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An evaluation of the two variable model for stream litter processing using data from southeastern Australia: How important is temperature?

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Introduction

The processing rate of terrestrial litter in streams has generally been described in terms of the negative exponential decay coefficient ($-k\,d^{-1}$) derived from the negative exponential equation $W = e^{-kD}$ where W is the proportion of the initial weight remaining after D days (PETERSEN & CUMMINS 1974, WEBSTER & BENFIELD 1986). HANSON et al. (1984) preferred the use of a two variable model, incorporating degree days as a second independent variable, to the single variable model. The expanded model, which takes the form $W = e^{-k(T)D}$, where T is a temperature variable such as degree days, proved an adequate fit to a greater proportion of the data sets they investigated, and allowed the processing rate coefficient to be calculated at a range of experimental temperatures rather than assuming that rate was temperature independent. They suggested that trends in temperature-dependent rate coefficients are useful in comparing differences in processing rates between sites and seasons.

The data set used by HANSON et al. (1984) to evaluate the two variable model was limited, being restricted to the results from 13 processing experiments. Of the 13, 5 were carried out in Gull Lake, at four different locations, 6 were carried out in the Augusta Creek catchment in Autumn 1974 each at a different location, and 2 in Augusta Creek in Autumn 1973 at a location different from those used in 1974. Only in two cases were two experiments performed at the same time and place, and in each of these the two experiments used different leaf species.

In this paper we analyse data from experiments on leaf processing in five southeastern Australian upland streams to evaluate the two variable processing model. This is a far larger data set, incorporating 130 separate processing experiments from 7 different sites, and 15 different leaf species.

Methods

Much of the data on which this study is based have been reported elsewhere and site details are fully reported in those studies, which are cited below. We have included data from two East Gippsland streams, Far Creek and Rooty Break Creek (CAMPBELL et al. 1991, CAMPBELL et al. 1992) and from forest and pasture sites on each of two streams near Melbourne, Loch River and Keppel Creek (CAMPBELL et al., in press). Finally we used some data collected from experiments in Kalatha Creek, a second order stony stream flowing through open mixed eucalypt forest near Glenburn, 60 km northeast of Melbourne.

All the experiments were carried out using packs of leaves fastened with buttoneers and elastic to terracotta capping bricks (see CAMPBELL et al. 1991, and CAMPBELL et al., in press b). The weights of the leaf packs varied depending on the leaf species and the particular experiment, and results from both fresh picked and abscissed leaves have been used in this analysis. For 6 of the 7 sites (Kalatha Creek being the exception) data from experiments commenced in at least 2 summers and at least 2 winters have been used. A sample of at least 3 leaf packs was collected 2 days after the packs were first placed in the stream and further samples taken at 4, 8, 16, and 30 days and then monthly until at least 70 % of the initial pack weight had been lost. The term "processing" in this paper incorporates both biological (invertebrate and microbial) processing and physical fragmentation of the leaves.

HANSON et al. expanded k(T) as $k(T) = b_0 + b_1T$ so that the two variable model, in log form becomes $\ln W_d = \ln W_0 - b_0D - b_1TD$ where W_d is the weight remaining after d days, W_0 is the weight at time 0, D is the time elapsed in days and TD is the accumulated degree days. There are some difficulties in fitting this model with a coefficient for $\ln W_0$ of 1, so we used the model $\ln W = b_0D + b_1D$ where $W = W_1/W_0$. Because the use of proportion of weight remaining may be influenced by distortion of the variances, a normal probability plot of the residuals was checked, and the studentized residuals were plotted against estimated values to ensure that the regression assumptions were not violated.

For each experiment the model was fitted by the least squares method using the SYSTAT computer package (WILKINSON 1990). The significance (p) level of the two coefficients, b_0 and b_1 were noted, as was the overall significance of the regression. In every case the overall significance was high ($p < 0.001$). Using $p = 0.05$ as the ac-

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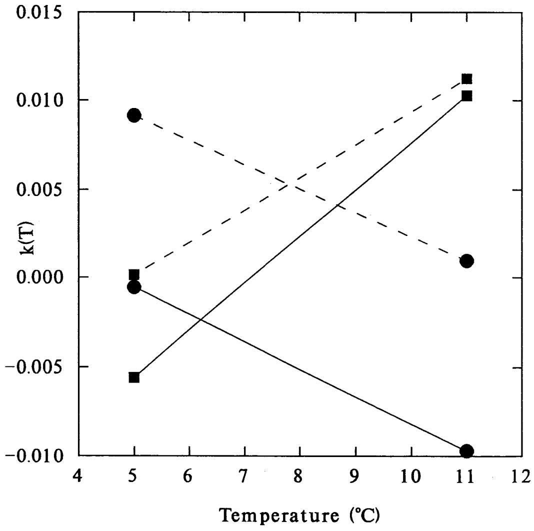

Fig. 1. Plot of k(T) against temperature for four experiments on leaf processing conducted at a site on Rooty Break Creek. Three experiments commenced in January 1990 (summer) and one, with 2.5 g packs, in July 1990 (winter). The four experiments were all conducted with fresh picked leaves of *Athersperma moschatum*, but each had a different pack size. The lines represent the results for 1.5 g (dashed line, square symbol), 2.0 g (solid line, round symbol), 2.5 g (dashed line, round symbol) and 3.0 g (solid line square symbol) packs.

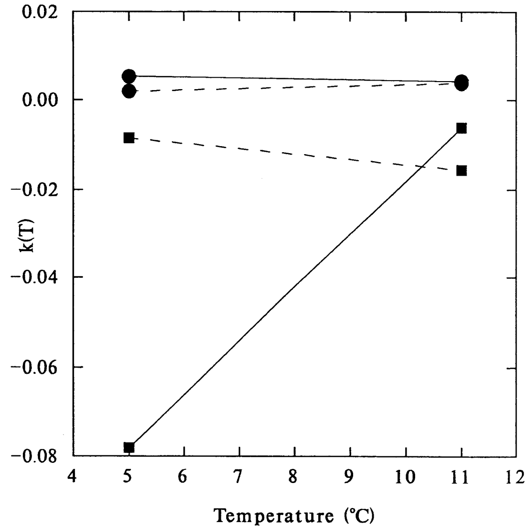

Fig. 2. Plot of k(T) against temperature for four experiments on leaf processing conducted at a site on Rooty Break Creek, commencing in January 1990. The four experiments were all conducted with fresh picked leaves of four different *Eucalyptus* species. The lines represent the results for *E. viminalis* (solid line, square symbol), *E. platyphylla* (dashed line, square symbol) *E. torelliana* (solid line, round symbol) and *E. hylandii* var. *campestris* (dashed line, square symbol).

cepted level of significance, each experiment was scored based on whether both, neither or only one of the coefficients was significant. Eight cases from Rooty Break Creek, in which both variables were either significant or not significant (i.e. in no case was there one significant and one non-significant variable) were selected, and values of k(T) were determined, using the expansion above, for temperatures at the top and bottom of the range encountered during the experiment. The trend in k(T) with increasing temperature was then plotted (Figs. 1 and 2).

Results

In the interpretation of the results, where neither b_0 or b_1 were significant either variable alone was sufficient to predict ln W, where both were significant both were necessary, and where either one alone was significant it alone was necessary. Of the 130 leaf experiments, in 69 cases neither variable was significant, and in 33 both were significant. Time alone was significant in 17 cases and accumulated temperature alone in 11 cases. This indicates that accumulated temperature was significantly related to the processing in 34 % of cases, while in 66 % it had either no effect (13 %) or the processing was adequately predicted by time alone (53 %). The eight data sets for which the change in k(T) with increasing temperature was plotted (Figs. 1 and 2) produced some plots in which k(T) was inversely related to temperature and some for which it was not.

Discussion

Our larger data set demonstrates weaknesses in several of the claims made for the two variable model by Hanson et al. (1974). The model does produce a satisfactory fit to the data in more cases than a single variable model. However, the more variables added to any linear regression model the better the fit to the data. Moreover every experiment we analysed in this study the overall regression was already highly significant ($p < 0.001$) with a single variable model. In about a third of the cases there was some benefit in adding the accumulated temperature term to the model, and while this constitutes an appreciable proportion of the experiments, in no case was the benefit

Table 1. Multiple r^2 values for regressions using three different models for the experiments on leaf processing in Rooty Break Creek for which accumulated temperature (T) was a significant variable (either alone or together with the time variable (D)) in the two variable model. Experiments are listed by leaf species and pack weight and season (S = summer, W = winter) if a particular leaf species was tested with different pack weights or in different seasons.

Experiment	Significant Variables	Multiple r^2		
		$\ln W = -kD$	$\ln W = -kT$	$\ln W = -kTD$
A. moschatum 2.5 g, S	T	0.925	0.939	0.948
A. moschatum 1.0 g, S	T, D	0.917	0.939	0.962
A. moschatum 3.0 g, S	T, D	0.841	0.861	0.889
A. moschatum 2.5 g, W	T, D	0.945	0.917	0.972
A. moschatum 3.0 g, S	T	0.836	0.855	0.859
A. moschatum 3.0 g, S	T, D	0.795	0.840	0.940
A. moschatum 3.0 g, W	T, D	0.961	0.941	0.980
A. moschatum 3.0 g, W	T, D	0.978	0.958	0.992
E. nitens, S	T, D	0.923	0.951	0.967
E. crebra, S	T	0.923	0.937	0.941
Elaeocarpus holopetalus	T	0.960	0.964	0.967

large. For example, at the Rooty Break Creek site, a total of twenty-six data sets were analysed, of these 11 had a significant accumulated temperature variable. The multiple r^2 values of the regressions for these cases are given in Table 1, with the r^2 values calculated using a single variable model based on time alone, a single variable model based on accumulated temperature alone and the two variable model. It is evident from the table that there is little difference in the r^2 values between the three models even for cases in which accumulated days are the only significant variable in the two variable model.

Hanson et al. suggested that, in the experiments which they carried out, those cases in which the addition of accumulated temperature to the model was not necessary based on the significance value of b_1, were cases where the temperature was stable for much of the experiment, or where the experiment was conducted for too short a time for the leaves to be adequately processed. That is not the case for our data. All of our experiments were conducted, as noted above, until at least 70% of initial leaf weight was lost. But even amongst experiments carried out at the same location at the same time there were differences in the relative significance of the two variables. For example 6 experiments using *Atherosperma moschatum* leaf packs of differing sizes (ranging from 0.5 to 3.0 g were conducted at Rooty Break Creek commencing in summer 1990. Of the six, three had neither variable significant, two had both variables significant and one had only the accumulated temperature variable significant. The experiments all continued for identical lengths of time, so it is not possible to invoke differences in temperature regime as an explanation of the differences in significance of b_1. The same type of pattern was also evident in the other sets of coincident experiments.

Hanson et al. (1984) found different patterns of change of k(T) with increasing temperature. In some experiments $k(T) \alpha T$ and in some cases $k(T) \alpha 1/T$. They had conducted only a single experiment at each site, and attributed differences in the trend of k(T) to differences in processing dynamics between sites. With the benefit a larger data set it appears that this is not the case. Figs. 1 and 2 plot the change in k(T) with temperature for two groups of coincident experiments at sites on Rooty Break Creek. In each figure only experiments for which neither b_0 nor b_1 were significant or both b_0 and b_1 were significant were plotted. Figure 1 plots data from four experiments with *Atherosperma moschatum* and Fig. 2 data for experiments with four different *Eucalyptus* species. From these data it is appears that, in southeastern Australian upland streams at least, the pattern of k(T) change with temperature is not a reflection of the processing dynamics at a site, or the processing dynamics associated with a particular leaf species at a site.

Overall we conclude that there is little benefit to be gained by adding an accumulated temperature variable to leaf processing models for southeastern Australian streams. The negative exponential model almost always, in our streams, adequately fits leaf processing data. An accumulated temperature variable does not bear a simple relationship to either site or leaf characteristics.

Acknowledgements

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References

Campbell, I. C., Cummins, K. W. & James, K. R., 1991: A preliminary investigation of seasonal differences in leaf decomposition patterns in Australian streams. – *Verh. Internat. Verein. Limnol.* **24:** 2071–2075.

Campbell, I. C., Enierga, G. M. & Fuchshuber, L., in press: The influence of pack size and position, leaf type, and shredder access on processing rate of *Atherosperma moschatum* leaves in an Australian cool temperate rainforest stream. – *Int. Rev. ges. Hydrobiol.* (submitted).

Campbell, I. C., James, K. R., Hart, B. T. & Devereaux, A., 1992: Allochthonous coarse particulate organic material in forest and pasture reaches of two southeastern Australian streams. I. Litter processing. – *Freshwat. Biol.* **27:** 353–365.

Hanson, B. J., Cummins, K. W., Barnes, J. R. & Carter, M. W., 1984: Leaf litter processing in aquatic systems: a two variable model. – *Hydrobiologia* **111:** 21–29.

Petersen, R. C. & Cummins, K. W., 1974: Leaf processing in a woodland stream. – *Freshwat. Biol.* **4:** 343–368.

Webster, J. R. & Benfield, E. F., 1986: Vascular plant breakdown in freshwater systems. – *Ann. Rev. Ecol. Syst.* **17:** 567–594.

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