Litter carbon dynamics analysis in forests in an arid ecosystem with a model incorporating the physical removal of litter

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Title: Litter carbon dynamics analysis in forests in an arid ecosystem with a model incorporating the physical removal of litter

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Abstract:

Arid land afforestation could be a countermeasure for global warming, and a project for developing and evaluating techniques for arid land afforestation and reforestation has been carried out in Sturt Meadows near Leonora, Western Australia. As a part of this project, the litter carbon dynamics were investigated at three *Acacia aneura* forest sites, using a litter carbon model incorporating the physical removal of litter by winds, floods, etc. Based on the field observation data of above ground plant biomass, annual litter fall, existing amount of the litter, and also litter decomposition rate constants separately obtained for leaf litter and woody litter, we investigated the carbon flows at these forest sites, especially the annual amount of litter physically removed from the sites by floods or winds. As a result, it is estimated that annual physical removal of litter amounted to 59% to 75% of the annual litter fall, and the litter removal rate constants were from 0.38 to 0.55 yr^{-1}. Roughly one third to a half of the existing litter is removed annually from the sites. There was also a tendency that as the canopy coverage decreases, the litter removal rate constant increases. For this type of ecosystem, which is susceptible to the run-off of water and strong winds, we consider the taking into account of the physical removal of the litter is essential for analyzing the carbon dynamics in the ecosystem.

1. Introduction

Arid land afforestation (Abe et al., 1997) is a way for planting trees in a large area without hindering food production, and thus can be considered as one of the few countermeasures for global warming. A project for developing and evaluating techniques for arid land afforestation and reforestation has been carried out in Sturt Meadows near Leonora, Western Australia (Abe et al., 1997; Yamada et al., 1999; Kojima et al., 2006). Several interesting results have been obtained and published, for example, Egashira et al. (2003) developed an integrated simulator of water transport and plant growth. Takahashi et al. (2003) investigated the water use efficiency of *Eucalyptus camaldulensis* which is considered as a promising species in arid land afforestation, and, Yamada et al. (2003) reported on hardpan blasting for making space for plant roots.

As a part of this project, we have been developing a litter and soil carbon dynamics model for arid land afforestation. In general, in forest ecosystems, litter and soil carbon play significant roles in carbon dynamics; usually litter and soil retain as much as or more carbon than that in plant bodies （Schlesinger, 1977; Houghton and Skole, 1990), and they might be sources of carbon dioxide, if the trees were cut and not re-planted. Thus, carbon dynamics models for forest ecosystems usually incorporate litter and soil carbon dynamics (e.g., Comins and McMurtrie, 1993; Friend et al., 1997; Ito and Oikawa, 2002).

In our preliminary investigation on the litter carbon dynamics of the project sites, Kumada et al. (2006) found that there is a possibility that a significant amount of litter is removed physically, i.e., by floods or winds, from the studied sites in Sturt Meadows. In arid ecosystems, forest physiognomy is usually sparse, thus, the litter in the forest is susceptible to winds or floods, and it is natural that a significant amount of litter is removed by these weather effects. This physical removal of litter is important when the carbon dynamics of its ecosystem are analyzed, because it not only reduces the input to the soil carbon, but it can also affect the ecosystem in many different ways.

There has been a lot of research on the transport of carbon in ecosystems (e.g., Schlesinger and Melack, 1981; Hope et al., 1994; Parks and Baker, 1997; Shibata et al., 2001; Vidal-Abarca et al., 2001; Dagg et al., 2004). These studies have suggested that transport of carbon either as particulate organic carbon (POC), dissolved organic carbon (DOC) or dissolved inorganic carbon (DIC) is not negligible in carbon flows in terrestrial ecosystems.

However, most models of carbon dynamics in forest ecosystems (e.g., Parton et al., 1987; Moorhead 1991; Comins and McMurtrie, 1993; Friend et al., 1997; Kirschbaum 1999; Chertov et al., 2001; Rasse et al., 2001; Ito and Oikawa, 2002) did not take into account the transport of carbon. Zhang et al. (2006) incorporated into their model the removal of litter by human activities, but not that by natural causes like winds.

Therefore, in order to clarify the carbon dynamics in arid forest ecosystems where the forest floor is susceptible to the weather, the development of a new kind of model incorporating the transport of litter and soil by winds or floods is needed.

In considering the physical removal of litter, the effect of forest physiognomy should be significant because dense forests reduce the strength of winds (e.g., Wang et al., 1997; Novak et al., 2000) and run-off is often reported to be related with canopy coverage (e.g., Kang et al., 2001; Bochet et al., 2006). Thus, in the application of the model, the relationship between canopy coverage and the physical removal of litter is investigated.

In forest ecosystems, distinguishing litter types is important. In general, litter is classified into several types: leaves, branches, bark, stems and roots, etc. In order to reproduce the dynamics of the litter, most forest models consider several different types of litter (e.g., Chertov et al., 2001; Rasse et al., 2001). In particular, the decomposition rates of woody litter such as branches and twigs are much slower than those for leaf litter (A’Connell, 1987; Jones et al., 1999; Mackensen, 2003), and thus the woody litter plays the dominant role in the long-term behavior of the litter carbon, and distinguishing between leaf and woody litter is necessary for a reasonable estimation of the litter carbon dynamics. Furthermore, it has been reported that litter decomposition rates were better fitted by dividing the litter into several components, which have a fast or slow decomposition rate, in a litter decomposition model (e.g., A’Connell, 1987). Thus, in our model, litter is divided into four sub-compartments according to the litter types and the decomposition rates, i.e., leaf or woody litter, and a fast or slow decomposition component of each type of litter.

In this study, a litter carbon dynamics model was developed that incorporated the physical removal of litter, and the carbon dynamics of several natural arid forest ecosystems having various canopy coverage were analyzed. The objective of this study is as follows.

(1) To analyze and estimate the litter carbon flows at study sites in Sturt Meadows.

(2) Especially, to estimate the annual amount of the physical removal of litter by floods, winds, etc. and the rate constants of removal,

(3) To determine if there is any relationship between canopy coverage and the rate of physical removal.

(4) To evaluate the effect of the physical removal on the carbon balances at the studied sites.

2. Methods

2.1 Site description

The research area is located in Sturt Meadows, near Leonora, 600 km east-northeast of Perth, Western Australia (latitude 28°40'S, longitude 120°58'E, Fig. 1). It is categorized as a typical arid zone. The average annual rainfall is 211.7 mm, fluctuating widely from less than 100 to about 500 mm (Yasuda et al., 2001). In particular, in the research area, runoff was often observed in heavy rains associated with thunderstorms and cyclones. Run-off, or flooding, occurs mainly due to the low soil water permeability in this area (Yamada et al., 2003; Kojima et al., 2006). The average topographical gradient of the research area is less than 1% (Abe et al., 2003), and a salt lake exists at the lowest elevation.

Suganuma et al. (2006a) have investigated the land cover in the research area, by analyzing satellite remote sensing data. It was found that the bare ground, vegetation area and water area occupied 55.4 %, 42.1% and 2.3 % of the study area, respectively. *Acacia aneura* natural forest, which is a dominant vegetation, occupied the majority of the woodland in the study area, accounting for 96.7 % of the vegetation area. *Acacia aneura* is an evergreen tree and has few understory plants. *Acacia aneura* is distributed widely in the research area, but the forest physiognomy of these forests is not uniform due to heterogeneous soil water conditions and geologic formations such as depth of the hardpan layer from the top soil. Another species in the research area, *Eucalyptus camaldulensis* forest resided in some wadis with a thick top soil layer, and accounted for only 2 % of the vegetation area. Therefore, we investigated carbon dynamics at several sites of natural *Acacia aneura* forests.

Of the several study sites of the project (Kojima, 2006), three sites were selected in natural *Acacia* forests, namely site 2, site 7 and site 12 (Fig. 2). The canopy coverages of these three sites were different, being 0.74, 0.84 and 0.16 for sites 2, 7 and 12 (Suganuma et al., 2006b), and classified as semi-dense, dense, and open forests, respectively. Site 12 is located on a gently inclined wash plain with occasional wandarrie banks, whereas sites 2 and 7 are located in flat areas. The areas of sites 2, 7 and 12 are 16 m × 80 m, 20 m × 20 m and 40 m × 100 m, respectively. According to locals, forests at the investigated sites have existed for at least 100 years. Pictures of the experimental sites are shown in Fig. 3.

A more detailed description of the research area and studied sites is available in Kojima et al. (2006).

2.2 Model description

2.2.1 Model structure

Fig. 4 shows the structure of the model. The aim of the model was to calculate the litter carbon dynamics at each experimental site, not for the individual tree or the whole study area.

The model consists of three major compartments of carbon pools: plant body (*WP*), litter (*WL*) and soil (*WS*). Litter is divided into two categories, leaf litter and other. The majority of the "other litter" is woody litter (branch, stem, twigs, etc.), so the category is renamed "woody litter." The leaf litter and woody litter are also divided into two sub-categories, according to their rate of decomposition. Thus, there are 4 sub-compartments for the litter pool, and they were denoted as WL_{ij}, where i represents the type of litter (i=1 for leaf and i=2 for woody) and j represents the decomposition rate (j=1 for fast, j=2 for slow).

Carbon flows between the compartments were as follows: Net Primary Production (*NPP*) enters the plant body, and the plant body produces litter as litter fall (*LF*). A portion of the litter is then removed physically by flood water or winds (*LR*). This physical removal is represented as "run-off" regardless of the cause, and a subscript "*run*" is used. Another portion of the litter is decomposed (*LD*). Some of the decomposed litter is transformed into soil organic matter (humus), and the rest is lost to respiration. As for the soil carbon, carbon input is the litter transformation and output is the respiration loss.

The annual litter production or litter fall, *LF*, was assumed to be proportional to the amount of carbon in the plant body and calculated as

$$LF = k_{LF}WP \qquad (1)$$

where WP is the amount of carbon in the plant [kg-C m^{-2}] and k_{LF} is the rate constant for litter fall [yr^{-1}]. Annual litter production $k_{LF}WP$ was then divided into two parts according to the type of litter. The mass fraction of either leaf or woody litter in the litter fall was denoted as f_i, (i=1 for leaf and i=2 for the woody litter), thus, the annual leaf litter production is $f_1\, k_{LF}WP$ (denoted as LF_1) and annual woody litter production is $f_2\, k_{LF}WP$ (denoted as LF_2).

The initial mass ratio of the fast and slow decomposition fractions is x_{ij}, where i indicates litter type (1 for leafy and 2 for woody) and j indicates the litter decomposition rates (1 for fast and 2 for slow), and the mass fraction of the j-th component in the i-th litter type is x_{ij}. These are summarized as follows: x_{11}: fast degrading mass fraction of leaf litter, x_{12}: slow degrading mass fraction of leaf litter, x_{21}: fast degrading mass fraction of woody litter, x_{22}: slow degrading mass fraction of woody litter. Note that $x_{11}+x_{12}=1$ and $x_{21}+x_{22}=1$, not $x_{11}+x_{12}+x_{21}+x_{22}=1$. Thus, $f_i x_{ij} k_{LF} WP$ (denoted as LF_{ij}) of carbon enters the ij-th sub-compartment of litter every year, and the following relationship holds.

$$LF = \sum_{j=1}^{2}\sum_{i=1}^{2} f_i x_{ij} k_{LF} WP \qquad (2)$$

The ij-th sub-compartment of the litter decomposes (either lost by respiration or transformed into soil carbon) at the rate of $k_{Ldecij}WL_{ij}$ (denoted as LD_{ij}), and is also lost by physical removal at the rate of $k_{run}WL_{ij}$ (denoted as LR_{ij}), where k_{Ldecij} and k_{run} are the first order rate constants [yr^{-1}]. The change in the amount of carbon in each sub-compartment of litter is then described as follows.

$$\frac{\mathrm{d}WL_{ij}}{\mathrm{d}t} = f_i x_{ij} k_{LF} WP - \left(k_{Ldec\,ij} + k_{run}\right) WL_{ij} \qquad (3)$$

We used different decomposition rate constants but the same physical removal rate constant for sub-compartments, because we do not have any information on the mobility of each sub-component. Change in the total amount of litter is then calculated as follows.

$$\frac{\mathrm{d}WL}{\mathrm{dt}} = \sum_{j=1}^{2}\sum_{i=1}^{2}\frac{\mathrm{d}WL_{ij}}{\mathrm{dt}} \qquad (4)$$

The annual physical removal of the litter, *LR*, was calculated as $k_{run}WL$, and was identical to the sum of $k_{run}WL_{ij}$,

$$LR = k_{run}WL = \sum_{j=1}^{2}\sum_{i=1}^{2} k_{run}WL_{ij} \qquad (5)$$

This paper only discusses the dynamics of litter. The carbon dynamics in soil were not analyzed. That is, only the part enclosed with the dot-dash line in Fig. 4 was investigated. Furthermore, only above ground processes were taken into consideration. It was assumed that the carbon pool in the plant body, *WP*, is a constant throughout the calculation.

2.2.2 Estimated parameters from the field investigations

The calculation uses parameters obtained from the field observation of the project (Yamada et al. 1999; Kojima et al., 2006). Table 1 shows the estimated values for carbon in the above ground plant body, *WP*(*AG*), in the litter, *WL*, the litter fall rate constant, k_{LF}, and also the fraction of the leaf litter, f_1, and woody litter, f_2, to litter production. Some details of the estimation of these values are given in Taniguchi (1998), Kobayashi (2003) and Suganuma et al. (2006b).

Table 2 shows the decomposition rate constants for each sub-compartment at each site. The rate constants were obtained by fitting the relative amounts of remaining leaf litter, $W_{leaf}(t)$, and branch litter, $W_{woody}(t)$, obtained in litter bag and litter tag studies, to the following equations.

$$W_{leaf}(\mathrm{t}) = x_{11}\exp(-k_{Ldec11}t) + x_{12}\exp(-k_{Ldec12}t) \qquad (6)$$

$$W_{woody}(\mathrm{t}) = x_{21}\exp(-k_{Ldec21}t) + x_{22}\exp(-k_{Ldec22}t) \qquad (7)$$

where x_{11} and x_{12} are the initial mass fractions of the fast decomposing and slow decomposing fraction of the leaf litter, and k_{Ldec11} and k_{Ldec12} are the corresponding decomposition rate constants, and similarly, x_{21} and x_{22} are the initial mass fractions of the fast decomposing and slow decomposing fraction of the woody litter, and k_{Ldec21} and k_{Ldec22} are the corresponding decomposition rate constants.

The rate constants for the fast decomposing fraction of leaf litter k_{Ldec11} at sites 2 and 7 and branch litter k_{Ldec21} at site 12 were not able to be obtained by fitting, due to the shortage of data in the first stage of the decomposition. Thus, it was assumed that the fast decomposing fraction of the litter would decompose instantaneously as it was produced, or in other words, infinite decomposition rates were assumed for the fast decomposing fraction of the litter at these sites.

3. Results and Discussion

3.1 Estimation of the amount of litter without physical removal

The investigation begins with the amount of litter when there is no physical removal (k_{run}=0). Calculated results of change in the amount of total litter for each litter type with an initial litter amount of zero are shown in Fig. 5. For sites 7 and 12, the total litter carbon pools nearly reach their steady values in one hundred years, and reach 80 % of the steady values in several tens of years. For site 2, the change is relatively slow due to a smaller k_{Ldec22}, but in two hundred years, the litter carbon pool is fairly close to its final value. The steady state amount of carbon is also estimated in *ij*-th litter pool, with k_{run}=0, using Eq. (8) and the total amount Eq. (9), and the results are shown in Table 3.

$$WL_{ij\infty} = \frac{f_i x_{ij} k_{LF} WP}{k_{Ldec\,ij}} \qquad (8)$$

$$WL_{\infty} = \sum_{j=1}^{2}\sum_{i=1}^{2} WL_{ij\infty} \qquad (9)$$

The estimated amounts of the steady state litter carbon with the assumption that there is no physical removal (WL_∞) were 6.3, 4.6 and 0.82 kg-C m^{-2}, whereas the observed values were 0.51, 0.75 and 0.086 kg-C m^{-2}, for sites 2, 7 and 12, respectively. The estimated values were 6 to 12 times larger than the observed values.

Considering the information from locals that the age of the forests are not less than 100 years, the discrepancy between the calculated and observed values cannot be ascribed to the youngness of the forests, and thus, we concluded that incorporation of the physical removal of litter to the model is essential for the analysis of the litter carbon dynamics of these sites.

Furthermore, from the Table 3, it is seen that the contribution of the woody litter to the total litter is significant. The estimated amount of carbon of leaf litter ($WL_{\infty 11}+WL_{\infty 12}$) and woody litter ($WL_{\infty 21}+WL_{\infty 22}$) ranged from 0.3 to 1.9 kg-C m^{-2} and 0.5 to 5.4 kg-C m^{-2}, respectively. Despite woody litter accounting for only 20% of the annual litter fall, the amount of woody litter carbon accounts for more than 58% of the evaluated steady state litter carbon, mainly due to the much slower decomposition rate compared with that of leaf litter.

3.2 Estimation of the amount of physical removal litter

As the estimated values of steady state litter carbon without any physical removal turned out to be much larger than the observed values, we tried to evaluate how much litter was removed physically from the sites.

In this investigation, we used the same value of k_{run}, the physical removal rate constants, for all the sub-compartments of the litter, as we did not have any information about the mobility of the leaf and woody litter. The steady state litter carbon when there is a physical removal of litter with a removal rate constant k_{run}, is thus calculated as follows.

$$WL_\infty^{(run)} = \sum_{j=1}^{2}\sum_{i=1}^{2}\frac{f_i x_{ij} k_{LF} WP}{k_{Ldec\,ij} + k_{run}} \qquad (10)$$

The removal constant k_{run} is then evaluated by making $WL_\infty^{(run)}$ equal to WL_{obs}, the observed amount of litter carbon.

Table 4 shows the estimated values of k_{run} together with LF (Litter Fall) and LR (Litter Removed) for three sites. Obtained k_{run} values were 0.43, 0.38 and 0.55 yr^{-1} for sites 2, 7, and 12, respectively. That is, roughly from one third to a half of the existing litter is estimated to be removed from the site. The amounts of annual physical removal of litter were estimated to be 0.22, 0.28 and 0.047 kg-C m^{-2} yr^{-1} for sites 2, 7 and 12, respectively. In other words, by incorporating the physical removal of litter and choosing the k_{run} values above, the amount of existing litter observed in the field was able to be reproduced by the model.

Comparing the canopy coverage and the estimated annual litter removal rate constant, k_{run}, it is seen that as the canopy coverage decreases, the removal rate constant increases. Although this finding is based on the observation of only three sites and more evidence may be needed, we consider this is reasonable because in forests with less canopy coverage, there should be fewer obstacles for the movement of the litter. Additionally, if the litter mobility is higher, then there should be less nutrients left for the forests and the canopy coverage should be less.

The ratio of the annual amount of the physical removal of litter to annual litter fall (LR/LF) is also shown in the Table 4. This ratio was 0.59, 0.66 and 0.75 for sites 2, 7 and 12, respectively. The annual physical removal amount was about three fifths to three quarters of the annual litter fall. The ratios of runoff were estimated separately for leaf (LR_1/LF_1) and woody litters (LR_2/LF_2), and ranged from 50 to 71 % and 87 to 92 %, respectively. That is, a higher ratio of litter-runoff was calculated for the woody litter than for the leaf litter.

This contradicts the fact that, in general, leaf litter is easier to move than woody litter. In our model, we assumed the same removal rate constants, k_{run}, for all the sub-compartments of the litter. Because of this restriction, the woody litter having slower decomposition rates was calculated as being easier to remove. In order to give in-depth analyses of litter runoff dynamics, it would be necessary to clarify the difference in mobility between leaf and woody litter fractions. Despite this discrepancy in our study, it is apparent that a significant amount of litter is physically removed from the sites.

3.3 Carbon balances

Fig. 6 shows the estimated carbon balance. Of the annual litter falls of 0.37, 0.43 and 0.063 kg-C m^{-2} yr^{-1}, 0.22, 0.28 and 0.047 kg-C m^{-2} yr^{-1} were estimated to be removed physically from the sites, and 0.15, 0.14 and 0.016 kg-C m^{-2} yr^{-1} were turned into soil or lost to respiration.

Nakane (1980) estimated the carbon balance in a Beech/Fir forest in a cold temperate climate, an evergreen oak forest in a warm temperate climate and a tropical rain forest. His estimates of annual litter fall were 0.20, 0.42 and 0.53 kg-C m^{-2} yr^{-1}, for Beech/Fir, evergreen oak and tropical rain forests, respectively. The carbon flows from litter were the same as the litter fall because no physical removal was considered. The estimated amounts of annual litter fall in the semi-dense (site 2) and dense (site 7) *Acacia aneura* forests in our project were in the same order of magnitude as the Beech/Fir, evergreen oak and tropical rain forests investigated by Nakane (1980), whereas the annual litter fall in the open forest (site 12) was one order smaller than the others. That is, as far as our study sites are concerned, it seems that the annual litter production or litter fall is not greatly different from those of temperate/tropical forests, as long as the canopy coverage is sufficiently high.

Carbon flows from the litter, to either soil or respiration, were, of course, smaller in our studies, due to physical removal of litter, than those reported in Nakane (1980). This probably causes less input to the soil and less soil carbon in our sites than for temperate/tropical forests, however, carbon dynamics in the soil is beyond the scope of this study, and we restricted our discussion to litter dynamics itself. Further investigation, including analysis of net primary production, plant growth, and below ground processes such as soil carbon dynamics and root respiration, and root litter dynamics will be necessary for attaining the whole picture of carbon balances at these sites.

4. Conclusions

A litter carbon dynamics model was constructed incorporating the physical removal of litter for analyzing carbon flows at our study sites in our research project in Sturt Meadows in Western Australia and the following were found.

(1) Estimated annual physically removed litter, i.e. litter removed by floods, winds, etc., amounted to 59, 66 and 75% of the annual litter fall for sites 2, 7 and 12 in *Acacia aneura* forests.

(2) Litter removal rate constants were 0.43, 0.38 and 0.55 yr^{-1}, for sites 2, 7, and 12; roughly one third to a half of the existing litter is estimated to be removed annually from the site.

(3) There was a tendency that as the canopy coverage decreases, the physical removal rate constants increase; higher mobility is estimated for less dense forests.

(4) It is suggested, from carbon balance analysis, that, due to physical removal, carbon flow from litter to either soil or to respiration may be much less than those in temperate or tropical forests.

We conclude that in this type of ecosystem, which is susceptible to the run-off of water and strong winds, taking into account of the physical removal of the litter is essential for analyzing the carbon dynamics in the ecosystem.

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Titles of the tables and figures

Table 1 Carbon pools, litter fall rate constant and fractions of the leaf litter and woody litter to litter production in Sturt Meadows.

Table 2 Litter decomposition parameters.

Table 3 Estimated value of the steady state amount of litter carbon without physical removal, and the observed value.

Table 4 Estimated rate constant for physical removal, k_{run}, and ratio of physically removed litter to litter fall.

Fig. 1 Location of research area in Western Australia.

Fig. 2 Location of study sites in Sturt Meadows.

Fig. 3 Appearance of forest physiognomy in study sites.

Fig. 3 (a) Site 2 (semi-dense forest)

Fig. 3 (b) Site 7 (dense forest)

Fig. 3 (c) Site 12 (open forest)

Fig. 4 Carbon flow diagram for litter part model.

Fig. 5 Transition of the litter amount without physical litter removal in several natural acacia forests. (- - - : leaf, ········ : woody, — : total)

Fig. 5 (a) Site 2

Fig. 5 (b) Site 7

Fig. 5 (c) Site 12

Fig. 6 Carbon amount and flux in several natural acacia forests with physical litter removal (Box: [kg-C m^{-2}], Flow: [kg-C m^{-2}yr^{-1}]). [a] This fraction of litter was assumed to decompose instantaneously.

Fig. 6 (a) Site 2

Fig. 6 (b) Site 7

Fig. 6 (c) Site 12

Table 1

Site	$WP(AG)$ [kg-C m^{-2}]	WL [kg-C m^{-2}]	k_{LF} [yr^{-1}]	f_1 [-]	f_2 [-]
Site 2	2.94	0.507	0.125	0.798	0.202
Site 7	3.41	0.749			
Site 12	0.500	0.0855			

Table 2

Site	x_{11} [-]	x_{21} [-]	k_{Ldec11} [yr^{-1}]	k_{Ldec12} [yr^{-1}]	k_{Ldec21} [yr^{-1}]	k_{Ldec22} [yr^{-1}]
Site 2	0.18	0.051	Infinite [a]	0.27	6.9	0.013
Site 7	0.15	0.061	Infinite [a]	0.15	4.3	0.030
Site 12	0.22	0.037	1.2	0.12	Infinite [a]	0.025

[a] The fast decomposing fraction was assumed to decompose instantaneously after litter fall.

Table 3

Site	$WL_{11\infty}$ [kg-C m^{-2}]	$WL_{12\infty}$ [kg-C m^{-2}]	$WL_{21\infty}$ [kg-C m^{-2}]	$WL_{22\infty}$ [kg-C m^{-2}]	WL_{∞} [kg-C m^{-2}]	WL_{obs} [kg-C m^{-2}]
Site 2	0 [a]	0.889	0.001	5.41	6.30	0.507
Site 7	0 [a]	1.93	0.001	2.69	4.62	0.749
Site 12	0.009	0.324	0 [a]	0.486	0.820	0.0855

[a] This fraction of litter was assumed to decompose instantaneously.

Table 4

Site	k_{run} [yr^{-1}]	LF [kg-C m^{-2}yr^{-1}]	LR [kg-C m^{-2}yr^{-1}]	LR_1/LF_1 [-]	LR_2/LF_2 [-]	LR/LF [-]	$WL_{\infty}^{(run)}$ [kg-C m^{-2}]
Site 2	0.425	0.367	0.215	0.50	0.92	0.59	0.507
Site 7	0.377	0.426	0.282	0.61	0.87	0.66	0.748
Site 12	0.550	0.063	0.047	0.71	0.92	0.75	0.0855

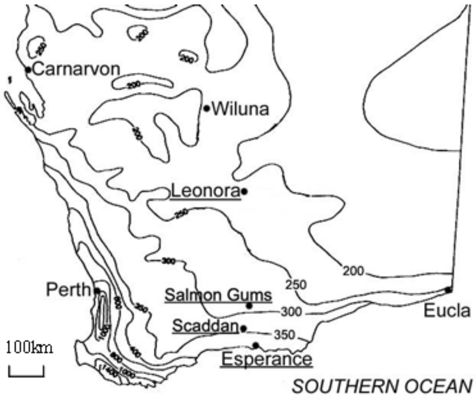

Carnarvon
200
200
200
200
Wiluna
Leonora
250
300
250
200
Perth
600
350
1000
Salmon Gums
300
Scaddan
350
Esperance
Eucla
100km
400
800
1400
1000
SOUTHERN OCEAN

Fig. 1

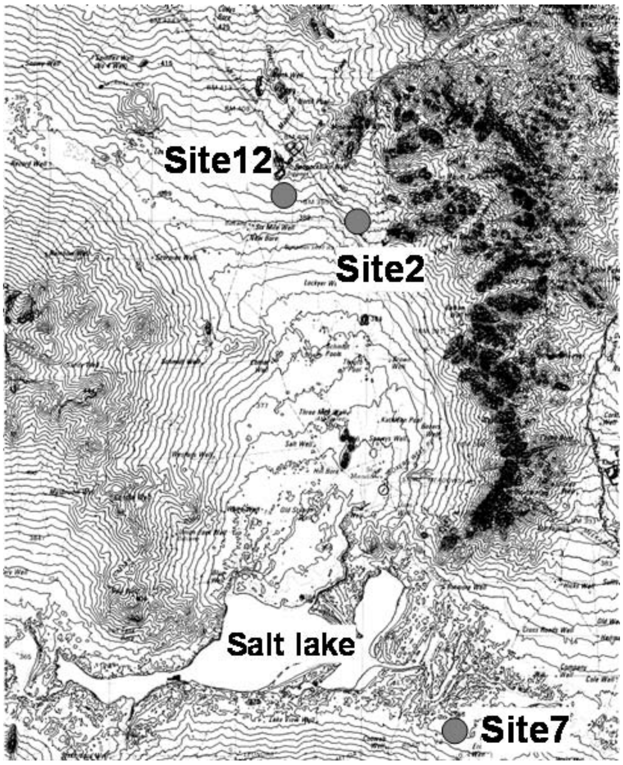


Fig. 2

Fig. 3 (a)

Fig. 3 (b)

Fig. 3 (c)

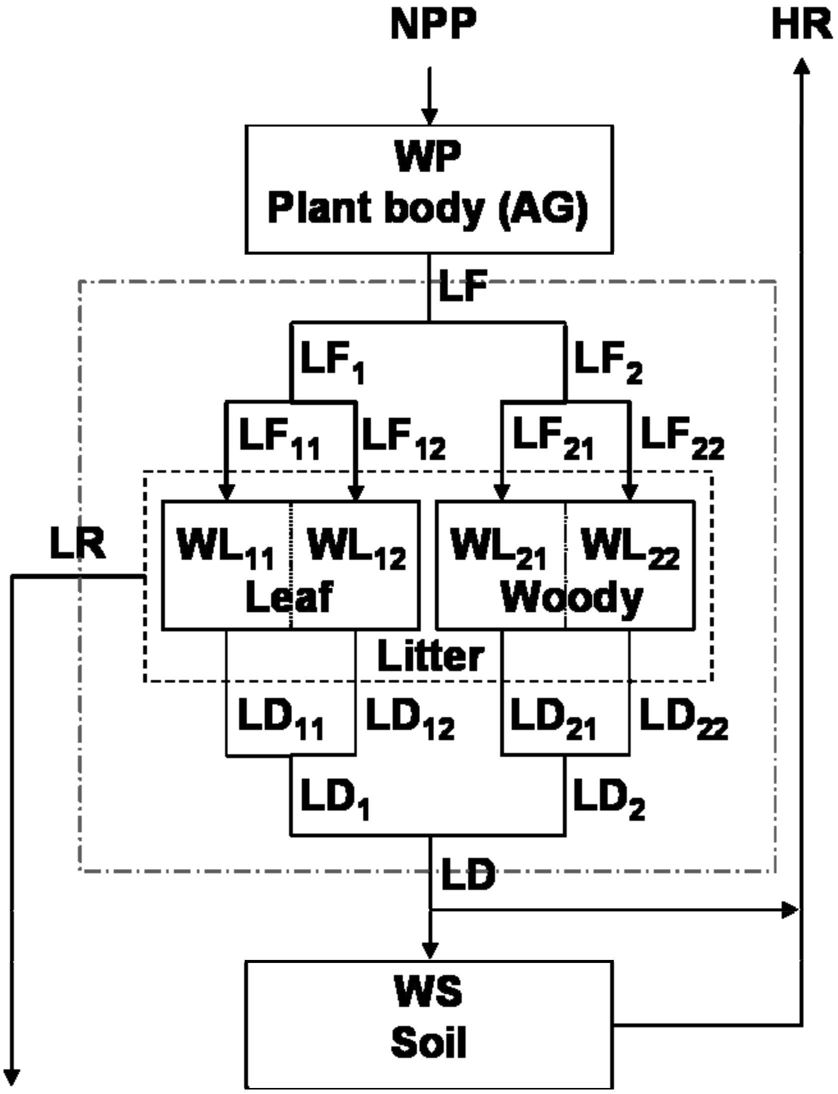

NPP
HR
WP
Plant body (AG)
LF
LF_1
LF_2
LF_{11}
LF_{12}
LF_{21}
LF_{22}
LR
WL_{11}
WL_{12}
Leaf
WL_{21}
WL_{22}
Woody
Litter
LD_{11}
LD_{12}
LD_{21}
LD_{22}
LD_1
LD_2
LD
WS
Soil

Fig. 4

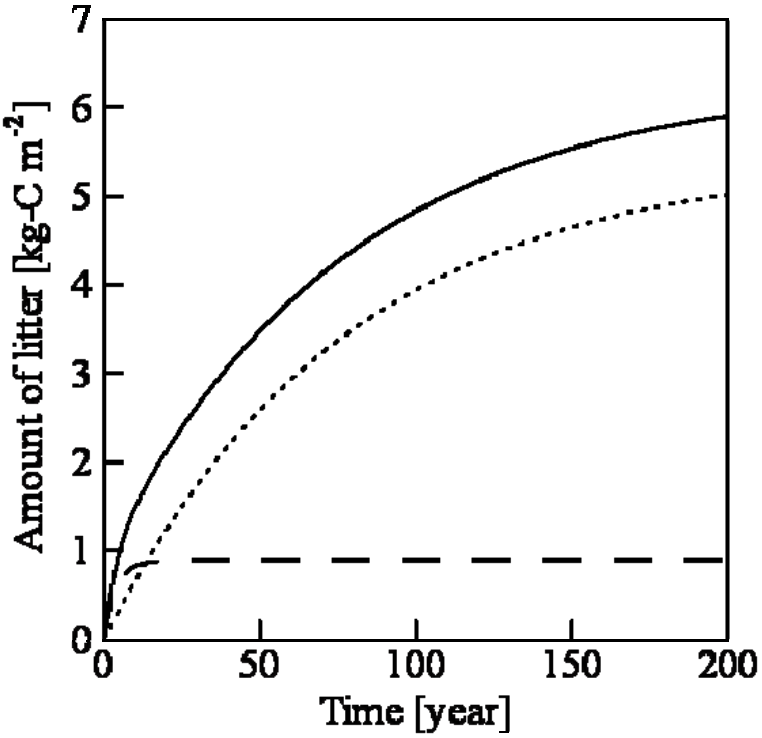
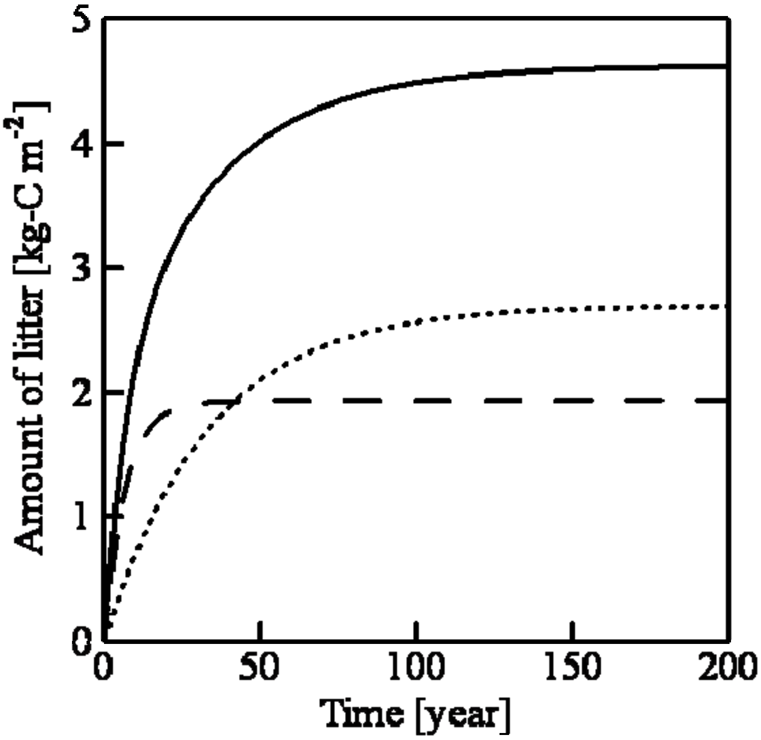


Fig. 5 (a)



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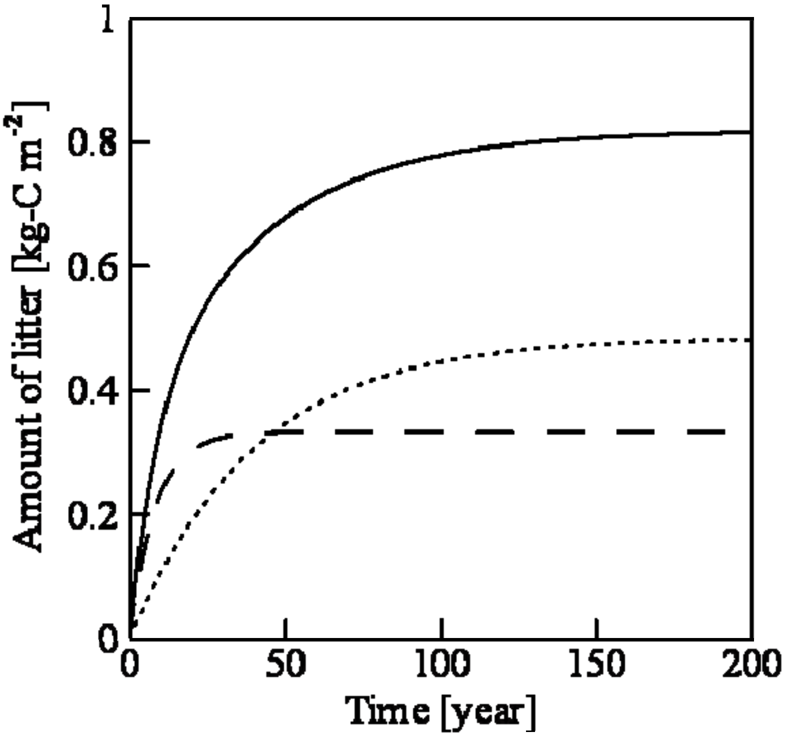

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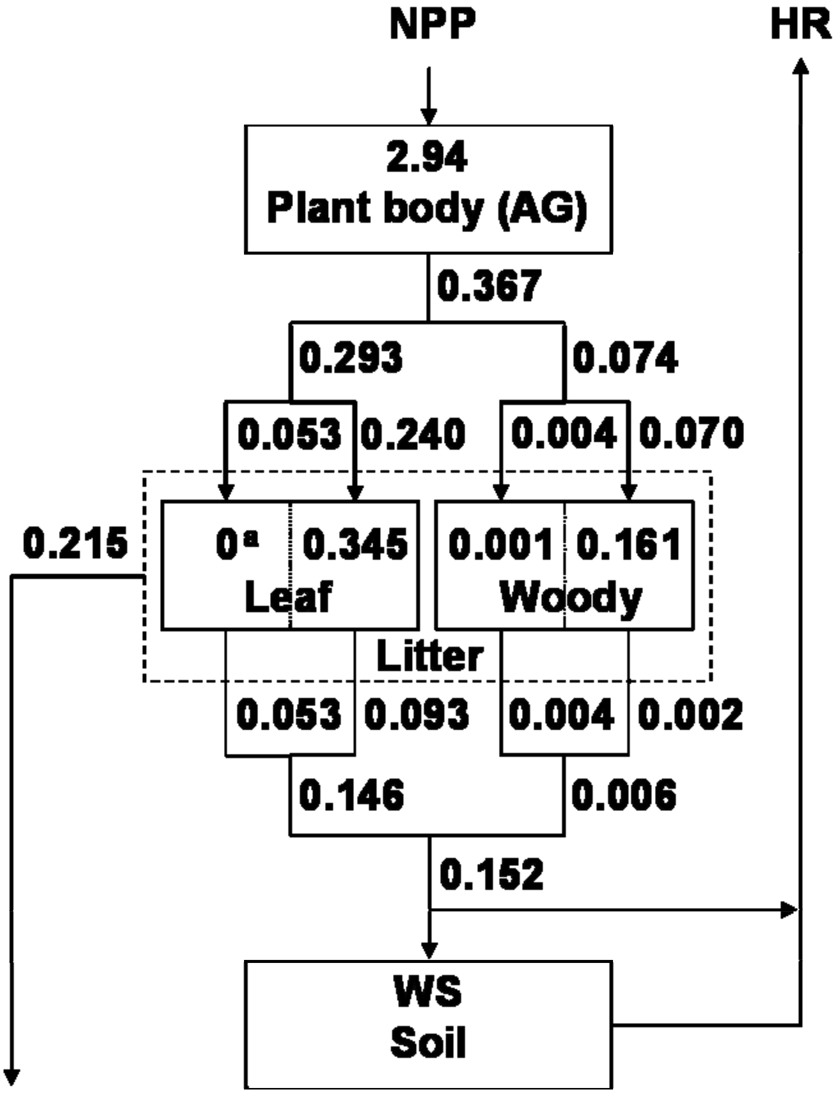
NPP
HR
2.94
Plant body (AG)
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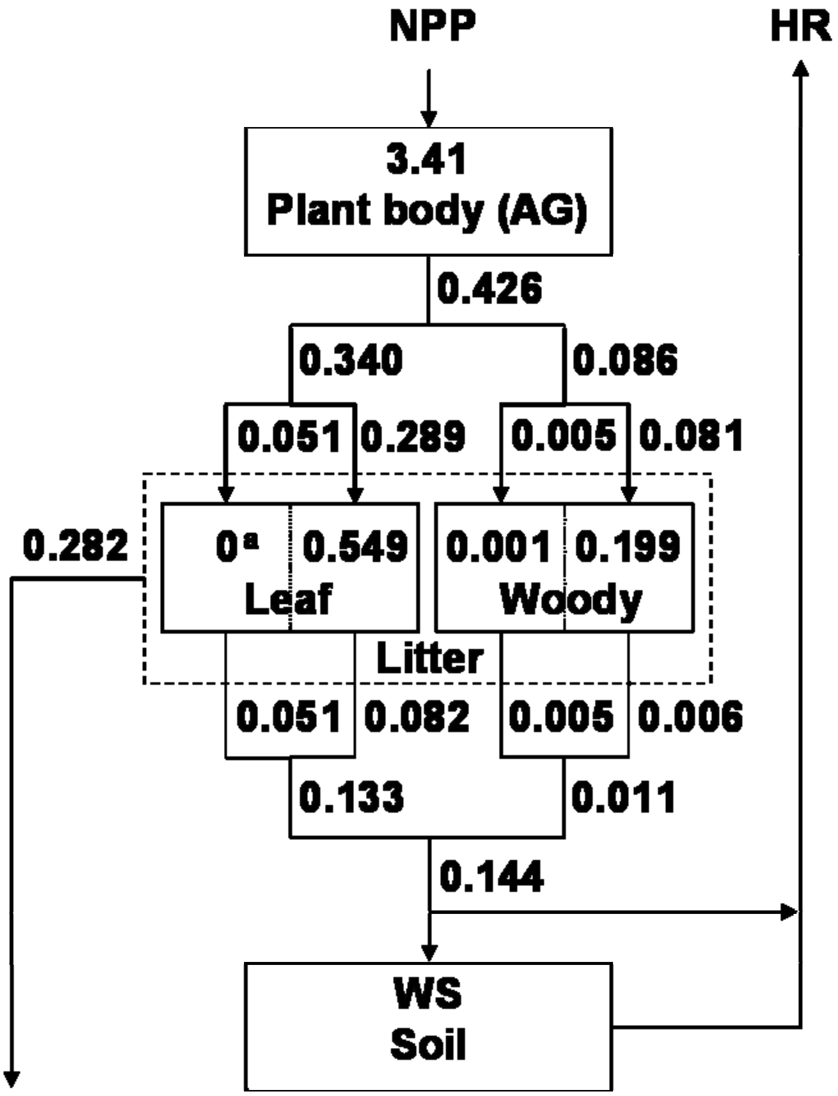
0.293
0.074
0.053
0.240
0.004
0.070
0.215
0ª
0.345
Leaf
0.001
0.161
Woody
Litter
0.053
0.093
0.004
0.002
0.146
0.006
0.152
WS
Soil

Fig. 6 (a)


NPP
HR
3.41
Plant body (AG)
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0.051
0.289
0.005
0.081
0.282
0ª
0.549
Leaf
0.001
0.199
Woody
Litter
0.051
0.082
0.005
0.006
0.133
0.011
0.144
WS
Soil

Fig. 6 (b)

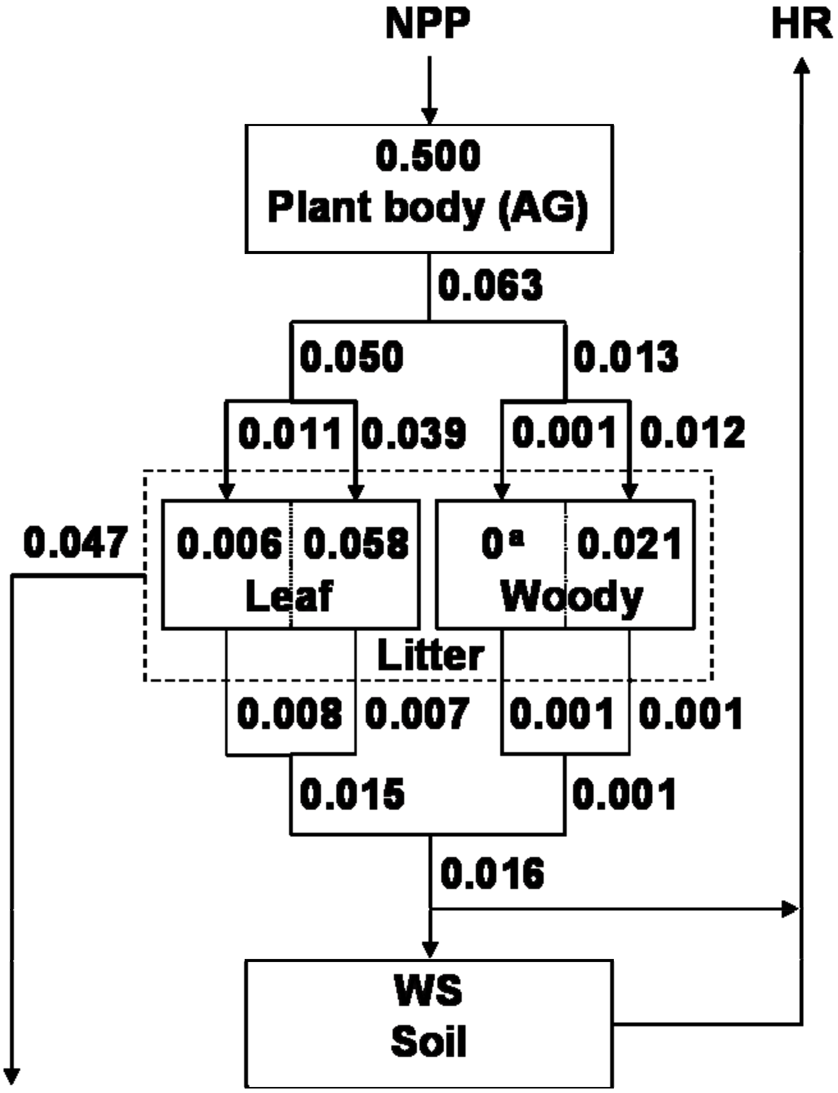
NPP
HR
0.500
Plant body (AG)
0.063
0.050
0.013
0.011
0.039
0.001
0.012
0.047
0.006
0.058
Leaf
0ᵃ
0.021
Woody
Litter
0.008
0.007
0.001
0.001
0.015
0.001
0.016
WS
Soil

Fig. 6 (c)