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Research was conducted at the University of Maryland to investigate carbon metabolic responses to deep and infrequent versus light and frequent irrigation in 'Providence' creeping bentgrass (*Agrostis stolonifera* L.). Irrigating creeping bentgrass at wilt, rather than daily to maintain moist soil, generally resulted in higher carbohydrate levels in leaves and roots, which may enable creeping bentgrass to better tolerate and recover from drought and other stresses.

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PURPOSE

The purpose of *USGA Turfgrass and Environmental Research Online* is to effectively communicate the results of research projects funded under USGA's Turfgrass and Environmental Research Program to all who can benefit from such knowledge. Since 1983, the USGA has funded more than 350 projects at a cost of $29 million. The private, non-profit research program provides funding opportunities to university faculty interested in working on environmental and turf management problems affecting golf courses. The outstanding playing conditions of today's golf courses are a direct result of ***using science to benefit golf***.

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Carbohydrate Metabolism in Creeping Bentgrass as Influenced by Two Summer Irrigation Practices

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SUMMARY

This field study was conducted to investigate carbon metabolic responses to deep and infrequent (DI) versus light and frequent (LF) irrigation in 'Providence' creeping bentgrass (*Agrostis stolonifera* L). Light frequent irrigation was performed daily to wet soil to a depth of 4 to 6 cm (1.6-2.4"), whereas deep infrequent irrigation was performed at leaf wilt to wet soil to a depth of 24 cm (> 9.5"). The creeping bentgrass was seeded into a sand-based rootzone in 2005 and was maintained as a putting green. Canopy net photosynthesis (Pn) and whole plant respiration (Rw) were monitored, and water soluble carbohydrates [WSC (i.e., glucose, fructose, and sucrose)], storage carbohydrates [SC (i.e., fructan and starch)], and total nonstructural carbohydrates [TNC (i.e., sum of water soluble and storage sugars)] in leaf and root tissue were quantified. The results indicate:

- Creeping bentgrass subjected to deep infrequent irrigation had a lower canopy net photosynthesis and generally similar whole respiration compared to light frequent-irrigated bentgrass.
- Deeply and infrequently irrigated bentgrass generally had greater levels of water soluble carbohydrate and total nonstructural carbohydrates in leaf tissue in 2006 and similar levels in 2007 compared to light infrequent-irrigated bentgrass. Leaf soluble carbobhydrate levels were higher in deep infrequent than light frequent-irrigated bentgrass in both years.
- Creeping bentgrass roots subjected to dry infrequent-irrigation generally had greater soluble carbohydrate and total nonstructural carbohydrate levels in both years than were found in light frequent-irrigated plants.
- Root water soluble carbohydrate (WSC) levels were higher (2006) or similar (2007) in deep infrequent versus light frequent-irrigated bentgrass.
- Irrigating creeping bentgrass at wilt, rather than daily to maintain moist soil, generally resulted in higher carbohydrate levels in leaves and roots, which may enable creeping bentgrass to better tolerate and recover from drought and other stresses.

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Careful water management is critical to growing quality creeping bentgrass during summer stress periods, especially in sand-based rootzones. Many golf course superintendents in the mid-Atlantic region and elsewhere irrigate creeping bentgrass greens either light and frequent or deep and infrequent. Light and frequent irrigation involves applying water before wilt is evident and maintaining soil moisture at or near field capacity (4). Deep and infrequent irrigation is defined as irrigating at the first signs of leaf wilt to replenish the rootzone with water (4). Deep and infrequent irrigation generally is recommended for maintaining cool-season grasses in summer (1, 4).

Carbohydrate metabolism in leaves and sheaths, including photosynthesis, respiration, and carbon translocation are major physiological processes that form the basis of healthy plant function. Creeping bentgrass summer performance may be improved by maximizing carbohydrate production through photosynthesis, while

Canopy net photosynthesis (Pn) and whole respiration (Rw) including plant and soil microbe respiration were measured on 2-to 3-week intervals using a portable gas exchange system.

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minimizing carbohydrate consumption from respiration (12). Total nonstructural carbohydrate (TNC) availability has been widely used as a physiological measure of stress tolerance, because carbohydrates provide energy and solutes for osmotic adjustment. The major total nonstructural carbohydrate found in grasses include water soluble (i.e., glucose, fructose, sucrose) and storage (i.e., starch and fructan) sugars.

Understanding the many physiological factors affecting rooting is critical, since roots can be a nutrient sink and obviously contribute to overall plant health maintenance. Efficient carbon allocation to roots might increase the probability of plant survival during periods of drought stress (2). Several investigations have found that turfgrass plants subjected to drought stress accumulate more carbohydrates in leaves, stems, and roots, compared to well-watered plants (2, 8, 9, 10).

Soil drying reduces the proportion of newly photosynthesized carbon allocated to leaves, while increasing the proportion of carbon allocated to tall fescue (*Festuca arundinaceae* Schreb.) roots (8, 10). This allocation of carbon to roots occurred to a greater extent in the more drought tolerant tall fescue cultivars evaluated (10). Similarly, DaCosta and Huang (2) reported that newly photosynthesized carbon increased during the early phase of drought stress in creeping bentgrass roots, but not in leaves and stems.

We are not aware of any field studies that have investigated carbon metabolism in creeping bentgrass maintained as a putting green in response to summer irrigation practices. Therefore, the objectives of this field study were:

Treatments	2006 June 7	June 21	July 4	July 26	Aug. 16	Sept. 7
	Photosynthesis rate (micromol s^{-1} m^{-2})					
LF [x]	6.7 a [z]	5.3 a	5.6 a	6.6 a	6.8 a	8.4 a
DI [y]	5.1 b	3.5 b	3.5 b	4.0 b	5.5 b	7.6 b
	Respiration rate (micromol s^{-1} m^{-2})					
LF	10.7 a	10.7 a	8.6 b	10.3 a	7.9 a	6.7 a
DI	10.5 a	8.8 b	9.9 a	9.5 a	6.6 a	7.3 a

Treatments	2007 May 31	July2	July 24	Aug. 14	Sept. 6
	Photosynthesis rate (micromol s^{-1} m^{-2})				
LF	4.1 a z	6.2 a	6.5 a	6.8 a	4.1 a
DI	2.2 b	3.6 b	5.1 b	5.0 b	4.3 a
	Respiration rate (micromol s^{-1} m^{-2})				
LF	11.5 a	8.8 a	8.7 a	8.9 a	9.8 a
DI	10.1 a	8.8 a	8.2 a	7.6 b	10.2 a

[x] Light and frequent (LF) irrigation was performed daily in the absence of rain to wet soil to 4 to 6 cm depth.
[y] Deep and infrequent (DI) irrigation was performed at leaf wilt to wet soil to a depth of 24 cm.
[z] Means in a column within each parameter followed by the same letter are not significantly different based on Fisher's protected least significant difference test (P= 0.05).

Table 1. Photosynthesis and respiration in response to light and frequent (LF) versus deep and infrequent (DI) irrigation in 'Providence' creeping bentgrass in 2006 and 2007.

a) to quantify canopy net photosynthesis and whole respiration rates and b) to quantify water soluble carbohydrates, storage carbohydrates, and total nonstructural carbohydrate levels in creeping bentgrass grown in a sand-based rootzone in response to light frequent versus deep infrequent irrigation in the summer.

Materials and Methods

This study was conducted on a research green built to USGA recommendations at the University of Maryland Turfgrass Research Facility in College Park in 2006 and 2007. Soil was a modified sand mix (97% sand, 1% silt, and 2% clay) with a pH of 6.5 and 1.0% organic matter. In September 2005, the study site was treated

Treatments	2006			
	June 15	July 13	Aug. 8	Sept. 7
	WSC [glucose ($mg.g^{-1}$ dry wt)]			
LF [x]	39.9 a [z]	48.6 a	39.4 b	40.4 b
DI [y]	34.5 a	50.4 a	52.6 a	44.1 a
	SC [glucose ($mg.g^{-1}$ dry wt)]			
LF	70.6 a	73.9 a	33.1 a	47.4 b
DI	70.9 a	70.5 a	33.8 a	52.7 a
	TNC [glucose ($mg.g^{-1}$ dry wt)]			
LF	110.5 a	122.5 a	72.6 b	88.0 b
DI	105.4 b	120.9 a	86.5 a	96.9 a

	2007				
	June 1	June 28	July 17	Aug. 15	Sept. 6
	WSC [glucose ($mg.g^{-1}$ dry wt)]				
LF	43.6 a [z]	43.1 a	36.4 b	33.4 b	44.0 a
DI	43.2 a	40.7 a	38.8 a	38.7 a	43.5 a
	SC [glucose ($mg.g^{-1}$ dry wt)]				
LF	83.4 b	88.4 a	101.0 a	88.6 a	79.7 b
DI	90.7 a	87.9 a	100.4 a	87.8 a	83.6 a
	TNC [glucose ($mg.g^{-1}$ dry wt)]				
LF	127.1 b	131.5 a	137.3 a	122.1 a	123.8 a
DI	133.8 a	128.2 a	139.1 a	126.4 a	127.1 a

[x] Light and frequent (LF) irrigation was performed daily in the absence of rain to wet soil to a 4 to 6 cm depth.

[y] Deep and infrequent (DI) irrigation was performed at leaf wilt to wet soil to a depth of 24 cm.

[z] Means in a column within each parameter followed by the same letter are not significantly different based on Fisher's protected least significant difference test (P 0.05).

Table 2. Water soluble carbohydrate (WSC), storage carbohydrate (SC), and total non-structural carbohydrate (TNC) in 'Providence' creeping bentgrass leaf tissue in response to light and frequent (LF) versus deep and infrequent (DI) irrigation in 2006 and 2007.

with glyphosate (Round-up) and the sod was removed to expose bare ground. The area was seeded with 'Providence' creeping bentgrass in September 2005. A total of 250 kg ha^{-1} N (5.0 lb N/1000 ft^2) was applied between September 20 and November 11, 2005. The bentgrass was fertilized biweekly with 4.9 kg ha^{-1} N (0.1 lb N/1000 ft^2) from urea between May 1 and June 7 and then weekly through August 24 for a total of 78.4 kg ha^{-1} N (1.6 lb N/1000 ft^2) during the experimental period in 2006.

In autumn 2006, the bentgrass was fertilized to provide a total of 71 kg ha^{-1} N (1.4 lb N/1000 ft^2). In 2007, the bentgrass was fertilized weekly with 4.9 kg ha^{-1} N (0.1 lb N/1000 ft^2) from urea between April 30 and August 27 to provide a total of 88.2 kg ha^{-1} N (1.8 lb N/1000 ft^2) during the experimental period. Iprodione (Chipco 26019) was applied biweekly in 2006 and 2007 to control dollar spot (*Sclerotinia homoeocarpa* F.T. Bennett) and brown patch (*Rhizoctonia solani* Kuhn). Deltamethrin (Deltaguard) was applied on July 26 and August 24, 2006 and July 18, 2007 to control sod webworm (*Crambus spp*). Turf was mowed to a height of 4 mm (0.158") about five times weekly and clippings were removed.

Each plot (1.8 X 2.4 m) was bordered by fiberglass edging set 10 cm deep in soil to minimize lateral movement of water. There also was a 60-cm creeping bentgrass perimeter border separating each individual plot. Each plot was individually irrigated between 7 and 8 AM using a hand-held hose. The quantity of water applied was monitored with a digital flow meter attachment. The two irrigation regimes assessed were light and frequent versus deep infrequent. In the light and frequent irrigation regime, water was applied daily to replace moisture lost due to evapotranspiration (ET). This ensured that soil was maintained in a moistened state to a depth of 4 to 6 cm (1.6-2.4") each morning. Evapotranspiration was estimated every 24 hours.

In the deep infrequent irrigation regime, water was provided at the first visual sign of leaf wilt as determined by the appearance of a bluish-gray leaf color. The frequency of irrigation was variable and depended on weather conditions. Therefore, deep infrequent irrigation frequency was sometimes as often as every three days or as infrequently as seven days. Since soil was dried to about the same level at wilt, a standard amount of water (11.6mm; 0.5") was applied to each deep infrequent-irrigated plot when irrigated. This amount of water wetted soil to a depth of 6 to 8 cm (2.4-3.2") within 5 minutes, and water penetrated to a depth 24 cm (> 9.5") within 20 minutes after irrigation ceased.

On sunny days, plots were hand syringed about three times daily depending on weather conditions. To minimize the impact of rain, two tarps were used to cover all eight plots prior to the onset of rain between May 22 and August 31, 2006 and 2007. However, some rain events occurred before plots could be covered. On those days, light infrequent-irrigated plots were not irrigated.

Canopy net photosynthesis (Pn) and whole respiration (Rw) including plant and soil microbe respiration were measured on 2-to 3-week intervals between June 7 and September 7, 2006 and on 3-to 4-week intervals between May 31 and September 6, 2007 using a portable gas exchange system (LI-6400). Clippings were the source of mostly leaf plus some sheath tissue used to measure water soluble carbohydrate and storage carbohydrate levels. Clipping were collected 2 to 9 days following deep infrequent irrigation on June 15, July 13, August 8, and September 7, 2006 and June 1 and 28, July 17, August 15, and September 6, 2007. Roots also were sampled by removing four soil cores (2.5 cm diam. x 20 cm deep) from each plot on the same dates. Tissues were analyzed for carbohydrates as described in Fu and Dernoeden (5). Treatment effects were determined by analysis of variance and significantly different means were separated by Fisher's protected least significant difference test (P=0.05).

Results

Creeping bentgrass subjected to deep infrequent irrigation had a lower canopy net photosynthesis on all six measuring dates in 2006, compared to light frequent-irrigated bentgrass.

Deep infrequent-irrigated bentgrass had a lower whole respiration on June 21, but a greater whole respiration on July 4, 2006, compared to light and frequent-irrigated bentgrass (Table 1). No differences in whole respiration were observed on the other four measuring dates between the two irrigation regimes in 2006.

In 2007, canopy net photosynthesis was lower on four measuring dates (May 31, July 2 and 24, and August 14) in deep infrequent versus light and frequent-irrigated bentgrass. No difference in canopy net photosynthesis was observed between regimes on September 6. Except on August 14, 2007 when whole respiration was lower in deep infrequent-irigated bentgrass, there were no differences in whole respiration between irrigation treatments in 2007.

Water soluble carbohydrate content in leaf

Treatments	June 15 (2006)	July 13 (2006)	Aug. 8 (2006)	Sept. 7 (2006)
	WSC [glucose (mg.g^{-1} dry wt)]			
LF [x]	36.0 b [z]	22.4 b	44.4 b	41.4 b
DI [y]	54.2 a	57.6 a	50.6 a	47.6 a
	SC [glucose (mg.g^{-1}dry wt)]			
LF	15.8 b	10.0 a	9.2 a	10.8 b
DI	21.8 a	11.6 a	10.6 a	15.0 a
	TNC [glucose (mg.g^{-1} dry wt)]			
LF	51.6 b	32.6 b	53.6 b	52.2 b
DI	75.8 a	69.0 a	61.2 a	62.8 a

Treatments	June 1 (2007)	June 28 (2007)	July 17 (2007)	Aug. 15 (2007)	Sept. 6 (2007)
	WSC [glucose (mg.g^{-1} dry wt)]				
LF	23.6 b [z]	24.0 a	17.5 a	17.7 a	20.3 a
DI	26.8 a	22.0 a	17.1 a	17.4 a	20.8 a
	SC [glucose (mg.g^{-1} dry wt)]				
LF	34.0 b	28.0 a	23.1 b	29.8 b	21.8 b
DI	44.5 a	28.2 a	28.5 a	33.3 a	25.1 a
	TNC [glucose (mg.g^{-1} dry wt)]				
LF	57.6 b	53.0 a	40.7 b	47.6 b	42.1 b
DI	71.6 a	49.2 a	45.6 a	50.7 a	46.0 a

[x] Light and frequent (LF) irrigation was performed daily in the absence of rain to wet soil to a 4 to 6 cm depth.

[y] Deep and infrequent (DI) irrigation was performed at leaf wilt to wet soil to a depth of 24 cm.

[z] Means in a column within each parameter followed by the same letter are not significantly different based on Fisher's protected least significant difference test (P=0.05).

Table 3. Water soluble carbohydrate (WSC), storage carbohydrate (SC), and total non-structural carbohydrate (TNC) in 'Providence' creeping bentgrass roots in response to light and frequent (LF) versus deep and infrequent (DI) irrigation in 2006 and 2007.

tissue was similar on June 15 and July 13, and greater on August 8 and September 7, 2006 in deep infrequent-irigated versus light and frequent-irrigated creeping bentgrass (Table 2). Creeping bentgrass subjected to deep infrequent irrigation had similar soluble carbohydrates levels in leaf tissue between June 15 and August 8, 2006 and a greater soluble carbohydrates in leaf tissue on September 7 compared to light and frequent-irrgated bentgrass.

Total nonstructural carbohydrate content in leaf tissue was less on June 15, similar on July 13, and greater on August 8 and September 7, 2006 for deep infrequent-irigated versus light and frequent-irrgated bentgrass. On the final rating date in 2006, water soluble carbohydrate, storage carbohydrates, and total nonstructural carbohydrates were greater in bentgrass leaf tissue subjected to deep infrequent-irigated than bentgrass receiving light frequent irrigation.

In 2007, deep infrequent-irigated bentgrass had greater water soluble carbohydrate in leaf tissue on two (July 17 and August 15) out of five measuring dates and similar water soluble carbohydrate on three dates (June 1 and 28, and September 6) compared to light and frequent-irrgated bentgrass (Table 2). Storage carbohydrate levels in leaf tissue were similar between June 28 and August 15, 2007 and greater on June 1 and September 6 in deep infrequent-irigated versus light and frequent-irrigated bentgrass. Creeping bentgrass subjected to deep infrequent irrigation had a greater amount of leaf total nonstructural carbohydrate on June 1, but similar total nonstructural carbohydrate levels on all other measuring dates compared to light and frequent-irrgated bentgrass. Unlike 2006, only storage carbohydrate levels were higher in deep infrequent-irigated bentgrass on the final measuring date.

Each plot (1.8 X 2.4 m) was bordered by fiberglass edging set 10-cm deep in soil to minimize lateral movement of water.

Creeping bentgrass subjected to deep infrequent irrigation had a greater water soluble carbohydrate and total nonstructural carbohydrate content in roots on all four measuring dates in 2006 compared to light and frequent-irrigated bentgrass (Table 3). Storage carbohydrate levels in roots were similar on July 13 and August 8 2006, but greater on June 15 and September 7, 2006 compared to light frequent-irrigated bentgrass.

In 2007, root water soluble carbohydrate was greater on June 1 in deep infrequent-irigated versus light and frequent-irrgated bentgrass (Table 3). No differences in root water soluble carbohydrate, however, were observed on the other four measuring dates between the two irrigation regimes in 2007. Creeping bentgrass subjected to deep infrequent irrigation had greater storage carbohydrate and total nonstructural carbohydrate levels in roots on four (June 1, July 17, August 15, and September 6) out of five 2007 measuring dates compared to light and frequent-irrigated bentgrass.

Discussion

During the study period in both years, soil moisture at the 0 to 10 cm (0-3.9") depth averaged 9.3% and 15.7% in deep infrequent-irigated and light and frequent-irrgated plots, respectively. Data showed that deep infrequent irrigation reduced canopy net photosynthesis in both years, but generally had no effect on whole respiration. It is likely that light and frequent irrigation encouraged more shoot growth, which would have resulted in a greater leaf surface area. A greater leaf area at the time of measurement may account for the higher canopy net photosynthesis rate in light and frequent-irrigated versus deep infrequent-irrigated bentgrass. Hence, photosynthesis was more sensitive to soil drying than respiration. Huang and Fu (8) previously reported that photosynthesis decreased in Kentucky bluegrass (*Poa pratensis* L.) and tall fescue plants subjected to complete drying of the soil profile in a greenhouse study. In a field study, however, it was shown that the canopy net photosynthesis rate in creeping bentgrass was similar, regardless of being irrigated three times per week at 40%, 60%, or 100% of actual evapotranspiration (3).

In the current study, only light frequent-irrigated plots were irrigated to 100% ET on rain-free days. While whole respiration remained similar between irrigation regimes in our study, Huang and Fu (8) reported that respiration decreased in Kentucky bluegrass and tall fescue beginning nine days after imposing drought stress in a greenhouse study. Maintaining healthy turf under limited water conditions may depend on the availability of carbohydrates. Leaf tissue from deep infrequent-irigated bentgrass contained higher levels of water soluble carbohydrates and total nonstructural carbohydrates than light and frequent-irrgated bentgrass on the final measurement date in September, 2006, whereas, storage carbohydrate levels in leaf tissue were higher on the final date in both years.

On the final measurement dates in September 2006 and 2007, soluble carbohydrates and total nonstructural carbohydrate levels in roots were higher in deep infrequent-irigated than in light and frequent-irrgated bentgrass. Root storage carbohydrate levels were on average 39% (2006) and 15% (2007) higher on the final measurement date in each year in deep infrequent-irigated versus light and frequent-irrgated bentgrass. On the final measurement date in each year, root total nonstructural carbohydrate levels were 9% to 20% higher in deep infrequent-irigated bentgrass.

DaCosta and Huang (2) subjected creeping bentgrass to drought stress for 6 to 18 days in a greenhouse and observed that the proportion of newly produced total nonstructural carbohydrate carbon was highest in roots, intermediate in stems, and lowest in leaves within 12 days of inducing drought. The present study showed that creeping bentgrass subjected to deep infrequent irrigation had root total nonstructural carbohydrate levels averaging 23% higher in both years compared to light and frequent-irrigated bentgrass. Therefore, although total nonstructural carbohydrate levels were greater in leaves, roots accumulated more total nonstructural carbohydrate when grown under deep infrequent irrigation. Hence, the results from our field studies are in agreement with greenhouse studies that have shown the total nonstructural carbohydrate levels in both leaves and roots increase in response to soil drying (2, 8, 9).

While not quantified, it is very likely that creeping bentgrass leaf growth was restricted more in deep infrequent-irrigated than light and frequent-irrigated plots. Since canopy net photosynthesis was less in deep infrequent-irigated bentgrass, the increases in carbohydrate levels of deep infrequent-irigated bentgrass leaves and roots likely were a result of a reduction in plant growth. That is, since growth was restricted by dry soil conditions, plants utilized less carbohydrate.

Maintenance of a favorable water status is essential for plants adapted to conditions with limited water availability. Osmotic adjustment is an

To minimize the impact of rain, two tarps were used to cover all eight plots prior to the onset of rain between May 22 and August 31, 2006 and 2007, however, some rain events occurred before plots could be covered. On those days, light infrequent-irrigated plots were not irrigated.

important physiological mechanism of water retention and cell turgor maintenance. The accumulation of solutes such as water soluble carbohydrate is associated with active osmotic adjustment when plants are subjected to soil water deficits (11). DaCosta and Huang (2) reported that creeping bentgrass plants osmotically adjust to dehydration stress by accumulating water soluble carbohydrate.

In this study, higher levels of water soluble carbohydrate were observed in leaves in 2006 (August 8 and September 7) and 2007 (July 17 and August 15). Higher water soluble carbohydrate levels also were observed in roots of deep infrequent versus light and frequent-irrgated bentgrass on all dates in 2006 and on June 1, 2007. These water soluble carbohydrate data suggest that creeping bentgrass plants subjected to deep infrequent irrigation were adapting to drought stress.

In summary, this field study showed that creeping bentgrass exhibited reduced canopy net photosynthesis, but generally unchanged whole respiration rates in response to deep infrequent-irigated. Deep infrequent irrigation resulted in higher levels of water soluble carbohydrate, storage carbohydrate, and total nonstructural carbohydrate in creeping bentgrass leaves in 2006 and higher soluble carbohydrates and total nonstructural carbohydrate levels in roots in both years. Carbohydrates accumulated more in deep infrequent-irrigated bentgrass since plant growth was restricted by frequent periods of wilt stress.

Higher water soluble carbohydrate levels in tissues of deep infrequent-irrigated creeping bentgrass likely contribute to improved drought tolerance by providing for a more negative osmotic pressure in tissues in response to prolonged periods of wilt stress. Accumulated total nonstructural carbohydrate also would be available to assist plants in their recovery from wilt and other stresses.

Acknowledgements

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