Eur. J. Hortic. Sci. *89*(6) | ISSN 1611-4426 print, 1611-4434 online | https://doi.org/10.17660/eJHS.2024/027 | © ISHS 2024

Original article

Growth and cation uptake in turf-type tall fescue (*Festuca arundinacea* Schreb.) are affected by low light intensity

Qian He[1] and Deying Li[2]

[1] College of Forestry and Landscape Architecture, South China Agricultural University, Guangzhou, China
[2] Department of Plant Sciences, North Dakota State University, Fargo, U.S.A.

Summary

Low light intensities adversely affect the growth of tall fescue (*Festuca arundinacea* Schreb.). The objective of this experiment was to understand the effects of low light intensity on tiller/leaf appearance rate, and on cation uptake. Single plants of two tall fescue cultivars, 'Tar Heel II' and 'Wolfpack', were established in plastic tubes and maintained in a greenhouse. The plants were subjected to shade treatment by covering with black knitted polyethylene cloth that allows 30% of full light to pass through without changing the light quality. Shade treatment reduced the biomass and stomatal density of tall fescue but did not affect stomatal conductivity. There was a greater reduction of root biomass (66%) than shoot biomass (47%). Shaded tall fescue also had a lower leaf appearance rate (0.132 leaf d^{-1}) than that in full light (0.139 leaf d^{-1}), which decreased to 0.065 leaf d^{-1} and 0.070 leaf d^{-1}, respectively, over 4 weeks. Similarly, tiller appearance rate in shade was 0.36 tiller d^{-1}, as compared to 0.42 tiller d^{-1} for full light, which decreased to 0.11 tiller d^{-1} and 0.18 tiller d^{-1}, respectively, 4 weeks after shade treatment. Shoot potassium concentration showed no difference in plants grown under shade or full light. Our results indicated that Fe content increased in leaves under shaded conditions. However, the optimum Fe content for managing tall fescue under such conditions is still unknown. Further research on the soil application of Fe and phytosiderophores to enhance shade tolerance is recommended.

Keywords
lawn, nutrient, shade, tiller, turfgrass

Significance of this study

What is already known on this subject?

- Tall fescue plants show decreased photosynthetic activity and slower growth under low light conditions. Shade-weakened tall fescue plants are more vulnerable to infestations by weeds and diseases.

What are the new findings?

- Under low light conditions, tall fescue root growth reduces more than shoot, while shoot Fe accumulations increase. These are considered important adaptation mechanisms.

What is the expected impact on horticulture?

- High density is critical for quality turfgrass. Management practices of tall fescue under shade conditions can be adjusted to improve root health and Fe availability in the soil.

Introduction

Low light intensities may negatively affect the growth of tall fescue (*Festuca arundinacea* Schreb.) despite its relatively strong shade tolerance as compared to other commonly used cool-season turfgrasses (Gilbert and DiPaola, 1985; Van Huylenbroeck et al., 1999; Gardner and Taylor, 2002). The influences of shade (light quality and quantity) (Wherley et al., 2005) on plants are manyfold, starting with lower net photosynthetic accumulations, followed by slower leaf appearance, decreased total leaf number, accelerated leaf senescence (Causin et al., 2006), reduced shoot and root biomass (Allard et al., 1991a), and ultimately lower tiller density (Allard et al., 1991a), all of which contribute to poor turf quality. Additionally, extended periods of shaded conditions make turfgrasses more vulnerable to certain diseases such as powdery mildew (Smith and Jackson, 1989) and result in slower recovery from damages caused by traffic and wear (Van Huylenbroeck and Van Bockstaele, 2001).

Woledge (1971) reported that the specific leaf area of forage-type tall fescue increased under shade resulting in an increased photosynthesis rate based on unit leaf dry weight, while the stomatal conductance and dark respiration rates decreased under the same conditions based on leaf area or dry weight. The apparent photosynthetic rate in the aging leaves of tall fescue decreased faster under shade compared to full light, resulting in a shortened leaf life span under shade (Woledge, 1971). Early research showed that the increase of leaf specific area in tall fescue under shade was due to the increases in air space and decreases in leaf thickness, as well as decreases in the volume of epidermis, vascular bundles, and mesophyll cells (Cohen et al., 1982; Allard et al., 1991a). The stomatal density of tall fescue leaves decreased under shade compared to full light exposure, but the number of stomata decreased more on the adaxial side than the abaxial side (Allard et al., 1991a). Carbon dioxide exchange rate as well as stomatal conductance decreased in tall fescue leaves, while chlorophyll content per unit dry weight of leaves increased under shade compared to full light (Allard et al., 1991b). He and Li (2021) reported that turf-type tall fescue cultivars showed a periclinal arrangement of chloroplasts against cell walls as a unique adaptation mechanism to low light intensity.

Managing turfgrass under shade requires multiple approaches. Adding artificial lights or periodically providing natural sunlight by opening the roof of a stadium or trans-

porting turfgrass modules outdoors is cost-prohibitive and is not widely used (Hunter et al., 2009). Understanding the impact of shade on plant growth is helpful in optimizing management practices in addition to using shade tolerant cultivars (Beard, 1997). Plant breeders can incorporate important traits for improving shade tolerance more effectively by understanding the shade-tolerance mechanisms and by using accurate and affordable assessment methods. Nelson et al. (1977) reported that tall fescue yield (aboveground biomass) components such as number of tillers/plant, yield/tiller, and leaf area expansion rate are not affected by the concentration of water-soluble carbohydrates in leaves and CO_2 exchange rate of leaves. However, the growth rate of the leaf elongation zone was faster in shaded leaves than in the full light due to the high sink strength of the elongation zone of leaves (Schnyder and Nelson, 1989), which is a genetically controlled trait (Wilhelm and Nelson, 1978; Volenec and Nelson, 1981). The tiller density and tillering rate was negatively correlated with yield/tillering (Zarrough et al., 1983a, b).

High shoot density and growth rate is desirable for turf-type tall fescue. The contributions of nutrient uptake to shoot growth, leaf and tiller appearance rates of tall fescue under shade are not clear. We report here the findings of shade effects on growth of turf-type tall fescue as well as the underlying mechanisms, such as the reduction of root biomass and mineral nutrients uptake/balance. The primary objective of this experiment was to understand the effects of low light intensity on tiller and leaf appearance rate and to find out if decreased photosynthesis capacity affect root biomass and cation nutrient uptakes in return.

Materials and methods

The experiment was conducted in a greenhouse at North Dakota State University (Fargo, ND). 'Tar Heel II' and 'Wolfpack' tall fescue cultivars, which showed different responses to shade (He and Li, 2021), were seeded in plastic tubes measuring 4 cm in diameter and 20 cm in depth. The growth medium was washed silicon sand. The plants were maintained at 25/15°C (day/night), 14 h/10 h (light/dark) photoperiod, and minimum midday PAR of 400 µmol m^{-2} s^{-1} supplemented from metal halide lamps. The average PAR during the light period was 322 µmol m^{-2} s^{-1}. The growth medium was maintained at field capacity by watering twice daily until the seeds germinated, when the watering was reduced to once daily. The seedlings were fertilized by watering with half strength Hoagland solution (Hothem et al., 2003) at 10 mL per tube twice a week. At the 2-leaf stage, the plants were thinned to one seedling per tube.

At the 4th leaf stage of the main tiller, full strength Hoagland solution was applied to the sand medium at 20 mL per tube every other day and the shade treatment was initiated. The shade was applied by covering the plants with black knitted polyethylene cloth (Grower's Solution, Cookeville, Tennessee, U.S.A.) that allowed 30% of full light to pass through. The light spectrum under shade was not changed compared to the untreated control. The light intensity and spectrum were confirmed by measurement using a quantum sensor (LI-190R, LI-COR Biosciences, Nebraska, U.S.A.) and a pyranometer (LI-200R, LI-COR Biosciences, Nebraska, U.S.A.). Plants without shade cover represented the untreated control. There was no difference in canopy temperatures between the shade treatments and controls based on frequent checking using type E thermocouple sensors.

To monitor the leaf senescence, on the day prior to the initiation of shade treatment and weekly thereafter for 4 weeks, the fourth fully developed leaves from the primary shoots were excised and placed in the leaf chamber of a LI-COR 6400 Portable Photosynthesis System (LI-COR Biosciences, Nebraska, U.S.A.) to measure stomatal conductance (g_s). During the measurement, the ambient CO_2 concentration was 340 µl L^{-1} and temperature was 25°C. Meanwhile, tiller number and leaf number on the primary shoot of the seedlings were recorded. A tiller was defined as one shoot with at least one fully developed leaf. A leaf with ligule and auricles exposed was considered as fully developed. Leaf appearance rate (LAR) (number of leaves $plant^{-1}$ d^{-1}) of the primary shoot and tiller appearance rate (TAR) (number of new tiller $plant^{-1}$ d^{-1}) were calculated based on the leaf and tiller number data. Both LAR and TAR parameters are traditionally used for the development of grass species (Mitchell, 1953; Silsbury, 1970). Stomatal density was determined by measuring the fourth, fifth and sixth fully developed leaves of the primary shoot at 4 weeks after shade (WAS). Briefly, a leaf sample was shaved with a razor blade while the leaf was submerged in a few drops of water on a glass slide to prepare the epidermal specimen. Both adaxial and abaxial epidermal specimens were observed under a light microscope (BX51TF, Olympus, Tokyo, Japan). The stomata density was counted for each field of view and recorded as number of stomata per unit area. Final measurements were made 4 weeks after the initiation of shade treatment.

At the end of each experiment, the shoot biomass was harvested by clipping at the soil surface. The roots were harvested by washing the sand off on a 2-mm sieve with tap water and rinsed with deionized water at the end. The root and shoot dry mass were recorded after drying at 68°C for 48 h. The dry tissues were ground to pass through a 0.178 mm sieve for nutrient analysis in tissues. The concentration of K, Ca, Mg, Na, and Fe in the tissues were analyzed using an AA7000w flame atomic absorption spectrophotometer (Beijing East & West Electronic Company, Beijing China) following dry ashing in a muffle furnace at 490°C for 8 h and digestion with 5 *M* aqua regia (Greweling, 1976; Jones et al., 1991).

The experiment was arranged in a randomized complete block design with three replicates and the experiment was conducted twice in two separate runs. Each shaded or full light treatment unit had 98 plants (one plant per tube). The data were subjected to analysis of variance (ANOVA) using mixed procedures in SAS 9.4 (SAS Institute, 2013) with the runs and the replicates within runs treated as random variables. The two runs were combined after testing the homogeneity of variance using the *F*-test. The data at different WAS were treated in the model as repeated measurements. Treatment means were separated using Tukey's significant difference (HSD) at the 0.05 probability level.

Results and discussion

Data from the two experimental runs had homogenous variances based on the *F*-test of the ratios of the error terms of the two runs (both had six degrees of freedom). There was no interaction between cultivar and shade treatment. Therefore, the data of two cultivars were pooled in the presentation to focus on the shade treatment main effects.

Shade treatment reduced the biomass of tall fescue (Table 1). There was a greater reduction of root (60%) than shoot biomass (50%). This indicates that aboveground growth of turf-type tall fescue had a sink priority under shade, which may be a mechanism to compensate for the reduced

Table 1. Shoot and root biomass of tall fescue cultivars 'Tar Heel II' and 'Wolfpack' as affected by shade that had 30% intensity of the full light.

		Root	Shoot
		g plant^{-1}	
Full sun		12.81a[z]	33.46a
Shade		4.36b	17.68b
		ANOVA	
Source of variance	*Df*	*P>F*	
Cultivar	1	0.9961	0.4349
Shade	1	**<0.0001**	**<0.0001**
Cultivar*Shade	1	0.6950	0.8876

[z] Means within the same column followed by a same letter are not different based on Tukey's significant difference (HSD) at 0.05 probability level.

Table 2. Stomatal density on adaxial and abaxial surfaces of the fourth, fifth, and sixth leaves of the primary tiller after four weeks of shade treatment. Results show the average of two tall fescue cultivars 'Tar Heel II' and 'Wolfpack' as affected by shade that had 30% intensity of the full light.

		Fourth		Fifth		Sixth	
		Adaxial	Abaxial	Adaxial	Abaxial	Adaxial	Abaxial
		Stomate mm^{-2}					
Full sun		84a	60a	82a	57a	74a	42a
Shade		72b	36b	66b	34b	61b	31b
		ANOVA					
Source of variance	*Df*	*P>F*					
		Adaxial			Abaxial		
Cultivar (C)	1	0.7208			0.6482		
Shade (S)	1	**<0.0001**			**<0.0001**		
Leaf position (L)	2	0.0821			0.1568		
C*L	2	0.4425			0.6242		
C*S	1	0.0397			0.0462		
S*L	2	0.6544			0.6852		
C*S*L	2	0.5459			0.6646		

Table 3. Leaf stomatal conductance of CO_2 for the average of tall fescue cultivars 'Tar Heel II' and 'Wolfpack' as affected by shade that had 30% intensity of the full light.

Treatment	WAS1[z]	WAS2	WAS3	WAS4
	mol m^{-2} s^{-1}			
Full sun	0.09a[y]	0.05a	0.05a	0.04a
Shade	0.10a	0.05a	0.04a	0.05a
	ANOVA			
Source of variance	*Df*	*P>F*		
Cultivar (C)	1	0.9724		
Shade (S)	1	0.6993		
Time (T)	3	**<0.0001**		
C*T	3	0.5731		
S*T	3	0.2793		
C*S	1	0.7984		
C*S*T	3	0.6369		

[z] WAS, week after shade.

[y] Means within the same column followed by a same letter are not different based on Tukey's significant difference (HSD) at 0.05 probability level.

photosynthesis capacity. However, such adaptation may be limited because the reduction of root growth over a long period of time potentially reduces the uptake of nutrients. The uptake of many essential mineral nutrients also depends on transpiration, which could be reduced by decreased stomatal density (Table 2) and stomatal conductance (Table 3) in newer leaves. Unlike the report by Allard et al. (1991b) and Woledge (1971), the shade treatment did not affect stomatal conductance in our experiment (Table 3). We attribute this discrepancy to the lower intensity of the full light treatment. In fact, results from Allard et al. (1991b) showed no difference in stomatal conductance between the treatments that had 60% and 30% of the full light (PPFD > 1,500 µmol m^{-2} s^{-1}) which was much higher than the full light intensity in our experiment. The research by Woledge (1971) was conducted outdoors in summer with a shade treatment allowing 26% of natural light passage. The decrease of stomatal conductance in time (Table 3) may be a result of leaf senescence, which may contribute to the decrease of the transpiration stream over time.

The shade treatment lowered the LAR (Table 4), which was also decreasing in time, indicating that the shade effects became more substantial over a longer period. These seemingly trend of stronger shade effects on LAR at week 2 and week 3 indicate that the source of photosynthesis became a more limiting factor over time. However, the shade by time interaction was not significant ($P = 0.09$). The interaction effects of cultivar and time for LAR suggests that the two cultivars may have different performance under shade (Table 4). At the initiation of shade, two cultivars did not have different LAR in respond to shade. At week 3, the 'Tar Heel II' had a LAR of 0.095 leaf d^{-1} while that of 'Wolfpack' was 0.089 leaf d^{-1} (data not shown in Table 4). As a result of slower LAR, TAR also decreased in the shade treatment (Table 5). However, the interaction between cultivar and time was not significant indicating that TAR was not affected by cultivar over the time period of this experiment (Table 5). The decreasing of LAR and TAR is in agreement with the reduction of apparent photosynthesis over time under shade (Woledge, 1971; He and Li, 2021).

Since we only measured LAR from the primary tiller, there could be no discussion of site filling which was found not sensitive to temperature and soil nutrients levels for many grasses including perennial ryegrass (*Lolium perenne*

Table 4. Primary shoot leaf appearance rate (LAR) for the average of tall fescue cultivars 'Tar Heel II' and 'Wolfpack' as affected by shade that had 30% intensity of the full light.

Treatment	WAS1[z]	WAS2	WAS3	WAS4
			Leaf d^{-1}	
Full sun	0.139a[y]	0.114a	0.092a	0.070a
Shade	0.132b	0.098b	0.075b	0.065b
		ANOVA		
Source of variance	*Df*		*P>F*	
Cultivar (C)	1		0.6206	
Shade (S)	1		**<0.0001**	
Time (T)	3		**<0.0001**	
C*T	3		**0.0005**	
S*T	3		0.0897	
C*S	1		0.7584	
C*S*T	3		0.5179	

[z] WAS, week after shade.

[y] Means within the same column followed by a same letter are not different based on Tukey's significant difference (HSD) at 0.05 probability level.

Table 5. Tiller appearance rate (TAR) for the average of tall fescue cultivars 'Tar Heel II' and 'Wolfpack' as affected by shade that had 30% intensity of the full light.

Treatment	WAS1[z]	WAS2	WAS3	WAS4
			Tiller/d	
Full sun	0.420a[y]	0.407a	0.252a	0.184a
Shade	0.363b	0.301b	0.160b	0.108b
		ANOVA		
Source of variance	*Df*		*P>F*	
Cultivar (C)	1		0.3183	
Shade (S)	1		**<0.0001**	
Time (T)	3		**<0.0001**	
C*T	3		0.3342	
S*T	3		**0.0180**	
C*S	1		0.3619	
C*S*T	3		0.5299	

[z] WAS, week after shade.

[y] Means within the same column followed by a same letter are not different based on Tukey's significant difference (HSD) at 0.05 probability level.

L.) (Davies and Thomas, 1983) but dependents on species or cultivars (Berone et al., 2008). However, under extended period of shade or after the canopy closing, site filling decreases in grasses (Davies and Thomas, 1983). Our results also indicated that the effect of increasing duration of shade was stronger for TAR than for primary shoot LAR. Therefore, source availability may be a limiting factor for tiller production. It was also reported that site filling decreases under continuous defoliation (Berone et al., 2008) or extended length of shade (Bahmani et al., 2000).

Leaves from full light and shaded plants showed no differences with respect to potassium and sodium content (Table 6). However, calcium and iron content were higher in shaded leaves compared to full light, whereas Mg content was lower in shaded leaves than in the leaves under full light (Table 6). Tall fescue leaves may have an adaptation mechanism to use energy to increase Fe uptake under shade. The increased transport of Fe to leaves may have contributed to the increase of Ca content in the shoots. It was reported that Fe uptake by monocotyledonous plants can increase Ca uptake/transport to shoots (Brown, 1978). Meanwhile, increases of Ca uptake often result in decreases of Mg uptake as reported earlier (Pritchard et al., 1964; Wallace and Mueller, 1980).

Two types of Fe uptake by plants are known, direct uptake of siderophore complexes of ferric Fe or reduction of Fe^{3+} to a more soluble ferrous (Fe^{2+}) form in soil prior to the uptake (crossing the endodermis). Grasses rely solely on the first mechanism (Schmidt, 1999). Therefore, Fe uptake in grass roots under shade needs the excretion of non-proteinogenic amino acids (phytosiderophores), and the transport of Fe to leaves is further regulated in coordination with Ca (Reid, 2001), which is not only an essential nutrient but also a signal involved in many physiological regulations (Demidchik et al., 2018). The results of our experiment did not show K differences in plant tissue under shade or full light. The results did show different Fe concentrations in leaf tissues under shade and full light although the optimum levels of Fe require further investigation. Therefore, further study on the application of K, Fe, as well as phytosiderophores to tall fescue may provide useful information for the management of tall fescue under low light intensity.

There were no differences in K and Na content in roots from plants growing under full light and shade (Table 7). This agrees with earlier findings on cool-season grasses. Jackson and Caldwell (1992) reported that K and ammonium uptake were not affected by low light intensity in *Agropyron desertorum*. Similar results were reported in barley (*Hordeum vulgare* L.) and wheat (*Triticum aestivum* L.) by Crapo and Ketellapper (1981) who attempted to explain the results by hypothesizing that the maintenance of existing tissues and processes had higher energy priority than the production of new tissue. However, research conducted by Cai et al. (2011) on the warm-season grass St. Augustinegrass [*Stenotaphrum secundatum* (Walt.) Kuntze] showed that K application enhanced growth and K concentration in leaves under shade. Wilson and Hill (1990) also reported that higher K concentration in leaves of bahiagrass (*Paspalum notatum* Fluege.) grown under tree shade compared to those grown in full sun light. The different responses to shade between C3 and C4 grasses have been well documented (Knapp, 1993; Kubasek et al., 2013). Special mechanisms for nutrient uptake include root phenotypic plasticity under low light intensity in *Poa* and *Bromus* (Wahl et al., 2001).

Unlike the case for leaves, Ca and Fe contents in the roots of grass grown in shade were lower than in the roots of grass grown in full light. However, the concentrations in

Table 6. Shoot cation content of tall fescue cultivars 'Tar Heel II' and 'Wolfpack' as affected by 4 weeks of shade that had 30% intensity of the full light.

Treatment		K	Na	Ca	Mg	Fe
				mg kg^{-1}		
Full sun		29,082a[z]	315a	6,250b	2,236a	348b
Shade		28,914a	312a	8,031a	2,024b	431a
			ANOVA			
Source of variance	*Df*			*P>F*		
Cultivar	1	0.7970	0.3776	0.9390	0.6580	0.9180
Shade	1	0.8037	0.8541	**0.0486**	**0.0088**	**0.0069**
Cultivar*Shade	1	0.8599	0.5961	0.9687	0.5793	0.0544

[z] Means within the same column followed by a same letter are not different based on Tukey's significant difference (HSD) at 0.05 probability level.

Table 7. Root cation content of tall fescue cultivars 'Tar Heel II' and 'Wolfpack' as affected by 4 weeks of shade that had 30% intensity of the full light.

Treatment		K	Na	Ca	Mg	Fe
				mg kg^{-1}		
Full sun		24,177a[z]	1,022a	6,369a	1,769a	928a
Shade		24,291a	1,015a	3,525b	1,684a	865b
			ANOVA			
Source of variance	*Df*			*P>F*		
Cultivar	1	0.8456	0.9717	0.4311	0.1509	0.9638
Shade	1	0.9531	0.8626	**0.0022**	0.2204	**0.0034**
Cultivar*Shade	1	0.9886	0.2376	0.5264	0.3938	0.8611

[z] Means within the same column followed by a same letter are not different based on Tukey's significant difference (HSD) at 0.05 probability level.

the whole plant calculated using the shoot and root biomass data showed no difference between full light and shade treatments. Therefore, it is possible that cations were taken up via mass flow into roots at similar rates between the shade and full light treatments (Gilliham et al., 2011). The cations then were selectively transported from roots to shoots (Wallace and Mueller, 1980), which is regulated by a complex process.

Conclusion

The results of this experiment showed that low light intensity reduced root growth more than shoot growth in two tall fescue cultivars. This indicated that carbohydrates from photosynthesis had a prioritized allocation to above ground growth under shaded conditions. However, such a strategy is not sustainable because leaf appearance and tillering rate decreased over time under shaded conditions resulting in a lower amount of photosynthates being supplied to the roots. Additionally, shade decreased the rate of transpiration. Ultimately, the nutrient uptake capacity of the roots under shaded conditions decreased.

Contrary to the reports for warm-season grasses, the K concentration in shoot tissues showed no difference in tall fescue grown under shade and full light. Therefore, extra application of K to tall fescue under shade is not justified. Our previous experiment as well as the current one on tall fescue indicated that Fe content increased in leaves under shaded conditions, which may be responsible for the increase of chlorophyll content on a dry weight basis in response to low light intensity. This, among other mechanisms, is very important for vigorous tall fescue growth in shade. Since the optimum Fe concentration in shaded leaves of tall fescue remains unknown, further research on the application of Fe and phytosiderophores is warranted.

References

Allard, G., Nelson, C.J., and Pallardy, S.G. (1991a). Shade effects on tall fescue: I. Leaf anatomy and dry matter partitioning. Crop Sci. *31*, 163–167. https://doi.org/10.2135/cropsci1991.0011183X003100010037x.

Allard, G., Nelson, C.J., and Pallardy, S.G. (1991b). Shade effects on growth of tall fescue: II. Leaf gas exchange characteristics. Crop Sci. *31*, 167–172. https://doi.org/10.2135/cropsci1991.0011183X003100010038x.

Bahmani, I., Hazard, L., Varlet-Grancher, C., Betin, M., Lemaire, G., Matthew, C., and Thom, E.R. (2000). Differences in tillering of long- and short-leaved perennial ryegrass genetic lines under full light and shade treatments. Crop Sci. *40*, 1095–1102. https://doi.org/10.2135/cropsci2000.4041095x.

Beard, J.B. (1997). Shade stresses and adaptation mechanisms of turfgrasses. Intl. Turfgrass Soc. Res. J. *8*, 1186–1195.

Berone, C.D., Lattanzi, F.A., Agnusdei, M.G., and Bertolotti, N. (2008). Growth of individual tillers and tillering rate of *Lolium perenne* and *Bromus stamineus* subjected to two defoliation frequencies in winter in Argentina. Grass For. Sci. *63*, 504–512. https://doi.org/10.1111/j.1365-2494.2008.00655.x.

Brown, J.C. (1978). Mechanism of iron uptake by plants. Plant Cell Environm. *1*, 249–257. https://doi.org/10.1111/j.1365-3040.1978.tb02037.x.

Cai, X., Trenholm, L.E., Kruse, J., and Sartain, J.B. (2011). Response of 'Captiva' St. Augustinegrass to shade and potassium. HortScience *46*, 1400–1403. https://doi.org/10.21273/HORTSCI.46.10.1400.

Causin, H.F., Jauregui, R.N., and Barneix, A.J. (2006). The effect of light spectral quality on leaf senescence and oxidative stress in wheat. Plant Sci. *171*, 24–33. https://doi.org/10.1016/j.plantsci.2006.02.009.

Cohen, C.J., Chilcote, D.O., and Frakes, R.V. (1982). Leaf anatomy and stomatal characteristics of four tall fescue selections differing in forage yield. Crop Sci. *22*, 704–708. https://doi.org/10.2135/cropsci1982.0011183X002200040002x.

Crapo, N.L., and Ketellapper, H.J. (1981). Metabolic priorities with respect to growth and mineral uptake in roots of *Hordeum*, *Triticum* and *Lycopersicon*. Am. J. Bot. *68*, 10–16. https://doi.org/10.1002/j.1537-2197.1981.tb06350.x.

Davies, A., and Thomas, H. (1983). Rates of leaf and tiller production in young spaced perennial ryegrass plants in relation to soil temperature and solar radiation. Ann. Bot. *51*, 591–597. https://doi.org/10.1093/oxfordjournals.aob.a086505.

Demidchik, V., Shabala, S., Isayenkov, S., Cuin, T.A., and Pottosin, I. (2018). Calcium transport across plant membranes: Mechanisms and functions. New Phytol. *220*, 49–69. https://doi.org/10.1111/nph.15266.

Gardner, D.S., and Taylor, J.A. (2002). Change over time in quality and cover of various turfgrass species and cultivars maintained in shade. HortTechnology *12*, 465–469. https://doi.org/10.21273/HORTTECH.12.3.465.

Gilbert, W.B., and DiPaola, J.M. (1985). Cool season turfgrass cultivars performance in the shade. Ch. 18. In Proc. Fifth Intl. Turfgrass Res. Conf., Avignon (France), July 1–5, 1985, F. Lemaire, ed.

Gilliham, M., Dayod, M., Hocking, B.J., Su, B., Conn, S.J., Kaiser, B.N., Leigh, R.A., and Tyerman, S.D. (2011). Calcium delivery and storage in plant leaves: Exploring the link with water flow. J. Exp. Bot. *62*, 2233–2250. https://doi.org/10.1093/jxb/err111.

Greweling, T. (1976). Chemical analysis of plant tissue. Search Agric. *6*(8), 1–35.

He Q., and Li, D. (2021). Assessing shade stress in leaves of turf-type tall fescue (*Festuca arundinacea* Schreb.). Photosynthetica *59*, 478–485. https://doi.org/10.32615/ps.2021.037.

Hothem, S.D., Marley, K.A., and Larson, R.A. (2003). Photochemistry in Hoagland's nutrient solution. J. Plant Nutr. *26*, 845–854. https://doi.org/10.1081/PLN-120018569.

Hunter, A., Shorten, R., and McDonagh, D. (2009). The effect of supplementary and replacement lighting on turfgrass growth and development. Intl. Turfgrass Soc. Res. J. *11*, 807–816.

Jackson, R.B., and Caldwell, M.M. (1992). Shading and the capture of localized sol nutrients: Nutrient contents, carbohydrates, and root uptake kinetics of a perennial tussock grass. Oecologia *91*, 457–462. https://doi.org/10.1007/BF00650316.

Jones, J.B., Wolf, B., and Mills, H.A. (1991). Plant Analysis Handbook (Athens, GA, U.S.A.: Micro-Macro Publ., Inc.).

Knapp, A.K. (1993). Gas exchange dynamics in C_3 and C_4 grasses: Consequence of differences in stomatal conductance. Ecology *74*, 113–123. https://doi.org/10.2307/1939506.

Kubasek, J., Urban, O., and Santrucek, J. (2013). C_4 plants use fluctuating light less efficiently than do C_3 plants: A study of growth, photosynthesis and carbon isotope discrimination. Physiol. Plant. *149*, 528–539. https://doi.org/10.1111/ppl.12057.

Mitchell, K.J. (1953). Influence of light and temperature on the growth of ryegrass (*Lolium* spp.) I. Pattern of vegetative development. Physiol. Plant. *6*, 21–46. https://doi.org/10.1111/j.1399-3054.1953.tb08930.x.

Nelson, C.J., Asay, K.H., and Sleper, D.A. (1977). Mechanisms of canopy development of all fescue genotypes. Crop Sci. *17*, 449–452. https://doi.org/10.2135/cropsci1977.0011183X001700030027x.

Pritchard, G.I., Pigden, W.J., and Folkins, L.P. (1964). Distribution of potassium, calcium, magnesium, and sodium in grasses at progressive stages of maturity. Can. J. Plant Sci. *44*, 318–324. https://doi.org/10.4141/cjps64-062.

Reid, R.J. (2001). Mechanisms of micronutrient uptake in plants. Austral. J. Plant Physiol. *28*, 659–666. https://doi.org/10.1071/PP01037.

Schmidt, W. (1999). Mechanisms and regulation of reduction-based iron uptake in plants. New Phytol. *141*, 1–26. https://doi.org/10.1046/j.1469-8137.1999.00331.x.

Schnyder, H., and Nelson, C.J. (1989). Growth rates and assimilate partitioning in the elongation zone of tall fescue leaf blades at high and low irradiance. Plant Physiol. *90*, 1201–1206. https://doi.org/10.1104/pp.90.3.1201.

Silsbury, J.H. (1970). Leaf growth in pasture grasses. Tropical Grasslands *4*, 17–36.

Smith, J.D., and Jackson, N. (1989). Fungal Diseases of Amenity Turf Grasses (London, U.K.: E. & F.N. Spon).

Van Huylenbroeck, J.M., and Van Bockstaele, E. (2001). Effects of shading on photosynthetic capacity and growth of turfgrass species. Intl. Turfgrass Soc. Res. J. *9*, 353–359.

Van Huylenbroeck, J.M., Lootents, P., and Van Bockstaele, E. (1999). Photosynthetic characteristics of perennial ryegrass and red fescue turfgrass cultivars. Grass For. Sci. *54*, 267–274. https://doi.org/10.1046/j.1365-2494.1999.00179.x.

Volenec, J.J., and Nelson, C.J. (1981). Cell dynamics in leaf meristems of contrasting tall fescue genotypes. Crop Sci. *21*, 381–385. https://doi.org/10.2135/cropsci1981.0011183X002100030007x.

Wahl, S., Ryser, P., and Edwards, P.J. (2001). Phenotypic plasticity of grass root anatomy in response to light intensity and nutrient supply. Ann. Bot. *88*, 1071–1078. https://doi.org/10.1006/anbo.2001.1551.

Wallace, A., and Mueller, R.T. (1980). Calcium uptake and distribution in plants. J. Plant Nutr. *2*, 247–256. https://doi.org/10.1080/01904168009362774.

Wherley, B.G., Gardner, D.S., and Metzger, J.D. (2005). Tall fescue photomorphogenesis as influenced by changes in the spectral composition and light intensity. Crop Sci. *45*, 562–568. https://doi.org/10.2135/cropsci2005.0562.

Wilhelm, W.W., and Nelson, C.J. (1978). Leaf growth, leaf aging, and photosynthetic rate of tall fescue genotypes. Crop Sci. *18*, 769–772. https://doi.org/10.2135/cropsci1978.0011183X001800050019x.

Wilson, J.R., and Hill, K. (1990). The growth of *Paspalum notatum* under the shade of an *Eucalyptus grandis* plantation canopy or in full sun. Tropical Grasslands *24*, 24–28.

Woledge, J. (1971). The effect of light intensity during growth on the subsequent rate of photosynthesis of leaves of tall fescue (*Festuca arundinacea* Schreb.). Ann. Bot. *35*, 311–322. https://doi.org/10.1093/oxfordjournals.aob.a084480.

Zarrough, K.M., Nelson, C.J., and Coutts, J.H. (1983a). Relationship between tillering and forage yield of tall fescue. I. Yield. Crop Sci. *23*, 333–337. https://doi.org/10.2135/cropsci1983.0011183X002300020036x.

Zarrough, K.M., Nelson, C.J., and Coutts, J.H. (1983b). Relationship between tillering and forage yield of tall fescue. II. Pattern of tillering. Crop Sci. *23*, 338–342. https://doi.org/10.2135/cropsci1983.0011183X002300020037x.

Received: Nov. 15, 2022
Accepted: Oct. 18, 2024

Addresses of authors:
Qian He[1] and Deying Li[2,*]
[1] College of Forestry and Landscape Architecture, South China Agricultural University, Guangzhou 510642, China
[2] Department of Plant Sciences, North Dakota State University, Fargo, ND 58108, U.S.A.
* Corresponding author; E-mail: deying.li@ndsu.edu