and Duckett (1980) that *Equisetum* sporophytes produce toxic chemicals which adversely affect the growth of *Equisetum* gametophytes.

Sporophyte extracts (1 g fresh sporophyte : 100 g distilled water) of *E. arvense, E. palustre* L. and *E. variegatum* Schl. ex Web. and Mohr all significantly reduced the germination of *Festuca rubra* ssp. *rubra* L. The relative potencies in reducing germination were: *E. arvense* = *E. palustre* > *E. variegatum*. This is in full agreement with the earlier work of Zelenchuk and Gelemei (1967).

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F. HYBRIDISATION, EVOLUTION AND TAXONOMY OF FERNS

Flavonoids as biochemical markers in fern taxonomy

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Many Cheilanthoid ferns (Polypodiaceae, Gymnogrammoideae) are characterised by a white or yellow layer of natural products (ceraceous indument) on their lower leaf surface. This farinose frond exudate consists mostly of flavonoid aglycones and sometimes also of diterpenses. They are excreted by and deposited on capitate cells of glandular trichomes.

Once the flavonoids forming the 'wax' of a given species have been analysed (bulk material required sometimes), further studies can be undertaken by comparative TLC. Minute frond fragments are sufficient to check specimens for constancy and significance of flavonoid patterns. Examples are given for the genus *Notholaena*.

Apart from some mostly quantitative infraspecific variability, the flavonoid profiles are constant and specific for species like *N. bryopoda, N. grayi, N. pallens* and others.

Some subspecific taxa also exhibit unique chemical profiles. ,For example, the two recognised varieties of *N. candida*, var. *candida* and var. *copelandii*, produce completely different flavonoids. In *N. californica*, two forms exist with either whitish or yellow farina. This is due to different exudate composition. Again, this reflects a remarkable difference in the biochemical capacity of both forms. It is suggested that they should be recognised as separate varieties. In *N. standleyi*, differences in geographic range, edaphic requirements, aspect, height and indument colour indicate that three distinct subgroups of this taxon exist. This is confirmed by statistical evaluation of their flavonoid patterns. These forms are regarded as chemical races (chemotypes).

The gametophyte in relation to colonising habit in Himalayan ferns: relevance to reproductive biology

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The Himalayas abound in a variety of ferns occupying diverse habitats from moist ravines and dripping rocks to sunny, open roadsides and forest margins extending from the foothills to nearly 3,500 m altitude. Fern sporophytes would be at the mercy of their gametophytes to the extent that they express any portion of the genome they convey. Furthermore, the regular sexual cycle might be expected to be restricted to the domain of specific habitats where sporophytic and gametophytic tolerances overlap. The homosporous ferns are unique in possessing potentially hermaphroditic gametophytes which allow the recurrence of intragametophytic selfing, generating thereby completely homozygous sporophytes. Studies on a large number of Himalayan ferns have revealed that the gametophyte generation offers a variety of adaptations, including particularly sequential emergence of gametangia and their duration, position of gametangia, populational characteristics of gametophytes derived from spores of a single sporophyte, and gametophyte–gametophyte interactions that either disproportionately favour or ensure intergametophytic mating.

The colonising and non-colonising species of ferns differ in their gametophyte characteristics. The data on the colonising species of Himalayan ferns are presented with particular reference to Lloyd's concept of predominance of intragametophytic selfing in colonising species of Hawaiian ferns (Holbrook-Walker and Lloyd 1973). There is seemingly a complex correlation between colonising habit, habitat, and ploidy level. The length of the gametophyte generation *per se* does not help in predicting the predominant mating system of a fern species. It is found that species with notably low gametophyte generation times, like *Polystichum* species, may possess gametophyte characteristics favouring intergametophytic mating. It is observed that populations of gametophytes contain a variable number of pure archegoniate prothalli, and the proportion of such prothalli amongst the total archegonia-bearing ones, constitutes a sensitive index to infer and compare the relative probabilities of intergametophytic mating between species, and between populations, genotypes and ecotypes within species.