Response of Giant Reed (*Arundo donax*) to Intermittent Shading

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A species' successful invasion into a new site depends on its ability to persist in the local environment. An experiment was conducted to examine the response of giant reed to intermittent periods of shading for 2 yr. Results indicate that giant reed persisted when exposed to significant shading (i.e., 90% reduction of full sun) and that shading also caused changes in a number of plant characteristics, such as stem height, internode length, leaf nitrogen, leaf chlorophyll content, specific leaf area, total leaf area per plant, and leaf life span. Estimates of leaf photosynthetic rates did not differ across shade levels. Giant reed's ability to persist and grow under intermittent low-light conditions implies that plants would be poised to take advantage of sun flecks and disturbances that create gaps within the resident plant community.

Nomenclature: Giant reed, *Arundo donax* L. ABKDO.

Key words: Establishment, invasion, photosynthesis, growth response, leaf life span.

The tall perennial grass giant reed (*Arundo donax* L.) is widely distributed throughout the region surrounding the Mediterranean Sea and eastward from there to China and Japan. This species was introduced around the world for a number of human uses. *Arundo donax* was widespread in the eastern United States in the late 1800s. It was reported to be in New York in 1868 (Anonymous 1868) and 1887 (American Florist Co 1889), in Mississippi in 1872 (Jones and Jones 1872), and in Virginia in 1874 (Gray 1874). *Arundo donax* appears to have been initially introduced into Southern California in the early 1800s (Hoshovsky 1987). It has been subsequently planted in other parts of the United States on more than one occasion (Perdue 1958). In some locations, it has escaped cultivation and become an invasive weed of riparian zones (Bell 1997). Plants in the United States appear to be a single genetic clone (Ahmad et al. 2008). Cook (1990) considers *A. donax* an emergent aquatic plant, and it is included on the noxious weed lists of California and Texas.

Richardson et al. (2000) proposed a schematic representation of six barriers that might limit the spread of plants once they become established in an area. Many of these barriers are environmental; that is, they relate to habitat conditions and how a species responds to specific external, biotic, and abiotic conditions. Light availability is an important factor that may limit plant growth. In natural environments, plants exhibit one of three strategies in response to shade (Smith 1981). Some plants avoid shade, some tolerate it, and others require it. Smith (1981) states that most herbaceous weeds in the temperate zone avoid shade, whereas some display characteristics that make them shade tolerant. *Arundo donax* was observed growing under low-light levels along Cache Creek, CA (mean, 5% of full sunlight; range, 2 and 15% of full sunlight; D. F. Spencer, unpublished data), and in widely variable light environments in three Southern California locations (Quinn and Holt, 2008). Little specific information on the *A. donax* response to shade or reduced light levels (but see Quinn and Holt 2008) is available. Thus, this study sought to answer the following question: How does *A. donax* respond to reduced light levels? This information may be used to help identify habitats that might be susceptible to successful establishment of *A. donax*.

Materials and Methods

Arundo donax rhizome sections were collected from plants growing adjacent to Cache Creek, CA, in March 26, 2002 (Spencer and Ksander 2005). One day after collection, five rhizome pieces (mean ± SD, 44 ± 13 g [0.097 ±0.029 lb] fresh wt, $N = 36$), each containing a single, nonsprouted bud, were planted in each of six large, fiberglass tubs (thus, there were 30 rhizome pieces used, five per tub by six tubs). The tubs (1.96 m by 1.22 m by 0.15 m [6.43 ft by 4.00 ft by 0.49 ft]) were filled with locally procured topsoil (Yolo clay loam, NO_3-N =

5.5 mg kg^{-1} [0.07 oz lb^{-1}]; Olsen PO$_4$-P, 14.0 mg kg^{-1}; exchangeable K, 60.0 mg kg^{-1}). The rhizome pieces did not have existing shoots growing from them. Plants were watered every 2 or 3 d by adding enough water to saturate the soil within the container. *Arundo donax* was allowed to grow under ambient conditions until June 26, 2002, when shade treatments were applied. A 2.2-m-tall frame was constructed around each tub using polyvinyl chloride pipes. The frame was covered with shade cloth (McConkey Co., Sumner, WA) producing the following levels of full sunlight (% FS): 10%, 20%, 30%, 40%, and 70% FS. Full sunlight (100%) was achieved by not covering the tub with any shade cloth. One tub was assigned to each light level, and rhizome sections were randomly assigned to each light level (tub). The shade cloth was removed from each tub from December to the following June to simulate the period when overstory trees may be without leaves, and thus, *A. donax* would be exposed to full sunlight. Conversely, the shade treatments were in place between late-June through November. The experiment was initiated in 2002, and the experimental treatments were applied for 2 yr, i.e., 2002 and 2003. In 2004, all shade cloth was removed, and all of the plants were exposed to full sunlight throughout the year.

During 2002, *A. donax* growth was monitored using a three-dimensional magnetic digitizer (3 Space Fastrak Digitizer, Polhemus, Colchester, VT) in conjunction with Floradig software (Hanan and Wang 2004). A detailed account of this procedure is given in Hanan and Wang (2004), but a brief description based on the one provided by Thornby et al. (2007) follows. The digitizer uses a known reference point to collect point data from a magnetic field. The point data are sent to the program, Floradig, which combines the data into a group of points representing the three-dimensional structure of the plant. In the case of *A. donax*, each point collected is assigned as either a node or one of five points on the surface of the leaf blade. Floradig constructs a hierarchy of points that resembles a map of the plant's topology and uses the three-dimensional coordinates of each point to calculate lengths, angles, and areas of each plant organ/structure (i.e., leaves, stems, internodes, nodes, etc.). The program also constructs a computer-searchable database, which includes the date that the plant structural information was collected. Using this information, we calculated stem height by summation of internode lengths and the total leaf area per plant. Measurements were collected on June 26; July 2, 16, 23, and 30; August 6 and 20; September 3 and 17; and October 3, 15, and 29. In addition, leaf chlorophyll content was measured using a Minolta 502 SPAD meter (Spectrum Technologies, East Plainfield, IL) on June 25; July 9, 16, 23, and 30; August 6, 13, and 20; September 3 and 17; October 3 and 15; and November 5. One leaf from each plant within a treatment was measured on each date. Readings from a Minolta 502 SPAD meter have been shown to be strongly related to *A. donax* leaf chlorophyll content (Spencer et al. 2008). On August 26, 2002, rates of photosynthesis and transpiration for leaves were measured on five plants within each light level using a LI-6400 (LI-COR, Lincoln, NE). Measurements were made at 500 μmol m^{-2} s^{-1} photosynthetically active radiation (PAR) using the internal light source. The mean leaf temperature was 26.6 C (SD = 1.3; $N = 30$) when the measurements were collected.

On September 9, 2002, one leaf from each plant within a treatment was collected, dried at 80 C for 48 h, ground to fine powder, and the C and N were determined with a Perkin-Elmer Model II CHN analyzer (Perkin-Elmer, Waltham, MA) with acetanilide used as the N standard. On November 22, 2002, all shoots were harvested. The number of leaves per stem was counted, and the combined weight of leaves and stems were measured following drying. During 2003, plants were exposed to the shade treatments. On October 8, 2003, 505 leaves (91, 83, 93, 83, 76, and 79 leaves at 10, 20, 30, 40, 70, and 100% FS, respectively) were collected, and individual leaf weights were determined following drying at 80 C for 48 h. A digital camera was used to photograph each leaf. Leaf images were analyzed using an image analysis program (SigmaScan Pro, SPSS, Inc., Chicago, IL). Leaf area was divided by leaf weight data to calculate specific leaf area (m^2 kg^{-1}). At the end of each growing season, the aboveground portions of the plants were cut off, and individual shoots (i.e., stems plus leaves) were dried. Harvests occurred before senescence on November 22, 2002; October 9, 2003; and November 29, 2004.

Statistical Analysis. Data were checked for homogeneity of variances and normality of error distributions before further analysis. When necessary to remove heterogeneity of variance, an appropriate transformation was applied before performing analysis. A mixed-model analysis for
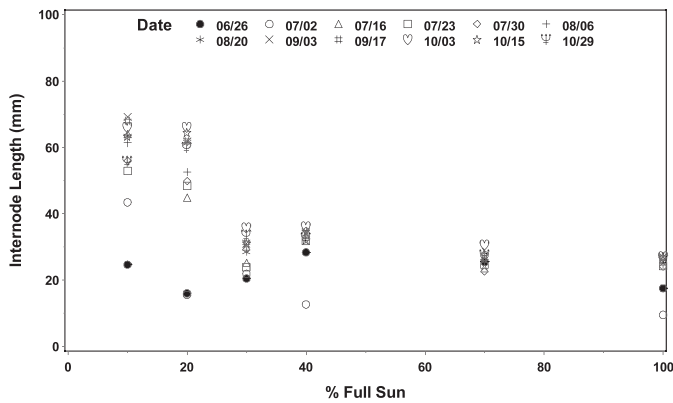
Figure 1. *Arundo donax* mean internode length on 12 dates for plants grown at different levels of full sunlight (% FS). Results of mixed-model ANOVA for repeated measures indicate that light level and sampling dates significantly influence mean internode length (P < 0.001). The interaction term was also significant (P < 0.001).

repeated measures was fitted using SAS software, PROC MIXED (SAS Institute, Cary, NC; Litell et al. 2006), considering light level and date as fixed effects and plants and stems as random effects. Significance testing was performed for all fixed effects and all possible interactions among them. Measurements taken on a whole-plant basis used "between" and "within-plants" variance measures. Tests were considered significant at a probability level below 0.05; however, exact probability levels for fixed-effect tests are shown in the results. For the biomass data determined at the end of each growing season, an ANOVA was calculated using PROC GLM in SAS (SAS Institute, Inc. 2004), with light level and harvest date as the treatments. Photosynthetic and transpiration rates and leaf nitrogen content were evaluated by linear regression against light level (% FS). Specific leaf area and leaf nitrogen-content data were analyzed using PROC REG to calculate linear regression against light level.

Leaf life spans were estimated by calculating the number of days between the date when a leaf was first digitized and the date it was last digitized (i.e., dead). A total of 415 leaf life spans were estimated in this manner. Life spans for leaves that had not died by the last date that the plants were digitized were considered right-censored values. There were 546 censored life spans. Leaf life spans were analyzed using Failure Time Analysis techniques (Dungan et al. 2003). Mean leaf life spans were estimated using the SAS procedure, LIFETEST, to compute the product-limit estimate of the survivor function for leaves at each light level (SAS Institute, Inc. 2004). The STRATA statement was used to compare survival curves for leaves at different light levels using the Wilcoxon test.
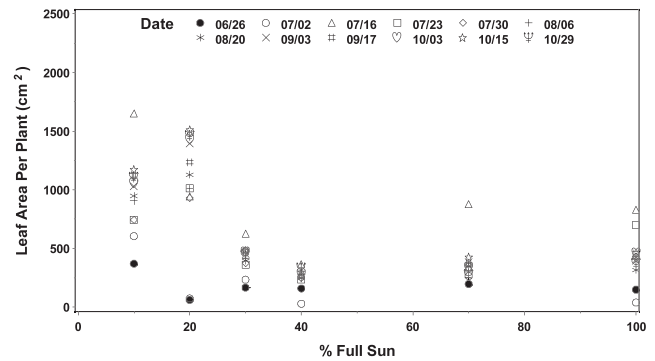

Figure 2. *Arundo donax* mean leaf area per plant on 12 dates for plants grown at different levels of full sunlight (% FS). Values are the mean ± standard error (SE). Results of mixed-model ANOVA for repeated measures indicate that light level and sampling dates significantly influence leaf area per plant (P < 0.001). The interaction term was also significant (P < 0.001).

Results

Aspects of *A. donax* architecture changed in response to shading. Internode length, stem height (data not shown), and the total area of leaves per plant increased significantly within 2 wk of the imposition of the shade treatments and remained that way for the rest of the growing season (Figures 1 and 2).

Leaf chlorophyll content increased by the first sampling date following imposition of the shade treatments (Table 1). Values for plants grown at 40% of full sunlight or less remained elevated compared with plants at 70 or 100% of full sun throughout the growing season. Leaf nitrogen was significantly higher at light levels below 30% full sun (Figure 3) as indicated by the significant regression coefficient (P < 0.001). Specific leaf area increased significantly (P = 0.0007) at lower light levels (Figure 4). Individual leaves persisted up to 20% longer as the light level decreased. Leaf life span was 79 ± 3 d at full sunlight and increased significantly (P < 0.0001, Wilcoxon chi-square test) as the light level decreased to a value of 95 ± 3 d at 10% full sunlight (Table 2). Photosynthetic rates measured at 500 μmol m^{-2} s^{-1} PAR for first-year leaves averaged 10.7 μmol CO_2 m^{-2} s^{-1}. Photosynthetic rates varied slightly but did not differ statistically (P = 0.1) across light levels (Table 3). A similar response was observed for transpiration rates (3.2 mmol H_2O m^{-2} s^{-1}), which were also not affected (P = 0.8) by the light level that the plants were grown under (Table 3).

Arundo donax shoot dry weight at the end of the growing season increased significantly over time (years; P < 0.001). Light level was not significant (P = 0.3). However, a significant interaction term for light level by time indicates that the effect of light level was not the same for all three growing seasons (Figure 5). Shoot dry weight increased

Table 1. Mean (± SE) chlorophyll concentration (SPAD units) for *A. donax* leaves at six light levels (% Full Sun). Readings for June 25 were taken the day before imposition of shading treatments. Results of mixed-model ANOVA indicate significant differences for light (P < 0.0001), date (P < 0.0001), and the interaction between light and date (P < 0.0001). One leaf from each plant at each light level was measured.

| % Full sun	June 25	July 9	July 16	July 23	July 30	August 6	August 13	August 20	September 3	September 17	October 3	October 15	November 5
10	29.7 ± 0.9	45.1 ± 1.7	39.3 ± 1.3	42.9 ± 0.8	34.9 ± 1.4	36.2 ± 1.9	40.2 ± 0.8	39.2 ± 1.1	35.2 ± 1.4	36.0 ± 1.7	35.4 ± 1.7	37.3 ± 1.2	36.7 ± 1.4
20	29.3 ± 1.9	45.8 ± 1.9	37.7 ± 1.6	39.0 ± 2.2	35.7 ± 2.1	40.8 ± 2.1	38.9 ± 1.9	39.4 ± 2.6	34.2 ± 4.1	38.6 ± 1.2	38.2 ± 1.8	38.6 ± 2.1	39.1 ± 1.3
30	30.9 ± 1.2	43.5 ± 2.0	45.7 ± 1.3	42.2 ± 1.6	32.7 ± 0.9	33.3 ± 1.3	36.4 ± 1.3	36.0 ± 1.0	35.2 ± 1.9	29.8 ± 1.5	31.6 ± 1.2	31.3 ± 1.9	24.6 ± 5.1
40	31.3 ± 4.1	39.3 ± 3.3	35.0 ± 3.3	38.2 ± 2.3	33.3 ± 2.8	32.3 ± 2.1	31.3 ± 1.6	32.1 ± 1.6	28.5 ± 1.3	29.0 ± 1.9	30.9 ± 1.2	32.9 ± 4.2	29.1 ± 4.4
70	33.7 ± 1.8	32.4 ± 1.5	32.0 ± 1.6	32.7 ± 1.3	29.3 ± 1.3	27.6 ± 1.6	28.0 ± 2.3	26.4 ± 1.8	27.8 ± 1.2	25.4 ± 1.3	25.2 ± 1.7	26.2 ± 1.8	21.8 ± 2.7
100	31.0 ± 1.3	30.4 ± 1.4	31.0 ± 1.0	30.4 ± 0.9	30.7 ± 1.0	23.6 ± 1.0	24.7 ± 0.8	25.6 ± 1.1	25.6 ± 2.5	24.7 ± 1.4	26.1 ± 1.6	27.0 ± 0.8	18.5 ± 2.8
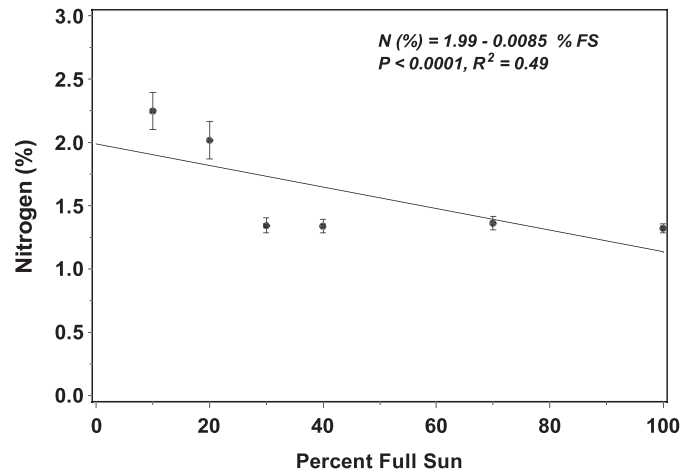
Figure 3. *Arundo donax* leaf N (%) for plants grown at different levels of full sunlight (% FS). The line represents the significant linear-regression equation. Values are the mean ± standard error (SE).

with light level during the second and third growing seasons. The light level effects were still evident after the third growing season when all of the plants received full sunlight.

Discussion

Arundo donax adjusted leaf chlorophyll content, leaf N content, specific leaf area, total leaf area per plant, leaf life span, internode length, and plant height in response to shading. These responses are similar to those reported for shade plants or plants grown under low-light levels
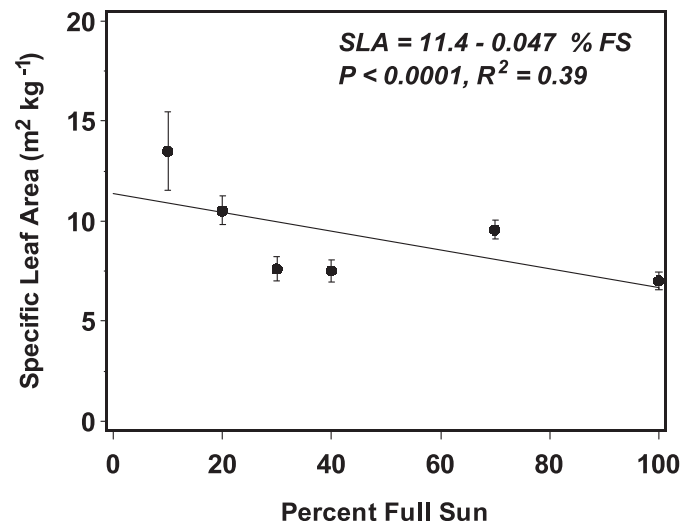

Figure 4. *Arundo donax* specific leaf area (m^2 kg^{-1}) for plants grown at different levels of full sunlight (% FS). The line represents the significant linear-regression equation. Values are the mean ± standard error (SE).

Table 2. Life spans for *A. donax* leaves at six light levels (% Full Sun). Results of the Wilcoxon test indicate that the survival curves differed significantly (P < 0.0001) across light levels.

% Full sun	Mean leaf life span	Leaf life span SE
	——————— d ———————	
100	79	3
70	82	3
40	96	4
30	84	3
20	97	4
10	95	3

Table 3. Photosynthetic rates and transpiration rates measured at 500 µmol m^{-2} s^{-1} photosynthetically active radiation for *A. donax* leaves grown at six light levels (% Full Sun). Results of linear regression indicate that neither photosynthetic rate (P = 0.1) nor transpiration rate (P = 0.8) differed significantly across light levels. Values are the mean ± SE.

% Full sun	Photosynthesis	Transpiration
	µmol CO_2 m^{-2} s^{-1}	mmol H_2O m^{-2} s^{-1}
100	9.6 ± 1.2	3.4 ± 0.4
70	9.9 ± 1.2	3.0 ± 0.5
40	12.2 ± 1.3	3.4 ± 0.5
30	10.8 ± 1.2	3.3 ± 0.6
20	9.1 ± 0.6	2.2 ± 0.1
10	13.1 ± 0.7	4.4 ± 0.7

(Boardman 1977). Photosynthetic rate measured at 500 µmol m^{-2} s^{-1} did not differ for leaves grown under a gradient of light levels ranging from 10 to 100% of full sun. This indicates that the photosynthetic capabilities of these leaves are equivalent, likely because of the increased levels of chlorophyll and leaf N in shade-grown leaves. Thus, leaves of *A. donax* growing in the shade would be fully capable of exploiting sun flecks (Skillman and Winter 1997).

Leaf life span was longer for *A. donax* growing under low-light levels (< 40% of full sun). This agrees with previous reports of the relationship between leaf life span and shading. Leaf life span declined with increasing light intensity for five species of tropical trees (Tong and Ng 2008). Leaf life spans can be 50 to 100% longer in shade-tolerant species than in species that require higher light for growth (Lusk and Warton 2007). Koike (1988) has suggested that shade-tolerant plants are likely to have more resources invested in leaf structural components, and this may explain the longer life span.

Results also agree with a previous field study, which included data on *A. donax* growth in three Southern California riparian habitats. Quinn and Holt (2008) planted *A. donax* into these habitats, which differed in the amount of sunlight received, among other factors. When averaged over three growing seasons, their data showed that *A. donax* was tallest at the site that received the lowest percentage of full sunlight (11% FS).

The fact that shoot dry weight increased at low light levels during the first, but not the second or third, growing seasons may be partially explained by the harvest of aboveground portions at the ends of the first and second growing seasons. Differences that may not have been large initially may have been amplified by the harvest made at the end of each growing season in the experiment. Plants growing at the lower light levels may not have had the same amount of stored underground reserves to allocate to new shoots. This agrees with the observation that plants at higher light levels produce more stems than do those at lower light levels. It appears that the individual stems that were produced possessed greater mass as well. One

implication of this is that plants growing in habitats with low light levels may not recover from damage as robustly as those growing in greater sunlight. This finding leads to the hypothesis that plants growing in reduced light may be more susceptible to management techniques that kill or remove biomass than are plants growing under full sunlight. These results may also apply to the success or failure of establishment of *A. donax* under natural conditions. Riparian habitats are subject to flooding, which may result in broken or damaged *A. donax* stems. Feeding on stems by unknown animals has also been reported for *A. donax* stems in California riparian habitats (Spencer 2012). Damage caused by either or both of these factors could differentially affect the success or failure of *A. donax* establishment in shaded or full sunlight habitats.
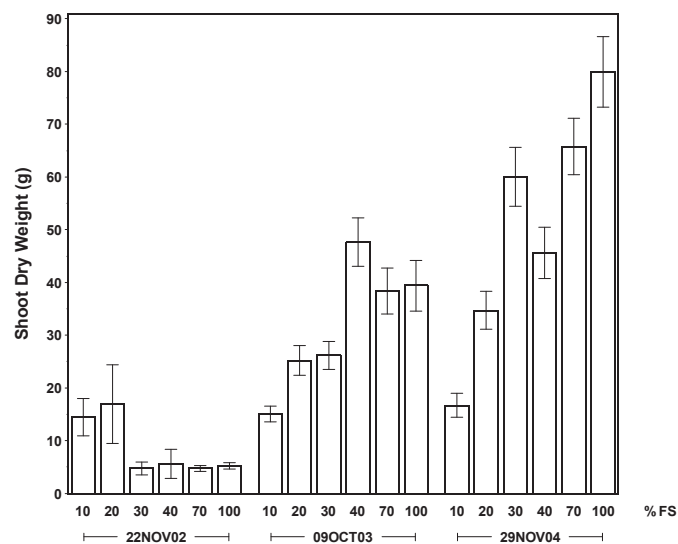

Figure 5. *Arundo donax* mean shoot weight at the end of the growing season for plants grown at different levels of full sunlight (% FS). Values are the mean ± standard error (SE).

Spencer et al. (2008) compared total leaf area and stem height for *A. donax* initially collected from two sites in Florida, one site in Texas, and two sites in California, grown under outdoor conditions in Northern California. They reported that total leaf area per plant did not differ for these plants regardless of their origin. The also reported that stem height and mean internode length were reduced for Florida plants from a variegated variety. Previous reports indicate low genetic diversity among U.S. *A. donax* species (Khudamrongsawat et al. 2004, Ahmad et al. 2008). Thus, it is likely that nonvariegated *A. donax* plants throughout the U.S. would respond to shading in a manner similar to the plants examined in this study.

Arundo donax displayed characteristics of both shade-avoiding species, (extreme extension growth of stems and petioles, increased specific leaf area) (Grime 1966) and shade-tolerating species (increased chlorophyll content) (Boardman 1977; Grime 1966). This blend of characteristics implies that the ability of *A. donax* to establish in riparian habitats may not be limited by light. Furthermore, restoration strategies that rely on planting shade-producing species as competitors (Funk and McDaniel 2010) may not result in communities resistant to invasion by *A. donax*.

Acknowledgments

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