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This Week's Citation Classic®

Scriber J M. Limiting effects of low leaf-water content on the nitrogen utilization, energy budget, and larval growth of *Hyalophora cecropia* (Lepidoptera: Saturniidae). *Oecologia* 28:269-87, 1977.
[Department of Entomology, Cornell University, Ithaca, NY]

Giant silkmoth larvae were reared on leaves of wild black cherry that contained variable amounts of leaf water but had the same total nitrogen content and caloric density. Larvae fed leaves with low water content grew more slowly and were less efficient at utilizing plant biomass, energy, and nitrogen than larvae fed leaves that were fully supplemented with water. Differences in leaf quality as indexed by leaf water are ecologically significant with large variation among and within individual trees. [The *SCI*® indicates that this paper has been cited in over 120 publications.]

J. Mark Scriber
Department of Entomology
Michigan State University
East Lansing, MI 48824-1115

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I find it ironic that the biggest source of experimental variation (and the major dilemma for my graduate thesis research at Cornell University) has become an important part of the foundation for the field called "nutritional ecology."[1] Leaf-water content as a significant and frustrating source of environmental variation, one that interfered with my search for a unifying principle in ecology, has itself become a classic issue. I wrote this paper 10 years ago, yet we are still struggling to control the environmental variation in order to elucidate the biochemical, physiological, and genetic mechanisms of differential foodplant use by insect herbivores, while assessing their ecological/evolutionary implications. The overwhelming effects of plant water content on food consumption and conversion efficiencies for insect growth greatly obfuscates the detection of physiological costs for insect detoxication or processing of allelochemics.[2]

Natural plant defensive chemistry and insect counteradaptations were approaching early bloom as an ecological field when Paul Feeny constructed a theoretical framework (the "plant apparency" concept).[3] Plant water content and nitrogen (although less glamorous than alkaloids, glucosinolates, cyanogenic glycosides, and other allelochemics) were tangentially included. Empirical correlates of this theoretically compelling ecological concept were subsequently described in later reviews that incorporated leaf nitrogen content and leaf water as key indices of plant leaf quality and insect growth performances.[4,5] These indices can now be used for most insect herbivores to predict the maximum growth rates that can be expected for insects, and they can help us understand why thermal unit accumulation alone is often inadequate for predicting individual and population growth rates.

The usefulness of water content for the differential classification of mature leaves of trees versus forbs was another (and unexpected) benefit that evolved from leaf-water analyses.[5] While these differences had been known for decades, the ecological significance of generally reduced growth rates of phytophagous insects on all tree leaves was perhaps not fully appreciated due to interest in other chemical effects.[1] It is not surprising that leaf water is physiologically, ecologically, and evolutionarily important to herbivorous insects; what was unexpected is that researchers did not consider water, perhaps because energy and nitrogen budgets had usually been calculated on a dry-weight basis. This paper may have reemphasized the significance of the high nutritional value of young leaves and the ecological advantages to phytophagous insects of spring feeding during leaf "flush" (a period sometimes called the "Feenyological window").

In summary I think that timeliness, subsequent recognition of an important but frequently overlooked chemical (dihydrogen oxide), and fortuitous circumstances led to this paper's ecological relevance. In an attempt to maintain a broad ecological perspective for what might otherwise have been a narrowly conceived feeding experiment, actual leaf composition was monitored throughout the day and night and at different seasons. The journal editors refused to permit inclusion of part of these data because of two missing data points from August 28, 1975. This corresponds to the morning of the birth of my second son; Bradley (and Brian) are doing fine today.

I think that if I were starting over, I would enroll in a graduate program in exercise physiology instead of foraging ecology (although both are enjoyable). In this way I could call "recreation" my job and insects my hobby, instead of the other way around.

1. **Slansky F & Rodriguez J G.** *Nutritional ecology of insects, mites and spiders.* New York: Wiley, 1987. 1016 p.
2. **Scriber J M & Feeny P P.** Growth of herbivorous caterpillars in relation to feeding specialization and to the growth form of their foodplants. *Ecology* 60:829-50, 1979. (Cited 70 times.)
3. **Feeny P P.** Plant apparency and chemical defense. *Recent Advan. Phytochem.* 10:1-40, 1976. (Cited 365 times.)
4. **Scriber J M & Slansky F.** The nutritional ecology of immature insects. *Annu. Rev. Entomol.* 26:183-211, 1981. (Cited 125 times.)
5. **Scriber J M.** Insect/plant interactions—host plant suitability. (Bell W & Carde R, eds.) *The chemical ecology of insects.* London: Chapman & Hall, 1984. p. 159-202.

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