

Photothermal controls of vegetative dormancy in *Poa secunda*

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Handling Editor: Zeng-Yu Wang

Funding information

U.S. Department of Agriculture, Grant/Award Number: 2017-67019-26370; Iowa Nutrient Research Center, Grant/Award Number: 2019-04

Abstract

Background: Summer vegetative dormancy is a desirable trait in cool-season grasses when they are interplanted with annual crops. Sandberg bluegrass (*Poa secunda* J. Presl.) shows summer dormancy, but the environmental cues that control dormancy remain unknown.

Methods: A controlled environment study using temperature and day length combinations of 32.2°C/15 h, 26.6°C/14 h, 21.1°C/13 h, and 15.5°C/12 h was conducted with *P. secunda* accessions PI232347, PI639272, and PI232348, and ‘Audubon’ red fescue as a nondormant control to determine the optimum treatment for dormancy induction. A second study using treatments of 26.6°C/14 h, 21.1°C/13 h, and 15.5°C/12 h was conducted to determine the thresholds for dormancy release. A third study used a factorial experiment with two temperatures (32.2°C and 15.5°C) and two day lengths (15 and 12 h) to differentiate between temperature and day length effects on dormancy induction.

Results: Of the four temperature and day length combinations, all except for 15.5°C/12 h resulted in dormancy by the end of 6 weeks, with 32.2°C/15 h inducing dormancy in only 17 days. Of the three treatments for dormancy release, 15.5°C/12 h broke dormancy the fastest in all accessions and released the most number of plants from dormancy. Considerable variation existed between accessions for the speed of dormancy release in the 21.1°C/13 h and 26.6°C/14 h treatments. The third study showed that temperature is the primary inducer for summer dormancy, while longer day length may promote dormancy under inductive temperatures.

Conclusions: This study identified the optimum photothermal for induction and release of summer dormancy in *P. secunda*, which will help future studies in elucidating the mechanism of summer dormancy.

KEYWORDS

controlled environment, dormancy induction, dormancy release, Sandberg bluegrass, summer dormancy

INTRODUCTION

Highly productive maize (*Zea mays* L.) and soybeans [*Glycine max* (L.) Merr.] dominate agriculture in the Midwestern United States, but are associated with water and soil quality issues. This is largely in part due to leaving fields fallow during the off-season, exposing the farmland to erosion, and the excessive amounts of fertilizers applied, which, without vegetation to intercept, is lost via leaching (Cassman et al., 2002; Porter et al., 2015). Cool-season turfgrasses used as perennial groundcovers (PGCs) have been identified

as a possible solution to ameliorate these consequences (Moore et al., 2019; Schlautman et al., 2021), and can support intensive agricultural production with minimal management (Flynn et al., 2013; Wiggans et al., 2012a). Cool-season turfgrass PGCs are uniquely suited to provide valuable ecosystem services to rehabilitate farmland. Primarily growing in the spring and fall when the weather is cool, their shallow but dense, fibrous root systems act as a net that intercepts excess nutrients during the most susceptible times of the year (Randall et al., 2003). In addition, during the main crop's growing season, PGCs can increase water

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retention and decrease surface evaporation (Wiggans et al., 2012b).

However, not all turfgrasses are compatible with the main crop when the two are intercropped. Several studies have found considerable yield losses when cool-season turfgrass PGCs are used in maize production without sufficient growth suppression (Box et al., 1980; Carreker et al., 1972; Harper et al., 1980). The selection of incompatible turfgrass PGCs can lead to decreased maize and soybean yields (Bartel et al., 2017a, 2017b). It is clear that, despite their preference for cool, moist growing environments, active growth of cool-season turfgrasses can occur well into the critical weed-free period (Zimdahl, 1988) for maize and soybeans. This critical weed-free period is the time when weeds must be managed to prevent the most amount of yield loss (Swanton & Weise, 1991). This growth overlap between PGC and the main crop can pose a threat to the yield potential of the main crops by altering the red/far-red light ratio that could trigger the shade avoidance response of maize/soybean seedlings, which may cause yield reduction to the main crop (Page et al., 2009, 2010). This is particularly true of contemporary, commercially available turfgrass cultivars, which historically have been bred for persistent growth year-round and esthetic appearance. It is vital to minimize the competition posed to the main crop by either suppressing the growth of PGC during the critical weed-free period or using turfgrasses that are not competitive during the crop growing season.

Poa secunda J. Presl. is a species included in the Sandberg bluegrass complex (Majerus et al., 2011) that shows a similar summer vegetative dormancy trait as that found in related species such as *Poa scabrella* Thurb. Benth (Laude, 1953) and *Poa bulbosa* L. (Ofir & Kigel, 1999). This summer dormancy, characterized by cessation of growth and onset of dormancy before unfavorable summer conditions, appears to be a trait adapted by cool-season perennial grasses to escape predictably long and dry Mediterranean summers (Balachowski et al., 2016; Volaire & Norton, 2006). In these grasses, summer dormancy appears to be triggered regardless of moisture availability and is controlled by increasing day length and probably high temperatures (Laude, 1953; Ofir & Kerem, 1982). In a 5-year study, summer dormancy in *P. scabrella* was found to be induced by high temperatures and long days in natural and artificial environments, with the onset of dormancy occurring within a 2-week window each year (Laude, 1953). Grasses that possess summer dormancy usually resume growth following the return of cooler temperatures and moisture, growing through the winter and early spring (Ofir & Kigel, 2003). Previous studies have suggested that summer dormancy in perennial temperate grasses can be broken with cooler temperatures and moisture, but cannot be broken with either factor alone (Laude, 1953; Volaire, 2002). Additionally, some level of moisture is required for grasses to maintain summer dormancy (Laude, 1953; McWilliam & Kramer, 1968; Ofir et al., 1967). It is likely that *P. secunda* has a similar dormancy behavior to *P. scabrella*, which did not break dormancy

for 3 weeks in the field despite steady, cool weather and would only resume growth when water was also provided (Laude, 1953). This type of dormancy is classified by Volaire and Norton (2006) as ecodormancy, where dormancy is governed by a specific set of environmental circumstances. This differs from endodormancy, when dormancy is controlled internally, and para-dormancy, when dormancy is controlled by an external biochemical stimulus. In many ways, summer ecodormancy is very similar to that of winter dormancy. Both are strategies for plants to avoid unfavorable growing conditions, often accompanied by dehydration and leaf senescence to prevent damage to surviving tissues (Gillespie & Volaire, 2017; Volaire & Norton, 2006). Dormancy induction, acquired by either decreasing photoperiod and temperature in the case of winter dormancy or the opposite for summer dormancy, leads to the plant retreating to a resting organ or buds, where it remains ready to grow when favorable conditions return (Gillespie & Volaire, 2017). Plants can also enhance their dormancy to protect themselves from inhospitable growing conditions, should favorable conditions return temporarily. Norton et al. (2006) found that orchardgrass/cocksfoot (*Dactylis glomerata* L.) and tall fescue had lessened growth reduction and foliage senescence, characteristics of summer dormancy when sown in the spring compared to the previous fall. They hypothesized that preparations for summer dormancy begin during the winter, allowing the plant to enter dormancy well before the wet season is over in the spring to avoid unsuitable summer conditions, only to resume growth when cooler fall temperatures and precipitation prevailed. Such reliable timing on both ends of a summer crop's growing season would be an extremely valuable tool if implemented in PGCs, allowing producers to plan their seasons more effectively.

Plant photosynthesis is driven by radiant energy, or light, and development is controlled by day length and thermal energy, or temperature (Liu & Heins, 2002). The combination of these signals can drive plant functions by inducing a photothermal response, relating to both light and temperature (Johansson et al., 2014). Several studies have detailed the photothermal controls behind *P. bulbosa* development and summer dormancy (Ofir & Kerem, 1982; Ofir & Kigel, 1999; Youngner, 1960), but the environmental cues that induce or release summer vegetative dormancy in *P. secunda* have not been well studied.

Identifying the photothermal thresholds in the induction and release of summer dormancy in *P. secunda* can enable the development of more compatible PGCs that minimize competition with summer crops while maintaining the benefits of PGC during the off-season. This study aims to identify the photothermal controls in *P. secunda* by subjecting selected accessions to different temperature and photoperiod treatment combinations. More specifically, the objectives of this project were to (1) identify the photothermal thresholds that control the induction and release of summer dormancy in genetically distinct accessions of *P. secunda* and (2) determine the role of

temperature or day length in summer dormancy induction in the same accessions of *P. secunda* as those used for objective 1.

MATERIALS AND METHODS

Plant materials

P. secunda accessions PI232347, PI232348, and PI639272 obtained from the Western Regional Plant Introduction Station (<https://npgsweb.ars-grin.gov/gringlobal/site?id=26>) and ‘Audubon’ red fescue (*Festuca rubra* L.) were prorogated from seed in the Horticulture Research Greenhouse at Iowa State University, Ames, IA. PI232347, PI232348, and PI639272 were selected based on previous field studies that found them to show minimal yield loss when intercropped with maize. PI232347 originates from Minnesota, PI232348 originates from Wyoming, and PI639272, also known as ‘Reliable’, originates from Utah. Seedlings were transplanted into 4-inch pots with LC1 soilless media (Sun Gro Horticulture, 2021) and grown in the same greenhouse mentioned above at 22.5°C/21.6°C (day/night) with a 16/8 h (day/night) photoperiod and a light intensity of approximately 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Experiment I: Study of the effect of photothermal combinations representative of the growing season on the induction of summer vegetative dormancy

After 2 months, 12 individuals from each accession were transferred into each of four growth chambers with temperature and day length treatment combinations of 32.2°C/15 h, 26.6°C/14 h, 21.1°C/13 h, and 15.5°C/12 h for 6 weeks. The light intensity in each growth chamber was maintained at approximately 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$. These treatments were designed to replicate field conditions during April (21.1°C/13 h), July (32.2°C/15 h), September (26.6°C/14 h), and October (15.5°C/12 h) in Boone, IA, where previous field experiments had been conducted and were based on historical weather data collected from the Boone Municipal Airport weather station. The experiment was a randomized complete block design and repeated four times by rotating treatments in different growth chambers. Consequently, a total of 48 plants for each accession were used for each treatment. The cultivar ‘Audubon’ of red fescue was used as a nondormant control. Plant pots were watered to saturation every 2–3 days to prevent moisture stress. Visual greenness ratings on a scale of 1–9 were made daily to measure the cessation of growth and onset of vegetative dormancy. A rating of 1 was equivalent to the grass having little to no green tissue, while a rating of 9 was equivalent to the grass being fully green, healthy, and actively growing. Stages of vegetative dormancy were determined as described in Ofir and Kigel (2003), with a 50% loss of green tissue considered as the first stage of dormancy as the grass progressed toward dormancy. A loss of 75% or more of

green tissue was considered the onset of full dormancy. These two stages are equivalent to a greenness rating of 5 and 2, respectively. Plants that had a majority of green tissue remaining were considered nondormant. Treatment responses were analyzed at $p < 0.05$ with a repeated-measures analysis of variance (ANOVA) using PROC MIXED in SAS version 9.4 (SAS Institute Inc., 2013).

Experiment II: Study of the effect of photothermal combinations representative of the growing season on the release of summer vegetative dormancy

Two-month-old *P. secunda* plants from the same accessions were propagated using the same methodology as the dormancy induction study and were placed into a growth chamber set at 32.2°C with a day length of 15 h. The light intensity in each growth chamber was maintained at approximately 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$. This photothermal combination was shown to be the most effective in inducing summer vegetative dormancy in the study described above. Once complete cessation of growth occurred in *P. secunda*, 10 plants from each accession were placed into each of three growth chambers with temperature and day length treatment combinations of 26.6°C/14 h, 21.1°C/13 h, and 15.5°C/12 h. Plants were arranged in a randomized complete block design with three replications, and a total of 30 plants of each accession were used for each treatment. Plant pots were watered to saturation every 2–3 days to prevent moisture stress. The number of plants that broke dormancy and the date on which dormancy was released were recorded for 3 weeks. The number of plants that broke dormancy was analyzed using the ANOVA procedure in SAS version 9.4 (SAS Institute Inc., 2013).

Experiment III: Study of the effect of day length or temperature on the induction of summer vegetative dormancy

To determine whether high temperature (32.2°C) or long day length (15 h) alone can induce summer vegetative dormancy in *P. secunda*, we carried out a 2 × 2 factorial study with two temperatures (32.2°C and 15.5°C) and two day lengths (15 and 12 h). Five 1-year-old plants each of PI232347 and PI639272 that were maintained in the greenhouse at 22.5°C/21.6°C (day/night) with a 16/8 h (day/night) photoperiod and a light intensity of approximately 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ were transferred to growth chambers that were programmed to provide the following treatments: 32.2°C/15 h, 32.2°C/12 h, 15.5°C/15 h, and 15.5°C/12 h. The experiment was replicated three times; thus, a total of 15 plants for each accession were treated. Plant pots were watered to saturation every 2–3 days to prevent moisture stress. Visual greenness ratings on a scale of 0–9 were performed to measure the cessation of growth and onset of dormancy. A rating of 0 was equivalent to the

grass having no green tissue, while a rating of 9 was equivalent to the grass being fully green, healthy, and growing. Treatment responses were analyzed at $p < 0.05$ with a repeated-measures ANOVA using PROC MIXED in SAS version 9.4.

RESULTS AND DISCUSSION

The effect of photothermal combinations representative of the growing season on the induction of vegetative dormancy

All treatments, except the 15.5°C/12 h treatment, resulted in a measurable cessation of growth by the end of the experiment. Cessation of growth in each accession was different from one to another over the duration of the experiment. It should be noted that the dip in greenness ratings immediately after transfer into the growth chambers was likely shock experienced by the plant, as ratings across all treatments were affected, but were recovered a few days later. The 32.2°C/15 h and 26.6°C/14 h treatments both induced dormancy in all *P. secunda* accessions, though it is clear that the 32.2°C/15 h treatment-induced dormancy at a much faster rate than the 26.6°C/14 h treatment. In PI232347 (Figure 1a), full dormancy was reached as quickly as 23 days. The first stage of dormancy was reached 13 days earlier in the 32.2°C/15 h treatment compared to the 26.6°C/14 h treatment. Full dormancy

was reached 16 days earlier in the 32.2°C/15 h treatment compared to the 26.6°C/14 h treatment. The 21.1°C/13 h treatment caused PI232347 to reach the first stage of dormancy, but only at the end of the 6 weeks, with initial cessation in growth occurring 5 weeks into the treatments.

PI232348 responded similarly (Figure 1b) to each treatment when compared to PI232347, though small differences were present. Full dormancy was reached in 22 days after transfer into the growth chambers in the 32.2°C/15 h treatment. The first stage of dormancy was reached 20 days earlier in the 32.2°C/15 h treatment compared to the 26.6°C/14 h treatment, and full dormancy was reached 21 days earlier in the 32.2°C/15 h treatment compared to the 26.6°C/14 h treatment. Despite the 32.2°C/15 h treatment inducing the first stage of dormancy at 11 days in both PI232347 and PI232348, the 26.6°C/14 h treatment took 5 additional days to induce PI232348 compared to PI232347. In the 26.6°C/14 h treatment alone, it appears that PI232347 enters dormancy more readily than PI232348, which maintained higher ratings of greenness for a longer period of time. Similar to PI232347, the 21.1°C/13 h treatment caused PI232348 to reach the first stage of dormancy at the end of the 6 weeks, but after 5 weeks of remaining nondormant.

PI639272 reached dormancy as quickly as 17 days in the 32.2°C/15 h treatment, 15 days earlier than the 26.6°C/14 h treatment (Figure 1c). The first stage of dormancy was reached in only 9 days after transfer into

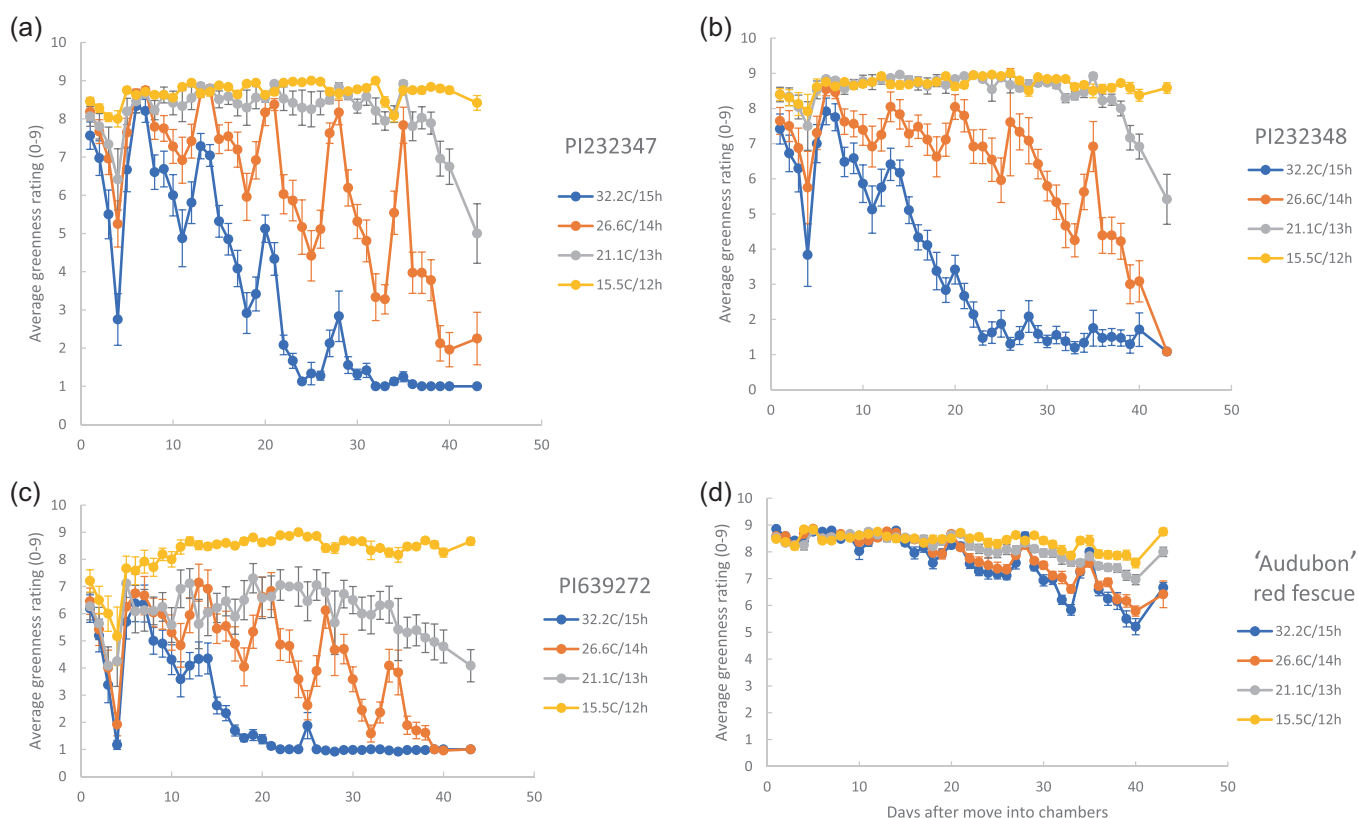


FIGURE 1 Cessation of growth over 6 weeks in PI232347 (a), PI232348 (b), PI639272 (c), and red fescue, cv. Audubon (d) under temperature and day length treatment combinations of 32.2°C/15 h, 26.6°C/14 h, 21.1°C/13 h, and 15.5°C/12 h. Each data point represents the average rating recorded across 48 individuals in all replications of the experiment. Each bar represents the standard error for a particular sampling date. A greenness rating of 5 indicates the first stage of dormancy, and a greenness rating of 2 indicates the onset of a full summer dormancy.

the growth chambers in the 32.2°C/15 h treatment, with the 26.6°C/14 h treatment reaching the same stage just 2 days later. Unlike PI232347 and PI232348, which maintained ratings above 8 in the 15.5°C/12 h and 21.1°C/13 h treatments until 38 days after transfer into the growth chambers, PI639272 showed a more proportional response to the temperature and day length treatments. This is evidenced by PI639272 maintaining ratings above 8 in the 15.5°C/12 h treatment, but maintaining ratings between 5 and 7 in the 21.1°C/13 h treatment for 38 days, after which it entered the first stage of dormancy. Though PI639272 did not reach full dormancy at 21.1°C/13 h, this growth pattern differed from the previous two accessions, which did not reach the first stage of vegetative dormancy with this treatment until the end of experimentation. In contrast, plants of the red fescue cultivar, ‘Audubon’ did not respond strongly to the temperature and day length treatments (Figure 1d).

Overall, dormancy was induced in *P. secunda* in both 32.2°C/15 h and 26.6°C/14 h treatments (Figure 2a–c), while plants of the red fescue cultivar, ‘Audubon’ did not

go to dormancy under any experimental conditions tested in this study (Figure 2d). The actual photothermal threshold for dormancy induction likely lies between 26.6°C/14 h and 21.1°C/13 h. However, it is clear that with increasing temperature and day length, dormancy is induced at a faster rate. What would have been considered the first stage of dormancy occurred near the end of the 6 weeks of experimentation when greenness rating for the ‘Audubon’ plants dipped close to 5 for the 32.2°C/15 h treatment. This is likely the result of abiotic stress caused by high temperatures as the optimum temperature range for cool-season grasses is between 15°C and 24°C (DiPaola & Beard, 1992). However, red fescue is not known for having summer dormancy.

The effect of photothermal combinations representative of the growing season on the release of vegetative dormancy

In this study, dormancy was considered to be broken when new green tissue started to appear. Across all accessions, the 15.5°C/12 h treatment broke dormancy at the highest frequency, with dormancy broken in just 3 days after plants were moved from the 32.2°C/15 h induction chamber to cooler treatment chambers. When treatments were held constant, there were no differences across accession response; however, differences were found between how each accession responded to each treatment (Table 1).

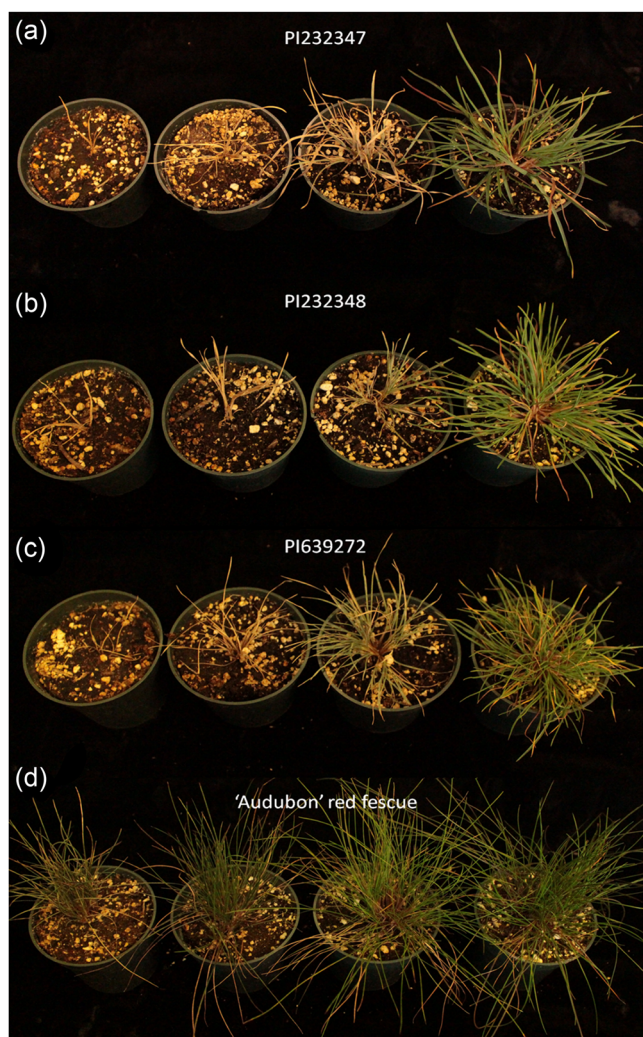


FIGURE 2 The effect of temperature and photoperiod on three *Poa secunda* accessions (a) PI232347, (b) PI232348, (c) PI639272, and (d) red fescue cv. ‘Audubon’. Each panel of four plants is arranged in treatment order of 32.2°C/15 h, 26.6°C/14 h, 21.1°C/13 h, and 15.5°C/12 h. Pictures were taken at the end of the 6-week experiment.

TABLE 1 Differences in dormancy release responses of *Poa secunda* J. Presl. accessions PI232347, PI232348, and PI639272 to 26.6°C/14 h, 21.1°C/13 h, and 15.5°C/12 h treatments after being induced to dormancy in a 32.2°C/15 h growth chamber.

Treatment	Comparison	$p > F$ (p value)
15.5°C/12 h	PI232347 vs. PI232348 vs. PI639272	0.72
21.1°C/13 h	PI232347 vs. PI232348 vs. PI639272	0.09
26.6°C/14 h	PI232347 vs. PI232348 vs. PI639272	0.21
Accession		
PI232347	15.5°C/12 h vs. 21.1°C/13 h vs. 26.6°C/14 h	0.0260
	15.5°C/12 h vs. 26.6°C/14 h	0.0114
	21.1°C/13 h vs. 26.6°C/14 h	0.4445
	15.5°C/12 h vs. 21.1°C/13 h	0.0319
PI232348	15.5°C/12 h vs. 21.1°C/13 h vs. 26.6°C/14 h	0.0025
	15.5°C/12 h vs. 26.6°C/14 h	0.0009
	21.1°C/13 h vs. 26.6°C/14 h	0.0078
	15.5°C/12 h vs. 21.1°C/13 h	0.0697
PI639272	15.5°C/12 h vs. 21.1°C/13 h vs. 26.6°C/14 h	0.0301
	15.5°C/12 h vs. 26.6°C/14 h	0.0145
	21.1°C/13 h vs. 26.6°C/14 h	0.0298
	15.5°C/12 h vs. 21.1°C/13 h	0.5913

PI232347 responded well to the 15.5°C/12 h treatment, with over 70% of plants resuming growth in 2 weeks, which was significantly higher than the two other treatments (Figure 3a). PI232347 did not respond very well to the 21.1°C/13 h treatment, with only 20% of plants breaking dormancy by the end of the third week. The 26.6°C/14 h was not effective at breaking dormancy, with only 3% of plants resuming growth at the end of experimentation.

PI232348 responded well to the 15.5°C/12 h treatment, and over 70% of plants resumed growth in 2 weeks, similar to PI232347. However, PI232348 responded better to the 21.1°C/13 h treatment, with over 40% of plants resuming growth by 2 weeks and over 60% at the end of the third week. The number of plants that resumed growth in the 15.5°C/12 h treatment was not statistically different from those in the 21.1°C/13 h treatment. Given the similar responses to treatments in the dormancy induction study, it is surprising to see that PI232348 breaks dormancy more readily than PI232347. Similar to the PI232347, the 26.6°C/14 h was not effective at breaking dormancy (Figure 3b), with only 7% of plants resuming growth by the end of experimentation, which was significantly lower than the other two treatments.

PI639272 readily broke dormancy, with both the 15.5°C/12 h and 21.1°C/13 h treatments releasing over 70% of plants from dormancy by the end of the third week (Figure 3c). The rate at which dormancy was broken was similar in these two treatments, with the 21.1°C/13 h treatment reaching similar numbers of plants released from dormancy to that of the 15.5°C/12 h treatment, just 1 or 2 days later. No differences were found between the number of plants that resumed growth in these two treatments. The 26.6°C/14 h treatment also broke dormancy in PI639272, unlike PI232347 and PI232348, with 27% of plants recovered by

the end of 3 weeks. However, the 26.6°C/14 h still had significantly fewer plants that resumed growth compared to the other two treatments. Our results suggest that the true photothermal threshold for breaking dormancy likely lies between 21.1°C/13 h and 26.6°C/14 h. Decreasing temperatures and day lengths were associated with faster rates of breaking dormancy, but considerable variation exists in how readily specific accessions respond to each treatment. A representative progressive view of dormancy release of a plant from each accession is shown in Figure 4.

While differences in summer dormancy behavior between perennial grass species have been well studied (Biddiscombe et al., 1977; Laude, 1953; Ofir & Kerem, 1982; Volaire et al., 2009), studies investigating differences in cultivars within grass species are limited. Malinowski et al. (2009) evaluated several cultivars of summer-dormant and summer-active tall fescue [*Lolium arundinaceum* (Schreb.) Darbysh.] and orchardgrass (*D. glomerata* L.) for biomass production and persistence. Summer-dormant cultivars in both species showed considerable variation in their summer dormancy indexes, a method of measuring plant productivity during the summer compared to a high-yielding cultivar of the same species as that described in Norton et al. (2009). Norton et al. (2009) only used two cultivars for each species evaluated in their study, but also found differences between summer dormant and nondormant cultivars.

The effect of day length or temperature on the induction of vegetative dormancy

While valuable information is gained from testing temperature and day length combinations that mimic

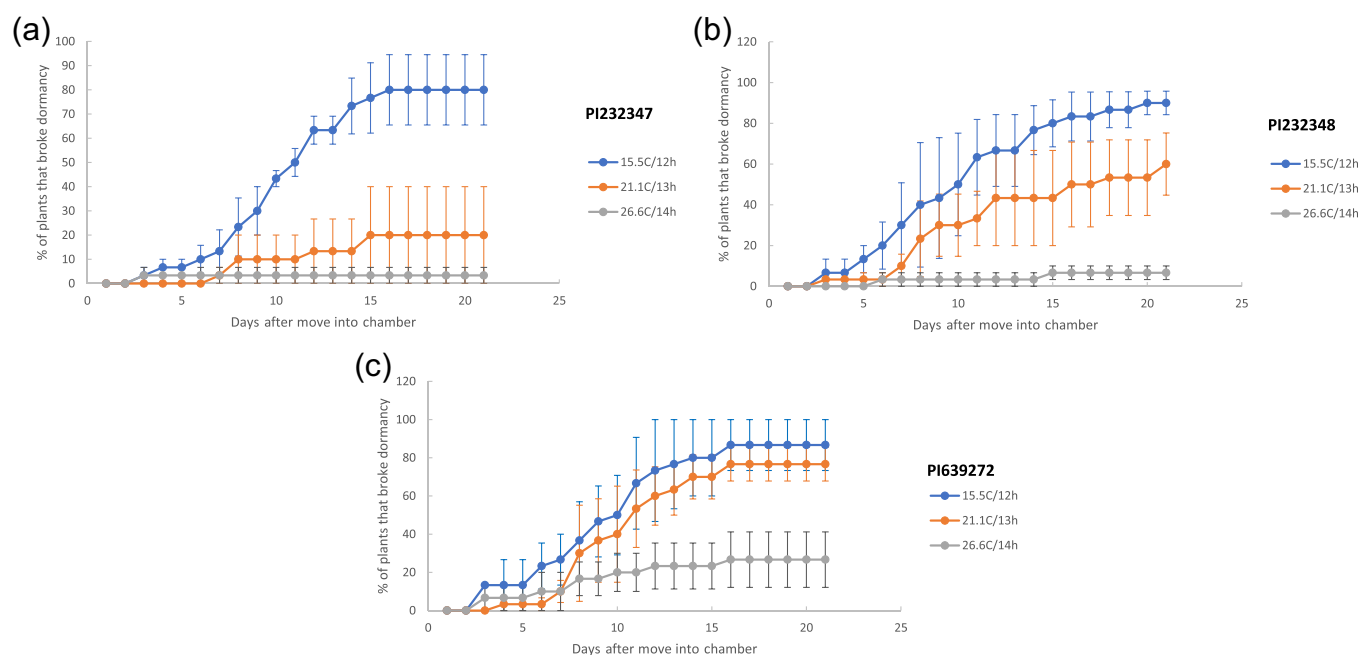


FIGURE 3 Percentage of plants in PI232347 (a), PI232348 (b), and PI639272 (c) that broke dormancy after 3 weeks in temperature and day length treatments of 26.6°C/14 h, 21.1°C/13 h, and 15.5°C/12 h. Each data point represents the average rating recorded across 30 individuals in all replications of the experiment. Each bar represents the standard error for a particular sampling date.

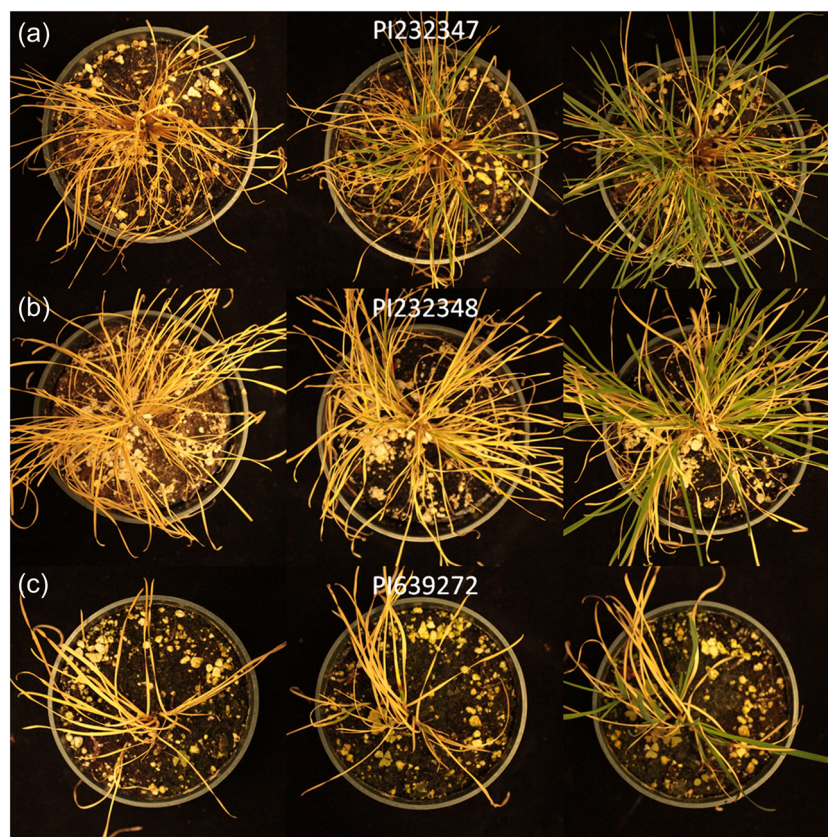


FIGURE 4 The effect of temperature and photoperiod on dormancy release of the three *Poa secunda* accessions (a) PI232347, (b) PI232348, and (c) PI639272 in the 15.5°C/12 h treatment, the most effective at releasing dormancy. Each panel of three pictures represents the same plant within each accession at 1, 8, and 17 days after transfer from the 32.2°C/15 h induction chamber to the 15.5°C/12 h treatment.

conditions in the field on inducing and breaking *P. secunda* vegetative dormancy, it is difficult to separate the effects between the two variables without using a factorial treatment design. Therefore, using the maximum and minimum temperatures and day lengths in combination with another can help quickly determine which effect was more important for inducing dormancy. Accessions of PI232347 and PI639272 were subjected to treatments of 32.2°C/15 h, 32.2°C/12 h, 15.5°C/15 h, and 15.5°C/12 h. PI232348 was not used due to its similar dormancy induction behavior to PI232347. After 31 days, patterns in cessation of growth were compared over time across each treatment combination. When analyzed with a repeated-measures ANOVA, temperature was found to be a significant factor ($p < 0.0001$) contributing to cessation of growth, while day length was not ($p = 0.71$). This indicates that temperature is likely more important for controlling dormancy induction. However, when looking at the differences in cessation of growth over time between the 32.2°C/15 h treatment (Figure 5a) and 32.2°C/12 h (Figure 5b), it appears that longer day length may enhance dormancy induction based on both PI232347 and PI639272 reaching full dormancy (a rating of 2 or below) 5 days earlier in the 32.2°C/15 h treatment. Neither accession achieved dormancy at 15.5°C with either a 15 or 12 h photoperiod (Figure 5c,d). While *P. secunda* and *P. bulbosa* are related species, this study suggests that they have opposite controls that regulate

their dormancy responses. Ofir and Kerem (1982) reported that in *P. bulbosa*, low-temperature delays the onset of dormancy but does not prevent it, and high temperatures enhance summer dormancy induced by long days with photoperiods of 11–12 h (Ofir & Kigel, 1999).

Unlike *P. bulbosa*, which reproduces primarily by the formation of bulbs at the stem base and bulbils in the seedhead, *P. secunda* produces true seed via facultative apomixis (Kelley et al., 2009; Kellogg, 1987), a distinct advantage over *P. bulbosa*. Kelley et al. (2009) showed that the ploidy level in *P. secunda* varies considerably between accessions examined, ranging from hexaploid to dactyploid. In many aspects, *P. secunda* is similar to Kentucky bluegrass (*P. pratensis* L.), a widely grown turf and forage grass with a facultative apomictic reproductive mode and high variability in ploidy levels. Interspecific hybridization among *Poa* species is common (Darmency & Gasquez, 1997; Kindiger, 2004a, 2004b; Pepin & Funk, 1971), and the resulting hybrids with complementary traits can be valuable germplasm for turf, forage, or as a PGC. The present study identified important environmental cues that control the induction and release of summer dormancy in *P. secunda* and established a robust method for summer dormancy assessment that will enable genetic analysis of summer dormancy in *P. secunda* and related *Poa* species.

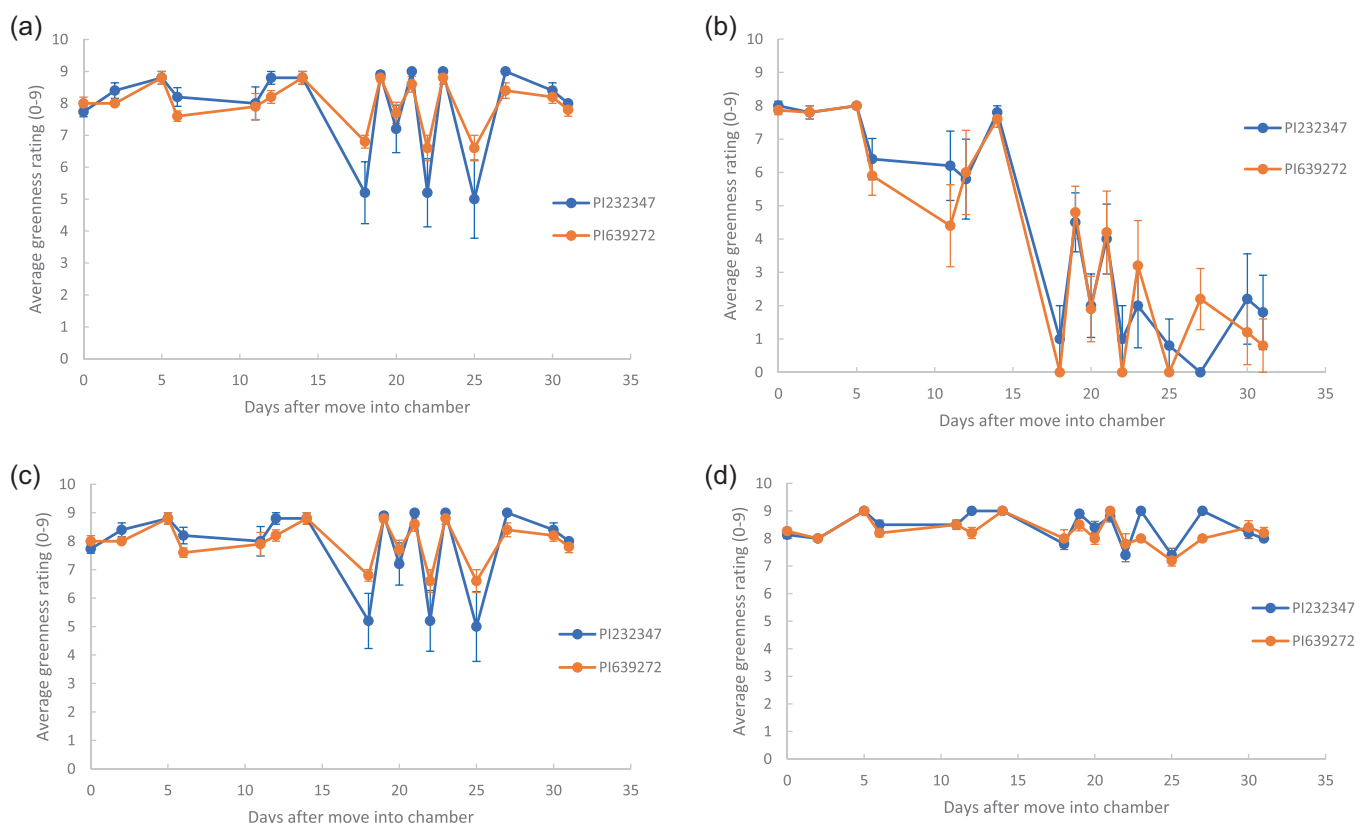


FIGURE 5 Cessation of growth in PI232347 and PI639272 when subjected to a 32.2°C/15 h (a), 32.2°C/12 h (b), 15.5°C/15 h (c), and 15.5°C/12 h (d) treatment for 31 days. Each dot represents the average of all ratings taken on that day for each accession across all replications. Each bar represents the standard error for a particular sampling date. A greenness rating of 5 indicates the first stage of dormancy, and a greenness rating of 2 indicates the onset of a full summer dormancy.

CONCLUSIONS

We identified photoperiod/temperature combinations that induce or release summer dormancy for three accessions of *P. secunda*. The 32.2°C/15 h combination is the most effective treatment for induction, while the 15.5°C/12 h combination is the most effective treatment for breaking dormancy. The photothermal threshold that controls vegetative summer dormancy in *P. secunda* likely lies between the treatment combinations of 21.1°C/13 h and 26.6°C/14 h, with increasing temperature and day length associated with increased rate of dormancy induction and decreasing temperature and day length associated with increased rate of breaking dormancy. The temperature was found to be the primary controlling factor behind dormancy induction, with day length possibly enhancing the rate of temperature-controlled summer dormancy. This study provides valuable information that can inform decisions on further developing cool-season perennial turfgrass PGCs. The experimental conditions that induce or release summer vegetative dormancy can be used to identify candidate genes responsible for summer dormancy induction or release with RNA-seq by generating summer-dormant *P. secunda* plants and breaking dormancy under controlled environments. Furthermore, the information obtained from this study can be used to assess summer dormancy in *P. secunda* under controlled environments, thus significantly shortening the screening time compared to

field screening, allowing faster development of more compatible cool-season turfgrass PGCs for use in agricultural cropping systems. Future studies should be directed at investigating if the temperature is also the primary controlling factor in breaking summer dormancy, screening additional *P. secunda* accessions to identify and characterize their respective dormancy behaviors, characterizing the genetic controls behind the photothermal thresholds identified, and how long *P. secunda* dormancy can last while remaining viable.

AUTHOR CONTRIBUTIONS

Allen A. Chen: Investigation and methodology; writing—original draft; formal analysis. **Shui-zhang Fei:** Funding acquisition; conceptualization; writing—original draft; writing—review and editing. **Andrew W. Lenssen:** Funding acquisition; conceptualization; writing—original draft. **Kenneth J. Moore:** Funding acquisition; conceptualization; writing—original draft.

ACKNOWLEDGMENTS

This study was supported by a grant from USDA-NIFA (Award Number 2017-67019-26370 to K. J. M., A. W. L., & S. F.) and a grant from the Iowa Nutrient Research Center (Grant no. 2019-04 to S. F., A. W. L., K. J. M., & A. A. C.). The authors would like to thank the Jacklin Seed Company for their generous support and are grateful to Pete Lawlor and Kaitlin Diggins for their invaluable assistance and efforts toward this project.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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How to cite this article: Chen, A. A., Fei, S.-z., Lenssen, A. W., & Moore, K. J. (2022). Photothermal controls of vegetative dormancy in *Poa secunda*. *Grassland Research*, 1(1), 43–52.
<https://doi.org/10.1002/glr2.12008>