = 0.41$ was more representative for tropical soils. Furthermore, this value is in accordance with estimates obtained elsewhere [e.g. $K_C = 0.41$ by Anderson and Domsch (1978)] under temperate conditions.

With regard to the FE method, Roscoe et al. (2006) observed that evaluations of MB-C in Brazil were normally based on K_{CE} (which have similar meaning to K_C but is related to FE method) varying from 0.30 to 0.38, and suggested that values lower than 0.33, as utilized by Vance et al. (1987) under temperate conditions, probably overestimate MB-C under tropical conditions. Roscoe et al. (2006) calibrated the relationship between FI and FE methods with MB-C measurements in several Brazilian studies, and suggested that a $K_{CE} = 0.40$ was more appropriated for tropical conditions. Therefore in this review, the MB-C measurements from different studies are standardized by using K_C and K_{CE} of 0.40.

Given its utility and robustness, the FI method (Jenkinson and Powlson, 1976) became a standard procedure for measuring MB-C, and has been used to confirm the reliability of other methods for MB-C measurements, including FE. Roscoe et al. (2006) compiled several studies performed in Brazil (Pfenning et al., 1992; Rodrigues et al., 1994; Feigl et al., 1995; Geraldies et al., 1995; Oliveira et al., 2001), adjusted the MB-C measurements on the basis of coefficient values of $K_C = 0.41$ and $K_{CE} = 0.40$, and obtained a correlation of 92% ($P < 0.01$), with a regression of $y = 1.02x$, showing that both FE and FI are equally suitable to measure MB-C. However, it has also been shown that, under tropical conditions, FE in general is less variable than FI (Pfenning et al., 1992) and more sensitive to total soil organic carbon (TSOC) (Rodrigues et al., 1994; Oliveira et al., 2001); therefore, it has been recommended for MB-C measurements in Brazil by the Brazilian Soil Science Society since 2004 (Roscoe et al., 2006).

Some important parameters may be derived from MB-C, such as the ratio of MB-C to the TSOC, known as the microbial quotient (MB-C/TSOC) (e.g. Insam and Domsch, 1988), and the metabolic quotient (qCO_2), which is the ratio of basal respiration (BR) to the total MB-C (e.g. Insam and Haselwandter, 1989). The MB-C/TSOC gives insight into the capability of a soil to support microbial growth, and it is expected that soils with better quality will have higher ratios of MB-C/TSOC. The qCO_2 indicates the efficiency by which soil microorganisms use C-resources in the soil, and it is expected that stressed soils will provide higher qCO_2 values than less-stressed soils (Insam and Haselwandter, 1989).

The FE method has also been used to determine nutrients other than C in the MB, following the same principle of measuring flushes after fumigation and dividing by a conversion coefficient (K). Therefore, MB-N (nitrogen) has been determined according to Brookes et al. (1985) with $K_N = 0.54$, the MB-P (phosphorus) according to Brookes et al. (1982) with $K_P = 0.40$, and the BM-S (sulfur) according to Strick and Nakas (1984) and Chapman (1987) with $K_S = 0.35$. In fact, it is possible to determine the MB-N with the FI method as well, but the results should be interpreted with caution due to nutrient immobilization during the incubation period.

3. The MB-C as indicator for soil quality

Concerns about agriculture sustainability have inspired myriad studies on MB-C and related parameters associated with soil chemical and physical characteristics, biodiversity and crop productivity as indicators of soil quality. Soil quality was first defined as the continued capacity of the soil to function as a vital living system, within ecosystems and land-use boundaries, to sustain biological productivity, promote air and water quality, and maintain plant, animal and human health (Sparling, 1997; Seybold et al., 1999). The MB-C is one of the most promising indicators of soil quality because it responds promptly to environmental changes, often much earlier than physical and chemical parameters, including TSOC and even crop productivity, consistently over seasonal fluctuations due to climatic conditions (Sparling, 1997; Balota et al., 1998; Seybold et al., 1999; Nogueira et al., 2006; Roscoe et al., 2006; Franchini et al., 2007; Hungria et al., 2009).

Additionally, MB-C/TSOC and qCO_2 may be used to indicate the soil vulnerability to disturbance in terms of resilience and resistance (Seybold et al., 1999). It is assumed that soil MB-C has low resistance if MB-C is significantly decreased after disturbances, but high resilience if the MB-C/TSOC and the qCO_2 are barely affected. High resilience is advantageous because after a stressful event in the soil, the MB-C and its related soil quality may recover with time. However, it is necessary to measure MB-C of a given soil under several circumstances before defining the thresholds of MB-C for optimal soil quality, mainly because MB-C is vulnerable to pedogenetic and climate conditions, and often varies significantly from one environment to another (Table 1). Therefore, the response ratios of MB-C with various treatments should be used to compare different studies (Sparling, 1997). In the following sub-sections, we discuss many of the MB-C studies performed in Brazil aiming at identifying management practices with relatively little impact on MB-C or soil quality.

3.1. Conceptual model to understand the role of MB-C in studies of soil quality

As mentioned before, the MB-C is a useful bioindicator of soil quality because it is sensitive and responds more rapidly to soil changes than any other agronomic parameter (Sparling, 1997; Balota et al., 1998; Nogueira et al., 2006; Franchini et al., 2007; Hungria et al., 2009). Based on MB-C measurements, measures may be taken to avoid soil degradation and loss of the soil quality, and consequently avoid losses in plant productivity. Fig. 1 shows a conceptual model of the responses of yield as a function of MB-C. Small losses in the MB-C do not relate directly to reductions in plant productivity due to a buffering capacity through soil resilience (Box III). Further decreases in the MB-C result in losses in N₂-fixation and arbuscular-mycorrhizal activities; however, crop productivity may be maintained by application of increasing rates of fertilizers (Box II). However, further decreases in MB-C and in soil quality may lead to lack of crop-productivity responses to fertilizers (Box I). On the other hand, if management practices stimulate MB-C, then plant productivity may increase due to stimulation of nutrient cycling and beneficial plant–microbe symbioses (Box IV).

3.2. Soil-tillage systems

Conventional tillage (CT)—the traditional system of ploughing, disking and harrowing before cropping—has damaged soil quality and crop productivity for decades in Brazil (Derpsch et al., 1991); therefore, as soon as they were aware of its advantages, farmers adopted no-tillage (NT), a cropping system minimizing soil turnover. Today, NT covers about 25.5 million ha (FEBRAPDP, 2008) and is often assumed to play a key role in sustainability, favoring

Table 1

Total soil organic C (TSOC, g kg⁻¹ soil), soil microbial biomass-C measured by FE method and FI method (MB-C, mg C kg⁻¹ soil), and microbial quotient (MB-C/TSOC, %) under different managements and biomes in Brazil.

Biome/management	TSOC	MB-C		MB-C/TSOC	Reference
		FE	FI		
Amazon/forest	10–76	254–797	320–1447	1.1–3.1	6, 11, 12, 16, 20
Amazon/perennial crop	12–24	166–567	159–171	1.2–2.4	16, 20
Amazon/pasture	16–42	93–623	336–2258	1.1–2.5	11, 12, 20
Amazon/agriculture	12	269	352	2.6	20
Cerrados/forest	3–45	101–1201	359–1386	0.9–5.5	5, 7, 13, 14, 15, 18, 20, 21, 25
Cerrados/perennial crop	17	175–564	131	0.8	14, 28
Cerrados/pasture	15–23	87–500	318	0.5–2.6	12, 13, 18
Cerrados/agriculture	3–33	46–322	99–214	0.5–2.0	10, 12, 13, 14, 15, 26, 27
Atlantic/forest	48–80	683–1520	–	2.1–2.8	2, 6
Atlantic/agriculture	8–28	491–591	21–359	0.1–2.3	1, 3, 4, 9, 17, 18, 22
Caatinga/forest	11–27	72–385	–	1.3–1.4	6, 23, 30
Caatinga/perennial crop	8–10	76–260	–	0.9–1.0	6, 23, 30
Caatinga/pasture	10	116	–	1.2	30
Caatinga/agriculture	8	76	–	1.0	30
Pampas/grassland	20–22	351–665	64	0.3–1.6	3, 24
Pampas/agriculture	13–16	170–298	39–299	0.2–2.3	3, 24, 29

The values of MB-C were standardized based on K_C and $K_{CE} = 0.40$.

References: 1. Balota et al. (1998), 2. Baretta et al. (2005), 3. Cattelan and Vidor (1990), 4. Cattelan et al. (1997a), 5. D'Andrea et al. (2002), 6. Feigl et al. (1995), 7. Ferreira et al. (2007), 8. Fialho et al. (2006), 9. Franchini et al. (2007), 10. Garcia et al. (2004), 11. Geraldies et al. (1995), 12. Luizão et al. (1999), 13. Marchiori-Junior and Melo (1999), 14. Matsuoka et al. (2003), 15. Mendes et al. (2003), 16. Moreira and Malavolta (2004), 17. Nogueira et al. (2006), 18. Oliveira et al. (2004), 18. Pereira et al. (2007), 20. Pfenning et al. (1992), 21. Rangel and Silva (2007), 22. Rodrigues et al. (1994), 23. Sampaio et al. (2008), 24. Santos et al. (2004), 25. Silva et al. (2007), 26. Souza et al. (2008a), 27. Souza et al. (2008b), 28. Theodoro et al. (2003), 29. Vargas et al. (2004), 30. Xavier et al. (2006).

TSOC conservation. Therefore, we gathered data on studies in Brazil and performed meta-analysis, consisting of calculations of the responses of ratios of MB-C to related parameters (i.e. TSOC, MB-C/TSOC, qCO_2) and of crop productivity. Readers are referred to [Gurvitch and Hedges \(2001\)](#) for data-gathering procedures and calculations. We treated CT as the control, and NT as the experimental treatment. The meta-analysis was based on 233 data points, from studies performed in almost all regions of Brazil, but mainly in the Atlantic Forest and Cerrados biomes. Data were gathered in 5-year intervals, over 25 years of NT implementation, via Scopus and Google Scholar until 21 November, 2008. When reading the output of a meta-analysis, a response may be regarded as positive if the response ratio (R) and the lower confidence interval (CI) are higher than 1, and negative if R and the higher CI are lower than 1.

The meta-analysis of NT effects ([Fig. 2a,b](#)) confirmed the hypothesis that MB-C is affected by NT at much earlier stages than is TSOC ([Balota et al., 1998, 2004a; Franchini et al., 2007](#)). The results showed that MB-C in NT system increased by 58% ($R = 1.58$) as early as the period 10–15 years, remaining stable up to 25 years

([Fig. 2a](#)). The trends for MB-C, averaged over a range of studies across Brazil, were lower than those determined by [Balota et al. \(1998\)](#), 118%, [Pereira et al. \(2007\)](#), of 114%, and [Franchini et al. \(2007\)](#), of 80%, in NT experiments in oxisols in southern Brazil, but were highly significant and consistently positive over the years ($R > 1$). Even though the response ratios of TSOC under NT were significantly higher than 1, there were no further increases in the TSOC over 25 years ([Fig. 2b](#)). Nevertheless, these results are consistent with model simulations by [Leite et al. \(2004\)](#), who parameterized the CENTURY-model for soil organic-matter dynamics under CT and NT conditions in Brazil, and predicted that, after 60 years of NT implementation, there would be an increase of 50% ($R = 1.50$) in the TSOC of NT in relation to CT ([Fig. 2b](#)).

According to [Insam and Haselwandter \(1989\)](#), secondary vegetation successions accumulate more organic matter, because there is an improved microbial metabolic efficiency (as measured by qCO_2) in the utilization of C residues. Likewise, long-term NT fields would accumulate more TSOC due to lower qCO_2 of the MB-C. Indeed, we demonstrated that qCO_2 was reduced in NT over time ([Fig. 2d](#)). It has been demonstrated that NT favors a higher ratio of fungi to prokaryotes because it does not shatter hyphal networks ([Beare, 1997; Frey et al., 1999; Bailey et al., 2002](#)). Fungi have a lower energy requirement for maintenance than prokaryotes, and thus transform substrate-C into microbial-C more efficiently ([Alvarez et al., 1995; Haynes, 1999](#)). Furthermore, we understand that NT provides better soil environmental conditions for microorganisms and plants; indeed this was confirmed by positive response ratios ($R > 1$) of MB-C/TSOC in the meta-analysis ([Fig. 2c](#)). Among the better conditions under NT are tempering of the daily temperature extremes, higher soil-moisture content and lower bulk density ([Voss and Sidiras, 1985; Hungria, 2000; Hungria and Vargas, 2000](#)). Therefore, considering the parameters of MB-C, MB-C/TSOC and qCO_2 as indicators for soil quality, clearly, we can conclude that NT gradually improves soil quality in relation to CT.

3.3. Crop rotations

To demonstrate an association between MB-C with soil quality as a function of crop rotation has proven to be a more difficult task.

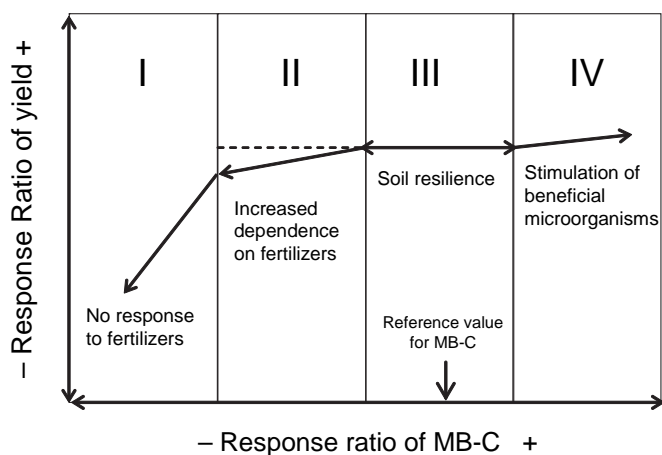


Fig. 1. Conceptual model depicting the relationships between changes in soil microbial biomass and plant productivity due to management practices.

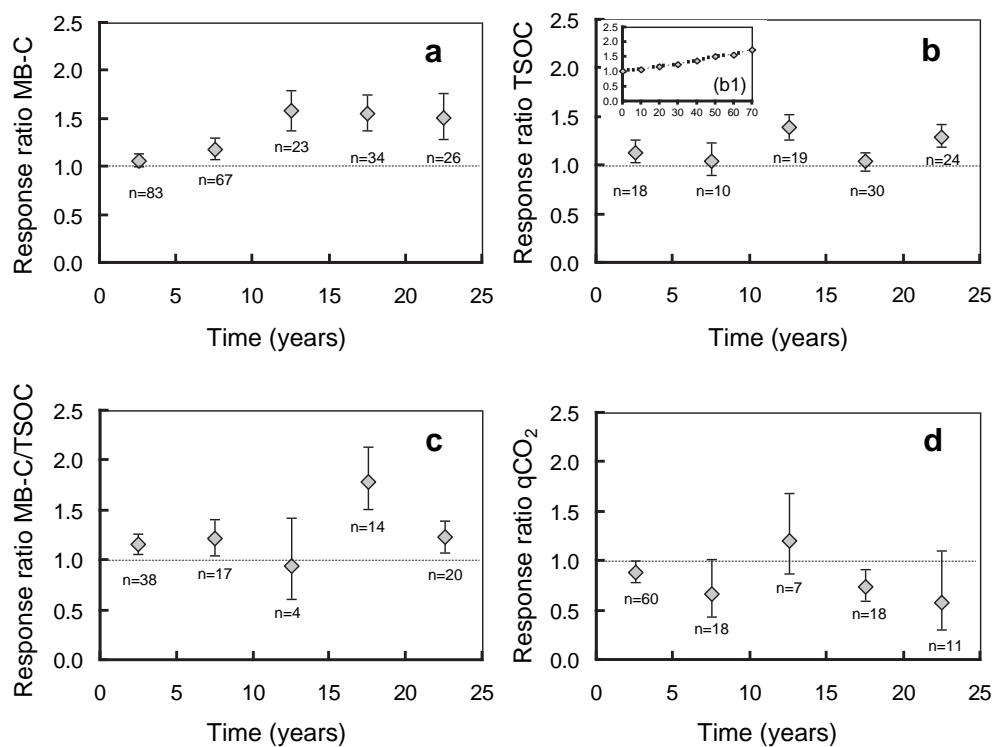


Fig. 2. Meta-analysis of the effects of no-tillage (NT) on (a) soil microbial biomass-C (MB-C), (b) total soil organic carbon (TSOC), (c) microbial quotient (MB-C/TSOC), and (d) metabolic quotient ($q\text{CO}_2$), over 25 years in Brazilian fields. Figure (b1) shows the response ratios applied to the output of model simulations of NT and conventional tillage (CT) by Leite et al. (2004). Meta-analysis was performed according to Gurevitch and Hedges (2001), considering CT as control and NT as treatment. Diamonds represent the estimates of response ratios in intervals of five years; bars indicate the 95% confidence intervals, and “n” is the number of independent data points. See Further reading for references on the meta-analysis.

Franchini et al. (2007) showed increases in MB-C in soybean [*Glycine max* L. (Merr.)] fields previously cultivated with legumes (lupine, *Lupinus albus* L.) in comparison with those previously cultivated with wheat (*Triticum aestivum* L.), and they found that crop rotations with higher ratios of legume to non-legume resulted in higher MB-C/TSOC values (Table 2). However, positive effects of legumes were not clearly identified in a large number of studies in Brazil (Table 2). Therefore, it has been proposed that differences in microbiological parameters due to crop rotation are detectable only in long-term trials (Franchini et al., 2007; Pereira et al., 2007), even under NT conditions.

Additional effects from crop rotations could result from shifts in rhizodeposition of organic compounds (Matson et al., 1997) variously stimulating or suppressing microbial communities. For example, flavonoids released by legumes into the rhizosphere elicit rhizobial and mycorrhizal symbioses (Hungria and Stacey, 1997; Hungria et al., 1997; Ferreira et al., 2000). There are also reports of the effects of crop rotations on the suppression of soil-borne plant pathogens in wheat (Santos et al., 2000), maize (Denti and Reis, 2001) and soybean (Hoffmann et al., 2004). Therefore, although effects of crop rotations on MB-C and related parameters have not been consistently observed in studies performed in Brazil (Table 2), there is strong evidence for qualitative changes in microbial communities (e.g. in diversity; Nogueira et al., 2006; Pereira et al., 2007), with positive overall effects on crop productivity.

3.4. Pastures

In Brazil, pastures are estimated to occupy up to 190 million ha, consisting mainly of the following systems: (i) permanent pastures (mainly *Brachiaria brizantha*, *Brachiaria decumbens* and *Paspalum*

notatum) with continuous grazing, (ii) pastures in rotation with annual crops (integrated pasture-crop management), typically found in the Cerrados (savannas) and Atlantic Forest biomes; and (iii) natural grasslands, typically found in southern Brazil and in the Pantanal (wetland) biome, but also in isolated areas across the country, including the Caatinga biome (a semi-arid environment). Because pasture productivity can decline to unsustainable conditions, defining attendant soil-quality parameters is important.

In southern Brazil, the natural grasslands generally have stronger ability to maintain MB-C than do cropped soils, regardless of species cropped and of the soil fertility status (Cattelan and Vidor, 1990); therefore, they have been used as reference standards for some soil-quality studies (Baretta et al., 2005; Conceição et al., 2005).

However, the conversion of forest to planted pastures in Amazon decreases soil MB-C as a result of the decrease of TSOC by burning, accelerated decomposition rates, and abundant release of soluble NO_3^- (Luizão et al., 1992, 1999; Geraldies et al., 1995). Interestingly, Cerri et al. (1985) and Luizão et al. (1999) demonstrated that changes are very dynamic, and despite initial losses, the MB-C in recently planted pastures increased up to the 5th year, and then declined slowly. Compared with natural forests, planted pastures may stimulate soil MB-C because of denser root systems (Alvarenga et al., 1999; Rangel and Silva, 2007), return of organic matter and nutrients as dung and urine (Haynes, 1999), and overall increased inputs of carbon from C_4 photosynthesis (Feigl et al., 1995, 2008). It has been shown by $\delta^{13}\text{C}$ studies that carbon rhizodeposition from pastures could support up to 82% of maintenance requirements of MB-C after 15 years of pasture (Feigl et al., 2008). Cerri et al. (2003, 2004) modeled soil organic-matter dynamics in pastures, and predicted long-term compensation for initial decreases after

Table 2

Crop rotations and their effects on the total soil organic C (TSOC, g C kg⁻¹ soil), soil microbial biomass-C (MB-C, mg C kg⁻¹ soil) and soil microbial biomass-N (MB-N, mg N kg⁻¹ soil) in areas of conventional tillage (CT) and no-tillage (NT) in studies performed in Brazil.

Crop Rotation	TSOC		MB-C		MB-N		Reference
	CT	NT	CT	NT	CT	NT	
Pigeon pea/maize	16		452				Cattelan and Vidor (1990)
Oat/faba bean/maize/cowpea	18		419				
Oat/maize	16		334				
Wheat/soybean [†]		22		545			Cattelan et al. (1997a)
Soybean [†] /oat/wheat		22		407			
Maize/soybean [†] /lupine/oat/wheat		22		541			
Maize/soybean [†] /lupine/wheat		22		518			
Wheat/soybean [§]	18	18	285	367			Cattelan et al. (1997b)
Wheat [§] /soybean	24	28	101	248	32	67	Balota et al. (1998)
Wheat [§] /maize	26	28	163	239	33	55	
Wheat/soybean [§]	24	28	187	635	29	48	
Wheat/maize [§]	26	28	202	669	20	41	
Common beans/maize/soybean/oat		42		446			Valpassos et al. (2001)
Soybean/maize	24		299				
Soybean/wheat [†]	14	18	135	215	19	29	Balota et al. (2003)
Maize/wheat [†]	15	21	155	238	19	23	
Cotton/wheat [†]	13	20	103	264	13	25	
Rice/soybean/maize	12		160		11		Santos et al. (2004)
Ryegrass/rice		20		241		21	
Wheat/soybean/wheat/maize		25		631		11	Nogueira et al. (2006)
Wheat/soybean		24		550		6	
Common beans/maize/common beans [†]	36		467				Fonseca et al. (2007)
Common beans/soybeans/common beans [†]	55		532				
Soybean [†] /wheat	21	24	262	521	41	111	Pereira et al. (2007)
Lupine/maize/oat/soybean/wheat/soybean [†]	19	22	272	625	42	102	
Soybean [†] /wheat	22	25	666	497	45	93	Hungria et al. (2009)
Soybean/wheat/lupine/maize [†] /oat/radish	23	28	510	624	46	104	

MB-C and MB-N measurements were performed at vegetative stage in the crops indicated by §, and at reproductive stage in the crops indicated by †. The values of MB-C were standardized based on K_C and $K_{CE} = 0.40$ and MB-N were calculated with $K_N = 0.54$. Table comprises average of MB-C whenever measurements were performed in different times or depth (up to 10 cm) and did not differ statistically. Crops species: Common beans (*Phaseolus vulgaris* L.); Cotton (*Gossypium hirsutum* L.); Cowpea (*Vigna unguiculata* L.); Faba bean (*Vicia faba* L.); Lupine (*Lupinus albus* L.); Maize (*Zea mays* L.); Oat (*Avena strigosa* Schreb.); Pigeon pea (*Cajanus cajan* L.); Radish (*Raphanus sativus* L.); Soybean (*Glycine max* L.); Wheat (*Triticum aestivum* L.); Rice (*Oryza sativa* L.); Ryegrass (*Lolium multiflorum* L.).

pasture conversion, such that, after 100 years, a pasture soil would have 54% more TSOC than the initial forest soil (Cerri et al., 2003, 2004). However, this model simulation was based on data obtained on a well-managed ranch unlike the majority of farms in the Amazon biome.

In the majority of studies performed in the Cerrados biome, permanent or integrated pasture-crop management and annual crops have shown lower values for MB-C, TSOC and MB-C/TSOC and higher qCO_2 than native Cerrados forest (e.g. Alvarenga et al., 1999; Oliveira et al., 2001, 2004; Valpassos et al., 2001; D'Andrea et al., 2002; Mercante, 2001; Mercante et al., 2004; Souza et al., 2006a,b; Lima et al., 2006; Araújo et al., 2007; Jakelaitis et al., 2008). Permanent pastures under appropriate management improved MB-C and related parameters in relation to annual cropping associated with soil disturbance, i.e. under CT (Marchiori-Junior and Melo, 1999; Souza et al., 2006a; Araújo et al., 2007; Rangel and Silva, 2007). However, permanent pastures and continuous grazing often cause soil-quality decline and reduce pasture productivity due to increased soil bulk density, nutrient depletion, and erosion (Valpassos et al., 2001; Oliveira et al., 2004; Jakelaitis et al., 2008). To recover areas under pasture, some farmers have adopted rotations with annual crops, expecting to combine advantages of both systems: soil liming and fertilization during cropping, and improvement of soil structure by the dense root systems of pastures, to give greater economic returns. In some cases, it has been shown that integrated pasture-crop management does not change MB-C in relation to permanent pastures (Mercante, 2001; Mercante et al., 2004; Souza et al., 2006b). However, several other studies evidenced that integrated pasture-crop management result in higher MB-C and MB-C/TSOC and lower qCO_2 than annual cropping (Oliveira et al., 2001; D'Andrea et al., 2002; Jakelaitis et al.,

2008). These changes in MB-C dynamics could be related with improved microbial functions, which could favour plant productivity.

There have been only a few studies on the effects of pastures on the Caatinga biome. Xavier et al. (2006) showed that a well-managed planted pasture significantly increased MB-C, particularly in the most surface layer in relation to native vegetation. Luna et al. (2008) showed that a well-managed and productive 25-year-old pasture doubled the MB-C when compared with a 40-year-old degraded pasture; the qCO_2 in the younger well-managed pasture was a sixth of that in the degraded pasture. Although none of these studies aimed at correlating MB-C with plant productivity, the differences in the magnitude of MB-C between different pastures highlighted the usefulness of MB-C as an indicator of soil quality.

3.5. Organic agriculture

There is an increasing demand for organic products, resulting in part from a growing awareness of environmental pollution, and Brazil devotes about 100,000 ha to organic agriculture, occupying the 34th position in the world ranking (Araújo et al., 2008). We found a few studies dealing with the effects of organic agriculture on soil MB-C, most of which were performed with permanent crops (Table 3). The majority of these studies indicated that organic agriculture improved soil quality by increasing MB-C and MB-C/TSOC and reducing qCO_2 , probably as a result of organic manure amendments and removal of agrochemicals application. Bettiol et al. (2002) showed that organic methods for growing tomatoes (*Lycopersicon esculentum* L.) resulted in two-fold higher soil respiratory activity than conventional methods, although colony counts of fungal, bacterial and actinomycete populations were

Table 3
Effects of organic farming on the microbial biomass-C (MB-C), MB-C/TSOC and qCO_2 ($mg\ CO_2-C\ g^{-1}\ MB-C$) in some perennial crops of Brazil.

Crop	Years	MB-C conventional ($mg\ C\ kg^{-1}\ soil$)	Increases/decreases due to organic system (%)			Reference
			MB-C	MB-C/TSOC	qCO_2	
Acerola	4	123	+37	-10	0	Xavier et al. (2006)
Acerola	1	121	+89	+120	-22	Araújo et al. (2008)
Acerola	2	143	+123	+60	-57	Araújo et al. (2008)
Acerola	6	127	+5	-20	+3	Sampaio et al. (2008)
Apple	7	606	+64	+48	-46	Figueiredo et al. (2006)
Apple	11	629	+54	+40	-36	Maluche-Baretta et al. (2007)
Coffee	5	412	+18	nd	nd	Theodoro et al. (2003)
Coffee	5	412	+15	nd	nd	Theodoro et al. (2003)
Sugarcane	5	1126	-4	nd	nd	Oliveira et al. (2007)

Increase was calculated as: $(Organic/Conventional - 1) \times 100$. Crop species: Acerola (*Malpighia glabra* L.); Apple (*Malus domestica* L. Borck); Coffee (*Coffea arabica* L.); Orange (*Citrus sinensis* (L.) Osbeck); Sugarcane (*Saccharum officinarum* L.) nd = not determined in the study.

similar in the two cropping systems. The changes in microbial activity are probably due to the addition of more rapidly decomposing organic amendments, i.e. animal manure (e.g. Souza et al., 2006c; Araújo et al., 2008). Although slower decomposition is generally desirable to preserve soil organic matter, for organic systems—which do not receive chemical fertilizers—faster rates of nutrient mineralization are desirable to support plant growth.

3.6. Agricultural use of industrial residues

Recent studies in Brazil have explored whether sewage and industrial sludge are suitably applicable to agricultural fields. We do not consider the effects of animal manures as industrial residues, even though they are commonly used in areas adjacent to swine- and poultry-production facilities. Table 4 shows the effects

Table 4
Effects of industrial and urban residues amendments on the microbial biomass-C (MB-C), MB-C/TSOC and qCO_2 ($mg\ CO_2-C\ g^{-1}\ MB-C$) in several soils of Brazil.

Residue/soil type	Dose ($t\ ha^{-1}$)	MB-C control ($mg\ C\ kg^{-1}\ soil$)	Increases/decreases due to residue amendment (%)			Reference
			MB-C	MB-C/TSOC	qCO_2	
Oven powder/clayey	1	143	27	nd	11	Melloni et al. (2001)
	2		186	nd	15	
	4		53	nd	-25	
Oven powder/sandy	1	285	-233	nd	216	Melloni et al. (2001)
	2		-50	nd	150	
	4		-66	nd	133	
PET fiber biosolid/clayey	6	266	101	20	-60	Trannin et al. (2007)
	12		120	20	-60	
	18		180	16	-100	
	24		204	16	-100	
Tannery sludge + lime/soil not informed	20	186	0	nd	nd	Passianoto et al. (2001)
	40		55	nd	nd	
	60		167	nd	nd	
Tannery sludge + chromium/soil not informed	20	186	11	nd	nd	Passianoto et al. (2001)
	40		100	nd	nd	
	60		122	nd	nd	
Textile sludge/clayey	6	286	-58	nd	0	Araújo and Monteiro (2006)
	19		-38	nd	11	
Sewage sludge/clayey	6	127	-12	nd	5	Vieira and Silva (2003)
	12		7	nd	-15	
	24		13	nd	-10	
	50		22	nd	-10	
Sewage sludge/clayey	6	171	105	nd	-5	Fernandes et al. (2005)
	12		140	nd	13	
	24		135	nd	13	
	50		140	nd	21	
Sewage Sludge/Loamy	30	50	27	33	66	Colodro et al. (2007)
	60		32	33	76	
Sewage biosolid 1/sandy	~17	43	400	10	-10	Lambais and Carmo (2008)
	~33		370	5	-5	
	~67		370	5	-5	
	~133		500	15	5	
Sewage biosolid 1/clayey	~17	90	-50	-10	5	Lambais and Carmo (2008)
	~33		-5	-5	10	
	~67		5	-5	5	
	~133		10	-7	5	
Sewage biosolid 2/sandy	~7	105	14	-2	5	Lambais and Carmo (2008)
	~13		43	0	10	
	~27		40	0	15	
	~55		114	0	5	
Sewage biosolid 2/clayey	~7	114	20	-3	5	Lambais and Carmo (2008)
	~13		0	0	5	
	~27		0	0	5	
	~55		0	0	10	

Increase was calculated as: $(Control/Application - 1) \times 100$; nd = not determined in the study; PET = polyethylene terephthalate.

of several industrial residues: oven powder (a product of the steel industry), PET fiber biosolid (organic residue from the production polyethylene terephthalate), tannery sludge with lime or with chromium (derived from leather production), textile sludge, and urban sewage sludges. There is evidence that soil texture differentially affects MB-C responses to application of various residues (c.f. Melloni et al., 2001; Lambais and Carmo, 2008), probably due differences in the aeration and compaction capacity of the soils (c.f. Minihoni and Cerri, 1987). Additionally, increasing doses of PET fiber biosolid and tannery sludge (c.f. Passianoto et al., 2001; Trannin et al., 2007) consistently stimulated MB-C, suggesting that these residues can be assimilated by microorganisms without major problems.

Vinasse, a byproduct of sugarcane–ethanol production, has shown to stimulate the degradation of xenobiotic compounds present in the soil. Prata et al. (2001) applied doses of 100 and 200 m³ ha⁻¹ of vinasse to sandy and clayey soils and found that the degradation of the herbicide ametryn at 28, 63 and 120 days was accelerated in both soils by vinasse application; 100 m³ ha⁻¹ was the most efficient treatment, possibly because higher doses inhibit specific groups of microorganisms. However, it is likely that benefits from vinasse application depend on soil conditions; for example, Minihoni and Cerri (1987) compared soils of three water-holding capacities (40, 60 and 80%) and observed that vinasse more effectively stimulated MB-C when the soil was maintained under drier conditions, probably due to increased O₂ availability for aerobic microorganisms.

It is clear that soil-quality responses depend on residue and soil type, and recommendations should thus be condition-specific.

3.7. Agrochemical application

Negative effects of fungicides were confirmed by Vieira et al. (2001), who showed that chlorothalonil applied to soil covered with oat residues decreased the MB-C by 80% after 26 days of incubation. However, Silva et al. (2005) observed only transitory effects of fungicides on MB-C; negative effects of metalaxyl and fenarimol commonly applied to vineyards (*Vitis vinifera*) on MB-C increased for 42 days, with no further effects after 119 days. Table 5 shows the results of several studies on the effects of herbicides applied to various crops and soils after incubation periods ranging from 2 weeks to 2 months. With no exception, herbicides compromised microbial survival and MB-C, and in most times there was a decrease in the efficiency in the use of C-resources in the soil, resulting in higher *q*CO₂ values (Table 5). Although there is evidence that herbicides have a lesser effect on MB-C than other agrochemicals such as fungicides, depending on the dose applied and crop canopy (c.f. Topp et al., 1997), herbicides may also have profound negative effects on beneficial microorganisms in the soil (e.g. rhizobial strains) (Cattelan and Hungria, 1994).

3.8. Burning

Despite the fact that crop burning is regulated by environmental laws in Brazil, this practice is common in several agricultural sectors. In the Cerrados, during the dry season, vegetation is occasionally ignited by lightning or fires are deliberately set to prepare new areas for cropping. To investigate effects of burning, Nardoto and Bustamante (2003) burned Cerrados vegetation in two dry seasons, and measured fluctuations in microbial activity. These authors observed that burning stimulated MB-C at the beginning of the raining season, but it decreased later, when the readily available C was depleted. They also observed that burning at dry season did not affect patterns of mineralization/immobilization when evaluated at the beginning of the rainy season, although it decreased the

inorganic-N cycled annually through mineralization (Nardoto and Bustamante, 2003). The Cerrados ecosystem may have adapted to natural burning over millennia; however, anthropogenic burning is more frequent and the effects on soil microbes may be substantially different.

In southern Brazil, farmers have burned natural grasslands yearly in winter for more than a century, arguing that it favors early re-growth in spring in comparison to fallow and mowing practices. Burning of grassland did not affect MB-C, TSOC or MB-C/TSOC, but resulted in lower metabolic efficiency (i.e. higher *q*CO₂ values), which could be associated with microbial adaptation to burning stress (Baretta et al., 2005).

In the Amazon region, many farmers practice itinerant agriculture, cutting trees for timber and burning branches and remaining trunks prior to planting crops. Such practices facilitate the implementation of agriculture but decrease soil MB-C by about 80% (Pfenning et al., 1992), resulting in declining productivity over a period of a few years and leading to eventual abandonment.

Sugarcane has been planted in Brazil since 1530 and, traditionally, mature fields are burned to minimize labor accidents during harvest. Cerri et al. (1991) observed huge losses of TSOC of sugarcane plantations in comparison with native forests. Given sugarcane's high capacity for dry-matter production, these TSOC losses are attributable to burning. Oliveira et al. (1999) stated that if the harvest is done mechanically without burning, 13–20 tons of straw (dry weight basis) per hectare would be left on the soil; therefore, it is not surprising that burning makes MB-C about 20% lower on a year basis (Mendoza et al., 2000).

4. Soil microbial functionality: the missing link in studies of MB-C for better soil quality

Natural and cultivated vegetation differs in the rate of plant growth and nutrient requirements therefore, one cannot directly assess productivity of the two ecosystems simply in terms of MB-C. However, it is possible to compare two similar plant structures (e.g. crops) and assess positive effects of MB-C on plant productivity. For that reason, data from studies on CT and NT systems can provide a good conceptual model to test hypotheses on benefits of MB-C. In this paper, we have demonstrated that NT significantly improves MB-C and its related parameters (Section 3.4), begging the question of whether that improvement results in higher plant productivity. To test that hypothesis, we plotted the response ratios of MB-C and of crop yield obtained from a number of long-term (5–22 years) NT versus CT experiments. Higher MB-C in the long-term increased crop yield with a slope of 0.1543 ($P = 0.013$) (Fig. 3). Indeed, several studies have shown that NT alters soil physical, chemical and biological properties (e.g. soil density or nutrient content due to microbial immobilization), reducing plant productivity in the beginning (e.g. Derpsch et al., 1991; Santos et al., 2007c); however, at later stages, both MB-C and yields were higher (Cattelan et al., 1997a; Valarini et al., 2004; Costa et al., 2006; Garcia et al., 2006; Franchini et al., 2007; Pereira et al., 2007). Another example was provided by Souza et al. (2008b), who compiled information from seven soybean-producing areas of Brazil, and obtained a significant correlation between plant biomass production and MB-C ($r = 0.609$, $P < 0.001$) and MB-N ($r = 0.613$, $P < 0.001$) (Souza et al., 2008b). These examples strengthen our hypothesis that MB-C is an indicator of soil quality, which in time, increases plant productivity (Section 3.2; Fig. 1), although the mechanisms are not completely clear yet, probably because they result from a combination of several abiotic and biotic processes. Higher yields may result from enhanced soil aggregation, increased total soil C and labile nutrients in MB-C, adequate release of mineralized nutrients, improved moisture and temperature stability, and improved symbioses.

Table 5
Effects of herbicides applied on the MB-C and qCO_2 in several crops cultivated in Brazil.

Herbicide	Crop/soil type	MB-C control (mg C kg ⁻¹ soil)		Increases/decreases due to herbicide (%)				Reference
		NT	CT	MB-C		qCO_2		
				NT	CT	NT	CT	
2,4-D	Sugarcane/sandy-clayey	438		2		-11		Reis et al. (2008)
Ametryn	Sugarcane/sandy-clayey	438		-18		71		Reis et al. (2008)
Ametryn + trifloxysulfuron-sodium	Sugarcane/sandy-clayey	438		-33		108		Reis et al. (2008)
Atrazine	Maize/clayey	251		-4		3		Jakelaitis et al. (2007)
Atrazine + nicosulfuron	Maize/clayey	251		-24 to -10		1 to 5		Jakelaitis et al. (2007)
Diuron	Orange/sandy	158		-3		nd		Dellamatrice and Monteiro (2004)
Diuron	Sand clay loamy	132		-154 to 6		-20 to 167		Vieira (1999)
Fluazifop-p-butyl	Common bean/maize/clayey	553	214	-62 to 2	-529 to -21	nd	34 to 232	Santos et al. (2005)
Fluazifop-p-butyl + Fomesafen	Common bean/maize/clayey	553	214	-7 to -8	-42 to -281	nd	80 to 392	Santos et al. (2005)
Fluazifop-p-butyl + fomesafen	Common bean/clayey	441	369	-396	-769	614	504	Santos et al. (2006)
Fomesafen	Common beans/maize/clayey	553	214	-38 to 9	-94 to -1	nd	3 to 99	Santos et al. (2005)
Fomesafen	Common beans/clayey	441	369	-91	-264	157	142	Santos et al. (2006)
Glyphosate	Soybean/sandy	87		18		-77		Zilli et al. (2007)
Glyphosate	Resistant ryegrass/clayey	236		-12		-13		Ferreira et al. (2006)
Glyphosate	Sensitive ryegrass/clayey	289		1		-11		Ferreira et al. (2006)
Glyphosate	Soybean/clayey	37		4		7		Zilli et al. (2008)
Glyphosate	Soybean/clayey	124		-50 to -8		-2 to 73		Santos et al. (2007b)
Glyphosate + Imazaquin	Soybean/sandy	87		-28		56		Zilli et al. (2007)
Imazaquin	Soybean/sandy	68		4		-57		Zilli et al. (2007)
Imazaquin	Soybean/clayey	37		27		-46		Zilli et al. (2008)
Sulfentrazone	Sugarcane/sand clay loamy	102		-40		22		Vivian et al. (2006)
Sulfentrazone	Soybean/sand clay loamy	256		-4		nd		Vieira et al. (2007)
Trifloxysulfuron-sodium	Sugarcane/sandy-clayey	438		-5		30		Reis et al. (2008)
Trifloxysulfuron-sodium	Velvet bean/clayey	283		1 to 17		-10 to -7		Santos et al. (2007a)
Trifluralin	Soybean/sandy	68		5		16		Zilli et al. (2007)

nd = not determined in the study. Crop species: Velvet bean (*Stizolobium aterrimum* Pit and Prac.) Orange (*Citrus sinensis* (L.) Osbeck) Sugarcane (*Saccharum officinarum* L.) Maize (*Zea mays* L.) Soybean (*Glycine max* L.) Common bean (*Phaseolus vulgaris* L.) Ryegrass (*Lolium multiflorum*). For those experiments with different measurements in time, we considered the last data of measurement.

We understand that a new challenge for soil microbiologists in the tropics is to upgrade the knowledge acquired from MB-C studies to the level of ecosystem-specific microbial functionality. Cultivated soils in general support a lower MB-C than forest soils. Intriguingly, if MB-C alone is taken as soil quality indicator, cultivated soils should consistently produce plant biomass at lower growth rates than forest soils. However, when forest soils are

converted to agriculture, plant diversity and the requirements in velocity of nutrient supply change. Our hypothesis is that, after disturbance by deforestation, cultivated soils tend to select fewer microbial individuals (i.e. lower MB-C, lower biodiversity) with higher effectiveness in promoting plant growth. Indeed, in the Cerrados biome, it has been shown that cultivated soils have less diversity in rhizobial strains than native forest soils, but produce higher numbers of nodules with improved efficiency of N_2 fixation by common bean (Grange, Ph.D. thesis, Universidade Federal do Paraná, 2005).

To predict responses in productivity in relation to changes in MB-C, we need a better understanding of the dynamics of nutrient cycling and microbial activity across ecosystems. MB-C varies positively with MB-N, MB-P and MB-S, but the ratios of these groups change as a function of soil management (Rodrigues et al., 1994; Balota et al., 2003; Duda et al., 2003; Souza et al., 2008b). For example, Balota et al. (2003) showed that NT systems increased MB-C by 100%, MB-N by 54% and MB-P by 39% in relation to CT systems, suggesting higher microbial activities and net mineralization in NT than in CT. In fact, during decomposition of residues, MB-C immobilizes P, N, S and other nutrients, functioning as a nutrient sink however, after breakdown of residues, it becomes a labile source of nutrients for plants (Haynes, 1999; Balota et al., 2003). Therefore, although immobilization is treated many times as a negative aspect of MB-C, it is actually temporary. If a management practice increases MB-N, it increases the efficiency of fertilizer use over time and prevents nutrient losses by leaching and volatilization (Haynes, 1999; Balota et al., 2003). In addition, in high P-fixing soils such as tropical oxisols, increases in MB-P following P-fertilization may be advantageous because MB-P is a much more labile form than soil fixed-P (Rheinheimer et al., 2000; Conte et al., 2002; Duda et al., 2003; Balota et al., 2003; Carneiro et al., 2004). It has

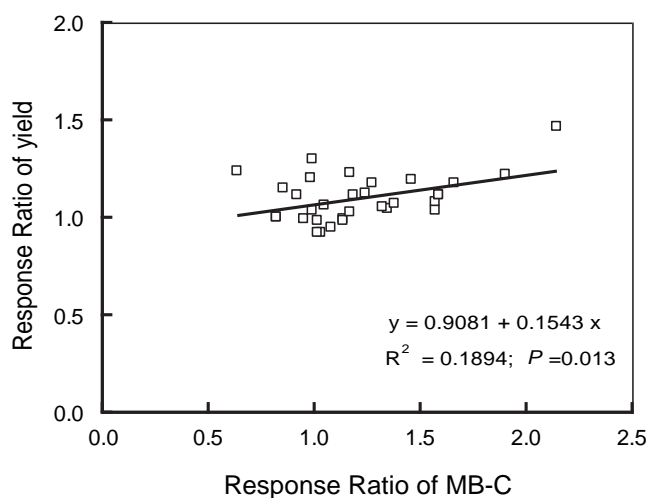


Fig. 3. Relationships between the response ratios of MB-C and yield to the effects of no-tillage (NT) system in 5–25 years lasting field experiments in Brazil. Response ratios were calculated according to Gurevitch and Hedges (2001), considering conventional tillage (CT) as control and NT as treatment. The values of data points were gathered from: Cattelan et al. (1997b), Valarini et al. (2004), Hungria et al. (2009), Costa et al. (2006), Garcia et al. (2006) and Pereira et al. (2007).

Table 6
Microbial biomass-C and enzymatic activity in soils under different managements in Brazil.

Vegetation type	MB-C $\mu\text{g g}^{-1}$	Carbon cycle		Nitrogen cycle		Phosphorus cycle		Sulfur cycle	Reference
		β -glucosidase (EC 3.2.1.21) $\mu\text{g PN g}^{-1} \text{h}^{-1}$	Cellulase (EC 3.2.1.4) $\mu\text{g GLg}^{-1} \text{d}^{-1}$	Urease (EC 3.5.1.5) $\mu\text{g N g}^{-1} \text{h}^{-1}$	Amidase (EC 3.5.1.4) $\mu\text{g GLg}^{-1} \text{d}^{-1}$	Ac. phosphatase (EC 3.1.3.2) $\mu\text{g PN g}^{-1} \text{h}^{-1}$	Alk. phosphatase (EC 3.1.3.1) $\mu\text{g PN g}^{-1} \text{h}^{-1}$	Arylsulfatase (EC 3.1.6.1) $\mu\text{g PN g}^{-1} \text{h}^{-1}$	
Caatinga	102	64	nd	nd	nd	335	166	nd	Wick et al. (2000)
Buffel grass	79	42	nd	nd	nd	264	124	nd	
Joazeiro	159	187	nd	nd	nd	389	384	nd	
Umbuzeiro	124	136	nd	nd	nd	403	199	nd	Matsuoka et al. (2003)
Cerrados	402	47	nd	nd	nd	383	nd	99	
Vineyard	153	41	nd	nd	nd	291	nd	34	
NT	99	52	nd	nd	nd	281	nd	17	Mendes et al. (2003)
Cerrados	444	26	nd	nd	nd	868	nd	73	
NT	214	52	nd	nd	nd	499	nd	48	
CT	125	24	nd	nd	nd	257	nd	16	Balota et al. (2004b)
CT 1	146	nd	118	nd	461	621	147	9	
CT 2	153	nd	94	nd	451	572	127	8	
CT 3	170	nd	86	nd	490	508	86	8	Trannin et al. (2007)
NT 1	286	nd	150	nd	670	792	186	19	
NT 2	303	nd	193	nd	750	832	207	33	
NT 3	269	nd	220	nd	929	852	187	28	Jakelaitis et al. (2008)
NT	432	783	nd	384	nd	601	nd	nd	
Pasture	329	863	nd	154	nd	692	nd	nd	
Cerrados	480	322	nd	nd	nd	374	191	nd	Jakelaitis et al. (2008)
Pasture	133	127	nd	nd	nd	317	33	nd	
NT	126	145	nd	nd	nd	354	148	nd	

nd = not determined in the study; PN = p-nitrophenol; GL = glucose; N = N-NH_4^+ ; Ac. = acid; Alk. = alkaline; NT, no-tillage; CT, conventional tillage. 1, 2 and 3 are different crop rotations, whose plant species were not informed. Plant species: Joazeiro (*Ziziphys joazeiro* Mart.); Umbuzeiro (*Spondias tuberosa* Arr. Com.), Buffel grass (*Cenchrus ciliaris* L.); Vineyard (within lines) (*Vitis vinifera* L.); Eucaliptus (*Eucaliptus* spp); Pasture (*Brachiaria* spp.).

also been shown that MB-P increases in soils receiving natural rock phosphate, a source of nutrients poorly available to roots (Duda et al., 2003). Although a cause-effect relationship has not been established, we found several studies showing that increases in MB-C are combined with increases in the activity of enzymes related to C, N, P and S nutrient cycles (Table 6).

We understand that MB-C plays a major role in soil sustainability and crop productivity through nutrient cycling (including N_2 fixation and mycorrhizal phosphate-foraging or microbial phosphate-solubilization; e.g. Duda et al., 2003; Pereira et al., 2007) and waste assimilation (i.e. degradation of xenobiotics; e.g. Prata et al., 2001), with a potential for biological control of pests and diseases of crops. For example, Costanza et al. (1997) described nutrient cycling as one ecosystem service, since it significantly contributes to the good functioning of human activities, and estimated the monetary value of nutrient cycling at US\$ 17,075 $\text{ha}^{-1} \text{year}^{-1}$ in 1994 dollars. We realize that implementation of a policy for monetary compensation for those who preserve ecosystems services may be difficult to implement. However, a link between the concepts of soil quality and ecosystem services, taking microbial functional diversity into consideration, could result in better designs for sustainable agriculture.

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