

Fire impact on C and N losses and charcoal production in a scrub oak ecosystem

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Abstract Fire profoundly modifies the terrestrial C cycle of about 40% of the Earth's land surface. The immediate effect of fire is that of a net loss of C as CO₂ gas and soot particles to the atmosphere. Nevertheless, a proportion of the ecosystem biomass is converted into charcoal, which contains highly recalcitrant molecular structures that contribute to long-term C storage. The present study aimed to assess simultaneously losses to the atmosphere and charcoal production rates of C and N compounds as a result of prescription fire in a Florida scrub-oak ecosystem. Pre-fire and post-fire charred and unburned organic matter stocks

were determined for vegetation leaves and stems, litter and soil in 20 sub-plots installed in a 30-ha area that was subjected to prescribed fire. Concentrations of C and N were determined, and fluxes among pools and to the atmosphere were derived from these measurements. Soil C and N stocks were unchanged by the fire. Post-fire standing dead biomass contained 30% and 12% of pre-fire vegetation C and N stocks, respectively. In litter, post-fire stocks contained 64% and 83% of pre-fire C and N stocks, respectively. Most of the difference in relative losses between vegetation and litter could be attributed to substantial litter fall of charred and unburned leaves during the fire event. Indeed, an estimated 21% of pre-fire vegetation leaf C was found in the post-fire litter, while the remaining 79% was lost to the atmosphere. About 3/4 of the fire-induced leaf litter fall was in the form of unburned tissue and the remainder was charcoal, which amounted to 5% of pre-fire leaf C stocks. Charcoal production ranged between 4% and 6% of the fire-affected biomass, i.e. the sum of charcoal production and atmospheric losses. This value is below the range of literature values for the transformation of plant tissue into stable soil organic matter through humification processes, which suggests that fire generates a smaller quantity of stable organic C than humification processes over decades and potentially centuries.

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Introduction

Fire profoundly modifies the terrestrial C cycle of about 40% of the Earth's land surface, whether naturally occurring or associated with agricultural practices (Chapin et al. 2002). The effect of fire on the C cycle is particularly important in light of the possibility that terrestrial ecosystems might act as C sinks for anthropogenic emissions of CO₂-C in the atmosphere. Ecosystem processes (plant growth and organic matter degradation) have a functioning timescale of decades. Therefore any potential mitigation of rising atmospheric CO₂ concentration by increasing C storage in terrestrial ecosystems must be evaluated over at least a century. Fire has two major impacts on C storage in terrestrial ecosystems that operate at very different timescales, making the assessment of the global effect of fire at century scale difficult.

On the one hand, fire induces an instantaneous loss of C as CO₂ gas and soot particles to the atmosphere, which drastically decreases C stocks in the ecosystem (Wirth et al. 2002a, b; Salgado et al. 1995). On the other hand, fire converts a fraction of biomass into charcoal, which contains highly recalcitrant black carbon (BC) (Derenne and Largeau 2002). These structures result from a loss of H and O, and a concentration of C and N in aromatic cycles and heterocyclic structures (Knicker et al. 1996; Baldock and Smernik 2002; Almendros et al. 2003). In this work, we did not focus on BC, which is understood to be the aromatic part of the organic matter continuum produced by fire. We concentrated on the whole material affected by fire and therefore we used the term 'charcoal'.

The amount of charcoal produced during a fire event is small in comparison with the atmospheric losses. The latter can reach 97% of the above-ground biomass in grassland ecosystems and from 72% to 84% in forest-type ecosystems (Kauffman et al. 1994). By contrast, recalcitrant charcoal production has been estimated to range from 0.6% to 8%, with most estimates below 2.5%

(Kuhlbusch and Crutzen 1995; Fearnside et al. 1999, 2001; Wirth et al. 2002b; Czimczik et al. 2003). Despite this low production rate, previous studies showed that pyrogenic carbon is abundant in some soils (Glaser and Amelung 2003). Its contribution to the ecosystem's C budget needs to be assessed. Therefore the instantaneous loss of C must be weighed against the formation of a small amount of recalcitrant material that can accumulate in terrestrial ecosystems and contribute to long-term C storage.

Numerous ecosystem fire studies have investigated atmospheric losses without addressing charcoal production (e.g., Wirth et al. 2002a, b; Van de Werf et al. 2003). Other studies have focussed on charcoal and BC production and quantification alone (Glaser et al. 2000; Skjemsstad et al. 2002; Lynch et al. 2004; Dai et al. 2005). This lack of combined measurements of atmospheric losses and charcoal production has led modelling and global budgeting studies to use proxies, such as the estimated BC/CO₂ ratio across fire types (Kuhlbusch and Crutzen 1995) and literature values from other sites (Ito 2005). The validity of such proxies is questionable. Not only is BC quantification highly method dependent (Masiello 2004; Schmidt et al. 2001), but in addition fire intensity, duration and effects depend on weather conditions associated with the regional climate and vegetation composition (Kuhlbusch et al. 1996; Fearnside et al. 2001; Wirth et al. 2002b; Gimeno-Garcia et al. 2004; Certini 2005). Combined measurements of atmospheric losses and charcoal production are therefore much needed to assess the impact of fire on the global C cycle. Such combined estimates were recently provided by Fearnside et al. (1999, 2001) for Amazonian forests. However, detailed quantification in a greater number of ecosystems is necessary. In addition, mechanistic models aiming at predicting C sequestration in 21st-century ecosystems will require multiple-flux information beyond simple quantification of fire-induced CO₂ losses and post-fire C stocks. In order to produce long-term predictions, such models typically require separate estimates of C fluxes from leaves, branches, stems, and soil litter (e.g., Rasse et al. 2001). These elements are therefore crucial for modelling fire effects.

The objective of the present study was to determine fire-induced losses to the atmosphere and charcoal production rates from the C and N stocks contained in a scrub oak ecosystem of Florida. In addition, we specified equations to assess fire-associated C fluxes from the separate ecosystem components, i.e. leaves, stems, litter and soils, which met the needs of mechanistic models.

Materials and methods

Study site and sampling

The study was conducted in the scrub oak ecosystem of Merritt Island National Wildlife Refuge, Florida. The climate is sub-tropical with a dry season extending from November to April and a wet season from May to October. The 100-year average annual precipitation is 1,310 mm year⁻¹ (Dijkstra et al. 2002). The ecosystem is dominated by six main shrub species: *Serenoa repens* (palmetto), three oak species (*Quercus myrtifolia*, *Q. chapmanii*, *Q. geminata*), *Lyonia ferruginea* and *Myrica cerifera*. On March 7th 2004, a prescribed fire was conducted on the Northern part of the island in a 30-ha area called “Shiloh”. The previous burning operation occurred 11 years prior to the present study and oaks were 2–3 m high. The prescribed burning was conducted at the end of the dry season when leaves were actively growing.

Soils at Shiloh are sand-dune Entisols classified as spodic Quartzipsamment, and belong to the *Paola fine sand* series (Myers and Ewel 1990; Schmalzer et al. 2001). In depressions between dunes the soil is slightly wetter and the vegetation composition differs slightly from that of the typical oak scrub. To minimise variability, sampling was conducted solely in upper-dune oak scrub, which represents the majority of the scrub oak ecosystem.

Measurements were performed along a north–south transect composed of 20 plots, 1 m² each and situated about 5 m apart. The effect of fire on C and N stocks in all organic matter compartments of the ecosystem were considered: soil surface, litter layer, and vegetation leaves and stems. Pre-and post-fire C and N

stocks were estimated through extensive sampling campaigns conducted in the month before and the week after the prescribed burning.

Fire was ignited on both the northwest corner and the east side of the 30-ha area. Fire from the east side became a heading fire driven by winds from the southeast. At the time of fire ignition, the air temperature was 28°C and wind speed varied between 3.5 and 4.1 m s⁻¹. The fire spreading rate ranged from 0.25 to 0.28 m s⁻¹. Flames reached an estimated height from 9 to 15 m.

In the present article we will consistently refer to pre-fire and post-fire material (vegetation, litter and soil) for the bulk material. We will use the terms “charcoal” and “charred” material, on the one hand, and “unburned” material, on the other hand, when referring to fractions of the post-fire material that can be visually identified as such. We will refer to “ash” exclusively as mineral ash free of remaining C and N.

Measurement of fire temperatures

Fire temperatures were estimated with sets of 16 thermosensitive paints (Tempil Division, Big Three Industries, Inc., So. Plainfield, NJ, USA), which cover a melting-point range from 79°C to 871°C (175–1,600 F). Paints were applied on copper tags and three sets of tags were placed in each plot: 50 cm above the soil in the vegetation, on the surface of the litter layer, and 2–3 cm below the soil surface.

As paints were sensitive to degradation by weather and displacement by animals, they were installed in the plots the day before the fire, and recovered three days after. The thermosensitive paint method has been successfully applied to ecosystem fires (Pérez and Moreno 1998; Gimeno-Garcia et al. 2004). Due to copper colour changes and partial heat alteration of paints, we grouped them into five temperature classes (<150°C, 150–350°C, 350–600°C, 600–800°C and >800°C) as these could be determined with more certainty.

Measurements of C and N stocks

Undisturbed soil samples were collected from 0 to 5 cm with a 5-cm diameter core for C, N and bulk

density measurements. Deeper soil sampling was not conducted because most studies indicate that fire does not significantly modify soil C and N stocks (Kauffman et al. 1994; Salgado et al. 1995; Roscoe et al. 2000). For each of the 20 plots, pre-fire soil was sampled outside the plot, less than 1 m away from the centre of the plot. Post-fire sampling was conducted within the plots. Soil samples were dried at 75°C during one week, weighed and ground to 200 μm . Elementary analyses for C and N were conducted with an elemental analyzer (Fisons Carlo Erba NA1500).

Litter sampling was conducted just before soil sampling inside a 27-cm diameter plastic ring centred on the soil sampling location. Pre-fire litter was collected outside the plots to avoid fire condition disturbance, as suggested by Caldwell et al. (2002). Pre- and post-fire litter samples were dried at 75°C. Post-fire litter was sieved into five fractions: >2 mm, 1–2 mm, 0.5–1 mm, 0.25–0.5 mm, <0.25 mm. Care was taken not to break the fragile charred leaves when sieving. In addition, seven samples of pre-fire litter were sieved in a similar fashion to serve as control. In one of the 20 plots, i.e. number 7, the post-fire surface soil appeared to have been disturbed by animal activity. Soil horizons were mixed, litter was almost absent, and the tag set that had been installed in the soil was retrieved on the soil surface. For these reasons, soil and litter data from this plot were not considered in the analyses.

Experimental steps of litter preparation are detailed in Fig. 1. The complete list of symbols and abbreviations is provided in Table 1.

Litter samples contained small amounts of mineral sand particles that were removed before analysis by flotation in distilled water (Fig. 1, step 1), as per Caldwell et al. (2002). The flotation method was applied to all <0.5 mm fractions of sieved pre- and post-fire litter where these mineral sand particles potentially accumulated. Sand-free litter samples were freeze-dried to avoid losses of dissolved organic matter. All litter samples were weighed and analysed for C and N contents. In the case of sieved litter samples, stocks were obtained from the total of the five litter size fractions. The unsieved pre-fire litter samples were corrected for sand content using the

average value obtained on the seven sieved samples of pre-fire litter.

As this ecosystem is periodically subjected to fire, both pre-fire and post-fire litter possibly contained ash in fine size fractions. To compute charcoal estimates (see below, 'Charcoal estimates' and 'Flux estimates to post-fire charred and unburned C pools'), we needed to correct the litter C concentration for this inorganic material (Fig. 1, step 2). We assumed that the >2 mm fraction of pre-fire litter did not contain any free ash and that its inorganic content represented the mineral-salt concentration of litter leaves (M , weight%). It was determined gravimetrically in seven subsamples after burning in a muffle furnace (900°C, 4 h). To calculate the free ash content of pre-fire litter, we assumed that it accumulated in fractions <0.5 mm. They were burned and the mass remaining (Rbf) was considered to be the free-ash (Abf) plus mineral-salt (M) content. Then ash content was computed as:

$$\text{Rbf} - M = \text{Abf}$$

The mean of the seven values represented 2.2% of the total litter weight and was used to correct C and N concentrations of pre-fire litter. For post-fire litter, residue content (rbf) was measured with fine-fraction. The ash content (aaf) was calculated as above and represented about 3.8% of the total litter weight. The C and N concentrations were corrected for each of the 19 plots.

Pre-fire plant biomass was assessed in the 20 plots by means of allometric relationships that were determined specifically for the vegetation of the Merritt Island National Wildlife Refuge (Table 2). Allometric relationships for the six main species were available either in the literature or in unpublished sources as mentioned in Table 2. These allometric relationships were established for trees with a diameter inferior to 20 mm. However, some trees exceeded this diameter class at Shiloh. Destructive sampling of six >20-mm trees, conducted outside of the experimental plots, confirmed that the allometric relationships held true for the larger oak trees. Sampling for this study was conducted at the end of March, while allometric relationships were

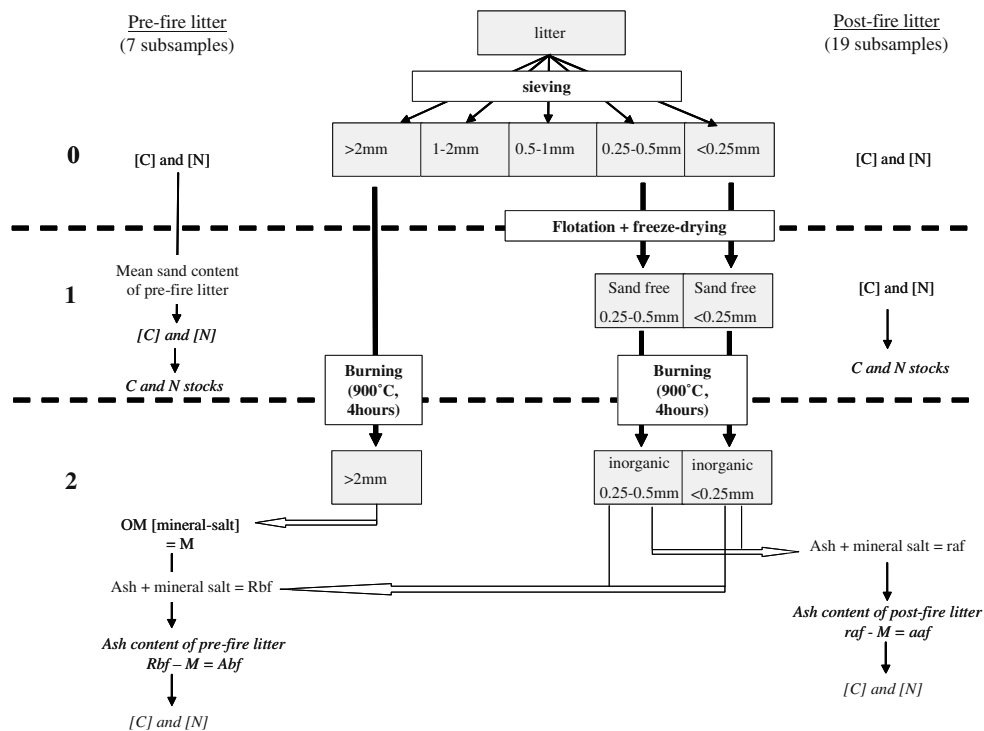


Fig. 1 Procedure for correcting litter C and N concentrations for sand and ash contents. Step '0' corresponds to the total collected litter, step '1' to the sand free litter and step

'2' to the litter without free ash and sand. Measurements (*roman*) and calculations (*italic*) applied to pre- and post-fire litter are on left and right sides, respectively

determined in June. This might have led to a slight overestimation of the leaf biomass.

Allometric relationships provide a non-destructive method particularly suited to fire studies where post-fire measurements must be conducted on the same undisturbed vegetation plots (Fearnside et al. 2001). Vegetation parameters required for the allometric relationships were recorded for each plant present within each 1-m² plot. Stem diameters were measured with a digital calliper as described by Dijkstra et al. (2002). For both shrub height and blade and rachis lengths we used a measuring tape (Gholz et al. 1999). Equations were derived for dry matter biomass of scrub-oak leaves and stems and palmetto blades and rachis. For each of the six main species, stem and leaf samples were randomly collected across Shiloh. Samples were dried at 75°C, milled at 200 μ m and analysed for C and N contents similarly to litter samples.

Post-fire standing biomass consisted exclusively of stems, which were manually harvested

within each plot. Samples were weighed, dried and reweighed for computing the residual moisture content. On these dried subsamples, C and N analyses were conducted on separated unburned and charcoal fractions, which were isolated as explained below. Allometric relationships were less reliable for low-biomass plots. Indeed, one such plot yielded a negative value for the difference between allometry-estimated pre-fire biomass and measured post-fire biomass. This plot was kept in the analysis not to bias the results towards higher biomass plots, but the pre-fire biomass was taken as equal to the measured post-fire biomass.

Charcoal estimates

Charcoal was visually identified as shiny and black-coloured material. Charred surfaces of standing stems were separated from the unburned interior sections by gentle scraping with a cutter blade. These fractions were weighed and the

Table 1 List of abbreviations and symbols for equation variables

Terms	Definition	Units
<i>Pre-fire</i>		
Rbf	average free ash + mineral salt residue content in fine pre-fire litter fraction	%
M	average mineral-salt concentration in pre-fire litter	%
Abf	average ash content in pre-fire litter	%
SL _{bf}	Pre-fire soil OM pool	g m ⁻²
ST _{bf}	Pre-fire stem OM pool	g m ⁻²
LF _{bf}	Pre-fire leaf OM pool	g m ⁻²
LIT _{bf}	Pre-fire litter OM pool	g m ⁻²
LITC _{bf}	C concentration of pre-fire litter	mg C g ⁻¹
LFC _{bf}	C concentration of pre-fire vegetation leaves	mg C g ⁻¹
<i>Post-fire</i>		
raf	residue content in fine post-fire litter fraction for each plot	%
aaf	ash content in fine post-fire litter fraction for each plot	%
LITC _{af}	C concentration of total bulk post-fire litter	mg C g ⁻¹
LITC _{ub}	C concentration of post-fire unburned litter	mg C g ⁻¹
LITC _{ch}	CC concentration of post-fire charred litter	mg C g ⁻¹
α	Proportion of charred material in post-fire litter	
β	Proportion of post-fire unburned litter originated from the canopy leaves	
SL _{af}	Post-fire soil OM pool	g m ⁻²
SL _{gas}	Soil OM lost to the atmosphere as gas and particle	g m ⁻²
ST _{ub}	Post-fire unburned standing stem pool	g m ⁻²
St _{ch}	Post-fire charred standing stem pool	g m ⁻²
ST _{gas}	Stem OM lost to the atmosphere as gas and particle	g m ⁻²
LF _{gas}	Leaf OM lost to the atmosphere as gas and particle	g m ⁻²
LIT _{af}	Total post-fire litter pool	g m ⁻²
LIT _{ub}	Post-fire unburned litter pool	g m ⁻²
LIT _{ch}	Post-fire charred litter pool	g m ⁻²
LIT _{gas}	Litter OM lost to the atmosphere as gas and particle	g m ⁻²
LF_LIT _{ub}	OM transferred from pre-fire canopy leaves to post-fire unburned litter	g m ⁻²
LF_LIT _{ch}	OM transferred from pre-fire canopy leaves to post-fire charred litter	g m ⁻²
LIT_LIT _{ub}	OM from pre-fire litter that remained in post-fire unburned litter	g m ⁻²
LIT_LIT _{ch}	OM from pre-fire litter that remained in post-fire charred litter	g m ⁻²

Table 2 Allometric relationships for the different species linking leaf and stem dry biomass (in g) to length of rachis and blades (L_{rachis} and L_{blade} , in cm), stem diameter (D , in mm) and plant height (H , in cm)

Species	Source	Measured parameters	Equations for stems or rachis dry mass (g m ⁻²)	Equations for leaves or blade dry mass (g m ⁻²)
<i>Serenoa repens</i>	Gholz et al. (1999)	rachis and blade length (cm), number of living fronds	Fronde number*(EXP(-10.38 + (2.72* LN(L_{rachis} + L_{blade}))))	Fronde number* ((0.85* L_{blade})- 13.31)
<i>Quercus myrtifolia</i> and <i>chapmanii</i>	Day et al. (1996)	Basal stem diameter (mm)	EXP(-2.537 + 2.969*LN(D))	EXP(-2.88 + 2.86*LN(D))
<i>Quercus geminata</i>	Day et al. (1996)	Basal stem diameter (mm)	EXP(-2.58602 + 2.90252*LN(D))	EXP(-1.72793 + 2.31391*LN(D))
<i>Lyonia ferruginea</i>	Sabina Dore, Personal communication	Basal stem diameter (mm)	0.0208*(D) ^{3.1103}	0.1261*(D) ^{2.1016}
<i>Myrica cerifera</i>	Sabina Dore, Personal communication	Height (cm)	10 [^] (-3.73 + 2.47*LOG10(H))	H *0.0867 + 1.29

proportion of charred vs. unburned fractions was estimated for each plot. Charred surfaces and unburned inside sections were analysed for C and N contents. Then C and N stocks in standing vegetation after fire were calculated.

The pre-fire litter proved charcoal free under visual identification. This observation was confirmed by the fact that the C concentration of the pre-fire litter was slightly lower than that of the post-fire unburned litter (data not shown). The opposite would have been expected if charcoal from previous fire events remained in the pre-fire litter. For these reasons, the pre-fire litter was considered charcoal free for our modelling exercise.

For post-fire litter, visual identification alone proved insufficient for charcoal quantification in the large post-fire litter samples, which contained intimately mixed charred, partially charred and unburned materials. We used the C concentration differences between post-fire unburned and charred litters to determine the charcoal content of litter samples. Incomplete combustion of organic matter leads to modifications of chemical structures. Above a temperature of 150°C, the C concentration increases under dehydration and aromatisation processes (Baldock and Smernik 2002; Almendros et al. 2003; Knicker et al. 1996). Standing-vegetation leaves falling during the fire event contributed to post-fire litter stocks. Therefore the difference between pre- and post-fire litter composition is not only due to charring, but also to litter fall during the fire event. Consequently, post-fire charred litter was compared to the post-fire unburned litter rather than to the pre-fire litter. Considering that the bulk post-fire litter is a mix of charred and unburned leaves, the proportion of charcoal material in the litter, α , was computed as:

$$\alpha = \frac{\text{LITC}_{\text{af}} - \text{LITC}_{\text{ub}}}{\text{LITC}_{\text{ch}} - \text{LITC}_{\text{ub}}} \quad (1)$$

where LITC stands for the C concentration of the litter (mg C g^{-1}), 'af' is for the total bulk post-fire litter, 'ch' the charred post-fire litter, 'ub' the unburned post-fire litter. Visual identification of charred and unburned material was conducted on post-fire litter material obtained from mixing six

randomly distributed samples collected across Shiloh outside of the experimental plots. A subsample was cautiously sieved into three size fractions, i.e. 0–1 mm, 1–2 mm, >2 mm, to avoid underestimating the contribution of smaller fractions. Colour was used to visually identify the charred litter fraction. Brown and black leaf particles were hand-picked separately for each size fraction. This was replicated five times. Unburned and charred fractions were analysed for total C content as described above.

Flux estimates to post-fire charred and unburned C pools

All ecosystem C fluxes were derived from the field observations and the measured pools, the latter comprising pre-fire leaves, stems, litter and soil, and post-fire charred and unburned standing stems, charred and unburned litter, and soil. Visual identification indicated that little to no leaves remained on the post-fire standing stems, and this pool was therefore ignored. We hypothesised that the soil exchanged biomass neither with the overlying litter nor with the above-ground vegetation during the fire event. This reasonable hypothesis was reinforced by the fact that soil C and N stocks were not significantly affected by fire, as described later. This first assumption allowed us to solve the soil system separately through mass balance:

$$\text{SL}_{\text{bf}} = \text{SL}_{\text{af}} + \text{SL}_{\text{gas}} \quad (2)$$

where SL_{bf} is the measured pre-fire soil pool (g m^{-2}), SL_{af} is the post-fire soil pool (g m^{-2}), and SL_{gas} (g m^{-2}) is the unknown loss to the atmosphere. The system was solved for both C and N components.

Visually, little or no stem material appeared to be transferred to the litter pool during fire, while large amounts of charred and unburned leaves were easily identified. Therefore, we ignored the flux from stems to litter during the fire event. This allowed us to solve the stem transformations separately through mass balance:

$$\text{ST}_{\text{bf}} = \text{ST}_{\text{ub}} + \text{ST}_{\text{ch}} + \text{ST}_{\text{gas}} \quad (3)$$

where ST_{bf} is the measured pre-fire stem pool ($g\ m^{-2}$), ST_{ub} is the measured post-fire unburned standing stem pool ($g\ m^{-2}$), ST_{ch} is the same for the charcoal component ($g\ m^{-2}$), and ST_{gas} is the unknown loss to the atmosphere ($g\ m^{-2}$), which is being computed through this equation. The system was solved for both C and N components.

The mass balance of the leaf-litter system can then be described through four equations:

$$LF_{bf} = LF_LIT_{ub} + LF_LIT_{ch} + LF_{gas} \quad (4)$$

$$LIT_{bf} = LIT_LIT_{ub} + LIT_LIT_{ch} + LIT_{gas} \quad (5)$$

$$LIT_{af} * \alpha = LF_LIT_{ch} + LIT_LIT_{ch} \quad (6)$$

$$LIT_{af} * (1 - \alpha) = LF_LIT_{ub} + LIT_LIT_{ub} \quad (7)$$

where LF_{bf} and LIT_{bf} are the measured pre-fire leaf and litter pools, respectively. LF_LIT_{ub} and LF_LIT_{ch} are the unknown fluxes from canopy leaves to unburned and charred litters ($g\ m^{-2}$), respectively. Similarly, LIT_LIT_{ub} and LIT_LIT_{ch} are the unknown fluxes from pre-fire litter to post-fire unburned and charred litters ($g\ m^{-2}$), respectively. LF_{gas} and LIT_{gas} are the unknown losses to the atmosphere from the canopy leaf and litter pools ($g\ m^{-2}$), respectively. LIT_{af} ($g\ m^{-2}$) is the measured post-fire litter and α is the quantifiable proportion of charcoal in post-fire litter as described in Eq. (1).

This set of four equations contains six unknown fluxes and therefore requires two additional equations for solving the system unequivocally. The first additional equation is derived from the observation that post-fire unburned litter is a mixture of unburned fallen canopy leaves and litter. The proportion, β of unburned litter that originates from the canopy leaves, can then be calculated by solving the following equation:

$$\beta = \frac{LITC_{ub} - LITC_{bf}}{LFC_{bf} - LITC_{bf}} \quad (8)$$

where LFC_{bf} ($mg\ C\ g^{-1}$) stands for the C concentration of pre-fire vegetation leaves and $LITC_{bf}$ ($mg\ C\ g^{-1}$) is the same for pre-fire litter. This equation requires the additional hypothesis

that C concentrations of post-fire unburned material remained identical to pre-fire values. The unknown flux from canopy leaves to unburned litter can then be deduced from β and the unburned litter value:

$$LIT_{ub} * \beta = LF_LIT_{ub} \quad (9)$$

The second additional equation is based on the hypothesis of Kuhlbusch and Crutzen (1995) that, within fire types, the ratio of BC to gas loss is constant. Here we assumed that the ratio of charcoal to gas loss is identical for leaves and litter. In that sense, we used the hypothesis of Kuhlbusch and Crutzen (1995) in a more restrictive way, as we applied it only to predominantly leaf-type material, i.e. vegetation leaves and litter. In addition, temperature regimes experienced during the fire event were quite similar for the standing vegetation and the litter, as we will later show in this article.

$$\frac{LF_LIT_{ch}}{LF_{gas}} = \frac{LIT_LIT_{ch}}{LIT_{gas}} \quad (10)$$

The set of six equations defined by (4–7) and (9) and (10) with six unknown fluxes was then solved using the MAPLE 8 software (Maplesoft).

Results

Pre-fire living biomass in scrub oak ecosystem

The 20-plot mean above-ground biomass density was $72 (\pm 90)\ Mg\ ha^{-1}$. The high variability is due to the small size of the experimental plots. The mean shrub density was $19.4 (\pm 9.9)\ stems\ m^{-2}$. The total biomass was 73.4% woody oak stems and palmetto rachis, and 26.6% oak leaves and palmetto blades (Table 3). *Quercus geminata* and *myrtifolia* represented 42.8% and 35.8% of the total biomass, respectively. The rest of the biomass was composed of *Lyonia ferruginea*, *Serenoa repens*, *Quercus chapmanii* and *Myrica cerifera*, at 8.5%, 8.2%, 4.5% and 0.2%, respectively.

Table 3 Pre-fire biomass and C and N concentrations and stocks in the dominant species of the scrub ecosystem

	Mean biomass (g m ⁻²)		C concentration (mg g ⁻¹)		N concentration (mg g ⁻¹)		C quantity (g m ⁻²)		N quantity (g m ⁻²)	
	Leaves (blade)	Stems (rachis)	Leaves (blade)	Stems (rachis)	Leaves (blade)	Stems (rachis)	Leaves (blade)	Stems (rachis)	Leaves (blade)	Stems (rachis)
<i>Serenoa repens</i>	189	332	465	471	13	5	88	156	3	2
<i>Q. myrtifolia</i>	802	1,708	500	481	7	5	401	822	13	8
<i>Q. geminata</i>	711	2,589	497	473	19	6	353	1,225	13	15
<i>Q. chapmanii</i>	101	201	485	470	19	5	49	95	2	1
<i>Lyonia ferruginea</i>	106	434	531	487	15	4	56	211	2	2
<i>Myrica cerifera</i>	5	6	493	482	20	7	3	3	0	0
Total biomass	1,914	5,270					950	2,512	32	27

Temperature measurements

Soil temperature at 2–3 cm remained below 100°C during fire (Fig. 2a). On the litter surface, recorded temperature ranged from 371 to 760°C with a mean of $493 \pm 112^\circ\text{C}$. This temperature range is contained within classes 3 and 4 (Fig. 2b).

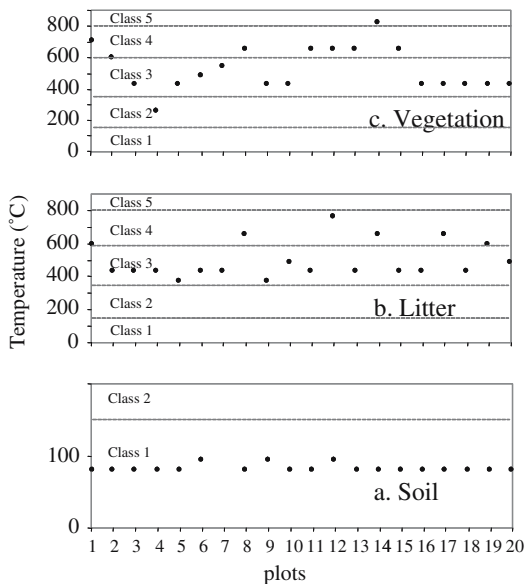


Fig. 2 Maximum temperatures reached during fire (in °C) and corresponding classes along the transect (a) in vegetation, (b) in litter, and (c) 2.5 cm below the soil surface. Temperature classes corresponded to: (1) below 150°C, (2) from 150 to 350°C, (3) from 350 to 600°C, (4) from 600 to 800°C and (5) above 800°C

Fire temperatures within the vegetation were more variable, ranging from 260 to 816°C with a mean of $524 \pm 137^\circ\text{C}$, and they belonged to classes 2, 3, 4 or 5 (Fig. 2c).

Fire-induced evolution of C and N stocks

Soil C and N stocks in the top 5 cm were not significantly affected by fire (Table 4). Mean carbon content was 62 mg C g soil⁻¹ in pre-fire soil and 70 mg C g soil⁻¹ in post-fire soil. Mean N content was 2 mg N g soil⁻¹ before fire and remained unchanged after fire. Nevertheless, this low increase in C concentration was more than compensated for by an inverse trend in bulk density. Indeed, C and N stocks decreased by 7% and 8%, respectively (Table 4). However, these changes proved non-significant according to paired *t*-tests ($P > 0.1$).

Fire significantly reduced litter C and N stocks by 36% and 17%, respectively (Table 4). Post-fire dead vegetation biomass was 23 Mg ha⁻¹. Significant correlations between pre- and post-fire values were observed for biomass, C and N stocks (Fig. 3a–c). Post-fire vegetation C represented 30% of its pre-fire value ($r^2 = 0.91$), while only 12% of N was preserved ($r^2 = 0.92$).

Atmospheric losses, as gas and particles, from vegetation, litter and soil represented 43.7% of initial C stocks, and 39.5% of initial N stocks. However, soil C and N stocks were not significantly

Table 4 Pre- and post-fire C and N stocks in the vegetation, litter and soil surface of the scrub ecosystem

Ecosystem OM pools	C (g m ⁻²)		N (g m ⁻²)	
	Before fire	After fire	Before fire	After fire
Vegetation	3,463	1,105**	60	7**
Litter	613	394***	14	12*
Soil surface	2,198	2,035 ^{NS}	83	76 ^{NS}
Total ecosystem	6,274	3,534	157	95

All units are in g m⁻². NS = non-significant and *, **, *** indicate significance levels at $P < 0.1$, $P < 0.01$ and $P < 0.001$, respectively, as determined by paired *t*-tests

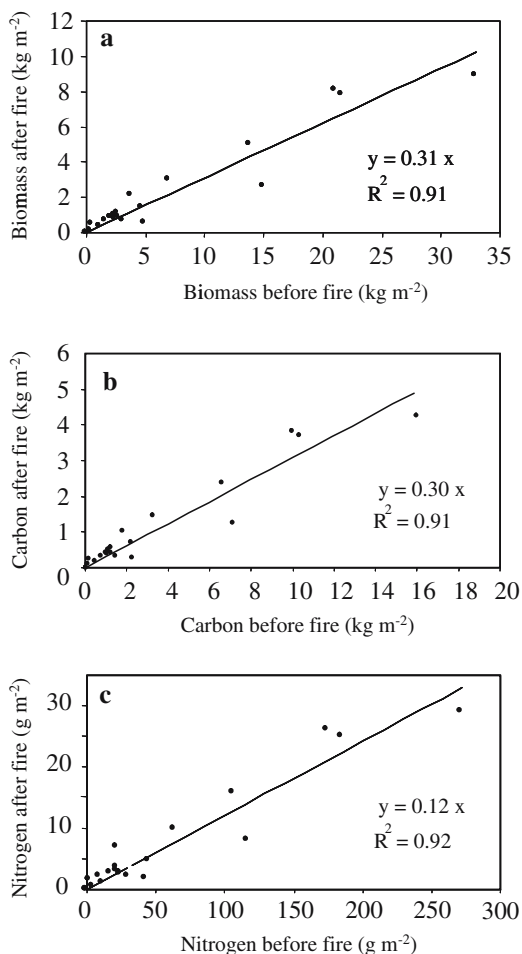


Fig. 3 Fire-induced evolution of (a) biomass, (b) C, and (c) N stocks in vegetation: remaining OM represents 31% of biomass ($r^2 = 0.91$), 30% of initial C ($r^2 = 0.91$), and 12% of initial N ($r^2 = 0.92$)

modified by fire. Vegetation and litter pools combined lost 63.4% and 74.6% of their initial C and N stocks, respectively (Fig. 4).

Charcoal production

Charcoal C and N contents of post-fire stems represented $2.4 \pm 1.8\%$ and $2.4 \pm 1.1\%$ of initial values, respectively. These values corresponded respectively to $5.6 \pm 4.2\%$ and $9.4 \pm 7.2\%$ of the post-fire standing dead C and N stocks. Charcoal percentage of standing dead stems was positively related to temperature classes measured in the vegetation (Fig. 5a, b).

Post-fire litter C concentrations ranged from 416 to 537 mg C g⁻¹, and corresponding N concentrations ranged from 12 to 17 mg N g⁻¹. Post-fire litter C concentrations were positively correlated to fire temperatures reached within the vegetation (Fig. 6).

Total post-fire litter contained 65.1%, 16.6% and 18.3% of material > 2 mm, 1–2 mm and < 1 mm, respectively (Table 5). Carbon concentrations of hand-picked charred and unburned particles were quite similar among these three fractions, averaging 584 mg C g⁻¹ for the charcoal particles and 459 mg C g⁻¹ for the unburned particles (Table 5). This confirms that a strong C-concentration shift was induced by fire, and that this signal was quite consistent throughout particle size distribution. For N, the fire-induced shift was much weaker, from 15 mg N g⁻¹ for the unburned particles to 16 mg N g⁻¹ for the charred particles (Table 5). In addition, N concentration significantly varied among size fractions with N enrichment in the finer fractions. Indeed, the size-fraction shift in N content appeared larger than the fire-induced one. For this reason, percentages of charcoal could be reliably derived from the mixing equation (1), while the small fire-induced N signal could not be used.

Fig. 4 Distribution of C and N pools in the scrub oak ecosystem before and after fire, as percentage of total initial quantities in ecosystem

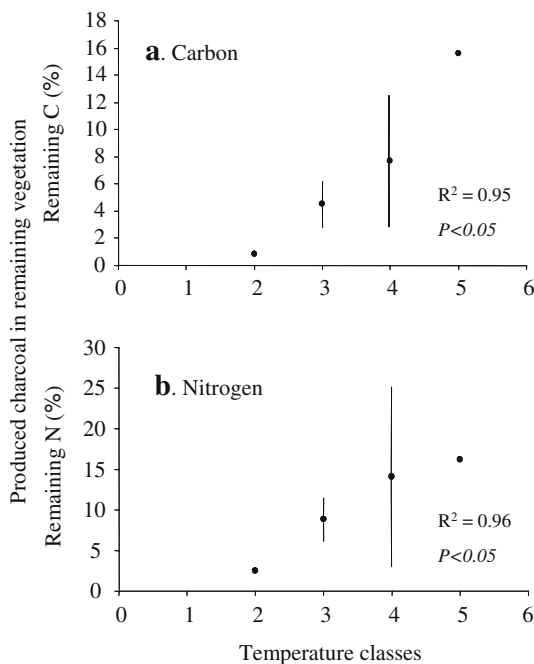
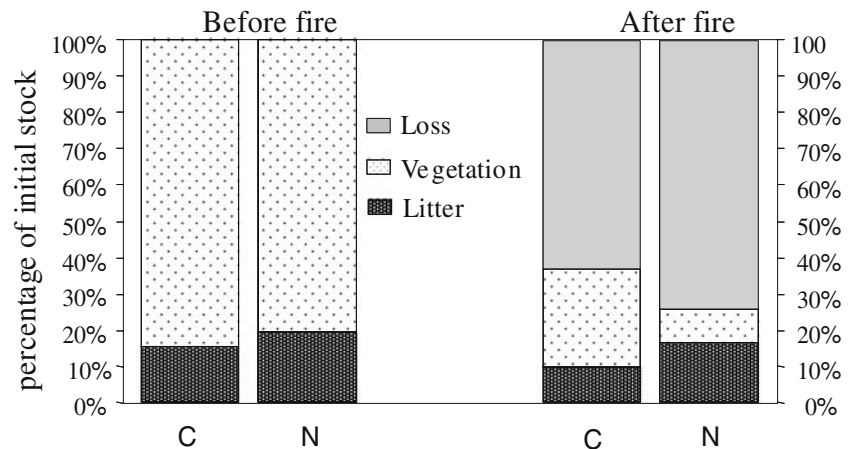


Fig. 5 Percentage of (a) charred C, and (b) charred N in remaining vegetation. Experimental plots were grouped per temperature class, and for each class charcoal-C or charcoal-N percentages were averaged. Standard deviations represented except for classes 2 and 5, which contained only one plot

The proportion of charcoal α was calculated with Eq. (1) and the C-shift values of Table 5. Mean proportion of charcoal for the 19 plots represented 17.6% of litter biomass, with a proportion of 11.6%, 12.4% and 41.0% in fraction >2 mm, 1–2 mm and <1 mm, respectively.

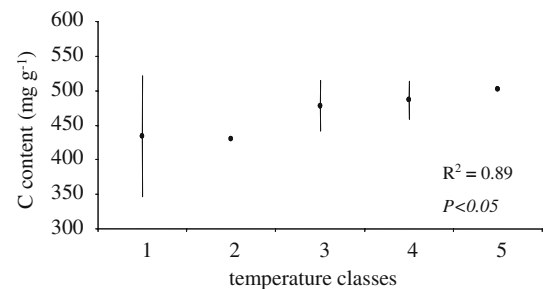


Fig. 6 C concentration of post-fire litter. Experimental plots were grouped per vegetation temperature class. C concentrations were averaged within each class. Standard deviations provided except for classes 2 and 5, which contained only one plot. Value corresponding to temperature class 1 is value of C concentration in pre-fire litter

Fire-induced fluxes in scrub oak ecosystem

Atmospheric C losses reached 56.2% from vegetation stems, 78.9% from vegetation leaves, and 68.9% from litter (Fig. 7). These values were estimated by solving Eqs. (3–10), which require multiple measured parameters. Standard errors of C and N concentration data were low, generally less than 1% of the average value. Biomass data had the highest relative standard errors, i.e. about 28%. However, all pre- and post-fire measurements were conducted on identical plots, which greatly reduced the uncertainty on the differential fluxes, as illustrated by the highly significant results of the paired *t*-tests (Table 4). We did not estimate error propagation in the set of Eqs. (3–10) notably because these equations describe a

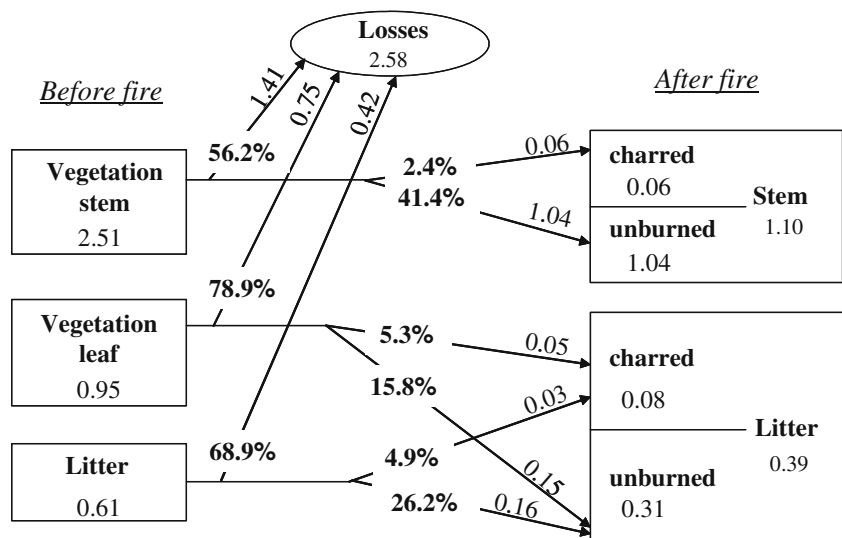
Table 5 Mean C and N concentrations in post-fire litter size-fraction of total ($n = 19$), charred ($n = 5$) and unburned ($n = 5$) material

Litter fraction	Proportion in post-fire litter %	Post-fire litter		Charred material		Unburned material		Charcoal proportion %
		Mean [C] (mg g ⁻¹)	Mean [N] (mg g ⁻¹)	Mean [C] (mg g ⁻¹)	Mean [N] (mg g ⁻¹)	Mean [C] (mg g ⁻¹)	Mean [N] (mg g ⁻¹)	
> 2 mm	65.1 (12.7)	479 (32)	13 (2)	590 (14)	15 (1)	465 (6)	14 (1)	11.6
1–2 mm	16.6 (5.3)	469 (41)	16 (1)	592 (9)	17 (1)	452 (3)	16 (0)	12.4
< 1 mm	18.3 (8.0)	489 (55)	20 (2)	554 (5)	19 (1)	441 (6)	17 (0)	41.0
Weighted means		478	15	584	16	459	15	17.6

Standard deviations are between brackets

Averaging was conducted on individual sample values ($n = 19$), each obtained from weighted means of litter fractions, and therefore are not exactly identical to weighted means of the per-litter-fraction values presented in the table

Fig. 7 Fire-induced modifications of C stocks and fluxes in the scrub oak ecosystem as derived from solving Eqs. (4–7) and (9) and (10). Absolute values are provided in kg C m⁻²



model where hypotheses carry non-quantifiable effects on the estimate.

On average, 2.4% of pre-fire vegetation stem C was transformed into charcoal, and 41.4% remained in standing dead biomass. About 21% of vegetation leaf C was transferred to the litter, with 5.3% as charcoal. In litter, charcoal production corresponded to 4.9% of initial C, while 26.2% remained in unburned litter. The proportion β of unburned leaves originating from vegetation was 44.2% of unburned litter after fire.

Remaining vegetation and litter C represented 33.2% of the pre-fire stock. Charcoal production from vegetation and litter C was 3.4% of the pre-

fire stock. This corresponds to a charcoal biomass of 244 g m⁻² or 136 g C m⁻². As explained above, corresponding N fluxes could not be estimated by model exercise. However, using the N contents of burned stems and burned litter, we estimated that total charcoal-N production was ~2.9 g N m⁻².

Discussion

Fire-induced losses and fluxes

Fire-induced biomass loss from the oak scrub vegetation to the atmosphere averaged 68% of the pre-fire stock. Burning efficiency is dependent

on the vegetation type. High biomass Amazonian forests were reported to lose only 35% of their initial biomass under the effect of fire (Graça et al. 1999). By contrast, herbaceous ecosystems can lose more than 90% of their above-ground biomass during fire events (Kauffman et al. 1994). Similarly, we observed in the present study that the burning efficiency of woody stems was much lower than that of foliage (Fig. 6). A high proportion of tree vs. fine-fuel and grass biomass decreases the burning efficiency (Barbosa and Fearnside 2005). Our results obtained in a dense oak-scrub ecosystem are quite consistent with the 70–80% biomass-loss estimates obtained in tropical dry forests and tree savannas (Kauffman et al. 1994, 2003). The dense canopy of the scrub oak reduces the growth of herbaceous species (Schmalzer and Hinkle 1996), which potentially explains that our measured burning efficiency was slightly lower than that observed in tropical dry forests.

Soil C and N contents were not significantly modified by fire in the oak scrub. A similar absence of fire effect on soil C and N stocks has been reported for other ecosystems (Kauffman et al. 1994; Roscoe et al. 2000), although some studies report significant losses (see review by Certini 2005). Our results are consistent with the limited increase in temperature at 2–3 cm depth, with maximum temperatures remaining below 100°C. The soil surface has good heat-insulation properties (Salgado et al. 1995; DeBano 2000), and no C losses from soils were reported when heated up to 150°C (Fernandez et al. 1997). Soil temperatures remain below 95°C as long as the soil water has not been entirely vaporised (Campbell et al. 1994; Certini 2005). Our results suggest that the soil surface still contained water, thereby preventing C loss through organic matter combustion. In addition, the heading fire was potentially too fast for a substantial heat front to move through the upper soil profile.

Fire-induced losses of C and N stocks from the scrub-oak vegetation and litter to the atmosphere (cf. Table 4) averaged 2,600 g C m⁻² and 55 g N m⁻². Relative to pre-fire biomass stocks, more N than C was lost. This observation appears contrary to findings that N is more preserved than C during the charring process (Knicker et al.

1996; Kuhlbusch et al. 1996; Almendros et al. 2003). In our study, N losses are due to preferential burning of N-rich organs rather than to preferential N loss within each organ. Indeed, we observed a 79% atmospheric loss of canopy leaves with a C/N ratio of 30 vs. a 56% atmospheric loss of stems with a C/N ratio of 95 (cf. Fig. 7 and Table 3).

Charcoal production

Conversion of pre-fire vegetation C stocks into charcoal-C reached 2.4% for stems, 5.3% for leaves, and 4.9% for litter (cf. Fig. 7). Adding stem and leaf contributions, 3.2% of pre-fire vegetation C stocks were converted into charcoal. This value does not differ greatly from those reported by Fearnside et al. (1999, 2001) for an Amazonian rainforest. In the scrub oak ecosystem, C-losses from biomass were about 21 times the amount of charcoal-C being produced. In Amazonian forests, this ratio ranges from 16 to 32 (Fearnside et al. 1999, 2001). The high variability of fire effects on the C budget, as reported in other studies (Fearnside et al. 2001), illustrates the need for specific studies both in terms of ecosystems and fire types.

The absence of charcoal in the pre-fire litter indicates that all charcoal disappears from the litter layer within a fire-return cycle, i.e. 11 years. No erosion is expected to occur in this flat landscape. Charred residues may have been mineralised or transferred to the soil as fine particles after physical degradation.

Charcoal production from above-ground biomass and litter was about 140 g C m⁻² or 11.7 mol C m⁻² during a typical scrub oak fire. However, only the BC fraction of the charcoal can be considered recalcitrant to biochemical alteration (Nguyen et al. 2004). BC percentage in charcoal is method-dependent, and until now no consensus exists concerning BC quantification (Schmidt et al. 2001; Masiello 2004). BC concentration, measured with chemical oxidation and solid-state ¹³C-NMR technique, was reported to be about 60% of organic carbon in a charred wood sample from Pompeii (Simpson and Hatcher 2004). Preliminary NMR investigations of our scrub-oak charcoal material (data not shown)

suggest that it is close in chemical structure to that analysed by Simpson and Hatcher (2004). This value implies that the production of recalcitrant BC in the oak scrub could potentially represent 7 mol C m^{-2} , which is within the range of values given by Wirth et al. (2002b). The BC values presented here are based on remaining charcoal and do not take into account the atmospheric losses of soot particles, which have been estimated to equal about 20% of the BC production (Kuhlbusch and Crutzen 1995). This implies that measurements of BC remaining in the ecosystem slightly underestimate BC production.

Implication for century-scale C budget

Assuming that the charcoal generated by the prescribed fire is resistant to degradation for at least 100 years, ten successive fire events during a century-long period would accumulate about $1,400 \text{ g charcoal-C m}^{-2}$ in the soil surface. This amount of charcoal C, although substantial, is certainly less than vegetation C stocks accrued over a century long-period without fire. Schmalzer and Hinkle (1996) reported that stem biomass in the oak scrub nearly tripled from 8-year-old to 25-year-old stands. This indicates that the young oak trees are in a productive growth stage at the time of the prescribed fires, i.e. around 10 years of age. In our case, a doubling of the stem biomass over an 11-year period would translate into an additional $2,500 \text{ g C m}^{-2}$ stored in the ecosystem. Although we do not have biomass estimates for stands that would be protected from fire for a century-long period, biomass-C accumulation in such a scenario would be much larger than the respective production of charcoal-C under the 10-year fire return cycles. Even if fire suppression would theoretically lead to a large increase in ecosystem C storage, we have to consider that fire is somewhat unavoidable in the scrub oak ecosystem, which means that the C-storage capacity of charred material has to be compared to that of the post-fire unburned material and not to that of the live biomass.

The ecosystem fire generates two new C pools: the atmospheric losses and the charcoal. For each C pool, the sum of both constitutes the fire products. In oak scrub, charcoal represents about

4% and 6% of fire products from stems and leaves, respectively. As discussed above, this estimate is affected by two uncertainties that somewhat cancel one another; not all charcoal is recalcitrant BC (Nguyen et al. 2004) and about 20% of the produced charcoal is lost to the atmosphere (Kuhlbusch and Crutzen 1995). In the scrub oak ecosystem, we assume that the post-fire unburned material decomposed similarly to plant residues that were not exposed to fire. Transformation of plant residues into soil organic matter (SOM) that is stable at the medium-term (>10 years) is also a fairly low-yield reaction. For corn, SOM stabilisation ratio ranged between 7.7% and 20% across nine different studies, as indicated in the review work of Bolinder et al. (1999). The longest corn experiments in these series, between 25 and 32 years, had stabilisation ratios that were in the upper range, which suggests that the resulting SOM is really stable over multiple decades to centuries. In other cropping systems and environmental conditions, stabilisation ratios were also reported to range between 7.6% and 21% (Kong et al. 2005 and references therein). Here we will make the conservative hypothesis that SOM stabilisation from plant residues in the scrub oak ecosystem is at the lowest end of these values, i.e. 7%. This conservative estimate is justified by the sandy nature of the soil and the entirely shoot-origin of the residues, which have both been associated with lower levels of SOM stabilisation potential (Rasse et al. 2005). Notwithstanding these uncertainties, it appears that the fire-induced stabilisation yield of oak-scrub biomass into charcoal (4–6%) is lower than the transformation yield of an equivalent mass of plant residues in stable SOC through humification processes (7%).

All recalcitrance is relative. Although a portion of SOM in soils is thousands of years old (Rumpel et al. 2002), most of the so-called stable fraction of SOM might only be so over periods of decades to centuries (Balesdent and Recous 1997). On the other hand, even BC is not totally inert and may also be mineralisable (Shindo 1991; Bird et al. 1999; Baldock and Smernik 2002; Hamer et al. 2004). In addition, the recalcitrance of BC is defined through thermal, chemical or photo-oxidative attacks (Schmidt and Noak 2000).

Whether such methods can actually discriminate mean residence time in soils is still an open question. Similar methods applied to isolate the recalcitrant SOM fraction have actually failed to find a strong link with mean residence time of the isolated compounds in natural environments (Balesdent 1996; Poirier et al. 2002). Over very long time scales, multiple centuries to millennia, BC is probably more recalcitrant than the stable SOM fraction of soils. Nevertheless, over a few decades to a century, it appears that the stabilisation of plant residue in the scrub oak ecosystem through the effect of fire might not exceed that occurring through humification processes.

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