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Pteridophytes of Iowa's Loess Hills — Adaptations to Dry Habitats

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Eleven species of pteridophytes and one hybrid occur in the Loess Hills of western Iowa. *Adiantum pedatum* L., *Athyrium filix-femina* (L.) Roth, *Camptosorus rhizophyllus* (L.) Link., *Cystopteris tenuis* (Michx.) Desv., *Cystopteris protrusa* (Weath.) Blasdell, and *Matteuccia struthiopteris* (L.) Todaro are widely distributed in Iowa, but restricted in this area to the most mesic woodlands, probably due to the drought sensitivity of their shallow rhizomes and above-ground gametophytes. *Equisetum hyemale* L. and *E. arvense* L. are common in riparian habitats and moist roadside ditches. These two species likely survive by maintaining contact with a permanent water table. *Equisetum laevigatum* A. Braun, *E. X ferrissii* Clute, *Botrychium virginianum* (L.) Sw., and a new species, *Botrychium* "prairie", inhabit native Loess Hills prairies. These *Equisetum* taxa avoid prairie drought through deep underground rhizomes, early senescence of aerial stems, and a low above-ground to below-ground biomass ratio. Underground gametophytes and rhizomes and early spring phenology are attributes allowing survival of the *Botrychium* species on the prairie. *B.* "prairie" of the subgenus *Botrychium* may be a Pleistocene relict.

INDEX DESCRIPTORS: Loess Hills, Pteridophytes, Ferns, *Botrychium*, *Equisetum*.

The Loess Hills bordering the Missouri River in western Iowa present the driest habitats in the state. Loess derived soils of the area dry out quickly, and natural rock outcroppings and the mesic microhabitats they provide are absent. Thus, it is not surprising that only 13 of Iowa's 65 pteridophyte taxa (Peck, 1976; 1984) occur in this region. It is of interest to examine those characteristics of pteridophytes that may limit their distribution in dry regions, to consider why certain species do occur here, and indeed, why a few thrive on the driest of the Loess Hills habitats, the native prairies.

PROCEDURE

Occurrence data of pteridophytes in counties containing the Loess Hills (Table 1) are derived from studies by Peck (1976, 1984) and from field studies in conjunction with biological surveys of the Loess Hills in 1981-83 sponsored by the Iowa State Preserves Advisory Board. Observations on pteridophyte ecology and reproduction are based on research in natural habitats in Iowa (Farrar and Gooch, 1975; Farrar, 1976; Carvey, 1977; Peck, 1980; Crist and Farrar, 1983; Rutz, 1982; Rutz and Farrar, 1984).

OBSERVATIONS and DISCUSSION

Pteridophytes reproduce sexually via free-living gametophyte plants which in most species are not tolerant of desiccation. Therefore, reproduction via spores generally requires a substrate that is continuously moist from the time of spore germination through gametophyte maturation and sporophyte production. This period is seldom shorter than six weeks under laboratory conditions and has been observed to be two to six months in natural habitats in Woodman Hollow, a forested canyon in Central Iowa (Farrar and Gooch, 1975; Peck 1980). These studies also showed a wide discrepancy among species in their propensity for reproduction via gametophytes. No evidence of gametophyte production for 8 of 14 species was seen during 10 years of study. Three of the species which did produce abundant gametophytes in Woodman Hollow, *Adiantum pedatum* L., *Cystopteris tenuis* (Michx.) Desv., and *Cystopteris protrusa* (Weath) Blasdell, are also present in the Loess Hills.

All of Iowa's pteridophytes are perennial; thus, regular reproduction via gametophytes is not necessary to maintain a sporophyte plant, once it is established. Furthermore, vegetative proliferation by rhizomes can in time produce clones that appear as large populations of individual plants. Theoretically, there is no limit to the age of such plants, given a stable habitat. Klekowski (1976), through excavation of underground rhizomes, determined that individual clones of

Osmunda regalis L. could be more than one hundred years old. Thus a rare success of gametophytic reproduction may suffice for initial establishment of a species in a given area, with subsequent maintenance and spread of the plants occurring through indefinite growth and branching of underground rhizomes.

Native prairies of Iowa's Loess Hills are the easternmost mixed grass prairies, dominated by little bluestem (*Andropogon scoparius*), side oats grama (*Bouteloua curtipendula*), hairy grama (*Bouteloua hirsuta*) and blue grama (*Bouteloua gracilis*). They also contain eastern disjunctions and range extensions of a number of Great Plains shrubs and forbs (see Novacek, 1985, for a discussion of the phytogeography of the Loess Hills and their relation to the Great Plains flora).

Despite this western aspect of the region, no primarily western ferns are present. This is probably due primarily to two factors: the northern latitude of the area and the absence of rock outcrops. Iowa is considerably north of the distributions of the many southwestern arid-land species of *Anemia*, *Cheilanthes*, *Notholeana*, *Pellaea*, and other genera (Mickel 1979). Absence of outcropping bedrock precludes the occurrence of most of these and Rocky Mountain cliff-dwelling species of *Asplenium*, *Woodsia*, and other genera. This hypothesis is supported by the occurrence of *Woodsia oregana* D. C. Eaton on Precambrian quartzite outcrops in Lyon County in extreme northwest Iowa, the only significant outcropping of bedrock in the western half of the state.

Table 1. Distribution of Pteridophyte species in the Loess Hills of Iowa

Species	Counties						
	Pl	Wo	Mo	Ha	Po	Mi	Fr
<i>Adiantum pedatum</i>			X		X		X
<i>Athyrium filix-femina</i>			X		X		
* <i>Botrychium</i> "prairie"	X	X	X		X		X
* <i>Botrychium virginianum</i>	X	X	X	X	X	X	X
<i>Camptosorus rhizophyllus</i>				X	X		X
<i>Cystopteris tenuis</i>		X	X		X		
<i>Cystopteris protrusa</i>	X	X	X	X	X		X
<i>Equisetum arvense</i>	X	X	X	X	X	X	X
<i>Equisetum hyemale</i>	X	X	X	X	X	X	X
* <i>Equisetum laevigatum</i>	X	X	X	X	X	X	X
* <i>Equisetum X ferrissii</i>	X	X	X	X	X	X	X
<i>Matteuccia struthiopteris</i>			X				

* Inhabitants of native Loess Hills prairies

Pl = Plymouth, Wo = Woodbury, Mo = Monona, Ha = Harrison, Po = Pottawattamie, Mi = Mills, Fr = Fremont

Forests occur on east and north facing slopes and in deep narrow valleys throughout the Loess Hills. Though forest cover in the region is greater today than at settlement, the most protected areas were forested even then (Thompson, 1981). These forests are largely dominated by bur oak (*Quercus macrocarpa*) but include more mesic species such as red oak (*Quercus rubra*), basswood (*Tilia americana*), and pawpaw (*Asimina triloba*) on the most protected slopes. These forests contain the woodland ferns *Adiantum pedatum* L., *Athyrium filix-femina* (L.) Roth, *Botrychium virginianum* (L.) Sw., *Camptosorus rhizophyllus* (L.) Link, *Cystopteris tenuis* (Michx.) Desv., *Cystopteris protrusa* (Weath) Blasdell, and *Matteuccia struthiopteris* (L.) Todaro. These are among the most widely distributed fern species in Iowa and may be presumed to be relatively more drought tolerant than, for example, species of *Dryopteris* and *Osmunda* which are limited to habitats of more or less permanent moisture in the eastern half of Iowa.

Equisetum arvense L. and *Equisetum hyemale* L. occur in riparian habitats along permanent streams and in low-lying roadside ditches. Both have rhizome systems capable of extending far below the surface, possibly as much as two meters (Borg, 1971; Rutz and Farrar, 1984). By maintaining contact with the water table, these species effectively escape the rigors of seasonal drought that are imposed upon the other pteridophytes of the area.

Four taxa of two genera grow in the driest of Iowa habitats, the native Loess Hills prairies. It is informative to consider how these four pteridophytes may be adapted to the dry prairie habitat and how they differ from the aforementioned species.

Equisetum laevigatum A. Braun is native to prairies and other open habitats throughout the western and midwestern United States (Mickel, 1979). It is characterized by deep underground rhizomes, a low above-ground to below-ground biomass ratio, and aerial stems that die back during periods of drought and in winter (Rutz, 1982). Survival in the prairie is thus accomplished through drought avoidance and underground perennation.

Equisetum X ferrissii Clute is the hybrid between *E. laevigatum* and *E. hyemale* (Hauke, 1963). Its aerial stems are more tardily senescent than those of *E. laevigatum*, but otherwise it possesses the same drought avoidance characteristics as that parent. *E. X ferrissii* occupies nearly the same distribution as *E. laevigatum* and occurs in native prairies throughout Iowa, generally at the base of slopes, below the position occupied by *E. laevigatum*. Both taxa occur commonly in roadside ditches throughout Iowa.

Sexual production of sporophytes of *E. laevigatum* or *E. X ferrissii* in nature has not been reliably documented (Duckett and Duckett, 1980; Rutz and Farrar, 1984), but their propensity for asexual reproduction is well known. Sprouting of detached sections of aerial stems of *Equisetum* is well documented (Hauke, 1963; Peck, 1980; Wagner and Hammitt, 1970), occurring within a few days, provided they are kept moist, and underground rhizome fragments regenerate equally as well (Rutz, 1982; Rutz and Farrar, 1984). Rutz and Farrar (1984) believe that rhizome fragments dispersed by road construction and maintenance activities are largely responsible for the high frequency of *Equisetum* in roadside ditches. Clonal expansion by rhizomes is also well documented; individual rhizomes may achieve several meters of growth in a single season (Borg, 1971; Rutz, 1982; Rutz and Farrar, 1984).

Persistence of these *Equisetum* taxa, even in dry prairie habitats, is clearly made possible by the vegetative capabilities of their deep underground rhizome systems. Why then are *E. arvense* and *E. hyemale*, with growth habits similar to the prairie taxa, absent from the prairie? This is unclear, but may be due to a greater above ground to below ground biomass ratio and to a longer persistence of aerial stems, particularly in the evergreen *E. hyemale*.

In a three year study in Woodman Hollow in central Iowa, Peck (1981) recorded maximum soil surface temperatures over 60 C on a south-facing hill prairie. At the same time, soil surface temperatures

in the surrounding woodland did not exceed 45 C, and those on a north-facing wooded slope reached a maximum of only 25 C. Similarly, in a study of prairie microhabitats in Freda Hafner Kettlehole Preserve in north-central Iowa, O'Keefe Van der Linden and Farrar (1983) reported simultaneous maxima of soil surface temperatures of 52 C in the prairie and 32 C in a nearby woodland in Ft. Defiance State Park. These data illustrate the extreme conditions that must be endured by organisms on or near the surface of prairie soils.

Rhizomes of most ferns, unlike those of *Equisetum*, are on the surface of their substrate or at most a few centimeters below the surface. Thus they are much more subject to extremes of drought and temperature. Perhaps this is why most fern species are limited to forests where protection from direct summer solar insolation is provided by the tree canopy. Furthermore, within the forest they are most prevalent on north and east slopes, where temperatures and evaporation are lowest.

Exceptions to the above are ferns of the genus *Botrychium*. They generally produce one leaf per year from a rhizome two to ten centimeters below ground. *Botrychium* (and *Ophioglossum* in the same family) also differs from other Iowa ferns in having underground gametophytes. Furthermore, both gametophytes and sporophytes are nourished by mycorrhizal fungi.

Given these characteristics, are *Botrychium* species better adapted for sexual reproduction in dry areas than are other ferns? Circumstantial evidence suggests that this is the case, at least with the two species of *Botrychium* occurring in the Loess Hills.

Botrychium virginianum (L.) Sw. is the most widespread fern species in Iowa. It occurs in all woodland types throughout Iowa and often is the only fern species present. It is the only species to appear naturally in recently established woodlands of the Iowa Lakeside Laboratory in northwestern Iowa and in small woodlots in central Iowa owned by the author, although *Adiantum pedatum*, *Athyrium filix-femina*, *Cystopteris tenuis*, *Dryopteris goldiana*, and *Matteuccia struthiopteris* grow well in these same areas when transplanted.

In the Loess Hills, *Botrychium virginianum* is common in all woodlands as large vigorous plants. It is also present on the native prairies, usually near the edge of advancing forests. Here, among prairie grasses and shrubs, it is greatly dwarfed, often only two to five centimeters tall. Nevertheless, these tiny sporophytes are frequently fertile. Possibly they are older than their size suggests and are stunted by the harsh conditions of the prairie habitat.

The most remarkable pteridophyte of the Loess Hills is a new species of *Botrychium* not yet described or named. This is a species of least grape ferns, the subgenus *Botrychium*. It was first discovered in Monona County, Iowa in 1982 (Fig. 1) and recognized by L. J. Eilers (Univ. of Northern Iowa) as a species new to Iowa. In the following two years, plants of this species were collected in five of the seven counties comprising the Loess Hills. Investigations by W. H. Wagner, Jr. (Univ. of Michigan, Ann Arbor) have led him to conclude that these plants represent a new species. In addition to the Iowa material, the species may be represented by specimens collected at three sites in Minnesota and three sites in Saskatchewan, Canada. Formal description and nomenclature for this species are being prepared by Wagner. For discussion in this paper it will be referred to as *Botrychium* "prairie".

Botrychium "prairie" is a tiny fern seldom more than five centimeters tall and frequently shorter than two centimeters (Fig. 2, 3). It is seen most frequently in association with the dwarfed forms of *B. virginianum*, under light shrub cover just beyond tree cover of advancing forests. It has also been found among dense grass cover in the open prairie and on all slope aspects of the prairie. Because of its size it is extremely difficult to detect among dense prairie grasses; thus, it may be questioned whether its apparent greater frequency under shrubs is an artifact of the greater ease of finding it in the lighter cover of this habitat. In any event, it is apparent that *B.* "prairie" is able to survive

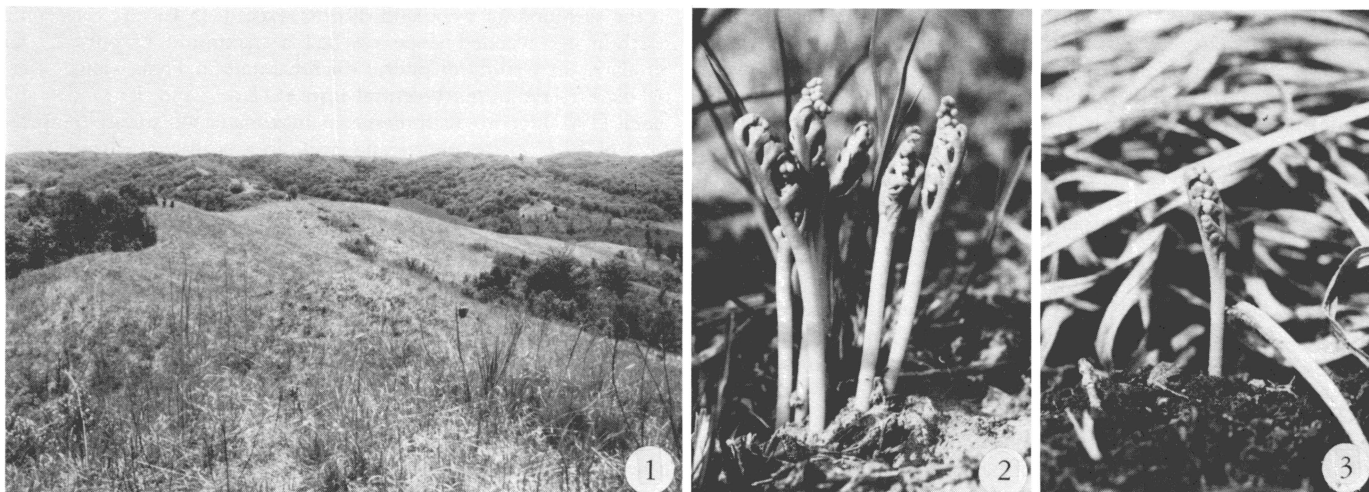


Fig. 1-3. Fig. 1 - Site of the initial discovery of *Botrychium* "prairie" in the Loess Hills Wildlife Area in Monona County, Iowa. Fig. 2 - *Botrychium* "prairie" occurring in a group of six individuals. Approximately life size. Fig. 3 - *Botrychium* "prairie" in its common occurrence as a single, small individual. Approximately life size.

the full rigor of the Loess Hills prairie habitat.

Like *B. virginianum*, *B.* "prairie" emerges in early spring and sheds its spores in late May and early June. By mid-June its leaves begin to wither and disappear. This phenology is in contrast to other species of the subgenus *Botrychium*, which mature and shed spores in summer to late fall. Other species of the subgenus also differ in habitat, growing in moist woodlands and meadows in northern latitudes and/or high elevations. Though contrasting with the norm for the subgenus, these characteristics in *B.* "prairie" are also compensating. By completing its above ground activity in early spring, *B.* "prairie", grows in the Loess Hills during a period when that habitat is similar to the habitat of related species in meadows of high latitudes and high elevations. Conceivably, ancestral *B.* "prairie", with a phenology and habitat more typical of the subgenus, might have occurred in the northern plains during the more northerly climatic periods of the Pleistocene and subsequently differentiated toward an earlier phenology, thus maintaining its period of aerial growth in a relatively cool, moist season.

The low number of pteridophyte taxa in the Loess Hills is not surprising considering the arid climate and absence of mesic microhabitats. Those present are testimony to pteridophyte capabilities of drought tolerance and drought avoidance, and of vegetative perennation. The success of *Botrychium* in prairie habitats adds new significance to the habit of subterranean reproduction in this genus.

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