GROWTH AND FLOWERING OF *DANTHONIA SERICEA* POPULATIONS[1]

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Abstract. Seasonal growth and flowering in relation to environmental stimuli were studied in 20 populations of *Danthonia sericea* Nutt. ranging from New Jersey to Georgia. Flowering in the natural habitat was correlated ($r = 0.988$) with latitude, but New Jersey transplant and greenhouse tests indicated that populations of this species can be separated into three groups on the basis of their habitat and flowering response mechanism. Populations with glabrous sheaths from bogs or wet areas next to rivers or ponds in New Jersey required only adequate air and soil temperatures for growth and subsequent flowering. In these wet habitats substrate temperature apparently serves as the environmental stimulus to which the plants respond. For the populations with pubescent sheaths occurring at openings or fringes of upland pine-oak forests on well-drained, sandy soils and for the glabrous populations occurring along stream borders and drainage areas adjacent to granite outcrops in Georgia, an additional requirement for specific photoperiods apparently exists.

INTRODUCTION

Danthonia sericea Nutt. is an ecologically variable species of the eastern United States, ranging from New Jersey to Florida and west to Louisiana. In a species with such a wide geographic-ecologic distribution, seasonal growth and development must be attuned to the particular habitat in which a population occurs. This may be accomplished by specific responses to temperature, photoperiod, or other environmental stimuli. Recognition of the importance of photoperiodism in plant-environment relationships dates back to the pioneering work of Garner and Allard (1920). Observing that some of the plants they studied had an extensive north-south distribution, they hypothesized that adjustment to such a wide range of conditions depended upon different physiological requirements of "types" developed as a result of natural selection. Among species of the Gramineae, Allard and Evans (1941), Olmsted (1944, 1945), Larsen (1947), McMillan (1956*a*, *b*, 1957, 1959, 1965, 1967), Quinn (1969), Quinn and Ward (1969), Ward (1969), and others have reported genetic variation in the growth and flowering of species-populations collected from varied geographic areas and grown in uniform environments.

Danthonia sericea is a perennial grass which commences vegetative growth in its natural habitat in early spring and flowers in late spring or early summer depending upon the latitude of the population. *Danthonia sericea* var. *sericea* occurs on acid, well-drained sandy soils in openings or along the fringes of pine-oak forests. It has villous sheaths and is also villous along the back of the lemma. This pubescent variety is distributed chiefly on the coastal plain, especially in sand barrens, from southern New Jersey to northern Florida and east to Kentucky and Louisiana (Hitchcock 1951).

Danthonia sericea var. *epilis* (Scribn.) Blomq. occurs in cedar bogs in the northern portion of its geographic range in southern New Jersey and along stream borders or in granite outcrops in Georgia. This variety has foliage with relatively glabrous sheaths and very thin lemmas that are villous only on the margins (Gleason and Cronquist 1963).

The purpose of this research was the investigation of seasonal growth and development of populations in relation to latitude and contrasting habitat types. The study utilized clones of *Danthonia sericea* collected from different latitudes and habitats and grown under transplant garden, greenhouse, and experimental photoperiod conditions.

METHODS AND MATERIALS

Clonal materials—transplant garden

In the summer of 1967 plants from 16 collection sites were transplanted to a uniform garden at the William L. Hutcheson Memorial Forest located approximately 1 mile east of East Millstone, N. J. (40° 30′ N, 74° 34′ W) on the Piedmont. The garden area is underlain by Triassic red shale of the Brunswick formation (Kummel 1940). The garden location is level with a moderately well-drained silt loam soil of pH 5.0 (1:5).

Annual mean temperature at a New Brunswick weather station approximately 9 miles east was 53.0°F (1963–68). During 1968 average minimum and maximum temperatures during January were 19.5° and 35.6°F and for July were 65.6° and 86.0°F. Sparkes and Buell (1955) found air temperature extremes of −8° and 112°F in a grassy old-field area near the garden area. Soil temperatures (4 cm below the surface) in the grassy old-field area ranged from 30° to 90°F (Sparkes and Buell 1955). The duration of the annual growing season is approximately 240 days (Monk 1961), and precipita-

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[1] Received August 3, 1970; accepted March 3, 1971.

tion during 1967, 1968, and 1969 totaled 49.06, 46.15, and 45.18 inches, respectively.

Collection areas provided both a latitudinal and a habitat-type sampling of *Danthonia sericea* populations (Fig. 1). *Danthonia sericea* var. *sericea* populations from New Jersey (NES, NGS, WNJS, BNJS, LNJS), Delaware (DLS), Virginia (GS, FS), North Carolina (NCS), South Carolina (SCS), and Georgia (RCS, RS) were studied. These populations occurred in uplands on well-drained, sandy soils (sand content ranging from 57% to 89%). Populations of the *epilis* taxon were collected in New Jersey (CHE, FRE, MFE, BAE) and Georgia (AME, LE, RCE). Soils or substrate for these populations generally consisted of 20–30 cm of a dense root and peat mat lying above a sandy or rocky substratum. One Georgia collection site (LSM) provided clones of both the *sericea* and *epilis* taxa as well as plants considered to be "intermediate" in diagnostic morphological characteristics. Soil pH for the 20 populations varied between 4.2 and 5.2 and was not correlated with either habitat type (bog or upland) or latitude of the population. Detailed descriptions of the collection sites are presented by Rotsettis (1970).

Samples from the collection sites each consisted of eight randomly chosen clones. Six of these clones were selected from each of the population collections and divided into three ramets each for planting in the transplant garden. The garden layout consisted of a randomized block design with three replicates. Each of the 16 populations was represented by one row within each replicate. Each row contained one ramet of each of the six clones of that population, with random distribution of clones within the row. Each of the rows was randomly distributed within each of the three replicates. The ramets were planted at 40-inch intervals, both between and within rows. The plants were watered when planted in the summer of 1967 and also at several other times during a dry period in the summer of 1968. Cultivation proceeded on a regular basis, and the garden was kept weed-free to insure maximum uniformity.

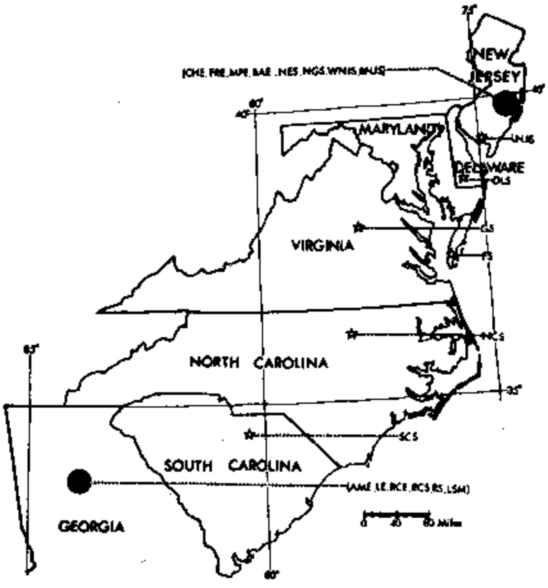

FIG. 1. Geographic location of populations of *Danthonia sericea* utilized in the various experiments. Stars indicate single populations, and the larger black circles denote a general area in which several populations were located.

Weekly phenology and height-growth readings were taken April through August in 1968. In 1969 weekly phenology and growth readings were terminated in June because of poor survival and growth of plants. Poor survival of several of the populations had necessitated another collection trip and subsequent replanting of material in the spring of 1968. The criteria used for phenological stages followed those of Quinn (1969).

Greenhouse readings

Extra clones from each population were divided where possible and placed in the greenhouse during the summer of 1967. Each plant was potted in a 1:1:1 mixture of soil, sand, and sphagnum peat in 6-inch clay pots. Plants were grown in one greenhouse room under semicontrolled environmental conditions. Temperature was controlled by a thermostat and a heater-air cooler system; humidity was controlled by an automatic mist system. Phenological readings were taken every 2 days from February 7 through June 20, 1968. Plants not flowering by this date were usually poor in vigor.

Plants were added to the greenhouse collection in the spring and summer of 1968. Phenology readings were taken on clones during the 1969 season (at irregular intervals from December 1968 through May 1969) and during the 1970 season (January 6 to June 20).

Photoperiod experiment

Representatives from 13 different populations were utilized. In most cases there were four clones (genotypes) per population, each with four ramets available for use under various experimental treatments. The photoperiods were chosen on the basis of estimated daylengths (including twilight) when floral induction was thought to occur at the collection sites. The four treatments included a 9-, 12-, and 15-hr and a "natural" daylength. Natural daylength referred to a photoperiod equal to the actual local daylength for each day (including twilight). This photoperiod was increased daily as the season progressed.

The photoperiod experiment consisted of a randomized block experimental design with four blocks, each containing one ramet of each of the four clones from each population. There were 11 rows of four plants within each of the four treatments. Each row contained ramets of only one population, except for several cases in which insufficient material prompted the placing of ramets of an additional population within the row. Rows were randomized within each treatment. The ramets were also randomized as to position within the row.

A bank of 200-w GE incandescent flood lamps was used to supplement and extend daylight conditions; light intensity was approximately 250 ft-c at pot surface. Black sheen cloth on 1.27-cm by 2.54-cm wooden frames (1.6 m long, 0.8 m wide, 1.0 m high) was used to cover the treatments during their respective nyctoperiods. All four treatments were uncovered at 8:00 AM and were subsequently covered at the various corresponding times. Covering time for the "natural" daylength treatment changed daily in relation to the daily increase in daylength. Each treatment received at least 9 hr of natural light supplemented with artificial light. Normal daytime temperature ranged between 70° and 78°F. Minimum temperature recorded was 61°F, and maximum recorded temperature during the experiment was 82°F. The photoperiod experiment began on December 19, 1968, the shortest day of the year, and terminated on May 25, 1969. Phenology readings were taken every 2 days. A rating system was devised to rank the overall vigor of each plant. Ratings of 0–10 were given on the basis of height, crown diameter, and general appearance. Vigor readings were taken on February 14 and May 25, 1969.

RESULTS AND ANALYSES

Field phenology

Mean dates of anthesis in 1970 for the *D. sericea* populations were approximated from previous observations of the development of reproductive culms under greenhouse, transplant garden, and field conditions and from field phenology records taken in 1967–70. When phenologic stages other than anthesis were observed in the field in 1970, dates of anthesis were estimated with an expected accuracy of ±3 days. Date of anthesis in the field was strikingly correlated ($r = 0.988^{**}$[2]) with latitude of collection site (Fig. 2). Since considerable intrapopulation variability was often observed, the date given is the peak date of anthesis for each population. In addition to genetic variation causing differences in date of anthesis of various clones within a population, environmentally imposed variation was observed in several populations. In general, when a population was growing along a shade-sun or moist-dry cline, earlier flowering was found in the sunny or drier microclimate.

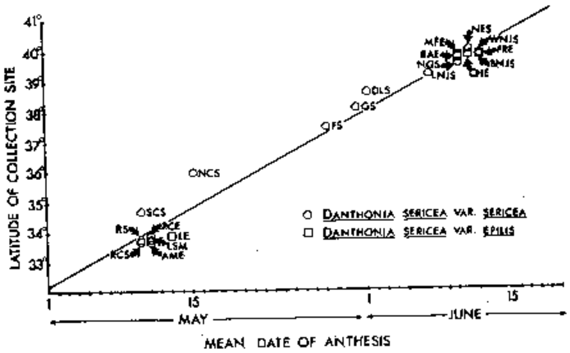

FIG. 2. Approximate dates of anthesis in 1970 in field populations of *Danthonia sericea* as a function of latitude of collection site ($r = 0.988^{**}$).

Transplant garden

Survival of plants in the transplant garden was evaluated from the mean number of plants per replicate alive, and equal to or greater than 3 cm tall, on June 19, 1968 (Fig. 3). This date marked the last week of phenology and height-growth readings before replacements for several populations were planted in 1968. Observations at this time should provide a fair representation (including subsequently replaced but living ramets) of survival under garden conditions. Survival rates were higher in populations of the *epilis* taxon than in most of the populations of the *sericea* taxon, probably because of edaphic conditions in the garden. *Danthonia sericea* var. *sericea* occupies well-drained, well-aerated sandy soil throughout its range and evidently will not tolerate a heavy soil with only fair drainage and aeration. Another factor affecting survival was frost heaving, which was particularly severe during the winter of 1968–69.

No correlation was apparent between latitude of collection site and survival (Fig. 3). Georgia populations of the *epilis* taxon had as good a survival

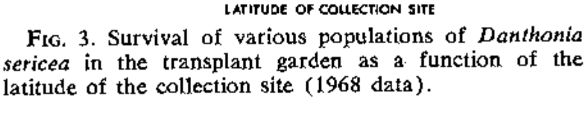

FIG. 3. Survival of various populations of *Danthonia sericea* in the transplant garden as a function of the latitude of the collection site (1968 data).

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[2] Statistical significance for each correlation coefficient will be indicated by ** for 0.01 and * for 0.05.

rate (if not better) as the New Jersey populations. Two Georgia populations (AME and LSM) had better survival than two of the New Jersey populations (CHE and MFE). Thus, Georgia *epilis* populations were apparently not at any disadvantage in their ability to survive the winter conditions of New Jersey.

Height-growth curves for three *D. s.* var. *epilis* populations (AME, FRE, and RCE) were generally sigmoid and tapered off approximately June 27 (Fig. 4). Plant height initially showed a rather moderate regular weekly increase, followed by a phase of maximum growth upon emergence of inflorescences. This maximum growth rate continued for 2–3 weeks and involved the elongation of the uppermost internodes of both initial and subsequent reproductive culms. Reproductive culms of one Georgia population (AME) were taller than those of the New Jersey (FRE) population (Fig. 4). The height-growth curve for the RCE population, another *epilis* population from Georgia, corresponded well with the height-growth curve for the FRE population.

Flowering in the transplant garden differed dramatically between the *epilis* and *sericea* taxa. Two-thirds of the *epilis* plants surviving at the end of the growing season flowered, but only two of the *sericea* plants were vigorous enough to flower (2 weeks later than most of the *epilis*). In the LSM rows *sericea*, *epilis*, and "intermediate" plants were included, and although *epilis* and intermediate plants flowered, neither of the *sericea* clones of LSM flowered.

Time of flowering did not differ significantly in northern and southern populations of *D. s.* var. *epilis* (Table 1). Several late-flowering CHE plants lacked vigor and developed abnormally and were not included in the calculations. Under the daylengths existing at the end of April and the first of May, temperature alone may be the controlling factor in the flowering of the *epilis* taxon. Thus, given the soil and air temperatures necessary for growth and development, populations of both northern and southern origin were able to flower at this time. In other words, if any photoperiod requirement existed, it had already been reached and surpassed.

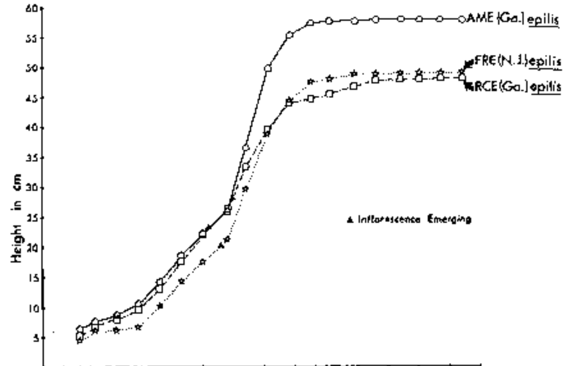

FIG. 4. Height growth of three *Danthonia sericea* var. *epilis* populations (AME, FRE, and RCE) growing in the transplant garden. Only plants that flowered were used in the compilation of data.

TABLE 1. Mean flowering time of *Danthonia sericea* var. *epilis* populations in the transplant garden at the Hutcheson Memorial Forest, East Millstone, N.J. (1968 data)

Population	Mean date of flag leaf stage	Mean date of inflorescence emerging stage	Mean date of inflorescence clear stage
New Jersey			
FRE	May 17.8	May 29.0	June 8.8
CHE	(June 21.4)	(July 1.4)	(July 10.6)
CHE (I only)	May 19.5	June 6.0	June 13.0
MFE	May 28.3	June 4.3	June 9.5
Average	May 21.9	June 2.8	June 10.4
Georgia			
LE	May 20.0	May 30.0	June 6.0
RCE	May 27.2	June 1.4	June 8.3
AME	May 18.8	May 24.7	June 4.8
Average	May 22.0	May 29.0	June 6.4
LSM[a]	May 21.6	May 27.2	June 8.8

[a] Combined data for *epilis* and "intermediate" clones.

Greenhouse

Greenhouse plants did not flower in 1967 after they were clipped back and divided in late summer. Flowering did not occur until February 1968 when a New Jersey population of *D. s.* var. *epilis* (FRE) began to flower. In general, clones of the *epilis* variant flowered earlier than those of the *sericea* variant (Table 2). There was a 3-month difference in time of flowering for the FRE population and the GS (Va. *sericea*) population. Within the *epilis* taxon earliest flowering occurred in the northern (N.J.) clones; southern (Ga.) material generally flowered later. Abbreviated phenological observations (only "inflorescence emerging" on varied numbers of plants) in 1970 further substantiated the above general trends.

Striking substantiation of the observed difference in phenological development between members of the *epilis* and *sericea* taxa came from observations on New Jersey plants from December 1968 to May 1969 (Table 3). Larger population samples were available at this time (two ramets each of 20 different clones per population). Flowering of New Jersey *epilis* populations occurred approximately 3 months earlier than flowering of New Jersey *sericea* plants (Table 3).

Variability in time of flowering under greenhouse conditions (following annual clipping in late summer) for the *epilis* variant was considerable during 1968, 1969, and 1970 and was especially evident in

TABLE 2. Phenology of populations of *Danthonia sericea* in the greenhouse from February 7, 1968 (day 0), to June 20, 1968

Population	Total plants used	Number of surviving plants	Percentage flowering (of surviving plants)	Mean number of days to: First date of flag leaf stage	Flag leaf stage	Inflorescence emerging stage	Inflorescence clear stage	Anthesis
FRE	4	4	100	2/7/68	3.75	8.50	12.00	14.50
CHE	4	4	100	2/21/68	16.50	21.00	37.30	42.75
LE	4	4	100	2/27/68	24.75	40.50	47.00	50.25
LSM[a]	4	4	100	2/27/68	34.75	41.00	48.25	53.25
AME	4	4	100	3/4/68	38.25	56.25	60.25	65.00
MFE	3	3	100	3/11/68	33.00	41.67	49.00	52.00
RCE	4	4	100	4/6/68	81.00	90.25	99.00	[c]
LSM[b]	4	4	100	4/9/68	90.25	102.00	112.00	[c]
LNJS	4	4	100	3/25/68	68.00	83.75	87.00	[c]
NCS	3	3	66.7	4/15/68	69.50	94.00	96.00	[c]
NES	4	4	100	4/15/68	71.50	92.00	96.00	[c]
FS	4	4	75	4/22/68	86.33	101.67	111.33	[c]
SCS	2	2	100	4/22/68	96.00	112.50	119.00	[c]
DLS	4	4	100	4/24/68	87.25	96.25	102.75	[c]
GS	4	4	100	4/27/68	86.00	106.75	112.50	[c]
RS	4	4	0	[d]	[d]	[d]	[d]	[d]

[a] LSM *epilis* plants.
[b] LSM intermediate plants.
[c] Anthesis did not occur on any date on which phenology readings were taken, and no visible evidence of this stage appeared (e.g., dried anthers, etc.).
[d] No flowering occurred in this population under greenhouse conditions.

TABLE 3. Flowering of four New Jersey populations of *Danthonia sericea* in the greenhouse (December 1968–April 1969)

Population	Taxon	Latitude of collection site	Date when flag leaf stage first observed
FRE	var. *epilis*	39° 50′	12/23/68
CHE	var. *epilis*	39° 49′ 30′	1/7/69
WNJS	var. *sericea*	39° 53′	3/28/69
BNJS	var. *sericea*	39° 46′	4/12/69

the early flowering New Jersey population FRE. First day of flag leaf stage was, respectively, February 7, 1968, December 23, 1968, and January 1, 1970.

Photoperiod experiment

Plants from several populations did not flower in any of the photoperiod treatments. This phenomenon seemed to be associated with poor vigor. All plants with a vigor reading of less than four on February 14, 1969, failed to flower.

Since flowering of certain FRE plants under experimental photoperiods began only 5 days after the experiment started, it is believed that some of the plants of this population were stimulated to flower before the experiment commenced. However, data for the FRE population under various photoperiods indicated some sort of quantitative flowering response to decreased daylengths. Mean date of flag leaf stage was earliest under a 9-hr photoperiod and was successively later under conditions of longer photoperiods. Flowering in clones of the CHE population (Table 4) indicated no qualitative photoperiod requirement, as flowering occurred simultaneously under all experimental photoperiods. These results failed to demonstrate even a quantitative response to daylength (in contrast to the FRE results).

In a southern *epilis* population (AME) flowering occurred only under a 15-hr photoperiod. Flowering of these AME plants occurred later than flowering in the New Jersey (FRE and CHE) populations. Georgia (LSM) *epilis* plants grown from seed also flowered later and only in the 15-hr and 12-hr treatments; earlier, and a larger percentage of flowering occurred in the 15-hr treatment.

Data for the *sericea* taxon are more difficult to interpret because of poor flowering under experimental conditions. In the LNJS population flowering occurred only under 15- and 12-hr photoperiods with earlier flowering under the 15-hr photoperiods.

One other population, intermediate clones of LSM, flowered under experimental photoperiods. Flowering occurred under every photoperiod except the 9-hr treatment.

DISCUSSION

Flowering in the natural habitat

Detailed climatological information is helpful in interpreting the adaptive significance of the close relation between time of flowering of *Danthonia sericea* under field conditions and the latitude of collection site (Fig. 2, $r = 0.988^{**}$). Weather-bureau data were obtained for stations closest to each of the sites. If sites were situated between two weather sta-

TABLE 4. Growth and flowering of populations of *Danthonia sericea* under experimental photoperiods in the greenhouse during the 1969 growing season

Population	Daylength (hr)	Total plants used	Number of surviving plants[a]	First date of:			Mean number of days to:			Total plants that flowered
				Fla.[b]	I.E.[b]	I.C.[b]	Fla.	I.E.	I.C.	
FRE	9	4	4	—[d]	12/26	1/9	8.3	12.0	28.0	4
	12	4	4	12/26	12/28	1/5	16.8	20.0	30.0	4
	15	4	4	12/26	1/3	1/7	21.0	25.8	33.0	4
	Nat.[c]	4	4	—	12/26	1/3	11.7	15.0	25.0	3
CHE	9	4	4	1/2	1/11	2/14	28.3	33.0	51.3	3
	12	4	4	1/2	1/5	1/19	17.3	22.3	39.7	3
	15	4	4	1/15	1/17	1/24	30.7	33.3	41.3	3
	Nat.	4	4	1/2	1/3	1/21	33.3	40.0	50.7	3
AME	9	2	2	—	—	—	—	—	—	0
	12	1	1	—	—	—	—	—	—	0
	15	2	2	1/28	2/4	2/10	45.0	49.0	60.0	2
	Nat.	2	1	—	—	—	—	—	—	0
LSM (*epilis*) seedlings	9	4	2	—	—	—	—	—	—	0
	12	4	2	2/22	2/24	3/12	65.0	67.0	76.0	1
	15	4	4	1/31	2/4	2/13	54.3	57.7	67.0	3
	Nat.	4	4	—	—	—	—	—	—	0
LSM int.	9	2	2	—	—	—	—	—	—	0
	12	2	2	2/20	2/22	3/4	65.0	67.0	76.0	1
	15	2	2	3/12	3/15	3/23	84.0	87.0	95.0	1
	Nat.	2	2	3/23	3/24	—	95.0	96.0	—	1
LNJS	9	4	4	—	—	—	—	—	—	0
	12	4	4	3/15	3/17	3/28	87.0	89.0	100.0	1
	15	4	4	—	2/16	2/22	56.0	59.0	65.0	1
	Nat.	4	4	—	—	—	—	—	—	0

[a] Number of surviving plants defined as those with a vigor rating of 1 or greater at termination of experiment on May 25, 1969.
[b] Fla. = flag leaf; I.E. = inflorescence emerging; I.C. = inflorescence clear.
[c] Nat. refers to a photoperiod equal to the actual daylength for each day (including twilight). This photoperiod was increased as the season progressed.
[d] A dash indicates that data are not available.

tions, average values were used to approximate the climatological conditions.

Temperature, more than any other environmental factor, appears strongly correlated with both latitude of collection site and time of flowering. Correlation coefficients of latitude of collection site with average (1948–68) last date in the spring with a temperature 28°F or less ($r = 0.893^{**}$) and degree-days[3] ($r = 0.920^{**}$) indicated that as the latitude increases, the last date of a temperature of 28°F or less gets later and the total warmth available for growth and flowering decreases. Given the above relationship, the close relation between the time of flowering (anthesis) and the latitude of the collection site seems explained by the distinct correlations of 1970 field anthesis with average last date of a temperature of 28°F or less ($r = 0.881^{**}$) and degree-days ($r = 0.987^{**}$).

Dates of 1970 field anthesis for Georgia and New Jersey differed by over 30 days (Fig. 2). Such a difference indicates that our populations of the *Danthonia sericea* complex either have no photoperiod requirement or do not possess the same photoperiod requirement. Since daylength in the spring increases as latitude increases, one would actually expect later flowering by southern populations than northern ones, if there were an absolute long-day requirement which was similar for all populations studied.

Habitat and flowering response mechanism

Populations of *Danthonia sericea* may be separated into three groups on the basis of their habitat and associated flowering responses: the New Jersey *epilis*, the Georgia *epilis*, and the *sericea* populations. Data from New Jersey *epilis* plants in the greenhouse (FRE, CHE, and MFE) indicated that if flowering in this taxon were controlled by a daylength requirement, initiation of the flowering process in the greenhouse would have occurred during the winter when daylengths are shortest and when plants are dormant under natural habitat conditions. For example, flowering of the FRE population began in early February in 1968 (Table 2), in late December in 1968 (Table 3), and in early January in 1970. Under experimental photoperiods (Table 4) clones of each of two populations (FRE, CHE) flowered almost simultaneously

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[3] When the mean temperature of a day in April, May, and June fell below 65°F, that value was subtracted from 65°F with the results accumulated toward a "degree-day" value.

regardless of the photoperiod. The flowering of the FRE and CHE populations at widely varying times under field, transplant garden, and greenhouse conditions was additional evidence for the lack of an absolute photoperiod requirement in growth and subsequent flowering. Earlier flowering in the greenhouse than in the field or in the transplant garden was probably brought about by higher greenhouse temperatures. Consistent with the evidence, a photoperiod requirement would not seem to be important adaptively in bog populations of *D. s.* var. *epilis* since substrate temperature could be a reliable "environmental stimulus-organism response" mechanism for initiation of growth and subsequent flowering. In the spring these bog habitats have a saturated substrate. Because of the high specific heat of water relative to that of sand particles, maximum substrate temperatures remain low for a longer period of time in the spring in bogs than in the sandy uplands. In Minnesota Reiners (1968) reported that spring soil temperatures rose very slowly in a heavily shaded cedar swamp and did not reach the levels of an oak forest and fen until mid-June. Thus, although air and surface soil in the uplands may get quite warm, the high amount of moisture in the bogs keeps the substrate cool. By the time soil temperatures are adequate for growth and flowering in these wet habitats, the danger of frost damage is probably extremely low.

Georgia *epilis* populations, on the other hand, reacted as long-day plants, as evidenced by their inability to flower under a 9-hr photoperiod (LSM, AME; Table 4), even though flowering occurred under longer daylength treatments. This would be the expected photoperiodic response, if there is one, since *Danthonia sericea* flowers in nature when daylength is increasing. Georgia *epilis* populations were also later in flowering under greenhouse conditions than the New Jersey *epilis* populations, but flowered simultaneously with the New Jersey *epilis* in the transplant garden under longer daylengths. A photoperiod requirement could be of adaptive value to Georgia *epilis* populations (AME, LE, LSM, RCE) growing on sandy, alternately wet-dry outcrop habitats in that premature warming of the outcrop on abnormally warm days in late winter or early spring would not trigger flowering and subsequent dormancy too early in the growing season. Genotypes which prematurely complete growth before the end of the growing season of the habitat area might be at a competitive disadvantage.

Evidence from the greenhouse-grown plants (Tables 2 and 3) and the experimental photoperiod study (Table 4) indicates that members of the *sericea* taxon (LNJS, NCS, NES, FS, DLS, SCS, GS) have a photoperiod requirement. These populations were considerably later in flowering under greenhouse conditions than the New Jersey *epilis* plants (Table 2) even though temperatures remained relatively constant in the greenhouse. Flowering of the LNJS population (Table 4) in the 12- and 15-hr, but not the 9-hr treatment provides additional evidence that the *sericea* taxon responds differentially to daylength. Since the *sericea* variant occurs on well-drained sandy soils, it is expected that these soils would warm up more rapidly in the spring than the wet soils on which the New Jersey *epilis* populations are found. Surface soil temperatures[4] as high as 74°F are attained by mid-April despite the fact that the average date of last temperature of 28°F or less for our New Jersey populations is April 15. Therefore, a long-day requirement would indeed be of survival value to these plants of the *sericea* variant, preventing possible frost damage.

Relevance to past studies

There is no one "expected" flowering response pattern for a latitudinal series of grass species-populations. If marked habitat variations are superimposed upon latitudinal differences, the ways in which populations of a species each attune growth and development to their specific habitats can be strikingly unique. Past studies by McMillan (1959, 1961) generally indicated that plants of different populations transplanted to a uniform garden may either be rather similar or quite different in their time of flowering. Flowering of *D. s.* var. *epilis* populations in our transplant garden corresponded to that reported for *Stipa spartea* and *S. comata* (McMillan 1959) and for *Stipa leucotricha* (McMillan 1961) in that all populations responded similarly. However, our subsequent greenhouse studies indicated that the southern *epilis* populations do respond differentially to daylength and that under the daylengths existing in New Jersey when soil and air temperatures were adequate for growth and development, the photoperiod requirement for the southern populations had already been reached and surpassed. We would predict that the same populations transplanted to a Georgia garden would show earlier flowering by the northern populations. Because of the longer growing season in Georgia, plants possessing a "maturity factor" (McMillan 1957) or a photoperiod requirement (southern populations of *Danthonia sericea*) would have competitive advantage in that flowering and cessation of growth too early in the season would not occur. On the other hand, those outcrop plants not flowering before the drop in monthly precipitation and the beginning of "the dry months" (McCormick and Platt 1964) in May would be at a selective disadvantage due to low seed set. Thus, *Danthonia sericea*, similar to *Stipa* and *Koeleria* species (McMil-

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[4] Data are courtesy of Rutgers Cranberry and Blueberry Research Lab, New Lisbon, N.J. 08064.

lan 1959, 1961), is a "cool-season" species with populations flowering sooner in southern than in northern habitats, and this study provides evidence that flowering time for these outcrop populations is apparently genetically fixed by a photoperiod requirement.

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