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SECONDARY COMPOUNDS IN PLANTS: PRIMARY FUNCTIONS

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Whittaker and Feeny (1971) expressed the view that defensive chemicals in plants originated as chemical wastes or chemical accidents resulting from mutation, with subsequent selection for increased production favoring the better-protected individuals. Thus they reinforced a current view among many ecologists that the function of certain secondary chemicals in plants is to repel or inhibit herbivores, pathogens, or competitors. Whittaker (1970) states: "The evolution of these substances is probably not, in fact, comprehensible except in an ecological context, including organisms other than the plants producing them." Regarding alkaloids in legumes, Janzen (1969) observed that there is no evidence that they are of direct metabolic importance to the adult plant. Ehrlich and Raven (1967) said that certain chemicals apparently perform no physiological function for the plants themselves but do act as potent insecticides or insect repellents. Recent papers by McKey (1974) and Freeland and Janzen (1974) further explore the relationships of plants, their secondary compounds, and predators. Although we feel that the evidence for the defensive use of secondary chemicals in plants is impressive, we argue here that other selective advantages for these substances exist and should be considered.

There are now substantial data showing that secondary compounds in plants exist in a state of dynamic equilibrium and are not static end products of metabolism. When labeled precursors of these compounds are introduced into plant systems and incorporated into secondary plant metabolites, the label is rapidly lost. The biological half-life may vary from a few minutes to a few days, and the radioactive label is subsequently incorporated into other primary and secondary metabolites or is lost as carbon dioxide. Loomis and associates (Loomis 1967; Burbott and Loomis 1969; Croteau, Burbott, and Loomis 1972) have demonstrated that the half-life of labeled monoterpenes in peppermint plants is several hours, the exact time depending on experimental conditions. They also showed daily fluctuations of terpene concentration in peppermint plants. Marrubiin, a sesquiterpene from horehound (*Marrubium vulgare*), turns over with a half-life of about 24 h (Abbondanza, Badiello, and Breccia 1965; Breccia and Badiello 1967). The metabolism and function of alkaloids in plants has recently been reviewed (Robinson 1974), and turnover times are similar to those of terpenes. For example, tomatine in tomato fruits has a half-life of about

6 days but disappears completely as the fruits mature (Sander 1956). Nicotine in tobacco has a half-life of 22 h (Leete and Bell 1959). Ricinine in the castor bean has an initial half-life of 4 h, but this is later increased to 6.7 days (Waller and Lee 1969) and the compound disappears completely from senescent plants (Skurský, Burselson, and Waller 1969; Lee and Waller 1972). Daily variations in alkaloid content have also been observed (Fairbairn and Suwal 1962; Fairbairn and Wassel 1964, 1967). Several newer techniques and problems concerning the introduction of radioactively labeled precursors into plant materials have been recently reviewed (Scott 1974). By growing seedlings in aqueous solutions of appropriate precursors, it was discovered that optimum times exist for incorporation of label into either single compounds or, in some cases, groups of compounds. For example, in *Vinca rosea* seedlings, C¹⁴ label introduced into the indole alkaloid tabersonine was redistributed into other alkaloids. After 6 days the presence of labeled tabersonine could no longer be observed. In the same seedlings, however, the amount of label in akuammicine (approximately 8% of the total) and vinervine (14%) remained unchanged from 9 h to 6 days.

The dynamic state of these chemicals in plants and the rapid rate of turnover suggests that these so-called secondary metabolic products are intimately involved with primary metabolic functions in the plants. Since many chemicals are recycled, the metabolic cost to the plant may be less than that originally envisaged by ecologists; in some cases, on the other hand, the requirement to maintain a certain level of toxic material by continual synthesis may represent an increased cost to the plant. Although 12% of fixed carbon per day in a tobacco plant may be used in nicotine biosynthesis, almost 40% of the nicotine in a plant is degraded in a 10-h photoperiod (Robinson 1974). When C¹⁴ and N¹⁵ labeled nictotines were fed to tobacco plants, the label appeared in amino acids, sugars, and organic acids (Tso and Jeffrey 1959, 1961), all of primary importance to the plant. In any case, it appears that the adaptive roles of at least some plant constituents are independent of selection pressure from the plant's enemies.

Since consideration of primary roles for secondary compounds has not been prevalent in the literature, we can make here only a few tentative suggestions. Fairbairn and El-Masry (1967) expressed the view of many biochemists when they concluded, after observing the surprisingly rapid changes in the pattern of toxic chemicals and disappearance of large quantities over short periods of time, "that they . . . are intermediaries in other, possibly important, metabolic processes." Robinson (1974) also concluded that alkaloids are active metabolites. Certainly toxic chemicals may act as carbon or nitrogen stores, and in their absence metabolic activity may be locally limited. In seeds of Mexican buckeye (*Ungnadia speciosa*), cyanolipids are present in amounts up to 15% dry weight. Within 3 days of germination all cyanolipids are gone (Seigler, unpublished data), suggesting that these secondary chemicals have acted in a storage capacity for essential chemicals. The same role has been assumed for alkaloids as a nitrogen source in legume seeds (Bell and Tirimanna 1965; Janzen 1969). A similar role may be performed by dhurrin, a cyanogenic compound in several *Sorghum* species where young seedlings have relatively high concentrations

which decrease rapidly with age. As the plant matures, the level of dhurrin reaches a plateau or increases slightly but decreases rapidly after pollination occurs (Kingsbury 1964 and references therein). This suggests that dhurrin acts as a nitrogen store used during seed production. The terpenes in *Juniperus pinchotii* undergo seasonal variation with an increase of the more volatile α - and γ -terpinenes and terpinolene during the summer with a corresponding decrease in citronellal and camphor (Adams 1970). As another example, in the California chaparral shrub *Heteromeles arbutifolia*, the seasonal variation of tannins and cyanogenic glucosides is correlated (Dement and Mooney 1974). Young leaves have high levels of both tannins and cyanogenic glucosides. Immature fruits also have high levels of both, but as the fruit matures tannins decline and the glucosides are shifted from the pulp to the seeds. This suggests that both types of compounds are readily transported and/or catabolized within the plant.

Finally, secondary chemicals may act as important regulators of biochemical processes. We know of their high activity in vitro. For example, flavonoids, which were until recently considered by many workers to be inactive secondary metabolic products, actually have pronounced effects on the vital processes of respiration and photosynthesis (Stenlid 1963, 1968, 1970; Mumford, Smith, and Castle 1961). Kaempferol at only 3×10^{-5} M causes a 50% inhibition of cyclic or noncyclic photophosphorylation in isolated chloroplasts of peas (Arntzen, Falkenthal, and Bobick 1974). A similar effect on oxidative phosphorylation has been demonstrated in isolated corn mitochondria (Koepe and Miller 1974). Robinson (1974) lists several effects that alkaloids have on biochemical processes in plants, and the possibility remains that they perform these functions in the plants that manufacture them. Del Moral (1972) rejected the hypothesis that phenolic compounds in sunflowers (*Helianthus annuus*) were selected principally for defense in favor of their role as regulators of metabolic systems when under stress. Thus if Del Moral is correct, the allelochemic properties of phenolics in *H. annuus* are secondary.

In summary, we wish to emphasize that the adaptive functions of natural products may be multiple and may involve metabolic functions as well as plant defense.

SUMMARY

Many natural products supposed by ecologists to exist as secondary metabolic products for protection of plants exist in dynamic equilibrium, with rapid turnover rates, involving cycles that include primary products such as sugars and amino acids. Therefore, natural selection of secondary chemicals may be for their role in primary metabolic processes as well as in defense.

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