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INFLUENCE OF SOLAR RADIATION AND PHOTOPERIOD ON FLOWER INITIATION OF SEASHORE PASPALUM (*PASPALUM VAGINATUM* SW.)

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Abbreviations: PAR, photosynthetically active radiation; PPFD, photosynthetic photon flux density

Keywords: turfgrass, seed production, grass reproduction

ABSTRACT

Production of seeded cultivars of seashore paspalum is possible but limited by length of growing season in the Pacific Northwest and low yield potential in the southern regions of USA. The timing and quantity of flowers play pivotal roles in the process of seed production. External factors of photoperiod and solar radiation were evaluated for their influences on flower initiation of seashore paspalum. The impact of solar radiation was determined by evaluating flowering habit of 11 genotypes of seashore paspalum in response to radiation levels of 100, 41, 27, and 13% of the non-shaded control in a greenhouse study. Eighty-nine genotypes from the USDA seashore paspalum germplasm collection were monitored for flowering habit for 15 weeks in a greenhouse receiving the natural photoperiod of Griffin, GA. In the radiation study, few flowers were produced at radiation levels of 27 and 13% of the non-shaded control, while most genotypes flowered readily under the 100% radiation treatment. Only a few genotypes tested flowered in response to the 41% radiation level treatment. Plants receiving weekly cumulative PAR (photosynthetically active radiation) of less than 90.2 mmol m^{-2} wk^{-1} did not flower. Flowering response to photoperiod varied greatly among genotypes. Flower initiation for the majority of the monitored genotypes increased dramatically as photoperiod reached 14 h and progressed to the longest photoperiod of 14.4 h. These findings indicate that seashore paspalum behaves as a long-day plant with a minimum light intensity of around 90.0 mmol m^{-2} of weekly cumulative PAR required for flower induction. Information obtained from this work should prove useful in improving the potential for production of seeded cultivars of seashore paspalum.

INTRODUCTION

Seashore paspalum (*Paspalum vaginatum* Sw.) is a perennial warm-season grass that has recently become popular as a turfgrass (Duncan, 1997; Morton, 1973). This species has great potential to enhance the aesthetic value of landscapes, and has been successfully used for soil stabilization and site reclamation (Duncan, 1997; Duncan and Carrow, 2000). As recently as 2000, a few researchers have suggested that seashore paspalum must be propagated vegetatively from sod or sprigs since establishment from seeds was not reliable (Duncan and Carrow, 2000). After years of breeding research focused on development of seeded cultivars, the first seeded cultivar 'Sea Spray' was released in 2003. It is the only seeded cultivar currently commercially available (Fricker et al., 2007). Sea Spray is produced in Oregon, USA, in a region that is known for its ability to produce high-quality seed of cool-season turf species. Considerable expertise and infrastructure for grass seed production exist in this region, but the climate is cool to temperate and production of seed from warm-season species such as seashore paspalum is challenging. Oregon has a cool growing season that typically limits the flowering period of seashore paspalum. Seed fields of seashore paspalum often suffer from winter injury which results in slow green-up in the spring. Delays in flowering push maturation of the seed crop closer to the onset of fall and winter rains typical of this region.

Logically the southern USA would be expected to be better suited for production of seashore paspalum since its growing season is warmer than that of the Pacific Northwest. However, seed production trials conducted in multiple locations in the southern United States have typically resulted in fewer flowers and lower seed yields than are achieved in Oregon in spite of its cooler growing season. In order to produce profitable seed yields, parental lines chosen for use in production fields whether in Oregon or Georgia must not only produce

functional and compatible reproductive organs but also must produce large numbers of flowers (Chastain and Young, 1998).

Changing environmental factors can affect and regulate flowering in plants. Photoperiod and temperature are the primary external factors known to induce flowering (Roberts and Struckmeyer, 1938; Rogers, 1950; Thompson, 1944). Measurement of photosynthetically active radiation is important to determine the effect of light on plant growth and flower induction (McCree, 1972a; 1972b; 1981). Photosynthetically active radiation (PAR) is the range of light (400 to 700 nm wavelength) that can be used by plants for photosynthesis (Commission Internationale de l'Eclairage, 1970). Photosynthetically active radiation is quantified by photosynthetic photon flux density (PPFD) and is reported as micromoles of photon per square meter per second. Latitude, season, and time of day influence PAR levels. Level of PAR can also be influenced by weather or objects that block direct sunlight.

A supply of photo-assimilates is prerequisite for flower initiation (Thomas and Vince-Prue, 1997). Hence, photosynthesis, which is affected by duration, intensity, and quality of light, plays a significant role in flower induction. High intensity light may affect the phytochrome action or the biosynthesis of the substances that promote flowering (Smith, 1975). In long-day species, such as *Lolium,* periods of low light intensity during the night are sufficient to induce flowering (Evans, 1958) Sucrose or glucose can be sufficient to substitute for low light intensity in some long-day plants; however, the requirement for high irradiance levels cannot be totally substituted by external energy (Brulfert et al., 1985).

For flowering plants (angiosperms), the time of flowering is critical for their reproductive success. Photoperiodism results in a synchrony of flower initiation within a population which

promotes genetic recombination by out crossing (Heide, 1985). Photoperiod is known to influence and regulate many aspects of plant development including formation of storage organs, leaf development, seed germination, and flower initiation (Thomas and Vince-Prue, 1984). Flowering plants are classified as long-day plants, short-day plants, and day-neutral plants (Thomas and Vince-Prue, 1997). A long-day plant flowers when the day length exceeds its critical photoperiod. These plants typically flower in late spring or early summer as days are getting longer. Short-day plants flower when the day lengths are less than their critical photoperiod and require a consolidated period of darkness (long nights) before floral development can begin. Day-neutral plants do not initiate flowering based on photoperiodism at all and flower regardless of the night length.

Knight (1955) reported that optimum seed production of dallisgrass (*Paspalum dilatatum* Poir.) occurred at 14 h photoperiod with a high night temperature of 18.3 to 21.1˚C. No seed formed under 8 h photoperiod, and erratic seed heads and incomplete flowering were observed under12 h photoperiod (Knight, 1955). An understanding of the flowering habits of germplasm lines is helpful to researchers who wish to select parents with synchronized flowering in order to promote crossing.

Limited information is currently available regarding the impact of photoperiod and solar radiation on flower induction of seashore paspalum. The goal of this research was to characterize the flowering habits of seashore paspalum and to identify parental lines best suited for potential production regions including the Southeastern and the Pacific Northwest regions of the USA. The specific objectives were to (1) determine the impact of solar radiation levels on flower initiation of seashore paspalum and (2) evaluate the USDA seashore paspalum germplasm collection for flowering response under the natural photoperiod of Griffin, Georgia.

MATERIALS AND METHODS

Effect of PAR level on floral induction. Impact of solar radiation level on flower induction was determined by monitoring the number of flowers initiated under different solar radiation levels. Two commercial cultivars, 'SeaIsle 1' and 'SeaIsle 2000', and nine breeding lines (Q36313, Hyb 7, PI647920, PI647892, PI647894, 03-501-46, 03-522-23, 03-528-126, 03-531-22) from The University of Georgia seashore paspalum breeding program were used in this study. Plant materials were established clonally from stolon nodes. Plants were grown in 10 x 10 cm pots and were maintained in a greenhouse with a temperature of 28 ±5/20 ±5˚C (day/night) without any artificial light supplementation. During the period of study, plants were never trimmed. Plants were irrigated twice daily and fertilized monthly with 28-7-14 (NPK) fertilizer (MacroN, Lesco, Ohio). In the greenhouse study, four levels of solar radiation 100 (no shade cloth), 41, 27, and 13% were created by using commercially available shade cloth designated as 60, 40, and 20% shade. Radiation levels were imposed on plants by placing PVC frames fitted with shade cloth covers over greenhouse flats each containing one replicate of the 11 genotypes. Quantum sensors (LI-190, LI-COR Environment, Lincoln, NE) were used to measure PAR under each level of solar radiation. PAR values were recorded using a Campbell Scientific 21X data logger (Campbell Scientific, Logan, UT) and summarized on a weekly basis. The flowers produced in each pot were recorded and removed weekly for 23 weeks. This experiment contained three replications and was repeated in time. Data were collected from the two trials (repetitions) from 25 Mar. to 26 Aug. and 1 Apr. to 2 Sept. 2011.

The experiment was statistically analyzed using analysis of variance (ANOVA) (SAS Institute, Cary, NC) as a split-plot design with the four radiation levels as main plots and the 11 genotypes as sub-plots. The flowering data collected at each of the 23 weeks (under different

photoperiods) were considered as repeated measures.

Effect of cumulative PAR on flower initiation. The actual solar radiation data collected during this study were also examined in an attempt to determine if there was evidence to support a minimum radiation level necessary for flowering in seashore paspalum. Hierarchical cluster analysis was used to divide the weekly data from all experimental units (reps/genotypes/radiation levels) into five discrete classes based on actual radiation level received. The numbers of flowers produced by each experimental unit were then graphically displayed by weekly sample dates for each radiation level class. Cluster analysis and graphic display of the results was accomplished using SAS JMP 8.0.2 (SAS Institute, Cary, NC).

Flowering response of USDA seashore paspalum germplasm collection. The flowering patterns of 88 genotypes from the USDA seashore paspalum germplasm collection were monitored for 15 weeks under natural photoperiods in a greenhouse experiment. Plant materials used in the study were established clonally from stolon nodes. All plants were grown in 10 x 10 cm pots and maintained without clipping in an air conditioned greenhouse maintained at 25 ±2/18 ±2˚C (day/night) temperature under natural photoperiod. Water was supplied twice daily by an automatic irrigation system and fertilizer applied monthly with a water soluble 28-7-14 (NPK) fertilizer (LESCO MacroN, Cleveland, Ohio). The experimental design was a completely randomized block and each genotype was replicated six times. The number of flowers occurring in each pot was recorded and flowers removed weekly for 15 weeks from May to September 2011, the most vigorous flowering period of seashore paspalum in Georgia. Data were analyzed using analysis of variance by SAS (SAS Institute, Cary, NC) and graphically displayed using SAS JMP 8.0.2 (SAS Institute, Cary, NC).

RESULTS

Solar radiation effect on flower initiation. The results of the analysis of variance were summarized and are presented in Table 1. The combined analysis indicated no differences between the two trials (repetitions) of this experiment. The four radiation treatments imposed created a wide range of radiation levels from 100% to 13% of the non-shaded control and significant differences ($P<0.001$) were found in the number of flowers produced in response to these radiation treatments. Genotypic differences in flower initiation ($P<0.001$) among the 11 genotypes tested were noted. The numbers of flowers initiated were highly significantly different ($P<0.001$) among dates indicating that changes in the natural day length over time significantly affected the flowering in seashore paspalum. The radiation by genotype interaction was also highly significantly different ($P<0.001$) indicating that genotypes responded differently in response to the radiation treatments. Table 2 shows the average weekly flowering response of each genotype in response to the four radiation levels averaged over the duration of the experiment. Few flowers were produced at radiation levels of 13, 29, and 41%. Flower production in most genotypes was low under any level of shade and no significant differences were observed among the three lowest irradiation treatments. Plants of 10 of the 11 genotypes produced significantly more flowers when grown under the highest irradiation (non-shaded) than when grown under shade. PI647920 and Q36313 appeared more low light tolerant than the other genotypes as evidenced by higher flower numbers at 41% ambient radiation levels. Experimental line 03-501-46 produced very few flowers regardless of radiation level.

Effect of cumulative PAR on flower initiation. PAR values ranged from 0 during the night to over 2000 μmol photons m^{-2} s^{-1} around 1400 h. Weekly cumulative PAR values over the entire period of the experiments were 226.5, 93.4, 61.8, and 28.9 mmol m^{-2} for the 100, 41, 27,

and 13% radiation treatments, respectively. Cluster analysis (data not shown) divided mean weekly PAR into discrete classes of 11.0-32.8, 32.9-64.4, 64.5-90.2, 90.3-189.7, and189.8-297.7 mmol m^{-2}. Experimental units receiving weekly cumulative PAR of less than 90.3 mmol m^{-2} did not flower (Fig. 1). However, flowering did occur when weekly cumulative PAR levels were between 90.3 to189.7 mmol m^{-2}. Greater flowering was observed at weekly cumulative PAR values of 189.8 to 297.7 mmol m^{-2}. These results provide support to the concept that seashore paspalum is not able to respond to normally inductive photoperiods when grown under low light intensity conditions.

Genotypic flowering response to photoperiod. The mean numbers of flowers produced weekly over 15 weeks by each of 88 genotypes of the USDA seashore paspalum collection were recorded (data not shown). Statistical analysis of this data showed significant genotypic differences ($P< 0.001$). Fig. 2 shows the overall response of the 88 genotypes in relation to photoperiod. Flowering increased rapidly as photoperiod increased above 13 h and peaked near the longest day of 14.4 h on 21 June. Flowering intensity then declined rapidly and reached a plateau as the photoperiod dropped below 14 h. Flowering response to photoperiod varied greatly among genotypes. Cluster analysis (data not shown) classified the 88 genotypes into seven groups according to the similarity of the flowering habit (Fig. 3). Flower initiation for the majority of the genotypes increased dramatically as photoperiod reached 14 h and progressed to the longest photoperiod of 14.4 h. Genotypes that clustered together as Group 4 included 'Collier', 'Excalibur', 'Kai Luna', and 'Wai Lua Kauai'. Peak flowering of genotypes in this group occurred during shorter photoperiods of less than 14.3 h (before 2 June). The genotypes classified as Group 2 flowered the least with no obvious peaks in response to changing photoperiod. Genotypes classified into Group 1 showed a second flowering peak in the middle of

August; however flowering was less intense than during the initial peak in June.

DISCUSSION

The information gained from these two studies suggests that lower light intensity does inhibit the initiation of flowering of seashore paspalum. During this experiment, plants maintained under low light intensity remained vegetative, and increased growth of above ground biomass. Longer internodes and fewer nodes were observed. Similarly Quedado and Friend (1978) reported that flowering of *Anagais arvensis* L. was increased by increasing irradiation up to 1900 μmol m^{-2} s^{-1} and that high photon density was required for flower induction. In the current study, it was difficult to separate the effects of solar radiation from photoperiod effects in a greenhouse radiation study since natural radiation levels varied with seasonal changes of photoperiod. Further studies with the ability to independently control light intensity and photoperiod are needed to better define the impact of light intensity on flowering in seashore paspalum. It should be noted that most growth chambers are not capable of producing light levels necessary for flowering of seashore paspalum.

Most genotypes of seashore paspalum flowered most intensely as day length increased to the longest day of the year (14.4 h). The percentage of plants flowering was the greatest (90%) around the longest day of the year. As day length decreased, the number of flowers produced steadily decreased. This finding provides support for the designation of seashore paspalum as a long-day plant, which initiates flowering when the day length is longer than the critical photoperiod (Thomas and Vince-Prue, 1997). Substantial genotypic differences in flowering habit were found in response to photoperiod among the 88 genotypes evaluated. This represents the first report of genotypic diversity in response to photoperiod and flowering time in seashore

paspalum. Approximately 25% of the lines evaluated flowered very little when exposed to the natural photoperiod of Griffin, Georgia. It is unknown if these lines require even longer photoperiods than were presented in this study or if they simply do not flower.

Nelson et al. (2010) proposed that induction of flowering in plants can be affected not only by length of the photoperiod, but also by the direction of change (increasing or decreasing) of the photoperiod. Photoperiodism affects both vegetative and reproductive growth (Hay and Heide, 1983). According to Slafer and Rawson (1996), increases in both photoperiod and temperature reduced time to heading of wheat. Torres and Lopez (2011) reported that *Tecoma stans* remained vegetative when grown under a 9 h photoperiod, only 30% of plants flowered when the photoperiod increased to 12 h, and all plants had visible buds and flowered under 14 and 16 h photoperiod. The findings reported here represent the first research to provide evidence that paspalum is a long-day plant. Future experiments should be conducted with a wider range of photoperiods and under controlled temperatures with high light intensity to more accurately determine the critical day-length and the influence of temperature on flower induction of seashore paspalum genotypes.

Based on the data presented, Collier, Excalibur, Kai Luna, and Wai Lua Kauai and possibly 'Cloister', 'Adalayd', and 'HI 10' could be classified as early flowering genotypes. All of these genotypes produced greater flower numbers than did the parents of Sea Spray under shorter photoperiods than those experienced in the production fields of Oregon. The use of earlier flowering parents in Oregon could improve yield stability of seashore paspalum seed production by providing more time for seed fill and maturation before the end of the growing season. Our data also suggest that photoperiod may restrict flowering of most seashore paspalum genotypes when grown in the southern USA. The identification and use of genotypes

capable of intense flowering under shorter photoperiods could greatly improve the potential for future seed production in the southeastern USA.

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Table 1. Summary of analysis of variance showing effects of trials (repetitions), solar radiation, genotype, and date on flower number of seashore paspalum in a greenhouse experiment conducted under natural photoperiod from March to September 2011.

Source of variation	df	Mean square
Trial (T)	1	0.01
Error a: Rep (T)	2	1.39
Radiation (R)	3	18.71***
T × R	3	0.47
Error b: Rep × R (T)	6	0.42
Genotype (G)	10	2.85***
T × G	10	4.20***
R × G	30	1.84***
T × R × G	30	2.98***
Error c: Rep × G (T × R)	80	2.13
Date (D)	22	5.09***
T × D	22	1.33**
R × D	66	3.80***
G × D	220	0.60
T × R × D	66	0.86*
T × G × D	220	0.67
R × G × D	660	0.52
T × R × G × D	660	0.57
Error d	3960	0.63

*, **, *** Significant at 0.05, 0.01, 0.001 probability levels, respectively.

Table 2. Least square mean of flower number of 11 genotypes in response of radiation levels over 23 weeks.

	Radiation level (percent of ambient)			
Genotype	**100%**	**41%**	**27%**	**13%**
			flower number[†]	
03-501-46	**0.01a**	**0.03a**	**0.00a**	**0.00a**
03-522-23	**0.04a**	**0.00b**	**0.00b**	**0.00b**
03-528-126	**0.71a**	**0.08b**	**0.05b**	**0.05b**
03-531-22	**0.17a**	**0.04b**	**0.02b**	**0.01b**
Hyb 7	**0.05a**	**0.00b**	**0.01b**	**0.00b**
PI 647892	**0.76a**	**0.04b**	**0.03b**	**0.00b**
PI 647894	**0.52a**	**0.06b**	**0.01b**	**0.00b**
PI 647920	**2.01a**	**0.49b**	**0.06c**	**0.01c**
Q36313	**1.23a**	**0.30b**	**0.09b**	**0.04b**
SI 1	**0.36a**	**0.04b**	**0.01b**	**0.00b**
SI 2000	**0.07a**	**0.00b**	**0.00b**	**0.00b**

[†] **Average number of flowers produced per pot per week. Means in the same row followed by the same letter are not considered different according Student's t-test at α=0.05.**

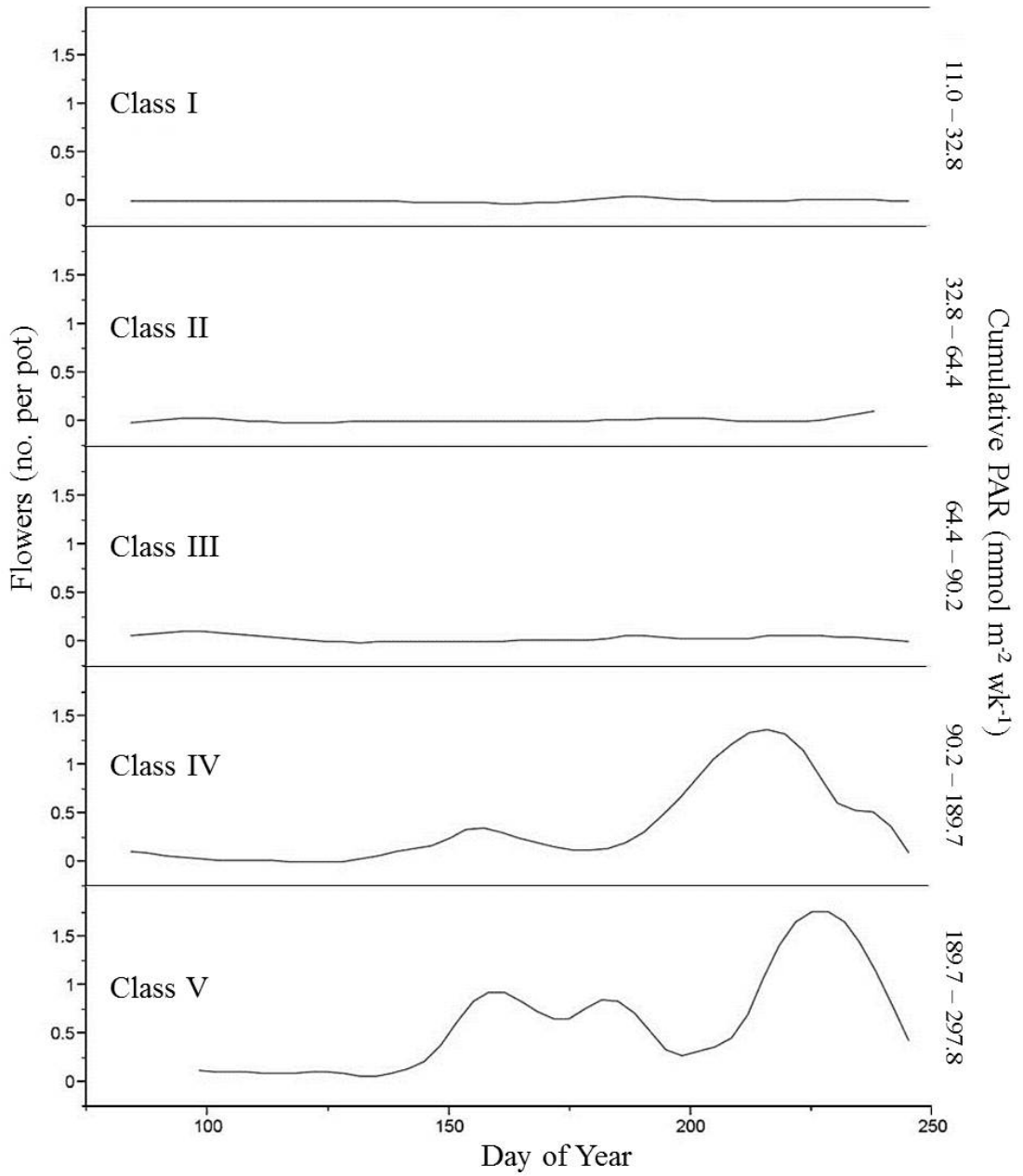

Fig. 1. The effect of weekly cumulative PAR on flower production. PAR has been divided into five discrete classes with seasonal flower response shown.

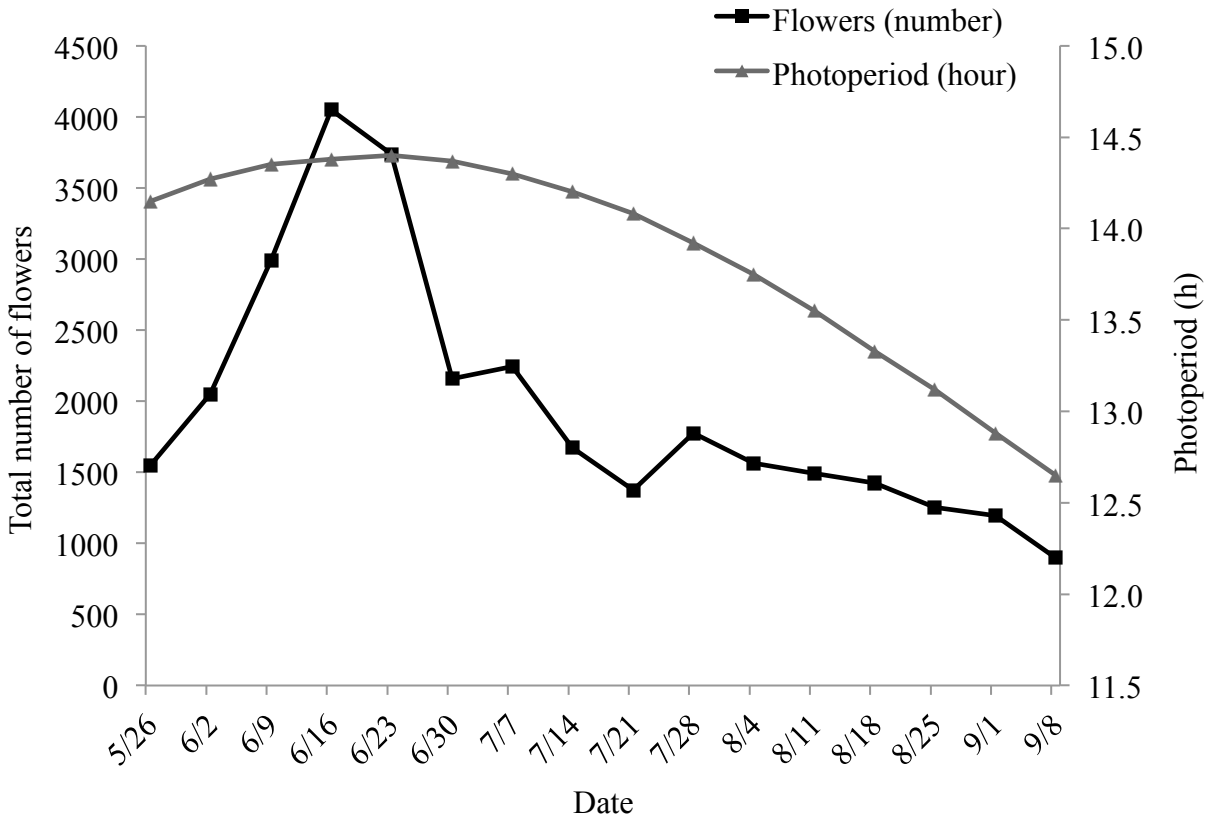

Fig. 2. Total number of flowers initiated on 88 genotypes in response to natural changes in photoperiod occurring from May to September 2011.