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Haploid sporophytes in *Athyrium filix-femina* (L.) Roth and evidence for somatic diploidization in one of them

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Abstract

Schneller J.J. 1982. Haploid sporophytes in *Athyrium filix-femina* (L.) Roth and evidence for somatic diploidization in one of them. *Botanica Helvetica* 93: 85-90. In off-spring of diploid *Athyrium filix-femina* ($2n = 80$) from natural locations three apogamously produced sporophytes were investigated. These plants were haploid with $x = 40$ chromosomes and were much smaller than diploids. None of the haploids developed any reproductive organs. In one plant, parts of some leaves were remarkably larger. The stomatal guard cells in these parts were nearly the same size as those in diploid *A. filix-femina*, whereas in the other parts of the leaf the guard cells were smaller, i.e. the same size as in the other haploids.

Introduction

Apogamy is not uncommon in sexual ferns. It was observed in various genera such as *Asplenium*, *Cystopteris*, *Doodia*, *Dryopteris*, *Phyllitis* (see Döpp 1967, Vida 1974) and *Ceratopteris* (Hickok 1979). Only in *Phyllitis scolopendrium* (L.) Newm. (Manton 1950) and *Ceratopteris richardii* Brongn. apogamy occurs at the haploid level ($x = 36$, $x = 39$ resp.) as far as could be seen. In this report haploid sporophytes of *Athyrium filix-femina* are described for the first time. In one of these haploids partial somatic polyploidization obviously occurred. This phenomenon is described and discussed together with apogamy.

Materials and Methods

Spores were collected from a cytologically examined diploid plant growing in nature (Nr. A-3, Horgenerberg, Kt. Zürich, Switzerland) and from a diploid plant now cultivated in my garden in Küsnacht (Nr. A-66, Küsnachterberg, Kt. Zürich).

In connection with breeding experiments started in 1974 a few dwarf sporophytes resulted. Two of them (A-3 h8, A-3 h9) remained very small but survived under nearly natural conditions

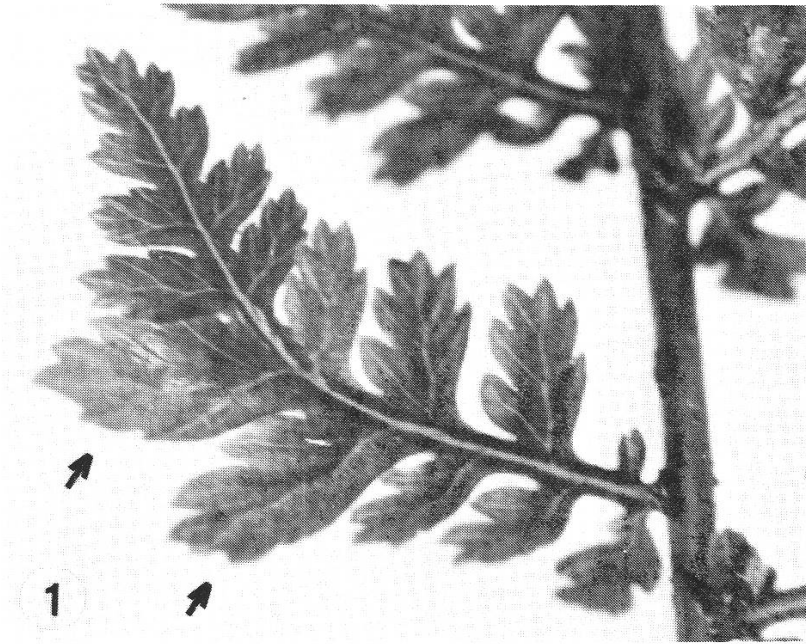


Fig.1. Pinna of haploid sporophyte Nr. A-3 h9 with «diploidized» pinnules (arrows).

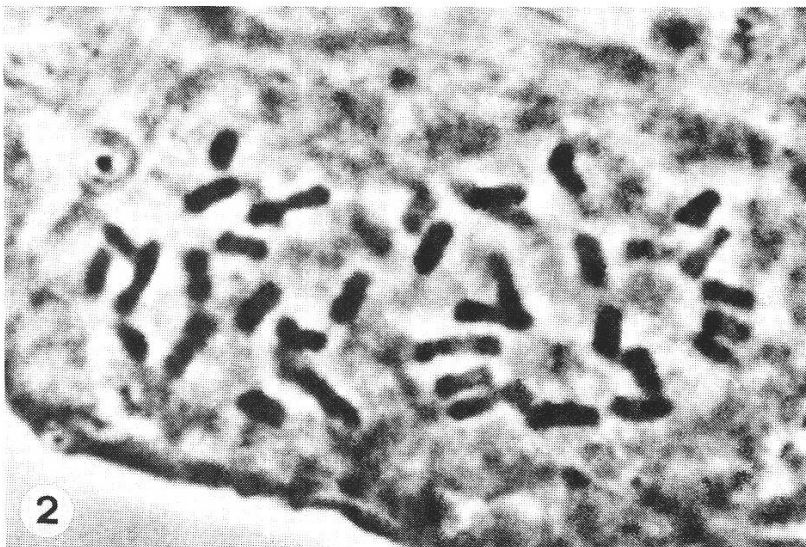


Fig. 2. Mitotic metaphase in a root tip of haploid sporophyte Nr. A-3 h9.

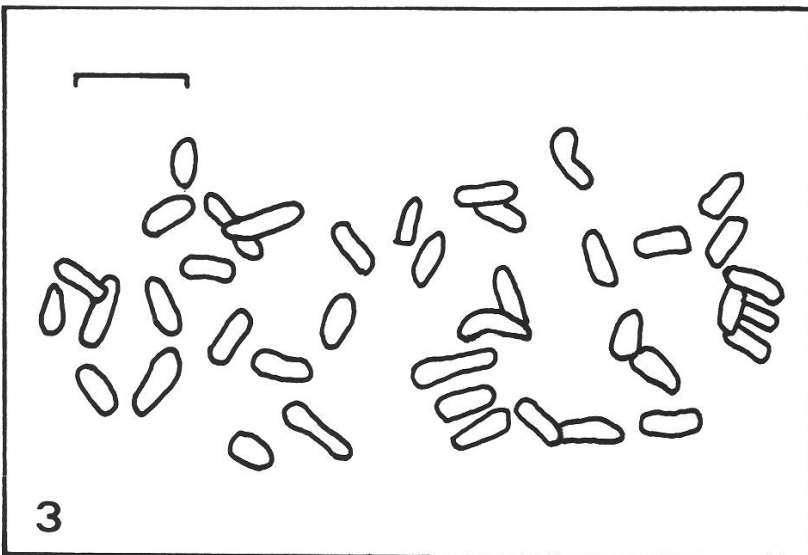


Fig. 3 Explanatory diagram of Fig. 2 showing 40 chromosomes. Scale 5 μ m.

in the Botanical Garden of the University of Zürich and are still alive (Oct. 1982). In 1981 and 1982 the chromosome number of these two dwarfs could be established.

In another breeding experiment started in 1978 a gametophyte strain (66 v) originating from plant Nr. A-66 was observed to develop a sporophyte apogamously.

For chromosome counts root tips of the sporophytes were used. The roots were pretreated with 0.1% aqueous solution of colchicine for 4 hours then fixed in pure ethanol: glacial acetic acid, 3:1, and hydrolyzed in 1 N HCl at 60°C for 15 min. The tips were stained with acetocarmine and squashed.

The epidermis was taken from living plants and observed in the fresh state. For comparison the epidermis of two known diploid plants (Nr. A-1, Nr. A-2, Horgenerberg) was studied. For the drawings of epidermal cells a Leitz microscope with drawing attachment was used. The photomicrographs were taken with a Zeiss photomicroscope.

Results

The cytological examination showed that the three different dwarf sporophytes (A-3 h8, A-3 h9, 66 v) were haploid with $x = 40$ chromosomes in the root tips (Fig. 2,3; Tab. 1).

Since it is well known that in many plants the size of stomatal cells (especially the guard cells) is correlated with the ploidy level, guard cells of the three haploids and of two diploids were measured and compared. A highly significant difference was observed (Tab. 1; Fig. 4 a, c).

A few leaves of the plant A-3 h9 showed pinnae with remarkably larger pinnules (Fig. 1). The guard cells in these parts are nearly the same size as guard cells in diploid plants (Tab. 1; Fig. 4b, c).

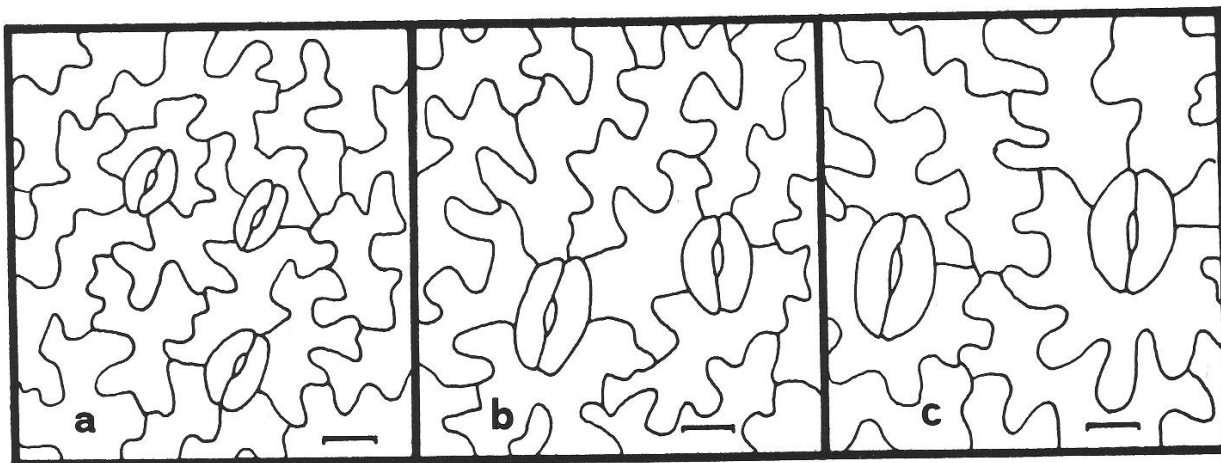


Fig. 4. Detail of lower epidermis of different plants. Scales 20 μ m.

- a. Haploid tissue of plant Nr. A-3 h9.
- b. «Diploidized» tissue of plant Nr. A-3 h9 (see Fig. 1).
- c. Epidermis of diploid plant Nr. A-1.

Table 1. Measurements of haploid and diploid sporophytes of *Athyrium filix-femina* (Of each plant 20 guard cells were measured)

Plant Nr.	chromosome number and ploidy level	leaf size cm	range of guard cells μm	mean of guard cell size (with standard deviation) μm
A-3 h8	40 (x)	9-12	26-36	31.7 (2.55)
A-3 h9	40 (x)	10-15	28-34	31.7 (2.23)
66 v	40 (x)	4- 5	28-34	30.2 (1.73)
A-1	80 (2x)	60-80	45-55	49.1 (2.82)
A-2	80 (2x)	60-80	41-49	45.9 (2.10)
A-3 h9 «diploidized» areas	(2x?)		40-49	44.8 (2.86)

Discussion

In previous investigations (Schneller 1979, Schneller and Schmid 1982) it could be shown that *Athyrium filix-femina* is a predominantly outbreeding species and that most of the plants found in nature are heterozygous. This was also the case in the two parent plants, A-3 and A-66, used in this investigation. It is noteworthy that at least some individual gametophyte strains (A-3 h8, A-3 h9, 66 v) originating from these two plants are able to develop haploid sporophytes by apogamy. However, gametophytes from eleven other parental individuals from natural locations (used in different experiments) were never observed to be apogamous.

The ability to form haploid gametophytes may be due to some change in genetic regulation and also due to the fact that the parents contain only a small amount of recessive deleterious alleles. The haploids are significantly smaller, a fact that is known also in haploids of higher plants (Zeven 1980).

The smallness of the haploids observed of *A. filix-femina* and the lack of reproducing organs may also be the result of weakly deleterious genes. This seems to be mainly the case in the 66 v plant, which lived less than half a year in a greenhouse and remained extremely small (Tab. 1). So far haploid *A. filix-femina* have not been found in nature. Besides the known examples, apogamy may be found in many other diploid, or allopolyploid, sexually reproducing fern species. Development of a sporophyte without involvement of sexual reproduction is one of the two important characteristics in the life cycle of many apomictic ferns. (The other is the ability to produce unreduced spores.)

There is considerable evidence for partial chromosome doubling in one of the haploids observed (A-3 h9). Although no chromosome count was possible because of the well differentiated leaf tissue the size of the guard cells and also of the other epidermal cells indicates the existence of diploid tissue (Tab. 1; Fig. 4a,b). It is noteworthy that the pinnules are larger compared with haploid ones (Fig. 1). The guard cells of the «diploid-

ized» tissue are nearly of the same size as guard cells of diploid plants (Fig. 4b,c). However, the plant A-3 h9 failed to develop sori either on the haploid or on the diploid parts.

Experimental studies on higher plants especially on *Nicotiana* show that some haploids tend to form chimeras with mixed haploid and diploid tissue on the same plant (Sunderland 1970). Such plants seem to be in some way genetically unstable. Chimeras of the same type could also be a consequence of competition between haploid and diploid cells originating through endopolyploidy.

Comparable observations in ferns were published by Vida (1974). An apogamously produced diploid offspring of an allotetraploid *Cystopteris fragilis* developed leaf areas with somatic polyploidization. In contrast to *Athyrium filix-femina* (A-3 h9) well developed sori with sporangia containing regular viable spores were produced on these areas, whereas the rest of the leaf developed only abortive spores in the sori. Hickok (1979) showed that during inbreeding experiments with *Ceratopteris richardii* some gametophyte strains were able to produce sporophytes apogamously. As in the case of *A. filix-femina*, A-3 h9, these haploids also show a tendency to partial somatic polyploidization.

Butters and Tryon (1948) described a naturally growing hybrid, *Woodsia* × *abbeae* (*W. ilvensis* × *cathcartiana*) in which the apical part of one frond was apparently fertile, whilst the basal portion developed abortive spores only. The epidermal cells of the fertile portion were about one third larger than those of the rest of the leaf blade. Butters and Tryon thought that the tissue in the upper, fertile part had changed to a tetraploid condition during leaf development and that therefore regular spores could be formed.

Somatic polyploidization may also be found in diploid *Athyrium filix-femina* or in *Athyrium*-hybrids. If spores are produced on the polyploid tissues it would allow either a polyploidization within the species or, in the case of hybrids, it would be an important step in the evolution of an allotetraploid *Athyrium* species.

I thank my wife for corrections and typing. I thank Mrs. Mary Fallen for reading the manuscript and for corrections.

Zusammenfassung

Im Zusammenhang mit fortpflanzungsbiologischen Untersuchungen bei *Athyrium filix-femina* ($2n = 80$) wurden apogam entstandene Sporophyten beobachtet. Diese erwiesen sich bei der zytologischen Kontrolle als haploid mit $x = 40$ Chromosomen in den Wurzelspitzen. Die haploiden Pflanzen waren viel kleiner als diploide. Zwei der Haplonten wuchsen mehr als 7 Jahre im Freien im Botanischen Garten Zürich und waren zum Zeitpunkt, als die Arbeit geschrieben wurde (Okt. 82), immer noch am Leben. Eine dritte haploide Pflanze war nur schwach lebensfähig; sie starb nach etwa halbjähriger Kultur im Gewächshaus. Diese Pflanze blieb sehr klein und entwickelte nur etwa 5 cm große Blätter.

Allen Haplonten war gemeinsam, daß sie keine Sori ausbildeten. Eine Linie, A-3 h9, fiel durch ihre Fähigkeit zu partieller somatischer Diploidisierung auf. Einige Fiederchen waren auffallend größer als die übrigen. Die Schließzellen an diesen Fiederchen erwiesen sich als fast gleich groß wie bei den diploiden Pflanzen. Auf den übrigen Teilen der Spreite

aber waren die Schließzellen viel kleiner und entsprachen in ihrer Größe jener der beiden Haplonten von *A. filix-femina*.

Ähnliche Erscheinungen wurden von anderen Autoren auch bei diploiden oder tetraploiden Farnen beobachtet. Das Auftreten von polyploidisiertem Gewebe dürfte, vor allem wenn darauf Sori und Sporen gebildet werden, für die Entstehung von Polyploidie bei einigen Farnen von Bedeutung sein.

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