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Mattson W J. Herbivory in relation to plant nitrogen content.
Annu. Rev. Ecol.Syst. 11:119-61, 1980.
[USDA Forest Service, North Central Experiment Station, St. Paul, MN]

Plants and their parts vary widely in N levels, reflecting specific adaptations to the spatially and temporally varying availability of N. This, in turn, has formed a basis for plant partitioning among herbivores, each of which employs different suites of adaptation for sequestering the dilute plant N. However, fleeting N availability has shaped not only the plants' nutritional, but also their antiherbivore properties, because growth and defense processes often compete for scarce resources—e.g., C in N-rich environments, and N in N-poor environments. [The *SCI*® indicates that this paper has been cited in more than 450 publications.]

Nitrogen—The Driving Element

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After finishing graduate work in the early 1970s, I began working on the population dynamics and impact of the forest tent caterpillar in northern Minnesota aspen forests. This experience triggered my latent interest in the effects of host plant quality on herbivores. Seeing the insect's mysterious, daily feeding rhythm, its inexplicable wholesale desertion of its "mother" tree at the third larval stage, and its ordered preferences for some plant species and clear aversion to others strongly reinforced ideas from the literature: plants are not inert, monolithic, green fodder. I became convinced that to understand the insect would require an understanding of its relationship with its hosts.

This led first to a paper on insects as regulators of forest primary production.[1] Further rumination on ideas gleaned from Janzen[2] and many others caused me to focus on the impact of plant N content on the ecology and evolution of phytophages, because protein limitation of herbivores seemed to be the common condition. Likewise, it appeared that plants themselves were generally N limited. Even more interestingly, variation in the availability of N impacted both nutritional and defensive plant properties.

In April 1978 I presented a lecture on this subject before the Central States Entomological Society. That event led directly to this article, because C.D. Michener (University of Kansas), who was associate editor for *Annual Reviews of Ecology and Systematics*, invited me to flesh out my lecture for consideration by *Annual Reviews*. Elated, I went home where I spent the next eight months reading and writing in order to assemble a comprehensive manuscript. To my dismay, I learned that it was twice as long as allowed. But a last-minute cancellation made room for nearly the whole thing.

This article grew out of an unusually rich intellectual atmosphere at the North Central Forest Experiment Station and the University of Minnesota. There were abundant seminars and informal discussion groups on biological and ecological theory and philosophy of science. This heady environment was enhanced by the varied disciplines and age classes of interacting scientists who were eager to promote and debate their different world views. I vividly remember the admonition of one particularly inspiring, sage colleague: write less; read and think more.

This article has been frequently cited probably because it was a timely, synthetic review addressing a broad subject. In many respects its conclusions are still current. Most authors cite it from the perspective of the importance of plant protein limitations on herbivores, which has been updated.[3] Fewer have cited it from the perspective of the concomitant influence of N availability on the evolution of plant defensive strategies and the expression of defensive properties and pathways, although that was its most novel contribution. However, this hypothesis was practically buried in the organizational framework. Furthermore, this idea was quickly captured and extended into, and hence superseded by, the more conceptually complete carbon-nutrient balance hypothesis,[4] the resource availability hypothesis,[5] and the growth-differentiation balance hypothesis of plant defense theory.[6] The article has also been cited for its speculation that a plant's seasonal growth pattern (e.g., determinate and indeterminate growth) affects what and how much it can allocate to defense, and hence its herbivory.

1. Mattson W J & Addy N D. Phytophagous insects as regulators of forest primary production. *Science* 190:515-22, 1975. (Cited 205 times.)
2. Janzen D H. Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica* 6:69-103, 1974. (Cited 225 times.)
3. Mattson W J & Scriber J M. Nutritional ecology of insect folivores of woody plants: nitrogen, water, fiber, and mineral considerations. (Slansky F, Jr. & Rodriguez J G, eds.) *Nutritional ecology of insects, mites, spiders and related invertebrates.* New York: Wiley, 1987. 1,016 p.
4. Bryant J P, Chapin F S & Klein D R. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40:357-68, 1983. (Cited 185 times.)
5. Coley P D, Bryant J P & Chapin F S. Resource availability and plant antiherbivore defense. *Science* 230:895-9, 1985. (Cited 265 times.)
6. Herms D A & Mattson W J. The dilemma of plants: to grow or defend. *Quart. Rev. Biol.* 67:283-335, 1992.
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