



Litter decomposition of six tree species on indigenous agroforestry farms in south-eastern Ethiopia in relation to litterfall carbon inputs and modelled soil respiration

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Abstract The indigenous agroforestry systems practised by smallholders in south-eastern Ethiopia have high biodiversity and productivity. However, little is known about their carbon (C) inputs and outputs. We carried out a 1-year litterbag study to determine leaf litter decomposition k constants for six woody species common to these agroforestry systems. The k values were then used to calculate the decomposition C losses from measured litterfall C fluxes and the results compared to modelled soil respiration (R_s) C losses. Litterbag weight loss at the end of the year was 100% or nearly so, k values 2.582–6.108 (yr^{-1}) and half-life 41–112 days. k values were significantly ($p = 0.023$) correlated with litter N contents, nearly so with C/N ratios ($p = 0.053$), but not with other nutrients (Ca, Mg and K), and negatively correlated with temperature ($p = 0.080$). Using species, farm elevation, temperature and litter quality as predictors, partial least squares regression explained 48% of the variation in k . Depending on species, estimated decomposition C losses from litterfall were 18 to 58% lower than annual litterfall C inputs. Using a heterotrophic respiration

(R_h) to R_s ratio of 0.5, modelled R_h C losses were 89 to 238% of litterfall decomposition C losses estimated using k values. However, using an R_h/R_s ratio of 0.27, which is appropriate for tropical humid forests, R_h C losses were 11 to 138% of estimated litterfall decomposition C losses. Our decomposition and soil respiration estimates indicate that litterfall is sufficient to maintain soil organic C contents and thereby the soil fertility of these unique agroforestry systems.

Keywords Litterbags · Litterfall · Partial least squares regression · Soil respiration · Tropics

Introduction

Interest in agroforestry has greatly increased recently because of food security issues and because of its potential for carbon (C) sequestration and hence climate change mitigation (Thangata and Hildebrand 2012; Mbow et al. 2014a, b). Although agroforestry is widely practised by smallholder farmers throughout Africa, there have been relatively few studies investigating the C cycle in African agroforestry systems in terms of litterfall production, litter decomposition and soil respiration.

Litterfall production and quality in agroforestry systems, as in general, varies with many factors including tree species, size and age, climate and

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season, and soil and management practice (Isaac et al. 2005; Isaac and Nair 2006; Hairiah et al. 2006; Das and Das 2010; Dawoe et al. 2010; Murovhi et al. 2012). Studies on litter decomposition in tropical agroforestry systems in Asia and South America have reported high but highly variable decomposition rates that are related to litter quality and climatic factors (Hairiah et al. 2006; Hossain et al. 2011; Jairo et al. 2017; Petit-Aldana et al. 2019). The rates are comparable to those reported for tropical forests (Powers et al. 2009; Waring 2012). Agroforestry related litter decomposition studies carried out in eastern Africa have shown that leaf litter decomposition also greatly differs among species, whether the trees are leguminous or not, the leaves are green or senesced, and on the season (Gindaba et al. 2004; Teklay 2004, 2007; Teklay and Malmer 2004; Mahari 2014; Abay 2018).

Soil respiration CO_2 effluxes are directly correlated to litterfall fluxes and litter decomposition rates and are driven by the same climatic factors (Raich and Schlesinger 1992; Raich and Tufekcioglu 2000; Bond-Lamberty and Thomson 2010). Field measurements of soil respiration rates from tropical agroforestry systems are few (Bae et al. 2013; Costa et al. 2018), but reported rates are high and similar to those reported for tropical humid forests (Oertel et al. 2016). Heterotrophic respiration, which measures the decomposition of soil organic matter, could be expected to show the most correspondence to litterfall and litter decomposition C fluxes.

Agroforestry has a long history in Ethiopia (Asfaw and Nigatu 1995). The indigenous systems practised today by small-holders on the escarpment of the Rift Valley in south-eastern Ethiopia are unique and have developed from natural forest through gradual intensification of land use centuries ago (Negash and Achalu 2008). They are characterised by a high diversity of fruit tree, shrub species and herbaceous food crops, and are highly productive (Negash et al. 2012).

The main objectives of this study were to determine the litter decomposition rates (k decay constants) of six woody species that are common in the indigenous agroforestry systems of south-eastern Ethiopia and to determine the dependence of k on litter quality factors and climate. We hypothesized that the k decay constants would differ among the six tree species because of differences in the initial chemical composition of the litter and that the k values would be correlated to

climate (mean annual temperature). Using the k values and measured C contents we also calculated litterbag decomposition losses of C and compared them with measured litterfall and modelled soil respiration C fluxes, hypothesizing that litterbag C loss would show correspondence with both. This study is part of a larger study that has dealt with the C budget of indigenous agroforestry systems in south-eastern Ethiopia (Negash et al. 2012, 2013a,b; Negash and Starr 2013, 2015; Negash and Kanninen 2015).

Material and methods

Study sites

The study was carried out in indigenous agroforestry systems practised on Rift Valley escarpment in the Gedeo zone in south-eastern Ethiopia ($6^\circ 10' \text{ N}$, $38^\circ 20' \text{ E}$). The elevation of the 14 study sites (smallholder farms) ranged from 1524 to 2190 m a.s.l. According to the Köppen-Geiger classification system, the climate is classified as tropical savanna with dry-winter characteristics (As). The mean monthly temperature recorded at Dilla weather station ($6^\circ 22' 49.6'' \text{ N}$, $38^\circ 18' 24.9'' \text{ E}$, 1515 m a.s.l.) is 18° C varying little during the year and the annual precipitation is about 1470 mm with a drier season from November to March (monthly rainfall < 100 mm) and two rainfall peaks, generally in May and October (Fig. 1). The soils in the study area are mainly Nitisols, i.e. relatively fertile, deep, well-drained red tropical soils with high clay and organic matter contents. For the

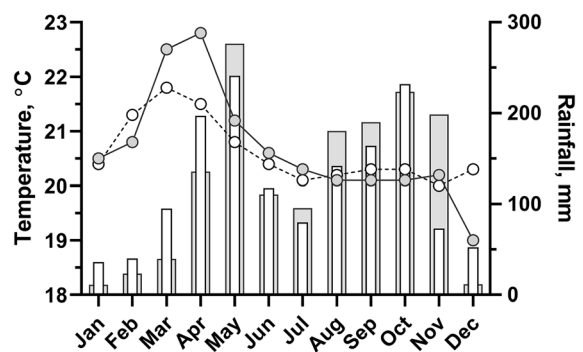


Fig. 1 Monthly mean (2005–2011; shaded) and 2011 (unshaded) temperatures (lines) and rainfall (bars) recorded at Dilla weather station ($6^\circ 22' 49.6'' \text{ N}$; $38^\circ 18' 24.9'' \text{ E}$; 1515 m a.s.l.) (Ethiopian National Meteorology Agency)

study farms, the soil texture of the 0–30 cm layer varied from loam to clay loam, clay contents from 17 to 58%, pH (in water) from 4.93 to 7.83, organic carbon content from 2.2 to 7.7%, and nitrogen content from 0.12 to 0.43%. Agroforestry dominates the land-use (94.5%) in the area with the remainder comprising grassland (1.4%), wetland (0.8%), natural forest (0.5%), plantations (0.1%) and others (2.7%).

Leaf litterfall and decomposition (litterbag dry weight loss) for four native tree species (*Cordia africana* Lam., *Croton macrostachyus* Del., *Erythrina brucei* Schweinf., *Millettia ferruginea* (Hochst.) Bak) and two non-native species (*Mangifera indica* L. and *Persea americana* Mill.) were determined in the field. These six species are the dominant species used in the agroforestry practised throughout the study area, typically accounting for > 70% of basal area and stem density and > 80% of the crown area (Negash et al. 2012). They provide fruits, fodder, fuel, shade for crops, and improve the microclimate for the growth of coffee (*Coffea arabica* L.) and enset (*Ensete ventricosum* (Welw.) Cheesman). *E. brucei* and *M. ferruginea* are also N-fixing species.

Litterfall

Monthly litterfall was collected at seventeen small-holder farms during 2010 (Negash et al. 2013a, b). For each of the six tree species, two or three farms were selected (farms where the trees were healthy, mature, and of good form). A litterfall trap was placed under the canopy of two trees of the selected species at each farm. The traps consisted of nylon netting (1 mm mesh diameter) draped over four 1.5 m tall wooden poles forming a 1 × 1 m collection area. To ensure complete collection, a stone was placed in the centre of the netting to weigh it down. At the end of each month the litterfall, which was mainly foliage, was collected. Litterfall other than leaves (e.g. small branches, flower, seeds) were removed before the remaining leaves were air-dried for a day and then, oven-dried (24 h at 65 °C), weighed and stored. Monthly litterfall fluxes (g m^{-2}) for each trap were calculated from the oven-dry mass and trap catch area (1 m^2).

At the end of the year, the stored leaf litterfall samples were composited by species and a subsample of each species taken and milled into a fine powder for chemical analysis. C contents were determined using the Walkley–Black method and nitrogen (N) contents

determined using the Kjeldahl method. Calcium (Ca), magnesium (Mg) and potassium (K) contents were determined after dry ashing and HCl acid digestion. Mg and Ca contents were determined using atomic absorption spectrophotometry and K by flame photometry. The analyses were performed in triplicate for each element and the mean values used in further calculations.

The monthly litterfall fluxes of C for each farm and species ($\text{LF}_{\text{C},i,j}$) were calculated as follows:

$$\text{LF}_{\text{C},i,j} = \text{LF}_{\text{DW},i,j} C_j / 100 \quad (1)$$

where $\text{LF}_{\text{DW},i,j}$ is the oven-dry weight litterfall flux (g m^{-2}) for the i^{th} month and j^{th} species and farm, and C_j is the annual C content (%) of litterfall for the j^{th} species averaged across the farms.

Litterbag incubation and k decay constants

Litterbags containing the combined monthly leaf litterfall collected in 2010 were installed at 14 of the farms on 1 January 2011. In the case of *C. macrostachyus*, *E. brucei*, *M. ferruginea* and *P. americana* there were two farms and in the case of *C. africana* and *M. indica* three farms (Table 1). The litterbags were prepared by inserting 200 g (± 0.01 g) of the oven-dried leaf litterfall material into 20 × 20 cm bags made from nylon netting having a mesh size of 1 mm. A labelled litterbag was installed at each corner of each litterfall trap using a small spade to make an incision at an angle of 45° and carefully inserting the bag to a depth of 15 cm. In total, 112 litterbags were placed out. A bag at each trap was retrieved on 31st March, 30th June, 30th September and 31st December, i.e. after 89, 180, 272 and 364 days respectively, and transported to the laboratory.

In the laboratory, the bags were carefully cut open and any ingrown roots and soil aggregates removed by hand. The remaining litter was gently rinsed with tap water to remove adhering soil particles, oven-dried (48 h at 55 °C) and weighed (± 0.01 g). The litter was then composited by species, ground into a fine powder and three sub-samples analysed for organic C and N contents using the same methods as described for litterfall. Species mean contents were used in subsequent calculations.

Table 1 Litterfall (initial litterbag material) carbon and nutrient contents and ratios by species. Species having the same lower case letter are not significantly different (ANOVA followed by Tukey's multiple comparison tests, $\alpha = 0.05$)

| Species | C, % | N, % | C/N | Ca, % | Mg, % | K, % |
|-----------------------------|------|-------------------|--------------------|---------------------|-------|---------------------|
| <i>Cordia africana</i> | 46.0 | 2.12 | 21.7 | 1.352 ^b | 0.529 | 0.691 ^{ab} |
| <i>Croton macrostachyus</i> | 48.0 | 2.97 ^a | 16.2 ^a | 3.524 ^a | 0.572 | 0.852 ^a |
| <i>Erythrina brucei</i> | 46.8 | 2.98 ^a | 15.7 ^{ab} | 3.817 ^a | 0.920 | 0.604 ^{bc} |
| <i>Mangifera indica</i> | 45.9 | 1.67 | 27.5 | 1.276 ^b | 0.679 | 0.401 ^{cd} |
| <i>Millettia ferruginea</i> | 49.8 | 2.72 | 18.3 ^b | 1.247 ^b | 0.783 | 0.605 ^{bc} |
| <i>Persea americana</i> | 50.4 | 1.40 | 36.0 | 1.914 ^{ab} | 0.731 | 0.330 ^d |

Decomposition constants were derived by fitting the following exponential decay equation to the litterbag weight loss data for each trap:

$$W_t/W_0 100 = 100e^{-kt} \quad (2)$$

where W_t = dry weight of remaining litter at time t (year fraction), W_0 = dry weight of litter at time 0, and k = litter decomposition decay rate constant (yr^{-1}). Equation 2 was fitted to the untransformed litterbag percentage weight remaining values using nonlinear regression analysis and the Y-intercepts forced through 100% (i.e. weight remaining at $t = 0$) (Adair et al. 2010).

Calculation of litterfall decomposition C loss fluxes

We used the litter decay constants to estimate how much of each month's litterfall flux (mean of the two traps) that was measured in 2010 would be remaining at the end of each subsequent month until the end of the year. These values were converted into monthly amounts of C remaining (g C m^{-2}) for each farm and species using Eq. 1. C contents (%) of the litterfall remaining at the end of each month were assumed to follow the mean C contents (%) of the litterbags measured during 2011. The C content of the litter remaining for the months between the measured at 0, 3, 6, 9 and 12 months was estimated using linear interpolation. Each month's litterfall was treated as a cohort such that the total amount of C in litterfall remaining (g C m^{-2}) at the end of each month was the sum of the current and previous month's amount of C remaining. For example, the total amount of C in the litterfall remaining in March was the sum of the amount of January's, February's and March's

remaining litterfall C. The monthly C loss (g C m^{-2}) from the litterfall through decomposition was then calculated as the difference between the monthly litterfall C flux and the estimated total amount of C remaining at the end of the month:

$$\text{LF}_{\text{Closs},j} = \text{LF}_{\text{C},j} - \sum_{(i=i)}^n (\text{LF}_{\text{Cremain},j}) \quad (3)$$

where $\text{LF}_{\text{Closs},j}$ = amount of litterfall C lost through decomposition at the end of the i^{th} month for the j^{th} species and farm, $\text{LF}_{\text{Cremain},j}$ = the amount of litterfall C remaining at the end of the i^{th} month for the j^{th} species and farm, and n = months up to the i^{th} month.

Modelled soil respiration fluxes

In the absence of measured soil respiration fluxes, we estimated soil respiration CO_2 -C fluxes for each farm using the linear regression models presented by Fung et al. (1987) and Raich and Schlesinger (1992). These simple models were used as they only require temperature data. The model by Fung et al. (1987) is for tropical/subtropical woody vegetation sites (Fung et al. 1987):

$$\text{Rs}_i/\text{Rs}_{\text{max}} = 0.78 T_i/T_{\text{max}} - 0.14 \quad r^2 = 0.64 \quad (4)$$

where Rs_i = mean monthly soil respiration (g C m^{-2} per day) for the i^{th} month, and Rs_{max} and T_{max} = maximum monthly soil respiration and temperature ($^{\circ}\text{C}$), respectively. For Rs_{max} we used a value of 3.0, which is based on values from Raich and Schlesinger (1992), Oertel et al. (2016) and Wood et al. (2013) for moist (humid) tropical forests.

The model by Raich and Schlesinger (1992) is global but data from tropical sites were included in the derivation of the model (Raich and Schlesinger, 1992):

$$R_s = 25.6T + 300 \quad r^2 = 0.42 \quad (5)$$

where R_s = annual soil respiration (g C m^{-2}) and T = mean annual temperature ($^{\circ}\text{C}$). Farm-wise 2011 mean temperatures were calculated from Dilla weather station ($6^{\circ} 22' 49.6'' \text{ N}$, $38^{\circ} 18' 24.9'' \text{ E}$, 1515 m a.s.l., Fig. 1) data using an adiabatic lapse rate correction value of 0.65°C per 100 m difference in elevation.

Statistical analysis

Significance testing for differences in the chemical characteristics of the litterfall samples among the six tree species was carried out using ANOVA and Tukey multiple comparison tests ($\alpha \leq 0.05$). Pearson correlation coefficients were employed to describe the degree of association between k and the individual variables (litter quality, and farm elevation and 2011 mean annual temperature). Partial least squares regression, PLS-R, was used to examine the combined effect and relative importance of all explanatory variables on k . Species was entered as a nominal variable. The SIMPLS method and leave-one-out cross-validation method were implemented. PLS-R extracts a set of orthogonal latent factors (vectors) from the predictor variables regardless of any multicollinearity among them to predict the dependent variable. The lowest root mean predicted residual sum of squares (PRESS) value was used to identify the optimal number of factors to use. Variable importance in projection (VIP) coefficients for the predictor variables reflect their importance to each of the latent factors and values > 0.8 indicate an important variable. The size of the model regression coefficients (using centred and scaled data) indicates the relative importance of each predictor and its sign (\pm) indicates the direction of the relationship between it and the latent factor. The goodness-of-fit of the actual and PLS-R predicted k values was examined by linear regression and the coefficient of determination (R^2).

For the nonlinear regression, ANOVA and correlation analyses we used GraphPad PRISM software (version 8.3.0 for Windows, GraphPad Software, San Diego, California, USA) and for the PLS-R analysis,

we used JMP software (JMP®, PRO 14.3.0. SAS Institute Inc., Cary, NC, USA).

Results

Other than C and Mg contents, significant differences in the chemical characteristics of the litterfall (initial litter material) among the species were found (Table 1). *C. macrostachyus*, *E. brucei* and *M. ferruginea* had higher N contents and lower C/N ratios than the other species. *C. macrostachyus* and *E. brucei* also had the highest Ca contents, although the difference from other species was not significant. *M. indica* and *P. americana* had the lowest K contents, the difference from other species being significant. Mg contents did not significantly differ among the species.

The exponential decay model (Fig. 2) explained 91.4–99.8% of species litterbag weight loss (Table 2). While there were too few data to allow for statistical testing of differences among the species, k values varied from 2.582 (*P. americana*, farm 44) to 6.108 (*M. ferruginea*, farm 13) (Table 2). The half-life (time to 50% weight loss) was the highest for *M. indica* (95–112 days), and the lowest for *M. ferruginea* (41–76 days) and *E. brucei* (52–67 days) (Table 2). The measured amount of litterbag weight remaining at the end of the year varied from 0 to 12% (*M. ferruginea*, farm 10) and the modelled amounts from 0.2 to 11% (*M. indica*, farm 51) (Fig. 2).

The k values significantly increased with the N content of the initial litter and correlations with litter initial C/N ratios (negative), farm elevation (positive) and temperature (negative) were nearly significant (Table 3). Interestingly, the correlations between the litterbag half-life values and the litter quality and environmental variables were stronger than those with the k values.

The PLS-R analysis using species and the ten other predictor variables indicated a 1-factor model (PRESS = 1.0182) that could explain 48% of the variation in the k values. The fit between the predicted and actual k values had an R^2 value of 48% (Fig. 3a). Of the six species only *E. brucei*, *M. indica* and *M. ferruginea* had VIP values > 0.8 , and of those *M. indica* and *M. ferruginea* had the greatest standardized model coefficients (Fig. 3b). Elevation, temperature, initial litter N, K and Mg contents, and C/N ratio had

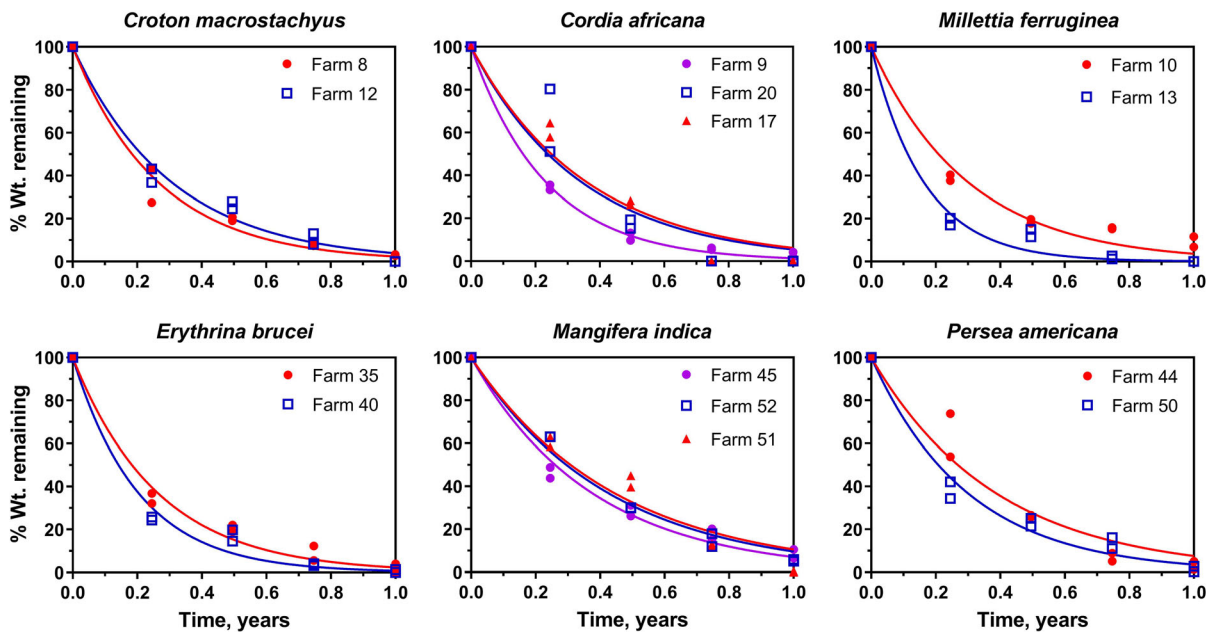


Fig. 2 Weight of litterbag remaining (as percentage of initial weight) for each species and farm plotted against time (year fraction), and the fitted exponential decay curves ($y = 100 e^{-kt}$) calculated using nonlinear regression (k values are given in Table 2)

Table 2 Farm elevation, mean temperature (2011), litterbag k decay constants, half-life (number of days until litterbag weight loss = 50%) and coefficient of determination (R^2) by farm and species

| Species | farm no | Elevation (m a.s.l.) | Temp. (°C) | k (yr ⁻¹) | Half-life (days) | R^2 (%) |
|-----------------------------|---------|----------------------|------------|-------------------------|------------------|-----------|
| <i>Cordia africana</i> | 9 | 2263 | 15.8 | 4.294 | 59 | 99.8 |
| <i>Cordia africana</i> | 17 | 2241 | 16.0 | 2.780 | 91 | 95.6 |
| <i>Cordia africana</i> | 20 | 2248 | 15.9 | 2.908 | 87 | 91.4 |
| <i>Croton macrostachyus</i> | 8 | 2169 | 16.4 | 3.753 | 67 | 99.3 |
| <i>Croton macrostachyus</i> | 12 | 2115 | 16.8 | 3.245 | 78 | 98.4 |
| <i>Erythrina brucei</i> | 35 | 1904 | 18.2 | 3.775 | 67 | 98.6 |
| <i>Erythrina brucei</i> | 40 | 1912 | 18.1 | 4.881 | 52 | 98.5 |
| <i>Mangifera indica</i> | 45 | 1673 | 19.7 | 2.662 | 95 | 98.5 |
| <i>Mangifera indica</i> | 51 | 1571 | 20.3 | 2.248 | 112 | 96.0 |
| <i>Mangifera indica</i> | 52 | 1521 | 20.6 | 2.347 | 108 | 98.7 |
| <i>Millettia ferruginea</i> | 10 | 2262 | 15.8 | 3.315 | 76 | 97.8 |
| <i>Millettia ferruginea</i> | 13 | 2207 | 16.2 | 6.108 | 41 | 98.7 |
| <i>Persea americana</i> | 44 | 1695 | 19.5 | 2.582 | 98 | 95.7 |
| <i>Persea americana</i> | 50 | 1697 | 19.5 | 3.334 | 76 | 98.1 |

VIP values > 0.8, indicating these were the most important predictors of k .

Litterfall C inputs were greater than the litterbag decomposition C losses for all six species, the difference varying between 14% (*E. brucei*)

and 58% (*M. indica*) (Fig. 4). The modelled soil respiration C losses at the end of the year were considerably greater than both litterfall C inputs and litterbag decomposition C losses. In comparison to litterbag C losses at the end of the year, Fung et al.

Table 3 Pearson correlation coefficients (r) and two-tailed p values describing the association between exponential decay model parameters (k and half-life) for litterbag weight loss and

farm elevation and mean temperature (2011) and chemical characteristics of litter. Significant ($\alpha < 0.05$) coefficients are in bold

| Decomposition parameter | Elevation | Temp | C | N | C/N | Ca | Mg | K |
|-------------------------|----------------|--------------|---------|----------------|--------------|---------|---------|---------|
| <i>k</i> | | | | | | | | |
| R | 0.485 | - 0.483 | 0.287 | 0.602 | - 0.526 | 0.267 | 0.361 | 0.366 |
| p | 0.079 | 0.080 | 0.320 | 0.023 | 0.053 | 0.356 | 0.205 | 0.199 |
| Half-life | | | | | | | | |
| R | - 0.597 | 0.594 | - 0.308 | - 0.687 | 0.589 | - 0.403 | - 0.312 | - 0.492 |
| p | 0.024 | 0.025 | 0.285 | 0.007 | 0.027 | 0.154 | 0.278 | 0.074 |

(Eq. 4) modelled R_s values were 123 to 510% greater than litterbag C losses; and 14 to 29% greater than R_s values modelled using the Raich and Schlesinger (1982) model (Eq. 5) (Fig. 4). Assuming an Rh/R_s ratio of 0.5, Rh C losses using the Raich and Schlesinger (1982) model (Eq. 5) were similar to litterbag decomposition C losses for *C. macrostachyus*, *C. africana* and *E. brucei* but greater for the other species. However, using an Rh/R_s ratio of 0.27 resulted in Rh values less than or similar to litterbag decomposition C losses.

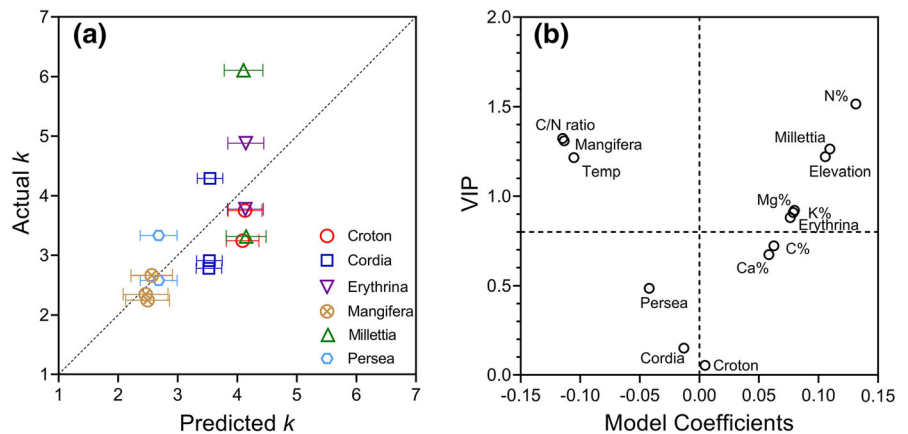
Discussion

The rapid decomposition of the leaf litter and resulting high k values we found are typical for tropical forests (Bernhard-Reversat 1982; Powers et al. 2009) and agroforestry systems (Hossain et al. 2011; Petit-Aldana et al. 2019; Jairo et al. 2017). The high k value for *M. ferruginea* recorded at farm 13, and the reason

for its deviation from the PLS-R predicted value was the result of the litterbag weight loss recorded at 3 months. Excluding the 3-month weight loss data resulted in a k value of 4.394, which compares well with the PLS-R predicted value of 4.303. This suggests that the k value for *M. ferruginea* recorded at farm 13 as given in Table 2 is erroneous. Nevertheless, the overall high k values we found undoubtedly reflect the effect of the higher temperatures on microbial activity and decomposition in the tropics (Zhang et al. 2008).

At the global (Zhang et al. 2008), European (Portillo-Estrada et al. 2016) and tropical (Salinas et al. 2010; Waring 2012; Bothwell et al. 2014) scales, k values are positively correlated to temperature. Therefore, the nearly significant negative correlation between k and annual temperature (positive for elevation) and the significant correlation between half-life and annual temperature (negative for half-life) were the opposite of that expected. However, the direct correlation between soil organic matter

Fig. 3 **a** Actual vs PLS-R predicted species k values (error bars are SEM; dotted line is the 1:1 line), and **b** PLS-R variable importance in projection (VIP) values vs model coefficients (using centred and scaled data; horizontal dotted line = VIP 0.8, values > 0.8 indicate an important predictor)



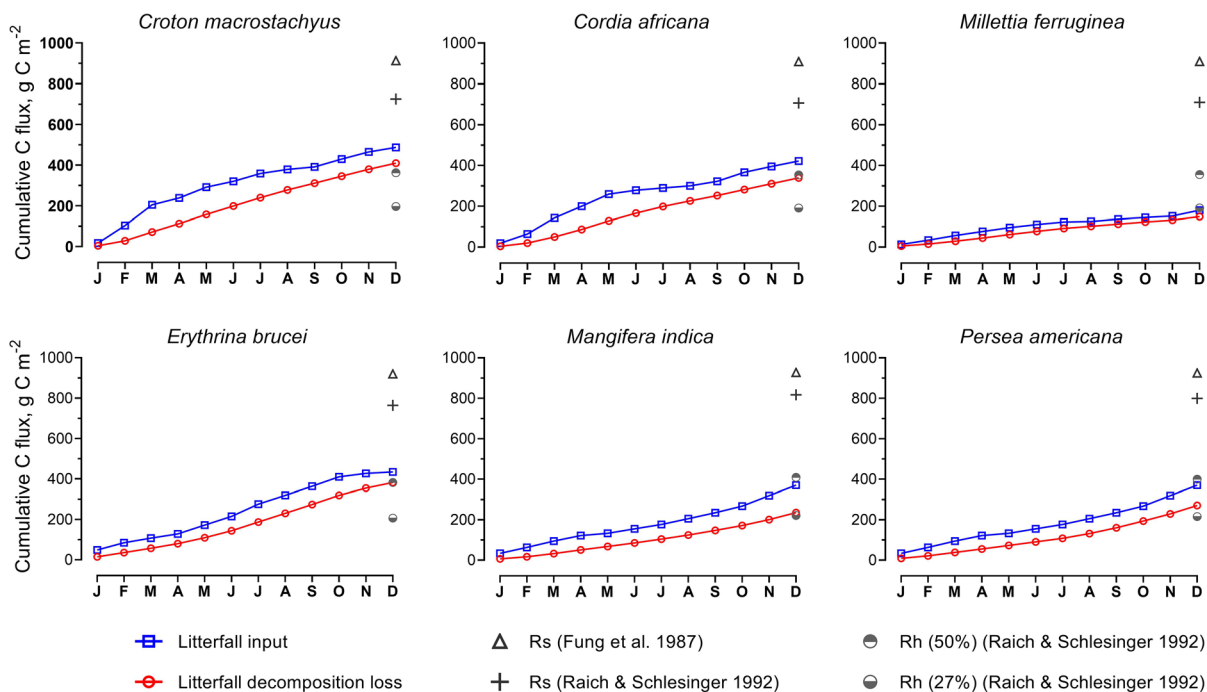


Fig. 4 Averaged cumulative monthly litterfall, litterbag decomposition loss and modelled soil respiration C fluxes for each of the six tree species studied. Litterfall C input values were calculated from measured litterfall fluxes (Negash and Starr, 2013) and measured C contents (Eq. 1); litterfall decomposition C losses were calculated from the litterfall fluxes, the litterbag k decay constants and measured C contents of the remaining

litter (Eq. 3); soil respiration (R_s) C fluxes calculated using the temperature-based models presented by Fung et al. (1987) for subtropical/subtropical woody vegetation biome (Eq. 4) and for global sites by Raich and Schlesinger (1982) (Eq. 5), and soil heterotrophic respiration (R_h) calculated from Raich and Schlesinger (1982) R_s values assuming R_h/R_s ratios of 50% and 27%

decomposition and temperature has been questioned. For example, the global decomposition rates of forest soil organic matter were shown to vary little with mean annual temperature (Giardina and Ryan 2000). Besides temperature, precipitation and evapotranspiration have also been found to be important climatic factors controlling decomposition at continental and global scales (Meentemeyer et al. 1982; Aerts 1997; Zhang et al. 2008). In a pan-tropical decomposition study, k values were found to be unrelated to mean annual temperature (MAT) but were strongly related to mean annual precipitation (MAP) (Powers et al. 2009). However, there was only a modest range in MAT but a large range in MAP in their study.

Whether the litterbags are placed on the surface or buried affects decomposition because of differences in temperature and moisture conditions. Powers et al. (2009) found that the decomposition of buried litterbags was faster than that of surface litterbags in drier (MAP < 3000 mm) tropical forests. As the

annual rainfall in the area is only some 1500 mm, it would suggest that the decomposition of our buried bags is faster than if they had been placed on the surface. We do not have rainfall data at the farm scale, but the variation among the farms is probably small and therefore also the variation in soil moisture. We, therefore, consider it unlikely that moisture conditions have had a controlling effect on our decomposition rates. However, a possible explanation for the weak negative dependence of k on temperature found in our study may be substrate availability and quality.

After a rapid loss of the more easily decomposable N-rich substances, decomposition becomes limited by the lignin content (Giardina and Ryan 2000). Litter decomposition rates are known to decrease with lignin contents (Zhang et al. 2008), and tropical forest litters tend to have higher lignin contents than temperate and subtropical litters (Bernhard-Reversat and Schwar 1997). Lignin contents were not determined in our study and therefore we cannot assess its importance in

controlling the observed decomposition rates. However, the significant correlation between k and initial litter N content, the nearly significant correlation between k and C/N ratio (correlation with half-life values were significant), and the results from the PLS-R analysis all indicate that litter N contents played an important role in controlling decomposition rates. The dependence of litter decomposition on N contents, at least during the early stages, is widely known (Berg and Laskowski 2006). The litter N contents of the six species are similar to values reported by others (Schaffer and Gaye 1989; Thorp et al. 1997; Gindaba et al. 2004; Tekay 2004; Tekay and Malmer 2004; Urban and Léchaudel 2005; Kotur and Keshava 2010, Mahari 2014; Abay 2018). Interestingly, the highest k values were associated with *E. brucei* and *M. ferruginea*, species that are nitrogen fixers.

C cycling in tropical forests has been considered to be more limited by litter contents of Ca, Mg and K than by N (Cleveland et al. 2011; Waring, 2012). However, the correlations between the litter contents of these elements and k were not significant in our study. *C. macrostachyus*, *E. brucei*, and *M. ferruginea* are deciduous species while *C. africana*, *M. indica* and *P. americana* are evergreen species. The generally greater k values for the former group of species compared to the latter group may thus be related to differences in leaf longevity and phenology (Cornwell et al. 2008; Salinas et al. 2010).

Our litterfall C inputs to the soil surface were greater than the litterbag decomposition C losses for all six species and modelled soil respiration C losses substantially greater than both. The greater R_s values calculated with the Fung et al. (1987) model compared to the Raich and Schlesinger (1982) model is at least partly related to the maximum monthly soil respiration ($R_{s_{max}}$, Eq. 4) value we used to convert the normalized values into absolute values for the farms. We used an $R_{s_{max}}$ value of $3 \text{ g m}^{-2} \text{ day}^{-1}$, which was based on soil respiration values presented by Raich and Schlesinger (1992), Oertel et al. (2016) and Wood et al. (2013) for tropical forests. However, daily mean soil respiration values across these studies varied between 2.4 and $6.0 \text{ g C m}^{-2} \text{ day}^{-1}$. Given the small variation in monthly temperature at our sites, we consider the $R_{s_{max}}$ value of $3 \text{ g m}^{-2} \text{ day}^{-1}$ to be a reasonable value for our purposes.

Heterotrophic respiration is generally considered to account for 50–60% of soil total respiration (Bond-

Lamberty and Thomson 2010). However, the Rh/R_s ratio may be much lower in the tropics than elsewhere. For instance, an average Rh/R_s ratio of 0.27 has been reported for tropical humid evergreen forests (Oertel et al. 2016). Using this value to partition our Raich and Schlesinger (1982) modelled R_s values resulted in C loss values that were more similar to our litterfall decomposition C losses, suggesting that an Rh/R_s ratio lower than 0.5 is more appropriate for the tropics. Furthermore, the sum of the mean autotrophic and heterotrophic soil respiration values reported by Oertel et al. (2016) for tropical humid evergreen forest ($873 \text{ g C m}^{-2} \text{ yr}^{-1}$) is similar to our estimated mean R_s value of $917 \text{ g C m}^{-2} \text{ yr}^{-1}$ based on litterfall production, litterbag C contents and decay k constants. The contribution of roots and belowground exudation of organic compounds to soil organic carbon contents in addition to the incorporation of aboveground litterfall, and therefore to Rh , is unknown. However, estimates of belowground biomass in the study farms are less than 25% of total biomass (Negash and Starr 2015).

Conclusions

The exponential decay constants (k) describing the weight loss of leaf litter for six woody species widely grown in the indigenous agroforestry systems of south-eastern Ethiopia are high compared to global values. The losses of litterfall carbon through decomposition calculated using the k values were less than litterfall production inputs for each species, indicating a net input of carbon to the soil. However, actual litter decomposition losses are likely to be less than the calculated values because litter is removed by the farmers for fuel and by grazing animals. Comparing soil respiration C effluxes, modelled using a simple temperature-based model, supported the notion that heterotrophic respiration accounts for considerably less of total soil respiration than the generally accepted value of 50%. To better evaluate the C dynamics and sequestration of these unique and diverse indigenous agroforestry systems there is a clear need for longer-term studies and field-based measurements of soil respiration. Nevertheless, efforts should be made to prevent their conversion to cash crop production with the resulting loss of woody species diversity, soil fertility and food security for the smallholder farmers.

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Declarations

Conflicts of interest None.

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