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Effect of temperature and litter quality on decomposition rate of *Pinus patula* needle litter

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Abstract

This study examined the mass loss and CO_2 production from *Pinus patula* (Schlecht et Cham) leaf litter collected from fertilized plots in the Mpumalanga Province. Litter decomposition increased with increasing temperature. Warming between 15 and 18 ºC significantly increased the amount of CO_2 emissions from the litter. Mass loss positively correlated with temperature levels. Nitrogen fertilizer applications had significant effects on litter decomposition rate but a minor effect on litter nitrogen quality. Litter quality was not a strong predictor of decomposition rates implying temperature is the major factor influencing the decomposition rate of *Pinus patula* needle litter. Results of this study are consistent with the hypothesis that the rate of nutrient cycling in non-limiting environments will increase, due primarily to an increase in litter decomposition as a result of increased temperatures.

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Keywords: Decomposition rate; Litter quality; Needle litter; *Pinus patula*; Temperature

1. Introduction

Litter decomposition forms an essential component of nutrient cycling processes and returns carbon (C) that was previously fixed in litter biomass as carbon dioxide (CO_2) into the atmosphere [1]. It is estimated that the nutrients released during litter decomposition can account for 67-87% of the total annual requirement of essential elements for forest plants [2]. Interest in the rate of litter decomposition has increased recently as it plays a major role in the dynamics of forest ecosystems.

The rate of litter decomposition is influenced by a number of factors including climate (temperature and moisture), litter quality and the nature and abundance of the decomposing organisms [3, 4].

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According to Swift *et al.* [3] the two most important factors are climate and the chemical nature of the litter. Climate is the dominant factor in areas subjected to unfavourable conditions, whereas litter quality largely prevails as the regulator under favourable conditions [5].

Different chemicals, their amounts and ratios have been shown to correlate with the decay rate of foliar litter and are used as substitutes for litter quality for example: Nitrogen (N) [6, 7], Lignin [8] and Lignin:N [4]. However, there is no universal litter quality index because litter decomposition depends on qualities which differ among species and plant parts. Geographical patterns of litter decomposition rates in major ecosystems types have been related to climate by Meentemeyer [9]. Results after 3 years of the Canadian Intersite Decomposition Experiment (CIDET), Moore *et al.* [10] showed that lignin:N ratio, mean annual temperature and mean precipitation were valuable parameters for predicting mass loss but the data after six-years [11] emphasized the dominance of climatic conditions over litter quality parameters in determining mass loss.

The global surface temperature is predicted to increase by 1.1-6.4 ºC within this century [12] as a result of climate change and coupled with other climatic parameters is expected to affect the litter decomposition rate. Thus, under a warmer climate the balance between ecosystem C fixation and decomposition may be altered potentially causing a dramatic increase in the flux of CO_2 from the soil to the atmosphere [13], even though the accuracy of any quantitative predictions of this flux is highly dependent on the assumed temperature sensitivity of decomposition [5]. Increases in temperatures are expected to increase decomposition rates, net N mineralization and nitrification [14]. Thus, elevated temperatures as a result of global warming have the potential to dramatically alter local ecosystems. In tropical regions, where high decomposition rates are compensated for by high primary production and lead to a relatively high soil C content understanding, the effects of increased temperatures on the C cycle are important especially in assessing the feedback of CO_2 to the atmosphere from these regions.

There are few studies on substrate quality (chemistry) and decomposition of leaf litter of exotic trees species in South Africa or in the other parts of East or Southern Africa. One example is the work by Lisanework and Michelsen [15] who studied decomposition and nutrient release in native forests and tree plantations using the litter bag technique. Another is a laboratory study by Lemma *et al.* [16] who studied substrate quality and decomposition of fresh leaf litter and fine roots of *Cupressus lusitanica, Pinus patula*, *Eucalyptus grandis* and native forest trees. In the Mpumalanga region of South Africa Dames [17] studied biotic factors and altitude effects on litter accumulation and decomposition. As far as we know, no study has been done to evaluate sensitivity of litter decomposition to litter quality and temperature in the Mpumalanga region especially under anticipated climate change scenarios. Therefore, the objectives of this study were (1) to determine the initial concentration of nitrogen (N) and carbon (C) in needle litter of *Pinus patula* collected from compartments in which six different nitrogen fertilizer treatments were applied in 2000 and 2002; (2) to characterize the changes in concentration of N and C of needle litter during the decomposition by comparing fresh litter with decaying litter; (3) to determine the effect of temperature and litter quality on the decomposition rate of *Pinus patula* needle litter; and (4) to determine the influence of fertilizer application on the decomposition rate of *Pinus patula* needle litter.

2. Materials and methods

2.1. Study area

Litter was collected from 18-year old second rotation *Pinus patula* (Schlecht et Cham) plantations located in the Ngodwana SAPPI plantation forest in the Mpumalanga province of South Africa (25° 34’ S, 30° 38’E). The province is situated in the eastern part of South Africa; it is a summer rainfall region with precipitation occurring mainly in the form of thunderstorms. The mean annual rainfall varies from

350 mm in the north east to 1600 mm on the escarpment. The region's proximity to the tropic of Capricorn and warm Mozambique current of the Indian Ocean results in a subtropical, frost-free climate in the low lying areas of the lowveld [18]. The study plots were located in Mamre, Elandshoogte and Mooifontein plantations. Mamre and Mooifontein have soil texture of clay loamy while Elandshoogte clay.Rainfall of about 1187 mm/yr is received in both Mamre and Mooifontein site while Elanshoogte receives 897 mm/yr. The criteria for selection were based on the fact that fertilizer trials were taking place in these plantations and fertilization was anticipated to affect the litter quality. The study plots underwent six fertilizer treatments and two replicates were used for each treatment. Only two replicates could be accommodated in the field design. The treatments were (1) Control: no fertilizer additions; (2) 100kg/ha Limestone Ammonium Nitrate (LAN) 28 % (N) applied when the trees were 11 years old; (3) 100kg/ha Urea 46 % (N) applied when the trees were 11 years old; (4) 100kg/ha LAN 28 % (N) applied when the trees were 13 years old; (5) 100kg/ha LAN 28 % (N) applied when the trees were 11 and 13 years old (Total of 200kg/ha); and (6) 100kg/ha Urea 46 % (N) applied when the trees were 11 and 13 years (Total of 200kg/ha N).

2.2. Litter collection

Newly shed needles were collected from *P. patula* plots in September 2007 which were subjected to six fertilizer treatments. The size of each plot is 576 m_2, containing 11 × 11 trees with a spacing of 2.4 × 2.4 m. A bulked sample of the surface litter, made up of five quadrats (each of size 0.25 m by 0.25 m) randomly placed were collected from each site, that is 36 samples (6 treatments × 2 replicates × 3 sites) in total.

2.3. Needle litter decomposition

The *P. patula* needles were weighed into 10 g samples and each sample inserted into 300 ml glass jars. The glass jars were covered tightly with screw caps and the needles were incubated at four temperature regimes (15º, 18º, 24º and 30 ºC) for 16 weeks. These temperatures were chosen to reflect current ambient (15 ºC), a likely change with global change (18 ºC) and extreme temperatures to measure the upper limits of decomposition rates. Subsamples of fresh needles collected from each plot were oven dried to constant mass at 65 ºC for 72 h and oven dry/fresh mass ratio was used to determine initial moisture content to convert fresh needle mass to dry weight and to express the decomposition parameters corrected on a dry mass basis. After 2, 5, 6, 8 and 16 weeks of incubation, two jars (representing two replicates) per each fertilization regime for three sites at four temperatures were retrieved (144 jars at each sampling date) and the needles were oven dried. Litter mass loss was determined by weighing oven dried samples and subtracting their mass from corrected oven dried mass. After 2, 6, 8, and 16 weeks the rate of CO_2 production was measured. To measure CO_2 flux from the needle litter at each incubation period, jars were removed (144 jars per each sampling date), opened and aerated for 10 minutes to release the CO_2 evolved. This approach was used because during a pilot experiment 0.1 M KOH solution used to capture CO_2 became saturated after 1 or 2 weeks of incubation hence a 2 hourly collection period of CO_2 was used at the end of each incubation period. The reasoning was that using this approach an instantaneous measure of CO_2 emission could be calculated, thus CO_2 data presented are not cumulative over the incubation period. The assumption is that the data are comparative across treatments, temperatures, time and sites using this approach. Test tubes containing 18 ml of 0.1 M KOH were inserted into the jars and closed tightly with screw caps and returned to the incubators. Controls were also set up by inserting test tubes into jars without needles. After 2 hours, test tubes were removed and the content titrated with 0.1 M HCl after addition of saturated $BaCl_2$ solution (1.44 ml per 18 ml KOH) using phenolphthalein as an indicator.

The difference in HCl consumption between the blank and the sample indicated the amount of adsorbed CO_2. Carbon dioxide emitted was calculated on the basis that 1 ml 0.1 M HCl is equivalent to 2.2 mg CO_2 [19]. Thus, the experimental design consisted of a factorial combination of three sites, six treatments, two replicates, four temperature regimes and five sampling dates, a total of 720 jars.

2.4. Elemental analysis

Subsamples of the litter from each study plot were oven dried at 65 ºC for 72 hours and ground in a laboratory mill (Retsch [Haan, Germany] ZM 100) to pass through a 0.5 mm screen. Total N and C concentrations were measured using freshly collected litter samples and samples after 16 weeks of incubation. Analyses were done at Bem laboratory in Cape Town, South Africa using a Leco Truspec CN analyzer.

2.5. Calculations and statistical analyses

Four-way ANOVAs were used to test for statistical ($p<0.05$) differences in CO_2 evolution and mass loss based on temperature, fertilizer treatment, site and duration of incubation. Three-way ANOVAs were used to test for statistical ($p<0.05$) differences in CO_2 evolution and mass loss based on temperature, fertilizer treatment and site at individual incubation periods. A three-way ANOVA was used to test for statistical differences in N (%) concentration in the needle litter that was incubating for 16 weeks based on temperature, fertilizer treatment and site. Two-way ANOVAs were used to test for statistical differences in C:N and N (%) concentrations of the needle litter with sites and fertilization level as main factors. Tukey's method was used for a pair-wise comparison between means. Pearson correlation coefficients were used to examine the relationships between mass loss, CO_2 evolution and litter chemistry. Correlation between temperature and N (%) accumulation was examined using the Pearson correlation coefficient. All statistical analyses were performed using R [20].

3. Results

3.1. Litter chemistry at the time of sampling

The total N content of the litter ranged from 1.20% at Elandshoogte to 1.60% at Mooifontein, and 1.38% at Mamre. Generally, the N concentrations in the litter differed significantly among sites with Elandshoogte having the lowest concentrations and Mooifontein the highest. Litter N concentrations increased in all the sites upon additional N supply with the highest relative response in Elandshoogte (6.67%), 5.27% for Mooifontein and lowest in Mamre (2.17%).The highest % increase was recorded for the site with the lowest N concentration for the control although these increases were not statistically significant. The form and amount of fertilizer applied did not affect litter N concentration at each site however; when the analyses for the three sites were pooled together the form and time of fertilizer application had a significant effect. The highest N (%) was recorded for the sites that were treated with Urea (46) at 11 and 13 years while the control recorded the lowest N concentration. The litter N concentration also varied with time of the fertilizer application where litter collected from sites fertilized at 13 years recorded higher N concentration than those of 11 years (Figure 1). Litter C concentration only varied from 68.2% to 69.6% and was not significantly different and therefore changes in litter C:N ratio mirrored those for litter N concentrations.

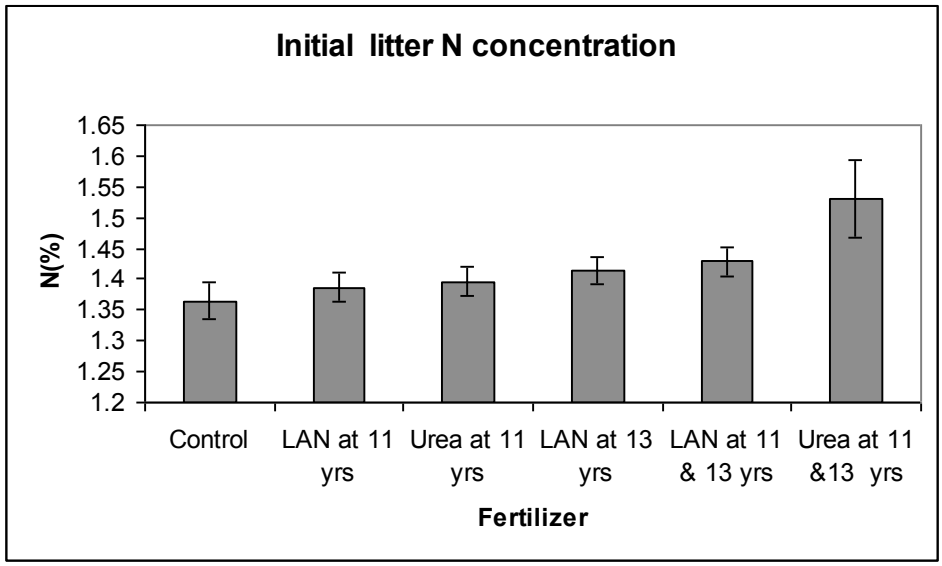

Figure 1 Initial nitrogen concentration of sites categorized according to the form of fertilizer and time of application since planting. Values are the means±SE derived from pooled data from three sites.

3.2. Litter chemistry changes over the 16 weeks of incubation

For all but 11 of 144 litter samples that were incubated at different temperatures for 16 weeks, there was an increase in N (%) concentration. Paired student's t-test result showed that there were significant differences between N concentration of the initial litter and after incubation for 16 weeks ($p<0.001$). The C:N ratio depended significantly on temperature ($p=0.03252$) and site ($p<0.01$). The paired student's t-test showed that in all cases there were significant differences between the initial and final C:N ratio of the litter ($p<0.001$). The C:N ratio drastically decreased after 16 weeks of incubation. For temperature, this variation in C:N was attributable to differences between 30 ºC and 15 ºC ($p=0.0339$) whereas site variation was due to differences between all three sites with Mooifontein having the lowest and Mamre the highest variation. Three-way ANOVA demonstrated that nitrogen accumulation depended significantly on temperature ($p=0.0082$), site ($p=0.0032$) and fertilization ($p=0.0291$). For temperature this variation was attributable to differences between 24 ºC and 15 ºC ($p=0.0490$) and 30 ºC and 15 ºC ($p=0.0062$); for fertilization the variation was attributable to differences between unfertilized and LAN (28) 11 yr plots ($p=0.0226$) and for site the variation was attributable only to differences between Mooifontein and Mamre ($p=0.0034$).

3.3. Rate of CO_2 production from decomposing litter

Carbon dioxide produced from litter varied significantly with temperature ($p<0.001$), fertilization ($p<0.001$) and duration of incubation ($p<0.001$) and there were significant interactions between all factors except site:time. Temperature accounted for much of the variability of CO_2 produced at all weeks except for week 6 where the fertilization effect was significant ($p<0.001$). However, significant two-and three-

way interactions on individual weeks indicated that the effect of temperature was frequently associated with fertilization or sites. Across all the three sites (Elandshoogte, Mamre and Mooifontein) the amount of CO_2 produced was generally higher for temperatures 24 ºC and 30 ºC compared to 15 ºCand 18 ºC. Carbon dioxide produced by samples incubated at 30 ºC in all the sites continued to increase from week 2 until week 8 and sharply declined at 16 weeks. There was a clear difference between CO_2 produced at 15 ºC and 18 ºC ($p<0.001$) with 87% of the data showing 18 ºC yielding more CO_2 than 15 ºC. The amount of CO_2 produced at high temperatures especially 30 ºC was significantly higher than that of 15 ºC and 18 ºC. The amount of CO_2 produced from the litter collected from the study plots in which N fertilizer was applied showed similar trends to the control with respect to temperature. ANOVA results indicate that fertilization is significant ($p=0.0088$). LAN (28) at 11 years, Urea (46) at 11 years and LAN (28) at 13 years were significantly different when compared with the control. The effect of fertilization is masked when the analysis was done at individual incubation periods, however, the fertilization effect was significant at week 6 ($p<0.001$).

In order to tease out the overall dominant variables influencing CO_2 emission, the total CO_2 emission, the total CO_2 calculated from addition of CO_2 levels at each incubation period was plotted (Figure 2). Cumulative CO_2 production (successive additions of CO_2 from week 2 up to week 16) varied significantly with temperature ($p<0.001$), while site and fertilization effects were not significant. The general trend was for the amount of CO_2 produced increased with an increase in temperature from 15 ºC up to 24 ºC and declined after 24 ºC. Correlation between cumulative CO_2 and temperature was significant ($r=0.6648$, $p<0.001$)**.** The amount of CO_2 produced was mainly influenced by temperature with high temperature leading to high production of CO_2. The effect of fertilization was not uniform across the weeks and the amount of CO_2 emission from the litter increased with duration of incubation.

3.4. Mass loss

Mass loss of the litter varied significantly with temperature ($p<0.001$), N fertilization ($p<0.001$), site ($p<0.001$) and duration of incubation ($p<0.001$). The higher order interactions (four-way) between all the factors were not significant even though some two-way interactions were significant: - temperature:time ($p<0.001$), fertilization:site ($p<0.001$) and time:site ($p=0.004$). When the analyses were done at each individual week, mass loss was significantly affected by temperature, fertilization and site at all time periods. Higher temperatures (24 ºC and 30 ºC) yielded mass loss that was significantly higher than that of 18 ºC and 15 ºC ($p<0.001$). Across all the sites mass loss of litter incubated at 18 ºC is higher than 15 ºC which is confirmed by 65 % of the data showing litter incubated at 18 ºC losing more mass than at 15 ºC ($p<0.001$). Generally litter incubated at 30 ºC lost more mass than that incubated at 15 ºC, 18 ºC and 24 ºC although some exceptions include litter collected from control plot in Mamre at week 6 and that of LAN at 11 yrs. N fertilization had a significant effect on mass loss ($p<0.001$). However, the pattern was not consistent with some levels of N fertilization showing no effect when compared with the control. For example the mass loss of the plot fertilized with Limestone Ammonium Nitrate (LAN) 28% at 11 years was not significantly different from the control ($p=0.6133$), a similar result was found when samples obtained from the plot fertilized with LAN (28%) at 13 years was compared with the control ($p=0.4436$). However, mass loss of plots fertilized with Urea (46) at 11 years, LAN (28) at 11 and 13 years and Urea (46) at 11 and 13 years showed significant difference from the control ($p<0.012$).

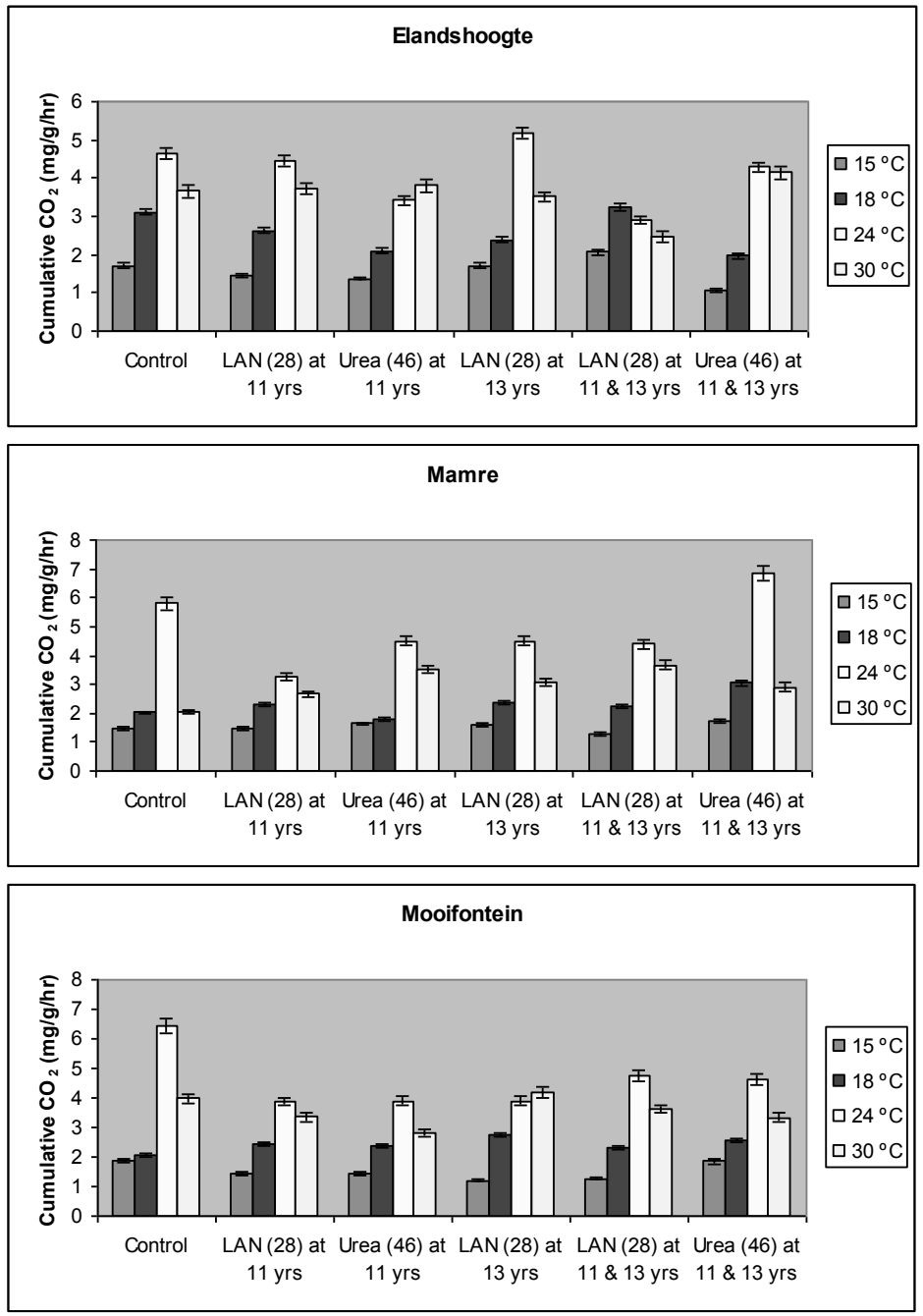

Figure 2 Cumulative CO2 emissions from three unfertilized (control) and fertilized sites incubated for 16 weeks at four temperatures.

Duration of incubation (time) effect on mass loss was significant ($p<0.001$). Generally mass loss increased as decomposition progressed. The highest mass loss was recorded at 16 weeks while at week two the lowest mass loss was recorded. Some exceptions include litter incubated at 15 ºC at week 8 for LAN at 11 and 13 yrs lost less mass than one at week 6.

Site was a significant factor affecting mass loss of the litter ($p<0.001$). Higher mass losses were recorded at the Mooifontein and Mamre sites than at the Elandshoogte site.

Generally mass loss was positively correlated with initial N (%) concentration of the needle litter. However, the correlation was extremely weak ($r=0.07$, $p=0.03$). When tested at each site, mass loss and N (%) correlation was only evident at Mooifontein. The correlation value also diminished as the decomposition progressed: $r=0.1$ after 8 weeks and after 16 weeks dropped to 0.07. However, there was significant correlation between cumulative mass loss and litter nitrogen concentration ($r=0.414$, $p<0.01$).

4. Discussion

4.1. Litter chemistry and nutrient dynamics

The litter N concentrations recorded in this study can be compared with other studies on the same species in the summer rainfall regions of South Africa. The N values recorded for needle litter (mean=1.42 %) were considerably higher than that found by Bird [21] in the Ermelo district of the Mpumalanga Highveld. Morris [22] working in *P. patula* plantations in Swaziland found mean litter N values of 1.25%. Lemma *et al.* [16] recorded a value of 0.56% using freshly fallen needle litter collected from *P. patula* in the Southwestern highlands of Ethiopia. Nitrogen concentrations of *P. patula* in this study varied greatly when compared with values of other pine species. Maggs [23] in *P. elliottii* stands found N concentrations of 0.33% and 0.59% for layers L and F2 respectively. Sharma and Pande [24] reported a value of 0.8% for pine plantations in India.

The differences in nutrient concentrations between those from the current study and those reported by various authors in the literature can be explained by the different species that were under investigation, site differences, degree to which the litter had been exposed to decomposition, seasonal variation and age of the trees. Phenologically different species may resorb N and phosphorus (P) before the abscission of leaves to redeploy in developing tissue in order to minimize nutrient losses [25] more so when plants experience nutrient deficiency [26]. For example Olbrich (1994) cited in Bird [21] found internal translocation in *P. patula* occurring at two distinct periods: spring to early summer and late summer to winter. Resorption and internal translocation will therefore reduce the foliar nutrient concentration and thus reduce the level of nutrients in the litter. The age of the stand from which the litter is collected influences the nutrient content of the litter. Morrison (1974) cited in Louw and Scholes [27] observed the influence of tree age on litter N content with the highest levels occurring at the age of approximately 30 years which possibly explains the difference in litter N content in the current study (1.42% N content from a 18 year old stand) and the results of Bird [21] of 1.01% N content from a *P. patula* stand of 16 year. Season is another factor that may affect the litter nutrient content. Louw and Scholes [27] report mean values of 1.24% foliar N during winter while, the value of 1.79% was reported during the summer period. The length of time that litter has been exposed to decomposers will influence the quantity of nutrients found in leaf litter, as illustrated by Lemma *et al.* [16]. They found that newly shed leaf litter had N concentrations of 0.56% while the litter from the Oe layer of the forest floor (decomposed) had N concentration of 1.6%. Similarly Maggs [23] found that in *P. eliiottii* forest floor the L (Litter) and F1 (first fermentation) layers were found to have 0.33 and 0.44% N respectively. The increase in N (%) during decomposition can be attributed to net loss of carbon in the form of CO_2 combined with microbial

immobilization [23,28]. The litter N concentration varied with the time and frequency of fertilizer application. Litter collected from plots fertilized at 13 years recorded higher N concentrations than those of 11 years, implying that the effect of fertilization on litter N concentration diminished as the time progressed. The litter collected from plots subjected to fertilization at 11 and 13 years recorded higher concentrations of N than those fertilized at only 11 or 13 years, this trend can possibly be explained by the residual effect of fertilization at 11 years double the amount. Crous *et al.* [29] found a significant effect of residual fertilizer on litter P levels when additional fertilizers were added to *P. patula* stands in Usutu, Swaziland. Similar results were found in *P. resinosa* stands which were fertilized with N for 9 years at Harvard forest, where the N concentration of litter continuously increased [30].

The relationship between litter chemistry and decomposition was investigated by comparing the chemistry of fresh leaf litter with the litter that was incubated for 16 weeks. The effect of temperature, fertilization and site on nutrient concentration was also investigated.

Decomposed litter showed higher N concentrations and lower C:N ratios compared with fresh leaf litter, consistent with the pattern documented in many other litterbag and laboratory studies [31, 16]. This pattern was attributed to net losses of C (or mass losses) combined with microbial immobilization (23, 28] and the slow biological breakdown of nitrogen-substituted lignin [5]. Temperature affected the N accumulation of the litter. Higher temperatures resulted in more accumulation of N. Hobbie [14] investigating the difference in N release of the litter incubated at 4 ºC and 10 ºC found initial N loss followed by N gain, followed by another period of N loss at 10 ºC, however the 4 ºC treatment litter did not exhibit a final period of N loss. However, Shaw and Harte [32] found no effect of warming on nitrogen release. Site also significantly affected N accumulation of the litter. This difference can possibly be explained by the fact that the initial amount of N concentration of the freshly fallen litter was different and therefore the effect is reflected on the decomposed litter. For example in a study by Ribeiro *et al.* [28] the litter with an initial higher concentration of N and P released higher proportions of these elements which is consistent with the current study where there was a positive correlation between the initial N concentration of the litter and the decomposed litter. The result of this study therefore supports the hypothesis that future climate warming will directly affect N and C cycling of the forests.

4.2. Rate of CO_2 production from the litter

Increasing atmospheric temperature may alter C cycling in forest ecosystems through changes in decomposition, and possibly act as a source of CO_2 to the atmosphere as positive feedback. This study mainly evaluated the effect of temperature on the rates of CO_2 production from litter at an early stage of decomposition. Temperature had a significant effect on rates of CO_2 production with higher temperatures resulting in higher production of CO_2 from the litter. Other studies [14, 33] have found CO_2 emissions from litter or soil to be strongly stimulated by temperature. Under a warming climate with possible increases in temperature of 1-3 ºC in the Southern African region, the amount of CO_2 emissions from the forest floor is expected to increase. Seasonal variation will be important in determining the pattern of CO_2 emission from the litter as there was marked difference in the amount of CO_2 produced at 30 ºC and 24 ºC when compared with litter incubated at 15 ºC and 18 ºC. At 30 ºC the CO_2 emission declined even though mass loss continued to increase. The amount of CO_2 emission was small (mg) relative to mass loss (g) and therefore continued increase in mass loss at 30 ºC even as CO_2 emission decreased can possibly be attributed to other metabolic changes taking place in the litter. Seasonal differences may also be important as during the drier, winter months or under drought conditions the composition of the microbial community may change with fungi becoming more dominant which may affect the amount of CO_2 production from the forest floor.

The amount of CO_2 produced was also affected by fertilization and duration of incubation. As time progressed, the amount of CO_2 produced increased in magnitude. This is in agreement with the results of Witkamp [34] who found positive correlations between the amount of CO_2 produced and time. Although temperature accounted for much of the variability of CO_2 produced, the significant two and three way interactions between temperature, fertilization, site and time indicated that the effect of temperature was not consistent across fertilization or sites. The effects of fertilization on decomposition rate of the litter and soil organic matter have been controversial. For example a study by Bradford *et al*. [35] found that P amendment stimulated decomposition rates while N fertilization suppressed decomposition of organic matter. In the context of feedback of CO_2 from the litter and soil as a result of global warming, the option of fertilizer application to forest plantation should be based on whether the amount on CO_2 emissions from the forest as a result of fertilization outweigh the amount of C that can be sequestered by the forest plantation. There was no significant effect of site on the amount of CO_2 produced from the litter collected from various study sites, a possible explanation for this is that the amounts of C in the litter collected from the different sites were more or less the same and therefore the amount of carbon respired in the form of CO_2 may reflect the carbon content of the litter collected from different study sites. Other studies have found significant site effects on factors affecting litter decomposition for example studies conducted in India by Kshattriya *et al*. [36] found that fungal and bacterial counts and invertase, amylase and cellulase enzyme activities were greatest on litter in low altitude sites when compared with high altitude sites. Decomposition at low altitude sites was found to be higher than high altitude sites in Mpumalanga region of South Africa [17] implying that places with different altitudes will have different rates of CO_2 emissions due to influence of altitude on temperature and microbial population and activity. In the current study although site effect was not significant the amount of CO_2 produced based on altitude of the site revealed that the site at lower altitude (Mooifontein) recorded higher amounts of CO_2 emissions than Elandshoogte and Mamre.

4.3. Mass loss

For terrestrial ecosystems, climate variables (temperature and moisture) have been found to be a rate-regulating factor of litter decomposition [37]. Temperature is often the primary factor determining rates of litter decomposition [8]. In the current study there were significant temperature effects on litter mass loss which are consistent with results of previous studies [38, 14] which found that mass loss and decomposition rates increased with an increase in temperature. A possible explanation for this pattern is the effect of increased temperature on microbial activity.

Witkamp [34] found that increased temperature increased the population of microorganisms and accelerated the amount of CO_2 produced from the litter. Witkamp [34] and Aerts and De Caluwe [39] found significant correlations between mass loss and respiration rates of the litter which is consistent with the current study where the correlation between cumulative mass loss and cumulative CO_2 emission was found to be positive ($r=0.212$) and significant when tested at 0.1 significant level ($p=0.0741$). Fierer *et al.* [40] attributed the majority of the C respired over relatively short incubation periods to loss of the soluble C fraction. The C loss in the form of CO_2 from the litter possibly explains the mass loss recorded during the study.

Mass loss of the litter and temperature exhibited linear relationship where litter incubated at 30 ºC recorded the highest mass loss and 15 ºC the lowest. Temperatures (15º, 18º, 24º and 30 ºC) were chosen bearing in mind that the study area currently experiences a mean annual temperature of 15 ºC and a possible temperature increase for the area of 3 ºC (Choice of 18 ºC). Temperatures 24 ºC and 30 ºC were included in the experiment to investigate the response of decomposition at higher temperatures.

Several studies have indicated that the chemical and biochemical quality of litter affects mass loss during decomposition [41, 42]. In many studies N concentration of the litter was strongly correlated with litter mass loss [34, 43]. Mass loss in the current study was found to be only very weakly correlate with N (%) of the litter. The quantity of N in the litter has been found to affect the activity of microorganisms. Litter with higher N concentrations is readily decomposed by microorganisms [3] and this possibly explains why litter with higher N lost more mass than those with lower N concentrations. The effect of N concentration on litter mass loss showed some variation as decomposition progressed. During the initial stage (2-8 weeks) the correlation between N % and mass loss was stronger than at the later decomposition phase (16 weeks). This is in agreement with Cotrufo *et al.* [44] who reported that litter mass loss was positively correlated with N concentration during the early phase of decomposition but the influence diminished at the later stage of decomposition. A possible explanation for the diminishing role of N in explaining mass loss of the litter as decomposition progressed is that N has been found to limit decomposition at high concentrations. Nitrogen at high concentrations reacts with lignin and polyphenols at late stages of decomposition creating more recalcitrant compounds [45], suppresses activity of lignin-degrading fungi [46] and decreases the amount of fungi and bacteria [47]. Other studies have shown that after an initial period during which various compounds are lost, the rate of decomposition decreases. This is caused by the accumulation of condensed or polymerized polyphenols which may originate from the litter or be synthesized by microorganisms [48, 17). Previous studies that have investigated the effects of fertilization on the rate of litter decomposition have been controversial. In this study fertilization had significant effects on mass loss of the litter in some cases. Litter from fertilized plots decomposed faster when compared with the control. This is consistent with some other studies (49,50]. The effects of fertilization on decomposition rate can possibly be explained by the effects of fertilizer on litter quality. Fertilization increased the N concentration of the litter, which in turn increased the amount of mass loss of the litter collected from fertilized plots. However, some fertilized plots did not show any differences when compared with the control. The inconsistent result may be due to the significant interaction between the site and fertilization treatment that was evident. Needle litter collected from different sites showed different magnitudes of mass loss. The difference in mass loss is possibly explained by differences in the amount of N contained in the litter collected from different sites. The sites (Mooifontein and Mamre) with high litter N concentration lost more mass than those at Elandshoogte with low N concentration. Initially litter that contained high amounts of N lost more mass than litter that contained low amounts of N. Litter collected from the sites on shale recorded more mass loss than from the site on andesite. The sites had different soil textures where litter collected from clay loam soils recorded more mass loss than Elandshoogte with a clay soil texture. Soil texture has been found to influence the rate of N mineralization and soil N concentration.

Nitrogen mineralization is generally more rapid in coarse than fine textured soils [51]. The rate of N mineralization possibly affected the nitrogen concentration of the litter and the effect reflected on mass loss of the litter. In this study the effect of site on mass loss was only related to litter chemistry and temperature of incubation but under field conditions the result may differ due to different factors affecting decomposition of the litter including both biotic and abiotic factors. Abiotic factors include the litters' physical structure, temperature, moisture, relative humidity and pH, while biotic factors include litter quality, microbial activity and the composition of the soil microorganisms and soil fauna [3]. Furthermore, the values of the mass loss in the laboratory may be underestimated because macrofauna like earthworms were not involved in the decomposition of the litter. Soil macrofauna are known to contribute significantly to the breakdown of leaf and needle litter by fragmentation which favours the colonization of bacteria and fungi by increasing the available surfaces and hence may accelerate decomposition [52; 53]. The differences in the amount of mass loss recorded in different sites reflects the

influence of site characteristics on decomposition rate of the litter which could have not been detected if the litter was collected from only one site.

Generally the amount of mass loss increased as decomposition progressed. Highest mass loss was recorded at week 16. This is possibly explained by loss of labile C fractions and other soluble fractions which are normally lost during the early decomposition phase [40]. As the time progresses there are usually the formation and accumulation of humic materials, which normally have a very slow rate of decomposition [3]. Li *et al.* [50] for example using *Dacryodes excelsa* leaf litter found that mass loss rate declined with the incubation time. Leaf litter decayed fast during the first 3 months and after 8 months of incubation the leaf mass loss slowed down and approached a constant value through the next 4 months of the study period. In the Mpumalanga region of South Africa rapid mass loss of *P. patula* litter occurred during the first six weeks. Mass loss of the current study is consistent with a previous study in Mpumalanga [17].

5. Conclusions

Decomposition rate of the litter was accelerated by an increase of 3 ºC in temperature implying that future warming will directly affect cycling of C and N in *P. patula* litter and soil of South Africa. The study confirms that there is a strong potential positive feedback inherent in the massive amounts of carbon that are currently tied up in the litter on the forest floor, an average litter thickness of 10 cm (range 3-35 cm) was observed in a study in the republic of South Africa in *Pinus patula* plantation [54]. The danger is that this could be released by global warming and adds to the CO_2 already in the atmosphere. The decomposition rate of the litter was more marked at higher temperatures (24 and 30 ºC) implying that seasonal variation will play a major role in the flux of CO_2 and mass loss of the litter.

The release of nitrogen from the litter increased with temperature therefore global warming will have an effect on nitrogen availability to the forest. Application of fertilizer differentially affected the decomposition rate of the litter as some fertilizer treatments were significantly different from the control while others were not. There is no simple explanation as to why this is the case.

The litter quality was not a strong predictor of litter decomposition rates implying that temperature will be the major factor influencing the decomposition rate of *P. patula* needle litter. Mass loss, CO_2 emission and nitrogen release of the *P. patula* needle litter appear to be strongly influenced by the site differences. Additionally, the decomposition of the litter is determined by the interplay of site, temperature and duration of incubation, therefore there is a need to develop models to assess the decomposition of the litter based on factor interactions.

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