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Comparative Ecology of *Woodsia scopulina* Sporophytes and Gametophytes

PAUL J. WATSON and MARGARITA VAZQUEZ*

Woodsia scopulina D. C. Eaton, an obligate rock fern, is widespread in the Rocky Mountains and has a few disjunct populations in eastern North America. This report concerns the ecology of *W. scopulina* gametophytes and sporophytes.

An understanding of the life history of any fern is incomplete as long as the functioning of its gametophytes remains obscure. Yet, the study of gametophyte ecology is in its infancy. Adaptations of gametophytes to cold and desiccation have been explored by Pickett (1914). Hill (1971) compared the habitat requirements for spore germination and gametophyte development for three ferns in Michigan. Gametophyte population divergence and general ecology have been studied by Cousens (1979).

Wagner and Sharp (1963) found that free-living *Vittaria* prothalli occurred in areas far north of their sporophytes. Since this discovery, several other genera of tropical ferns have been found to possess gametophytes with geographic ranges much more extensive than the sporophyte (Wagner & Evers, 1963; Farrar, 1967; McAlpin & Farrar, 1978). Page (1979) sums up much of the research on fern gametophyte ecology.

Gametophyte ecology is, of course, microecology. We find this a fascinating and unusual level at which to study plant ecology, a science in which investigation of systems at the macro level is the norm.

PROCEDURES

Our study areas consisted of xeromesic to xeric talus slopes and rock outcrops in the immediate vicinity of Bigfork, Montana. These rocky sites represent typical *Woodsia scopulina* habitat, and many hundreds of sporophytes as well as thousands of gametophytes are found there. *Cystopteris fragilis* (L.) Bernh. also occurs at the sites; however, it is only a minor contaminant of the nearly pure *W. scopulina* fern communities. Other herbaceous plants are only sparsely distributed on the sites. Shrubs such as Mountain Spray (*Holodiscus discolor* (Pursh) Maxim.), Serviceberry (*Amelanchier alnifolia* Nutt.), and Rocky Mountain Maple (*Acer glabrum* Torr.) occur, especially on the less disturbed sections of the talus slopes. Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco.) also occurs sparingly. A rich moss flora is present on the talus and the rock outcrops.

We explored the microhabitats of numerous *W. scopulina* gametophytes, gametophytes harboring juvenile sporophytes (in which the sporophytes' leaves were still dichotomous, not yet resembling those of the mature sporophyte), young, sterile sporophytes, and fully-developed, fertile sporophytes. For each of these life cycle phases, we noted such environmental factors as substrate composition and pH, sunlight exposure, and nearby plant associates. Consistently occurring differences in the habitat of each of the four phases were recorded.

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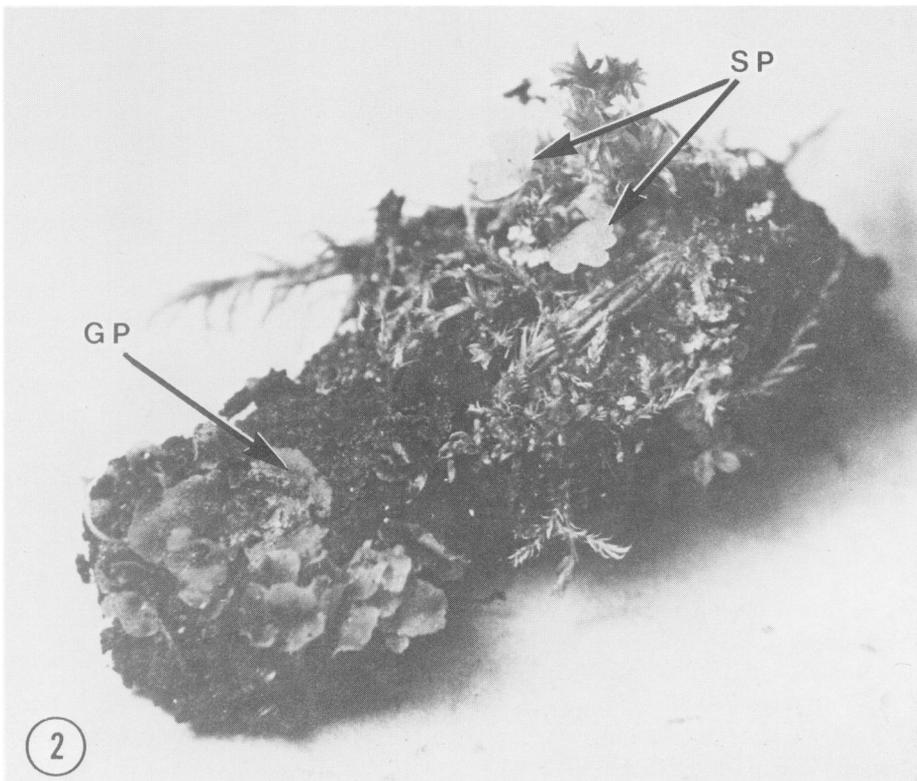


FIG. 1. Talus hollows where *Woodsia scopulina* gametophytes are found. FIG. 2. Two clumps of soil illustrating juvenile sporophytes (SP) in association with mosses and gametophytes (GP) growing on bare soil.

Quantitative data on the substrate preferences of gametophytes were gathered by examining all the cave-like talus hollows on a chosen talus slope. Sixty-one hollows were inspected. For each, the presence or absence of gametophytes and nature of the substrate (bare soil, litter on soil, moss and litter on soil, etc.) were recorded. (We define litter as decomposing but still recognizable plant material upon soil or rock surfaces.)

In order to compare the habitat preferences of *W. scopulina* gametophytes and sporophytes with those of a typical mesophytic forest fern, we familiarized ourselves with the habitats of the life cycle phases of *Athyrium filix-femina* (L.) Roth. The study sites for this fern were located in the moister forested areas of the University of Montana Biological Station, approximately 12 miles south of Bigfork.

RESULTS

The puberulent, slightly sticky gametophytes of *W. scopulina* were found only in cave-like hollows on the talus slopes (*Fig. 1*) and in crevices on rock cliffs and tables. These talus hollows and rock crevices contain various amounts of soil, bare rock, mosses, and litter. Gametophytes existed only on bare soil over rock (*Fig. 2*). Gametophytes usually were found within talus hollows containing obvious patches of bare soil (23 out of 29 hollows), but seldom were found in hollows with soil mostly covered by litter or mosses (5 out of 32 hollows). Gametophytes were never found in hollows lacking soil. A mere dusting of soil about a millimeter thick was enough to support gametophytes. Soil pH readings from gametophyte substrates ranged from 6.4 to 7.2.

Gametophytes in the various populations were sparse to dense, and were not closely associated with other plants, even with the young, leafy moss shoots. Favorable gametophyte habitats typically were sheltered from direct sunlight. However, gametophytes did not grow so far back in hollows and crevices that illumination was too heavily diminished, even if other environmental conditions were favorable. Gametophytes were oriented with their apical notches farthest from the opening of the crevice or hollow. Most gametophytes did not lie flat on the substrate, but had the apical two-thirds of their thalli slanted steeply upwards (*Fig. 3*).

Populations of gametophytes giving rise to juvenile sporophytes also grew in the crevices and hollows, but the soil substrate often was not bare (*Fig. 2*). This phase of *W. scopulina* was usually associated with the moss *Brachythecium velutinum* (Hedw.) B.S.G. This small, pleurocarpous moss grew sparingly around gametophytes with new juvenile sporophytes but more robustly around those with more advanced juvenile sporophytes having two or three well-developed leaves (in the latter case the gametophytic tissue was still visible but totally chlorotic). Where *B. velutinum* grew densely, a second moss, *Encalypta vulgaris* Hedw., often occurred intermixed with it. Occasionally, a thin layer of litter also covered the soil. Clusters of tiny juvenile sporophytes grew from gametophytes positioned in the more illuminated portions of the microhabitat as, for example, near the front of talus hollows, but still out of direct sunlight. Those gametophytes furthest back in such a hollow often had few or no sporophytes.

Young, sterile sporophytes were seen growing only out of talus hollows, rock crevices, and upon rock tables. When seen growing upon a rock table, examination of the plants' bases showed them to be anchored to at least a small crack or other irregularity in the rock. These sporophytes usually grew in close association with several mosses such as *Dicranum scoparium* (L.) Hedw., *Rhytidiadelphus triquetrus* (Hedw.) Warnst., *Tortula muralis* Hedw., *Homalothecium* sp., and *Brachythecium* sp. Openings that harbored young, sterile sporophytes supported only one per opening.

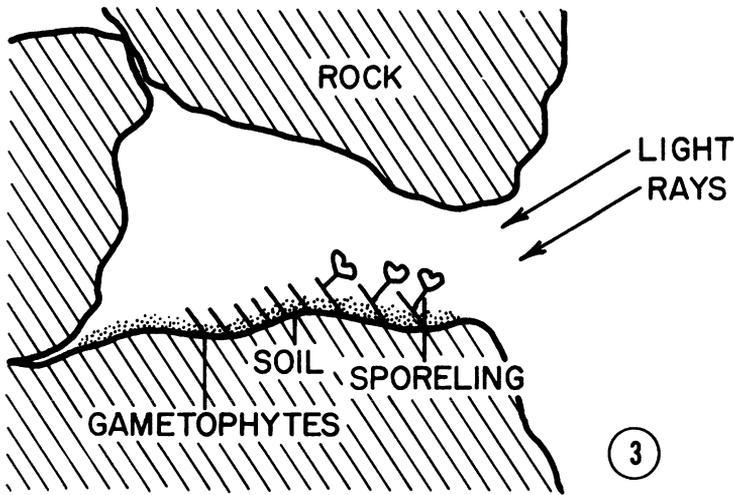


FIG. 3. Position of gametophytes and juvenile sporophytes within a typical talus hollow.

Fully developed, fertile sporophytes of *W. scopulina* were found growing out of talus hollows, rock crevices, and from irregularities on rock tables and cliffs. Their fronds always extended completely out of the rock opening of their origin, but grew in filtered to direct sunlight, depending on the presence of overstory shrubs or trees. Mature sporophytes had huge systems of fine roots. These roots were much greater in extent and density than we expected for a fern so small as *W. scopulina*. The roots never grew on bare rock. Instead, they grew within a layer of soil over rock and spread down into even the thinnest layers of soil between rocks. Thick mats of the same mosses associated with young, sterile sporophytes commonly covered the soil substrate. *Woodsia* sporophytes were not associated with thick growths of grasses and did not occur on sites with a great abundance of deciduous litter. The pH of the soil substrates we tested ranged from 6.2 to 6.8.

The prothalli of *Athyrium filix-femina* were found only on bare soil or moist, heavily rotted wood in shady microhabitats. As was true for *W. scopulina* gametophytes, *A. filix-femina* gametophytes did not grow among mosses or upon forest litter.

Sporophytes of *A. filix-femina* occurred in mesic forest conditions, often beneath gaps in the tree canopy. Mature sporophytes grew in association with many herbs, shrubs, and thick layers of mosses.

DISCUSSION

We conclude that there are at least three salient differences in the ecologies of *Woodsia scopulina* gametophytes and sporophytes: (1) Gametophytes become established only in secluded microhabitats where sunlight is diffuse for most or all of the day. Sporophytes, on the contrary, can tolerate exposure to intense direct sunlight for many hours each day. (2) Competitive abilities of the two generations differ. Gametophytes cannot coexist with other plant growth, including the mere leafy shoots of small bryophytes. On the other hand, even the youngest sporophytes are often surrounded by mosses with no apparent ill effects. Association with mosses may even benefit sporophytes by reducing desiccation of their roots. Sporophytes also grow well in close proximity to widely spaced herbaceous and woody angiosperms. (3) Gametophytes cannot grow upon or under litter, but sporophytes are not disadvantaged by moderate litter accumulations.

The above conclusions conflict with certain general statements in the literature, such as that by Nayar and Kaur (1971) who claim that "sporophytes and gametophytes have nearly the same ecological requirements."

The first difference in ecological requirements mentioned above is a function of place and, of course, results from sporophytes growing towards sunlight. Gametophytes typically orient towards sunlight, but they do not grow towards it to any extent. The latter two ecological differences mentioned above are a function of time rather than place. The microhabitats that provide suitable conditions for gametophytic growth contain patches of fresh, bare soil in talus hollows and rock crevices. Such microhabitats are ephemeral and exist due to very recent accumulation of dust and soil or to soil-churning rock movements. Sporophytes grow in the same places, but after other plant life has invaded and litter has accumulated.

Although the sporophytes of *W. scopulina* and *A. filix-femina* are adapted to different habitats, their gametophytes exist in strikingly similar habitats. Gametophytes of both genera grow on bare substrates in relatively moist and shady microhabitats. Difference in the sporophytes' yet similarity in the gametophytes' habitat requirements of these two ferns suggests that specialization of the haploid generation of *W. scopulina* has lagged behind that of the diploid phase. This observation reinforces the concept that the evolution of ferns is primarily a diploid affair (Wagner, pers. comm.). It also is in harmony with the suggestion of Cousens (1979) that a potential exists for some degree of independent evolution by the two generations. Cousens' suggestion is based upon the observation of Pray (1968) that differences among populations of *Pellaea andromediifolia* gametophytes were not correlated with differences in the sporophyte generation. *Woodsia scopulina* gametophytes are evolutionary conservatives, developing only in the most mesic, forest-like microhabitat available on the otherwise xeric, rocky macrohabitat to which the sporophyte has become adapted.

Nonetheless, it may be that *Woodsia* gametophytes have made modest advances towards becoming xerophytes. Unicellular glandular hairs and a slightly sticky surface coating may be desiccation-inhibiting adaptations. (We note however that Stokey (1951) states that hairs of this type are widely distributed and usually not of generic significance.) Also, the nonoccurrence of *Woodsia* gametophytes on rotting wood in the immediate vicinity of the study sites indicates that spore germination on this substrate has been selected against. Perhaps the ability to grow on wood has been traded for some xerophytic adaptation.

Our studies suggest that the frequency and abundance of *W. scopulina* gametophytes in suitable microsites is greater than that of *A. filix-femina* gametophytes. This has interesting implications. Perhaps ferns that do not reproduce extensively by means of their rhizome system, such as *W. scopulina*, produce gametophytes of greater vigor than ferns capable of such asexual reproduction and dispersal, such as *A. filix-femina*.

In a study of this type, the tremendous individual mortality due to random phenomena and intraspecific competition that may take place as plants of a species struggle to advance from one developmental stage to another becomes highly evident. For example, only those spores of *W. scopulina* that happen to land on properly illuminated bare soil in specially protected areas among rocks will germinate and develop into gametophytes. Spore wastage must be incredibly high. Of the gametophytes that do develop, some are not in the right portion of the microhabitat to give rise to new sporophytes, such as gametophytes found towards the inner recesses of talus hollows. The threshold light intensity allowing gametophyte development may be too low for the growth of new sporophytes. Alternatively, it may be that not enough free water reaches the deeper parts of talus hollows to allow much sperm transfer from antheridia to archegonia. Thus, innumerable gametophytes are also wasted. Further, out of the mats of juvenile sporophytes that arise from part of a gametophyte population, only one ultimately survives to occupy the crevice or hollow as a young, sterile and latter as a fertile plant.

In *W. scopulina*, almost all intraspecific competition takes place between juvenile sporophytes. New sporophytes promptly kill their parent gametophytes, possibly by secreting a toxic chemical or by parasitism, thereby avoiding competition from other sporophytes that otherwise might arise on the same gametophyte. Competition between juvenile sporophytes of different gametophytes probably is mostly for available light. The reason most intraspecific competition takes place between juvenile sporophytes is because of the small size and spotty distribution of microhabitats suitable to nurture the birth, growth, and continued survival of *W. scopulina* sporophytes.

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REVIEW

“FERNS, FERN ALLIES AND CONIFERS OF AUSTRALIA,” by H. T. Clifford and J. Constantine. xviii + 150 pp. illustr. University of Queensland Press. 1980. ISBN 0-7022-1447-7. \$24.25.— Although this book is subtitled “A Laboratory Manual,” and does contain illustrations of morphological details, it is a good introduction to the pteridophyta of Australia, and, by extension, to the Old World tropics. Two-thirds of the book concerns pteridophyta. For those interested in identifying Australian ferns and fern allies, there are keys down to species, interesting and useful generic descriptions with notes on habitats, and tables of distribution by species within Australia and Tasmania. Species descriptions are missing, and are not really compensated for in the brief keys to species. Fortunately, the genera of Australian ferns are diverse and mostly with only a few species, and so identification is likely to be easy in most cases. References and literature cited, a table of vegetative characteristics of major vascular plant groups, a list of synonyms of Australian pteridophyta with the names accepted by the authors, a short glossary, and an index conclude this useful work.—*D. B. L.*