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Research Article

Environmental Influences on Growth and Reproduction of Invasive *Commelina benghalensis*

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Commelina benghalensis (Benghal dayflower) is a noxious weed that is invading agricultural systems in the southeastern United States. We investigated the influences of nutrition, light, and photoperiod on growth and reproductive output of *C. benghalensis*. In the first experimental series, plants were grown under high or low soil nutrition combined with either full light or simulated shade. Lowered nutrition strongly inhibited vegetative growth and aboveground spathe production. Similar but smaller effects were exerted by a 50% reduction in light, simulating conditions within a developing canopy. In the second series of experiments, *C. benghalensis* plants were exposed to different photoperiod conditions that produced short- and long-day plants growing in similar photosynthetic periods. A short-day photoperiod decreased time to flowering by several days and led to a 40 to 60% reduction in vegetative growth, but reproduction above and below ground was unchanged. Collectively, the results indicate that (1) fertility management in highly weathered soils may strongly constrain competitiveness of *C. benghalensis*; (2) shorter photoperiods will limit vegetative competitiveness later in the growing seasons of most crops; and (3) the high degree of reproductive plasticity and output possessed by *C. benghalensis* will likely cause continual persistence problems in agricultural fields.

1. Introduction

Commelina benghalensis L. is among the world's worst weeds in agricultural systems, with infestations occurring in 25 crops in 29 countries. In the US, it became established in Florida in the early 1930s [1] and is now moving northward. The prevalence in Georgia has led to challenges with *Commelina benghalensis* control in cotton (*Gossypium hirsutum* L.) and peanut (*Arachis hypogaea* L.) production [2], as infestations have commonly caused 60% to 100% yield reductions [3, 4]. And there are observations indicating that *C. benghalensis* may be spreading further northward as far as North Carolina [5].

A key to *C. benghalensis* invasiveness is its reproductive flexibility. In its native geographical areas, that is, tropical Asia, Africa, and the Pacific Islands, *C. benghalensis* grows as a perennial, but it can survive as an annual in temperate regions [6]. It is fast growing and a prolific seed producer [7]. Both aerial and subterranean seeds are produced in dimorphic flowers [8], and seeds have variable dormancy and germination characteristics [9, 10]. Furthermore, *C. benghalensis* has the ability to regenerate from stem fragments [11]. These characteristics, plus a high degree of tolerance to glyphosate [12], make *C. benghalensis* exceptionally difficult to control in agronomic systems when it becomes established.

We are investigating environmental effects on *C. Benghalensis* growth and development. The purpose is to gain insights into factors that influence its competitiveness and persistence, which are keys for assessment of the risk of invasions and formation of long-term control strategies. In recent experiments, it was found that seeds of *C. benghalensis* can persist in soil for up to four years in areas extending from Florida and Georgia to North Carolina [13]. This implied that the management programs must prevent seed

production for that period of time to effectively reduce seed banks. In further agroecological studies, it was found that control of *C. benghalensis* will be especially problematic in sustainable farming systems not using herbicides [14]. The viability of *C. benghalensis* seed acquired during grazing or consumption of fresh hay is not reduced during animal digestion and generation of manure, so there is no restraint on seed dispersal. Also, vegetative regeneration was near its maximum in the temperature range typical in summers in the southeastern US, severely limiting the potential effectiveness of cultivation.

In the study described in this paper, we examine *C. benghalensis* responses to several environmental variables that can be related to prediction of field behavior. Two of the variables examined, light and photoperiod, required that experiments be conducted in controlled-environment growth chambers. Specific questions were being addressed. One was "how are growth and development of *C. benghalensis* altered by changes in nutrition and light?" Crops are fertilized at different levels, so the magnitude of the fertility response would help predict cropping systems where *C. benghalensis* would be more or less aggressive. Exposure to low light will reveal the extent that growth and development might be expected in crop understories or small gaps in crop populations. Another question was "how is *C. benghalensis* affected by altered photoperiod?" With current warming patterns [15, 16], cropping seasons can be extended, unless a counterbalancing effect is exerted by shorter day lengths. To assess responses in a worst case scenario, the environmental treatments were imposed under relatively high temperatures of 30–35°C, a temperature range common in the southeastern states in the US, when crop interference by weeds most often occurs, and a range where *C. benghalensis* exists [17].

2. Materials and Methods

2.1. Nutrition and Shade. Experiments were conducted in walk-in environmental chambers at the Southeastern Plant Environment Laboratory, Raleigh, NC. Large aerial seeds of *C. benghalensis* were germinated in 6 L plastic pots (25 cm diameter) containing Norfolk sandy loam soil (kaolinitic, thermic Typic Kandiudults, bulk density 1.2 g cm^{-3} and pH 6.1). Prior to sowing, seeds were disinfected by soaking in 5% bleach solution (0.25% NaOCl) for 5 min, rinsed with water, and then scarified with a blade to break physical dormancy and enhance germination [18]. Seeds were germinated at a constant day/night temperature of 30/30°C, with a 9 h photoperiod. Treatments were imposed just after seedlings were thinned to two per pot at the one-leaf stage (approximately 10 days after seeding). The treatments examined *C. benghalensis* responses at two nutrient levels and under two light intensities. Lighting was provided at either full (600 μmol m^{-2} s^{-1}) or reduced (324 μmol m^{-2} s^{-1}) PPFD, provided by a combination of incandescent and fluorescent lamps. Reduced lighting was achieved by covering the area with a shade cloth. PPFD was measured with a LI-191 Line Quantum Sensor (LI-COR Biosciences, Lincoln, NE). The daily light and dark periods were maintained from 08:00 to 17:00 h and 17:00 to 08:00 h, respectively. The aerial temperature was held constant at 30°C. Soil temperatures were monitored continuously at a 2 cm depth in the pots using temperature probes (WatchDog A-Series Data Loggers, Spectrum Technologies). Soil temperatures were within a ±3°C range of aerial temperatures under all treatments.

The experimental design was a split-plot with light intensity as the main plot and nutrient level as the subplot. Each light treatment was subdivided into two nutrient treatments. Pots with high nutrition received 200 mL of complete Hoagland nutrient solution [19] every day, and pots with low nutrient level received 200 mL of the same solution once a week, with deionized water added on the other days. Each pot was flushed with deionised water prior to nutrient additions to minimize residual nutrient accumulation. Three pots from each treatment combination were randomly selected and harvested at 14, 28, 35, 42, 49, and 56 d after treatments started. At harvests, plants were separated into aerial and subterranean tissues. The tissues were further separated into aerial vegetative (shoots and leaves), aerial reproductive (aerial spathes), subterranean vegetative (roots), and subterranean reproductive (rhizomes and spathes). All tissues were dried to a constant mass at 60°C in a drying oven and weighed afterwards. To avoid seed dissemination, aerial fruits were collected prior to dehiscence throughout the treatment period. Plant height, number of leaves, and leaf area were also measured at time of harvest. A standard Li-Cor model LI-3100C Area Meter (LI-COR Biosciences, Lincoln, NE) was used to measure leaf area per plant. There were 3 replications for each treatment and the experiment was conducted twice. Data were analyzed using the GLIMMIX procedure in SAS version 9.3 (SAS Institute, Inc., Cary, NC). Mean separation was performed using Tukey's honest significant difference (HSD) at $\alpha = 0.05$.

2.2. Photoperiod. Photoperiod experiments also were conducted in growth chambers at the Southeastern Plant Environment Laboratory. Seed treatment, germination, seedling establishment conditions, and soil were the same as described previously. In this circumstance, plants were exposed to five temperature-photoperiod regimes established in five reach-in environmental chambers. Twelve pots were kept in each chamber.

The five day/night temperature-photoperiod regimes included 30/22°C with long-day (12 h), 30/22°C with short-day (9 h), 35/28°C with long-day, 35/28°C with short-day, and a constant day/night temperature at 30°C with short-day. Each growth chamber was programmed with one unique combination of day/night temperature and photoperiod. In the short-day regime, day and night periods were maintained from 08:00 to 17:00 h and from 17:00 to 08:00 h, respectively. Illumination during day hours was provided by a combination of incandescent and fluorescent lamps with a PPFD of 600 μmol m^{-2} s^{-1}. The long-day regime was achieved by imposing the 3 h night interruption with incandescent lighting (from 00:00 to 03:00 h by incandescent lamps generating a nonphotosynthetic PPFD of 40 μmol m^{-2} s^{-1}). By disrupting continuous night hours, the night interruption leads to similar flowering transition effects as those occurring with actual long-day hours [20]. But, with similar photosynthetic

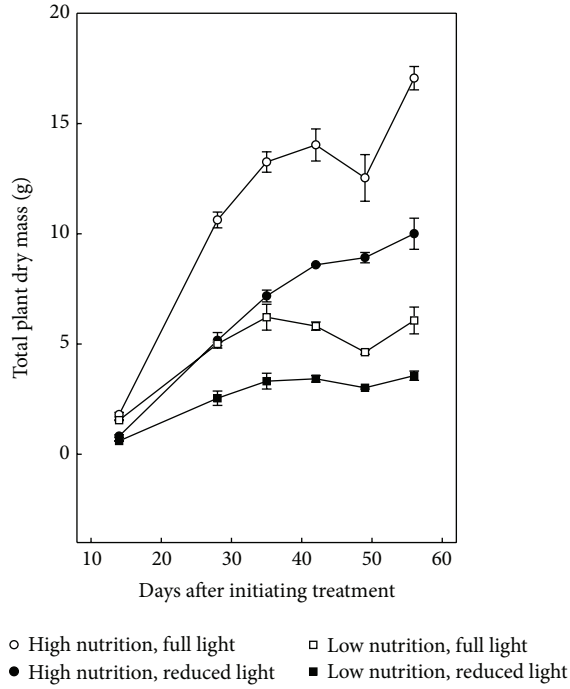

Figure 1: Effects of nutrition level and light intensity on total dry mass of *C. benghalensis*. Data points are means of six replicates, and bars indicate standard errors of the mean.

period lengths, the conditions allow the physiological effects exerted by vegetative/reproductive shifts to be evaluated alone. The night interruption technique has been used in many experiments over the years in controlled environment to suppress flowering of crop plants [19].

Plants were watered twice daily with 150 mL deionized water and once every other day with 200 mL complete Hoagland nutrient solution [19]. The plants thus were growing under high nutrition similar to that in the previous nutrition experiments. Three pots from each chamber were randomly selected and harvested at 14, 28, 42, and 56 d after treatment. Tissues were separated and processed as described previously. The experiment was repeated twice and data were combined and analyzed using the GLM procedure in SAS 9.3. (SAS Institute, Inc., Cary, NC).

3. Results and Discussion

3.1. Responses to Nutrition and Reduced Light. *C. benghalensis* whole-plant mass accumulation increased greatly with a higher level of nutrition (Figure 1), especially under full light. Increased growth included increases in root mass and plant height (Figures 2(a) and 2(b)). Impacts on leaf morphology were particularly pronounced, as the number of leaves and the leaf area per plant were considerably greater in plants receiving higher nutrition, regardless of light intensity (Figures 2(c) and 2(d)). This response is typical for fast-growing plants under high nutrition, where shoot growth is often stimulated more than root growth, resulting in an increase in the shoot to root growth ratio [21, 22].

Reproduction of *C. benghalensis* was also greater at high nutrition. Time to flowering was not changed (data not shown), but the number of aerial spathes was constantly greater in plants grown in high nutrition after the first sampling date, and by the end of the 56 day experiment, it was 3 times greater than that with low nutrition (Table 1). In contrast, the statistical analyses indicated that production of subterranean spathes varied little between the two nutrition levels.

The fertility responses are especially relevant for field responses in the southeastern US because soils are highly weathered with inherently low nutrition [23], and fertility requirements can be very different among cropping systems. Based on studies done with a number of higher plant species, it has been proposed that weed invasiveness is strongly linked with increased growth rates under improved resource conditions, but that invasive species may not outperform native or noninvasive species when resources are limited [24–27]. The strong response of *C. benghalensis* to increased nutrition in our experiments suggests that it would be much more aggressive in cropping systems with high rates of fertilization like those with corn (130–170 kg N/ha) and much less so in crops grown with lower fertilizer additions like N_2-fixing soybean that often receives low amounts of fertilizer (<33 kg N/ha) if any at all.

There are circumstances where weed species might acquire nitrogen from alternative sources. Experiments using ^{15}N natural abundance, for example, found that weeds could obtain large amounts of nitrogen transferred from N_2-fixing soybean [28]. However, because transfer occurred through and was dependent on soil-borne mycorrhizae, this type of alternative nitrogen acquisition would not be available to *C. benghalensis*. Our recent analyses have indicated that it is not a mycorrhizal host species (Riar, unpublished observation). Therefore, growth and competitiveness of *C. benghalensis* would primarily be influenced by fertilization in the crop system.

Shading was used in this study to examine *C. benghalensis* growth and reproductive output under reduced light, in an attempt to simulate conditions that exist when growing concurrently with a developing leaf canopy. Shading greatly reduced total biomass of *C. benghalensis* (Figure 1) when plants received the same nutrition level. Similarly, root mass was consistently less in shaded plants, especially under the high nutrition treatment (Figure 2(a)). Low light conditions tended to increase plant height, but differences were not statistically significant (Figure 2(b)). Shading had little effect on total leaf number and leaf area per plant (Figures 2(c) and 2(d)) but because leaf canopy mass was decreased substantially, shaded plants had much thinner leaves. This evidently reflects a morphological compensation response, where decreased amounts of available photosynthate are prioritized to maximize photosynthetic surface. In past experiments by others, greater specific leaf area and leaf area ratio were observed under reduced light conditions with jimsonweed (*Datura stramonium* L.), velvetleaf (*Abutilon theophrasti* Medik.), and soybean [29]. Thinner leaves and a less dense canopy evidently are an important adaptation of

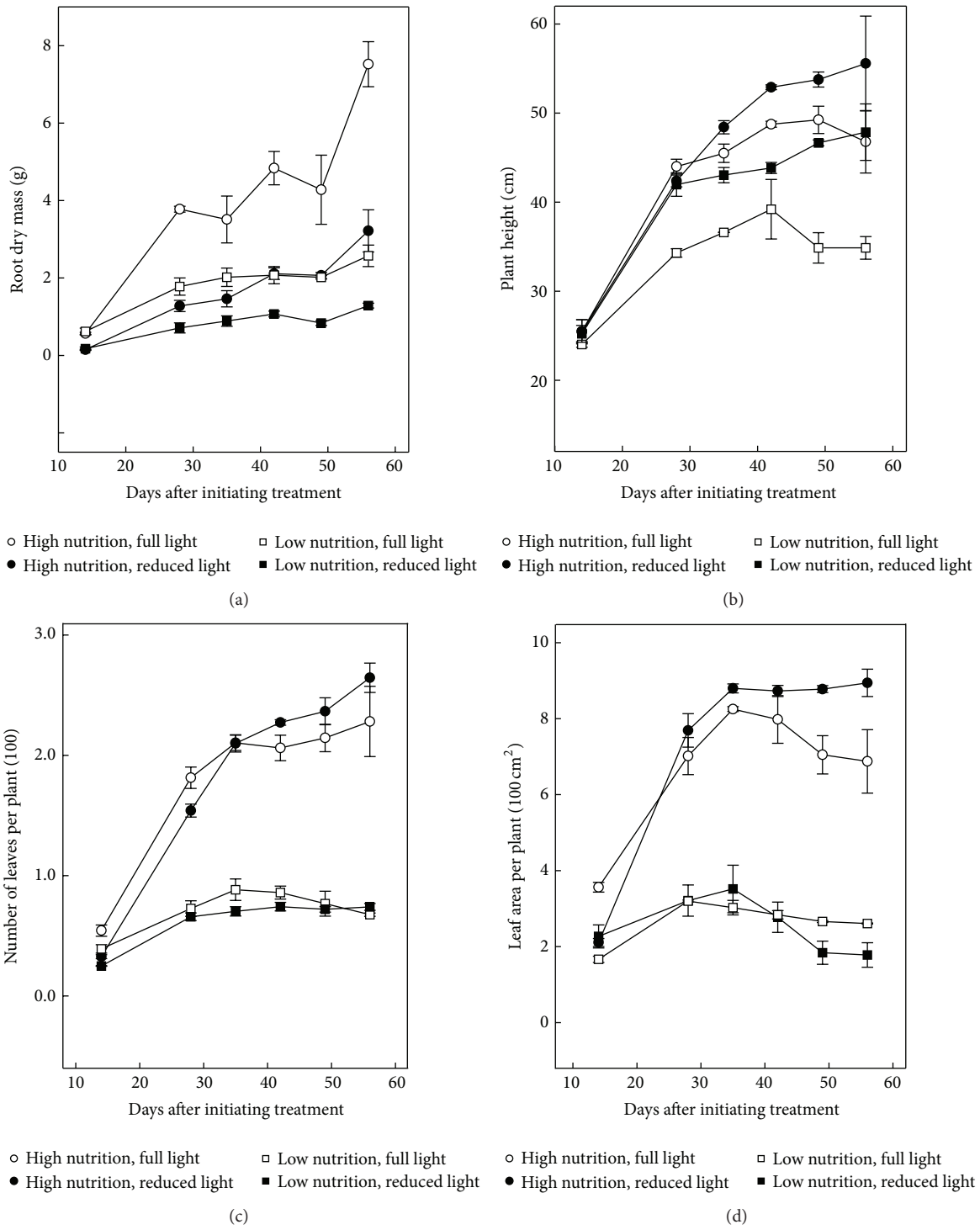

Figure 2: Effects of nutrition level and light intensity on (a) root dry mass, (b) plant height, (c) number of leaves per plant, and (d) leaf area per plant of *C. benghalensis*. Data points are means of six replicates, and bars indicate standard errors of the mean.

plants growing under shaded conditions that permits light penetration to lower leaves [30, 31].

As was the case with altered nutrition, shading had no impact on initiation of flowering (data not shown), but there were significant decreases in aerial spathe production (Table 1). Subterranean spathe production tended to be suppressed slightly by shading, but most of the observed differences were not statistically significant (Table 1).

The degrees of adjustment in spathe production above and below ground with plants that received low nutrition and those under shading indicate that *C. benghalensis* shifts to a "survival" strategy when resources are limited [32]. Even

Table 1: Effects of nutrient supply and light on *C. benghalensis* aerial and subterranean spathe production.

Treatment		Aerial spathes					Subterranean spathes				
		Days after treatment					Days after treatment				
Nutrient[a]	Light[b]	28	35	42	49	56	28	35	42	49	56
		Number of spathes plant^{-1}									
High	Full	132[c]	251	286	379	558	16	23	34	55	80
High	Shade	68	150	212	284	398	7	13	26	37	54
Low	Full	65	115	126	124	150	11	20	30	35	52
Low	Shade	38	66	92	90	124	5	13	22	29	41
$HSD_{0.05}$[d]		81	56	61	75	35	NS	NS	NS	NS	30

[a]Plants treated with high nutrient level received complete Hoagland's nutrient solution on a daily basis; plants treated with low nutrient level received complete Hoagland's nutrient solution once a week.
[b]PPFD under full light was at 600 μmol m^{-2} s^{-1}; PPFD under shade was at 324 μmol m^{-2} s^{-1}.
[c]Values are means of six replicates.
[d]Tukey's honest significant difference at $\alpha = 0.05$.

with severely reduced growth and restriction of aboveground spathe production, belowground reproduction tended to be maintained. On an individual plant basis, this increases the likelihood of genetic persistence, mainly because of less predation than occurs above ground. From an agronomic viewpoint, genetic persistence equates with a high likelihood of persistence in field soils. Difficulties with eradication of *C. benghalensis* in agricultural fields are clearly implied.

3.2. Response to Altered Photoperiod. Little has been published about *C. benghalensis*'s photoperiod sensitivity, particularly in the high temperature range where its growth and potential interference with crops are the greatest. High temperature interactions with photoperiod are becoming more important with global warming, as extension of high temperatures into months with shorter photoperiods could result in growth and reproductive characteristics unlike those in summer months. These experiments were specifically designed (a) to examine whether flowering was photoperiod sensitive and (b) to determine the extent that vegetative growth and reproductive output were altered by short days. All of the photoperiod treatments were imposed with plants growing under high nutrition.

Flowering of *C. benghalensis* was altered in short days (Figure 3). With the shortened light period of 9 hours and at the high temperature of 35/28°C, flowering occurred at day 27 whereas with long-day plants (with the night interruption) flowering occurred 3 days later at day 30. With the 9-hour light period and 30/22°C temperature, the short-day plants flowered at day 33 compared to day 40 with the long-day plants. Plants growing in the 30/30°C temperature also flowered sooner in short days, in this case on day 29, when compared to short-day plants at 30/26°C. The difference in short-day and long-day flowering with *C. benghalensis* contrasts with the much stronger suppression of flowering in soybean (*Glycine max* L.) and tobacco (*Nicotiana tabacum* L.) under similar conditions with a night interruption [33, 34].

Even though short-day plants flowered only a few days earlier than long-day plants, whole plant growth was greatly reduced for plants exposed to short days (Figure 4). As might have been predicted from earlier studies examining *C. benghalensis* response to high temperature [17, 35], growth processes were enhanced at the high 35/28°C temperature. However, mass of short-day plants, when compared to long-day plants, was decreased by about 40% at 56 d in 35/28°C and growth was decreased 60% by short days in the slower growing plants at 30/22°C. The decreases in plant mass were accompanied by decreases in root mass (Figure 5(a)), plant height (Figure 5(b)), and total leaf area (Figure 5(d)) compared to plants in the long-day photoperiod. Effects on the number of leaves were not as consistent, with reductions in leaf number occurring in short-day plants at 30/22°C but not at 35/28°C by the final 56-day harvest (Figure 5(c)). Taken as a whole, our results are at odds with a previous study where it was concluded that photoperiod would not greatly affect growth of *C. benghalensis* [36].

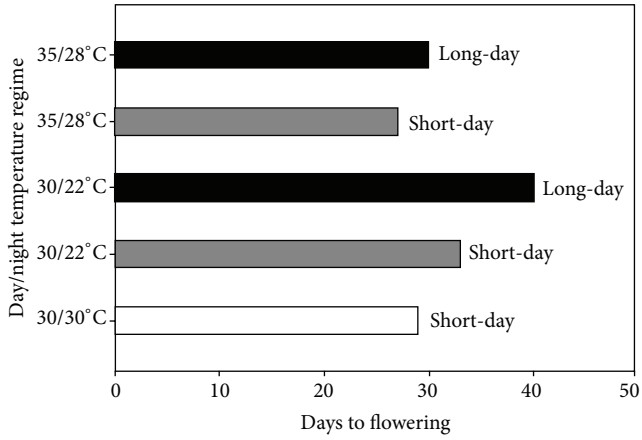

Figure 3: Photoperiod effects on time of flowering of *C. benghalensis* plants. Long-day plants (LD) were exposed to a 9 h light period and a 3 h night interruption with nonphotosynthetic light to suppress flowering. Short-day plants (SD) were exposed only to the 9 h light period.

Reproductive performance in the short-day plants was statistically similar to that in the long-day plants at in 35/28°C and 30/22°C temperatures. Thus, reproductive data for the short- and long-day plants were combined (Table 2).

Table 2: Effects of three temperature regimes on *C. benghalensis* aerial and subterranean spathe production. Data for the photoperiod treatments were similar, statistically, so they were combined.

Temperature regime	Aerial spathes			Subterranean spathes		
	Days after treatment			Days after treatment		
	28	42	56	28	42	56
°C	Number of spathes plant^{-1}					
35/28[a]	18[b]	68	87	4	30	31
30/22	22	94	120	1	15	22
30/30	42	84	98	5	25	37
$HSD_{0.05}$[c]	4	15	20	1	5	5

[a]Numbers indicate day/night temperatures.
[b]Values are means of 24 replicates. Photoperiod effects were nonsignificant at the 35/28 and 30/22°C temperatures, so data were pooled for each temperature regime.
[c]Tukey's honest significant difference at $\alpha = 0.05$.

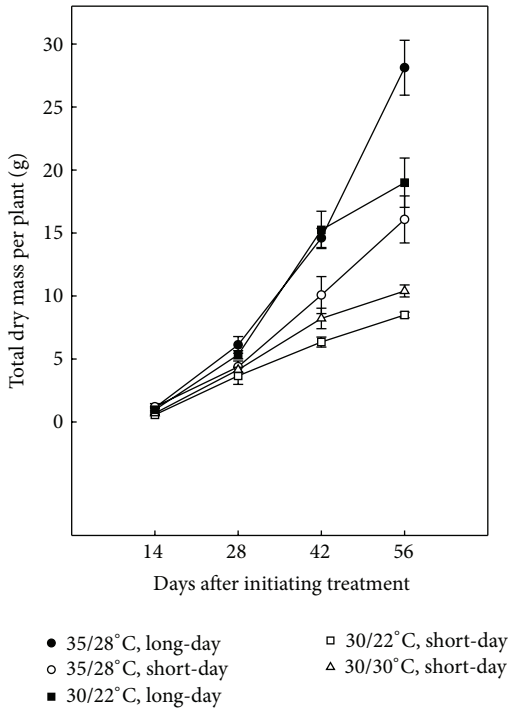

Figure 4: Effects of day/night temperature regime and altered photoperiod on total dry mass of *C. benghalensis*. The long-day treatment was imposed by a 3 h nonphotosynthetic night interruption in the middle of dark periods. LD: long-day; SD: short-day. Data points are means of six replicates, and bars indicate standard errors of the mean.

Some differences in the number of reproductive structures occurred among temperatures. At the higher temperature of 35/28°C, the higher vegetative mass (Figure 4) was associated with lower production of aerial spathes and greater production of belowground spathes.

As indicated above with low fertility or shaded plants, it is quite evident that *C. benghalensis* retains an ability to sustain a high level of reproductive output in high temperature ranges, in this case even when whole plant growth is constrained by the physiological response to a shorter photoperiod. This resilience in reproduction is obviously of concern when it is considered that one of the biggest challenges in weed management is to limit seed production in agronomic fields, reducing the long-term soil seed bank. Studies have shown that as many as 8,000 to 12,000 seeds m^{-2} can be produced by *C. benghalensis* [7], and the seeds can remain viable for at least 3 to 4 years [13].

4. Conclusions

Much is unknown about how the invasive weed *C. benghalensis* interacts with the environment. These experiments with different nutrition, low light, and photoperiod treatments offer new insights into environmental factors that enhance or suppress the invasiveness of *C. benghalensis* in agricultural systems. One insight is that *C. benghalensis* competitiveness and reproduction are strongly increased by the high nutrition typically used with grain crops. A valid containment strategy with large infestations of *C. benghalensis* would be to grow a series of crops with low or no added nitrogen fertilizer, like soybean or an N_2-fixing pasture. It should be emphasized that substantial growth and especially reproductive output still occurred at lower nutrition in our experiments, so it is anticipated that a degree of weed pressure will persist.

A second insight is that vegetative growth is suppressed under short days, even when flowering shifts only a few days. Thus, *C. benghalensis* competitiveness is likely to be reduced when germination and growth occur during shorter photoperiods outside of normal crop growing seasons, even though high temperatures may become more prevalent. A third important observation is that, regardless of the type of environment it faces, *C. benghalensis* exhibits a substantial reproductive capability, and this is true even when vegetative growth is suppressed by nutrition, low light, or a photoperiod shift. Underground reproduction appears to be particularly resilient. The persistent reproductive output underscores the importance of intensive management strategies to prevent introduction of *C. benghalensis* into agricultural fields.

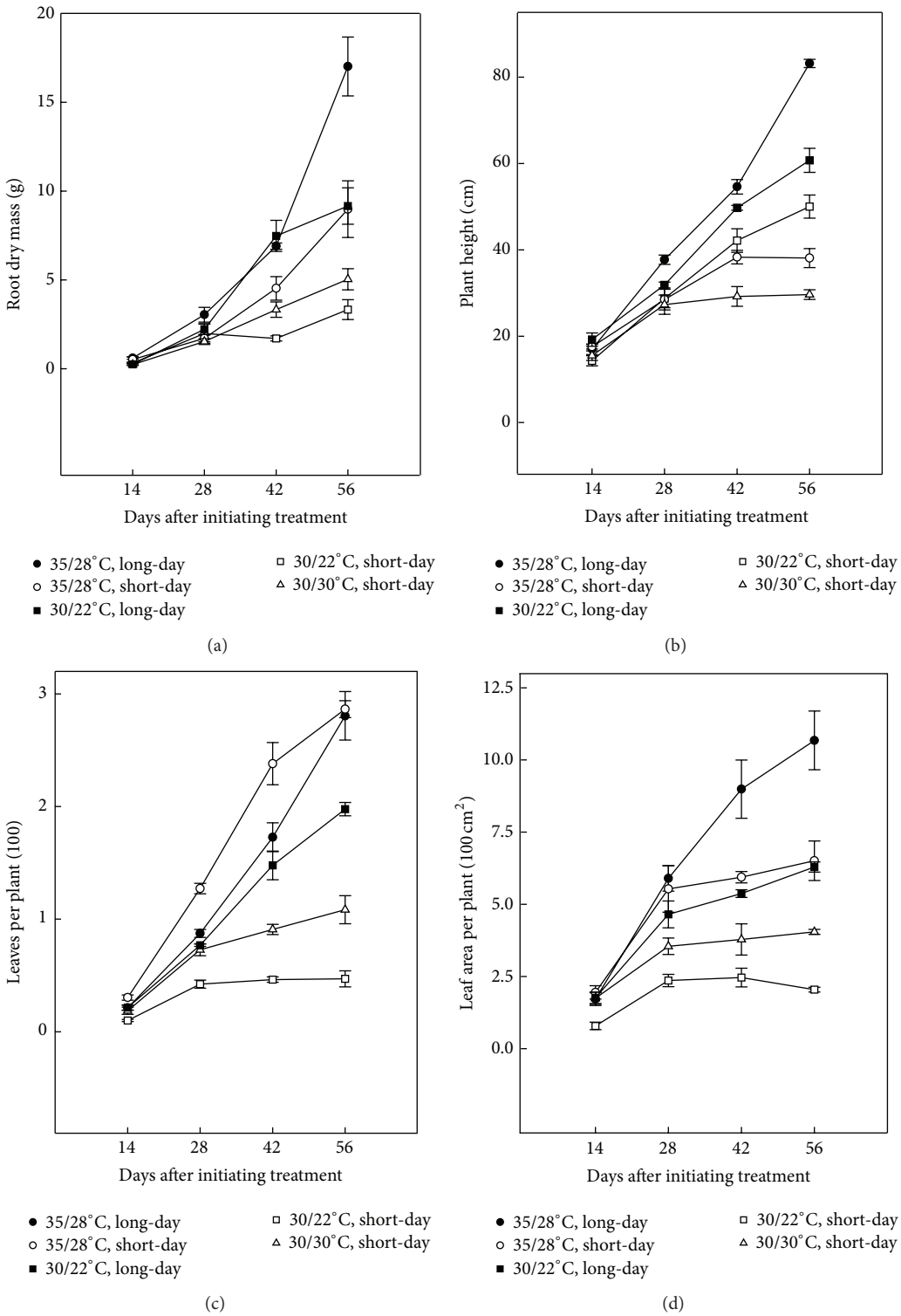

Figure 5: Effects of day/night temperature regime and altered photoperiod on (a) root dry mass, (b) plant height, (c) number of leaves per plant, and (d) leaf area per plant of *C. benghalensis*. The long-day treatment was imposed by a 3 h nonphotosynthetic night interruption in the middle of dark periods. LD: long-day; SD: short-day. Data points are means of six replicates, and bars indicate standard errors.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

Acknowledgments

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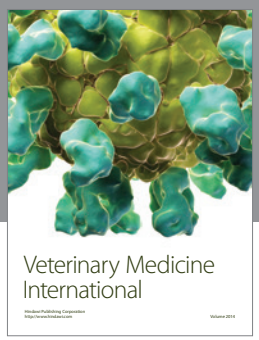

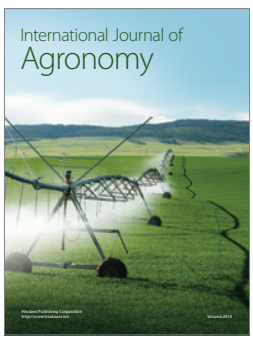

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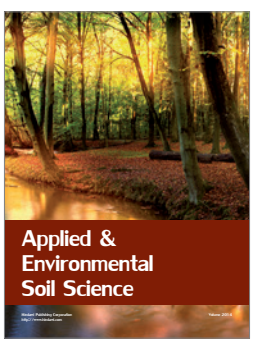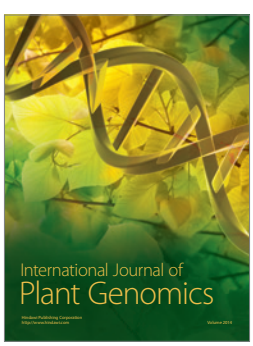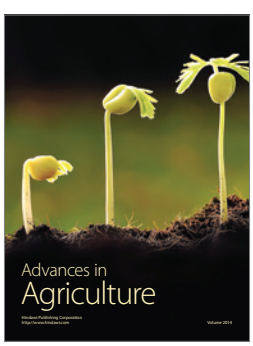
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