Leaf litter decomposition rates increase with rising mean annual temperature in Hawaiian tropical montane wet forests

Decomposing litter in forest ecosystems supplies nutrients to plants, carbon to heterotrophic soil microorganisms and is a large source of CO_2 to the atmosphere. Despite its essential role in carbon and nutrient cycling, the temperature sensitivity of leaf litter decay in tropical forest ecosystems remains poorly resolved, especially in tropical montane wet forests where the warming trend may be amplified compared to tropical wet forests at lower elevations. We quantified leaf litter decomposition rates along a highly constrained 5.2 °C mean annual temperature (MAT) gradient in tropical montane wet forests on the Island of Hawaii. Dominant vegetation, substrate type and age, soil moisture, and disturbance history are all nearly constant across this gradient, allowing us to isolate the effect of rising MAT on leaf litter decomposition and nutrient release. Leaf litter decomposition rates were a positive linear function of MAT, causing the residence time of leaf litter on the forest floor to decline by ~31 days for each 1 °C increase in MAT. Our estimate of the Q_{10} temperature coefficient for leaf litter decomposition was 2.17, within the commonly reported range for heterotrophic organic matter decomposition (1.5 – 2.5) across a broad range of ecosystems. The percentage of leaf litter nitrogen (N) remaining after six months declined linearly with increasing MAT from ~ 88% of initial N at the coolest site to ~74% at the warmest site. The lack of net N immobilization during all three litter collection periods at all MAT plots indicates that N was not limiting to leaf litter decomposition, regardless of temperature. These results suggest that leaf litter decay in tropical montane wet forests may be more sensitive to rising MAT than in tropical lowland wet forests, and that increased rates of N release from decomposing litter could delay or prevent progressive N limitation to net primary productivity with climate warming.

1   **Title:** Leaf litter decomposition rates increase with rising mean annual temperature in Hawaiian

2   tropical montane wet forests.

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Introduction:

11   Litter decomposition is a fundamental biogeochemical process influencing rates of carbon

12   and nutrient cycling in forest ecosystems (Perry et al. 2008). Global syntheses indicate that

13   temperature is a primary factor controlling litter decay rates (Aerts 1997, Gholz et al. 2000, Adair

14   et al. 2008), but these datasets are dominated by temperate forest ecosystems. The factors

15   controlling litter decomposition in tropical wet forest ecosystems are less well studied (Cusack et

16   al. 2009, Wieder et al. 2009) and data from tropical montane wet forests are particularly sparse

17   (Malhi et al. 2010). The paucity of litter decomposition data from tropical montane wet forests

18   represents a significant gap in knowledge given recent evidence that litter decomposition in

19   montane tropical wet forests may be more sensitive to rising temperature than in lowland tropical

20   wet forests (Waring 2012) and that warming in the tropics may be occurring faster at higher

21   elevations (Giambelluca et al. 2008).

22   One of the more tractable approaches to estimate the temperature sensitivity of litter decay in

23   forests is through the use of elevation gradients, which can be powerful tools to examine climatic

24   controls on ecosystem functioning (Malhi et al. 2010). Observational studies along elevation

25   transects substitute space for time by examining litter decay rates in forests across a range of

26   temperature environments, and so have the advantage of representing the long-term, integrated

27   response of decomposition to changing mean annual temperature (MAT). Elevation gradients are

28   seldom a perfect proxy for climate warming, however, because other factors that influence

29   ecosystem processes may also vary with elevation, including plant species composition,

30   precipitation and soil moisture, geologic substrate, and soil chemical and physical properties.

31   These potentially confounding factors can complicate efforts to isolate the influence of

32   temperature on ecosystem functioning along elevation gradients (Wood et al. 2012).

33   We know of only two studies that have specifically examined the effect of temperature on leaf

34   litter decomposition along elevation transects in the tropics (Scowcroft et al. 2008, Salinas et al.

35   2011), both of which indicate that temperature is a primary factor controlling leaf litter

36   decomposition rates. However, the two studies vary widely in their estimates of the apparent Q_{10}

37   temperature coefficient, the proportional change in litter decay rate due to a 10 $^{\circ}$C increase in

38   temperature, potentially because of the confounding effects of precipitation and soil moisture,

39   which also exert a strong control on litter decay (Schuur 2001). For example, precipitation

40   differences with elevation in Salinas et al. (2011) resulted in a three-fold variation in mean annual

41   soil moisture across sites of different elevation. Relatively few litter decomposition studies and

42   the wide range of results from those studies highlight the need for more research aimed at

43   isolating the influence of temperature on leaf litter decay in the carbon dense and highly

44   productive tropical montane wet forest biome.

45   Here we present results of a leaf litter decomposition experiment across a well-constrained

46   5.2 °C MAT gradient consisting of nine permanent plots in native-dominated tropical montane

47   wet forests spanning 800 m elevation along the eastern slope of Mauna Kea Volcano on the Island

48   of Hawaii. Many potentially confounding factors remain constant across this MAT gradient, such

49   as dominant canopy tree species, disturbance history, soil water content, geological substrate and

50   soil type (Litton et al. 2011, Iwashita et al. 2013, Selmants et al. 2014). We examined decay of a

51   common substrate (senescent *Metrosideros polymorpha* [Myrtaceae] leaves from a mid-elevation

52   plot) across the MAT gradient over a six-month time period to address two main research

53   questions: (*i*) Does rising MAT increase rates of leaf litter decomposition in tropical montane wet

54   forests when other environmental factors are held constant?; and (*ii*) does variation in MAT alter

55   the rate of nitrogen (N) release from decomposing leaf litter in tropical montane wet forests?

56   **Materials and methods:**

57 *Study sites*

58   We tested the effect of rising MAT on leaf litter decomposition rates by using a highly

59 constrained MAT gradient along the eastern flank of Mauna Kea volcano on the Island of Hawaii.

60 This MAT gradient consists of nine permanent 20 x 20 m plots in native-dominated tropical

61 montane wet forests spanning 800 – 1600 m in elevation, which corresponds to a 5.2 °C MAT

62 gradient (13.8 - 18.2 °C). All nine MAT plots are similar in factors other than mean annual

63 temperature that can affect ecosystem processes, including vegetation, disturbance history, soils,

64 parent material, and soil water balance (Litton et al. 2011, Iwashita et al. 2013, Selmants et al.

65 2014). Specifically, all nine MAT plots are in moderately aggrading mature forests with a canopy

66 dominated by *M. polymorpha* and a mid-story dominated by three species of tree fern (*Cibotium*

67 spp.). Soils are all well-drained Acrudoxic Hydrudands according to USDA Soil Classification

68 System, and are all derived from ~20,000 year-old volcanic ash deposits on top of a Pleistocene-

69 age lava flow dominated by the minerals hawaiite and mugearite (Wolfe and Morris 1996, Litton

70 et al. 2011). Rainfall is not constant across the MAT gradient, but tends to decrease with

71 elevation (Table 1). However, potential evapotranspiration also decreases with elevation (Table

72 1; Giambelluca et al. 2014), which results in near constant mean annual soil water content across

73 the gradient (Litton et al. 2011). Solar radiation is also nearly constant across the MAT gradient

74 (Table 1), and all MAT plots are below the trade wind inversion layer (Cao et al. 2007). The

75 seven lower elevation MAT plots are in the Hawaii Experimental Tropical Forest and were

76 accessed by permission from the USDA Forests Service and the State of Hawaii Department of

77 Land and Natural Resources. The two highest elevation MAT plots are in the Hakalau Forest

78 National Wildlife Refuge and were accessed by permission from the US Fish and Wildlife

79 Service.

80 *Experimental design*

81   We examined the effect of MAT on leaf litter decomposition by following the decay of

82   senescent *M. polymorpha* leaves in each of the nine MAT plots for a six month period (June to

83   December, 2012). Rainfall is fairly evenly distributed throughout the year on windward slopes in

84   the Hawaiian Islands (Giambelluca et al. 2013) and seasonal changes in solar zenith angle,

85   although much less pronounced than in higher latitude temperate regions, lead to slightly warmer

86   air temperatures in summer months than in winter (Giambelluca et al. 2014).

87   We used intact senescent *M. polymorpha* leaves sorted from oven-dried litterfall samples

88   collected monthly in elevated trays at 1116 m (16.1 °C; Table 1) from July 2010 through March

89   2012. These leaves were composited and well mixed for construction of individual litterbags. We

90   used litter collected from one species at a single elevation as a standard substrate to isolate the

91   effect of MAT on litter decay by minimizing variation in litter nutrient concentration. Each

92   litterbag was 10 x15 cm, constructed of fiberglass screen with 1.5 mm mesh size and contained ~

93   2.5g of well-mixed senescent *M. polymorpha* leaves. We deployed 15 litterbags per MAT plot in

94   June of 2012. We placed a cluster of three litterbags tethered with nylon fishing line to a central

95   stake in five 5x5 m subplots within each MAT plot, resulting in five replicate litterbags for each

96   collection period in each MAT plot. All litterbags were placed on the soil surface (top of the O

97   horizon). We collected litterbags at one, three, and six months after initial placement. After each

98   collection, litter was oven-dried at 70 °C, weighed and finely ground in a ball mill for chemical

99   analysis. We did not correct for ash-free dry mass, but, because they were placed on top of the

100   undisturbed O horizon, there was no evidence of soil accumulation on either litterbag surfaces or

101   litter itself. Total N of initial, undecomposed leaf litter and of partially decomposed litter from the

102   three collection periods was determined by combustion using a Costech Elemental Analyzer at

103   the University of Hawaii at Hilo Analytical Laboratory (Costech Analytical Technologies,

104   Valencia, CA USA).

105   *Data analysis*

106   We estimated the decomposition rate of *M. polymorpha* leaf litter for each of the five replicate

107   litterbag clusters within each MAT plot by fitting a single-pool negative exponential model to the

108   litter mass data (Olson 2007) using non-linear regression with initial mass fixed at the measured

109   value (Adair et al. 2010):

110                                    $X(t) = e^{-kt}$ (1)

111   where $X(t)$ is the proportional mass remaining at time t (in days) and k is the decomposition rate.

112   The proportional initial mass, $X(0)$, is equal to 1 by definition and so is not estimated as a model

113   parameter (Adair et al. 2010). The mean residence time of leaf litter on the forest floor was

114   calculated as $1/k$ for each set of litterbags. We calculated the Q_{10} temperature coefficient for litter

115   decomposition rates across the MAT gradient as:

116                                    $Q_{10} = (R_2/R_1)^{10/(T_2-T_1)}$ (2)

117   Where Q_{10} is the proportional change in k due to a $10°$C increase in MAT, R_1 and R_2 are

118   regression-derived estimates of k at the coolest and warmest MAT plots, and T_1 and T_2 are MAT

119   values of the coolest and warmest MAT plots (13 °C and 18.2 °C, respectively). The proportion

120   of initial N remaining at the end of the six-month incubation period was calculated by dividing

121   the mass of N in litter collected after six months by the mass of N in the initial undecomposed

122   litter (Schuur 2001).

123   We used ordinary least-squares linear regression to determine whether leaf litter

124   decomposition rate (k), leaf litter residence time ($1/k$) and the percentage of leaf litter N

125   remaining after six months varied significantly as a function of MAT. The plot (n = 9) was the

126   smallest experimental unit to which the treatment (MAT) was applied, and so we use within-plot

127   means of the five replicate litterbag clusters as the response variable for all linear regression

128   analyses. We also used regression analysis at the plot level to determine whether annual rainfall

129   and soil water content were significant predictors of leaf litter decay rates across the MAT

130   gradient. We calculated 95% confidence intervals of the percentage of initial N remaining in leaf

131   litter after one, three and six months to examine net N mineralization and net N immobilization at

132   each stage of decomposition across the MAT gradient. For all statistical tests, we set $\alpha = 0.05$ and

133   confirmed that the assumptions of normality and homoscedasticity were met. All statistical

134   analyses were performed in R version 3.0.2 (R Core Team, 2013).

135   **Results:**

136   Leaf litter decomposition rate (k) ranged from 1.67×10^{-3} d^{-1} to 4.03×10^{-3} d^{-1} across the MAT

137   gradient and k was a positive linear function of MAT ($R^2 = 0.65$, $p < 0.01$). Decomposition rates

138   increased by 0.21×10^{-3} d^{-1} for each 1° C increase in MAT. Consequently, leaf litter residence

139   time declined by 31 days for each 1° C increase in MAT (Fig. 1). The estimated Q_{10} for leaf litter

140   decomposition was 2.17.

141   Initial N concentration of mixed *M. polymorpha* litter was 8.5 mg g^{-1}. After six months of

142   decomposition, the percentage of N remaining in decomposing *M. polymorpha* leaves declined

143   significantly as a function of increasing MAT (Fig. 2), from ~ 88% of initial N at the coolest site

144   to ~74% of initial N at the warmest site, a decline of approximately two percentage points for

145   each 1 °C increase in MAT. Nitrogen remaining in leaf litter was never significantly larger than

146   100% at any stage of decomposition within any of the nine MAT plots (Fig. 3), indicating there

147   was no net N immobilization in decaying leaf litter. Neither annual rainfall nor soil water content

148   during the six month experiment period (Table 1) were significant predictors of leaf litter decay

149   rates ($R^2 = 0.013$, $p = 0.34$ for annual rainfall; $R^2 = 0.03$, $p = 0.67$ for soil water content).

150   **Discussion:**

151   Quantifying the temperature sensitivity of leaf litter decomposition and nutrient release is

152   critical to understanding how forest ecosystem processes will respond to climate change. We used

153   a highly constrained MAT gradient to demonstrate that both mass loss and N release during leaf

154   litter decay increase linearly in response to rising MAT in Hawaiian tropical montane wet forests.

155   Globally, there is evidence that leaf litter decay is slowed by cool temperatures in tropical

156   montane forests (Waring 2012) and that climate warming in the tropics is occurring faster at

157   higher elevations (Bradley et al. 2004, Giambelluca et al. 2008). When combined with results

158   presented here, this evidence suggests leaf litter decomposition rates in tropical montane wet

159   forests may increase substantially with climate warming in the coming decades.

160   The rates of leaf litter decomposition reported here (1.67×10^{-3} d^{-1} to 4.03×10^{-3} d^{-1} across the

161   MAT gradient) are consistent with other studies in montane wet forests in Hawaii (Hobbie and

162   Vitousek 2000, Schuur 2001, Scowcroft et al. 2008) and well within the two orders of magnitude

163   range of 3×10^{-4} d^{-1} to 3×10^{-2} d^{-1} reported for tropical wet forests globally (Gholz et al. 2000,

164   Cusack et al. 2009, Waring 2012). There are a number of factors aside from temperature that can

165   affect leaf litter decomposition rates in tropical montane wet forests, most notably leaching from

166   precipitation (Wieder et al. 2009), soil oxygen availability related to soil water content (Schuur

167   2001) and leaf litter chemistry (Wieder et al. 2009, Salinas et al. 2011). By decomposing a

168   common substrate across a highly constrained MAT gradient, we were able to isolate the effect of

169   temperature by largely controlling for the effects of precipitation, soil moisture, initial litter

170   chemistry and other potential confounding factors, demonstrating a strong linear increase in leaf

171   litter decomposition rate with rising MAT. This increase in leaf litter decay rate is in line with,

172   and likely contributes to, the substantial increase in soil-surface CO_2 efflux across this MAT

173   gradient (Litton et al. 2011). Notably, soil organic carbon storage remains constant across the

174   MAT gradient despite increased rates of litter decay and soil-surface CO_2 efflux with rising MAT

175   (Selmants et al. 2014, Giardina et al. 2014).

176   The Q_{10} temperature coefficient, which describes the rate of change in a biological or

177   chemical process over a 10° C interval, often falls within the range of 1.5 - 2.5 when applied to

178   heterotrophic processes such as organic matter decomposition (Reiners 1968, Kätterer et al. 1998,

179   Gholz et al. 2000, Hyvönen et al. 2005, Zhou et al. 2009). Our Q_{10} estimate for leaf litter

180   decomposition (2.17) is within this range, and is similar to the Q_{10} estimate for soil-surface CO_2

181   efflux (2.26) across the same MAT gradient (Litton et al. 2011), suggesting a consistent response

182   of carbon cycling rates to rising temperature in tropical montane wet forests. In contrast to our

183   results, Salinas et al. (2011) estimated a Q_{10} for leaf litter decay of 3.06 in five tropical forest

184   plots across an elevation gradient spanning 12.8 °C (11.1 – 23.9 °C). Although there is wide

185   variation in estimates of apparent Q_{10} from litter decomposition studies (Gholz et al. 2000, Adair

186   et al. 2008), we suggest the Salinas et al. (2011) estimate of litter decay Q_{10} is ~ 40% higher than

187   ours largely because of confounding factors related to site selection and data analysis technique.

188   First, the lowest temperature site in the Salinas et al. (2011) study was also the driest, with a

189   mean annual soil moisture nearly three-fold lower than the mean of the other four sites,

190   potentially depressing k for this low temperature site. In contrast, mean annual soil moisture is

191   nearly constant across our MAT gradient (Litton et al. 2011). Although there was some variation

192   in soil water content among our MAT plots during the six-month period when leaf litter was

193   decomposing, the driest plots during the experiment period were in the middle of our gradient

194   and the percentage variation in soil moisture was an order of magnitude less than that of Salinas

195   et al. (2011). Second, Salinas et al. (2011) used linear regression of log-transformed mass loss

196   data to estimate decomposition rates, which can result in sizable overestimates of k depending on

197   error structure (Adair et al. 2010). We used non-linear regression of untransformed

198   decomposition data, which consistently yields accurate k estimates (Adair et al. 2010). The

199   potential confounding effect of a three-fold variation in soil moisture combined with the use of

200 log-transformed mass loss data in the Salinas et al. (2011) study suggest that their estimate of

201 apparent Q_{10} may be artificially inflated.

202   We found no evidence of N limitation to leaf litter decomposition across the MAT gradient.

203 At all stages of decomposition, the proportion of initial N remaining in decomposing leaf litter

204 never significantly exceeded 100% at any of the MAT plots. This evidence is consistent with

205 results from a fertilization experiment at a site near the middle of our MAT gradient, in which

206 individual additions of N and phosphorus (P) had no effect on *M. polymorpha* leaf litter

207 decomposition and combined N and P additions had only a weak positive effect (Hobbie and

208 Vitousek 2000). We also found an overall trend of increased rates of N release from decomposing

209 litter with rising MAT. Taken together, this evidence suggests that warming will increase rates of

210 N cycling and availability in these forests, a response consistent with results from warming

211 experiments across a wide range of forest and grassland ecosystems (Rustad et al. 2001). We did

212 not measure leaf litter phosphorus (P) dynamics in this study, so it remains unclear how rates of P

213 release from decomposing leaf litter respond to rising MAT. However, since P does not directly

214 limit *M. polymorpha* leaf litter decomposition at a site near the middle of our gradient (Hobbie

215 and Vitousek 2000), we consider it likely that increasing rates of leaf litter decay with rising MAT

216 will increase rates of P release and availability similar to the trend for N documented here.

217   Results from this leaf litter decomposition experiment across a well-constrained MAT

218 gradient have two potentially countervailing implications for how the carbon balance of tropical

219 montane wet forests will respond to climate warming, at least within the MAT range studied here

220 and where increasing temperature does not drive significant, concomitant changes in leaf litter

221 chemistry or soil water balance. First, our results indicate that warming will increase rates of leaf

222 litter decay in tropical montane wet forests, which explains part of the warming-induced increase

223 in rates of soil-surface CO_2 efflux to the atmosphere (Litton et al. 2011). At the same time, these

224 results suggest that more rapid decomposition with warming should also increase rates of nutrient

225 release from decaying leaf litter, at least in forest ecosystems where decomposition is not

226 currently nutrient limited. The availability of nutrients may strongly regulate whether ecosystem

227 carbon sequestration keeps pace with rising atmospheric CO_2 concentrations (Luo et al. 2004).

228 An increase in rates of nutrient release from decaying leaf litter with climate warming, as

229 suggested by our results, could delay or even prevent the onset of progressive nutrient limitation

230 of ecosystem carbon sequestration.

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Environmental characteristics of the nine permanent plots along a 5.2 °C mean annual temperature gradient in tropical montane wet forests on the Island of Hawaii.

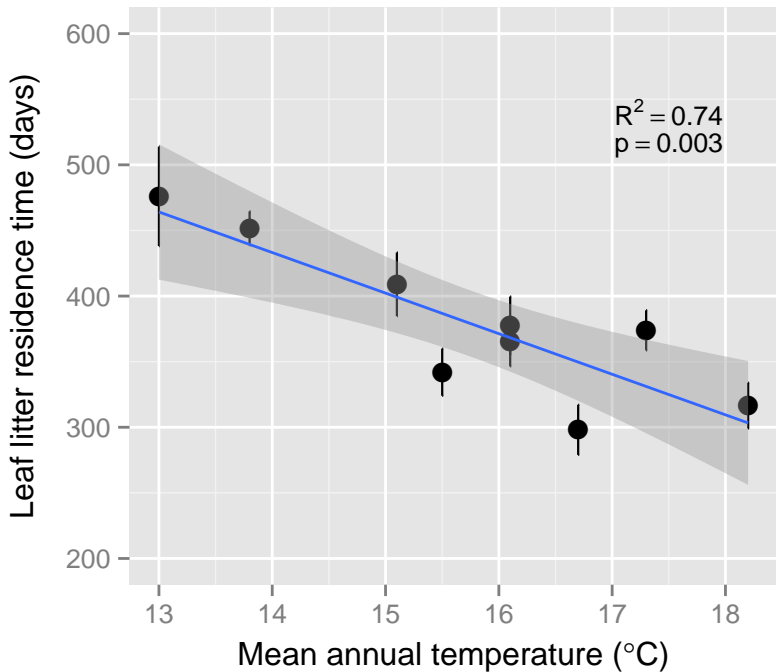
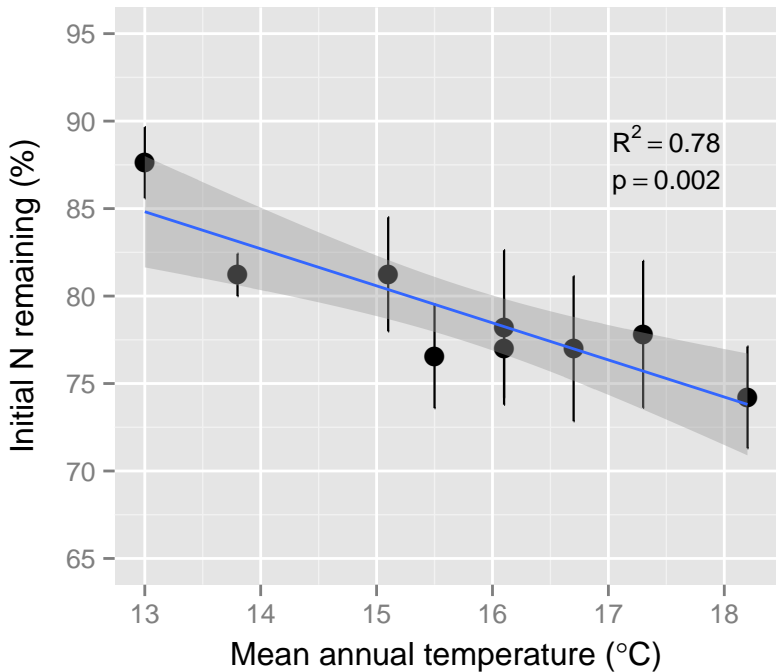
[a]Mean annual air temperature and mean annual soil volumetric water content from Litton et al. (2011).

[b]Mean monthly soil volumetric water content during the leaf litter decomposition experiment (June to December, 2012).

[c]Mean annual rainfall estimates from Giambelluca et al. (2013)

[d]Mean annual potential evapotranspiration and solar radiation estimates from Giambelluca et al. (2014).

MAT Plot	Elevation (m)	Air temperature (°C)[a]	Rainfall (mm y^{-1})[b]	Soil VWC: annual (m^3 m^{-3})[a]	Soil VWC: experiment (m^3 m^{-3})[b]	Potential evapotranspiration (mm y^{-1})[c]	Solar radiation (W m^{-2} y^{-1})[c]
1	800	18.2	4570	0.55	0.67	2298	201.1
2	934	17.3	4292	0.55	0.64	2232	200.9
3	1024	16.7	3975	0.57	0.63	2214	202.4
4	1116	16.1	3734	0.48	0.61	2127	204.9
5	1116	16.1	3433	0.51	0.47	2137	210.1
6	1204	15.5	3181	0.40	0.42	2211	214.5
7	1274	15.1	3101	0.51	0.44	2234	216.2
8	1468	13.8	4119	0.55	0.61	1888	202.6
9	1600	13.0	3282	0.57	0.60	1961	213.1

Leaf litter residence time across a mean annual temperature gradient on the Island of Hawaii.

Nitrogen remaining in leaf litter after six months of decomposition across a mean annual temperature gradient on the Island of Hawaii.

Nitrogen remaining in decomposing leaf litter at three stages of decomposition across a mean annual temperature gradient on the Island of Hawaii.