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Patterns of Sporophyte Maturation Dates in the Pottiaceae (Bryopsida)¹

RICHARD H. ZANDER²

Abstract. Patterns of sporophyte maturation dates (SMDs) in the Pottiaceae correlate with sexual condition, latitude, date of regional precipitation maximum, habitat and taxonomic group. Most closely related species have SMDs at about the same time (at the month or season level of resolution), but many species complexes, sections, genera and suprageneric taxa have distinctive SMDs that may be used as taxonomic characters. An eurychronic group of mostly dioicous, largely hygrophilic species shows a relatively great differentiation of SMDs between geographic regions.

A review of the literature on sporophyte maturation dates (SMDs) in taxa of the Pottiaceae was undertaken to determine its possible taxonomic value. Major floristic studies of the Bryopsida, since the time of Hedwig, commonly give the season or month(s) of sporophyte capsule maturity as part of the species description, yet seldom is this characteristic used in distinguishing taxa. Near the turn of the century, several studies (Arnell, 1875, 1905; Grimme, 1903; Krieger, 1915) of moss phenology sought to compare dates of sporophyte maturation in taxa but were handicapped by the small number of species for which information was known. Since then, many floristic studies have included phenological information, and this paper summarizes the data on the family Pottiaceae given in 10 major floristic manuals concerning widely scattered areas of the North Temperate Zone of both Old and New Worlds.

The probable intent of early authors was to provide data for mosses comparable to times of anthesis in flowering plants. However, because syngamy in mosses occurs up to one year or more before the date of capsule dehiscence, while in angiosperms it occurs just after anthesis, information about sporophyte maturation dates cannot be directly used to estimate degree of temporal reproductive isolation of taxa by different fertilization times. As has been emphasized by Forman (1965), Greene (1960) and Scott et al. (1976), species-specific variations in time of fertilization and of SMD have been described for relatively few mosses. Forman (1965) and Greene (1960) suggested notational systems for recording phenological stages of the life cycles.

Previous large-scale studies comparing times of fertilization and of sporophyte maturation have dealt with only a few species of each of many families of mosses and involve only one or two floristic regions. Grimme (1903) compared Arnell's (1875) data from Scandinavia with that given by Limpricht (1890–1894) for Germany, Austria and Switzerland and found that sporophyte development in German mosses usually took a longer time than did Scandinavian mosses of the same species. Fertilization occurred one or two months earlier in Germany. This was apparently related to the longer growing season of the southern areas. He also concluded from his own obser-

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vations that maturation of gametoecea (= "inflorescences") in German mosses occurred over a short period of the year, peculiar to each taxon. Each species appeared to have a distinctive duration of sporophyte development lasting between four and 24 months. In the Pottiaceae, species in Germany usually took 10–13 months to complete sporophyte development, but some annual species took as short a time as six months, and one species, *Didymodon rigidulus* Hedw., took 16–19 months.

Krieger (1915) supported Grimme's (1903) observation that climate differences associated with latitude correlate well with time of fertilization and duration of sporophyte development in German mosses, and noted that altitude was another major factor influencing dates. Edaphic factors appeared to have little influence except that very wet habitats had somewhat shorter duration of sporophyte development. The usual duration of sporophyte development in the Pottiaceae, given as 12–13 months, was the same as that of most other families he studied. Krieger noted that individuals within the same polster may deviate considerably in duration of sporophyte development, e.g. in one clump of *Tortula muralis* Hedw. sporophytes with somewhat longer setae had capsule dehiscence delayed up to a week.

Arnell (1905) separated *Polytrichum* into two phenologically different groups, one requiring about 13 months for sporophyte development and capsule dehiscence occurring in July or early August, and the other taking seven to ten months for sporophyte development and dehiscing in winter or early spring. Arnell also compared dates of fertilization and of sporophyte maturation between populations of species in Germany and Sweden and found, as did Grimme (1903), that both fertilization date and SMD were earlier in Germany. Although many German populations did show a somewhat longer duration of sporophyte development than did Swedish populations of the same species, the reverse was true in other species.

Towle (1905, 1906) considered her phenological studies in Vermont to have taxonomic importance. She suggested that certain *Mnium* species were closely related because of very similar dates of fertilization and spore discharge, and *Atrichum* and *Polytrichum* were distinguished by phenology. Towle and Gilbert (1904) noted that populations of two *Polytrichum* species in Vermont had the same duration of sporophyte development that was reported by Grimme (1903) for European populations.

Only relatively recently have further studies been made of dates of fertilization and sporophyte maturation, and few of these deal directly with taxonomic problems (Forman, 1965). Jones (1947), in part using phenological characters, distinguished between two species of *Ulota* in the United Kingdom. Tallis (1959) studied *Rhacomitrium lanuginosum* (Hedw.) Brid. in the field in the United Kingdom, noting that young capsules develop in September and early October at lower altitudes but two to six weeks later at higher altitudes. They ripen the next year, earlier at low altitudes. Greene (1960) advocated phenological studies using herbarium specimens, noting that little change occurs in phenological state of the specimens on drying. Greene and Greene (1960) used phenological characters to distinguish between *Pylaisiella polyantha* (Hedw.) Grout and *Hypnum cupressiforme* (Wils.) Schimp. in the United Kingdom. The laboratory experiments of Benson-Evans (1961, 1964) indicated that the seasonal production of gametangia in many liverwort species is related to relative daylength, some being long- and others short-day plants, while in the moss *Polytrichum* and the liverwort *Cryptothallus* temperature alone induced gametangial formation. However, short days stimulated development of capsule and spore production in *Polytrichum*.

Belkengren (1962) suggested that starvation, through lack of photosynthesis and

shortage of nutrients, induced gametangial formation in cultures of *Leptodictyum riparium* (Hedw.) Warnst. Monroe (1965) found that low temperature (10°C), not day length, is the important factor influencing the initiation of gametangia in *Funaria hygrometrica* Hedw. According to Schuster (1966, p. 189), the majority of hepatic species in the Northern Hemisphere form mature sporophytes during the period March to June.

Lemmon (1968) studied the phenology of *Astomum* and *Weissia* species in the southeastern United States. The three species studied usually had mature sporophytes at different dates, separated by two weeks to a month. Internal genetic barriers to outcrossing, in addition to microgeographic and temporal barriers, were assumed to usually act to keep the species and races distinct; however, some hybrids were found.

Johnsen's (1969) phenological study of *Orthotrichum anomalum* Hedw. in northern Arizona showed that most sporophytes matured (being operculate but post-meiotic) in early spring during wet and cold weather but final maturation and dehiscence of the capsule occurred during the late spring to early summer drought. Culture studies indicated that time of gametangial initiation and sporophyte development are independent of photoperiod and temperature. Hughes and Wiggin (1969) found that the sporophyte of *Phascum cuspidatum* Hedw. grown under laboratory conditions could mature in as little as 35 days after fertilization. Clarke and Greene (1970) studied two *Pohlia* species in the Arctic, the United Kingdom and on the island of South Georgia in the south Atlantic Ocean. They found strong latitudinal effects on time of sporophyte development. Longton (1972) reviewed literature relating effects of photoperiod and temperature on initiation of gametangial development, noting that reproductive cycles seem to be largely under environmental control. He correlated reproduction of Antarctic species of *Polytrichum* and *Psilopilum* with temperature, finding that dehiscence of gametangia occurred earlier in more favorable climates. Anderson's (1974) review indicated that mosses are dependent either on temperature regimes or endogenous rhythms for control of gametangial initiation. Zehr (1969) found photoperiodism to control the formation of gametangia in several species of bryophytes.

Variation between sporophyte maturation dates of closely related species in one geographic location may indicate different times of gametangial maturation. Indeed, Lemmon (1968) felt that a difference of usually two weeks between SMDs of *Astomum muhlenbergianum* (Sw.) Grout and *A. ludovicianum* (Sull.) Sull. and of about one month between these dates and that of *Weissia controversa* Hedw. is sufficient evidence to indicate a large degree of temporal reproductive isolation between the three species. However, at the level of resolution given by most authors of taxonomic treatments, most closely related species appear to overlap in SMDs.

The family Pottiaceae has many of the taxonomic problems common to the Bryopsida, including over classification through geographic (Touw, 1974) and pigeonhole (Grout, 1938) species concepts, paucity of revisionary studies (Anderson, 1963), lack of biological basis for the species concept (Greene, 1976; Steere & Inoue, 1972) or for that of the genus (Anderson, 1974), apparent lack of parallelism of evolution of the sporophyte and the gametophyte (Anderson, 1963), typological concepts of morphology (Zander, 1977) and over reliance on the constancy of certain taxonomic characteristics (Zander, 1977, 1978a,b). The family has, in addition, certain features that are not peculiar to the family but in toto boggle the taxonomist. These include interspecific and intergeneric hybridization (reviewed by Anderson, 1974), a high incidence of intra- and interspecific polyploid series (Fritsch, 1972; Steere, 1972), apomixis and

sterility (Gemmell, 1950; Saito, 1975; Whitehouse, 1966), and polymorphism associated with variation in climate and habitat (Lazarenko, 1963; Lazarenko & Lesnyak, 1972; Zander, 1977, 1978a,b). This paper evaluates sporophyte maturation dates in the Pottiaceae as yet another character that may be used to segregate taxa in this taxonomically difficult family.

METHODS AND PRESENTATION OF DATA

Information on sporophyte maturation dates in the Pottiaceae was extracted from 17 taxonomic and floristic papers in ten major floristic studies. Only areas of the north temperate zone were studied: North America (Craig, 1939; Grout, 1938–1939; Steere, 1938a,b, 1939; Wareham, 1939—all papers contributed to Grout's Moss Flora of North America North of Mexico), Pennsylvania (Jennings, 1951), Indiana (Welch, 1957), Utah (Flowers, 1973); Scandinavia and Finland (Nyholm, 1956); United Kingdom and Ireland (Dixon, 1924); Germany, Austria and Switzerland (Limpricht, 1890–1894); France (Husnot, 1884–1894); U.S.S.R. (Savicz-Ljubitzkaja & Smirnova, 1970); and Japan (Saito, 1973, 1975). The data given here concern 36 genera, representing the major subfamilies and tribes of the Pottiaceae recognized by recent authors (reviewed by Saito, 1975). Crosby and Magill (1977) assign 91 genera to the Pottiaceae in the Dictionary of Mosses.

The degree of resolution of dates of sporophyte maturation given by each author is usually within a consecutive two- or three-month range. This wide span may be, in part, due to latitudinal, elevational or local climatic differences within each floristic area studied. The reports were nearly always given as consecutive months or seasons. Some similarity of data between authors may indicate a degree of cribbing or uncritical acceptance of the data of other authors; however, one might expect at most use of earlier data only as guides—most data did show at least minor variation between authors. I have assumed that phrases used by various authors indicating date of mature capsules, ripe spores, "fruiting," etc., are all equivalent to what I am here calling sporophyte maturation date (SMD). Very close or identical dates given for each of many species by many authors support this, and much variation may be correlated with environmental factors, as noted below.

The names and authorities of taxa and synonymy is that accepted by the Index Muscorum (van der Wijk et al., 1959–1969) excepting certain recent revisions (Delgadillo, 1975; Robinson, 1970; Saito, 1973, 1975; Zander, 1977, 1978a,b). For ease in comparing traditionally accepted taxa, I have made some attempt to preserve certain narrow taxonomic concepts. Thus *Trichostomopsis* is retained here, though recently merged with *Didymodon* (Zander, 1978b) but several species of *Barbula* are recognized in *Didymodon* following Zander (1978b). *Desmatodon plinthobius* is recognized in *Tortula* for reasons discussed below. *Weissia hedwigii* Crum replaces *W. microstoma* (Hedw.) C. Muell. (Crum, 1971). Essentially tropical species that were cited by some authors, but not included in this study, are *Barbula agraria* Hedw., *B. indica* (Hook.) Spreng. and *Trichostomum jamaicense* (Mitt.) Jaeg.

Table 1 reviews the data on sporophyte maturation dates of species and infraspecific taxa of Pottiaceae, and Figure 1 summarizes this data in a graphic manner. Table 1 lists (at left) species and infraspecific taxa of Pottiaceae, and (at right) gives the number of reports (of a total of 10 possible, corresponding to the 10 floristic treatments consulted) that give a date or period of sporophyte maturation for that taxon. In general the larger the number of reports, the more widely distributed is the taxon in the North Temperate Zone. The central 12 columns are the months of the year, beginning with March, and every three months is grouped into a season. The calendar equivalency is inexact but adequate for the degree of resolution involved. Numbers in the 12 columns refer to numbers of reports mentioning sporophyte maturation during each month. Reports given only as seasons are presented in the table as all three consecutive months of that season. Reports giving an "early," "mid-" or "late" season citation are shown here as a single month at the appropriate time. Because seasons were given by authors far more commonly than were months, the numbers in Table 1 are often in groups of threes.

In Figure 1 the categories in the largest type face (above) refer to the vertical set of graphs directly below, excepting Cinclidotoideae, Leptodontieae and Trichostomeae, which are intercalated to save space. Within each graph is the name of the taxon, the total number of species and reports dealt with (the latter in parentheses) and a double graph that should be read against the percentage marks to the far right. The graphs are divided into four seasons, beginning with spring, and each season is divided into three months as in Table 1. Each graph includes two

TABLE 1. Sporophyte maturation dates of North Temperate Zone Pottiaceae. The twelve columns give number of reports for each taxon (from among 10 floristic treatments consulted) for each month of the year, beginning on the left with March. D = dioicous, M = monoicous, D-M = heteroicous.

	Spring			Summer			Autumn			Winter			Total reports
	M	A	M	J	J	A	S	O	N	D	J	F	
Pottioideae													
Pottieae													
<i>Acaulon</i>													
<i>muticum</i> D	6	4	4			1	1	1	3	6	6	6	6
var. <i>rufescens</i> D	1									1	1	1	1
<i>schimperianum</i> D-M										1	1	1	1
<i>triquetrum</i> D	6	1	1						1	1	1	1	6
<i>Phascum</i>													
<i>crucicolle</i> M	5	4	4							1	1	1	5
<i>cuspidatum</i> M	8	7	7	1						1	1	1	8
<i>floerkeanum</i> M							1	1	3	3	3	3	5
<i>Aloina</i>													
<i>aloides</i> D	1	1	1				1	1	3	5	5	5	5
var. <i>ambigua</i> D-M	2	2					3	3	3	5	5	5	5
<i>brevirostris</i> D-M				1	1	2	2	2	4				5
<i>rigida</i> D-M	1	1	1						2	3	3	3	4
<i>Crossidium</i>													
<i>aberrans</i> D-M										1	1	1	1
<i>squamiferum</i> D-M	4	3	2										4
var. <i>pottioideum</i> M	2												2
<i>Pterygoneurum</i>													
<i>lamellatum</i> M	4	4	3										4
<i>ovatum</i> M	5	2	2							1	1	2	7
<i>subsessile</i> M	3	1	1									1	4
<i>Pottia</i>													
<i>arizonica</i> M	1												1
<i>bryoides</i> M	5	5	5							2	2	2	6
<i>davalliana</i> M	1	1	1				2	2	2	2	2	2	5
subsp. <i>commutata</i> M	1	1	1	1						3	3	3	3
<i>fosbergii</i> M	1	1	1										1
<i>heimei</i> M	2	2	6	2		1							7
<i>intermedia</i> M	2	1	1						2	4	4	4	4
<i>lanceolata</i> M	6	6	5										6
<i>mutica</i> M	1	1	1	1						1	1	1	3
<i>nevadensis</i> M			1	1									1
<i>recta</i> M	3	3	3							2	2	2	4
<i>starkeana</i> M	4	2	2							1	1	4	6
<i>truncata</i> M	6	6	6				4	4	6	6	6	6	7
<i>viridifolia</i> M	1	1	1							2	2	2	2
<i>wilsonii</i> M	1	1	1							2	2	2	2
subsp. <i>asperula</i> M										1	1	1	1
var. <i>crinita</i> M	1	2	1							2	2	2	3
<i>Desmatodon</i>													
<i>cernuus</i> M				3	5	4							6
<i>convolutus</i> M	6	6	6							1	1	1	6
<i>latifolius</i> M				6	6	6	1	1	1				7
<i>laueri</i> M				4	6	3	1						6

TABLE 1. Continued.

	Spring			Summer			Autumn			Winter			Total reports
	M	A	M	J	J	A	S	O	N	D	J	F	
<i>leucostomus</i> M				3	5	4							6
<i>obtusifolius</i> M	3	3	4	6	3	4	2	2	2				8
<i>porteri</i> D	2												2
<i>systylius</i> M				2	4	2							4
<i>Tortula</i>													
<i>amplexa</i> D						1							1
<i>buyssonii</i> M				1	1	1							1
<i>canescens</i> M	4	3	2								1		4
<i>cuneifolia</i> M	3	3	4										4
<i>ferganensis</i> D				1	1	1							1
<i>fragilis</i> D						1							1
<i>guepinii</i> M	1	1	1										1
<i>inermis</i> M	4	5	5	2									5
<i>intermedia</i> D	3	3	4	3	2	2							6
<i>laevipila</i> M	1			5	3	2							5
<i>latifolia</i> D	4	3	2	2	1	1							5
<i>lingulata</i> D				1	1	1							1
<i>marginata</i> D	4	4	4										4
<i>mucronifolia</i> M				2	3	6							6
<i>muralis</i> M	5	6	6	5	3	2							8
var. <i>aestiva</i> M				1	1	1							1
<i>norvegica</i> D				2	2	2							2
<i>plinthobius</i> D-M	1	1	1										1
<i>princeps</i> M	6	6	6	1									6
<i>revolutifolia</i> M				1	1	1							1
<i>revolvens</i> M	1	1	1										1
<i>ruralis</i> D	5	5	6	4	1	2	1						8
subsp. <i>ruraliformis</i> D	1	1	1	1	1	1							1
<i>sinensis</i> M				3	4	3			1				4
<i>subulata</i> D-M	2	2	2	5	3	1							6
var. <i>angustata</i> M				1									1
<i>thianschanica</i> M				1	1	1							1
<i>transcaspica</i> M	1	1	1										1
<i>vahliana</i> M	3	3	3										3
<i>virescens</i> D	2	1	2	1									3
<i>Stegonia</i>													
<i>latifolia</i> M	2	2	2	4	4	4	1						7
<i>Weisiopsis</i>													
<i>anomala</i> M									1	1	1	1	1
Barbuleae													
<i>Barbula</i> sect. <i>Barbula</i>													
<i>unguiculata</i> D	8	3	3						1	6	6	6	9
sect. <i>Revolutae</i>													
<i>revoluta</i> D	4	4	4	1	1	1							4
var. <i>hornschuchiana</i> D	5	5	5										5
sect. <i>Streblotrichum</i>													
<i>bicolor</i> D				1	1	3							3
<i>convoluta</i> D	5	5	6	4	1	1							6
<i>coreense</i> D				1	1	1							1
<i>crocea</i> D				1	1	1	4	4	3				4
<i>enderesii</i> D				1	1	1	2						3
<i>horrinervis</i> D							1	1	1				1

TABLE I. Continued.

	Spring			Summer			Autumn			Winter			Total reports
	M	A	M	J	J	A	S	O	N	D	J	F	
<i>Hymenostylium</i>													
<i>recurvirostrum</i> D	1	1	1	3	3	6	4	5	5				9
var. <i>aurantiacum</i> D							1	1	1	1	1	1	1
<i>Molendoa</i>													
<i>hornschuchiana</i> D				1	1	3							3
<i>sendtneriana</i> D				1	2	2	1	1	1				4
<i>Pleuroweisia</i>													
<i>schliephackei</i> D				1	1	2							2
Leptodontieae													
<i>Leptodontium</i>													
<i>flexifolium</i> D	4	2	1				1	1	1	1	1	1	4
Trichostomoideae													
Tortelleae													
<i>Tortella</i>													
<i>flavovirens</i> D	6	6	6										6
var. <i>viridiflava</i> D	1	1	1										1
<i>fragilis</i> D				2	3	3							3
<i>humilis</i> M	4	4	5	5	2	2							6
<i>inclinata</i> D	2	3	3	1	1	1							4
<i>inflexa</i> D	3	3	3										3
<i>japonica</i> M							1	1	1				1
<i>tortuosa</i> D	1	1	4	8	5	5							8
<i>Pleurochaete</i>													
<i>squarrosa</i> D	2	2	3	3									5
<i>Oxystegus</i>													
<i>tenuirostris</i> D	1	1	1				6	6	8	2	2	2	9
<i>Pseudosymblepharis</i>													
<i>angustata</i> D							1	1	1				1
Trichostomeae													
<i>Astomum</i>													
<i>crispum</i> M	6	6	6							1	1	1	6
var. <i>sterile</i> M												1	1
<i>exertum</i> M	1	1	1										1
<i>ludovicianum</i> M	1												1
<i>mittenii</i> M	1												1
<i>muhlenbergianum</i> M	2	1	1										3
<i>multicapsulare</i> M	3	3	3										3
<i>Weissia</i> subg. <i>Hymenostomum</i>													
<i>atrocaulis</i> M				1	1	1	1	1	1				1
<i>edentula</i> M	1	1	1				1	1	1				1
<i>hedwigii</i> M	7	7	7	2									7
<i>newcomeri</i> M	1	1	1										1
<i>rostellata</i> M	2	1	1				1	1	1	2	2	2	4
<i>squarrosa</i> M	1						1	1	1	4	4	4	5
<i>tortilis</i> M	5	4	4										5
subg. <i>Weissia</i>													
<i>controversa</i> M	8	8	8				1	1	1				8

TABLE 1. Continued.

	Spring			Summer			Autumn			Winter			Total reports
	M	A	M	J	J	A	S	O	N	D	J	F	
<i>fallax</i> M	1	1	1										1
<i>longidens</i> M	1	1	1										1
<i>planifolia</i> M							1	1	1				1
<i>rutilans</i> M	5	5	5										5
subsp. <i>ganderi</i> M				1	1	1	1	1	1				2
<i>tyrrena</i> M	1	1	1										1
<i>wimmeriana</i> M	1	1	2	3	2	2							3
<i>Aschisma</i>													
<i>carniolicum</i> M										1	1	1	1
<i>Trichostomum</i>													
<i>brachydontium</i> D	4	4	4										4
subsp. <i>mutabile</i> D	2	2	1										2
<i>caespitosum</i> M	3	3	3										3
<i>crispulum</i> D	5	5	4	1						1	1	1	6
<i>platyphyllum</i> D	1												1
<i>spirale</i> M									1				1
<i>triumphans</i> M				1	1	1							1
var. <i>pallidisetum</i> M				1	1								1
<i>viridulum</i> D				1	2	1							2
<i>Timmiella</i>													
<i>anomala</i> M	1	1	1	4	4	5	1	1	1				5
<i>barbuloides</i> D	1	1	1	2	2	2							2
<i>flexiseta</i> D				3	3	3							3
Cinclidotoideae													
<i>Cinclidotus</i>													
<i>aquaticus</i> D	2	2	2										2
<i>fontinaloides</i> D	1	1	1	4	4	4				1	1	1	5
<i>riparius</i> D				2	3	3							3
<i>Dialytrichia</i>													
<i>mucronata</i> D	3	3	3	1									3

lines, these occasionally overlapping. The thicker line refers to the number of taxa with mature sporophytes during each month expressed as a percentage of total taxa involved, and is filled in below with stippling to facilitate comparison between graphs. The thin line refers to the number of reports upon which the values that are indicated by the bold line are at any one time based, expressed as a percentage of total reports involved. This last value gives some indication of the geographic range of the data reported. The sum of the percentages given for the seasons of the year usually exceed 100 percent because many taxa have SMDs that include more than one season.

GENERIC AND SUPRAGENERIC TAXONOMY AND SMD

A comparison of the graphs of the suprageneric taxa in Figure 1 summarizes the trends in sporophyte maturation dates. The Trichostomoideae have mainly spring SMDs (the included tribes being little different in this respect); the Pleuroweisiae mature in midyear; the Barbuleae have a weak modality, somewhat similar to that of the Pleuroweisiae; and the Pottiae have SMDs mainly in spring but also in summer

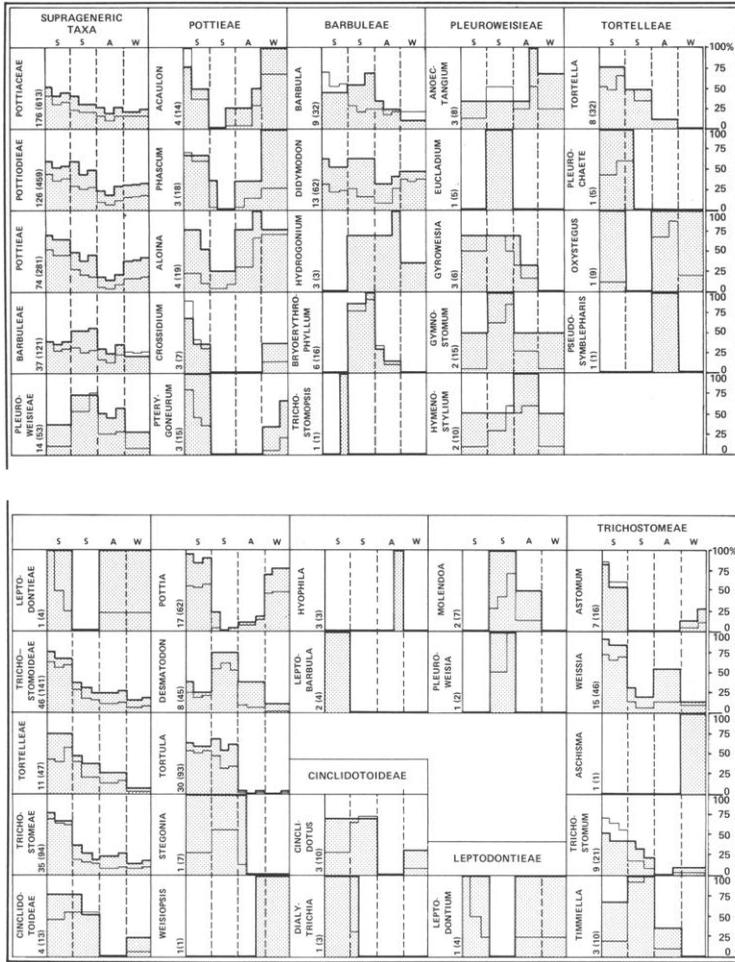


FIGURE 1. Summary of sporophyte maturation dates in genera and suprageneric taxa of Pottiaceae. Given are total number of species and infraspecific taxa for each genus or higher category and, in parentheses, total number of reports. Bold lines (stippled-in below) refer to number of species and infraspecific taxa with mature sporophytes at any one time expressed as a percentage of total species and infraspecific taxa. Thin lines indicate number of reports for each period expressed as a percentage of total reports (a crude estimate of geographic area involved). The charts begin on left (top to bottom) with the season of spring and the month of March as in Table 1.

and winter. The Cinclidotoideae have spring and summer SMDs. The Leptodontieae are poorly known but apparently have mainly spring SMDs in north-temperate areas.

Sporophyte maturation dates often correlate at the generic level with regional climate (as described by Critchfield, 1960; Trewartha, 1937; Walter, 1973) and characteristic habitat. Although mosses usually liberate spores in dry weather, when wind turbulence may enhance dispersal (Ingold, 1965), most species of Pottiaceae do not have mature sporophytes in late summer or autumn. This characteristic may be due to the stress-tolerant ruderal (Grime, 1977) nature of many Pottiaceae species and an

increase in competition from annual vascular plants, together with a general lack, then, of moist, bare soil for colonization. Snow melt may be an important source of moisture sufficiently constant to ensure protonemal establishment, and spores are dispersed when annual dry periods commence. The precipitation maximum for humid, continental warm-summer climates, areas most studied, is during spring or summer (Critchfield, 1960). Nearly all species of variable, dry, midlatitude, lowland habitats have SMDs in winter, spring or early summer. Correlation with various precipitation maxima is also apparent in spore discharge dates of lichens, according to data given by Pyatt (1969).

The most common variation in vernal sporophyte maturation modality is emphasis on either winter and spring dates, e.g. by *Acaulon*, *Phascum*, *Pterygoneurum*, *Pottia*, *Aloina* and *Crossidium* or on spring and summer dates, e.g. *Tortula*, *Stegonia*, *Tortella*, *Pleurochaete* and *Trichostomum*. The first four genera of the former group are considered annuals, commonly found in extreme ruderal situations of bare earth or among grasses. Grimme (1903) gave durations for sporophyte development of 9 and of 7–10 months, respectively, for two species of *Phascum*, and of 6–8 and 7–9 months for two species of *Pottia*. However, he noted that two taxa of *Aloina* need 12 months to complete sporophyte maturation. Flowers (1973) observed the fertilization time of *Pterygoneurum* species in Utah to occur in the autumn, with capsule maturation by early spring. *Aschisma* may observe the same general wintertime requirement for SMD as do annual species of Pottiaceae. *Aloina* and *Crossidium* may have similar SMDs because of their common habitat in arid and semiarid regions, perhaps being affected by the occurrence of moderate snowfall in steppe regions and the winter precipitation maximum in Mediterranean climates. However, they differ strongly in SMDs from species of *Tortula* of similar regions, in that these lack winter SMDs. One might suppose that a genetic difference between the genera is operating. Spore dispersal in annuals probably involves a mechanism other than wind, as in those adaptations for short dispersal distances of atelochorous and synapterospermous species of vascular plants discussed by van der Pijl (1972).

Those genera with SMDs mainly in spring and early summer are in two taxonomically distinctive groups. In the first, *Tortula* and *Stegonia* are closely related. The habitats occupied by the numerous species of the former genus are diverse, but the SMDs are very similar. *Stegonia* is an alpine genus and its SMDs are probably retarded by the short growing season. Recently, *Crumia* Schof. was placed by Schofield (1966) near *Tortula* on morphological grounds. Its spring SMD also supports this disposition. The second group consists of *Tortella*, *Pleurochaete* and *Trichostomum*; these are also closely related to each other. In view of the diversity of habitats of the many species in this group, the restriction to spring and summer in these taxa, as in *Tortula*, may be related to temperature or photoperiod rather than to precipitation. Sporophytes of *Weissia* and *Astomum* are commonly thought to develop very quickly (Crum, 1973; Lemmon, 1968); however, Grimme (1903) gave 11–12 and 10–12 months, respectively, for sporophyte development in species of these genera. These longer spans, if correct, may account for the similarity of their graphs in Figure 1 with that of the closely related *Trichostomum*.

Hygrophilic taxa, such as those found in seepage, on moist ledges or near waterfalls, typically have SMDs in summer or autumn (Figure 1). Genera of this sort include *Hydrogonium*, *Bryoerythrophyllum*, *Hyophila*, *Cinclidotus* and most genera of the Pleuroweisiae, including *Anoectangium*, *Eucladium*, *Gyroweisia*, *Gymnostomum*, *Hymenostylium*, *Molendoa* and *Pleuroweisia*. Both Chen (1941) and Hilpert (1933)

recognized the Hyophileae as a tribe separate from the Barbuleae; however, phenological data are not supportive of taxonomic segregation, as these may only reflect the typical hygrophilic habitat. The Pleuroweisieae itself appears to be polyphyletic on morphological grounds (Zander, 1977), and its phenology may be strongly influenced by the wet habitats of most species. The relative dryness of habitat during summer might greatly affect the maturation cycles of hygrophiles, in that appropriate substrate for new growth is then well exposed and, as noted, by Johnsen (1969) for *Orthotrichum anomalum*, final maturation and dehiscence of the capsule may await a period of drying. Interestingly, all the above genera except *Cinclidotus*, *Anoectangium*, *Hymenostylium* and *Pleuroweisia* are reported (Saito, 1975; Zander, 1977, 1978a) to have specialized propagula. These are rare in most genera of Trichostomoideae and Pottiaceae but are common in the genera *Barbula* and *Didymodon*. Their presence may be related to the same factors in the habitat that determine midyear SMDs. *Dialytrichia* is usually considered closely related to the hydrophilous genus *Cinclidotus* but lacks late summer or autumn SMDs. This is possibly because *D. mucronata* (Brid.) Broth. is a stream-bank species and does not grow immersed in water as do species of *Cinclidotus*. Limpricht (1890–1894) put *Dialytrichia* and *Cinclidotus* in separate families, the Pottiaceae and Grimmiaceae, respectively, recognizing major differences between the two genera in capsule anatomy. Thus, the phenological differences may be due to phylogenetic relationships rather than to different habitats.

Genera that have SMDs mainly in late summer or autumn, but which are not commonly thought of as hygrophilic include: *Aloina*, *Desmatodon*, *Barbula*, *Didymodon*, *Pseudosymblypharis* and *Timmiella*. Some of these include montane-northern species with a much shortened growing season, and others have species apparently responding to autumnal maximum precipitation in monsoon Japan or in interior continental steppes. The modality in the graph of sporophyte maturation dates in *Aloina* (Figure 1) may be explained by the overlapping of data from all species in autumn (Table 1). Characteristic SMDs for *Aloina* is actually winter to spring, as it is for related genera, and may correspond to the winter precipitation maximum typical of Mediterranean climates (Critchfield, 1960), such as occurs in parts of southwestern United States where species of *Aloina* are widely distributed. Although the precipitation maximum for interior continental plains, arid and semiarid deserts and steppes at midlatitudes occurs in summer, areas with moderate snowfall may be more constantly moist during winter and early spring, judging from data given by Johnsen (1969). Most taxa of *Desmatodon* have mainly midyear SMDs (Table 1). Habitat data (especially that of Flowers, 1973) indicates that these are mainly steppe or montane taxa.

Although *Barbula* and *Didymodon* species are scarcely mesophytes in appearance, those species that liberate spores mainly in late summer or autumn are taxa of interior montane regions with short growing seasons, except *D. spadiceus* (Mitt.) Limpr., which is a hygrophile, and *B. horrinervis* K.Saito, which may be responding to the dry summers and wet autumns of Japan. The secondary peak of spore liberation time in *Weissia* is due to reports (Saito, 1975) of bimodal SMDs (spring and autumn) in two Japanese species, probably on account of a secondary maximum in precipitation in early summer—the “*Baiu* rains”—in Japan (Critchfield, 1960). The midyear modality of *Timmiella* is difficult to explain. Although this genus is often found in relatively evenly moist habitats, it occurs mainly in regions with autumn or winter precipitation maxima. In other genera some species that lack midyear SMDs also often grow in evenly moist areas, e.g. *Pottia heimeii* (Hedw.) Fűrnr. in Hampe.

Some genera—*Leptodontium*, *Oxystegus*, *Gymnostomum* and *Didymodon*—appear to produce sporophytes about equally throughout the year. The first two genera mentioned contain only one species for which data are known and the second only two species. The indication of number of reports in Figure 1 for each month (thin line on graph) may be a better indication of peak in SMD. *Oxystegus tenuirostris* (Hook. & Tayl.) A.J.E.Sm. is a species of moist habitats and should be considered typical of hygrophilic species with late summer and autumn SMDs. The rather undistinctive graph of *Didymodon* may be due to the large variation in geographic range and in climate optima of the species. The genus includes several often polymorphic species that occupy a wide latitude and climatic range. The appearance that *Weisiopsis* is out of place in the Pottiaeae may be false, since the graph is of only one species, and, like *Aschisma*, the genus may observe an annual SMD. Allowing for influences of habitat and latitude, the major similarities and differences between taxa in SMDs appear to be worthwhile additional characteristics that, in large part, support the generic and suprageneric scheme followed here, which is mainly that of Saito (1975). However, although the hygrophilic tribe Pleuroweisieae has a characteristic SMD range, this phenology is duplicated by unrelated hygrophilic taxa. The phenology, thus, does not counter morphological evidence suggesting that the Pleuroweisieae is polyphyletic.

INTERSPECIFIC RELATIONSHIPS AND SMD

Two species which, following van der Wijk et al. (1959–1969), are included here in *Desmatodon* have SMDs rather different from the typical midyear dates of the other species of the genus (type species = *D. latifolius* (Hedw.) Brid.). *Desmatodon obtusifolius* (Schwaegr.) Schimp. has been recognized in the genus *Tortula* in recent studies by Nyholm (1956), Saito (1973) and Savicz-Ljubitskaja and Smirnova (1970), and this disposition would correlate with habitat and phenological data. The other species, *D. porteri* James in Aust., is unusual for the genus in that it is dioicous and has an areolation of small, very papillose leaf cells, unlike those of typical *Desmatodon* species. Future studies may do well to recognize both taxa as species of *Tortula*.

Most of the 30 taxa of *Tortula* treated here show either a spring or a summer SMD. There appears to be no correlation of dates with sexual condition (Table 1), but a correlation is evident with geographic distribution (as given by Podpěra, 1954; Savicz-Ljubitskaja & Smirnova, 1970). Taxa of *Tortula* that have summertime SMDs characteristically occur only in areas of short growing season, such as circumboreal areas or montane to alpine regions, or in midlatitude continental steppes affected by summer rainfall maximum. *Tortula virescens* (DeNot.) DeNot. is the only exception. Taxa with dates in spring are mainly in areas with long growing seasons. These regions include Mediterranean or marine climates, which are very dry in summer and wet in winter, or moist, central lowlands which have spring or summer precipitation maxima but no distinct dry season. Exceptions include *T. amplexa* (Lesq.) Steere and *T. fragilis* Tayl., which have been only poorly studied, and *T. laevipila* (Brid.) Schwaegr., for which retarded SMDs may be somehow related to its unusual corticolous habitat. The SMDs fail to support recognition of Visotska's (1967) proposed subfamily Tortuloideae, which is based on a chromosome number of $x = 12$ and was to contain *Tortula*, *Aloina* and *Crossidium*. This subfamily is also criticized on cytological grounds by Nyholm and Wigh (1973) because several species of *Tortula* have a basic chromosome number of $x = 13$.

Tortula plinthobius (Sull. & Lesq.) Broth. is usually recognized in *Desmatodon*, but on phenological and morphological grounds it is better considered a *Tortula*. Flowers (1973) asserted that the only reliable character distinguishing this species and *T. muralis* Hedw. is the short peristome of the former. Although many authors describe *T. plinthobius* as dioicous and *T. muralis* as monoicous, Flowers (1973) considered the former occasionally monoicous and the latter occasionally dioicous. I have found one specimen of *T. muralis* to be both autoicous and (apparently) rhizautoicous in the same sod.

From the available data (Table 1), the sections of *Barbula* have distinctive SMDs. Section *Barbula* has SMDs in winter and early spring, section *Revolutae* mainly in spring, and section *Streblotrichum* from spring to autumn. In the last section the taxon with its SMD in spring is a widespread, lowland species of dry, mainly ruderal habitats, while the taxa with SMDs in summer or autumn are montane species, except *B. horrinervis*, which is probably responding to the autumn precipitation maximum in Japan.

The genus *Didymodon* is here treated as emended by Saito (1975). Although the SMDs in the genus are heterogeneous, many closely related species have similar dates. In section *Graciles*, *Didymodon fallax* (Hedw.) Zander, *D. rigidicaulis* (C.Muell.) K.Saito and *D. tophaceus* (Brid.) Lisa have largely wintertime SMDs. The latter species is hygrophilic but does not have mature sporophytes in late summer and fall as do most other hygrophiles. This situation may be due to a very close relationship with *D. fallax* that may not exclude considerable genetic interchange. In section *Vineales*, *D. vinealis* (Brid.) Zander and its var. *flaccidus* (B.S.G.) Zander have spring-time SMDs. In section *Didymodon*, *D. acutus* (Brid.) K.Saito and *D. luridus* Hornsch. in Spreng. are closely related and have SMDs largely in winter. The latter species is a hygrophile and may be related to *D. acutus* in the same way that *D. tophaceus* is related to *D. fallax*. In the same section, *D. icmadophyllus* (Schimp. ex C.Muell.) K. Saito and *D. nigrescens* (Mitt.) K.Saito are montane or northern species with SMDs largely in summer; *D. rigidulus* Hedw., like *D. acutus* and *D. fallax*, has SMDs that span three seasons, probably because of the great distributional range. Propagula are commonly produced by *D. rigidulus* and may be a factor favoring variation in regional SMDs. I have not studied the sectional taxonomic relationships of the montane *D. lamyanus* (Schimp.) Thér. and the hygrophile *D. spadiceus* (Mitt.) Limpr. Dixon (1924) used date of capsule maturity as a character in distinguishing between *D. fallax*, *D. rigidulus* and *D. vinealis* in the United Kingdom.

The genus *Didymodon* is dioicous. If variation in SMDs actually reflects variation in fertilization times then an explanation for such variation based on adaptation to reduce outcrossing might account for the heterogeneous SMDs. It is difficult to ignore, however, the evident correlations in other genera of SMD with climate, including length of growing season and season of precipitation maximum, even if such correlations are not immediately evident for groups of species in *Didymodon*. Probably both genetics and regional climate influence SMDs in *Didymodon*.

I have recently (Zander, 1977) synonymized *Gymnostomum aeruginosum* Sm. and *G. calcareum* Nees & Hornsch., noting many characters that appear to change along a gradient in plant stature, a phenomenon that results in rather different appearance of plants representing the large (typical *G. aeruginosum*) and the small (facies *G. calcareum*) ends of the cline. Since the synonymy is somewhat controversial (several pers. comms.), phenological data are kept separate in Table 1. Weak differences between the two expressions in SMDs are evident and may be due to the fact that the

facies *G. calcareum* grows in somewhat drier climates; it is more common in Mediterranean climates than typical *G. aeruginosum*.

In *Tortella*, as in *Tortula*, the species with largely northern distributions—*T. tortuosa* (Hedw.) Limpr. and *T. fragilis* (Hook. & Wils.) Limpr.—show comparatively retarded SMDs in comparison with those of midlatitude distribution. The autumn date of *T. japonica* (Besch.) Broth. is probably due to the Japanese autumn precipitation maximum.

The effect of variation in monthly precipitation on date of sporophyte maturation may be rather large in India, where seasonal differences in rainfall are striking because of very wet summers due to monsoon winds. Maximum precipitation at Allahabad, India, occurs during the period July to September, reaching a peak of more than 300 mm during August, but not surpassing 50 mm during any one of the other nine months of the year (Critchfield, 1960). Gangulee (1972) gave "fruiting" dates for 21 of the 73 species of Pottiaceae included in his moss flora of Eastern India. These dates occurred only from July through December, mostly during the period of August to October, and concerned mainly hygrophiles. None of the dates given conflicted with data assembled here for the same or related species in other areas of the world. Taxa known to have SMDs typically from late winter to early summer, such as *Acaulon*, *Crossidium*, *Tortula* and *Tortella*, are apparently sterile, rare or absent from eastern India according to Gangulee (1972), although Chopra (1975) lists for western Himalayan and montane regions of India many species of genera characteristically with turn-of-the-year SMDs.

Future study of the sporophyte maturation dates of other critical genera, e.g. *Gymnostomiella* Fleisch., *Husnotiella* Card., *Luisierella* Thér. & P.-Vard., *Neohyphila* Crum, *Splachnobryum* C. Muell. and *Tuerckheimia* Broth., as well as of many unusual species, many be of aid in pointing out relationships.

SEXUAL CONDITION

Of genera with six or more taxa, *Didymodon* and *Barbula* are entirely dioicous (Table 1) and have internally heterogeneous SMDs. *Pottia*, *Desmatodon*, *Astomum* and *Weissia* are almost entirely monoicous; *Tortula* is about half monoicous and half dioicous species; and *Bryoerythrophyllum*, *Tortella* and *Trichostomum* have at least some monoicous species. These last eight genera are relatively homogeneous and narrow in SMDs. If Krieger's (1915) estimate of 12–13 months as the typical duration of sporophyte development in the Pottiaceae is valid, then fertilization and sporophyte maturation both commonly take place about the same time. Such is true for the majority of Hepaticae in the Northern Hemisphere, according to Schuster (1966, p. 189). If SMDs are a reflection of fertilization dates, then temporal heterogeneity in dioicous genera might be an adaptation toward genetic isolation of their species, or at least of their species complexes, through lessened chance of outcrossing.

To examine the possibility that the dioicous or monoicous condition might be correlated with dates of sporophyte maturation, I made some simple calculations. Of the 176 species and infraspecific taxa considered, about half were dioicous and half monoicous, a balance that matches the estimate of Khanna (1964) for bryophytes as a whole. For the 86 dioicous taxa, the total number of months during which sporophyte maturation occurred is 399, with a mean of 4.64 months per taxon. There were 3.45 reports per taxon (a crude measure of geographic range). For the 82 monoicous taxa, the months totaled 344, with a mean of 4.20 months per taxon. There were 3.57 reports per taxon. The eight taxa that are each heteroicous (variably dioicous or monoicous)

TABLE 2. Comparisons of number of specific and infraspecific taxa per month of sporophyte maturation date (SMD) span and per number of reports (a measure of range).

SMD Span: Number of months	Number of taxa		Geographic range: Number of reports	Number of taxa	
	Dioicous	Monoicous		Dioicous	Monoicous
1	9	7	1	29	29
2	0	3	2	8	5
3	31	32	3	10	8
4	8	8	4	10	9
5	1	1	5	8	9
6	21	20	6	9	11
7	4	6	7	4	6
8	0	0	8	4	4
9	11	5	9	4	1
10	1	0		86	82
11	0	0			
12	0	0			
	86	82			

have a mean of 4.88 months per taxon and 3.38 reports per taxon, but the sample is too small to be comparable. The duration of SMD, i.e. span in time that mature capsules are present in the North Temperate Zone, in dioicous taxa is slightly longer than in monoicous taxa, which is statistically significant at $P < 0.05$ by Student's "t" test. But the indication that monoicous taxa are somewhat more widely distributed is not significant. Dealing only with endemic or very local species, the difference between the number of months of sporophyte maturation of dioicous and monoicous taxa, each known only from a single report, is not statistically significant by a "t" test. Endemic and narrowly distributed taxa were then eliminated by restricting calculations to widespread taxa, i.e. those having five or more total reports. Of these, the 26 dioicous taxa were found to have a SMD span of 6.77 months per taxon and 6.39 reports per taxon. The 31 monoicous taxa had a figure of only 5.55 months per taxon but 6.26 reports per taxon. The difference of more than one month between durations of SMD in these widespread dioicous and monoicous taxa is statistically significant at $P < 0.01$. The difference in number of reports between widespread dioicous and monoicous taxa is not statistically significant. A comparison of number of taxa per category of number of reports (Table 2) also indicates that the range of widespread dioicous taxa is little different from that of widespread monoicous taxa.

Table 2 shows that, of 86 dioicous taxa, 12 of them each span nine or more months in the north temperate zone, while, of 82 monoicous taxa, only five do so. Except for these taxa of unusually long SMDs in the North Temperate Zone, Table 2 shows similarity in distribution of data between dioicous and monoicous taxa. Most of the 17 eurychronic taxa (i.e. those with nine month or greater SMD span) do not exceed two consecutive seasons of duration of SMD in any one geographic area. The seasons of SMDs for the 17 eurychronic taxa are shown in Table 3. In Table 3 the dioicous taxa are separated into 2 groups: A, of hygrophilic taxa with largely summer or autumn SMDs, and B, all other dioicous taxa, mainly calciphiles, ruderals or taxa of arid lands. Group C includes all monoicous eurychronic taxa. The number of reports of each season for each region is totaled in the lower portion of the table. The highest numbers show up mainly in summer and autumn, apparently on account of the many hygro-

TABLE 3. Continued.

	N. Am.	Penn.	Ind.	Utah	U.S.S.R.	Fenn.	U.K. & I.	Germ.	Fran.	Jap.	Cons. mo.
C—Monoicous Taxa											
<i>Desmatodon obtusifolius</i>	b-c	a	a-c		b	b	b	a-b	b	a-b	4
<i>Pottia davalliana</i>	a, c-d	a, c-d			c	c	d	d	a	a, c-d	3
<i>P. truncata</i>	b				a, c-d	a, c-d	c-d	a, c-d	a-b	b-c	4
<i>Timmiella anomala</i>					b	c	d	d-a	d-a		4
<i>Weissia rostellata</i>					c						4
Total of season reports for Groups A, B & C.	5	2	1	2	4	3	2	6	11	2	
	4	1	2	0	8	4	6	7	4	4	
	7	4	3	2	8	7	7	6	1	5	
	4	2	1	2	5	3	6	7	7	2	
Total of season reports for Groups B & C only.	5	3	2	2	2	2	2	5	8	2	
	2	0	1	0	3	1	1	2	2	4	
	3	2	2	1	7	6	3	5	0	2	
	4	2	1	2	4	3	6	7	5	1	
Regional precipitation maximum	a-b (E, N. Am.)	a-b	a-b	b	b (steppes)	d	d	a-b	d	c	

{ Spring (a)
Summer (b)
Autumn (c)
Winter (d)

{ Spring (a)
Summer (b)
Autumn (c)
Winter (d)

philic species with SMDs that characteristically occur at that time. A second total, given below the first, excludes the hygrophilic taxa and shows a more balanced distribution of season reports, although summer is the least likely season for these taxa. What Table 3 demonstrates well is that, in addition to infraspecific variation of SMDs between geographic areas, this variation in SMDs appears to correlate somewhat with regional climate. Although the sample is small, SMDs are usually most common during or just after the season of regional maximum precipitation. This is clearly exaggerated in France, which has strong seasonal contrasts in rainfall in the south. A "t" test comparing widespread (with 5 or more reports) dioicous and monoicous taxa, one that is similar to that above but from which the data concerning taxa with nine or more months of SMD span were eliminated, showed no statistical difference in SMD duration. Thus the average of a month longer duration in SMDs in dioicous taxa appears to be due largely to the small eurychronic group of taxa, preponderantly dioicous species with rather different SMDs in different floristic regions.

In similar studies involving data gathered from previous floristic works of other authors, Gemmell (1950, 1952) found that, in the United Kingdom, dioicous species were more variable and more widespread than monoicous species and were of two distinct types—very widely or very narrowly distributed species. Also, distribution curves were bimodal in dioicous species and unimodal in monoicous species. My data, derived in a somewhat different fashion and concerning the entire North Temperate Zone, fail to support Gemmell's assertion that dioicous species are more widespread than monoicous species, at least for the Pottiaceae. Also, Table 2, describing number of taxa per category of number of reports, shows no remarkable difference between dioicous and monoicous taxa in modality or any bimodality in respect to narrow and wide geographic distribution.

LITERATURE CITED

- ANDERSON, L. E. 1963. Modern species concepts: mosses. *THE BRYOLOGIST* 66: 107–119.
 ———. 1974. Bryology, 1947–1972. *Ann. Missouri Bot. Gard.* 61: 56–85.
 ARNELL, H. W. 1875. *De Scandinaviska Löfmossornas Kalendarium*. Upsala Univ. Årsskrift. *Math. Nat.* 4: 1–129.
 ———. 1905. Phenological observations on mosses. *THE BRYOLOGIST* 8: 41–44.
 BELKENGREN, R. O. 1962. Growth and sexual reproduction of the moss *Amblystegium riparium* under sterile conditions. *Amer. Jour. Bot.* 49: 567–571.
 BENSON-EVANS, K. 1961. Environmental factors and bryophytes. *Nature* 191: 255–260.
 ———. 1964. Physiology of the reproduction of bryophytes. *THE BRYOLOGIST* 67: 431–445.
 CHEN, P.-C. 1941. Studien über die ostasiatischen Arten der Pottiaceae, I–II. *Hedwigia* 80: 1–76; 141–322.
 CHOPRA, R. S. 1975. *Taxonomy of Indian Mosses (An Introduction)*. *Chronica Botanica*, New Delhi.
 CLARKE, G. C. S. & S. W. GREENE. 1970. Reproductive performance of two species of *Pohlia* at widely separated stations. *Trans. Brit. Bryol. Soc.* 6: 114–128.
 CRAIG, E. J. 1939. *Aloina*, pp. 211–215 in A. J. Grout (ed.), *Moss Flora of North America North of Mexico*. Vol. 1(4). Newfane, Vt.
 CRITCHFIELD, H. J. 1960. *General Climatology*, Third Edition. Englewood Cliffs, N.J.
 CROSBY, M. R. & R. E. MAGILL. 1977. *A Dictionary of Mosses*. Missouri Botanical Garden, St. Louis.
 CRUM, H. 1971. Nomenclatural changes in the Musci. *THE BRYOLOGIST* 74: 165–174.
 ———. 1973. Mosses of the Great Lakes Forest. *Contr. Univ. Michigan Herbarium* 10: i–iii, 1–404.
 DELGADILLO M., C. 1975. Taxonomic revision of *Aloina*, *Aloinella* and *Crossidium* (Musci). *THE BRYOLOGIST* 78: 245–303.

- DIXON, H. N. 1924. The Student's Handbook of British Mosses, Ed. 3. London.
- FLOWERS, S. 1973. Mosses: Utah & the West. A. Holmgren (ed.). Brigham Young Univ. Press, Provo, Utah.
- FORMAN, R. T. T. 1965. A system of studying moss phenology. *THE BRYOLOGIST* 68: 289-300.
- FRITSCH, R. 1972. Chromosomenzahlen der Bryophyten, eine Übersicht und Diskussion ihres Aussagewertes für das System. *Wiss. Zeitschr. Friedrich-Schiller Univ. Jena, Math.-Naturwiss. Reihe* 21: 839-944.
- GANGULEE, H. C. 1972. Mosses of Eastern India and Adjacent Regions, a Monograph. Fascicle 3 (Syrhophodontales, Pottiales & Dicranales). Publ. by Author, Calcutta.
- GEMMELL, A. R. 1950. Studies on the Bryophyta. I. The influence of sexual mechanism on varietal production and distribution of British Musci. *New Phytol.* 49: 64-71.
- . 1952. Studies in the Bryophyta. II. The distribution of the sexual groups of British mosses. *New Phytol.* 51: 77-89.
- GREENE, S. W. 1960. The maturation cycle, or the stages of development of gametangia and capsules in mosses. *Trans. Brit. Bryol. Soc.* 3: 736-745.
- . 1976. Are we satisfied with the rate at which bryophyte taxonomy is developing? *Jour. Hattori Bot. Lab.* 41: 1-6.
- & D. M. GREENE. 1960. An assessment of some characters distinguishing *Pylaisia polyantha* (Hedw.) B.&S. from *Hypnum cupressiforme* Hedw. var. *resupinatum* (Wils.) Schp. *Trans. Brit. Bryol. Soc.* 3: 715-724.
- GRIME, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Amer. Nat.* 111: 1169-1194.
- GRIMME, A. 1903. Über die Blüthezeit deutscher Laubmoose und die Entwicklungsdauer ihrer Sporogone. *Hedwigia* 42: 1-75.
- GROUT, A. J. 1938. The species concept. *THE BRYOLOGIST* 41: 49-50.
- . 1938-1939. Moss Flora of North America North of Mexico. I(3): 137-192, pl. 69-90; I(4): 193-264, pl. 91-129. Newfane, Vt.
- HILPERT, F. 1933. Studien zur Systematik der Trichostomaceen. *Bot. Centralb. Beih.* 50(2): 585-706.
- HUGHES, J. G. & A. J. A. WIGGIN. 1969. Light intensity and sexual reproduction in *Phascum cuspidatum* Hedw. *Trans. Brit. Bryol. Soc.* 5: 823-826.
- HUSNOT, T. 1884-1894. *Muscologia Gallica*. Paris.
- INGOLD, C. T. 1965. *Spore Liberation*. Oxford Univ. Press, London.
- JENNINGS, O. E. 1951. *A Manual of the Mosses of Western Pennsylvania and Adjacent Regions*, Ed. 2. Amer. Midl. Nat. Monogr. 6. Notre Dame, Ind.
- JOHNSON, A. B. 1969. Phenological and environmental observations on stands of *Orthotrichum anomalum*. *THE BRYOLOGIST* 72: 397-403.
- JONES, E. W. 1947. The time of fruiting of *Ulota bruchii* Hornsch. and *U. crispa* Brid. *Trans. Brit. Bryol. Soc.* 1: 20-21.
- KHANNA, K. R. 1964. Differential evolutionary activity in bryophytes. *Evolution* 18: 652-670.
- KRIEGER, W. 1915. Über die Dauer der Sporogonentwicklung bei den Laubmoosen. *Hedwigia* 57: 154-199.
- LAZARENKO, A. S. 1963. Dynamics of quantitative variation in the sporophyte of *Desmatodon randii* (Kenn.) Lazar. in a natural population and monosporic cultures. *Bull. Moscow Soc. Naturalists, Biol. Ser.* V. 68: 133-148.
- & E. N. LESNYAK. 1972. A comparative study of two moss sibling species—*Desmatodon cernuus* (Hüb.) B.S.G.—*D. ucrainicus* Laz. (Contribution to the problem of infrastructure of the moss species.) *Zhurnal Obschei Biologii (Jour. Gen. Biol.)* 33(6): 657-667.
- LEMMON, B. A. E. 1968. Cytological Investigations in the Genus *Weissia* in Southeastern United States. Ph.D. Dissertation, Dept. of Botany & Plant Pathology, Louisiana State Univ.
- LIMPRICHT, K. G. 1890-1904. *Die Laubmoose Deutschlands, Oesterreichs und der Schweiz*. Leipzig.
- LONGTON, R. 1972. Reproduction of Antarctic mosses in the genera *Polytrichum* and *Psilopilum* with particular reference to temperature. *Brit. Antarct. Surv. Bull.* 27: 51-96.
- MONROE, J. H. 1965. Some factors evoking formation of sex organs in *Funaria*. *THE BRYOLOGIST* 68: 337-339.
- NYHOLM, E. 1956. *Illustrated Moss Flora of Fennoscandia*. II. Musci. Fasc. II. Lund, Sweden.
- & K. WIGH. 1973. Cytotaxonomical studies in some Turkish mosses. *Lindbergia* 2: 105-113.
- PODPĚRA, J. 1954. *Conspectus Muscorum Europaeorum*. Prague.

- PYATT, F. B. 1969. Studies of the periodicity of spore discharge and germination in lichens. *THE BRYOLOGIST* 72: 48-53.
- ROBINSON, H. 1970. A revision of the moss genus *Trichostomopsis*. *Phytologia* 20: 184-191.
- SAITO, K. 1973. Memoir of the Japanese Pottiaceae (I). Subfamily Pottioideae. *Bull. Nat. Sci. Mus. Tokyo* 16: 61-91.
- . 1975. A monograph of Japanese Pottiaceae (Musci). *Jour. Hattori Bot. Lab.* 39: 373-537.
- SAVICZ-LJUBITZKAJA, L. L. & Z. N. SMIRNOVA. 1970. Handbook of the Mosses of the U.S.S.R. Komarov Bot. Inst., Acad. Sci. U.S.S.R., Leningrad.
- SCHOFIELD, W. B. 1966. *Crumia*, a new genus of the Pottiaceae endemic to western North America. *Canad. Jour. Bot.* 44: 609-614.
- SCHUSTER, R. M. 1966. The Hepaticae and Anthocerotae of North America East of the Hundredth Meridian. Vol. 1. New York.
- SCOTT, G. A. M., I. G. STONE & C. ROSSER. 1976. The Mosses of Southern Australia. Academic Press, New York.
- STEERE, W. C. 1938a. *Barbula*, pp. 173-185 in A. J. Grout, Moss Flora of North America North of Mexico. Vol. I(3). Newfane, Vt.
- . 1938b. *Didymodon*, pp. 185-190 in A. J. Grout, Moss Flora of North America North of Mexico. Vol. I(3). Newfane, Vt.
- . 1939. *Tortula*, pp. 228-246 in A. J. Grout, Moss Flora of North America North of Mexico. Vol. I(4). Newfane, Vt.
- . 1972. Chromosome numbers in bryophytes. *Jour. Hattori Bot. Lab.* 35: 99-125.
- & H. INOUE. 1972. Distributional patterns and speciation of bryophytes in the circum-Pacific regions: introduction. *Jour. Hattori Bot. Lab.* 36: 1-2.
- TALLIS, J. H. 1959. Studies on the biology and ecology of *Rhacomitrium lanuginosum* Brid. II. Growth, reproduction and physiology. *Jour. Ecol.* 47: 325-350.
- TOUW, A. 1974. Some notes on taxonomic and floristic research on exotic mosses. *Jour. Hattori Bot. Lab.* 38: 123-128.
- TOWLE, P. M. 1905. Notes on the fruiting season of *Catharinea*. *THE BRYOLOGIST* 8: 44-45.
- . 1906. Notes on the life history of the Mniums. *THE BRYOLOGIST* 9: 54-56.
- & A. E. GILBERT. 1904. The fruiting season of the hair-cap moss. *THE BRYOLOGIST* 7: 35-36.
- TREWARTHA, G. T. 1937. An Introduction to Weather and Climate. New York.
- VAN DER PIJL, L. 1972. Principles of Dispersal in Higher Plants, Ed. 2. Springer-Verlag, New York.
- VAN DER WIJK, R., W. D. MARGADANT & P. A. FLORSCHÜTZ. 1959-1969. Index Muscorum. *Regn. Veg.* 17, 26, 33, 48, 65. Utrecht.
- VISOTSKA, E. I. 1967. A survey of the chromosome numbers in mosses of the Ukrainian SSR. *Cytologia i Genetica* 1(4): 30-39.
- WALTER, H. 1973. Vegetation of the Earth in Relation to Climate and the Eco-Physiological Conditions, Ed. 2. J. Wieser (transl.). Springer-Verlag, New York.
- WAREHAM, R. T. 1939. *Pottia*, pp. 197-208 in A. J. Grout, Moss Flora of North America North of Mexico. Vol. I(4). Newfane, Vt.
- WELCH, W. 1957. Mosses of Indiana, an Illustrated Manual. Indianapolis.
- WHITEHOUSE, H. L. K. 1966. The occurrence of tubers in European mosses. *Trans. Brit. Bryol. Soc.* 5: 103-116.
- ZANDER, R. H. 1977. The tribe Pleuroweisieae (Pottiaceae, Musci) in Middle America. *THE BRYOLOGIST* 80: 233-269.
- . 1978a. A synopsis of *Bryoerythrophyllum* and *Morinia* (Pottiaceae) in the New World. *THE BRYOLOGIST* 81: 539-560.
- . 1978b. New combinations in *Didymodon* (Musci) and a key to the taxa in North America north of Mexico. *Phytologia* 41: 11-32.
- ZEHR, D. R. 1979. Phenology of selected bryophytes in southern Illinois. *THE BRYOLOGIST* 82: 29-36.