Journal of Horticultural Science & Biotechnology (2000) **75** (1) 72—78

Response of Chinese water chestnut (*Eleocharis dulcis* (Burm. f.) Hensch) to photoperiod

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SUMMARY

As a crop new to the western world, opportunities for production of Chinese water chestnut have barely been exploited. In China, over the latitude range 21° to 34°N it is planted in spring and harvested in autumn. Opportunities exist to extend its cultivation to new climates, where growth throughout the year is not constrained by low temperature, but may be constrained by photoperiod. To study the response of Chinese water chestnut to photoperiod, six experiments were conducted in tropical central Queensland. One set focussed on planting early in spring, with long-day treatments superimposed. Another set investigated autumn and winter plantings, also with superimposed long-days, and the third compared the performance of Chinese water chestnut under constant or decreasing photoperiods, ranging from 8 h to 20 h, in light-out chambers. Corm formation was strongly retarded by long days but promoted by the photoperiods which were shorter than a critical maximum. The critical photoperiod was between 12.0—12.5 h, below which corm formation was rapid, and above which it was non-existent, or minimal if combined with cool (<21° mean) temperature. Under short days, to the detriment of stem growth, significantly more dry matter was allocated to corms and rhizomes. The latter provided potential corm sites. The response of corm formation and rhizome production to photoperiods shorter than the critical was more pronounced the more extended the treatment period. The data provide evidence for the ability to manipulate timing of harvest at the field scale to extend availability of fresh produce on the market.

Chinese water chestnut *(Eleocharis dulcis* (Burm. f.) Hensch) is widely cultivated in eastern Asia for its sweet, juicy and crisp corm. The growth and development of this crop is complete within 210—240 frost-free days, and it is usually planted in spring or summer, depending on the crop rotation, and is harvested in winter (Hodge and Bisset, 1955). Three types of stems — green stem, rhizome and corm — play important roles in the life cycle of Chinese water chestnut. The above-ground green stems perform photosynthesis and provide carbohydrates for the whole plant. The underground rhizomes, which send out daughter plants with green stems, determine the size of canopy. The corms, which are formed at the tips of the later-produced rhizomes, are reserve organs and responsible for year-to-year propagation. Rhizomes follow two developmental pathways. One is to produce daughter plants when the rhizome tip grows upwards. The other is to form corms through the swelling and accumulation of dry matter at their tips. To date, there is no known report on the triggering factors that signal the switch in rhizome development.

Light is one of the important environmental factors in the development of plants. The effects of light may result from variations in wavelength, intensity or duration (photoperiod). For many species, photoperiod plays an important role in the formation of underground organs (Vince-Prue, 1975; Struik *et al.*, 1988; Demagante and Vander Zaag, 1988; Alvarenga and Valio, 1989). For example, tuberization of potato is favoured by days shorter than a critical photoperiod, although the critical photoperiod varies from cultivar to cultivar (Ewing and Struik, 1992). Observations on the production of Chinese water chestnut in Australia suggest that corm formation is associated with shortening photoperiod and cool temperature (i.e. corms are formed from mid-summer onwards, and plants senesce in early autumn) however, this is only conjecture. The objective of our study was to investigate the response of Chinese water chestnut to photoperiod, with special focus on corm formation. With this knowledge, it should be feasible to superimpose objective field-based photoperiod treatments to manipulate the timing of corm formation, and harvest, and extend seasonal supply of Chinese water chestnut to the market.

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MATERIALS AND METHODS

Most experiments were run at Rockhampton (23° 23'S, 150° 29'E) in 1996, 1997 and 1998, while one (Experiment 1) was run at Mackay (21° 07'S, 149° 10'E) in 1996. Representative weather data and sunrise and sunset times are presented in Tables I and II and specific experimental details are summarized in Table III.

Materials and planting

In all but one experiment a single Chinese water chestnut clone collected from China in 1994 was used. Two other clones were used in Experiment 5. In each experiment in Rockhampton the procedures were as follows:

Seed corms were surface disinfected in 30% calcium hypochlorite solution (1.2% active chlorine) for 20 min, rinsed and placed side by side in metal trays, and covered with sterilized sand and a 1 cm layer of water. After germination the plants were planted out into

TABLE I
Monthly mean temperatures recorded at Rockhampton (1996-1997) and Mackay (1996)

	Temperature (°C)			
	Rockhampton[y]		Mackay[z]	
Month	Max	Min	Max	Min
January	31.3	22.1	31.4	22.2
February	32.7	22.3	30.3	20.0
March	30.3	20.7	28.7	20.4
April	29.1	18.2	29.1	19.2
May	25.6	15.2	26.5	15.4
June	23.8	12.2	25.1	13.6
July	23.0	10.0	23.5	8.7
August	24.8	11.4	24.6	11.4
September	29.1	13.9	28.2	10.9
October	28.9	17.4	27.2	18.3
November	32.2	19.1	30.8	18.4
December	32.3	22.3	32.0	21.6

[y]Temperature at Rockhampton was recorded by the Bureau of Rockhampton Meteorology.
[z]Temperature for Mackay was recorded by the Bureau of Sugar Experimental Station.

sandy loam soil (15 min steam-sterilized, pH 6.0) which was mixed with slow-release N and P fertilizer (N 13.9% as NH_4^+; total P 12.7%) at 5 g kg^{-1}.The soil was placed in polystyrene boxes (80 cm wide, 40 cm long, 22 cm deep) to a depth of 10 cm for full growth cycle experiments or into plastic boxes to a depth of 5 cm (12 cm wide, 17 cm long, 8 cm deep) for short-season experiments. All experiments in Rockhampton, with the exception of Experiment 2, were conducted within a net house that reduced incident photosynthetically active radiation by ca. 40%. After planting four plants into the soil to a depth of approximately 7.5 cm for full growth cycle experiments, or three plants to a depth of 3-4 cm for shorter experiments, the soil was flooded with tap water for one day, drained off the next and reflooded to 5-10 cm or 2-3 cm, respectively, above soil level within one week. This depth was maintained throughout the growing season. For comparisons between extended photoperiods and natural daylength, incandescent lamps (60 W, one per 1.3 m^2 floor space) were installed 1.5 m above the boxes and were programmed to turn on one hour before sunset and off at the predetermined time according to the duration of the photoperiod extension. Untreated boxes were isolated from those with photoperiod extension.

The experiments comparing natural daylength with shortened and lengthened photoperiods were under-taken in purpose-built black plastic chambers. All long photoperiod and short photoperiod treatments received 9 h natural light from 0900 hours to 1800 hours in Experiment 6, and 7 h 0930 hours to 1630 hours in Experiments 4 and 5. For the remainder of each day the chambers were covered with light-proof black plastic, and the incandescent lights programmed to provide the desired photoperiod treatments. Incandescent lamps did not provide more than 5 µmol m^{-2} s^{-1} PAR at the top of the canopy, and therefore were considered not to contribute to photosynthesis. Air temperature within the chambers was on average 1-2 K higher than air temperature outside.

Non-destructive sampling for initiation of corms, by way of feeling in the soil, was undertaken weekly in Rockhampton experiments. Sequential and final destructive harvests involved separating out plant components (i.e. daughter plants, rhizomes, roots, stems, and corms sorted by size and maturity - white as immature, brown/black as mature), counting parts and calculating percentages of corm-bearing plants and corm maturity index (the number of mature corms/total number of corms).

Following measurement of fresh weights, plant parts were separately oven-dried for 72 h at 70°C for determination of dry weight. In Experiments 3 and 6, sugars of fresh corm flesh were extracted according to the method described by Bhadula and Sawhney (1989) and measured according to the technique of Chaykin (1966). Fresh corm flesh (0.1 g) was ground and extracted with 10 ml of 80% ethanol at 95°C for 20 min. After cooling, samples were centrifuged at 10,000 rpm for 10 min. The super-natant was collected and the pellet was extracted again by repeating the procedure. The supernatant from two extractions was pooled for soluble sugar content measurement (glucose was used as the standard). The pellet was then hydrolyzed with 10 ml 4.5 N H_2SO_4 for 1 h in a boiling-water bath. After cooling and diluting to volume, the solution was filtered through a hardened filter paper. The filtrate was collected for insoluble sugar content measurement using the same method as for soluble sugar content measurement. Starch was used as the standard for insoluble sugar. Total carbohydrate content was considered as the sum of soluble and insoluble sugars.

In Experiments 2 and 4, with a portable refractometer °Brix was measured on juice expressed with a garlic press from fresh corms. The juice was centrifuged at 10,000 rpm for 10 min before °Brix measurement.

Analyses of variance, and regression analyses were conducted on the data using SAS computer programs (SAS Institute, 1993) for the relevant experimental designs.

The six experiments

In total six experiments were undertaken, and details specific to each are presented in Table III.

Experiment 1 was set up to determine whether plants would initiate corms during the short days of spring growth within the tropics. Seed corms from sequential harvests were planted within one week of harvest over

TABLE II
Duration of daylight[z] (in hours) for half-months at Rockhampton and Mackay. The latitudes at Rockhampton and Mackay are 23° 23'S and 21° 07'S respectively

Town	January		February		March		April	
Rockhampton	13.54	13.34	13.07	12.80	12.47	12.10	11.83	11.50
Mackay	13.38	13.18	12.96	12.73	12.42	12.10	11.88	11.57
	May		June		July		August	
Rockhampton	11.13	10.90	10.76	10.66	10.76	11.00	11.23	11.60
Mackay	11.24	11.03	10.92	10.82	10.92	11.13	11.34	11.67
	September		October		November		December	
Rockhampton	11.83	12.20	12.57	12.84	13.17	13.40	13.54	13.57
Mackay	11.88	12.20	12.52	12.74	13.06	13.27	13.38	13.39

[z]Data were interpolated from the data presented in *The World Almanac and Book of Facts 1997.*

TABLE III

Summary of planting dates, treatments, sample size and harvest dates for each of six experiments

Experiment	Date		Treatments	Sample size/treatment		Harvest dates	
	Planted	Treatments imposed		Sequential harvest	Final harvest	Sequential	Final
1.	8 July-22 Nov 1996	Immediately	Planting date with natural daylength (ND)	20-40 plants for corm initiation	None	35-99 DAT*	-
2.	29 July-14 Oct 1997	Immediately	Planting dates with ND or 15.7-18.5 h extended photoperiod	5 plants non-destructive for corm initiation	25 plants	Weekly	19-21 Dec 1997 (65-144 DAT)
3.	13 Feb 1996	23 April after ND	ND or 20 h extended photoperiod. One half extended photoperiod shifted to ND on 29 Julv	6 plants	6 plants	15 July (83 DAT) 27 August (126 DAT)	24 Sept 1996 (154 DAT)
4.	10 Nov 1997	30 Nov after 16 h photo-period	8 h, 12 h, 16 h, 20 h, 24 h, 13-11 h with 15 minute weekly decre-ments	10 plants	15 plants	21 Dec (21 DAT) 11 Jan (42 DAT)	2 Feb 1998 (63 DAT)
5.	8 Jan 1998	Immediately	Two clones in each of 8 h, 12 h, 16 h, 20 h, 24 h, 12.5-11 h with 15 minute weekly decrements, ND (13.5-11.5 h)	3 plants	3 plants	12 Feb (33 DAT) - 9 April (89 DAT) (weekly)	16 Apr 1998 (96 DAT)
6.	2 Nov 1996	23 Jan after 16 h from 15 Dec and ND til then	Initially 11.0 h, 11.5 h, 12.0 h, 12.5 h, 16 h, ND (13.6-11.0 h) and then on 9 March to ND	8 plants	8 plants	7 Feb (15 DAT) 22 Feb (30 DAT) 8 Mar (45 DAT)	9 May 1998 (106 DAT)

*DAT = days after treatment began.

the period July to November 1996 in Mackay in metal trays filled with soil. Shortly before plants were transplanted to the field (when stems were 20–30 cm tall), 20–40 plants were sampled at random for detection of newly-formed corms.

Experiment 2 compared the effects of long daylengths (15.7–18.5 h) vs. natural daylengths (10.7–13.5 h) on biweekly sequential plantings of successively harvested corms from Mackay over the period 29 July to 14 October 1997 – a period when both natural daylength and ambient temperature were increasing. All plants were harvested over the period 19–21 December, 1997.

Experiment 3 compared the effects of long (20 h) vs. natural shortening and then lengthening days (i.e. prior to and after the winter solstice: 12.3–10.7–12.1 h) on flowering, corm initiation and dry matter partitioning. On one occasion (100 d after starting the long-day treatment) some plants were shifted from the long-day treatment to natural daylength.

Experiment 4 was undertaken to quantify the effects on corm initiation and early dry-matter partitioning of constant photoperiods (8, 12, 16, 20, 24 h) and a shortening photoperiod (13 h to 11 h in weekly 15 min decrements, giving an average 12 h photoperiod over the nine-week experiment.) This experiment was run from November 1997 to January 1998 when temperatures were increasing.

Experiment 5 was similar in objective to Experiment 4, with almost identical treatments plus a natural daylength treatment. Two cultivars, multiplied in Australia but obtained from Singapore and Thailand, were included in the experiment, which was run from 8 January until 16 April 1998, over a period of decreasing temperature and daylength. Weekly destructive harvests were taken commencing on 12 February 1998.

Experiment 6 allowed comparison of six photoperiod treatments (16, 12.5, 12.0, 11.5, 11.0 h and natural daylength 12.8–13.6–11.0 h). Before imposing the photo-period treatments, all plants except those in the natural daylength treatment were equilibrated under 16 h long days for one month following germination and early growth. The six treatments were run for 45 d from 23 January 1997, followed by transfer to either natural daylength (12.4–11.0 h) or a 20 h photoperiod for a further two months before final harvest.

RESULTS

Spring-season induction and superimposed long photoperiods

Under naturally lengthening days, corm initiation was evident until the mean natural daylength during the

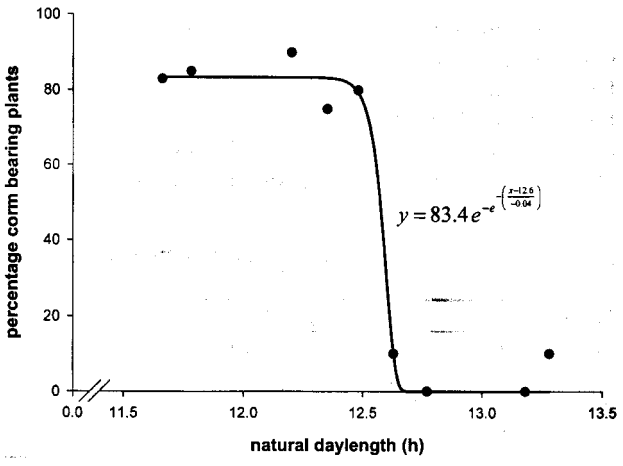

FIG. 1

Effect of natural daylength (from planting to evaluation) on the percentage of corm bearing plants in Experiment 1. (Fitted Gompertz equation, $r^2 = 0.984$, $P \leq 0.001$).

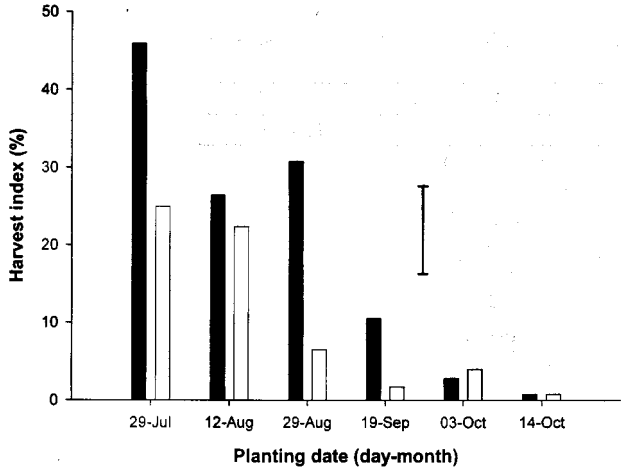

FIG. 2
Harvest indices of Chinese water chestnut plants (mean value per box) grown under natural days (solid bars - 10.7-13.5) and extended photoperiods (open bars - 15.7-18.5 h) and planted on six occasions in Experiment 2. (Bar represents LSD, P≤0.05).

period of plant growth (Experiment 1 — Figure 1) exceeded 12.5 h, after which corm initiation was negligible.

A similar short-day induction of corms was evident in Experiment 2, where the propensity to form corms in the shorter daylengths of earlier plantings was reflected in their higher harvest indices (Figure 2). However, if the requirement for short days were absolute, then imposition of a long photoperiod treatment should inhibit corm initiation. The data show that the long photoperiod treatment (18.5—15.7 h) did not entirely prevent corm formation, for the harvest index of the late July planting long photoperiod treatment reached 25%, compared with 46% in the natural short-day treatment. These data suggest that either the requirement for short days for corm initiation may be substituted in part by the cooler temperatures of August and September than October (Table I) or that corm initiation is inevitable after a vegetative period of sufficient duration, or, perhaps, a combination of the two.

Total biomass declined with later planting dates as a consequence of the shorter growth period to harvest (Figure 3), but a notable increase in biomass was evident between the plantings of October 3 and 14 almost certainly due to the inhibition of corm initiation, and greater investment in stem, and therefore, photosynthetic tissue.

Autumn and winter season induction and superimposed long photoperiods

The short days of autumn in Experiment 3 (12.3—11.4 h) to which plants were subjected before the long photoperiod (20 h) treatment commenced, resulted in corm initiation in both the natural daylength and long-photoperiod treatments. Four weeks after the long-photoperiod treatment began, two thirds of plants in both the long photoperiod and natural daylength had initiated corms. However, by final harvest (154 d after implementing the treatment — DAT) the proportion of plants that had initiated corms under the long photo-period remained the same while under ND all plants had by then formed corms.

The number of corms initiated per plant under ND increased from 10 to 25 over the 70 d sampling period (Figure 4) but no corm initiation was evident in plants one month after their shift from LD to ND. After a further month of ND, the total number of corms on plants shifted from LD to ND was similar to that of plants originally under ND. However, the proportion of mature corms (20%) was much less in the plants that experienced fewer ND than in those (85%) in ND for the whole period, most likely due to the longer maturation period from initiation to harvest in the ND treatment.

Fresh weight of total and mature corms under LD and ND showed the same pattern as the numbers of total and mature corms, but the fresh weight of total corms for the plants shifted from LD to ND was not proportional to the total number of corms. This was because of the large number of small, immature corms (data not presented).

The fresh weight per mature corm averaged 3.17 ± 0.25 g for plants under ND, but decreased in

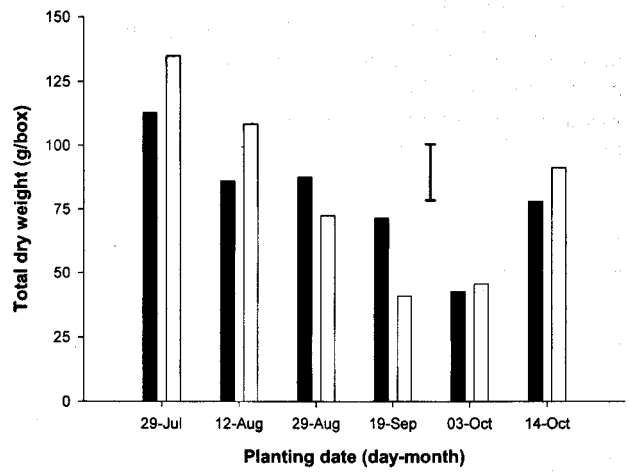

FIG. 3
Total dry weight of Chinese water chestnut plants (value per box) as affected by natural days (solid bars - 10.7-13.5 h) and extended photoperiods (open bars - 15.7-18.5 h) and six planting dates in Experiment 2. (Bar represents LSD, P≤0.05).

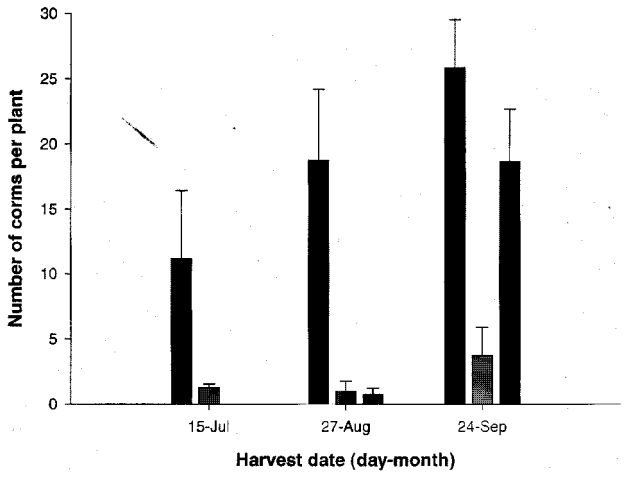

FIG. 4
Total numbers of corms per plant measured on three dates in Experiment 3, under natural days (first columns, 13.0-10.7-12.1 h, dark shading), under long days (second columns, 20 h, light shading) and in plants shifted from LD to ND on 29 July (third columns, dark shading, for the two later dates). Bars represent SE.

TABLE I V

Total plant dry matter, and partitioning for Chinese water chestnut plants grown under different photoperiods and determined at three occasions in Experiment 4

Weeks after treatment	Photoperiod (h)	Dry wt (g/plant)	Dry-matter partitioning (%)[y]			
		Total	Stem	Root	Rhizone	New corm
3	8 h	1.54	92.9 ab	6.84 a	0.32 a	0
	12 h	1.97	90.3 b	9.12 a	0.55 a	0
	13-11 h	n.d.	n.s.	n.d.	n.d.	n.d.
	16 h	1.22	93.3 a	6.73 a	0 a	0
	20 h	1.44	90.6 ab	8.92 a	0.45 a	0
	24 h	1.35	91.7 a	8.20 a	0.13 a	0
6	8 h	1.73 b	90.4 b	6.37 a	0.94 a	2.30 a
	12 h	1.24 b	93.9 ab	5.85 a	0.25 ab	0 b
	13-11 h	2.63 ab	92.5 ab	7.36 a	0.16 b	0 b
	16 h	3.28 a	92.7 ab	6.86 a	0.41 ab	0 b
	20 h	2.47 ab	92.3 ab	7.42 a	0.31 ab	0 b
	24 h	2.12 ab	95.9 a	3.94 a	0.14 b	0 b
9	8 h	2.16	82.0 b	5.45 b	3.39 a	9.18 a
	12 h	3.22	88.0 ab	5.65 b	1.24 b	5.07 ab
	13-11 h	2.72	91.7 a	6.11 ab	1.44 b	0.76 b
	16 h	3.35	94.3 a	5.57 b	0.09c	0 b
	20 h	3.84	90.7 a	9.04 a	0.23c	0 b
	24 h	3.14	93.7 a	6.11 ab	0.14 c	0 b

[Y]Data were transformed using arcsin $\sqrt{p}$, where p is a proportion, prior to statistical analysis, and the means were transformed back to percent when reported in the table. Means within columns within a sample date with the same letter are not significantly different at $P = 0.05$ level according to Duncan's multiple range test.

plants under long photoperiods from 2.13 ± 1.33 g to 0.88 ± 0.19 g. This loss of fresh weight was matched by a loss in total sugar concentration over the same 2.5 month period in mature corms (from 23.6 ± 2.4 to 16.4 ± 2.2 g per 100 g fresh weight), at a time when sugar concentration of mature corms under ND stabilized at 24 ± 3.2 g per 100 g fresh weight. Two months after shifting plants from LD to ND, their sugar concentration recovered to values similar to ND plants.

Evidently, therefore, further corm initiation was effectively blocked after plants were transferred from SD to 20 h photoperiods, although a few new corms were found even in this treatment by the last harvest. In contrast, the SD conditions (12.3-10.7-12.1 h), prior to and after the winter solstice, favoured corm initiation and growth. Visual response to the shift from 20 h photoperiod to ND occurred between one and two months after the shift.

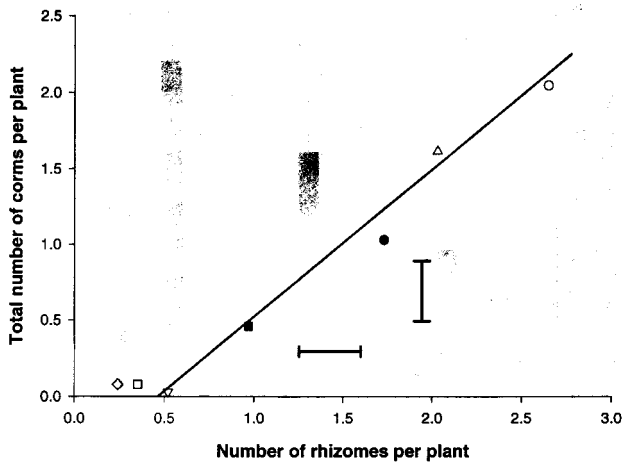

FIG. 5

Relationship between average number of corms and number of rhizomes per plant as affected by photoperiod treatments in Experiment 5. (○ = 8 h, △ = 12 h, ▽ = 16 h, □ = 20 h, ◇ = 24 h, ● = 12.5-11 h, ■ = ND). Linear regression for daylength treatments <20 h, y = 0.96x - 0.49, r^2 = 0.983**. (Bars represent LSD, $P \leq 0.05$)

Short-term photoperiod treatments

Following corm germination under a 16 h photoperiod for three weeks in Experiment 4, transfer to photoperiods of 12 h or fewer resulted in corm formation within nine weeks, and within six weeks under 8 h photoperiod (Table IV). A few corms under the 8 h photoperiod were observed to be directly formed on mother corms, i.e. without rhizomes.

The earlier corm initiation under the 8 h photoperiod led to less investment in stem biomass, as was also evident for the 12 h photoperiod treatment at 9 WAT (Table IV). Corm formation was also accompanied by greater rhizome biomass, but root dry weight did not vary systematically across sample dates or treatments.

The lesser investment in corm dry matter by the 13-11 h reducing photoperiod than under the constant 12 h photoperiod (over the nine-week experiment the average photoperiod was identical in both treatments) suggests that the critical photoperiod for corm initiation in that experiment was between 12 h and 13 h. The constant 12 h treatment would have begun induction immediately after transfer from the 16 h pre-experimental period while the 13-11 h reducing treatment would have initiated some time later, once the critical photoperiod was reached. The data suggest that the

TABLE V

Number of rhizomes and corms and dry weight of corms of Chinese water chestnut determined after 45 d under photoperiod treatments and natural days in Experiment 6

Photoperiod (h)	No. of rhizomes/box	No. of corms/box	Wt of corms (g/box)
11.0	26.5 a	15.8 a	8.7 ab
11.5	17.3 abc	14.8 a	6.2 be
12.0	21.5 ab	13.3 ab	4.7c
12.5	11.5c	8.0c	4.5c
ND	16.8 bc	12.5 abc	10.5 a
16	10.8c	8.8 bc	3.3c

ND stands for natural daylength (12.8-13.7-12.4 h). There were four plants in each box. Means within columns with the same letter are not significantly different at $P = 0.05$ level according to Duncan's multiple range test.

TABLE VI

Effect of final photoperiod (last 60 d of Experiment 6) on corm (mature and immature) and rhizome numbers, and dry weights (g), per box at final harvest

	Mature corms		Immature corms		Rhizomes	
Final photoperiod treatment	No.	Wt	No.	Wt	No.	Wt
LD (20 h)	9.6	8.9	0.2	0.0	16.6	0.84
ND (12.4-11.0 h)	10.4	10.	4.1	0.4	23.6	1.17
Difference	n.s.	n.s.	**	**	*	n.s.

n.s. Non significant, *Significant at P<0.05, **Significant at P<0.01.

inducing effects of short photoperiod treatments (8–12 h) were closely related to exposure time. Shorter days required fewer inductive cycles for corm formation than did longer days below the critical photoperiod, and the longer the SD treatment was in place, the stronger the inductive effect.

Photoperiods of 16 h or greater essentially inhibited corm initiation in Experiment 5 (Figure 5), although very few (on average <0.1 per plant) were found even in the 24 h treatment. It was only in the clone originating from Thailand that corms were initiated under 16, 20 and 24 h treatments. The number of corms per plant was closely related to the number of rhizomes per plant (Figure 5) and, as in previous experiments, shorter days produced significantly less vegetative biomass and consequentially greater harvest indices (data not presented). Shorter days induced more rhizomes but these provided potential sites for corm formation, and not for the production of daughter plants. Corms were observed 47 DAT in the 8 h and 12 h photoperiod treatments, 68 DAT in the shortening photoperiod and 89 DAT under natural days, indicative of the quantitative response to photoperiod for corm initiation.

The final experiment (Experiment 6) also compared the performance of water chestnuts subjected to a number of photoperiod treatments, and followed by shifts to natural daylength (ND) or a 20 h (LD) photoperiod. Corms were present 15 DAT in the 11–12.5 h photoperiod treatments and by 45 DAT even the 16 h treatment had corms (Table V). Excluding data from the ND treatment, there was a quantitative response of corm and rhizome dry weight to photoperiod; the shorter the photoperiod the greater the dry weight. By the harvest 61 d after the shift from SD to LD or ND, the number and size of mature corms was not affected by either the initial nor final photoperiod treatment (data for final photoperiod treatment given in Table VI). In contrast, the number of immature corms, and their weight, were significantly greater in the plants shifted to ND rather than to LD. The same trend was so for rhizomes. Rhizomes and immature corms were evidently initiated after the imposition of the ND treatment, but to a much lesser extent in the LD treatment.

DISCUSSION

Our data show that, as for many other plant species (Vince-Prue, 1975; Ewing, 1978; Alvarenga and Valio, 1989; Han *et al.,* 1991), Chinese water chestnut exhibited marked quantitative responses to photoperiods, which were most evident for corm formation. Most photoperiodic induction of storage organs, with the exception of bulbs in the genus *Allium,* show a short-day response (Vince-Prue, 1975) and our data confirm this for Chinese water chestnut. In contrast with most species, however, it is likely that the stems in Chinese water chestnut, and not the leaves, perceive the photoperiodic stimulus, for leaves in this species are reduced to very minor bracts.

Constant short days ('13 h), shortening days from 13 h to 11.0 h or from 12.5 to 11.0 h, or short natural days (11.0 to 13.7 h) brought about corm formation soon after their imposition. The smaller biomass associated with early corm formation (Figure 3) was in line with data for potato, relating early tuber formation to reduced canopy size (Midmore, 1992). The changing pattern of natural days, whether shortening or lengthening, seemed less important for corm formation than the length of day being below a critical maximum for corm formation. However, this critical value, which is probably between 12–12.5 h, is still not known. The small proportion of plants with corms when the mean day-length reached 13.28 h (Figure 1) may reflect the tendency for corm initiation at photoperiods greater than 12.5 h in response to a decreasing photoperiod, as occurred after the summer solstice. Such a precise response to photoperiod has been shown to exist in flowering of sugarcane (Midmore, 1980), and may be evident for other tropical and subtropical species.

The determination of critical photoperiod will be subject to the modifying effects of such factors as temperature and irradiance level. For example, cooler temperature and high irradiance raise the critical photoperiod in potato (Ewing and Struik, 1992). Within our experiments, which were conducted under ambient temperatures at various times throughout the year, it is not possible to specify the nature of a temperature x photoperiod interaction. However, the initiation of admittedly few corms under photoperiods greater than the presumed critical, especially when ambient temperature was cooler closer to harvest (e.g. in Experiment 5 vs. Experiment 4), does suggest that cooler temperature may substitute for shorter days below the critical. As an alternative, though, water chestnut plants might initiate corms under any photoperiod following a sufficient period of vegetative growth. Our data indicate that initiation took place under photoperiod >13 h by 91 d after planting in Experiment 2, 89 d in Experiment 5, 104 d in Experiment 6 and not at all by 83 d in Experiment 4. It may well be that corm initiation can take place, irrespective of current photoperiod, as a conditioned response to Chinese water chestnuts.

Among photoperiods shorter than the critical value, the shortest photoperiod tended to induce more strongly corm formation. The development of sessile corms formed on the mother corm under the 8 h photoperiod in Experiment 4 was indicative of conditions highly inductive for corm formation, as shown for potato under similar conditions (Ewing and Stuick, 1992).

The minimum number of inductive cycles (days) for each photoperiod could not be clarified in the present experiments since the process of corm induction and subsequent corm initiation and development were not separated. The overall tendency that fewer short-day cycles are required if the photoperiods are much shorter than the critical photoperiod is in line with that reported for other short day species (Ewing and Struik, 1992). Data from Experiment 5, relating date of corm initiation to actual photoperiod, do provide some insights into the possible duration for juvenility and induction and appearance of corms. In the ND treatment, corms were visible 89 DAT, approximately two weeks after daylength would have shortened to less than 12 h. Assuming photoperiods greater than the critical do not contribute to corm induction (a large assumption, but valid in simplifying the argument) and that the critical photoperiod is 12 h then the response time to the critical photoperiod is two weeks. If that were so, then the juvenile stage of plants in Experiment 5 would be approximately 33 d, for the 8 h and 12 h treatments initiated corms by 47 DAT. On this basis, the artificially decreasing photoperiod treatment would have been ready to respond to the shortest days (11 h) effective 28 d DAT, however, corm initiation was delayed by three weeks compared with the constant 12 h or 8 h treatments. This implies that photoperiods greater than the critical do contribute to corm initiation, once the juvenile period has passed.

Hastening effects of a shortening photoperiod (simulating the natural progression in daylength) on corm formation were not observed within the short time frame in Experiment 4. One half of plants in each of the 12 h and 13–11 h shortening photoperiod were induced to initiate corms. Indeed, the 12 h constant photoperiod resulted in more dry matter being partitioned to corms (Table IV). This suggests that the induction to corm formation took place a little earlier under 12 h constant photoperiod. Perhaps, while some of the corms that had initiated under 12 h constant photoperiod had entered into an enlargement stage, most corms were just being initiated under 13–11 h changing photoperiod by 8 WAT.

The loss of corm fresh weight and decline in corm sugar content in plants transferred from short to long days in Experiment 3 suggests that photoperiods should remain inductive after corm initiation for sustained corm growth. The loss of corm weight noted could reflect resorption and redistribution of biomass to other plant parts, as noted for potato tubers after photoperiods were changed, following tuber initiation and some tuber growth, from inductive to non-inductive (Ewing and Struik, 1992).

The data presented here suggest that for corm formation, Chinese water chestnut is a quantitative short-day plant. Corm formation was essentially pre-vented by photoperiods of 16 h and longer but enhanced by photoperiods which are short in relation to the critical photoperiod. The critical photoperiod during the conduct of our experiments was in the range 12–12.5 h. From a practical standpoint, imposition of daylength extension in the field could delay corm initiation with a consequent delay in harvest if the effects of shorter than natural daylengths at delayed corm induction do not over-compensate for the absolute delay in corm initiation. In tropical regions, delaying corm initiation by way of daylength extension (>16 h) could delay the harvest period into the autumn and winter period. We believe that this may lead to sweeter corms at harvest. In regions outside of the tropics, where curtailment of growth is dictated by onset of frosts, shortening the daylength (<10 h) could hasten corm initiation and extend the period available for corm growth and lead to greater corm yield. These two practical approaches could result in both an extension of the natural harvest period and supply of fresh Chinese water chestnut corms to the market.

We thank the Rural Industries Research and Development Corporation for partial funding, the CQU Plant Sciences Group with help in construction of photoperiod chambers, Mr Greg Gunning for supply of corms, and AusAID for provision of a scholarship to Mei Li.

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(Accepted 1 August 1999)