Journal of Chemical Ecology, Vol. 14, No. 1, 1988

LIGHT-INDUCED VARIATION IN PHENOLIC LEVELS IN FOLIAGE OF RAIN-FOREST PLANTS. I. Chemical Changes

SIMON MOLE,[1] JANE A.M. ROSS,[2] and PETER G. WATERMAN

Phytochemistry Research Laboratories
Department of Pharmacy, University of Strathclyde
Glasgow G1 1XW, Scotland, U.K.

(Received August 18, 1986; accepted December 17, 1986)

Abstract—Levels of phenolic secondary metabolites in the leaves of four west African rain-forest plants, *Acacia pennata*, *Cynometra leonensis*, *Diopyros thomasii*, and *Trema guineensis*, were correlated with incident light intensity at both the inter- and intraindividual level. Enhanced phenolic levels under high light intensity appeared to be due to production of both polyphenolics (condensed and hydrolyzable tannins) and simple phenolics. In *Trema guineensis*, where it is possible to separate leaves in terms of both their age and the light incident upon them, condensed tannin production progressed differently during the development of "sun" and "shade" leaves, suggesting continuing production of new oligomers in the former but not in the latter. The results of this study suggest that the production of phenolics in relation to variation in incident light is a finely tuned process, which must be explained in terms of plant physiology and intermediate metabolism rather than in terms of resource allocation or a direct response to herbivory.

Key Words—Phenolics, tannins, light enhancement, overflow metabolism, *Acacia pennata, Cynometra leonensis, Diopyros thomasii, Trema guineensis.*

INTRODUCTION

Considerable emphasis has been placed on the role of phenolic compounds, particularly polyphenolics (e.g., tannins), in the defense of plants against herbivores (Feeny, 1970; 1976; Rhoades and Cates, 1976; Rhoades, 1979; Baldwin and Schultz, 1983; Zucker, 1983; Harborne, 1985). The mode of action

[1] Present address: Department of Biochemistry, Purdue University, West Lafayette, Indiana 47907.
[2] Present address: Department of Biological Sciences, Njala University College, Njala, Sierre Leone.

0098-0331/88/0100-0001$06.00/0

generally associated with tannins has been that of digestibility reduction, providing plants with a quantitative defense (sensu Feeny, 1976) against herbivory by sequestering the protein in herbivore diets as insoluble tannin–protein complexes or by inhibiting digestive enzymes (Rhoades, 1979; Pierpoint, 1985). While there is considerable evidence for avoidance of high levels of tannins in food selection by many mammalian herbivores (Mole and Waterman, 1986), convincing support for digestibility-reducing effects has not generally been forthcoming from in vivo studies (Bernays, 1978; Berenbaum, 1983; Mole and Waterman, 1986), and evidence at the molecular level now indicates that animal digestive systems have evolved ways to counter the potential antinutritional effects of tannins on dietary proteins (Martin and Martin, 1984; Mehansho et al., 1985; Mole and Waterman, 1985). In short, the notion (Feeny, 1976; Rhoades and Cates, 1976) that tannins provide plants with a costly but relatively impregnable defense against herbivores is compromised by currently available evidence. While the production of tannins by a species may be optimized at a constant constitutive level, there is evidence that the quantities produced by an individual are variable and may be under metabolic control (Schultz, 1983; Baldwin and Schultz, 1983). On the assumption that such variation is of adaptive value in terms of plant fitness, then an understanding of the conditions that influence the production of tannins may help us appreciate their role(s).

If it is accepted that tannins have no metabolic or physiologic roles, it is in terms of constraints upon availability of fixed carbon and energy for their metabolism that explanations for their level of production will have to be sought. The starting point for the present work is the report (Waterman et al., 1984) that individuals of the tree *Barteria fistulosa* (Passifloraceae) growing in rainforest clearings respond to the higher light intensity of that environment by an increase in levels of phenolics in their foliage in comparison to individuals growing under the forest canopy. Specifically, the condensed tannin component of foliar total phenolics was shown to be enhanced by high light intensity. Waterman et al. (1984) suggested possible explanations for this phenomenon in terms of passive or active response of biosynthetic processes directly to variation in the light environment or indirectly to variability of herbivore pressure on *B. fistulosa* situated in different light environments. Given the highly effective defense *B. fistulosa* obtains against insect herbivores through an obligate mutualistic association with pseudomyrmicine ants (Janzen, 1972) a direct relationship between light intensity and condensed tannin production was considered the more likely explanation in this case.

A positive association between increasing light intensity and levels of phenolics has been recognized for some time (Hillis and Swain, 1959; McClure, 1985), but only in the last few years has it received attention in the ecological literature. Woodhead (1981) showed that the total phenolic content of *Sorghum*