physiologically active compounds from higher plants and fungi which would have complimented ongoing work such as that described. This programme was to have involved the staff and interests of both the Royal Botanic Gardens and CAB International Mycological Institute. Both institutions will sadly miss his cheerful self, his ideas and his enthusiasm.

REFERENCES

1. Cooper-Driver, G. A. and Swain, T. (1976) *Nature* **260,** 604.
2. Fellows, L. E. (1987) *Chem. Brit.* **23,** 842.
3. Tyms, A. S., Berrie, E. M., Ryder, T. A., Nash, R. J., Hegarty, M. P., Taylor, D. L., Mobberley, M. A., Davis, J. M., Bell, E. A., Jefferies, D. J., Taylor-Robinson, D. and Fellows, L. E. (1987) *Lancet* 1025.
4. Nash, R. J., Fellows, L. E., Dring, J. V., Stirton, C. H., Carter, D., Hegarty, M. P. and Bell, E. A. (1988) *Phytochemistry* **27,** 1403.
5. Rothschild, M., Nash, R. J. and Bell, E. A. (1986) *Phytochemistry* **25,** 1853.

TANNINS—CHEMICAL ECOLOGY IN ACTION

(A tribute to the contributions of Professor Tony Swain)

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The name of Tony Swain is well known to all scientists, young or old, who have more than a passing interest in either the chemistry of tannins or in their potential to influence the feeding behaviour of herbivores. His contributions to these topics span four decades and many continue to be widely cited. In this tribute it is not my intention to list and discuss all of these but to highlight a few that illustrate the diversity of his interests. These will not include his review papers [i.e. 1–3] but will concentrate on his own original work.

For my first selections I go back to 1959, when Tony was working in Cambridge. In that year he published, in collaboration with W. E. Hillis, two papers on the phenolic constituents of *Prunus domestica.* These were not the first papers Tony had produced on phenolic compounds as he had previously worked closely with E. C. Bate-Smith. However, I feel that it is these papers that mark the real beginning of Tony's contribution to chemical ecology.

The first of these papers [4] dealt solely with methods of analysis of phenolic compounds. It included a whole battery of procedures (Folin–Denis, butanol/HCl or leucoanthocyanin reagent, vanillin reagent) through which the authors tried to assess the phenolic profile of their plant material. Despite the inherent problems involved with all of these assays due to critical operating conditions and non-stoichiometric reactions (which Tony recognised), the strategy adopted in this paper remained, until the 1980's, the 'norm' for most quantitative studies of tannins and other phenolics.

The second paper [5] was particularly revealing of Tony's attitude to his research. His initial remit had been to investigate why Victoria plums sometimes underwent deleterious changes due to excessive lignification of the stone and surrounding flesh. What was finally reported was a far more wide-ranging set of observations including (a) that extensive changes occurred in tannin concentrations and astringency during fruit ripening; (b) changes in tannin levels occurred during leaf development; (c) shaded leaves produced less tannins than sun leaves; (d) healthy leaves produced more tannins than unhealthy leaves. Now, thirty years on, the importance of observations (b–d) are beginning to attract great attention as we recognise that many extrinsic factors (biotic and abiotic) can influence the synthesis of phenolic compounds with consequences for a plant's resistance to pests and pathogens.

The next two papers I have selected mark Tony's collaboration with Judith Goldstein. In the first of these [6] he returned to the problem of changes in astringency during fruit ripening, studying not only the plum but also apple, pear, banana, grape and persimmon. Tannin measurements were based on the same colorimetric measures adopted previously [4] but now they were used not only singly but as ratios in an attempt to gather information on changing tannin structures. The conclusion reached, that decreasing astringency in ripening fruits is due to increasing polymerization, remains plausible although recent work suggests other mechanisms whereby astringency may be reduced during fruit ripening without this happening.

The second paper with Goldstein [7] is, in my view, one of the most significant Tony produced. It deals directly with the ability of tannins to interact with the protein β-glucosidase. The exciting thing about the results were that they showed clearly that the concept of an irreversibly bound tannin-protein complex was not tenable. 'Strong' complexes between tannins and this enzyme were readily disrupted by surfactants, PVP and variation in ionic strength of solutions. Unfortunately this work was never adequately followed up and its implications were either missed or ignored when, later, the role of tannins as non-reversible digestion inhibitors was being woven into the folk-lore of chemical ecology. It is only now, twenty years later, that the importance of high gut pH, natural surfactants (lecithins, bile acids), mucoproteins, variation in the specificity of tannin-protein interactions, and soluble tanning-protein complexes in modifying the activity of tannins are at last being thoroughly explored.

By the 1970's Tony's work on tannins had tended to move out of the laboratory into the field with a number of studies concerned with the feeding ecology of wild animals in relation to the biochemistry of their food plants. One of the first, and the best, of these was the study [8], carried out in Richmond Park, on the biochemistry of bracken in relation to its palatability to a ruminant mammal (deer) and a phytophagous insect (locust). The results implicated tannins and cyanogenesis as feeding deterrents, operating primarily at different periods of the growing season and with different effects on the two herbivores. This was a timely reminder of the dangers of considering individual products of secondary metabolism in isolation, something a herbivore cannot do!

At about the same time Tony published a short paper [9] on the impact of alkaloids and tannins on food selection by the black-and-white colobus monkey in the Kibale Forest in Uganda. I do not regard this as one of his best papers; in retrospect the tannin levels reported for all food and non-food plants (except one) were so low that there was little chance of them having any influence on feeding. However, this paper did point to the potential value of colobine monkeys in investigating the influence of leaf chemistry of food selection by mammalian herbivores in tropical rain forests as a counterpart to similar studies being carried out on large herbivores in tropical savanna and temperate/boreal ecosystems. On a personal level I have cause to be very grateful to Tony for his considerable generosity in subsequently leaving me to further develop studies on the biochemical basis of food selection by colobine monkeys and encouraging my efforts in this endeavour.

The final two papers I have selected further develop Tony's wide interests in the chemical ecology of herbivory. In his work with Buchsbaum and Valiela [10] he produced our most comprehensive set of data on large grazing birds through the study of Canada geese food selection in coastal salt marshes. Results suggested that phenolic compounds were a negative influence on food choice on wild animals and avoidance of both hydrolysable and condensed tannins was confirmed in feeding trials with captive geese.

Lastly, I would draw attention to a paper [11] published after Tony's death in which he and his co-workers report on an extensive study of the feeding ecology of the rhesus monkey in Pakistan. This is, I believe, the most comprehensive study to date on a non-colobine primate in a natural environment. The mainly terrestrial rhesus is shown to behave in the same way as other primates; selecting a diet low in tannins and high in nutrients. By contrast to most colobines the availability of nutrients does not appear to be a major constraint on food selection and as a consequence of this and because of its monogastric digestive system avoidance of tannins appears particularly well defined in this primate.

This has been a brief and personal view of Tony's contribution to the study of tannins and their ecological importance. It has covered the era in which tannins have progressed from being of interest primarily to the tanner and vintner to their present position centre-stage! Throughout this period Tony's papers have been essential reading to all who have ventured into the biochemistry of tannins and he is justly regarded as a pioneer in the quest to understand the physiological and ecological significance of these fascinating but frustrating molecules.

REFERENCES

1. Swain, T. (1977) *Ann. Rev. Plant Physiol.* **28,** 479.
2. Swain, T. (1978) *Biochemical Aspects of Plant and Animal Co-evolution* (Harborne, J. B., ed.), p. 3. Academic Press, London.
3. Swain, T. (1979) *Herbivores: their Interactions with Secondary Plant Metabolites* (Rosenthal, G. A. and Janzen, D. H., eds), p. 657. Academic Press, New York.
4. Swain, T. and Hillis, W. E. (1959) *J. Sci. Food Agric.* **10,** 63.
5. Hillis, W. E. and Swain, T. (1959) *J. Sci. Food Agric.* **10,** 135.
6. Goldstein, J. L. and Swain, T. (1963) *Phytochemistry* **2,** 371.
7. Goldstein, J. L. and Swain, T. (1965) *Phytochemistry* **4,** 185.
8. Cooper-Driver, G., Finch, S., Swain, T. and Bernays, E. A. (1977) *Biochem. Syst. Ecol.* **5,** 177.
9. Oates, J. F., Swain, T. and Zantovska, J. (1977) *Biochem. Syst. Ecol.* **5,** 317.
10. Buchsbaum, R., Valiela, I. and Swain, T. (1984) *Oecologia* **63,** 343.
11. Marks, D. L., Swain, T., Goldstein, S., Richard, A. and Leighton, M. (1988) *J. Chem. Ecol.* **14,** 213.