Edaphic Factors and Flower Colour Distribution in the Anemoneae (Ranunculaceae)

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Abstract: Variation patterns of flower colour in some species of the Anemoneae can be correlated with edaphic variables. These examples are used in the argument that discriminative pollination through colour responsive pollen vectors is not the sole cause for non-randomness in intra-specific flower colour distributions. Some possible reasons for genetic linkage between genes controlling edaphic responses and genes controlling flower pigmentation are discussed.

Among the factors which help to maintain flower colours in natural populations, a single one, namely the response of animal pollinators to flower colour signals has been studied almost exclusively. Zoophily tends to promote monomorphism for the most catching colour and rare occurrences of polymorphism provide the student with information on variables that can affect pollinator choice. Among such variables are population structure (see e.g. Levin 1972) or climate (see e.g. Mogford 1974). In cases where pollinator discrimination as to flower colour is relaxed or altogether inoperative, a wider polymorphism may reveal itself. The causes underlying the non-randomness of polymorphic patterns in such cases are none too evident. Frias et al. (1975) studied such patterns in Eschscholtzia californica in Chile and assume that the contrasting flower colour alleles here are firmly lodged components in gene complexes adapted to dissimilar climatic and edaphic conditions.

So far unexplained affinities of different flower colour forms to specific soils have also been reported in the Anemoneae (Ranunculaceae). In Pulsatilla alpina (L.) Delarbree the form known as subsp. alpina with a purplish and white perianth is a widely distributed calcicole, while the yellow flowered more localized subsp. apiifolia (Scop.) Nyma

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is a calcifuge (DAMBOLDT & ZIMMERMANN 1974). In *Anemone coronaria* L. in Israel monomorphic scarlet flowered colonies are widely distributed on all soil types. Polymorphic populations, on the other hand, in which the majority of plants are purple and violet flowered and which also contain pink, white, and scarlet flowered individuals, are restricted to enclaves of unleached mineral rich terra rossa overlying dolomite or to cool heavy alluvial soils, all within the evergreen Mediterranean maquis belt (HOROVITZ et al. 1975). A third grouping, in which only white and pale pink flowered plants co-occur with scarlets, is restricted to leached terra rossas or basaltic soils in the sub-Mediterranean park forest belt. Polymorphic, many-coloured, as well as monomorphic scarlet flowered populations of *Anemone coronaria* L. and *A. pavonina* LAM. are also reported in Greece but here edaphic distributions have not been studied in detail. *Hepatica nobilis* SCHREB. var. *japonica* NAKAI of variable flower colours has a white flowered polyploid race: var. *pubescens* HIRO, which is restricted to calcareous soils in western Japan (HARA 1962).

The conspicuous flower coloration in all these cases is undoubtedly an aid in the attraction of a wide range of insects. In the examples given, flowers do not contain nectar and are foraged for pollen only. However, *Pulsatilla alpina* (DAMBOLDT & ZIMMERMANN 1974) and *Anemone coronaria* are characteristically protogynous and can therefore not be pollinated by the strictly pollen foraging insects that are renowned for their colour responses. The phenomenon of “deceit”, which is sometimes invoked to account for bee pollination in nectarless protogynous pollen flowers, has not been observed as a regular feature in *Anemone coronaria* in Israel. In this species the important pollen vectors are those insects which use the flowers for shelter and move indiscriminately from male-stage flowers, in which they become coated with pollen, to female stage flowers. In the area studied these include only a minority of bees, such as male individuals of an *Eucera* sp. in certain localities, and range otherwise from pollen eating beetles to predaceous anthocorid bugs. Though the latter are deemed insufficiently hairy for pollen transport and do not figure in the pollination literature (but see PORSCH 1958), they are ideally suited to the needs of the protogynous pollen flower and merit closer study. It has not been established in how far this compound fauna of shelter seeking insects exercises any colour discrimination based on e.g. camouflage (see COVICH 1974). For the present purpose it is assumed that there is little or no discrimination as to flower colour on the part of the pollinator. Moreover, in Middle Eastern *Anemone coronaria*, much of the pollen transport and pollination is effected by air currents.

Further surveys in the *Anemoneae* and collation of the available