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Aspects of spore release of *Asplenium ruta-muraria* with reference to some other woodland ferns: *Athyrium filix-femina*, *Dryopteris filix-mas*, and *Polystichum aculeatum*

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Abstract

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A relatively small portion of spores is released from the fertile leaves of *Asplenium ruta-muraria* after a single phase of wetting and drying. This is due to the relatively ineffective annulus movement. To empty all the sori this process has to be repeated many times. Therefore, the spores are retained for a long time on the leaves and can thus be dispersed over the entire season. In *Dryopteris filix-mas* and *Polystichum aculeatum* the sori are empty after a few phases of wetting and drying. *Athyrium filix-femina* lies somewhat between *D. filix-mas* and *A. ruta-muraria*. In contrast to the other species the sporangia of *A. ruta-muraria* remain open after drying and the sporangial walls form two cup-like parts, in which spores may be kept. It could be seen that not only the annulus movement but also wind-induced shaking of the leaves (ballanemochory), physical energy of raindrops, and liquid water (hydrochory) are important means for spore dispersal. Moving the leaves (by wind or rain) has the effect that spores drop from the cup-like parts of the sporangium. Short distance dispersal and the different dispersal agents in *A. ruta-muraria* seem to be significant for success in reaching safe sites which are small fissures and cervices in almost vertical limestone rocks or man-made walls. In the other species, wind dispersal and a more effective annulus movement may be responsible for a wider distribution of the spores. The safe sites of these species (small, well protected patches of bare soil) are more widely scattered.

Key words: Dispersal, annulus efficacy, spore release, ecology, *Asplenium ruta-muraria*, *Athyrium*, *Dryopteris*, *Polystichum*, Pteridophyta.

Introduction

In ferns and many other cryptogams spores are diaspores. Studying the significance of diaspores three main aspects have to be considered: 1) production, 2) release and 3) likelihood (and success) to reach safe sites.

Several investigations dealing with spore-production in homosporous ferns have been published (Conway 1957, Cousens 1988, Tryon 1986; for ref. see also Kramer et al. 1995). The principle of spore release by cohesion mechanisms in the annulus of leptosporangiate ferns has been known for a long time [Renner 1915, Ursprung 1903 (including references of earlier investigations), Ursprung 1915]. Many textbooks or chapters in books dealing with dispersal in ferns refer to the general statements made in these earlier publications. It was Haider (1954) who improved some of the former general ideas and introduced a more detailed view of the physiological base of spore release. A more recent review of the topic has been written by Straka (1962). However, investigations on selected species which also consider different aspects of spore release and dispersal are almost absent.

In the present investigation a more precise view of the potential for spore release and some aspects of dispersal mainly in *Asplenium ruta-muraria* will be given. Some results from *A. ruta-muraria* will be compared with investigations with *Athyrium filix-femina*, *Dryopteris filix-mas*, and *Polystichum aculeatum*. The characteristics of spore release are discussed in relation to spore production and to dispersal vectors on one side and in relation to success (reaching the safe site) of the spores on the other. One further objective was to find out whether species-specific characteristics of spore dispersal are correlated with ecological (habitat) conditions.

Material

Ripe leaves of *Asplenium ruta-muraria* s.str. used in the experiments were obtained from a man-made wall near the University of Zürich Botanic Garden. Leaves of *A. ruta-muraria* ssp. *dolomiticum* were gathered from plants cultivated in the University Botanical Institute (collected in Alpe Grünwald, Südtirol, Italy). For some tests dried material of *A. ruta-muraria* from my private herbarium (population Spitzliweg, Erlenbach, Kt. Zürich) has been used. For the experiments with *Dryopteris filix-mas*, *Athyrium filix-femina*, and *Polystichum aculeatum* fresh, ripe leaves were collected from my garden in Küsnacht (Kt. Zürich).

The methods and experiments will be described in different parts of the following section (results) to avoid too many repetitions.

Results

Estimation of spore production of Asplenium ruta-muraria

To estimate the spore production, a mean-sized plant (5 leaves, approximately 8 cm tall) was selected and the area of sori, the number of sporangia and spores was approximately estimated. Based on this a typical plant produces about 10 million spores in one year.

The release of spores from leaves of Asplenium ruta-muraria compared with Dryopteris filix-mas

To study the release of spores (effect of the annulus) in sheltered conditions fresh leaves of *A. ruta-muraria* s.str. and ssp. *dolomiticum* and ripe pinnules of *Dryopteris filix-mas* were fixed with Scotch tape at the tips on the covers of plastic boxes (7 × 10 × 20 cm). The leaves therefore hung vertically about 4–5 cm from bottom of the

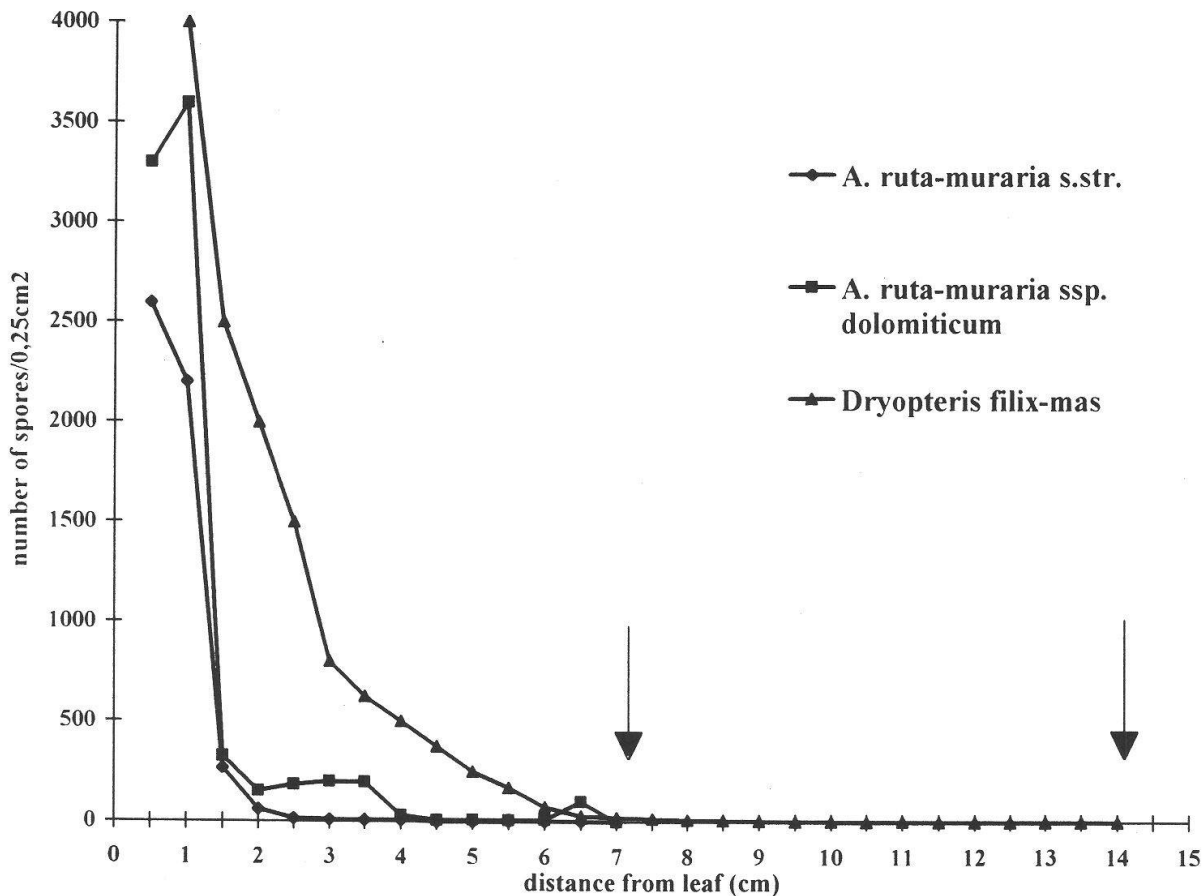


Fig. 1. Dispersal of spores released from leaves of *Asplenium ruta-muraria* and *Dryopteris filix-mas*. The leaves were mounted vertically $\pm 10-20$ cm above the bottom. Arrows: maximal distances of spores from a leaf of *A. ruta-muraria* and one from *Dryopteris filix-mas*.

box. At the bottom slides were mounted with double sided Scotch tape to collect the spores after the action of the annuli. After 24 h the distance of the released spores from the point of intersection of the vertical axis (given by the hanging leaf) and the bottom of the box was measured. The result shows (Fig. 1) that most spores are found close to the leaf. The role of the annulus seems to be to disseminate the spores into the wind rather than to sling them away from the leaf. The comparison with *Dryopteris filix-mas* shows that its annulus is more effective in projecting spores (Fig. 1).

Differences in annulus movement between Asplenium ruta-muraria and the other selected ferns

To study the annulus movements during desiccation and wetting, sori were observed under a dissecting microscope and a light microscope. In *A. ruta-muraria* the speed of opening of the annulus during desiccation is relatively slow. This seems to be true for sporangia opening for the first time and also for those that have already opened before. The drying annulus slowly extends and bends slightly backwards. Then with a few relatively short jolts the annulus moves slightly back again and forms a wide bow, the sporangium is then not fully closed. After this the annulus normally stretches again slowly and remains, when completely dry, more or less stretched. During such a process

only some of the spores will be ejected and some will remain in the sporangium. They may be released after a next step of wetting and drying or later or by some other mechanisms (see next sections).

In *Dryopteris filix-mas*, *Athyrium filix-femina*, and *Polystichum aculeatum* the drying annulus (opening for the first time or reopening) extends and bends relatively slowly backwards as in *A. ruta-muraria*. In contrast to this species it jumps quickly back to a nearly closed position in which it then remains. Consequently the spores will be ejected more effectively (see also Schneller 1985) than in *A. ruta-muraria* (Fig. 1).

Repeated spore release

It is known that the annulus movement is based on physical conditions and can be repeated whenever the sporangium is moistened for at least about ten minutes and then dried again. To know more about the consequences of repeated desiccation and wetting leaf fragments of *Asplenium ruta-muraria* (one or two pinnules) bearing sori were used. The pinnules were put on to slides with the sori directed downwards. After the first release (using fresh material at the beginning) and the first count of free spores, the parts were moistened in a few drops of water and put on a clean slide. After they were dry the released spores were counted. This experiment was repeated until nearly all the sporangia were empty (Fig. 2). After each procedure also a few empty, released sporangia could be observed.

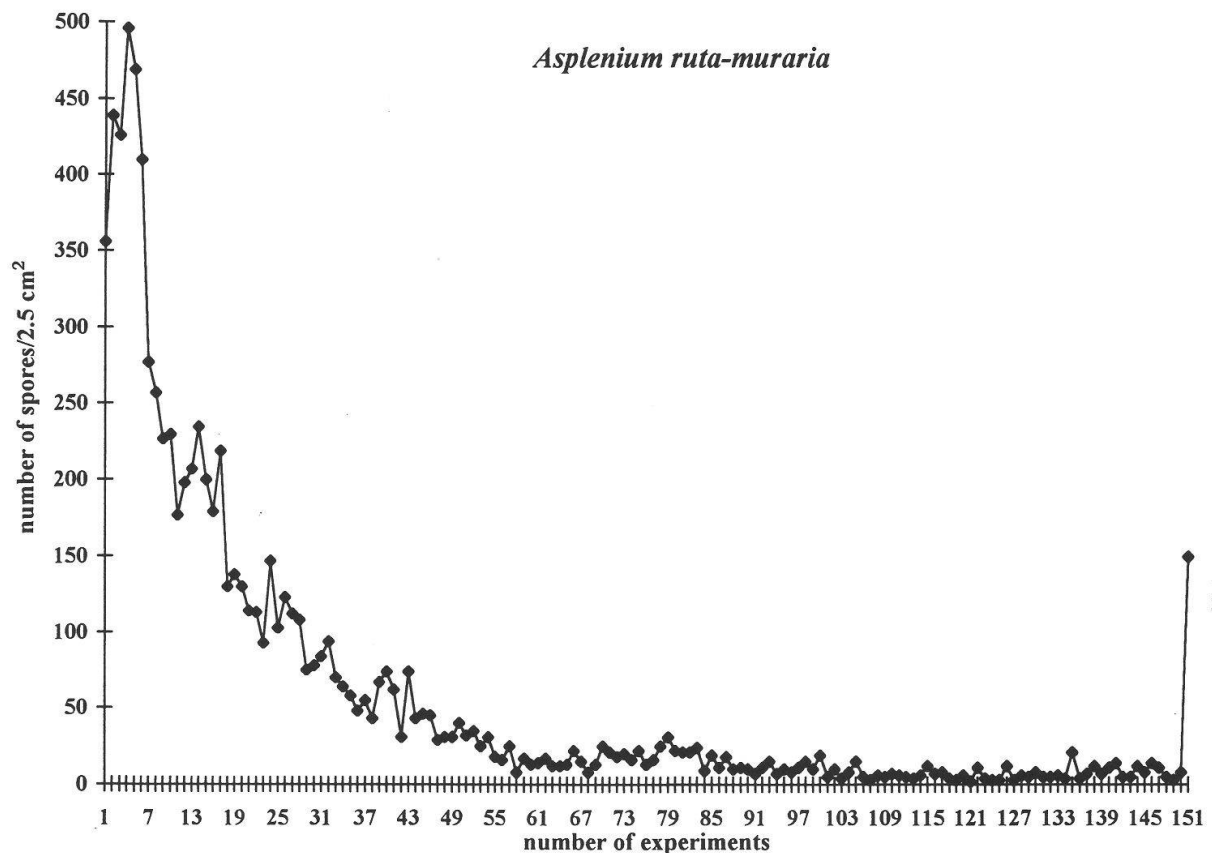


Fig. 2. Spore release of *Asplenium ruta-muraria* after repeated drying and wetting. After 150 runs the number of spores remaining was counted.

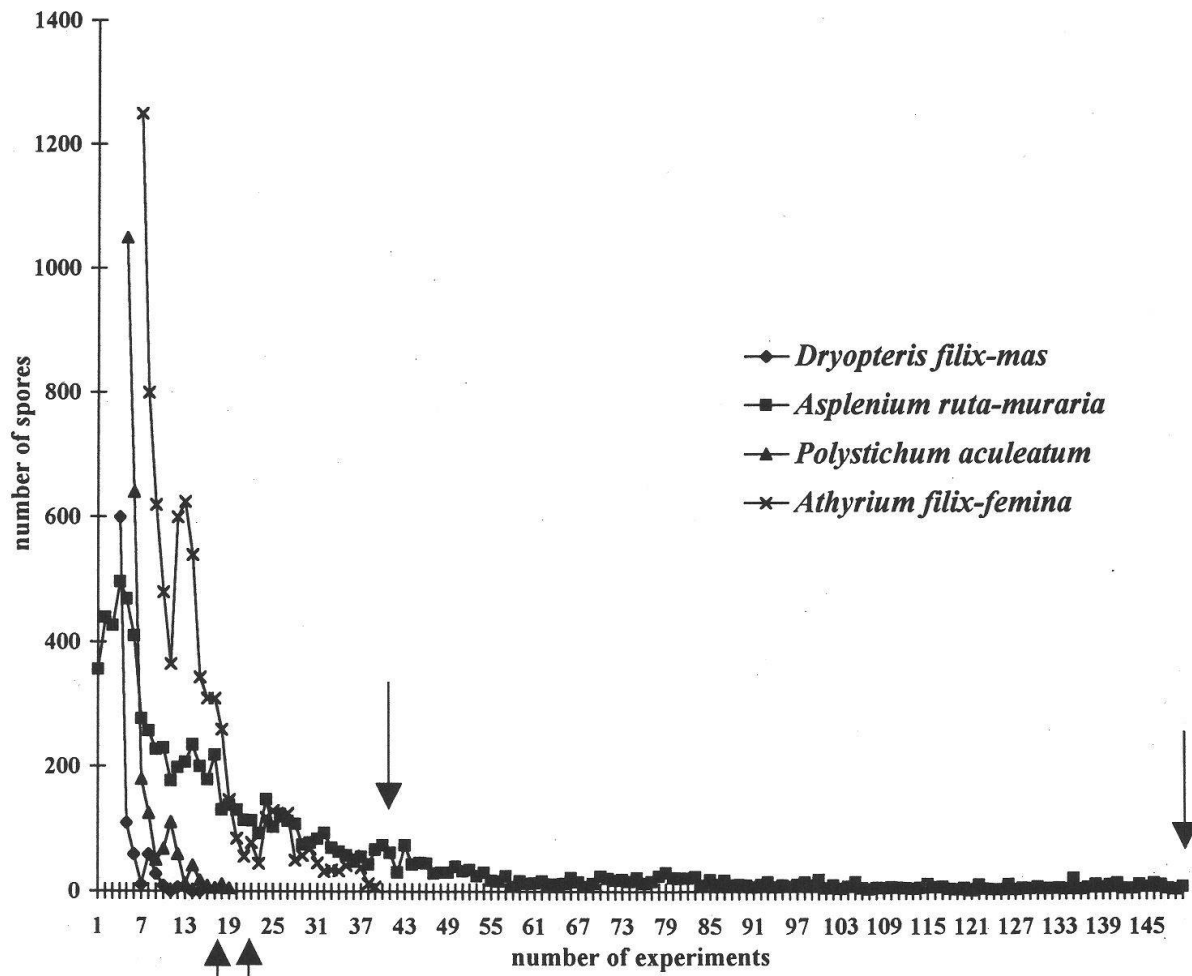


Fig. 3. Spore release after repeating drying and wetting of the sori. Comparison between *Asplenium ruta-muraria*, *Dryopteris filix-mas*, *Polystichum aculeatum* and *Athyrium filix-femina*. Arrows: completed spore release of the different taxa.

The same kind of experiments was carried out with *Athyrium filix-femina*, *Dryopteris filix-mas*, and *Polystichum aculeatum*. The results (Fig. 3) show that there are remarkable differences between these species.

The influence of air humidity on sporangia movements in Asplenium ruta-muraria

When enclosing dried leaves (with the sporangia open) for a few hours in a vessel with high humidity (at least 90%), it could be observed that the sporangia closed. When transferred again into dryer conditions (humidity of 50% or less) the sporangia open again. For the functioning of the annulus mechanism liquid water does not seem to be absolutely necessary; high humidity is sufficient to close sporangia. Observations done in nature confirmed the experimental results. To check the potential for spore release three small pieces from a fresh leaf (one pinnule, 12 mm²) were kept for two hours in a vessel with 100% humidity. Then the pinnules – with sori directed downwards on a slide – were brought into dryer air. The number of released spores was counted. After ten repeats of the experiments on average 58 spores were released (which is less than 1% of the estimated total).

Effectiveness of spore dispersal due to desiccation in comparison to the influence of mechanical movements

Three pinnules of *Asplenium ruta-muraria* (each $\pm 15 \text{ mm}^2$, with the sori downward, on a slide) while still attached to the leaf stipe were kept at 100% humidity to induce the closing of the sporangia and then dried to open the sporangia. The spores which had fallen on to the slide were counted and removed. Then the dry parts were shaken by holding the stipe and by tapping 30 times. The newly released spores were collected and counted. The reason for this procedure lies in the assumption than in nature leaves will be moved and shaken by currents of air. This procedure was repeated 10 times. With drying alone 141 spores were released while tapped pinnules released 1493 spores.

A further experiment consisted of wetting three fertile pinnules still attached to the leaf with liquid water. After drying the released spores were counted. Then the leaf was tapped 30 times and again the released spores were counted (Fig. 4).

Liquid water as vector for spore dispersal in Asplenium ruta-muraria

To study the potential for water dispersal 8 pinnules with sori were used. The pinnules were attached to the rachis and stipe so that they could easily be manipulated. The treatment consisted of rinsing water from a wash-bottle over the previously dry pinnules. The water drops then were collected on blotting paper on which the released spores could be counted. After wetting the pinnules were put on a slide (sorus downward) on which they dried once more. The released spores were counted. These two steps (watering and drying) were repeated 10 times. The results show that drying is the more effective dispersal mechanism but also rinsing the leaves leads to spore release (Fig. 5).

Leaves in nature are exposed to rain and drops often form at the tips of the pinnae and pinnules. During rain spores accumulate in these drops. Such drops were collected on blotting paper. Eight samples (drops collected at the tips of pinnules) taken in nature at the beginning of a rainfall contained on average 62 spores.

Spore release in Asplenium ruta-muraria when combining different factors

To test the effects of different factors together an experiment was carried out with repeated changes in drying, tapping and rinsing the leaves with water. The leaf used contained 8 pinnules. It could be seen that tapping led to the most effective spore release followed by drying and rinsing (Fig. 6).

Leaf and sporangial characteristics as mechanisms for the dispersal of Asplenium ruta-muraria in nature

In natural habitats the sori are borne adaxially and more or less covered and arranged horizontally or they are directed towards the substrate. The sporangia are therefore turned downwards. This is obviously relevant for dispersal in *Asplenium ruta-muraria* and must be seen in connection with the following explanation. When drying the sori the movement of the annuli lasts only a relative short time. If the air is not extremely humid the sporangia will be open in about ten to fifteen minutes. Two extreme stages of the annulus during desiccation are shown in the figures 7a and 7b. If the weather remains dry and no rain falls the sporangia remain open (Fig. 7b). The annulus is nearly straight or slightly bent backwards at the tip. The rest of the sporangial cells forms an upper and basal 'cup' (Fig. 7b) in which some spores remain, the rest being released by the slow annulus movements. When humidity increases and/or the leaves get soaked the sporangia

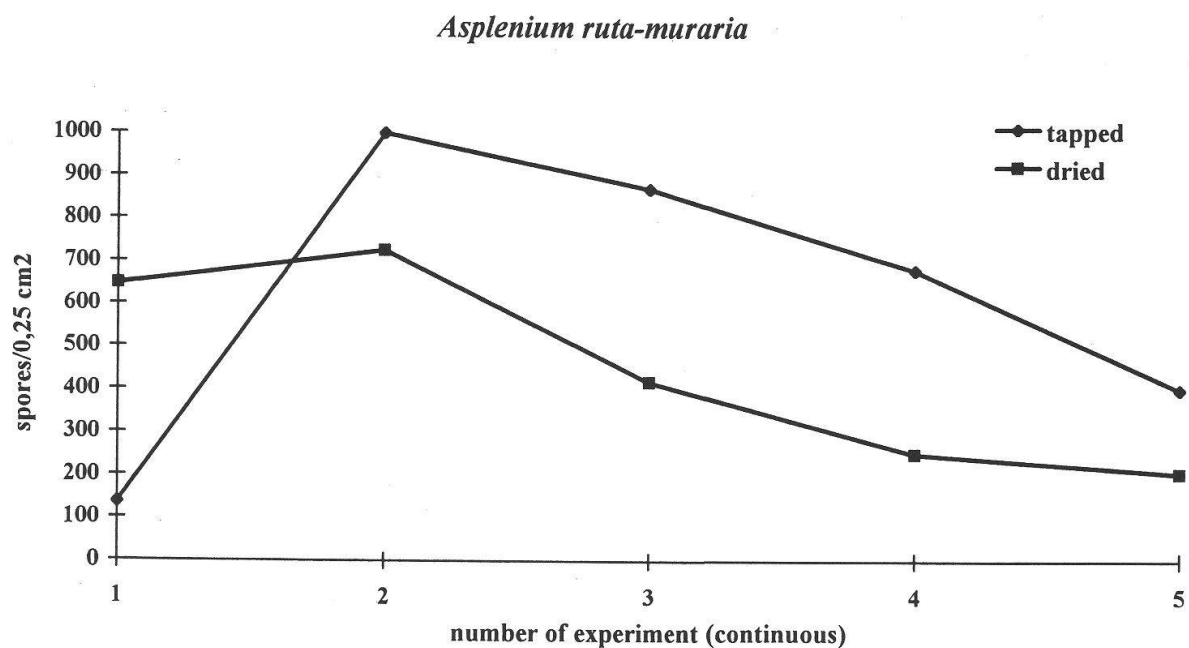


Fig. 4. *Asplenium ruta-muraria*: total number of spores after initial tapping and then after wetting and drying the pinnules. Pinnule number: three; area of sori 2 cm².

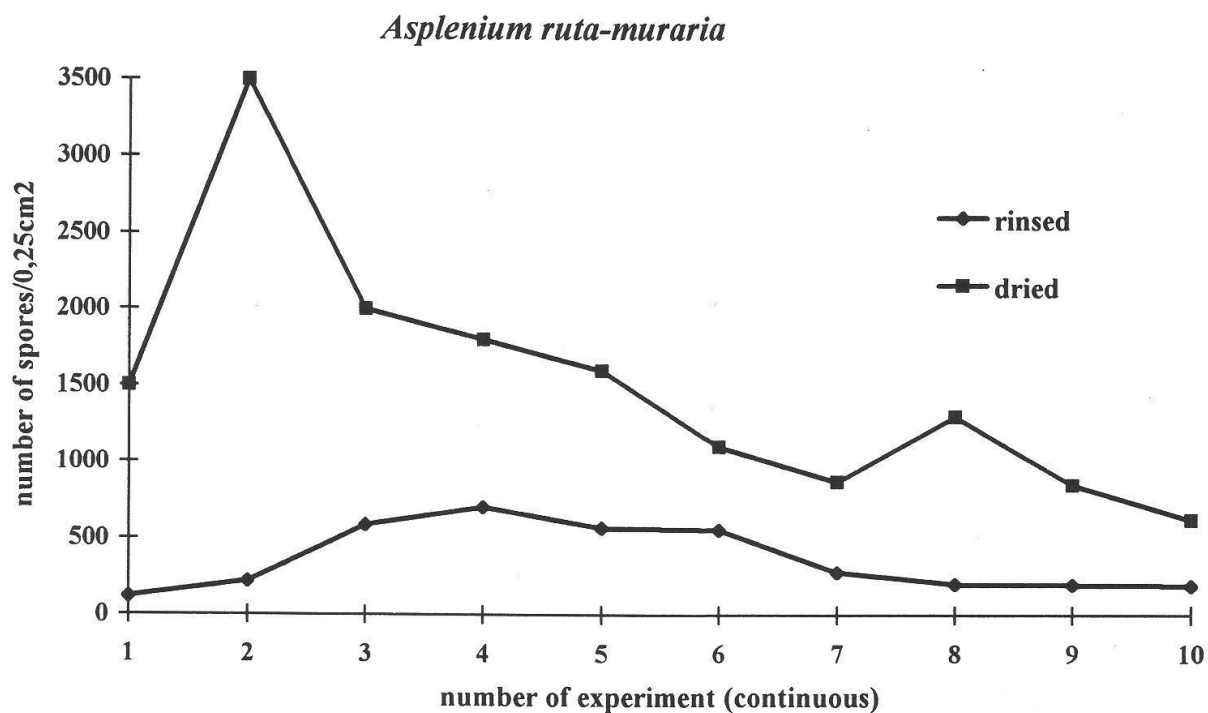


Fig. 5. *Asplenium ruta-muraria*: total number of spores counted after initial rinsing with water and drying. Pinnules: eight; total area of sori ± 6 cm².

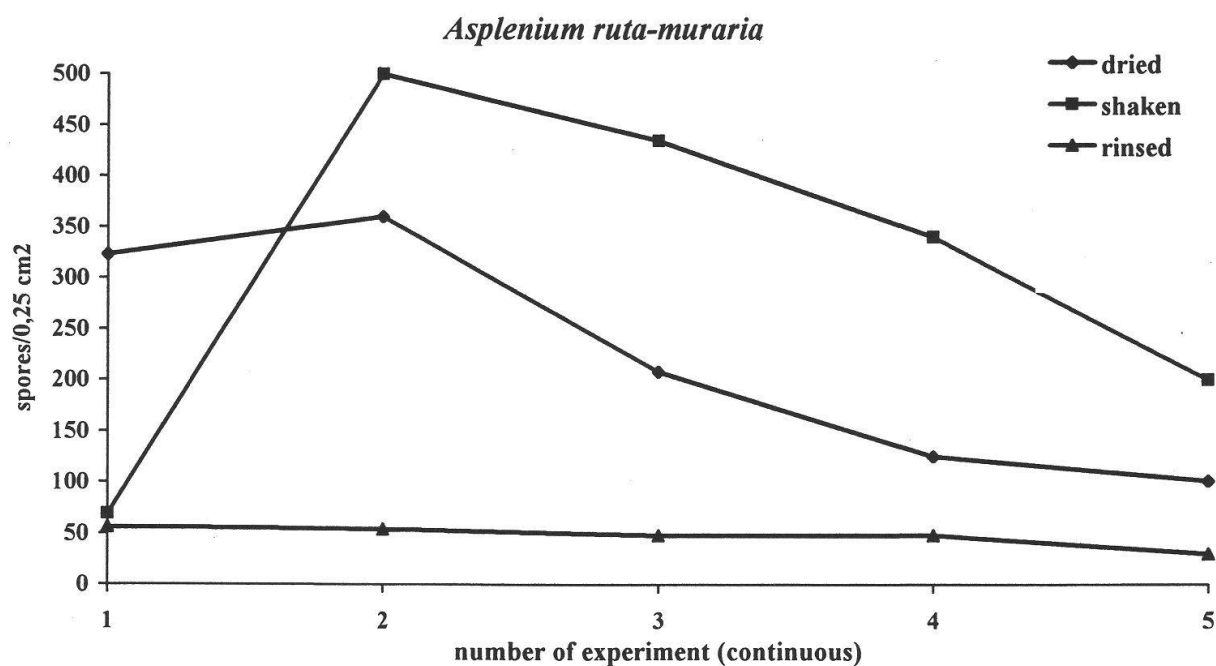


Fig. 6. *Asplenium ruta-muraria*: mean of total spores counted after initial tapping followed by wetting and drying and by rinsing with water. Plants: two with leaves reduced to three pinnules.

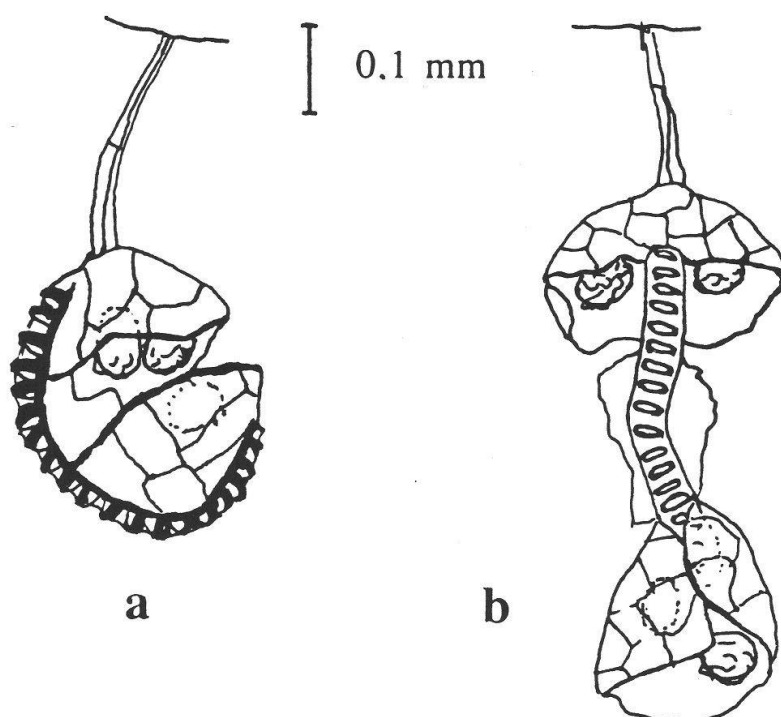


Fig. 7. Sporangia of *A. ruta-muraria* in a more or less natural position (oriented downwards). a) closed wet sporangium containing few spores. b) open sporangium when dry containing few spores. Note the two cup-like parts.

close. It could be observed in nature that even after hours of rain the sorus was not totally wet, however, the sporangia may close by the humidity of the air.

Sporebank in nature

In small crevices and fissures of man-made walls colonized by *A. ruta-muraria* prothalli and young sporophytes can sometimes be observed. This very restricted micro-habitat contains the safe sites. Three soil samples from such fissures and crevices in a population near University Botanic Garden were collected. The samples were spread out in small plastic boxes with covers and kept at room temperature in the laboratory near a north facing window. They were watered when necessary. After three weeks at least 50 or more germinated spores per square-centimeter could be observed. It is very likely that due to rainwater and air currents enough spores reach the safe sites and may germinate. When the conditions are favourable they may form a persistent spore bank. Spores kept at room temperature remain viable for at least three years.

Discussion

Most homosporous ferns produce large numbers of spores (Tryon 1986, Cousens 1988, Kramer et al. 1995). The number of spores produced mainly depends on the size of the plant. In the relatively small species *Asplenium ruta-muraria* (mean size of a fertile leaf ± 8 cm long) there is an annual production of about 10 million spores per plant. In *Athyrium filix-femina* about 75–100 million spores per plant will be produced (Schneller 1979). About the same number of spores will be found on a well-developed plant of *Dryopteris filix-mas* or *Polystichum aculeatum*. In general, homosporous ferns (as many other cryptogams) have evolved the strategy of producing high numbers of small diaspores thus compensating for a high loss. Most of the spores are deposited in close vicinity to the source (Schneller 1975, Conant 1978). However, the production of high numbers of small diaspores makes long-distance dispersal possible. As shown for recent volcanic islands like Krakatau (Ernst 1934) or Surtsey (Fridriksson 1975) successful long-distance dispersal does occur.

When scanning textbooks or articles dealing with spore dispersal in homosporous ferns the role of the annulus and wind dispersal is emphasized. Animal dispersal is discussed only in a few cases (Tryon 1985, Walker 1985). The influence of rain and water on dispersal has, so far, been mentioned for the first time in Suter (1985) and Suter & Schneller (1986).

When comparing the influence of the annulus in different species, differences can be observed. In experiments with *D. filix-mas* and *P. aculeatum* the sori are empty after only a few phases of wetting and drying (Fig. 2). The speed of the annulus movement, especially the closing, during drying is much faster than in *A. ruta-muraria* and thus seems to be mainly responsible for the greater effectiveness in catapulting spores (Schneller 1975). For *D. filix-mas* and *P. aculeatum* it can be assumed that in nature the sori are empty after a short time and spore rain occurs only for a few weeks during the season. When interpreting the experiments with *A. filix-femina* it can be concluded that the spore rain lasts for a longer time than in *D. filix-mas* and *P. aculeatum*. However, when collecting old leaves some spores may persist in the sori. Some of these spores may remain and will eventually reach the soil near to the parent plant.

The safe sites of these three species consists of small well protected patches of bare soil within woods. The somewhat more effective dispersal mechanism may be important

for reaching the safe sites. The temporally relatively short but effective spore rain in late summer may allow spore germination in the same year. But, at the same time, an effective persistent spore bank may be formed (Dyer and Lindsay 1992).

In *A. ruta-muraria*, even on old leaves (for instance on leaves of the previous season which are still present at the beginning of the new vegetation period), numerous spores are found. Because of the relatively limited action of the annulus when drying, the spores are not catapulted away from the sporangia as observed in *D. filix-mas*, *P. aculeatum* and *A. filix-femina*. For *A. ruta-muraria* the somewhat slower action of the annulus allows a long lasting dispersal of spores (Figs. 2, 3). This means that spores will be released throughout the whole year. Observations in nature supports this. The long lasting spore release is due to the fact that the annulus mechanism is not very effective and not all the spores in the sporangia are freed at the same time. The position of some sporangia within the dense sorus may also be responsible for a retarded spore release. After each phase of humidity induced annulus mechanism a few sporangia will also be released thus reducing the density of sporangia in the sorus.

The investigations with *A. ruta-muraria* shows that not only the annulus and wind (although they are important factors) but other factors or a combination of factors play a role in spore dispersal. The sporangia remain open when dry. The two halves of the sporangia form 'cups' which are turned downwards (because the sorus is found on the lower side of the leaf) (Fig. 7b). The spores placed within these two cups may simply just fall out (due to gravity). The procedure of opening of the sporangia is characterized by some jerky movements which may shake the already open but spore containing sporangia and allow spores to fall out. Some spores in the open sporangia may be kept in the 'cups' (Fig. 7b) until the leaf is moved. Such a situation has been simulated in experiments by tapping the pinnules. In *A. ruta-muraria* it could be seen that when combining the different types of spore release shaking the leaves (after the sporangia have opened) seems to be a very effective factor for dispersing spores.

It can be assumed that for the interpretation of the results not the total number of spores is relevant but their proportion (Figs. 4, 6). The low numbers of spores at the beginning of experiments when the leaves were tapped (Figs. 4, 6) may be due to the fact that at the beginning the open sori had already been emptied by natural conditions before gathering.

In nature, two situations lead to mechanical movements (shaking) of leaves. One is the wind. In the natural habitat of *A. ruta-muraria* (on steep rocks and man-made walls) there are often upwinds during warm weather but also downwinds occur. Wind may shake the leaves thus releasing the spores from the already open sporangia (Fig. 7b). In this case, one can speak of ballanemochory. The second situation is found when it rains. Falling raindrops have sufficient energy to shake parts or whole leaves. Since the sporangia are on the underside of the leaves, they will not normally be hit directly by raindrops but open sporangia will loose spores because of the mechanical influence of raindrops. If the humidity is high, however, the sporangia will close and the spores will be kept in the sporangia. However, some spores laying between the sporangia will be washed out of the leaves especially when the rain lasts for hours or days. As already shown by Suter & Schneller (1987), raindrops or water running down from leaves may transport spores away from each leaf. So also hydrochory seems to be at least partially responsible for dispersal. Spores in a film of water are more likely to reach the microsites such as crevices in walls or rocks (safe sites) which are suitable for germination, gametophyte and sporophyte development. A not strictly seasonally restricted release of spores allows dispersal for quite a long time. The ability to use different means of short-distance

dispersal such as a relatively weak active ejection by the annulus, the passive dispersal by leaf movements due to wind or raindrops and the partial hydrochory are seen as important adaptations in the colonizing and establishing strategy of *A. ruta-muraria*. The safe sites are confined to very restricted places such as rock crevices, fine fissures or small gaps in walls. Safe sites are more likely to be reached by spores from donors nearby than from those more distant.

Transport by wind is possible because of the small size of the diaspores. Wind is the vector which allows long-distance dispersal and it may be important for founding new populations (Schneller and Holderegger 1995), but it plays a secondary role in the establishment of local colonies.

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