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Author(s): W. G. Whitford, V. Meentemeyer, T. R. Seastedt, K. Cromack, Jr., D. A. Crossley, Jr., P. Santos, R. L. Todd and J. B. Waide

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¹ Manuscript received 24 January 1980; accepted 19 August 1980.

² Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721 USA.

³ Department of Zoology, Brigham Young University, Provo, Utah 84602 USA.

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EXCEPTIONS TO THE AET MODEL: DESERTS AND CLEAR-CUT FOREST¹

W. G. Whitford², V. Meentemeyer³, T. R. Seastedt⁴, K. Cromack, Jr.⁵, D. A. Crossley, Jr.⁴, P. Santos^{2,7}, R. L. Todd⁴, and J. B. Waide⁶

Meentemeyer (1978) developed a model for decomposition of litter as a function of actual evapotranspiration (AET) and lignin content. This model is a series of linear relationships differentiated by lignin content. Meentemeyer tested this model with existing data from a number of temperate and boreal forest sites. However, in his discussion of the model, Meentemeyer (1978) suggested that these relationships might not apply in deserts. Here, we show that the attractive correlation between AET and decomposition does not necessarily apply to all vegetation types nor to severely disturbed sites. Decomposition is higher than predicted by the AET model in deserts where AET is low, and lower than predicted for a mesic clear-cut forest where AET values are higher than uncut forests. We suggest that the attractive simplicity of the AET decomposition relationship fails in these systems because it does not account for marked changes in microclimate produced by ecosystem perturbation like clear-cutting, or for biotic adaptations in desert ecosystems.

Decomposition Rates on Clear-cut and Hardwood Forests at Coweeta

Decomposition rates of forest litter have previously been studied at the Coweeta Hydrologic Laboratory in the southern Appalachian Mountains in North Carolina, USA (Cromack and Monk 1975). Those data were previously used in development of the AET model. In 1977, a hardwood watershed (WS 7) was cable logged and clear-cut, and litter decomposition rates

were measured in 1978 using litter bags. Decomposition rates were concurrently measured on an adjacent hardwood watershed (WS 2). AET was calculated using the Thornwaite method from temperature and precipitation data collected on the clear-cut watershed. These AET values were then compared with decomposition rates of two species of litter measured in 1978 and earlier (Table 1). Dogwood (*Cornus florida*) leaf litter with 4.9% lignin and chestnut oak (*Quercus prinus*) leaf litter with 25.5% lignin were selected because of differences in lignin content (Cromack and Monk 1975). While lignin content appears strongly to influence decomposition rates, between-year differences should be predictable on the basis of differences in AET. The AET model predicted lower decomposition rates on WS 2 in 1978 due primarily to reduced rainfall, and was validated by lower measured rates of decomposition. However, the model predicted higher decomposition rates on WS 7 following clear-cutting, primarily because of higher temperatures, but the measured rates were substantially lower than predicted. (The AET value used here is a modeled value, and may differ from the AET measured by the United States Forest Service for entire watersheds at Coweeta.) Summer average maximum temperatures at the litter-soil interface on WS 7 in 1978 were about 40°C (R. L. Todd and J. B. Waide, *personal observation*). These high temperatures adversely affected faunal densities (Seastedt and Crossley 1981).

R. L. Todd and J. B. Waide (*personal observation*) measured CO₂ evolution and ATP amounts in litter and soil as indicators of microbial activity on WS 7 before and after clear-cutting. They did not find any significant changes resulting from the perturbation, suggesting that the rate of decomposition of organic matter in the entire soil profile was not appreciably altered. However, we suspect that microbial activity in the uppermost litter horizons where the litter bags

TABLE 1. Actual and predicted annual mass loss (%) of dogwood and chestnut oak litter on various Coweeta watersheds based on the AET model (derived from Meentemeyer 1978: Fig. 3).

| Site | Percent mass loss after one year | | | | AET value (mm) |
|--------------------------------------------------|----------------------------------|-----------|--------------|-----------|----------------|
| | Dogwood | | Chestnut oak | | |
| | Actual | Predicted | Actual | Predicted | |
| WS 18 (Hardwood forest, 2-yr average, 1969–1971) | 71.6 | 62.8 | 45.4 | 40.9 | 713 |
| WS 2 (Hardwood forest, 1977–1978) | 47.1 | 56.6 | 26.9 | 36.7 | 647 |
| WS 7 (Clear-cut forest, 1977–1978) | 42.0 | 65.4 | 19.4 | 42.6 | 741 |

were located was adversely affected by diurnal and longer term wetting and drying cycles that occurred on the clear-cut watershed (Witkamp and Frank 1970). Thus, reduced decomposition rates of the litter were attributed to reduced faunal comminution and, perhaps, to reduced microfloral respiration activity. Certainly the clear-cut watershed experienced pulses of extreme temperatures and moisture.

Decomposition Rates in Deserts

In desert ecosystems there are many factors which affect decomposition rates which cannot be predicted using the AET model alone. The clear-cut watershed at Coweeta is in several respects similar to a desert ecosystem. Low leaf area and surface temperature extremes are notable similarities, yet there are many differences. In deserts a portion of the annual litter fall is buried via interactions between animal activities, wind and water. Litter buried in the soil has been displaced to a new environment and should therefore have a different fate and different rate of decomposition than does surface litter (Santos and Whitford 1981).

Santos found that rainfall and soil temperature accounted for <50% of the variation in mass loss of buried creosotebush leaf litter. When arthropods were

excluded, precipitation and air temperature explained 90% of the variation. Santos and Whitford (1981) also found that >50% of the surface organic matter disappeared during the growing season (April–October), over which total rainfall amounted to 137 mm. Between August and October, $57.4 \pm 7.7\%$ of litter in surface bags disappeared, with a total AET for that period of 33 mm. Much of that loss was attributed to foraging subterranean termites.

Short-term litter bag studies indicate that mixed litter in a desert ecosystem decomposes at a rate equal to or greater than that observed over a comparable time interval for litter in Southeastern forest ecosystems (Table 2). Using the annual AET from the White Sands Monument (272.4 mm) (Table 2) and lignin values of 10% and 50%, Meentemeyer's (1978) model predicts percent litter mass loss of 14.21% to 18.23% in this desert. Percent mass losses during the summer months were double this figure and only the winter mass losses approached the annual predicted mass loss based on AET and lignin content.

In the Chihuahuan and Sonoran deserts, activity by the surface foraging subterranean termites of the genus *Gnathamitermes* varies as a function of soil temperature and moisture (Johnson and Whitford 1975, La Fage et al. 1976). W. G. Whitford (*personal observation*) found that from mid-August through October (1979) percent mass losses of a perennial grass, fluff-grass, *Erioneuron pulchellum*, and an annual, *Lepidium lasiocarpum*, on plots with termites eliminated were $26.05 \pm 5.75\%$ and $24.4 \pm 10.05\%$, respectively. Where termites were present, $75.79 \pm 2.20\%$ and $63.95 \pm 18.8\%$ of the mass disappeared. This is a 2.9- and 2.6-fold greater rate with termites present. Interestingly, this is almost exactly the magnitude by which the AET model underestimates the reported rates for deserts. In the natural litter, which was primarily creosotebush leaves and stems plus grass and forb fragments, etc., termites removed 20% more material than disappeared in the absence of termites.

Why should AET be a good predictor of organic matter loss in forests but not in deserts? Preliminary

TABLE 2. Percent mass loss of surface litter bags ($N = 10$ for each date) placed on gypsum dunes at White Sands National Monument, Otero County, New Mexico, in relation to AET values. Each bag contained thirty grams of oven-dried litter composed of equal portions of green stems of Mormon tea (*Ephedra trifurca*) leaves and small twigs of skunkbush sumac (*Rhus trilobata*) and green stems of rabbit brush (*Chrysothamnus nauseosus*).

| Duration of experiment | Loss of mass (%) | AET (mm) |
|---------------------------|------------------|----------|
| January–February (59 d) | 19.6 | 32.0 |
| March–April (61 d) | 25.5 | 5.4 |
| June–July (61 d) | 30.4 | 39.0 |
| 15 July–October (102 d) | 38.7 | 93.4 |
| November–February (120 d) | 30.1 | 102.6 |
| | | 272.4 |

studies by W. G. Whitford and his co-workers (*personal observation*) have shown that mean soil temperature at 10-cm depth explained approximately 50% of the variation in organic matter loss. However, their data are only for short-term studies and losses in mass from creosotebush litter are initially high. Soil surface temperatures in midsummer reach 60–65°C and remain there for 3–5 h/d. High temperatures and intense radiation could cause breakdown and volatilization of breakdown products, especially of the wax layers and resins on the leaves of desert plants like creosotebush, but would also cause intense drying and a harsh environment for microarthropods.

In another study, W. G. Whitford and co-workers (*personal observation*) found that, in July, surface litter moisture content (by mass) increased during the night and by 2 h after sunrise was 6%. By midday the moisture content was a fraction of 1%. They found significant populations of oribatids and other microarthropods in the litter at 0800 but not at midday nor in the evening. It needs to be emphasized here that soil biota live where humidities of 90% or greater persist even in very dry soil. Also soil organisms can migrate vertically and can go into and out of anhydrobiosis to escape harsh surface conditions. Even in deserts, in summer, there are "windows" of moderate surface microclimates in litter, of 2–4 h duration, when organisms like oribatids, collembola, etc. can feed rapidly and transport quantities of material into lower soil for digestion and excretion. The nature and causes of these "windows" needs additional research. Vapor movement upward from warm soil to surface litter cooled at night, a process called distillation, causes, with dew, the condensation of moisture on litter. Intense biological activity is thereby possible daily, but not for all soil organisms.

Conclusions

Meentemeyer (1978) recognized that AET was only a correlate of some of the actual regulators of decomposition processes. Clearly, these regulators are microbial activity, faunal consumption, and interactions between microbes and fauna that stimulate both biotic and physical breakdown of litter (e.g., Witkamp and Crossley 1966, Witkamp 1969, Vossbrink et al. 1979). When temperatures exceed the tolerance limits of the forest biota, as likely occurred on the clear-cut watershed, then decomposition rates are slowed. In environmentally harsh systems such as deserts, the biota have evolved mechanisms that ameliorate environmental restraints on feeding activity, resulting in decomposition rates greater than predicted by the AET model. AET is generally a good predictor of decomposition rates because it is strongly correlated

with biotic decomposition processes within a given range of temperature and moisture values. If these values are exceeded, or if behavioral adaptations of the biota circumvent abiotic constraints, then the relationship between AET and decomposition no longer holds.

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² Department of Biology, New Mexico State University, Las Cruces, New Mexico 88003 USA.

³ Department of Geography, University of Georgia, Athens, Georgia 30602 USA.

⁴ Institute of Ecology, University of Georgia, Athens, Georgia 30602 USA.

⁵ Department of Forest Sciences, Oregon State University, Corvallis, Oregon 97330 USA.

⁶ Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee 37830 USA.

⁷ Permanent address: Departamento de Ecologia, Instituto de Biociencias, U.N.E.S.P. Campus de Rio Claro, Caixa postal 178, 13.500 Rio Claro, Sao Paulo, Brazil.