Soil carbon dynamics during secondary succession in a semi-arid Mediterranean environment

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Abstract

Clarifying which factors cause an increase or decrease in soil organic carbon (SOC) after agricultural abandonment requires integration of data on the temporal dynamics of the plant community and SOC. A chronosequence of abandoned vineyards was studied on a volcanic island (Pantelleria, Italy). Vegetation in the abandoned fields was initially dominated by annual and perennial herbs, then by Hyparrhenia hirta (L.) Stapf, and finally by woody communities. As a consequence, the dominant photosynthetic pathway changed from C3 to C4 and then back to C3.

Conversion of a plant community dominated by one photosynthetic pathway to another changes the $^{13}C/^{12}C$ ratio of inputs to soil organic carbon (SOC). Using the time since abandonment and the shift in belowground $\delta^{13}C$ of SOC relative to the aboveground $\delta^{13}C$ plant community, we estimated SOC turnover rate.

SOC content (g kg$^{-1}$) increased linearly ($R^2 = 0.79$ and 0.73 for 0–15 and 15–30 cm soil depth) with the age of abandonment, increasing from 12 g kg$^{-1}$ in cultivated vineyards to as high as 26 g kg$^{-1}$ in the last stage of the succession.

$\delta^{13}C$ increased in the bulk soil and its three fractions during succession, but only for soil fractions the effects of soil depth and its interaction with succession age were significant. Polynomial curves described the change in $\delta^{13}C$ over the chronosequence for both depths. $\delta^{13}C$ in the bulk soil had increased from $-28\%$ to $-24\%$ by 30 yr after abandonment for both depths but then decreased to $-26\%$ at 60 yr after abandonment (corresponding with maturity of the woody plant community). Overall, the results indicate that abandoned vineyards on volcanic soil in a semi-arid environment are C sinks and that C storage in these soils is closely related to plant succession.

1 Introduction

Because of human activities, the concentration of atmospheric CO$_2$ is increasing rapidly while the long-term storage capacity of terrestrial and ocean ecosystems is
declining (Canadell et al., 2007). Understanding the role played by soil in global C
dynamics requires estimation of soil carbon (C) stocks. Because more C is stored in
the soil than in vegetation or the atmosphere (Eswaran et al., 2000), changes in soil C
content could greatly affect the atmosphere (Lal, 2004).

The effects of the conversion of natural soil to cropland or pasture on C storage are
well known (Del Galdo et al., 2003; Desjardins et al., 2004; Romkens et al., 1999). In
contrast, less is known about the dynamics of soil organic carbon (SOC) after agricul-
tural abandonment, and this is especially true for Mediterranean areas (Alberti et al.,
2011; La Mantia et al., 2007). There is some evidence that abandonment of agricultural
land and the subsequent regeneration of forests through secondary succession may
return C storage to the pre-agricultural levels, although the rate of recovery depends on
the time one considers and whether the land was previously used for crops or pasture
(Post and Kwon, 2000; Guo and Gifford, 2002).

A major factor affecting the dynamics of SOC after the abandonment of an agricul-
tural land is climate (Alberti et al., 2011). Zhang (2007) found that abandonment led to
an increase in SOC in a favourable (medium rainfall and high temperatures that sup-
ported high primary productivity) climate but a decrease in SOC in an unfavourable
climate. This finding, however, was not confirmed by other experimental evidence.
For example, abandonment under climatic conditions that limit primary production (a
Mediterranean climate) caused an increase in the soil C_stock (Alberti et al., 2011). Sim-
ilarly, a lack of soil disturbance in a semiarid environment resulted in an increase of C
in the soil surface (Alvaro-Fuentes et al., 2009).

Furthermore, the increase of SOC concentration is determined by the incorporation
of new organic matter in the coarse fraction and the reduction of mineralisation pro-
cesses in the finest ones (Ouédraogo et al., 2005; Barbera et al., 2010). Regardless, it
is not clear whether SOC content can continue to increase as a function of time since
agricultural abandonment or whether there is some limit. Whether SOC accumulates
or decreases greatly depends on how interactions between climate and soil type affect
SOC mineralisation rates and/or accumulation in soil.
SOC mineralization can be reduced within soil aggregates in comparison to bulk soil, and the formation and turnover of soil aggregates are affected by agricultural abandonment and other changes in land management (Schimel et al., 1995). There is still lack of knowledge on how management conditions and their abandonment affect aggregate formation and the protection of SOC. Generally, micro-aggregates (<250 µm; Tisdall and Oades, 1982) are relatively stable and are bound by persistent polysaccharide-based glues produced by roots and microbes and by calcium bridges. On the other hand, micro-aggregates are bound into macro-aggregates (>250 µm) by a network of roots and hyphae. Therefore, macro-aggregate stability is thought to respond more rapidly to changes in land use. Several authors have reported that the aggregate stability and SOC content of stable macro-aggregates were higher in native grassland than in cultivated fields (Cambardella and Elliott, 1992; Six et al., 2002). Others reported a higher mean residence time of SOC for reduced-tilled soils (Six et al., 2002; Collins et al., 1999), and the increased residence time was attributed to an increased physical protection of soil aggregates in the absence of disturbance.

As noted, the physical protection of SOC provided by aggregates favours SOC accumulation whereas cultivation tends to break aggregates apart and therefore increases SOC mineralization. The inclusion of SOC in soil aggregates and the mineralization of SOC in broken aggregates is accompanied by changes in the chemical structure of SOC. These processes have been studied with the aid of δ^{13}C analysis (Buzek et al., 2009; Desjardins et al., 1994, 2004, 2006; Wookey et al., 2002).

After agricultural abandonment, old fields are “spontaneously” colonized by various plants, a gradual process during which different plant communities develop (secondary succession). In general, annual and perennial herb communities dominate early and are then partially or completely replaced by perennial grasses, shrubs, and/or trees. These changes within a plant community characterized by a switch from one photosynthetic pathway to another modify the $^{13}C/^{12}C$ ratio ($\delta^{13}C$) of inputs to SOC. Using the time since perturbation and the shift in belowground $\delta^{13}C$ of SOC relative to the aboveground $\delta^{13}C$ of the plant community, researchers can estimate the SOC turnover rate.
SOC turnover rates have been estimated when C4-dominated natural grasslands were converted to C3 annual crops and perennial pastures (Balesdent et al., 1990; Follet et al., 1997), or when C3-dominated natural forests and grasslands were converted to C4 annual crops and perennial pastures (Balesdent et al., 1987; Gregorich et al., 1995; Jastrow et al., 1996), but no data are available for secondary successions characterized by a C3-C4-C3 pathway. When separated on the basis of chemical composition, aggregate size, or particle density, SOC fractions have been shown to differ in age and thus in turnover rate (Balesdent et al., 1990; Jastrow et al., 1996).

The present study analyses the change in soil carbon stock along a secondary succession after agricultural abandonment, and describes differences in SOC turnover rates along succession for all soil fractions. The evaluation of SOC turnover using changes in the natural abundance of $\delta^{13}$C contributes to the knowledge on aggregate formation and the protection of SOC under different management systems, and provides data on SOC turnover along a C3-C4-C3 succession pathway.

2 Materials and methods

2.1 Study and sampling area

The study was carried out in cultivated and abandoned terraced vineyards on Pantelleria Island (Italy), which is situated in the rift of the Sicilian Channel (83 km² surface area; 36°44′ N, 11°57′ E) (Fig. 1a). Pantelleria is of volcanic origin, its highest summit is Montagna Grande (836 m a.s.l.), and its surface rocks are mainly acidic, silicic volcanites (pantellerites and trachytes). Most of the diffused soils are Lithosols, Regosols (mainly “escalic”), and Cambisols (mainly “vitric”) (C. Dazzi, personal communication, 2011). The island is semi-arid (Thornthwaite and Mather, 1955) with a typical Mediterranean climate: most of the annual mean precipitation (409 mm) falls between October and February; monthly average temperatures range from 25.6°C (August) to 11.7°C (January).
Except for the most recent lava flows, Pantelleria has over the centuries been almost entirely terraced for agriculture. Currently, only about 20% of these terraces are still cultivated with grapevine, caper, and olive trees (Rühl, 2007), while the rest have been abandoned by agriculture. This abandonment has continued since the 1950s; it first affected the most inaccessible and marginal areas, and then the more accessible ones. Because of secondary succession dynamics, natural vegetation has spread spontaneously into the old fields.

The rapidity and course of these colonization processes depend on various factors such as exposure (Rühl et al., 2006), the presence of favourable microsites for germination and growth of woody species (safe-site-effect), and the distance of seed sources from the old field (neighbourhood-effect; Rühl and Schnittler, 2011). Thus, the current landscape of Pantelleria is characterized by a mosaic of patches of old fields differing in abandonment age and degree of woody colonization.

Succession dynamics on Pantelleria can be “slow” or “fast” but in any case lead to the formation of the same maquis-wood community dominated by Quercus ilex L. (Rühl et al., 2006). Old fields characterized by “fast” succession dynamics are north-facing and/or are located near woody source communities. For the first 5 yr after abandonment, these fields are dominated by annual and perennial herbs. Then, the cover of woody species increases rapidly, so that shrub communities are present about 15–20 yr after abandonment, with the most common species being Arbutus unedo L., Cistus L. sp. pl., Erica arborea L., Erica multiflora L., Phillyrea latifolia L., Pistacia lentiscus L., and Quercus ilex. Old fields characterized by “slow” succession dynamics, in contrast, are south-facing and/or are located far from woody seed sources; in these fields, colonization by woody species is slower and often follows an intermediate stage that is dominated by the C4 grass Hyparrhenia hirta (L.) Stapf. Apart from the community dominated by H. hirta, all other communities occurring during local secondary succession are dominated by C3 plants.

The sampling area was situated on a south-facing slope where still-cultivated and abandoned terraced vineyards were present in close proximity to each other (no more
than 10 m). Environmental factors such as geological substrate, soil type (in terms of soil texture), exposure values, etc., can be regarded as homogeneous for all samples.

Soil samples were taken in seven terraces which represent all stages of secondary succession of vine old fields (chronosequence approach). In fact, the selected terraces host different plant communities (herb community, *Hyparrhenia* grassland, *Hyparrhenia* grassland with shrubs, shrubland, and maquis) as a function of their abandonment age and their distance from woody seed sources (Table 1 and Fig. 1b).


### 2.2 Soil sampling and processing

In each of the seven terraces, three soil samples were collected at 0–15 cm and 15–30 cm depth, respectively (randomly in an area of about 20 m²). The soil was air-dried and passed through a 2-mm sieve. To reduce the error tolerance to less than ±5 %, 2–4 kg of soil (Hitz et al., 2002) was collected per sample. The soil texture was 60 % sand, 25 % silt, and 15 % clay, and did not statistically differ among soil samples and depths.

Soil $C_{stock}$ (Mg ha$^{-1}$) was calculated as:

$$C_{stock} \text{(Mg ha}^{-1}) = BD \cdot C_{conc} \cdot D \cdot CF_{coarse}$$

where $C_{conc}$ is carbon concentration (g/100 g), BD is bulk density (Mg m$^{-3}$), $D$ is depth thickness (m), and CF is a correction factor (1–(Gravel % + Stone %)/100).

Wet aggregate-size fractions, without prior chemical dispersion, were isolated by mechanical shaking of 100 g of air-dried fine soil on a column of sieves with pore sizes >250, 250–25, and <25 µm using a Shaker AS 200 Sieve (RETSCH analytical, 203-mm sieves) (amplitude of 2 cm, frequency of 1.6 Hz and a water flux of 2 l min$^{-1}$). After the physical fractionation, we distinguished three main aggregates of soil based on size: >250 µm (macro-aggregates, of “particulate organic matter” POM), 25–250 µm (micro-aggregates), and <25 µm (silt and clay fraction).
3 Chemical analysis

For each soil fraction, the relative weight distribution, the C content, and $\delta^{13}C$ abundance were measured. Total N was measured only for the bulk soil (passed through a 1-mm sieve). Because of its volcanic origin, the soil contained no carbonates, which facilitated high accuracy in determining C isotope composition.

SOC content was analysed by the Walkley-Black method (Walkley and Black, 1934). For the $\delta^{13}C$ analysis, an EA-IRMS (elemental analyser isotope ratio mass spectrometry) was used. The reference material used for analysis was IA-R001 (Iso-Analytical Limited wheat flour standard, $\delta^{13}C_{V-PDB} = -26.43\%$). IA-R001 is traceable to IAEA-CH-6 (cane sugar, $\delta^{13}C_{V-PDB} = -10.43\%$). IA-R001, IA-R005 (Iso-Analytical Limited beet sugar standard, $\delta^{13}C_{V-PDB} = -26.03\%$), and IA-R006 (Iso-Analytical Limited cane sugar standard, $\delta^{13}C_{V-PDB} = -11.64\%$) were used as quality control samples for the analysis. The International Atomic Energy Agency (IAEA), Vienna, distribute IAEA-CH-6 as a reference standard material.

The results of the isotope analysis are expressed as a $\delta$ value (‰) relative to the international Pee Dee Belemnite standard as follows:

$$\delta(\text{‰}) = \frac{R_s - R_{st}}{R_{st}} \cdot 1000$$

(2)

where $\delta = \delta^{13}C$, $R = ^{13}C/^{12}C$, $s =$ sample, and $st =$ standard.

4 Data analysis

Natural abundance of $\delta^{13}C$ was measured and used to determine the proportion of C in SOC that was derived from the new crop (independently in C3 or C4) and how much C remained from the previous crop in each soil fraction. These proportions were calculated by the mixing equation (Gearing, 1991):
New carbon derived (N_{cd}) (\%) = \frac{(\delta^{13}C_{new} - \delta^{13}C_{old})}{(\delta^{13}C_{biomass new species} - \delta^{13}C_{old})} \quad (3)

and

Old carbon derived (O_{cd}) (\%) = 1 - N_{cd} \quad (4)

where \( N_{cd} \) is the fraction of C derived from the present vegetation type, \( \delta^{13}C_{new} \) is the isotope ratio of the soil sample, \( \delta^{13}C_{biomass new species} \) is the isotope ratio of the colonizing species (-11.3 ± 0.15 ‰), and \( \delta^{13}C_{old} \) is the isotopic ratio of the previous vegetation type (-27.5 ± 2.1 ‰, 27.1 ± 1.6 ‰, and 27.2 ± 1.6 ‰), respectively for vineyard, shrub, and wood (Table 1 and Fig. 1a).

Turnover of SOC (mean resident time in years, MRT) was determined by taking the reciprocal of the first order rate constant \( k \) (Eq. 5) according to Balesdent and Mariotti (1996) and Dorodnikov et al. (2007).

The mass of new carbon additions was calculated both for bulk soil and each fraction (Eq. 6).

5 Statistical analysis

The data for mass content, total soil C, new crop-derived C, C content, and C concentration for each fraction were analysed by analysis of variance (ANOVA) for a completely randomized block. Differences between means were tested with the LSD test at \( P < 0.05 \). SAS statistical programs were used (SAS Institute, 2001). Time since the abandonment was regressed against new and old carbon derived in the same plot both for bulk soil and its fractions.
6 Results

6.1 Total C and N

SOC content (g kg\(^{-1}\)) increased linearly \(R^2 = 0.79\) and 0.73 for 0–15 and 15–30 cm soil depth) with the age of abandonment; it increased from 12 g kg\(^{-1}\) in the cultivated vineyard (terrace 1) to 26 g kg\(^{-1}\) in the vineyard abandoned 60 yr earlier (terrace 7) (Fig. 2). There was no interaction between age and depth, and SOC content was greater near the surface (0–15 cm) than deeper (15–30 cm) in the soil (Fig. 2); after 60 yr of abandonment, SOC content was 28 g kg\(^{-1}\) at 0–15 cm and 26 g kg\(^{-1}\) at 15–30 cm. Nitrogen content also increased with abandonment age, but with a highly significant interaction between depth and age such that the two regressions converged 60 yr after abandonment (Table 2) (Fig. 3).

6.2 \(\delta^{13}\)C values in bulk soil and fractions

\(\delta^{13}\)C values in bulk soil and in the three fractions were significantly affected by succession (years since abandonment) (Table 2). Depth and its interaction with succession were significant for the fractions but not for the bulk soil (Table 2).

Changes in \(\delta^{13}\)C values for the two depths over the course of the secondary succession were described by highly significant polynomial curves \(R^2 = 0.78\) for 0–15 cm and 0.73 for 15–30 cm) (Fig. 4). \(\delta^{13}\)C values in the bulk soil increased from \(-28\%\) at time of abandonment to \(-24\%\) at 30 yr after abandonment for both soil depths. \(\delta^{13}\)C values subsequently decreased to \(-26\%\) 60 yr after abandonment, corresponding to the maturity of the woody community. A similar trend occurred for both macro and micro-aggregates at both depths (Tables 3 and 4). Silt-clay aggregate did not reduce variability across all period of investigation and maintains the same trend of bulk soil, macro and micro-aggregate fractions.
6.3 Soil and C mass of the three soil fractions

The mass of macro-aggregates (>250 µm) was greater than that of the two smaller fractions and did not change substantially with abandonment age at either depth (Fig. 5); the large quantity of sand in this fraction probably limits further aggregation. In contrast, the mass of the micro-aggregates (25–250 µm) increased while that of the smallest fraction (<25 µm) decreased during the 60 yr after abandonment. For the two depths, 500 and 450 g kg\(^{-1}\) of smallest fraction were measured, respectively, in the still cultivated vineyard where soil is frequently subjected to rotary tillage that breaks apart the micro- and macro-aggregates.

Following abandonment, SOC content changed more in the intermediate soil fractions (25–250 µm) than in the larger or smaller fraction; in the intermediate fraction, SOC content jumped from <5 g kg\(^{-1}\) of C from 0 to 25 yr after abandonment to >10 g kg\(^{-1}\) of C from 30 to 60 yr after abandonment (Table 3). The SOC content of micro-aggregates, except for vineyard in the 15–30 soil layer did not show any statistical differences underlining the high stability of SOC in this fraction. Also POM carbon (>250 µm fraction) was stable in the deeper layer (except for vineyard system).

6.4 SOC derived from the “new crop” in bulk soil and in fractions

The effect of change of vegetation (from C3 to C4 and again to C3) was easily explained by estimates of carbon derived from soil in the chronosequence. At both depths in the bulk soil, the proportion of carbon derived from new vegetation increased linearly (\(R^2 = 0.83\)) and the proportion derived from old vegetation decreased linearly (\(R^2 = 0.78\)) with time since abandonment (Fig. 6). The quantity of old SOC was greater than that of new SOC until year 40 but the opposite was true at year 45 and later in the chronosequence. The trend was similar for macro-aggregates (>250 µm) (Fig. 6) except that the quantity of new carbon exceeded old carbon about 35 yr after abandonment. Perhaps the content of old carbon declined faster in the macro-aggregates.
than in the bulk soil because this fraction has a high sand content and probably a high mineralization rate.

In the other two fractions, the two lines either intersected or at least met much later after abandonment (Fig. 6).

### 6.5 SOC turnover

The quantity of old C in the bulk soil was relatively constant for the first 30 yr after abandonment and then decreased when woody plants increased, as indicated by the switch from C4 to C3 plants (Fig. 7); differences in old C did not statistically differ at either depth up to year 30. The quantity of new SOC in the bulk soil increased rapidly after year 30 (Fig. 7).

The contribution of new C in the other fractions decreased proportionally with fraction size (Fig. 7). In the smallest fraction, new C addition was inconsequential and did not statistically differ over time (Fig. 7).

In all fractions and at both depths, the mineralization coefficient ($k$) was high up to year 30, i.e. up to the time when the plant community switched from being dominated by C4 to C3 plants (Fig. 8).

The average mineralization coefficient for C3 and C4 biomass addition confirms that the values were higher for C4 than for C3 species at both depth (Table 5). Consequently, the MRT was lower for SOC for the C4 than C3 community. MRT values tended to be higher in the intermediate (250–25 µm) fraction in the C3 plant community, but the trend of aggregation along chronosequence must also be considered.

### 7 Discussion

In the semi-arid Mediterranean environment, where climate is one of the major driving forces for determining both rate of vegetation community turnover within secondary succession, and the period necessary to complete conversion (new steady state),
knowledge of $C_{stock}$ and the resilience of the soil must be increased. The results of the current study indicate that, following abandonment of vineyards on volcanic soil in a semi-arid Mediterranean area, the soil acts as a C sink. This finding is consistent with previous reports on semi-arid environments (Desjardins et al., 1994; Lisboa et al., 2009). The pattern of SOC distribution in the different fractions of the volcanic soil of the current study was slightly different from the pattern observed on semi-arid vertisols (Barbera et al., 2010).

Secondary succession is often accompanied by changes in soil structure that affect C storage. In the last stages of a succession, the increase in litter and roots can cause an increase in macro-aggregates and therefore an increase in the total $C_{stock}$ (Tisdall and Oades, 1982). The volcanic soil in the current study contained a large percentage of sand, which may explain why macro-aggregates increased only slightly in the chronosequence and were not associated with the increase in SOC. The increase in SOC was also not associated with the silt-clay fraction (<25 µm), which declined steeply along the chronosequence. In contrast, the increase in SOC was associated with the substantial increase in the intermediate aggregates (the micro-aggregates, 25–250 µm). Previous reports indicated that the micro-aggregate and silt-clay fractions contribute to SOC increase and stabilization (Six et al., 2002), but in the Pantelleria case study silt and clay fraction was incorporated in the micro aggregate fraction during the renaturalization processes must be considered. According to Six et al. (2002), the micro-aggregate fraction was more enriched than the other fractions in new carbon at the end of the studied chronosequence. In the current study, reduction in quantity of silt-clay aggregates did not apparently compromise carbon accumulation; in fact, the finest fraction was stabilized into micro-aggregate determining also a decrease of the mineralization coefficient ($k$) and an increase of MRT ($1/k$) of this fraction. A previous report indicated that the silt-clay fraction seems to be very important in maintaining the oldest soil $C_{stock}$ (Del Galdo et al., 2003).

In the chronosequence of the current study, new carbon gradually replaced old carbon in the different soil fractions. New carbon became dominant about 40 yr after
abandonment in the macro-aggregates and after nearly 50 yr in the micro-aggregates. In the silt-clay fraction, however, new and old carbon were nearly equivalent 60 yr after abandonment. According to Marin-Spiotta et al. (2009), the organic carbon in macro-aggregates and micro-aggregates are relatively unprotected and are consequently more sensitive to the influence of vegetation dynamics after land abandonment. The current results demonstrate that the SOC sequestration potential is lower for C4 than for C3 plant communities, which is due to the lower primary productivity and the high lignin content of C4 Hyparrhenia hirta (Wynn et al., 2007).

Moreover, the current study documented an increase in total soil nitrogen with time since abandonment, and this finding is consistent with other studies of succession in Mediterranean regions (Robertson and Vitousek, 1981; Bonet, 2004). This increase in nitrogen has been attributed to a progressive inhibition of nitrification (Carreira et al., 1994) and also to limited leaching under semi-arid conditions (Parfitt et al., 2003; Scott et al., 1999). Other studies in semi-arid regions showed that C losses may occur only if there is a substantial decrease in soil $N_{stock}$ and that the rate of change in both of these stocks is related to annual rainfall (Halliday et al., 2003; Kirschbaum et al., 2008).

The current results have some implications for the understanding of carbon cycle in semi-arid Mediterranean environments. The replacement of cultivation with other species and/or abandonment and renaturalization are interesting practices aimed to the carbon stock improvement, even if further studies need to improve data set to allow the predictions to be more reliable.

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References


Table 1. Characteristics of the abandoned vineyards (terraces 2–7) in this study. Terrace 1 was still under cultivation. Values for $\delta^{13}$C are from the above-ground plant biomass. “Close” and “Distant” woody seed sources were $<50$ m and $>100$ m, respectively, from the sampled field.

<table>
<thead>
<tr>
<th>Terrace</th>
<th>Abandonment (years)</th>
<th>$\delta^{13}$C (‰) (biomass)</th>
<th>Vegetation</th>
<th>Woody seed source</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>cultivated</td>
<td>27.5 ± 2.1</td>
<td>Vineyard</td>
<td>Close</td>
</tr>
<tr>
<td>2</td>
<td>15</td>
<td>11.1 ± 1.2</td>
<td><em>Hyparrhenia hirta</em> grassland (without woody individuals)</td>
<td>Close</td>
</tr>
<tr>
<td>3</td>
<td>28</td>
<td>16.1 ± 1.9</td>
<td>Mosaic of 50% <em>Hyparrhenia hirta</em> grassland mixed with 50% shrub cover (<em>Euphorbia dendroides, Cistus creticus, Phillyrea latifolia, Quercus ilex</em>)</td>
<td>Close</td>
</tr>
<tr>
<td>4</td>
<td>30</td>
<td>27.1 ± 1.6</td>
<td>Shrubland of <em>Cistus creticus</em> and <em>Euphorbia dendroides</em></td>
<td>Close</td>
</tr>
<tr>
<td>5</td>
<td>35</td>
<td>11.1 ± 1.2</td>
<td><em>Hyparrhenia hirta</em> grassland (without woody individuals)</td>
<td>Distant</td>
</tr>
<tr>
<td>6</td>
<td>40</td>
<td>16.1 ± 1.9</td>
<td>Mosaic of 50% <em>Hyparrhenia hirta</em> grassland mixed with 50% shrub cover (<em>Phagnalon saxatile, Phillyrea latifolia, Rubus ulmifolius</em>)</td>
<td>Distant</td>
</tr>
<tr>
<td>7</td>
<td>60</td>
<td>27.2 ± 1.6</td>
<td><em>Quercus ilex</em> and <em>Phillyrea latifolia</em> maquis</td>
<td>Close</td>
</tr>
</tbody>
</table>
Table 2. Results of statistical analysis for the effects of succession (years of abandonment), soil depth, and their interaction on SOC (g kg\(^{-1}\) of bulk soil) and \(\delta^{13}C\) for bulk soil and soil fractions. Single and double asterisk indicate \(P < 0.05\) and 0.01, respectively in ANOVA, ns indicates \(P > 0.05\).

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>SOC</th>
<th>(\delta^{13}C)</th>
<th>N</th>
<th>SOC</th>
<th>(\delta^{13}C)</th>
<th>SOC</th>
<th>(\delta^{13}C)</th>
<th>SOC</th>
<th>(\delta^{13}C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Succession ((S))</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>**</td>
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<td>**</td>
</tr>
<tr>
<td>Depth ((D))</td>
<td>*</td>
<td>ns</td>
<td>**</td>
<td>*</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>(S \times D)</td>
<td>ns</td>
<td>ns</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>**</td>
</tr>
</tbody>
</table>
Table 3. SOC (g C kg\(^{-1}\) bulk soil) and \(\delta^{13}\)C in bulk soil and fractions in the seven terraces of the chronosequence at 0–15 cm depth. Values in a column followed by different letters are significantly different (\(P < 0.05\)).

<table>
<thead>
<tr>
<th>Terrace</th>
<th>(\delta^{13})C</th>
<th>SOC</th>
<th>(\delta^{13})C</th>
<th>SOC</th>
<th>(\delta^{13})C</th>
<th>SOC</th>
<th>(\delta^{13})C</th>
<th>SOC</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>-28.08 a</td>
<td>17.7 b</td>
<td>-28.40 a</td>
<td>7.0 b</td>
<td>-28.10 a</td>
<td>3.5 b</td>
<td>-27.90 a</td>
<td>7.2 a</td>
</tr>
<tr>
<td>2</td>
<td>-26.34 b</td>
<td>16.2 b</td>
<td>-26.70 b</td>
<td>8.9 b</td>
<td>-27.11 a</td>
<td>5.1 b</td>
<td>-25.70 a</td>
<td>2.2 b</td>
</tr>
<tr>
<td>3</td>
<td>-24.85 c</td>
<td>18.1 ab</td>
<td>-24.26 c</td>
<td>11.5 a</td>
<td>-26.00 a</td>
<td>4.2 b</td>
<td>-25.77 a</td>
<td>2.4 b</td>
</tr>
<tr>
<td>4</td>
<td>-24.18 c</td>
<td>20.1 ab</td>
<td>-23.64 c</td>
<td>13.8 a</td>
<td>-24.61 a</td>
<td>4.9 b</td>
<td>-24.59 b</td>
<td>1.4 b</td>
</tr>
<tr>
<td>5</td>
<td>23.39 c</td>
<td>20.0 a</td>
<td>-23.49 c</td>
<td>7.6 b</td>
<td>-23.34 b</td>
<td>10.0 a</td>
<td>-23.93 b</td>
<td>2.2 b</td>
</tr>
<tr>
<td>6</td>
<td>-25.74 b</td>
<td>26.4 a</td>
<td>-26.86 b</td>
<td>10.0 a</td>
<td>-26.70 a</td>
<td>11.5 a</td>
<td>-26.49 a</td>
<td>4.9 b</td>
</tr>
<tr>
<td>7</td>
<td>-26.62 b</td>
<td>28.7 a</td>
<td>-27.10 b</td>
<td>11.0 a</td>
<td>-26.36 a</td>
<td>15.0 a</td>
<td>-25.98 a</td>
<td>2.6 b</td>
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</tbody>
</table>
Table 4. SOC (g C kg\(^{-1}\) bulk soil) and \(\delta^{13}\)C in bulk soil and fractions in the seven terraces of the chronosequence at 15–30 cm depth. Values in a column followed by different letters are significantly different (\(P < 0.05\)).

<table>
<thead>
<tr>
<th>Terrace</th>
<th>(\delta^{13})C</th>
<th>SOC</th>
<th>(\delta^{13})C</th>
<th>SOC</th>
<th>(\delta^{13})C</th>
<th>SOC</th>
<th>(\delta^{13})C</th>
<th>SOC</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>−27.48</td>
<td>a</td>
<td>11.7 b</td>
<td>5.2</td>
<td>b    26.96 a</td>
<td>2.5</td>
<td>b</td>
<td>27.32 a</td>
</tr>
<tr>
<td>2</td>
<td>−25.88</td>
<td>b</td>
<td>13.1 b</td>
<td>9.5</td>
<td>a    24.96 b</td>
<td>2.7</td>
<td>b</td>
<td>24.69 b</td>
</tr>
<tr>
<td>3</td>
<td>−23.90</td>
<td>c</td>
<td>12.7 ab</td>
<td>8.5</td>
<td>a    25.75 b</td>
<td>3.5</td>
<td>b</td>
<td>25.65 b</td>
</tr>
<tr>
<td>4</td>
<td>−24.27</td>
<td>c</td>
<td>19.9 ab</td>
<td>13.3</td>
<td>a</td>
<td>24.44 b</td>
<td>2.9</td>
<td>b</td>
</tr>
<tr>
<td>5</td>
<td>−22.81</td>
<td>c</td>
<td>19.3 a</td>
<td>9.3</td>
<td>a    22.95 b</td>
<td>6.3</td>
<td>a</td>
<td>23.81 b</td>
</tr>
<tr>
<td>6</td>
<td>−25.70</td>
<td>b</td>
<td>21.0 b</td>
<td>9.3</td>
<td>a    26.58 a</td>
<td>9.9</td>
<td>a</td>
<td>26.51 a</td>
</tr>
</tbody>
</table>
Table 5. Mineralization coefficients ($k$, per year) and mean residence times (MRT, $1/k$) for organic carbon in the bulk soil and soil fractions as affected by soil depth and dominant plant community (C4 or C3) in the chronosequence.

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>Plant community</th>
<th>$k$</th>
<th>MRT</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Bulk soil</td>
<td>&gt;250 (µm)</td>
<td>250–25 (µm)</td>
</tr>
<tr>
<td>0–15</td>
<td>C4</td>
<td>0.0181</td>
<td>0.0108</td>
</tr>
<tr>
<td></td>
<td>C3</td>
<td>0.0026</td>
<td>0.0112</td>
</tr>
<tr>
<td>15–30</td>
<td>C4</td>
<td>0.0157</td>
<td>0.0091</td>
</tr>
<tr>
<td></td>
<td>C3</td>
<td>0.0032</td>
<td>0.0102</td>
</tr>
</tbody>
</table>
Fig. 1. Aerial photograph of Pantelleria Island (A) and plant succession after vineyard abandonment (V, Vineyard; H, Hyparrhenia hirta; S, Shrubs; T, Trees). H is a C4 community and V, S, and T are C3 communities (B).
Fig. 2. SOC (g kg$^{-1}$) along the chronosequence at the two depths (○ 0–15 cm; ● 15–30 cm).
Fig. 3. Total nitrogen (g kg$^{-1}$) along the chronosequence for the two depths (○ 0–15 cm; • 15–30 cm).
Fig. 4. $\delta^{13}$C values along the chronosequence for the two depths (○ 0–15 cm; ● 15–30 cm).
Fig. 5. Masses (g kg$^{-1}$) of three soil fractions along the chronosequence at 0–15 cm and 15–30 cm soil depth.
Fig. 6. New ■ and old □ carbon derived (%) for bulk soil and fractions at two depths along the chronosequence. The dominance of the C4 and C3 plants in the succession is indicated by arrows (➡C4 stage; ➩C3 stage) (0–15 cm layer, top; 15–30 cm layer, bottom).
Fig. 7. New ■ and old □ carbon (Mg ha\(^{-1}\)) for bulk soil and fractions at two depths in the chronosequence. The dominance of the C4 and C3 plants in the succession is indicated by arrows (➡C4 stage; ➩C3 stage) (0–15 cm layer, top; 15–30 cm layer, bottom).
Fig. 8. New ■ and old □ carbon mineralization coefficients ($k$, per year) for bulk soil and fractions at two depths in the chronosequence. The dominance of the C4 and C3 plants in the succession is indicated by arrows (➡C4 stage; ➩C3 stage) (0–15 cm layer, top; 15–30 cm layer, bottom).