

**REPRODUCTIVE STRATEGIES AND POPULATION STRUCTURE
IN THE ENDANGERED PTERIDOPHYTE *TRICHOMANES
SPECIOSUM* (HYMENOPHYLLACEAE: PTERIDOPHYTA)**

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Keywords: Glacial refugia, gametophyte, historical biogeography, dispersal, filmy-fern.

ABSTRACT

Trichomanes speciosum Willd. (Hymenophyllaceae) is unique amongst European ferns in that the gametophyte generation can survive indefinitely in the absence of the sporophyte, propagate vegetatively and disperse locally. Reproductive success, both in terms of spore production and sporophytic recruitment currently vary widely across the species' broad, disjunct range, declining from south to north and west to east. Reproductive success would appear to be controlled largely by climatic factors, although genetic components also must be considered. Detailed study of populations throughout the species' range, over a 15 year period, have led to a greater understanding of growth rates, powers of dispersal and the reproductive strategies currently operating. Using this knowledge, the extent and pattern of genetic variation regionally and locally, i.e. within sites, can be used to infer the routes and mechanisms of colonisation and subsequent reproductive history.

Many sites for this species have been considered as glacial refugia, i.e., supporting relictual populations through cycles of glaciation throughout the Tertiary. The validity of these claims is tested using molecular and other data.

INTRODUCTION

Trichomanes speciosum Willd. (syn. *Vandenboschia speciosa* (Willd.) Kunkel), the Killarney Fern, is the sole native European representative of the genus *Trichomanes sensu lato* (Tutin *et al.*, 1993) and the largest of the region's filmy-ferns (Hymenophyllaceae). It has been considered one of the continent's most vulnerable plant species, threatened both by habitat destruction and long the victim of over-collection, and has been accorded legal protection throughout its range under the Bern Convention (Anon, 1979) and E.C. Habitats Directive (Anon, 1992).

Trichomanes speciosum is unique amongst European ferns in that its gametophytic generation is perennial, gemmiferous and capable of persisting and dispersing in the absence of a sporophyte. This 'gametophytic independence' is apparently a very rare condition amongst homosporous ferns, and known in three families, all widespread as epiphytes in tropical regions: the Vittariaceae, the Grammitidaceae, and the Hymenophyllaceae. However, gametophytic independence is apparently only well developed in those rare species found at the temperate extremes of these families'

ranges (Rumsey & Sheffield, 1996).

Independent gametophytes of a *Trichomanes* species were first tentatively identified from eastern North America by Wagner & Evers (1963) and confirmed by Farrar (1967, 1985, 1992) who identified a distinct taxon, *T. intricatum* Farrar (Farrar, 1992) represented solely by gametophyte populations. This taxon was found to exist far to the north of the line of the last glacial maximum, indicating it clearly had the ability to disperse over some distance, even if sporophytes and hence spores were currently not produced. The other widespread North American species of *Trichomanes* have been found as gametophyte populations but always in close proximity to sites in which sporophytes are present (Farrar, 1993). The situation in Europe falls between these extremes and differs in scale, in that both generations of *T. speciosum* are known, but the gametophyte has an extensive range (hundreds of kilometres) beyond that of the sporophyte.

Reproductive Potential and Strategies

The sporophyte of *T. speciosum* has a long-running, branching rhizome, at intervals bearing fronds which are functional for 4 or more years, and may persist for longer. Rhizome growth rates are heavily dependant on the plant's nutrient status and climatic environment but main axes may elongate by over 30 cm per annum, although usually by much less. Suppressed side branches borne in the sporophyll axils allow for steady patch formation should the leader not find suitable habitat and die. This growth form allows a guerrilla-type growth strategy similar to that employed by species of *Lycopodium* to exploit patchy environments (Callaghan *et al.*, 1986). Specialised mechanisms of vegetative propagation are absent (viviparous plantlets have been recorded twice in cultivated material over two centuries of observation (Druery, 1910; Ensoll, pers comm.)). Rhizome fragmentation, dislodgement and re-growth are likely to be infrequent but significant events. Extensive, intricate and usually dense patches form with time. Within these it is generally impossible to determine the number of individuals present without recourse to molecular techniques. Individual clones covering several hundred square metres have been recorded by the authors in the Azores, obviously indicative of considerable antiquity. However, colony size is not necessarily an accurate indication of age. Several British colonies known for over a century are very restricted in size, their maximal extent presumably determined by the extent of the micro-features that they grow in.

Unlike many European ferns *Trichomanes speciosum* is not fertile annually once mature. Indeed Ratcliffe *et al.*, (1993) reported that the majority of British sporophytes had never been seen to be fertile. Detailed investigation of fertility is difficult and in many cases not desirable because of the nature of the sites occupied. However, during the last decade four Welsh and two English sporophytes known to the authors have at least attempted to produce spores. Involucrets have formed but the receptacular bristle upon which the sporangia are spirally borne has, in at least two of the sites, not extended and no spores have formed as a consequence. This receptacular bristle structure has a basal meristem and presumably continues to elongate and produce new sporangia until a certain trigger, perhaps desiccation causing sporangial dehiscence, causes it to cease. Its failure to develop in marginal British sites may have climatic cause, such as exposure to cold. This and the factors determining the onset of fertility are almost certainly complex and have not been established for *T. speciosum*. Anecdotal evidence would seem to suggest that sporophytes in extreme shade are less regularly fertile and,

as most plants at the more northern and marginal extremes of the species range are progressively restricted to more sheltered and hence usually darker microsites, this alone may account for the reduction in northern fertility. Considerable variation exists in the degree of fertility, i.e. the number of involucre produced – dictated by frond stature and dissection, and the number of sporangia produced per involucre, as outlined above. Sporophytes in northern and more easterly British sites are invariably small and relatively poorly dissected, reducing sporing potential. Calculations based on observation of the number of fertile fronds known in all British populations for one year, an estimated mean number of involucre per frond and numbers of sporangia per involucre, suggested that the total British spore production per decade would be considerably less than that produced by a single healthy adult *Athyrium filix-femina* in one year (Rumsey, 1994) ! The species is thus likely to be a poor coloniser by spore or vegetative means.

Sporophyte recruitment parallels the pattern of spore production in that there is a marked reduction in the production of sporophytes northwards, i.e. into northern France and the British Isles and even more markedly, eastwards into continental Europe. Thus within the wetter portions of Macaronesia the species functions as a “normal” pteridophyte, completing its life cycle from spore to spore, whereas elsewhere the cycle progressively breaks down, until over much of the species extensive distribution in northern and continental Europe the gametophyte is effectively functionally independent. Immature sporophytes have rarely been noted within the British Isles and show high levels of mortality (Rumsey, 1994), although recent years have perhaps shown an increased incidence in their production (“Sentinel”, 2003; Rumsey, unpubl.) which may be a reflection of the run of warm but wet summers and milder winters experienced in the British Isles. Immature sporophytes have also been reported in central Europe, eg. Rasbach *et al.*, 1994 which indicates that gametangial production and normal function are occurring in at least some “independent” gametophytic clones. Given a potentially indefinite gametophytic lifespan the probability must be that sporophytes would form, although perhaps extremely infrequently, in the vast majority of populations.

Sporophytic production and recruitment almost certainly is predominantly a reflection of the rate and extent of gametangial production. The archegoniophore is a comparatively massive, differentiated, multicellular structure unlike the simple irregular branching filamentous structure it is borne on. The processes triggering its initiation are unknown but rates of cell growth and light/nutrient availability might be implicated. The smaller antheridia are more regularly produced and may persist in a non-dehisced state for many months. Rumsey & Sheffield (1996) summarised knowledge on the *in situ* and *ex situ* production of gametangia by different British gametophyte clones over a 5 year period. They identified consistent sterility, or super-fertility, of some clones, even when sub-divided and grown apart under similar but not rigorously controlled growth conditions, suggesting a significant genetic component to gametangial production, but with no clear geographical, ecological or discernible historical basis. Locally this may complicate considerations of the effect of climatic and other external factors on gametangial production but broad regional differences, which are reflected in sporophyte recruitment, are still apparent.

Understanding the Current Distribution- Refugia or Recent Colonisation?

First detected as recently as 1989 (Rumsey *et al.*, 1990; 1991), subsequent survey has

revealed the gametophyte to be widespread but extremely localised within the British Isles, significantly occurring in many areas from which the sporophyte had never been reported (Rumsey *et al.*, 1998). Similarly, as the distinctive habit and habitat of the gametophyte became known, discoveries across northern continental Europe rapidly followed, e.g. Vogel *et al.*, 1993; Rasbach *et al.*, 1994; Bennert *et al.*, 1994; Bujnoch & Kottke, 1994; Kirsch & Bennert, 1996; Horn & Elsner, 1997; Huck, 1997; Reichling, 1997; Boudrie, 2001; Krippel, 2001, Loriot *et al.*, 2002, Kottke, 2003, etc.

Initial reports were from deeply dissected sandstone massifs, such as the Petite Suisse of Luxembourg, the northern Vosges and the Elbsandsteingebirge, all areas noted for the occurrence of other rare, disjunct 'Atlantic' taxa (*sensu* Ratcliffe, 1968) but particularly the filmy-fern *Hymenophyllum tunbrigense* (L.) Sm. (Richards & Evans, 1972). In these disjunct areas *H. tunbrigense* has been considered to be a Tertiary relict (Drude, 1902; Klein, 1926). Subsequent examination has revealed the gametophyte of *Trichomanes speciosum* to be more widely distributed and in less "exceptional" landforms and habitats in intervening regions in western and Central Europe, such that the recorded distribution of the species is now much less discontinuous and more extensive than previously realised. This raises interesting questions as to when this broader gametophyte distribution was achieved and from where?

The broad continental and northern-European distribution of *Trichomanes speciosum* may have been achieved as a result of a wave of post-glacial migration from southern and western refugia, or conversely from limited diffusion from a range of more northerly peri-glacial refugia, or indeed result from an amalgam of both. Sites containing gametophytes alone may thus represent recent arrivals, or the tenacious survivors of a species uniquely suited to coping with a sub-optimal climate. Sadly, few relevant sub-fossil or palynological finds are known, or are realistically to be expected. Comparison with the distribution of other taxa can be informative, but elucidation of the species quaternary history is largely reliant on molecular studies of the pattern, extent and structure of genetic variation throughout the species range. Knowledge of the comparative reproductive and dispersive capabilities of the different generations can then be used to infer whether sporophytes were likely to be present historically in areas from which they are now unknown.

Generally our expectation must be that sites which have been suitable for the peri-glacial survival of a particular species are likely to have allowed the survival of a suite of taxa, and that this community, or many of its distinctive components may well recur in other disjunct refugial sites. The peculiar biology of *Trichomanes speciosum* and its ability to grow in conditions that are not conducive to the survival of all other vascular plants may, however, mean that it is a special case.

We also expect refugial sites to support greater genetic diversity than those which have been recently colonised. A potential confounding factor is that of severe bottlenecking – low or no diversity may result from loss over time/genetic drift, as well as by founder effects. We must also consider that an efficiently vegetatively-reproducing organism of narrow ecological amplitude might effectively block niches and thus prevent the arrival of other individuals ("the first in wins"). Variation may then be reliant on the rates of mutation in the various ramets, although these would be expected to accrue with time, meeting our original expectation. Ancient refugial sites, if isolated, might be expected to show private variation, i.e. unique to them, although post-glacial dispersion, if efficient, will obscure such patterns.

Refugia or Not?

Several disjunct areas are now known to support very small populations of *Trichomanes speciosum*, many of which have been discovered comparatively recently. Within these the relative proportion of sporophytes vs. gametophytes differs but many show comparably low levels of sporophytic presence and association of a suite of Atlantic species. Do they and their associated species show similar levels and patterns of genetic diversity and what can this reveal as to their history?

Southern Spain

Trichomanes speciosum was first discovered in Southern Spain by Richards (1934) and is now known from a very limited range of sierras leading inland from the coast near Algeciras, northwards to near Cortes de la Frontera (Rumsey & Vogel, 1998; Garrido Díaz & Hidalgo Maqueda, 1998). Currently nine populations are known to be extant, more than half (5) of which are thought to support fewer than 10 discrete sporophyte clumps each. Only one site (Sierra de Montecoche) currently contains gametophytes in the absence of sporophytes. The species main concentration is in the Sierra de Ojén and its westward continuation, the Sierra de Saladavieja. Here a total of approaching 200 distinct mature regularly fertile sporophytic clumps, closely associated with small localised areas of gametophyte and numerous juvenile sporophytes, occur in 12 distinct sub-populations by parallel small watercourses. High levels of mortality, with extreme reductions, at least in sporophyte populations, linked with the cycles of cork-oak harvesting and climatic variation, have been documented in the recent past (Molesworth-Allen, 1977).

Allozymic study of material from 3 sites: Sierra de Ojén (4 sub-populations), the Valle del Río de la Miel and the Sierra de Montecoche, indicates that each site had alleles not shared with the other sites (Table 1) and that the large Sierra de Ojén site contained at least 16 different multilocus phenotypes (MLPs), 10 of which were present in the largest sampled sub-population. The observed differences between closely adjacent watercourses may indicate low levels of gene-flow even over such restricted ranges but patterns indicate the likelihood of intergametophytic mating within these sub-populations, with the fern fully completing its life cycle and behaving in a “normal” pteridophytic fashion, unlike populations further north in its range.

These small populations co-exist with a limited range of Macaronesian bryophytes unknown elsewhere in Mainland Europe (Rumsey & Vogel, 1999) as well as other pteridophyte taxa, including *Calcita macrocarpa*, *Diplazium caudatum*, *Pteris incompleta* and previously *Dryopteris guanchica* – the latter suggesting a closest affinity with the Canarian flora. This floristic enclave, with fragmentary representation on the adjacent North African coast and into the Rif mountains, either represents the vestige of a once wider coastal African/Canarian/Iberian distribution fragmented by aridification and the increase of the Saharan desert area, or, and less likely, represents independent post-glacial (re-)colonisation by the many and varied Macaronesian floral elements. All potentially are highly dispersible given the small size of their diaspores.

Alpi Apuane, Italy

Trichomanes speciosum was found, new to the Italian flora, only as recently as 1976 (Ferrarini, 1977). Subsequently a total of five “populations” have been detected growing within the stream gorge of the Valle de Serra and its side valleys, close to the town of Serravezza (Marchetti, in Ferrarini *et al.*, 1986). Few discrete individual mature

Table 1. Distribution of multilocus phenotypes (MLPs) in southern Spanish *Trichomanes speciosum* populations (figures represent the number of apparently discrete individuals possessing that MLP).

Allozyme Phenotype				Site					
PGM	IDH	6-PGD	MDH	Miel	Ojén 1	Ojén 2	Ojén 3	Ojén 4	Monte-coche
A	A	A	A						2
A	A	A	B		5	9			
A	A	A	D		3			1	
A	A	A	E		3	1		2	
A	A	B	B		2	2	3	4	
A	A	B	D					4	
A	A	B	E			4			
A	A	B	F					1	
A	A	D	B					1	
A	B	A	E		4				
A	B	B	-					1	
B	A	A	B		26	1			
B	A	B	E		1				
B	A	B	F		1				
B	B	C	E		1				
B	C	A	A	1					

sporophytes are known but at least one is extensive and regularly highly fertile. The known sporophytes share a distinctive and apparently unique morphology.

Initial researches indicate a wider distribution of the gametophyte (Rumsey & Vogel, unpubl.), perhaps paralleling that of another disjunct Atlantic element, the filmy-fern *Hymenophyllum tunbrigense*, for which ca. 70 sites are known in the communes of Massa, Montignoso, Stazzema, Pietrasanta, as well as Serravezza (Pichi-Sermolli, 1936; Marchetti, 1992). Sporophytic recruitment has been observed in sites containing mature sporophytes but not in sites currently only known to support gametophyte populations.

Unfortunately only a limited range of material has been available for analysis. Both localities from which multiple samples have been taken support more than one MLP (3 & 5) with patterns consistent with the occurrence of intergametophytic mating.

Sporophytes are currently unknown in the most genetically diverse of these sites. One allele in the enzyme PGM has not to date been recovered in any other *Trichomanes speciosum* population throughout its global range.

All the evidence would thus tend to argue that this area must be considered refugial.

Southwest Scotland

In contrast to the Iberian and Italian sites this area was heavily glaciated and the species occurrence here must result from post-glacial (re-) colonization. It is thus instructive to compare the patterns of distribution and extent of genetic variation with the almost certainly refugial areas above and more equivocal areas.

Fewer than 20 discrete sporophyte plants have been detected in Scotland since its first discovery in 1863 (Babington, 1863) and less than half this number are known to be extant. Only one of these colonies has ever been seen to produce spores and most are, or were, very limited in size and extent. However, the gametophyte generation is widespread and may be locally abundant. Recent recruitment of sporophytes has been seen to occur both in sites containing mature sporophytes and also in at least one site where these were absent.

Genetic diversity of the species at this the northern-most limit of its distribution was studied by Rumsey *et al.*, (1999). 121 samples from 37 populations in 22 sites were examined and 7 allozyme MLPs were detected. Two of these MLPs covered large areas (>30 km in total extent), while the others were restricted to one, or rarely few, localities. No site was found to contain more than one MLP. Whether this is evidence for blocking of available niches by the first arrival, or merely a reflection of the extreme rarity of propagules of other MLPs arriving in occupied sites is unclear and may require experimental verification through deliberate introduction. The extent of MLPs was not correlated with presence /absence of sporophytes. Where they extend over many kilometres, in some cases on separate islands, the only credible means of dispersal is by spore. Where sporophytes are currently unknown such a distribution indicates their past presence, and a greater fertility than in the recorded past. Sporophytes may have occurred as long ago as in the sub-atlantic period, or during brief warm/wet phases subsequently – such as we appear to be experiencing currently. Very broad distributions must indicate considerable age given the poor dispersal powers shown by both generations of this organism. It is tempting to speculate that geographical extent could be correlated with arrival time but many conflicting factors have also to be considered.

Communities in glaciated and un-glaciated areas share many rare and disjunct taxa and their presence alone is un-informative as to refugial status, but the population structure and genetic make-up of these taxa is much more revealing. Many of the Macaronesian bryophytic taxa show disjunctions to southwest Scotland, but the majority of these diocious species are represented by one sex alone in the British Isles, yet exist in mixed sex populations and fruit in southern (refugial?) areas. Such a pattern might be expected given extremely rare long-range post-glacial dispersal events to the north.

Central Europe

Rumsey *et al.*, (1998) examined allozymic diversity in 35 sites from the then easternmost known extent of the species distribution in the Elbsandsteingebirge on the Czech- German border, through Germany to the French border in the northern Vosges mountains. The extensive distribution of some MLPs, as in Scotland, indicated that

sporophytes almost certainly must have been present in the past. The majority of sites supported single MLPs ; however some sites in the pfälzerwald supported multiple MLPs, some of which are indicative of past inter-gametophytic mating and thus by inference sporophyte production. From the allozyme data alone Rumsey *et al.*, (1998) suggested that post-glacial spread was more likely but were unable to exclude the possibility that some at least of these locations may have acted as refugia for the species. The levels of intra-population variation, even though low, and the presence of unique simple banding patterns for two enzyme systems (ACON, 6-PGD), gave support to this notion but the proximity of glacial forelands to many of the current localities suggested survival was less likely (Vogel *et al.*, 1993). Subsequent work by Rumsey *et al.* (in prep.), sequencing of the chloroplast DNA haplotypes first reported by Rumsey *et al.* (1996) has provided additional evidence which would appear to strengthen the case for, at least limited, peri-glacial survival. Macaronesian island refugia show a major dichotomy between the Azores in the north, and Madeira and the Canaries to the south. Minor haplotype variants link some Canarian populations with those from southern Iberia, supporting the broad floristic links already known. Investigated areas of Europe on the western Atlantic seaboard from Brittany northwards show a mix of the haplotypic variants found in the southern refugial sites, although not an intimate one (i.e. sites contain single haplotypes in all cases). The overall picture created is in contrast with the usual pattern of Northern Purity – Southern Richness reported by Hewitt (1999) and others. Interestingly, central Europe is uniformly of the Azorean, believed to be ancestral, type, in spite of the fact that all of the nearest spore sources (Spain, Italy) are of the contrasting major haplotype. If the distribution were the result of post-glacial immigration one might expect a similar pattern to that shown in northwest Europe, with all of the refugia and particularly the most proximal to be involved. Unique minor variants also exist within central Europe, for example in Luxembourg, where they cover an extensive area indicative of a long period of occupation and/or past sporophyte presence. Extremely severe conditions in proximity to sites and the growth and reproductive strategies of *Trichomanes speciosum* may explain the lack of expected diversity in these putatively refugial areas.

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