Amer. J. Bot. 71(2): 203–209. 1984.

FLOWERING PHENOLOGY AT BIG RUN BOG, WEST VIRGINIA[1]

R. KELMAN WIEDER, CHARLENE A. BENNETT, AND GERALD E. LANG

Department of Biology, West Virginia University, Morgantown, West Virginia 26506

ABSTRACT

In each of four major plant communities at Big Run Bog, a 15-ha *Sphagnum*-dominated wetland in the Appalachian Mountains of West Virginia, the flowering phenology of 21 species was measured by counting the number of flowering stems at frequent intervals throughout the growing season. The four plant communities exhibited no consistent differences with regard to the patterns of flowering phenology. Mean flowering duration was 30 days for all species, and was 32 and 31 days for wind- and insect-pollinated species, respectively. Peak flowering times for the 21 species were randomly distributed throughout the growing season. Results from Big Run Bog are not markedly different from those reported for other bogs in North America.

PHENOLOGY, the study of periodically occurring natural phenomena and their relation to climate and changes in season, is a central focus of several aspects of ecology. Patterns of flowering phenology have long intrigued naturalists and ecologists (Clarke, 1893; Robertson, 1895, 1924). Here we report data on the flowering phenology at Big Run Bog, a minerotrophic very poor fen located in the unglaciated Appalachian Plateaus Physiographic Province (Fenneman, 1938) of West Virginia. Big Run Bog is near the southern limit of the distribution of bogs/poor fens in eastern North America (Cameron, 1968; Goodwin and Niering, 1975; Mundale, 1981). Many plant species that are typically present in the ombrotrophic bogs of the glaciated regions of eastern North America are absent from Big Run Bog. In addition, many of the species at Big Run Bog are not typically found in the more northern bogs. Some of the plant species at Big Run Bog, including *Carex canescens, Gentiana linearis, Nemopanthus mucronata, Vaccinium oxycoccos,* and *Menyanthes trifoliata,* approach their southern limits in the mountain wetlands of West Virginia (cf. Wieder, McCormick and Lang, 1981). Typically, the vegetation is distributed across the surface of one of these mountain wetlands in a mosaic of distinct plant communities (e.g., Darlington, 1943; Robinette, 1964; Fortney, 1975; Wieder et al., 1981; Walbridge, 1982). At Big Run Bog, four major plant communities were identified (Wieder et al., 1981) and an abbreviated list of the species composition of these communities is given in Table 1.

In this paper, flowering phenology at Big Run Bog is discussed on two different scales of resolution. First, we compare the four plant communities with regard to overall patterns of flowering phenology, although we had no a priori reason to expect to find intercommunity differences. Second, we combine the data from the four communities at Big Run Bog to make comparisons with flowering phenologies reported for more northern ombrotrophic bogs in Ontario (Judd, 1958), British Columbia (Pojar, 1974), and Maine (Heinrich, 1976). Studies contrasting patterns of flowering phenology among different ecosystems have suggested that specific patterns of flowering phenology may be characteristic of specific ecosystem types (Pojar, 1974; Heinrich, 1976). If this is indeed true, then Big Run Bog should exhibit patterns similar to the more northern bogs. Alternatively, considerably divergent patterns for Big Run Bog would suggest that patterns of flowering phenology within a particular ecosystem type can be altered by variations in plant species composition among individual sites.

STUDY SITE—Big Run Bog (39°07′N, 79°35′W) is a 15-ha wetland located at an elevation of about 980 m within a 291-ha forested watershed in the Monongahela National Forest. Climatological data for the region were approximated from a national weather station at Canaan Valley, West Virginia, 15 km east of Big Run Bog at an elevation of 991 m (NOAA, 1946–1981). Based on 35 years of observation, mean annual precipitation is 133

[1] Received for publication 12 February 1983; revision accepted 25 July 1983.

We wish to thank J. B. McGraw and A. L. Chester for their thoughtful comments on the manuscript. E. L. Clark, A. M. McCormick, and M. P. Nebiolo assisted in the field work. This study was supported by the U.S. Army Corps of Engineers.

TABLE 1. *Abbreviated list of the species composition of the four major plant communities at Big Run Bog. Values are mean percent cover and are taken mainly from Wieder et al. (1981); percent cover values with an asterisk are from Walbridge (1982) and represent species that were not encountered in a particular community in the sampling of Wieder et al. (1981). Pollination mode was determined by consulting Proctor and Yeo (1972) and Pojar (1974): I, W, and S denote insect-, wind-, and self-pollinated species, respectively.*

Species	Pollination mode	Community			
		Polytrichum-Carex canescens	*Polytrichum-shrub*	*Sphagnum-Eriophorum virginicum*	*Sphagnum-shrub*
SHRUBS					
Hypericum densiflorum	I	1.4*	1.8	0.1	
Ilex verticellata	I	1.6*	3.3	0.5	5.3
Nemopanthus mucronata	I		0.6*	0.3	0.1
Pyrus arbutifolia	I		4.7	1.1	0.5
Rubus hispidus	I	2.5	47.0	29.4	17.4
Vaccinium myrtilloides	I		0.3	0.6	0.1
Vaccinium oxycoccos	I			5.4	3.0*
Viburnum cassinoides	I		0.5	0.1	0.1
HERBS					
Agrostis hyemalis	W			0.2*	1.0*
Agrostis perrennans	W				0.5*
Carex canescens	W	75.6	9.8	0.2	1.0
Carex folliculata	W	0.2*	3.5	1.4	1.7
Carex trisperma	W		2.0*	2.0*	0.7*
*Danthonia compressa***	W				
Drosera rotundifolia	S			0.2	0.1
Eriophorum virginicum	W	0.6*	0.6	38.7	5.0
Gentiana linearis	I		0.7		0.1
Juncus brevicaudatus	W	0.2*	0.5	4.4	4.3
Juncus effusus	W	1.0*	1.8	0.2	1.7
Rhynchospora alba	W		6.0*	19.4*	1.8*
Solidago uliginosa	I		1.4	9.2	2.9
MOSSES					
Polytrichum spp.		71.0	76.6	5.5	23.7
Sphagnum spp.		33.4	25.2	93.8	64.1

** *Danthonia compressa* was not encountered by either Wieder et al. (1981) or Walbridge (1982) in any of the four communities, but was encountered in the present study.

cm and mean annual temperature is 7.9 C. The average number of days between 0 C frosts is 97, from 2 June through 7 September.

Sphagnum and *Polytrichum* mosses cover 59 and 27%, respectively, of the wetland surface (Wieder et al., 1981). Both genera are very productive (Wieder and Lang, 1983) and are important in the production of peat, which has accumulated to a maximum depth of 225 cm and has been radiocarbon dated to 13,080 ± 420 yr B.P. (Wieder, 1982). Because Big Run Bog receives water and nutrients from the surrounding upland portions of the watershed, the wetland is not a true ombrotrophic bog, but rather is a minerotrophic fen (Wieder, 1982). Surface waters within Big Run Bog have an average pH of 4.02 and an average calcium concentration of 0.8 mg/l (Wieder, 1982). Thus, Big Run Bog, although a fen, has both vegetational and chemical similarities to the more northern ombrotrophic bogs (Jeglum, Boissonneau and Haavisto, 1974; Moore and Bellamy, 1974).

METHODS—Flowering phenology was assessed by establishing one 2 × 50-m transect in each of the four major plant communities at Big Run Bog (Table 1). Using this design, we were able not only to compare aspects of flowering phenology among the four communities, but also to combine the data from the four communities to examine patterns of flowering phenology at Big Run Bog as a whole.

The perimeter of each transect was delineated by placing permanent flags at 5-m intervals along the outer edges. At 3 to 6-day intervals from 13 May through 25 September the total number of flowering stems of each species was counted in each transect. Any stem containing flowers with exerted stamens or stigmas that were not brown, dried, or shriveled was regarded as flowering. For upright shrubs; the main shoot emerging from the ground was considered to be a single stem. For *Rubus hispidus*, a trailing shrub, each floricane was considered to be a single stem. For *Vaccinium oxycoccos*, each shoot with a terminal

TABLE 2. *Comparison of flowering phenologies among the four major plant communities at Big Run Bog. Precise definitions of peak day, duration of flowering, and peak value are given in the text. Community designations are: PC* = Polytrichum-C. canescens; *PS* = Polytrichum-*shrub; SE* = Sphagnum-E. virginicum; *SS* = Sphagnum-*shrub.*

	Peak day				Duration of flowering (days)				Peak value			
Species	PC	PS	SE	SS	PC	PS	SE	SS	PC	PS	SE	SS
Carex canescens	146	149	146		30	11	27		8,589	15	92	
Carex folliculata	162	162	162	162	17	17	10	14	42	724	42	195
Carex trisperma			156	159			4	7			27	157
Eriophorum virginicum	198	202	195	202	32	48	50	48	5	257	733	707
Gentiana linearis	245	230			23	20			5	2		
Hypericum densiflorum	223	208			60	58			75	33		
Ilex verticellata		188	188			13	16			12	3	
Juncus brevicaudatus	226	223	226	226	19	23	33	33	15	124	325	77
Juncus effusus	183		183	173	54		40	40	129		319	34
Nemopanthus mucronata			156	159			11	1			4	1
Pyrus arbutifolia		149	149	156		21	14	14		298	30	45
Rhynchospora alba		208	198	198		36	48	43		99	4,151	9,258
Rubus hispidus	208	198	190	190	43	44	36	39	20	131	337	207
Solidago uliginosa			245	245			46	43			23	37
Vaccinium myrtilloides	149	149			21	30			5	28		
Vaccinium oxycoccos			173	177			22	37			1,132	3,352

cluster of flowers was counted as a single flowering stem.

RESULTS AND DISCUSSION—Of the 21 vascular plant species encountered in the four transects at Big Run Bog, ten species (all dicots) are insect-pollinated, ten species (all monocots) are wind-pollinated, and 1 species (*Drosera rotundifolia*) is primarily self-pollinated (Table 1). Pojar (1974) found that in two bogs on Vancouver Island 58 and 57% of the species were insect-pollinated and 38 and 40% of the species were wind-pollinated, while in a salt marsh and a subalpine meadow 22 and 67% of the species, respectively, were insect-pollinated and 55 and 22%, respectively, were wind-pollinated. Pojar (1974) suggested that in some ecosystems the flora is strongly dominated by either insect- or wind-pollinated species, but in bogs there may be more of a balance between insect- and wind-pollinated species. Such a balance is clearly evident at Big Run Bog. Although the respective floras of the bog, woodland, and roadside habitats studied by Heinrich (1976) appeared to be dominated by insect-pollinated species, grasses, sedges, and rushes which are primarily wind-pollinated were conspicuously absent from his species lists, suggesting that these families were completely excluded from his analysis.

At Big Run Bog, we expected that for each species, intercommunity differences in the maximum number of flowering stems that were recorded in a transect on a particular day (peak value) should have reflected differences in the relative abundance of that species among the four communities. However, for most species, peak value data in Table 2 and percent cover data in Table 1 provided a different ranking among the four communities. Discrepancies between Tables 1 and 2 may have been a result of method: percent cover was determined from a series of quadrats scattered throughout each community, but peak value was determined from a single transect located within one relatively small area of each community. Alternatively, differences between the two Tables may indicate that spatial variation in a species' abundance (measured as percent cover) may not necessarily be reflected in a corresponding variation in flowering stem abundance (measured as peak value). Or simply, that vigor in flowering is not related to abundance.

For each species that occurred in at least two communities at Big Run Bog, potential differences among communities with regard to flowering phenology were assessed by examining two quantitative aspects: the day of the year when the maximum number of flowering stems was counted in a particular community (peak day) and the number of days between the onset of flowering and the last date on which flowering stems were recorded in a particular community (duration of flowering). For 9 out of the 16 species that occurred in more than one community, the maximum difference between communities in peak day of flowering was four or less (Table 2). Although for 5 of the 16 species, intercommunity differences in peak day of flowering were ten or more days, these large differences were obtained for species that had low flowering abundance (peak value) either in

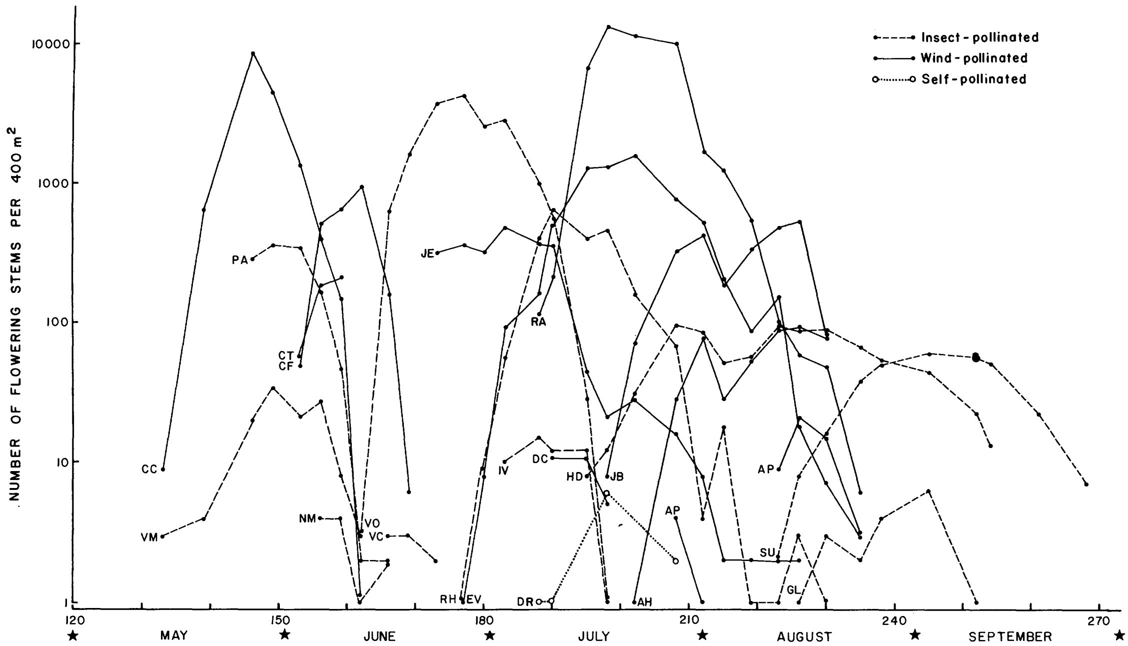

Fig. 1. Flowering phenology curves for the 21 vascular plant species encountered at Big Run Bog. Each curve is identified by the first letters of the genus and specific epithet listed in Table 1. Numbers on the x-axis are the day of the year; months are separated by stars.

general (*Gentiana linearis*) or in one particular community (*Juncus effusus, Rhynchospora alba, Rubus hispidus*). For these latter three species, if the community with the lowest peak value was excluded, maximum differences in peak day of flowering were considerably reduced.

Differences among communities with regard to the duration of flowering of a given species also appeared to reflect differences in relative flowering abundance among transects. If for each species in Table 2 the communities were ranked from highest to lowest for both the duration of flowering and peak value, for 12 of the 16 species the community with the longest flowering season also had the largest peak value, and for 13 of the 16 species the community with the shortest flowering season also had the smallest peak value. The consistency of the duration-peak value relationship is more closely related to probability than to flowering biology. In comparison to communities with low flowering abundance, communities with high flowering abundance have a greater probability that some individuals will flower very early or very late based on sheer numbers alone.

At Big Run Bog, we did not observe a shift of several species within one community toward either an earlier or a later peak day of flowering or toward either a shorter or a longer flowering season compared to species in a different community. These types of shifts were observed in a comparison of two adjacent first-year fallow fields in Indiana, and the shifts were attributed to differences between the two fields in soil moisture and temperature regimes (Swieringa and Wilson, 1972). In contrast to Swieringa and Wilson's (1972) comparisons of two highly disturbed fields, at Big Run Bog known intercommunity differences in species composition, water chemistry, peat chemistry, and the physical properties of peat (Wieder, 1982) had no consistent effects on overall patterns of flowering phenology.

The data from the four communities were combined to examine overall patterns of flowering phenology (Fig. 1). For each species, no flowering stems were observed on the sampling date before the first plotted point or on the sampling date after the last plotted point. The general shape of the flowering curves for a given species depends on several factors, including the number of flowers that come into bloom (stamens and/or stigmas expanded) on a particular day; the number of flowers that terminated blooming (stamens and/or stigmas dry up) on a particular day, and the average lifetime of individual flowers. The fairly steep ascent of the flowering curves of several of the species in Fig. 1 suggests that the onset of blooming

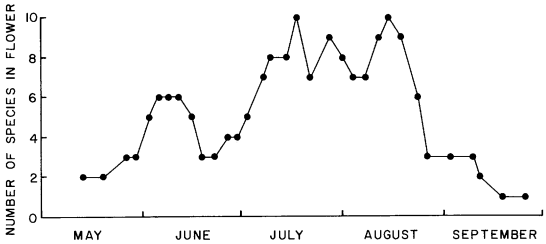

Fig. 2. Number of species in flower on a particular day throughout the flowering season at Big Run Bog.

is a pulsed event in which many flowers come into bloom within a short period of time (cf. Thompson, 1980; Rabinowitz et al., 1981).

Flowering at Big Run Bog began in mid-May and continued through late September (Fig. 1). The temporal extent of the flowering season corresponded well with the 1981 frost-free season measured at nearby Canaan Valley, which lasted from 21 May through 25 September (NOAA, 1981). The 136-day flowering season at Big Run Bog was comparable to the 131-day flowering season in the Ontario bog studied by Judd (1958), but was shorter than the 160- and 163-day flowering seasons at the two bogs studied by Pojar (1974) and the 159-day composite average of the four bogs examined by Heinrich (1976). The average duration of flowering of the 21 species at Big Run Bog was 30 days, as compared to 28 days for an Ontario bog (Judd, 1958), to average values of 32 and 27 days for two bogs in British Columbia (Pojar, 1974), and a composite average of 25 days for four Maine bogs (Heinrich, 1976). Mean flowering duration of wind-pollinated species has been shown to be shorter than for insect-pollinated species in bogs (Pojar, 1974), a woodland and a roadside habitat (Hienrich, 1976), and a tallgrass prairie (Rabinowitz et al., 1981). This was not the case at Big Run Bog where mean flowering duration was 32 days for wind-pollinated species and 31 days for insect-pollinated species.

In comparing data from his study with those of Pojar (1974) and of Judd (1958), Heinrich (1976) suggested that bog species tend to flower in an unbroken progression, such that the number of species in flower on a particular day over the course of the flowering season is relatively constant. A contrasting pattern was obtained for a salt marsh (Pojar, 1974), and a woodland and a roadside habitat (Heinrich, 1976) where in each system a relatively large portion of the entire species complement tended to flower during a relatively short proportion of the flowering season. In the salt marsh and roadside habitats, the fairly sharp peak in the number of species flowering coincidently was more or less associated with the warmest portion of the flowering season, whereas in the woodland system the peak occurred prior to canopy closure. At Big Run Bog, the number of species in flower showed a small peak in early June and a broader and slightly higher peak from mid-July through mid-August during which up to ten species were in flower simultaneously (Fig. 2). However, the peaks in Fig. 2 are not especially sharp and the general flatness of the curve is similar to the pattern for the bogs examined by Judd (1958), Pojar (1974), and Heinrich (1976).

Using the statistical procedure of Poole and Rathcke (1979), we determined that the distribution of peak flowering times of the 21 species encountered at Big Run Bog was random, as opposed to either regular or clumped (Table 3). Moreover, random distributions were also obtained by considering subsets of the entire species complement, i.e., wind-pollinated species, insect-pollinated species, and sedges and rushes (Table 3). Similar results were obtained by Rabinowitz et al. (1981) for a Missouri tallgrass prairie in which wind-pollinated species, insect-pollinated species, grasses, composites, and legumes each exhibited a random distribution of peak flowering times.

The analysis described by Poole and Rathcke (1979) was intended as a method of statistically

TABLE 3. *Poole-Rathcke analysis of dispersion of peak flowering for all species at Big Run Bog and for wind-pollinated species, insect-pollinated species, and sedges and rushes. Equations and conventions follow Poole and Rathcke (1979). P is the sample variance of the distances between peak flowering days between temporally adjacent species. E(P) is the expected value of P under the null hypothesis of randomly dispersed peaks. The ratio P/E(P) is the dispersion index which if significantly different from 1.0 indicates nonrandom dispersion of peaks. Significance was tested by comparing the value kP/E(P) with a chi-square value with k degrees of freedom at the 0.05 level. NS denotes not significant.*

Group	k	E(P)	P	P/E(P)	
All species	21	0.00189	0.00223	1.180	NS
Wind-pollinated species	10	0.00689	0.00288	0.418	NS
Insect-pollinated species	10	0.00689	0.00469	0.680	NS
Sedges and rushes	7	0.01215	0.00463	0.381	NS

addressing the concept that natural selection should ultimately result in the uniform staggering of flowering periods throughout the growing season as a means of minimizing both competition for pollinators and interspecific hybridization (Mosquin, 1971; Heinrich and Raven, 1972; Frankie, Baker and Opler, 1973; Stiles, 1977). The relevance and generality of the Poole-Rathcke approach have been questioned on several grounds. A basic assumption that remains untested is that each day of the flowering season is equally suitable for flowering (Rabinowitz et al., 1981). Stiles (1979) suggested that species specific physiological constraints may preclude the attainment of a statistically uniform distribution of flowering periods. Moreover, Gleeson (1981) noted that a random or even an aggregated distribution of flowering periods may be sufficient to minimize competitive forces to a tolerably low level. In addition, the Poole-Rathcke test is intuitively more reasonable when examining an assemblage of species pollinated by the same insect group than in multiple pollinator systems (Gleeson, 1981; Rabinowitz et al., 1981).

Cole (1981) pointed out that because the shapes of flowering curves differ considerably among species (e.g., Fig. 1), the distribution of flowering peaks, whether random, clumped, or uniform, cannot be used to draw unequivocal inferences about ecologically more relevant questions regarding temporal and spatial pattern in flowering periods (cf. Thompson, 1980; Rabinowitz et al., 1981). Quantitative methods for assessing the distribution and overlap of flowering periods are not well developed. Thus, at Big Run Bog, although we have shown that peak flowering times are randomly distributed (Table 3), we can say little about the distribution and overlap of flowering periods.

In summary, within Big Run Bog, the four plant communities exhibited no consistent differences with regard to patterns of flowering phenology. Despite the conspicuous absence of several plant species that are typical of northern bogs, and the presence of several species that are not typical of northern bogs, many aspects of flowering at Big Run Bog, including the relative proportion of wind- and insect-pollinated species, the mean duration of flowering, and the pattern of the progression of flowering over the season, are not markedly different from those patterns reported for northern bogs and may be characteristic of bogs/poor fens in general.

LITERATURE CITED

CAMERON, C. C. 1968. Peat. *In* Mineral resources of the Appalachian Region, pp. 136–145. U.S. Geol. Surv. Prof. Pap. 580.

CLARKE, H. T. 1893. The philosophy of flower seasons. Amer. Nat. 27: 769–781.

COLE, B. J. 1981. Overlap, regularity, and flowering phenologies. Amer. Nat. 117: 993–997.

DARLINGTON, H. C. 1943. Vegetation and substrate of Cranberry Glades, West Virginia. Bot. Gaz. 104: 371–393.

FENNEMAN, N. M. 1938. Physiography of eastern United States. McGraw-Hill Book Company, Inc., New York.

FORTNEY, R. H. 1974. The vegetation of Canaan Valley, West Virginia, a taxonomic and ecological study. Ph.D. thesis, West Virginia University, Morgantown.

FRANKIE, G. W., M. G. BAKER, AND P. A. OPLER. 1974. Tropical plant phenology: applications for studies in community ecology. *In* H. Lieth [ed.], Phenology and seasonality modeling, pp. 287–296. Springer-Verlag, Berlin.

GLEESON, S. K. 1981. Character displacement in flowering phenologies. Oecologia (Berlin) 51: 294–295.

GOODWIN, R. H., AND W. A. NIERING. 1975. Inland Wetlands of the United States. Natural History Theme Studies, Number 2, National Park Service, USDA, Washington, D.C.

HEINRICH, B. 1976. Flowering phenologies: bog, woodland, and disturbed habitats. Ecology 57: 890–899.

———, AND P. A. RAVEN. 1972. Energetics and pollination ecology. Science 176: 597–602.

JEGLUM, J. K., A. N. BOISSONNEAU, AND V. F. HAAVISTO. 1974. Toward a wetland classification for Ontario. Information Report 0-X-215, Great Lakes Forest Research Centre, Canadian Forestry Service, Department of the Environment, Sault Ste. Marie, Ontario.

JUDD, W. W. 1958. Studies of the Byron Bog in southwestern Ontario. II. The succession and duration of blooming in plants. Can. Field-Nat. 72: 119–121.

MOORE, P. D., AND D. J. BELLAMY. 1974. Peatlands. Springer-Verlag, New York.

MOSQUIN, T. 1971. Competition for pollinators as a stimulus for the evolution of flowering time. Oikos 22: 398–402.

MUNDALE, S. M. (ED.). 1981. Energy from peatlands: options and impacts. Center for Urban and Regional Affairs, University of Minnesota, Minneapolis.

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 1946–1981. Climatological data. Annual summaries. West Virginia. Environmental Data and Information Service, National Climatic Center, Asheville, North Carolina.

POJAR, J. 1974. Reproductive dynamics of four plant communities of southwestern British Columbia. Can. J. Bot. 52: 1819–1834.

POOLE, R. W., AND B. J. RATHCKE. 1979. Regularity, randomness, and aggregation in flowering phenologies. Science 203: 470–471.

PROCTOR, M., AND P. YEO. 1972. The pollination of flowers. Taplinger, New York.

RABINOWITZ, D., J. K. RAPP, V. L. SORK, B. J. RATHCKE, G. A. REESE, AND J. C. WEAVER. 1981. Phenological properties of wind- and insect-pollinated prairie plants. Ecology 62: 49–56.

ROBERTSON, C. 1895. The philosophy of flower seasons, and the phaenological relations of the entomophilous flora and the anthopilous insect fauna. Amer. Nat. 29: 97–117.

———. 1924. Phenology of entomophilous flowers. Ecology 5: 393–407.

ROBINETTE, S. L. 1964. Plant ecology of an Allegheny mountain swamp. M.S. thesis, West Virginia University, Morgantown.

STILES, F. G. 1977. Coadapted competitors: the flowering seasons of hummingbird pollinated plants in a tropical forest. Science 198: 1177–1178.

———. 1979. Reply to Poole and Rathcke. Science 203: 471.

SWIERINGA, S., AND R. E. WILSON. 1972. Phenodynamic analyses of two first-year old fields. Amer. J. Bot. 59: 367–372.

THOMPSON, J. D. 1980. Skewed flowering distributions and pollinator attraction. Ecology 61: 572–579.

WALBRIDGE, M. R. 1982. Vegetation patterning and community distribution in four high-elevation headwater wetlands in West Virginia. M.S. thesis, West Virginia University, Morgantown.

WIEDER, R. K. 1982. Biogeochemical relationships in *Sphagnum*-dominated wetlands in West Virginia. Ph.D. thesis. West Virginia University, Morgantown.

———, AND G. E. LANG. 1983. Net primary production of the dominant bryophytes in a *Sphagnum*-dominated wetland in West Virginia. The Bryologist 86: 276–284.

———, A. M. MCCORMICK, AND G. E. LANG. 1981. Vegetational analysis of Big Run Bog, a nonglaciated *Sphagnum* bog in West Virginia. Castanea 46: 16–29.