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12. We thank Drs. H. Schindler and O. Kempenich-Pinto of the Volcani Institute of Agricultural Research, Rehovot, and Dr. B. A. Peleg of the Kimron Veterinary Institute, Beit Dagan, for the demonstration of useful techniques.

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Photoperiod Evidence in the Introduction of Xanthium (Cocklebur) to Australia

Abstract. *North American populations of cocklebur* Xanthium strumarium L. *are diverse in form and show critical dark periods ranging from 7.75 to 10.75 hours (critical photoperiods of 13.25 to 16.25 hours). South American cockleburs also are diverse in form and response. American cockleburs are adapted to diverse ecosystems, which suggests that they are indigenous. In contrast, the widespread Australian populations known as Noogoora Burr are all of the* chinense *morphological complex and respond uniformly to photoperiod. Plants from southern Louisiana and Australia are nearly identical in external form and in critical dark period of 10.5 hours. Probably the Australian Noogoora Burr and the Indian monsoon form arrived in their present countries after 1800 as contaminants in cottonseed from the Mississippi Delta region.*

Explosive spread of weedy species, such as cocklebur *Xanthium strumarium* L. (*1*) is a worldwide occurrence. Assessment of the problem is required in order to predict potential population spread in newly disturbed ecosystems. Certain populations that are currently restricted may have potential for rapid and broad increases in their distribution if they are accidentally or purposely introduced into a new area. As man continues to disturb natural ecosystems, new areas for exploitation will increase. In Australia, apparently an array of disturbed ecosystems in a broad range of latitudes permitted the intrusion of a uniform type of cocklebur. However, in America, *Xanthium* is latitudinally diverse and originally was probably indigenous primarily occupying sites subjected to disturbance along streams and beaches.

The pattern of photoperiodic differentiation among *Xanthium* populations of North America includes critical dark periods ranging from 7.75 to 10.75 hours (critical photoperiods of 13.25 to 16.25 hours) (*2*). Those in south central North America (Texas, Mexico) between latitudes of 18° and 35° vary in their critical dark periods from 9.0 to 10.75 hours. Although the range of latitudes in Australia (and India) is similar to that of Texas and Mexico, the distribution of *Xanthium* does not reflect similar patterns of adaptation.

Three Australian populations of *X. strumarium*, named Noogoora Burr, in the *chinense* morphological complex (*1*), were compared with populations originating in North America, South America, and India. The three Australian populations represent latitudinal extremes, near Darwin at Borroloola, Northern Territory, 16°S, and at Wodonga, Victoria, 36°S, and a central location near Brisbane (Indooroopilly, Queensland, 28°S). The Brisbane location is near the point of reported introduction (*3*). Collections from Córdoba, northern Argentina, and from Salto, Uruguay, at latitudes 31° to 33°S, represent the common complex of South America, *cavanillesii.* An Indian collection from Chandigarh, approximately the same latitude as Austin, Texas (30°N), represents the most common complex of India, *chinense.*

Seedlings germinated in sand (burs soaked overnight in a dilute solution of Consan-20, a fungicide) were kept under continuous light at 30°C during the day and 24°C during the night until they were exposed to dark periods (*4*). The 2-week-old seedlings were transplanted into polystyrene cups of fine sandy loam and given weekly nutrient additions. Five 60-day-old seedlings of each population were placed in Percival growth chambers operated at 30°C during the day and 24°C during the night at night lengths of 9, 9.75, and 10.5 hours. After each 7-day period, the night length was increased by 15 minutes so that the range of night lengths varied from 9 to 11 hours. Before comparison of photoperiods, 45-day-old plants were tested in 11-hour dark periods and proved to be sufficiently mature (ripeness-to-flower) for inducibility.

Plants of the three Australian populations were morphologically and behaviorally uniform (Table 1) and were indistinguishable from the Indian population. They showed floral induction in dark periods of 10.5 or more hours, but they failed to be induced at dark periods of 10.25 hours or less. A similar photoperiod status for other Indian plants has been reported by Kaul (*5*, *6*).

The South American collections (*cavanillesii* complex) (Table 1) were diverse in their response to photoperiod. Each population showed a specific dark-period requirement.

All Texas populations studied were in the *italicum* complex, but photoperiods included patterns similar to each of the above populations. Plants from Austin, Texas, showed a 10.5-hour critical dark period and those from more western sites at the same latitude showed 9.75- and 10.25-hour critical dark periods.

The above comparison of plants from approximately the same latitude in Australia, India, North America, and South America showed photoperiod variation only among plants of the Americas. The uniformity of the Australian and Indian plants suggests their introduction from a common source.

Because Ray and Alexander (*2*) had not shown a 10.5-hour critical dark period in the morphological complex *chinense* in North America, it appeared that the Australian plants might have originated elsewhere or were the product of genetic selection after their introduction. However, Ray and Alexander (*2*) showed critical dark periods ranging from 8.0 hours for *chinense* plants in Michigan to 10.0 to 10.25 hours for *chinense* plants in northern Mississippi, central Alabama, and Georgia. Their study did not include plants from Louisiana or areas in Mississippi and Alabama adjacent to the Gulf of Mexico. If the gradient in the length of the critical dark period continued to vary latitudinally, it seemed reasonable that plants requiring 10.5-hour dark periods might occur adjacent to the Gulf of Mexico and that the Mississippi Delta might harbor the type of cocklebur that has successfully colonized Australia and India.

To determine whether 10.5-hour dark periods are required for flowering by *chinense* plants in the United States, samples were transplanted from six populations in southern Louisiana in late July 1970 (Fig. 1). Five Collections of *chinense* plants included: LaRose (29°25′N, 90°21′W), LaFourche Parish; Pecan Island (29°45′N, 92° 30′W), Vermillion Parish; Lake Charles (30°15′N, 93°20′W), Calcasieu Parish; Frost (30°20′N, 91°10′W), Livingston Parish; and LeBeau (30°40′N, 91°50′W), St. Landry Parish. A sixth collection near the Texas border at Johnson's Bayou (29°45′N, 93°40′W), Cameron Parish, was closer to the *italicum* complex. The collections at LaRose, southwest of New Orleans, and at Frost, east of Baton Rouge, were in the Mississippi Delta region and were separated from each other by only a degree of latitude.

The sample plants showed no floral induction at five of the six sites in late July. At the Lake Charles population, a number of plants were in various stages of flowering and bur production, suggesting the possible inclusion of plants that are day neutral in their flowering or were induced by short dark periods. The natural dark periods were near 9.5 hours at the time of collecting. For the Lake Charles population, the sample plants included only those that showed no floral development at the time of collecting.

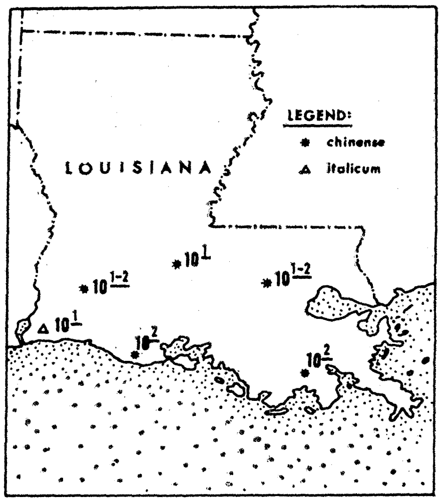

Fig. 1. Geographical distribution of critical night length in populations of *Xanthium strumarium* from southern Louisiana. For each population the critical night length is indicated in hours, and, by superscript, quarters of an hour: 10^{1} indicates 10.25 hours, 10^{2} indicates 10.5 hours, and 10^{1-2} indicates a combination of different critical nights.

The plants were kept under natural day lengths enroute to Austin, Texas, because southern Louisiana is approximately at the same latitude as Austin and, therefore, has the same day-length sequence. The plants were potted in polystyrene cups of fine sandy loam, given regular nutrient additions, and kept under continuous light for 3 weeks prior to testing. None of the plants, including those from the Lake Charles population that had included some flowering individuals, produced flower buds under continuous illumination, indicating that they had not been induced under natural dark periods. For the photoperiod test, four or five plants of each of the populations were placed under dark periods of 10.25, 10.5, and 10.75 hours at 30°C during the day and 24°C during the night.

All of the Louisiana plants were induced to flower in 10.5- and 10.75-hour dark periods, but only a few were induced at 10.25 hours during an 18-day test period (Fig. 1). The *italicum* population from Johnson's Bayou produced macroscopic buds uniformly under the 10.25-hour dark periods. Only one *chinense* plant, in the LeBeau population, produced macroscopic buds during 18 days of 10.25-hour dark periods, but the remaining plants from LeBeau produced them subsequently in 2 to 4 days after the 10.25-hour series was changed to one of 10.5-hour dark periods. Only the two most southerly populations of *chinense* plants, Pecan Island and LaRose, uniformly showed no bud development until 10 days after the transfer to 10.5-hour dark periods. The populations from Frost and Lake Charles included some plants that gave a response typical of plants from LeBeau and others that gave a response typical of plants from LaRose and Pecan Island. All of the *chinense* plants were either 10.25- or 10.5-hour types. Australian plants that were removed from the out-of-doors planting in mid-August also reacted as the 10.5-hour plants did, showing no bud development during 18 days at 10.25 hours and none subsequently in 10.5-hour nights for 10 days.

Out-of-doors at Austin, Texas, 30 *chinense* plants representing the Australian and Indian populations (Table 1) and 40 transplants from Louisiana produced macroscopic flower buds in late August to early September. Although the Australian and Indian plants had been germinated under natural conditions in March, and a second series in June, they remained vegetative until the dark periods extended between 10.25 and 10.5 hours in late August, buds appearing almost synchronously from 29 August to 3 September. The Louisiana plants showed greater variation in time of flowering.

The similarity of plants from Australia, India, and Louisiana extended to chemical parameters (7). The sesquiterpene lactones were compared fo

Table 1. Photoperiod in populations of *Xanthium strumarium.*

Geographic position	Morphological complex	Critical night length (hours)	Date of bud appearance at Austin, Texas
	Borroloola, Northern Territory, Australia		
16°S 135°E	*chinense*	10.5	30 August–3 September
	Indooroopilly, Queensland, Australia		
28°S 153°E	*chinense*	10.5	29 August–2 September
	Wodonga, Victoria, Australia		
36°S 148°E	*chinense*	10.5	31 August–2 September
	Chandighar, India		
30°N 77°E	*chinense*	10.5	29 August–3 September
	Córdoba, Argentina		
33°S 66°W	*cavanillesii*	9.75	8 August–15 August*
	Salto, Uruguay		
31°S 57°W	*cavanillesii*	10.25	15 August–22 August
	Marfa, Texas		
30°N 104°W	*italicum*	9.75	8 August–19 August†
	Del Rio, Texas		
29°N 101°W	*italicum*	10.25	19 August–22 August
	Austin, Texas		
30°N 98°W	*italicum*	10.5	29 August–30 August

* Plants germinated after 22 June to replace those that initiated flower buds between 5 May and 21 May. † Plants germinated after 22 June to replace those that initiated flower buds between 5 May and 16 May.

plants from the three Australian populations, the Indian population, and two Louisiana populations (Johnson's Bayou, *italicum*; Pecan Island, *chinense*). Additional plants from Kentucky (*chinense*), Mexico (*italicum*), and Argentina (*cavanillesii*) were compared.

Nuclear magnetic resonance spectra of crude syrups from plants from Australia, India, and Pecan Island, Louisiana, were nearly identical, but no two other populations showed patterns that were as nearly identical. The uniformity of the sesquiterpene lactone content of *chinense* plants from Australia, India, and Louisiana was interpreted to indicate closer affinity of these plants to one another than to the *chinense* plants of Kentucky or to those of the other morphological complexes. Although the chemical affinity suggested that the Pecan Island population was similar to the Noogoora Burr and the monsoon form, the length of the Pecan Island bur prickles indicated that it probably was not the population providing the original seed.

The Noogoora Burr was introduced to Australia with cottonseed sent from India (*3*). The seed was reportedly American cotton, which suggests that the original introduction to India may have been with cottonseed from America. *Xanthium* was first reported in India by Roxburgh in 1812 from Patna according to Kaul (*5, 6*) and first reported from Australia near Brisbane in 1845 to 1860 (*3*). Because the original introduction to Australia was reportedly with seed of American cotton, Everist (*3*) doubted that the Australian pest was the same one that is a weed throughout India, as now seems certain.

Although other types of *Xanthium* have been introduced to Australia and India, the *chinense* complex appears to be the most widespread and most serious pest (*8*). The success of the Noogoora Burr in Australia and the monsoon form (*5, 6*) in India probably lies in its floral induction being delayed until near the end of a long vegetative period even though seeds germinated under inductive photoperiods. Everist (*9*) indicates that the Noogoora Burr at Indooroopilly, near Brisbane, does not begin to flower until February or later although it may germinate anytime between October and February (this pattern is similar to that demonstrated for Indooroopilly plants in the Northern Hemisphere for the comparable period, April to August). Kaul (*5*) reports that the monsoon form at Varanasi, India, germinates in late June or early July and flowers in August. Similar response was demonstrated at Austin, Texas, for plants germinated in June. The success of the *chinense* plants in Australia and in India probably resulted from attributes that were of selective advantage to plants from the Mississippi Delta.

If the southeastern United States was the source of the seed that has produced the Noogoora Burr of Australia and the "monsoon form" of India, as appears likely, a similar broad expansion of this type has not occurred in North America. Although the *chinense* complex occurs in the islands of the Caribbean (*1*), it is absent from most of Texas and Mexico at latitudes comparable to those of India and Australia.

The question of whether *Xanthium* is introduced or native to America has been raised (*1*), but the broad range of photoperiod types showing correlation with latitude and local habitat suggests long-term adaptation to conditions in the Americas. Undoubtedly the burs have been moved about considerably, but the ultimate survival of a population in a given site involves adaptive values that would eliminate many types of exotic *Xanthium*. For example, material from Chicago, Illinois, and from Pullman, Washington, flower in central Texas in April, soon after germination since they are continuously under inductive photoperiods at that latitude. The resultant plants produce one or two burs by late May and are at a selective disadvantage when compared with the local Texas population that may germinate as early as February and flower in late August. At lower latitudes, selective premiums are probably placed upon a population germinating as early as possible, remaining vegetative until near the end of the long growing season, and yielding maximum bur production prior to cold or drought conditions. A population from the cotton-growing areas along the Mississippi Delta in the early 1800's probably had these attributes necessary for the successful invasion of diverse sites at lower latitudes in Australia and India when accidentally introduced with cottonseed. The multitude of variants in *Xanthium* that show adaptation to different latitudes and to different habitats in North America may have had and still possess attributes for explosive invasion when introduced to disturbed ecosystems in other parts of the world.

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References and Notes

1. The terminology follows that of D. Löve and P. Dansereau [*Can. J. Bot.* **37**, 173 (1959)] who regarded all races of *Xanthium* (except *X. spinosum* which was not included in the present study) as being within *X. strumarium*. As they indicated, morphological intermediates between the named types are common and the classification is, therefore, somewhat arbitrary. They recognized the following morphological "complexes:" *cavanillesii, chinense, echinatum, italicum, orientale, oviforme, pensylvanicum*, and *strumarium*. They regarded all of the complexes to be of American origin except *strumarium*, which they felt to be of Mediterranean-European origin. They point out that *X. pungens*, the name that has been used for Noogoora Burr in Australia, is synonymous with *X. chinense*. Similarity of different "complex" types in photoperiodic response was shown → P. M. Ray and W. E. Alexander [*Amer. J. Bot.* **53**, 806 (1966)].
2. *Xanthium strumarium* is commonly reported to be a short-day plant with a photoperiod requirement of 15.5 hours (8.5-hour critical night length), but these reports are usually based on physiological studies of one or a few strains from the vicinity of Chicago, Illinois, latitude 42°N. P. M. Ray and W. E. Alexander (*1*) documented a latitudinal shift in photoperiodic response from New York and Minnesota with apparent critical night length of 7.75 to 8.5 hours and from Georgia to Texas, 9.5 to 10.5 hours. C. McMillan [*Science* **165**, 292 (196 → *Amer. J. Bot.* **57**, 881 (1970)] has shown a latitudinal gradient in Texas from 9.5- to 10.75-hour critical nights and variation among Mexican populations from 9.0- to 10.75-hour critical nights.
3. S. L. Everist [*Queensland Nat.* **16**, 49 (1960)] reports that *Xanthium* (Noogoora Burr) was introduced to Australia at Noogoora Station near Brisbane, probably between 1845 and 1860. By 1879, 500 acres were infested. Everist reports that the Noogoora Burr replaced prickly pear (*Opuntia*) as the most serious weed pest in Queensland.
4. The growth chambers were programmed for 10 hours at 30°C during the period of higher light intensity (24,200 to 26,400 lu/m^2) allowing 2 hours for transition during the morning and 2 hours in the evening. All chambers received 12 hours of higher light intensity from a combination of fluorescent and incandescent lamps. Light period extensions were with incandescent lamps only.
5. V. Kaul, *Trop. Ecol.* **6**, 72 (1965).
6. Kaul (*5*) has studied *Xanthium* from diverse sites in India. His collections of a monsoon form resemble the Australia plants in leaf and bur morphology and in photoperiod. The monsoon form is the most common type of *Xanthium* in India. Kaul (unpublished data) reports that various collections of the monsoon form from diverse latitudes show the same photoperiod. The plants from Chandigarh in the present study are typical of the monsoon form.
7. The sesquiterpene lactones in the crude syrups were compared by nuclear magnetic resonance analysis using the techniques of T. Mabry, in *Phytochemical Phylogeny*, J. B. Harborne, Ed. (Academic Press, London, 1970).
8. N. Hannon (unpublished data) reports that three types of *Xanthium* are common in New South Wales but that the Noogoora Burr is the most widespread. S. L. Everist (unpublished data) reports that only Noogoora Burr occurs in Queensland and that it is a widespread and abundant weed.
9. S. L. Everist, unpublished data.
10. I thank R. Parsons, S. L. Everist, and N. Byrnes (Australia), P. S. Ramakrishnan (India), W. S. Birkhead (South America), V. Bryant (Washington), J. E. Winstead (Kentucky), and T. Gillespie (Illinois) for seed collections. S. Graw prepared the leaf extracts for nuclear magnetic resonance spectra analysis by E. Szatkowski and E. Rodriguez. I thank T. Mabry for the use of the nuclear magnetic resonance equipment. I appreciated the assistance of R. Fontenot and J. and K. McMillan in the collection of Louisiana material. J. N. Thompson, director of the Balcones Research Center, provided maintenance of facilities for photoperiod study. M. C. Johnston has given valuable comments on the manuscript.

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