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CYANOGENESIS IN LOTUS

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It would be very misleading to write only about *Lotus* species and so part of this brief review will be of a general nature.

Many plants which are not normally regarded as being cyanogenic are capable of metabolizing labelled exogenous HCN and therefore it appears likely that HCN commonly occurs in plants and needs to be detoxified.

Why does HCN occur commonly in plants? The suggestion that its major role was in asparagine biosynthesis is no longer tenable because it is now known that a glutamine-dependent asparagine synthetase is probably concerned with the normal pathway. On the other hand, an even more fundamental role for endogenous HCN has emerged recently. The reduction of nitrate to nitrite is the limiting step in nitrate assimilation in plants and there is strong evidence for the *in vivo* regulation of nitrate reductase by cyanide in *Chlorella*. Furthermore, there is other evidence that HCN plays a part in nitrate reductase regulation in *Zea*, *Sorghum* and *Triticum* and so, at present at least, there are very good reasons why plants should have a readily available source of HCN and a means of detoxifying excess. Cyanogenic glycosides and lipids may well be the normal source of HCN; certainly there are good reasons for concluding that these substances are widely distributed in flowering and non-flowering plants, usually at concentrations below the normal level of detection.

The Character of Cyanogenesis

The evolution of what we call cyanogenic species is more readily explicable in terms of the over-production of existing substances rather than as the sporadic occurrence of new ones. In *Trifolium repens*, for example, the difference between cyanoglucosidic and acyanoglucosidic plants appears to be regulatory and not result from a structural gene mutation. The questions we must ask, therefore, are (1) why do some species produce an excess of cyanoglucoside over their requirements for primary metabolism and (2) why are some species polymorphic?

By studying the polymorphic species *T. repens* and *Lotus corniculatus* it may well be possible to answer both questions at the same time. Evidence from several sources suggests that damage to leaf tissue of cyanogenic plants is deleterious. This damage can result from grazing, freezing or from osmotic shock. There is, therefore, selection against cyanogenesis. On the other hand, we have direct evidence that cyanogenesis in L. corniculatus and T. repens does have a protective function against herbivores both in the laboratory and in natural habitats. In other species a defensive role has also been demonstrated, for example, the cyanogenic form of the bracken fern (Pteridium aquilinum (L.) Kuhn) in Richmond Park, Surrey, England is not grazed by deer or by sheep.

It is clear that the cyanoglucoside itself may be the deterrent to some herbivores whereas it is the HCN released when the plant is damaged which gives rise to the deterrent effect against other organisms. These results show that cyanogenesis must be regarded as a toxic and not a digestibility reducing system, and as qualitative or 'unapparent' in the sense suggested by Feeny.

Stability of the Phenotype

We are now satisfied that there are two types of cyanogenic L. corniculatus. One type has a stable phenotype whereas the other has the ability to change phenotype in response to environmental stress, particularly of temperature. There are different frequencies of stable and unstable plants in different populations. The genetics of this instability is being studied. (See also last years Lotus Newsletter - note by Borsos et al; Blaim in publications list).

Cyanogenesis in Natural Populations of Lotus corniculatus

Recently our approach has been to study habitats in which there are consistent differences (in time) in the frequency distribution of cyanogenic and acyanogenic plants over short distances (less than 1 km) and attempt to discover the selective agents responsible. This work has involved detailed recording of the climatic, biotic and edaphic factors in these habitats. As a result we are now convinced that selective grazing is the predominant agent determining the distribution of cyanogenic L. corniculatus on the south-west coast of Holy Island (off Anglesey, N. Wales). It is clear, however, that the situation is markedly different on the island of Birsay, Orkney Islands, where soil moisture stress is the principle factor associated with the distribution of the cyanogenic form.

On Holy Island we have discovered phenotype x habitat (area) interactions which are so large that no simple hypothesis explaining cyanogenesis is possible.

Conclusions

In general, there is good evidence that cyanogenesis acts as a protection against herbivores in some plants, but in those polymorphic species which have been studied it is equally clear that selective grazing of the cyanogenic form is not intense enough for the species to become monomorphic for cyanogenesis. Many other factors exert selection on cyanogenesis and so when studying the variation in natural populations interpretations must in general be confined to the plants and areas actually studied. Different plants in different habitats may respond to selection in entirely different ways and therefore contrary explanations of the role of cyanogenesis within species, let alone between species, are only to be expected.

To save space no references have been included in this brief review. Please see Jones, D.A., Keymer, R.J. and Ellis, W.M. 1978. Cyanogenesis in plants and animal feeding. In Biochemical Aspects of Plant and Animal Coevolution. Edited by J.B. Harborne. Academic Press, and the *Lotus* publication list in this issue of the Newsletter.