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Isozyme variation within and between *Taraxacum* agamospecies in a single locality

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Three isozyme systems were analysed in 97 individuals of *Taraxacum* randomly sampled from 100 m^2 of mature sand dune on the north-east coast of England. Ten agamospecies were identified in the sample and another ten occurred nearby. There was no variation found in the sample for tyrosinase or acid phosphatase. For esterase each agamospecies was found to be different and variation was found within five agamospecies. For these variable agamospecies the mean percentage variability was 19 per cent. Variation was found in two out of three offspring families, where the mean percentage variability was 22 per cent. A high level of homozygosity was found among the offspring of mothers heterozygous for tyrosinase.

INTRODUCTION

Genetic variation can arise during the course of asexual reproduction in a variety of parthenogenetic animals (*e.g.*, Vepsalainen and Jarvinen, 1979). Many plant taxa are agamospermous and it is important to investigate the variation generated between siblings of agamospermous parents and to discover the extent of the variation within genetic lineages approximated by agamospecies. The genus *Taraxacum* (Dandelions) consists of some 2000 species, of which 90 per cent are agamospermous. Within the genus it has been suggested that the 22 members of the section *Hamata* have arisen from a single founder, as all share an unusual cytological marker which should be lost by sexuality (Mogie and Richards, 1983). It would seem that agamospermous *Taraxacum* can generate sufficient morphological variability for discrete lineages to be recognised as agamospecies.

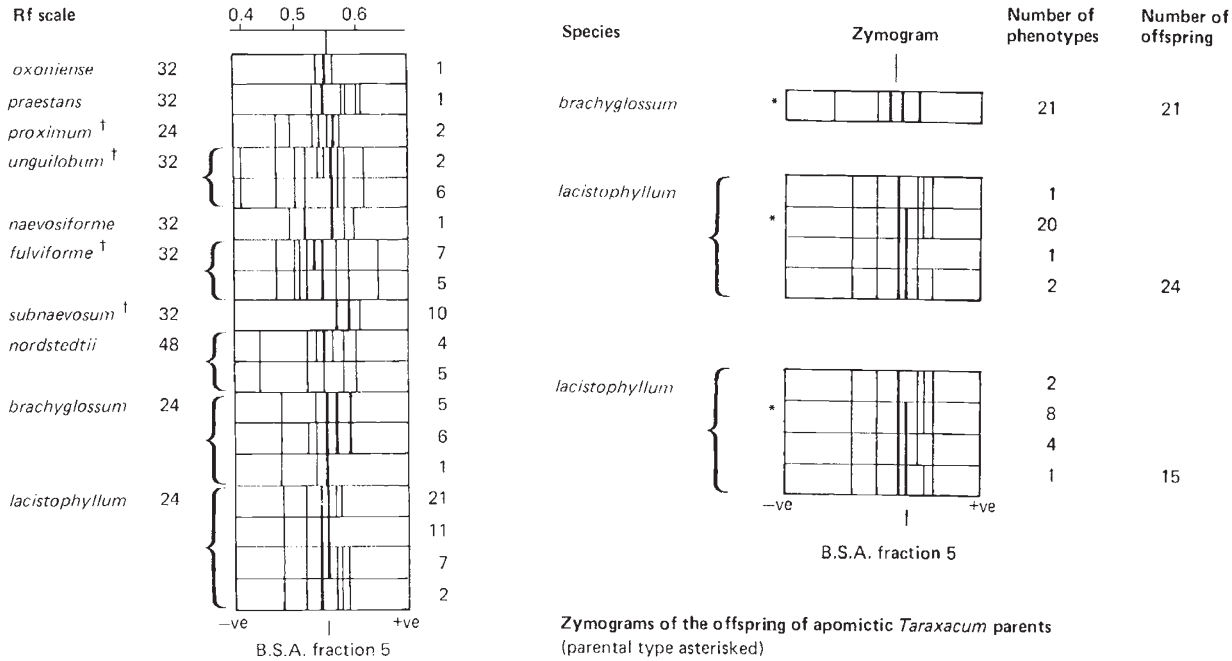
A study was undertaken of the variation of isozymes found within and between *Taraxacum* agamospecies occurring within a single locality and within the offspring of single parents. It was hoped to establish whether isozyme variation occurs within agamospecies, and whether and at what rate *de novo* variation originates within obligately agamospermous familes.

METHODS

100 m^2 of stable sand dune grassland was selected for sampling at Druridge Bay, Northumberland (GR 45/276 962) where demographic studies were in progress (Ford, 1985). One hundred plants, chosen as those nearest to the 1 m intersections of a grid were dug up, potted in John Innes: No. 3 Compost in 12 cm plastic pots and grown under glass in frost-free conditions. From each of two individuals of *Taraxacum lacistophyllum* (Dahlst.) R. and one of *T. brachyglossum* (Dahslt) Dahlst. 25 seedlings were grown to maturity at 10°C constant temperature, and 12 hour days.

Plants were identified to agamospecies level by AJR as they flowered. All plants were tested for agamospermy by "emasculation"; the distal three-quarters of a minimum of 5 capitulum buds/plant was excised about 3 days before anthesis, when the buds are about 1.5 cm in length. All plants were able to achieve more than 90 per cent seed-set after this treatment, which removes both anthers and styles; although emasculated buds sometimes aborted it was considered that all were obligate agamosperms. Four of the 10 agamospecies identified produce no pollen (fig. 1).

Electrophoretic studies were based on leaf extracts taken from fully developed, but not senes-



Taraxacum species, chromosome number, zymogram, number in population sample (total = 97)
†indicates those species in which pollen is absent

Zymograms of the offspring of apomictic *Taraxacum* parents (parental type asterisked)

Figure 1 Esterase zymograms for 97 parental individuals and 60 offspring from three parents of 10 *Taraxacum* agamospecies from a Northumberland sand-dune. Chromosome number, and presence or absence of pollen is given for each species, and the number of individuals represented by each zymogram is also given. Both parents of *T. lacistophyllum* had the same 7 banded zymogram, which is the commonest type in the offspring. The gels run to the right. BSA is the Bovine serum albumin standard run with each.

cent leaves during January to June (it is difficult to obtain useful results during the rest of the year for reasons that are not understood). For each system, each plant was tested at least 4 times, and many were tested 10 times over a two year period. No variation was detected within an individual. Electrophoretic techniques were based on Scandalios (1969), modified by Ford, and by Mogie (1982), as described by Hughes and Richards (1985). Three enzyme systems were investigated; esterase, acid phosphatase, and tyrosinase. It is not possible to demonstrate that visualised bands in these systems are heritable and allelic with respect to each other in an agamosperm, for test crosses cannot be made. Lyman and Ellstrand (1984) identify their loci, and infer inheritance by reference to Roose and Gottlieb (1976) who worked on the "related species" *Tragopogon* spp. We believe *Tragopogon* is too distantly related to *Taraxacum* for confident comparisons of electrophoretic bands to be made. Hughes and Richards (1985) study the inheritance of electrophoretic bands visualised in 12 enzyme systems for diploid sexual *Taraxaca* in section Taraxacum (Vulgaria). They show that tyrosinase and acid phosphatase each have a locus with single banded homozygotes and double banded heterozygotes. Esterase is complex with many loci, at least four of which have been analysed; EST-4 is monomorphic; EST-1 and EST-3 have an active allele and a null allele, and EST-2 has three alleles, one null, and the other two with very similar mobility to each other. In no case did individuals of different agamospecies share the same zymogram type.

Electrophoretic variation within an agamospecies was expressed as a percentage (the number of phenotypes divided by the number of individuals, times 100). Thus if 10 individuals had three electrophoretic phenotypes between them the variation would be expressed as 33 per cent. The agamospecies sampled were statistically

homogeneous for the frequency of electrophoretic variability ($\chi^2 = 3.94$, df = 5). Between 15 and 20 electrophoretic bands were identified for esterase within the total sample, although no single individual possessed more than 10 bands. Many more esterase loci occur in the total sample than the four identified by Hughes and Richards (loc. cit.) which were based on six bands. However the inheritance of the bands presented here cannot be studied as all the plants are agamospermous.

Three families of 25 siblings each were tested electrophoretically for all three systems. No variation was detected for acid phosphatase, for which all the individuals in the population and all the offspring showed the same monomorphic isozyme phenotype. However in tyrosinase considerable variation was observed (table 1). All 10 agamospecies and 97 individuals displayed the same isozyme phenotype, interpreted as a two banded heterozygote, T1, T2. Of the offspring in the *T. brachyglossum* family, 62 per cent showed non-parental single banded phenotypes, all except one of these having the same slow moving band. Of the two *T. lacistophyllum* families, 22 per cent and 62 per cent of the offspring showed non-parental single banded zymograms; in these, the differences between the numbers of the two presumptive homozygotes were not statistically separable.

A much lower rate of sibling variation was detected for esterase (fig. 1). The 21 seedlings from a parent of *T. brachyglossum* that were tested all had the parental phenotype. Parents of two families of *T. lacistophyllum* had the seven banded phenotype. In one family 20 out of 24 offspring had this phenotype, the remaining 4 having one of 3 non-parental phenotypes. In the other family, 8 out of 15 offspring had the parental phenotype, the remaining seven having one out of three non-parental phenotypes. Four non-parental phenotypes occurred in the total progeny of *T. lacistophyllum*. One of these variants was found in the parental population, but the two commonest parental types were absent from the offspring (which came from parents of a rare morph).

Table 1 Presumptive genotypes of offspring families from three parents for the tyrosinase locus, for which all parents were heterozygous T^1T^2

		brachy-glossum	lacisto-phyllum 1	lacisto-phyllum 2
offspring	T^1T^2	8	18	5
	T^1T^1	12	3	5
	T^2T^2	1	2	3
		21	23	13

CONCLUSIONS

First, the work provides evidence that *Taraxacum* agamospecies normally coexist, in contrast to the work of some theoreticians (see Janzen, 1977, and von Hofsten, 1954). Within the study locality different agamospecies varied from each other in their esterase zymograms, but not in their acid phosphatase or their tyrosinase zymograms.

Secondly, five agamospecies showed intraspecific variation for esterase, although one agamospecies showed no variation amongst ten individuals. Two interpretations are possible, though these are not mutually exclusive: (1) that the agamospecies are polyphyletic; (2) that lineages represented by agamospecies are capable of generating some enzyme variation between generations.

The within family variation for esterase occurred between siblings in two out of three families at an average rate of 45 per cent overall. All three parents were obligate agamosperms and it is suggested that some variation can occur between parents and offspring in these agamospermous clones.

REFERENCES

FORD, H. 1985. Life History strategies in two coexisting agamospecies of dandelion. *Biol. J. Linn. Soc, 25*, 169-186.

VON HOFSTEN, C. G. 1954. *Studies on the genus Taraxacum (Wigg.) with special reference to the group Vulgaria De., in Scandinavia. L.T.S. Forlag*, Stockholm.

HUGHES, J. AND RICHARDS, A. J. 1985. Isozyme inheritance in diploid *Taraxacum* hybrids. *Heredity, 54*, 245-249.

JANZEN, D. H. 1977. What are Dandelions and aphids? *Amer. Nat., 113*, 156-157.

LYMAN, J. C. AND ELLSTRAND, N. C. 1984. Clonal diversity in *Taraxacum officinale* (compositae), an apomict. *Heredity, 53*, 1-10.

MOGIE, M. 1982. The status of *Taraxacum* agamospecies. Ph.D. Thesis, the University of Newcastle upon Tyne.

MOGIE, M. AND RICHARDS, A. J. 1983. Satellited chromosomes, systematics and phylogeny in Taraxacum (Asteraceae). *Pl. Syst. Evol., 141*, 219-229.

RICHARDS, A. J. 1972. *The Taraxacum flora of the British Isles. Watsonia, 9*, (suppl.), 1-141.

ROOSE, M. L. AND GOOTLEIB, L. D. 1976. Genetic and biochemical consequences of polyploidy in *Tragopogon. Evolution*, 30, 818-830.

SCANDALIOS, J. G. 1969. Genetic control of multiple molecular forms of emzymes in plants: a review. *Biochem. Genet., 3*, 37-79.

VEPSALAINEN, K. AND JARVINEN, O. 1979. Apomictic parthenogenesis and the pattern of the environment. *Amer. Zoo., 19*, 739-751.