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LIGHT-INDUCED VARIATION IN PHENOLIC LEVELS IN FOLIAGE OF RAIN-FOREST PLANTS. II. Potential Significance to Herbivores

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Abstract—The allelochemic activity of the polyphenolics isolated from the leaves of four west African rain-forest plants, *Acacia pennata*, *Cynometra leonensis*, *Diospyros thomasii*, and *Trema guineensis*, was examined by means of protein precipitation experiments to estimate their specific activity as precipitants. Results indicated that light-induced phenol synthesis in the more heavily insolated foliage of a species led to greater protein-precipitating capacity in these leaves. It is considered doubtful that this produced a quantitative difference in protein availability to an herbivore as, on average, even in the most shaded leaves there was sufficient tannin present to precipitate all the foliar protein. However, taking into account the considerable variability inherent in the results obtained and the adaptations herbivores possess to circumvent the antinutritional properties of tannins, it was concluded that shaded foliage was generally likely to present a nutritionally more acceptable food package on a statistical basis but that acceptable leaves could be found from throughout the light continuum encountered in any of the species studied.

Key Words—Foliar phenolics, condensed tannins, light enhancement, protein precipitation, herbivory, variable plant chemistry.

INTRODUCTION

In the preceding paper (Mole et al., 1988) evidence was presented for a positive correlation between the production of phenolic secondary metabolites and incident light intensity in the leaves of four west African plants, *Acacia pennata*, *Cynometra leonensis* (both Leguminosae), *Diospyros thomasii* (Ebenaceae), and

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Trema guineensis (Ulmaceae). In all four species enhanced phenolic levels in insolated leaves seemed to carry a significant contribution from increased condensed tannin (CT) synthesis; in the case of *D. thomasii* it also included increased production of hydrolyzable tannins (HT).

The ability of tannins to act as antifeedants has been widely considered to occur through their interaction with proteins (Zucker, 1983). The antifeedant activity could be due to astringency of tannins in the mouth (Bate-Smith, 1972; Lea and Arnold, 1978), but most authors assume that tannins exert their activity through inhibiting the action of proteases and other digestive enzymes in the gut and by generally insolubilizing proteins as precipitates (Rhoades, 1979; Mitaru et al., 1984; Sekiya et al., 1984; Beart et al., 1985). Thus it has been widely assumed that animals avoid feeding on tannin-containing plants to avoid inhibiting the processes of digestion.

Martin and Martin (1984) and Mole and Waterman (1985) have shown how tannin-protein precipitates may be solubilized by surfactants naturally present in the gut. While indicating potential adaptations for feeding on tannin-containing plants, this evidence does not show that tannins do not combine with proteins in vivo. Indeed, there is clear evidence that tannins do bind to proteins to form soluble complexes (Van Buren and Robinson, 1969), and so the process of digestion may still be subject to inhibition under conditions where precipitates do not form. Furthermore, evidence indicating that tannins and other phenolics can promote digestion in soluble systems (Neucere et al., 1978; Mole and Waterman, 1985; Oh and Hoff, 1986a) may now need to be reassesssed in light of evidence that tannins have the potential to disrupt sequential proteolytic systems involving inactive zymogen precursors (Oh and Hoff, 1986b).

Thus, none of the available evidence contradicts the notion that tannins will bind to proteins in vivo as they do in vitro, and there is evidence supporting complex formation in vivo (Mitaru et al., 1984). Analysis of feces shows a particular tendency for tannins to prevent digestion of proline-rich proteins ingested in the diet (Eggum and Christensen, 1975; Mole et al., unpublished results). It has recently been proposed (Butler et al., 1986) that mammals might counteract the effects of tannins by means of proline-rich proteins secreted in saliva, binding preferentially with them and so preventing interaction with other proteins.

Recent reviews (Bernays, 1981; Mole, 1986; Mole and Waterman, 1986) suggest that typical insect or mammalian herbivores tend to avoid consuming levels of tannin above an acceptable level for that species. This holds whether the herbivore has a high average intake (tannin specialist) or a low to zero average intake (nonspecialist). There are exceptions, but this generalization holds in the majority of cases.

Thus, despite evidence for counteradaptations (Martin and Martin, 1984; Mole and Waterman, 1985; Butler et al., 1986), the quantitative argument concerning the effects of tannins in vivo still holds true. An excessive intake of