

## THE BIOLOGY OF CANADIAN WEEDS. 56. *Xanthium strumarium* L.

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*Xanthium strumarium* L. is an annual weed found in all provinces of Canada except Newfoundland, and throughout the temperate and subtropical regions of the world. It occurs in ruderal habitats, waste places, agricultural fields, and along watercourses, beaches and coastal dunes. Throughout its range, populations vary widely in fruit size and morphology and in photoperiodic requirements. It has been used extensively as an experimental plant in studies of floral induction, leaf development, stomatal control, seed germination, and biological control.

Key words: Cocklebur, reproductive biology, weed, *Xanthium*

[La biologie des mauvaises herbes du Canada. 56 *Xanthium strumarium*]

Titre abrégé: *Xanthium strumarium*

*Xanthium strumarium* L. est une mauvaise herbe annuelle qui se retrouve dans toutes les provinces du Canada, sauf à Terre-Neuve, ainsi que dans toutes les régions tempérées et subtropicales du monde. Elle préfère les habitats rudéraux, les dépotoirs, les champs cultivés mais se retrouve aussi le long des cours d'eau, sur les plages et les dunes côtières. La taille et la morphologie du fruit ainsi que les exigences photopériodiques de cette plante varient largement selon sa distribution. Elle a fait l'objet de nombreuses expériences sur l'anthogénèse, le développement des feuilles, le mode de fonctionnement des stomates, la germination et la lutte biologique.

Mots clés: Lampourde, biologie de la reproduction, mauvaise herbe, *Xanthium*.

### 1. Name

*Xanthium strumarium* L. — **cocklebur** (Alex et al. 1980), **clotbur**, **ditchbur**, **sheepbur**, **noogoora bur** (Holm et al. 1977); **lampourde glouteron** (Alex et al. 1980). Compositae, composite family, Composées.

### 2. Description and Account of Variation

(a) Annual herb 20–150 cm tall with a tap root, spreading by seeds only (Fig. 1); stems erect, ridged, rough-hairy, usually branched, spotted with purple; cotyledons 6.0–7.5 mm long, narrow (Figs. 1b, 2a), often persisting on older plants; leaves simple, sometimes opposite at lowest node but alternate above, triangular-ovate to

broadly ovate with three prominent veins, margins toothed or lobed, both surfaces rough-pubescent; petioles nearly as long as blades; flowers small, green, unisexual; staminate and pistillate heads in separate clusters in axils of leaves and at ends of branches and main stem (Fig. 2b); staminate heads in short spikes or racemes, many-flowered with separate phyllaries and cylindrical receptacle; pistillate heads below staminate heads on axis, hairy, with two pistillate flowers enclosed within a spiny involucre; fruit (Fig. 2c) a hard, woody bur, 1–2 cm long, ovoid-globose, covered with spines, glandular-pubescent, ending in two stout, incurved beaks, brown at maturity, containing two achenes; ach-

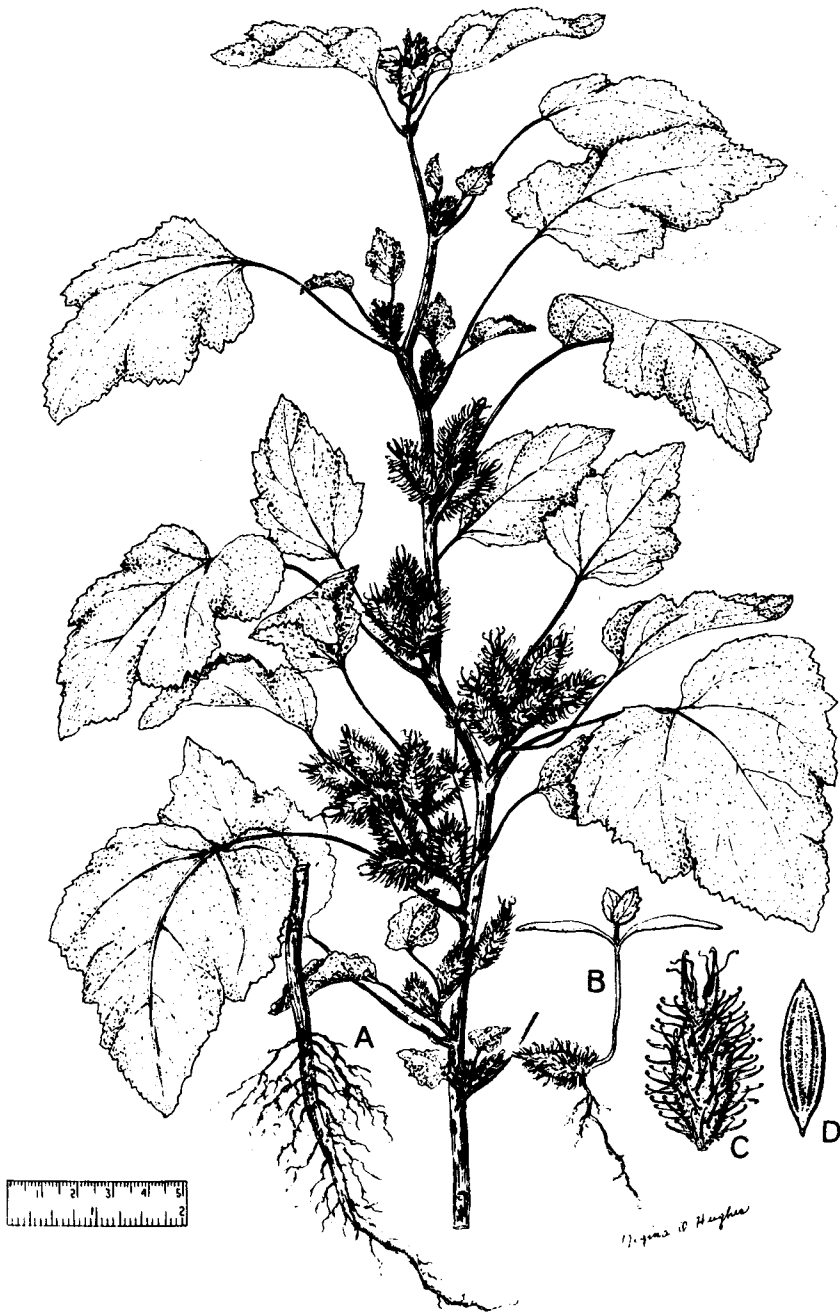


Fig. 1. *Xanthium strumarium* L. A, Habit ( $\times 0.5$ ); B, seedling ( $\times 0.5$ ); C, bur ( $\times 1.25$ ); D, seed ( $\times 1.5$ ). Source: Reed and Hughes (1970), originally captioned *X. pensylvanicum*.

enes oblong, flattened, 0.4–2.2 mm long, one often larger than the other, gray to dark brown.

There is extensive variation, both within and between *Xanthium* populations, in fruit size, pubescence, the number and length of spines, and the degree to which the beaks and spines are hooked (Löve and Dansereau 1959; Nadeau 1961; Hicks 1971). More than 20 *Xanthium* species have been recognized in North America primarily on the basis of these differences in bur morphology (Millsbaugh and Sherff 1919; Hicks 1971). The revised classification of *Xanthium* taxa by Löve and Dansereau (1959) is now widely accepted but remains provisional. Löve and Dansereau (1959) reduced the number of *Xanthium* species to two: *X. strumarium* L., an extremely variable species in the section *Xanthium* (= *Euxanthium* DC.) and *X. spinosum* L., a more homogeneous species in the section *Acanthoxanthium* DC. They recognized two subspecies within *X. strumarium*, *strumarium* and *cavanillesii* (Schouw) D. Löve and P. Dansereau, which are geographically separate and morphologically distinct. The center of distribution of the former subspecies is Mediterranean-Eurasian, while that of the latter is American. Löve and Dansereau (1959) also described several infraspecific taxa within *X. strumarium*, as well as seven complexes based on geographical distribution and bur morphology: *strumarium*, *cavanillesii*, *oviforme*, *echinatum*, *chinense*, *pensylvanicum-italicum* and *orientale*. They suggested that the latter six complexes are all derived from subspecies *cavanillesii*, and are thus native to America although reintroductions between the Old and the New World have undoubtedly occurred. Nadeau (1961) on the basis of further studies is in general agreement with this taxonomic treatment. The *strumarium* and *cavanillesii* complexes are widespread and extend to three continents, whereas the others are more regional. All the complexes except *cavan-*

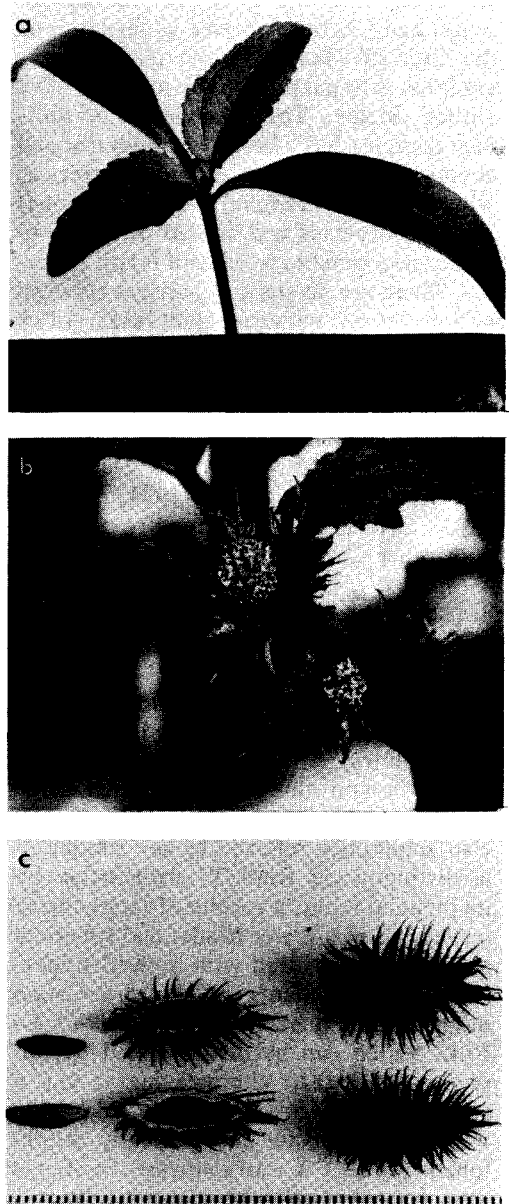


Fig. 2. (a) Three-week-old seedling; (b) male and female inflorescence; and (c) fruit and seed of *X. strumarium*.

*illesii* and *oviforme* have been reported in Canada, with the greatest diversity in the east (Löve and Dansereau 1959). The *ca-*

*vanillesii* complex is found throughout South and Central America as far north as the Gulf of Mexico, while the *oviforme* complex is found principally in the western United States. The *pensylvanicum-italicum* complex has a broad geographical and ecological distribution in North America, whereas the *echinatum*, *chinese* and *orientale* complexes are limited primarily to shores and beaches in eastern North America. There are no sterility barriers between subspecies or between complexes (Löve and Dansereau 1959; Hicks 1971; McMillan 1974, 1975a). All *Xanthium* taxa examined to date are tetraploid with a chromosome number of  $2n = 36$  (Darlington and Wylie 1955; Löve and Dansereau 1959; Nadeau 1961; Hicks 1971).

(b) *X. strumarium* is not readily confused with other Canadian plants when mature. *X. spinosum* is similar in appearance but has stout, three-pronged spines at the stem nodes and in the leaf axils. *X. spinosum* is not common in Canada, although it has an almost worldwide distribution (Holm et al. 1977). It is primarily a weed of pastures or meadows, whereas *X. strumarium* is most common along shores and in cultivated areas. *Arctium minus* (Hill) Bernh., also sometimes referred to as "clotbur," is distinguished from *X. strumarium* by its biennial habit, a rosette of large coarse leaves, purple flower heads, and spherical burs densely covered with hooked spines. Nonflowering plants of *X. strumarium* might also be mistaken for *Iva xanthifolia* Nutt., which can be distinguished by opposite rather than alternate leaves and a smooth stem, or *Ambrosia trifida* L., which has opposite and generally deeply lobed leaves. *X. strumarium* seedlings may be confused with those of *Datura stramonium* L. which have similar long, narrow cotyledons and broad, oval leaves. However *D. stramonium* seedlings may be distinguished by their strong, sour odor and smooth, hairless stems and leaves. The bur, or remnant of a bur, which usually clings to the root of *X. strumarium* seed-

lings is also a distinguishing feature.

(c) In addition to variation in bur size and morphology, populations of *X. strumarium* show considerable variation in the photoperiodic requirement for floral induction (Ray and Alexander 1966; McMillan 1975a). *X. strumarium* is a short-day plant, and in North America the critical night length increases with decreasing latitude from about 7.5 h in northern populations to above 10 h in the south. Plants from higher latitudes in the United States also have higher levels of chlorophyll, due to a greater number of chloroplasts with more total membrane surface area, than plants from lower latitudes (Abdulrahman and Winstead 1977). In India, critical night lengths range between 8 and 11 h, but day neutral forms also occur (Kaul 1965a, 1971). Kaul (1971) found critical night lengths to be specific to the different seasonal forms of *X. strumarium* in India irrespective of latitude of origin. Although Moran and Marshall (1978) noted a high degree of allozyme uniformity over 13 enzymic loci within Australian populations of *Xanthium*, they did distinguish genetic differences between the *chinense*, *cavanillesii*, *pensylvanicum*, and *italicum* races. These genetic differences between complexes were reflected in their distinct morpho-physiological characteristics when plants were grown in a common garden (McMillan 1975b).

### 3. Economic Importance

(a) *Detrimental* — *X. strumarium* is a major weed of soybeans and cotton in the United States (Cooley and Smith 1973; Barrentine 1974). It has recently become a troublesome weed in soybean fields in parts of southern Ontario. Worldwide, it is a minor weed of 11 crops in 28 countries (Holm et al. 1977). Infestations of *X. strumarium* in soybeans can cause severe (60–75%) losses due to a decreased yield, increased moisture content of the beans at harvest, and the presence of foreign material (Anderson and McWhorter 1976).

*X. strumarium* is often found around barnyards and at the edge of farm ponds and can be a particular nuisance in livestock production (Holm et al. 1977). The burs become entangled in the manes and tails of farm animals and contaminate the wool of sheep, decreasing its value (Hasan 1974; Wapshere 1974). The seed and young seedling contain carboxyatractyloside, located in the cotyledons, which is poisonous to livestock (Kingsbury 1964; Holm et al. 1977). The toxicity diminishes rapidly after germination and the disappearance of carboxyatractyloside is associated with metabolic activity in the cotyledons (Cole et al. 1980). Adult plants are not readily eaten by animals due to their rough texture but their actual nutritional value compares favorably to that of oats (Marten and Anderson 1975; Holm et al. 1977).

The *Xanthium* genus is closely related to the *Ambrosia* (ragweed) genus, both being in the tribe Ambrosieae, and *X. strumarium* produces a large amount of pollen which is highly antigenic (Reddi et al. 1980). The glandular hairs on the leaves and stem secrete a substance which causes contact dermatitis in allergic individuals (King 1966).

(b) *Beneficial* — Fruits of *X. strumarium* were once a source of medicinal drugs in Europe and are at present in India (Kaul 1965a). The genus name is derived from the Greek root "*Xanthos*" which means "yellow," and the plant may have been used to produce a dye (Hicks 1971).

(c) *Legislation* — *X. strumarium* is listed as a noxious weed in the Provincial Weeds Act of Manitoba only (Anonymous 1973).

#### 4. Geographical Distribution

*X. strumarium* is found in all provinces of Canada except Newfoundland (Fig. 3). It is widespread throughout the United States (Reed and Hughes 1970), Europe and Asia, and occurs in parts of South America and Africa, Australia and the Pacific Islands (Holm et al. 1977).

#### 5. Habitat

(a) *Climatic requirements* — The distribution of *X. strumarium* extends from latitude 53°N to 33°S (Holm et al. 1977). It is found most often in the temperate zone but also in subtropical and mediterranean climates (Holm et al. 1977). It is not common in mountainous regions (Löve and Dansereau 1959). Kaul (1967) reviews the traits of *Xanthium* that contribute to its widespread geographic and environmental distribution. The latitudinal and altitudinal limits of its distribution are determined by the interaction between climate and photoperiod (Ray and Alexander 1966). Fruit production increases with plant size (Kaul 1965c) and even very young plants will flower and set seed under an inductive (short-day) photoperiod (Ray and Alexander 1966; Salisbury 1969). Therefore, late germination and a long critical night length prevent precocious flowering and inadequate seed production. High temperatures (35°C or greater), particularly during the dark period, inhibit floral induction (Leonard et al. 1981). On the other hand, in the northern part of its range, low autumnal temperatures and early frosts select for early germination and a short critical night length so that there will be sufficient time between flower formation and fruit maturation. In addition, low temperatures, particularly at night, retard flower and fruit development and increase the perceived critical night length (Ray and Alexander 1966). These conflicting selection pressures result in nearly synchronous germination and flowering at the northern end of its range (Löve and Dansereau 1959).

(b) *Substratum* — *X. strumarium* is tolerant of a variety of soil conditions ranging from moist clay to dry sand, but prefers compact sandy soil, slightly moist below the surface, with a small amount of organic matter (Löve and Dansereau 1959; Kaul 1965c). However, ruderal populations in southern Ontario are more common on fine-textured clays and clay-loams than on coarser soils (Alex and Switzer 1976). In



Fig. 3. Canadian distribution of *Xanthium strumarium* from specimens in the following herbaria: UBC; ALTA; SASK; WN; HAM; CAN; DAO; UNB; DAL; ACAD (herbaria abbreviations as in Holmgren et al. 1981).

India, *X. strumarium* will germinate and grow at a range of soil pH from 5.2 to 8.0 and tolerates frequent flooding and saline conditions (Kaul 1961, 1965c). Rooting depth in *X. strumarium* increases with the depth of the water table (Kaul 1968); on a well-drained silty clay loam Davis et al. (1965) report roots extending laterally 2.1 m and down to 1.2 m. Plants achieve good growth with water tables ranging from 5 cm above to 90 cm below the soil surface (Kaul 1961, 1968). Plants tolerate flooding at all stages of growth. Roots of plants grown under anaerobic conditions develop larger air spaces in the cortex and are less suberized than roots of plants grown under aerobic conditions (Kaul 1961, 1968).

(c) *Communities in which the species occur* — *X. strumarium* occurs in waste places, along roadsides, railway embankments, watercourses, beaches and coastal

dunes, field edges and within cultivated fields. It prefers open communities and will disappear if shaded or crowded (Löve and Dansereau 1959; Kaul 1971). It will not flower or fruit in full shade (Kaul 1971). In ruderal and agricultural habitats, *X. strumarium* is found in association with annual, biennial or short-lived perennial weeds; along beaches and flood plains its associates are beach and dune species (Löve and Dansereau 1959; Nadeau 1961; Hicks 1971). Löve and Dansereau (1959) and Nadeau (1961) have described in detail the range of beach communities within which *X. strumarium* occurs in eastern North America.

## 6. History

Löve and Dansereau (1959) identify the center of origin of *Xanthium* as Central or South America, from which many of the

complexes have spread northward. The native North American *Xanthium* taxa originally grew primarily along shores and rivers and the fruits were dispersed by water or occasionally by animals (Löve and Dansereau 1959). The activities of man created both newly disturbed habitats and new modes of dispersal and enabled previously isolated populations to interbreed. Moreover, Eurasian races appear to have been inadvertently introduced (Löve and Dansereau 1959), such as with Manchurian soybeans (Millsbaugh and Sherff 1919). Occasional crossing between groups followed by inbreeding and stabilization has led to strong differentiation of local populations as well as great variability over a wide geographic range (Löve and Dansereau 1959). In North America the greatest number of distinct *Xanthium* groups is found in the northeast, where Löve and Dansereau (1959) suggest a great deal of interbreeding and subsequent dispersal of new forms may have taken place. Löve and Dansereau (1959) attribute the lack of speciation and the absence of sterility barriers in *X. strumarium* to the fact that it is uniformly tetraploid.

In Canada, the earliest herbarium specimens of *X. strumarium* from CAN, DAO, and MTMG (herbaria abbreviations as in Holmgren et al. 1981) were collected in Quebec in 1821, in Ontario in 1862, in Manitoba in 1873, in Alberta in 1879, in Saskatchewan and British Columbia in 1906, and in Prince Edward Island in 1914. Löve and Dansereau (1959) refer to Canadian specimens of *X. strumarium* described by Linnaeus (1753) and Miller (1768). Specimens of *X. spinosum* were also collected in British Columbia, Ontario and New Brunswick in the late 1800s, but this species is now uncommon in Canada. The distribution of *X. strumarium* seems to be expanding in Ontario from the southwestern counties, where it is most common northeastward as the range in which soybeans are grown expands (Weaver, unpubl. data). The growth cycle of *X. strumarium*

can be completed in soybeans because it normally germinates at the same time that the crop is sown, soybeans do not provide excessive shading, and the harvest is late enough to permit the fruits to mature.

## 7. Growth and Development

(a) *Morphology* — The cotyledons of *X. strumarium* are large, fleshy, and photosynthetically active and enable the seedling to become established quickly (King 1966). Maksymowych (1973) provides a comprehensive summary of leaf development during the life of the plant. Short glandular hairs are scattered over the aerial parts of the plant, giving it a rough texture which makes it unpalatable to grazing animals (Hicks 1971; Marten and Anderson 1975). These glandular hairs exude a sticky substance responsible for the plant's distinctive odour (Hicks 1971). The hooked spines on the burs cling to animal fur, human clothing and other material and facilitate dispersal. Air bubbles also lodge between the spines and increase the buoyancy of the burs in water (Kaul 1961, 1965a).

(b) *Perennation* — *X. strumarium* is an annual and overwinters as seeds on or below the surface of the soil.

(c) *Physiological data* — *X. strumarium* has been used extensively in physiological studies of floral induction (Salisbury 1969; Gaunt and Plumpton 1980). It is a short-day plant and generally will not flower under photoperiods longer than 14 h (McMillan 1975a). Populations vary in critical night length with latitude of origin and some show a quantitative rather than qualitative short-day response (Ray and Alexander 1966). Leaves are most responsive to photoperiod at the stage of rapid elongation and cellular differentiation of the lamina (Maksymowych 1959, 1973). Flowering can ordinarily be induced by only one to three photoperiodic cycles early in the life cycle (Kaul 1971). Light flashes longer than 1 min during the dark period inhibit floral induction, but the plant generally does not respond to twilight

at either end of the dark period (Salisbury 1981). Plants subjected to continuous illumination can live as long as 18 mo, attaining great size and producing large numbers of seeds if put under an inductive photoperiod (Kaul 1971). The ratio of male to female flowers is influenced by the number of inductive cycles, with mostly staminate flowers formed after one to three cycles and the number of pistillate flowers, as well as the rate of flower maturation, increasing with increasing numbers of cycles (Leonard et al. 1981).

*X. strumarium* has the  $C_3$  photosynthetic pathway (Sharkey and Raschke 1981). The stomata respond primarily to light rather than changes in the intercellular concentration of  $CO_2$  (Sharkey and Raschke 1981) but the overall control of stomatal response is complex (Raschke 1976). Chloroplasts are present in every cell type from guard cells to transfer cells (Al-Dabbagh Khudairi 1977). Longstreth and Kramer (1980) found transpiration rates and leaf conductance values of *X. strumarium* to be greater than those of soybean (*Glycine max* L., also a  $C_3$  plant) at any given day after planting. Leaf water potential of *X. strumarium* varies diurnally and seasonally, but is not significantly affected by high density in pure stands or by competition with soybeans (Scott and Geddes 1979). Floral induction and flowering do not affect the rate of transpiration, leaf water potential, leaf conductance or photosynthetic response (Longstreth and Kramer 1980). Water use efficiency, the ratio of a plant's photosynthetic and transpiration rates, is positively correlated with seed production (Lechowicz unpubl. data).

Mineral nutrients, especially nitrogen, are also an important influence on reproduction in *Xanthium* (Neidle 1939; Salisbury 1969). *Xanthium* can assimilate both nitrate and ammonia nitrogen and can store nitrogen reserves as nitrate in its tissues (Wallace and Pate 1967). Just prior to flowering the total nitrogen concentration

of *Xanthium* plants was 1.54% in root tissues, 2.20% in stems, and 4.49% in leaves; of these totals 0.13% in roots, 0.26% in stems, and 0.13% in leaves were nitrate nitrogen (Campbell 1924). At maturity nitrate nitrogen was zero in all tissues and nitrogen concentrations were 0.69% in roots, 0.29% in stems, 1.96% in leaves, and 1.79% in fruits suggesting that nitrogen was preferentially reallocated to fruits. The seeds, with nitrogen concentrations of 6.6%, account for fully 95% of the nitrogen invested in fruits (Blais and Lechowicz unpubl. data). Neidle (1939) has shown that nitrogen availability can limit production of both male and female inflorescences.

(d) *Phenology* — Seed germination of *X. strumarium* generally takes place in the latter half of May in southern Ontario (Weaver unpubl. data), but may be delayed until early July along flood plains in the Champlain-St. Lawrence region of Quebec (Löve and Dansereau 1959). In Illinois, seedlings emerge abundantly from April through mid-May and in lesser numbers through June (Stoller and Wax 1973). Smaller flushes of germination may occur throughout the summer with adequate moisture. In experimental plantings on 26 May 1980 at 5 cm depth in St. Rosalie clay, seedling emergence ranged from 9 to 14 days with a mean of 10 days (Lechowicz unpubl. data). On average, the seedlings had formed their first true leaves by day 14 from planting. Flowering begins in early to mid-August, regardless of plant age or size, and fruits continue to mature until a killing frost occurs. The burs are dispersed during autumn and winter or occasionally remain on the dry branches until spring.

(e) *Mycorrhiza* — No information is available on the presence or absence of mycorrhiza on *X. strumarium*.

## 8. Reproduction

(a) *Floral biology* — The staminate heads of *X. strumarium* are located above the pistillate heads on the main axis and side

shoots, an arrangement favoring inbreeding. It is wind pollinated, self-compatible and predominantly self-pollinated (Löve and Dansereau 1959; Hicks 1971; Moran and Marshall 1978). Moran and Marshall (1978) found the outcrossing rate in natural populations to be less than 12% and possibly zero. Nadeau (1961) points out that in natural populations outcrossing can arise because of the interwoven branches of adjacent plants. There is no apomixis in *Xanthium*, although it was once suspected to occur (Symons 1926; Hicks 1975). In a Quebec experimental garden, individual plants produced from 611 to 1488 male inflorescences (Lechowicz unpubl. data). The 100–150 male florets in each staminate head shed their pollen in gradual, centripetal succession, beginning a few days before the stigmata are receptive (Hicks 1971). Pollen is discharged by filament enlargement, elongation and subsequent splitting of the anther sacs. The pollen grains are 22–38  $\mu\text{m}$  in diameter, non-adhesive, and slightly sculptured with weakly developed spines (Nadeau 1961; Hicks 1971). There have been no published reports of insect pollinators of *X. strumarium*, but insect visitors have frequently been observed in an experimental garden near Montreal (Lechowicz unpubl. data).

(b) *Seed production and dispersal* — Estimates of fruit production by a single, vigorous, open-grown plant of *X. strumarium* range from 500 in Illinois (Hicks 1971), to 2300 burs in India (Kaul 1965a) and as high as 5400 burs in a well-watered, nutrient-rich experimental garden in Quebec (Lechowicz unpubl. data). The number of fruits produced is entirely dependent upon the amount of vegetative growth at the time of floral initiation. Nadeau (1961) reports that natural populations in Vermont produced up to 24 fruits per secondary branch and up to 18 branches per plant. Plants sown in rows in the field in southwestern Ontario at 2-wk intervals from 15 May to 15 July flowered simultaneously in

mid-August, and produced an average of 400 burs per plant from the earliest planting and 80 burs per plant from the latest planting (Weaver unpubl. data). Mean reproductive effort was 40–50%, based on total bur weight as a proportion of total plant weight, regardless of planting date. The mean reproductive effort in a Quebec experimental garden was comparable and can be further partitioned since the seeds on average account for only 38% of bur weight (Lechowicz unpubl. data). Average fruit production in dense, pure stands has been estimated as 71–586 burs per plant or about 200–300 burs per square metre in India (Kaul 1965b). Total fruit production is negatively correlated with bur length, husk weight and seed weight, whereas bur length is positively correlated with seed weight (Hare 1980). Each fruit normally contains two seeds although rare cases of three or more seeds per fruit have been reported (Kaul 1965b; Hicks 1971).

Fruits of plants growing along rivers or beaches are easily dispersed by water because the burs are buoyant and will remain floating for up to 30 days (Kaul 1961, 1965a). The spiny burs are also dispersed by becoming entangled in animal hair or adhering to human clothing and other materials.

(c) *Viability of seeds and germination* — The two seeds within each bur usually differ in both size and germination requirements (Kaul 1965b; Hicks 1971). In a Quebec population the larger seed averaged 0.06 g compared to 0.05 g for the smaller (Lechowicz unpubl. data). The smaller seed is often pushed up in the locule toward the beaked end of the fruit and exhibits innate dormancy. The larger, “lower” seed normally germinates in the spring following production, whereas the “upper” seed does not germinate until later in the season or, more frequently, the following year. However, in some populations the seeds do not differ in position within the bur and as many as 73% of sown fruits may produce “twin” seedlings

(Hicks 1971). Two seedlings emerging from the same bur are often equal in size and vigour (Symons 1926). Seed viability in most populations is at least 80%, and usually greater, at the time of production (Kaul 1965b; Stoller and Wax 1973; Wapshere 1974).

The dormancy and germination requirements of seeds of *X. strumarium* have been studied extensively. Lower seeds often require overwintering or several months of afterripening for germination (Hicks 1971), although populations vary in germination requirements and freshly-harvested seeds may germinate under favorable conditions (Weaver unpubl. data). After 12–16 wk of dry storage, only the lower seeds will germinate at 21°C, whereas both seeds will germinate at 30°C (Kaul 1965b). Percentage and rate of germination are maximum at alternating temperatures of 30/20° or 33/25°C and at 1–8 cm below the soil surface. Light is not required for germination and seedlings seldom emerge from seeds lying on the soil surface or buried 15 cm or more below the soil surface (Kaul 1965b; Stoller and Wax 1973, 1974). Seeds of *X. strumarium* have a high moisture requirement for germination and show little germination in soils at less than 75% of field capacity, but are able to absorb moisture at high osmotic concentrations (Kaul 1968). Dormancy of the upper seed has been attributed to impermeability of the seed coat to oxygen (Davis 1930) and to the presence of germination inhibitors (Porter and Wareing 1974). Upper seeds can be induced to germinate by presoaking in water at 23°C in darkness for up to eight days (Esashi et al. 1976) or by the exogenous application of ethylene (Satoh and Esashi 1980). Germination of both upper and lower seeds is promoted by microbial decay, by pricking the testa, by acid scarification for 3–5 min, or by exposure to high temperature (50°C) for 10 days (Kaul 1965b). Secondary dormancy is induced in both upper and lower seeds by holding in water or water-logged

soil at low oxygen pressure and high temperature (30–35°C) for 50 days or more (Kaul 1965b). Subsequent chilling at 3–7°C will break secondary dormancy (Esashi and Tsukada 1978). Nondormant seeds exhibit an endogenous rhythm with germination flushes at 16-h periods (Satoh and Esashi 1978).

There is little information available on the longevity of seeds of *X. strumarium*. Viability of seeds from populations in India decreased markedly after 18 mo of storage, regardless of storage conditions (Kaul 1965b). The viability of buried seeds from populations in the southern United States decreased from 99% at harvest to 66% after 6 mo of burial and 18% after 30 mo of burial, regardless of depth of burial from 8–38 cm below the soil surface (Egley and Chandler 1978). However, seed viability remained 100% and germination increased from 61 to 92% after 30 mo of dry storage at 4°C. Stoller and Wax (1974) found that *Xanthium* fruits overwintered in the soil at depths from 2.5 to 15.2 cm showed germination between about 50% and 90% in laboratory tests. Wapshere (1974) found that seeds from plants of *X. strumarium* growing along the coast of Australia did not survive more than a few years when buried deeply in the soil, and that 98% of viable seeds were found in the top 5 cm of soil.

(d) *Vegetative reproduction* — *X. strumarium* is an annual and does not reproduce vegetatively.

## 9. Hybrids

All of the infraspecific taxa recognized by Löve and Dansereau (1959) and Nadeau (1961) within the extremely variable species *X. strumarium* interbreed readily with normal chromosome pairings and a chromosome number of  $2n = 36$  (Nadeau 1961; Hicks 1971; Ray and Alexander 1966). Hicks (1971) found over 90% of pollen grains to be viable in crosses between several complexes found in North America. McMillan (1973), however, re-

ported only partial fertility of progeny between Asiatic and American parents. Reciprocal  $F_1$  progenies between various complexes are intermediate between parental types in leaf and bur morphology, photoperiodic requirements, and chemical composition (Nadeau 1961; McMillan 1974; McMillan et al. 1976). The ease of producing new photoperiodic responses between introduced and indigenous types suggests that the species has great potential for colonizing new areas and expanding its range.

Efforts at hybridization between *X. strumarium* and *X. spinosum* have not been successful (McMillan 1975a,b). There are no reports in the botanical literature of other interspecific hybrids involving *X. strumarium*.

### 10. Population Dynamics

Two types of population of *X. strumarium* are found which may differ in their dynamics. Populations located along shores or watercourses tend to be small, ephemeral and homogeneous; populations in ruderal habitats, agricultural fields or waste areas tend to be large, dense and heterogeneous, with tall, vigorous plants producing an abundance of seed (Löve and Dansereau 1959; Nadeau 1961; Hicks 1971). In the first type dispersal is mainly by water, whereas in the second it is anthropogenic. Both types of population, however, occupy unstable habitats and are continually shifting to newly disturbed areas.

Under favorable conditions *X. strumarium* can quickly colonize new habitats due to its high germination rate and rapid growth (Kaul 1965c). In ruderal habitats in India, 70–80% of sown burs produced seedlings within 4–5 days of sowing and seedling morality was only 1%, resulting in pure stands with densities averaging 100 plants per square metre and an average seed production of 200–300 seeds per square metre (Kaul 1965b,c). Plants which have been stunted by lack of nutrients or

saline conditions will still produce some viable seeds.

Wapshere (1974) studied the effects of density on plant size in pure stands in Australia and found that basal stem diameter, the number of side shoots and the number of fruits per plant increased with increasing nearest-neighbour distances from 0.15 to 1.80 m. Plants more than 1.80 m apart were unaffected by intraspecific competition, and had 20 or more side shoots with approximately 100 fruits per shoot.

*X. strumarium* is an extremely competitive weed in crops such as soybeans and cotton (Cooley and Smith 1973; Barrentine 1974). Estimates of soybean yield reduction due to infestations of *X. strumarium*, sown at densities of 1–3 plants per square metre, range from 52 to 75% (McWhorter and Hartwig 1972; Barrentine 1974). Soybean yields in the southern United States increased 6% for each 10% reduction in dense natural stands of *X. strumarium* (Anderson and McWhorter 1976).

### 11. Response to Herbicides and Other Chemicals

*X. strumarium* is susceptible to a number of soil- and foliar-applied herbicides commonly used for the selective control of broad-leaved weeds in field crops (Anonymous 1981). Metribuzin applied preplant incorporated (0.3–0.5 kg/ha) or preemergence (0.4–1.1 kg/ha), bentazon applied postemergence (0.6–1.1 kg/ha) and acifluorfen applied postemergence (1.1 kg/ha) effectively control *X. strumarium* in soybeans (McWhorter and Anderson 1976a,b; Weaver 1980). Bentazon is more effective at high temperature (35°C) and relative humidity (96%) and with an adjuvant (Wills 1976). Atrazine (1.1 kg/ha), cyanazine (1.6–2.2 kg/ha) and dicamba (0.28–0.56 kg/ha) applied preemergence and 2,4-DB (1.1 kg/ha) applied postemergence provide good control of *X. strumarium* in corn (McGlamery and Slife 1976; McGlamery and Zajicek 1979). Repeated applications at slightly lower rates are often more ef-

fective than single applications of postemergence herbicides, particularly for plants taller than 25 cm (McWhorter and Anderson 1976a; Overton et al. 1979).

## 12. Response to Other Human Manipulations

Young plants of *X. strumarium* regenerate readily from the lower nodes if trampled, clipped or otherwise injured. Fruit on older plants or shoots which have been cut or damaged will continue to ripen provided fertilization has occurred prior to the injury (Kaul 1965c). Seeds from immature, green fruits with a moisture content of 52% showed 46% germination as compared to 80% germination for seeds from fully mature fruits with a moisture content of 8.5% (Kaul 1965c).

## 13. Responses to Parasites

(a) *Insects* — Hare and Futuyma (1978) studied factors which affect seed predation of *X. strumarium* by two insects found in North America: a moth, *Phaneta imbridana* Fernald (Lepidoptera: Tortricidae) and a trypetid fly, *Euaresta aequalis* (Loew) (Diptera: Tephritidae). The moth oviposits on the surface of the bur and the larvae bore through the bur wall to attack the seeds, whereas the fly oviposits through the bur wall directly onto one of the seeds. Seed damage in New York populations due to the moth varied from 0 to 28% and damage due to the fly from 0 to 42%, with combined damage varying from 4 to 89% over 3 yr (Hare and Futuyma 1978). The level of predation was greatly affected by between-population variation in bur size and shape, with the moth more sensitive to spine length and the fly more sensitive to bur length (Hare 1980). In general, seed predation was more common in populations with smaller burs because large burs have thicker walls and longer spines and are more difficult to penetrate (Hare 1980).

Two species of stem-boring cerambycid beetles (Coleoptera: Cerambycidae) were imported to Australia in an attempt at bi-

ological control of *X. strumarium* (Wapshere 1974). *Mecas saturnina* Le Conte is native to the southern United States and *Nupserha vexator* (Pasc) to India. Both beetles oviposit at the top of the stems and the larvae bore down through the pith and overwinter in the root. Neither insect adapted well to the Australian climate or gave sufficient control to prevent seeding except in very small plants. Large, branched plants will produce seeds on any shoot which has not been attacked. Multiple attacks result in larval mortality because only one larva can occupy the root (Wapshere 1974).

(b) *Fungi* — The rust *Puccinia xanthii* Schw. is an obligate parasite of species of *Xanthium* and *Ambrosia* and occurs throughout the United States, southern Canada and parts of Europe (Conners 1967; Hasan 1974). It attacks all aerial parts of the plant except the flowers. The telia cause deformation of the leaves, splitting of the petiole and stem epidermis, and finally leaf drop. Infected plants mature more rapidly than healthy plants and show decreased transpiration, dry weight, bur production, and percent germination (Hasan 1974). The spores overwinter on dead plant parts.

Conners (1967) also lists *Septoria xanthii* Desm. as occurring on *Xanthium* in Canada. The following fungi occur on *Xanthium* in the United States (Anonymous 1960): *Albugo tragopogonis* Pers. ex S.F. Gray, *Botrytis cinerea* Pers. ex Fr., *Cercospora xanthicola* Heald & Wolf, *Colletotrichum xanthii* Halst., *Diaporthe arctii* (Lasch) Nits., *Erysiphe cichoracearum* DC, *Mycosphaerella xanthicola* (Cke. & Harkn.) Lindau, *Phymatotrichum omnivorum* (Shear) Dug., *Plasmopara halstedii* (Farl.) Berl. & Det., *Puccinia canaliculata* (Schw.) Lagh. and *Rhodospora xanthii* Pk. A powdery mildew, *Erysiphe* sp., is conspicuously frequent on plants of the *chinense* complex in Texas (McMillan 1975b).

(c) *Nematodes* — The following are found on *X. strumarium* in the United States (Anonymous 1960): *Aphelenchoides ritzema-bosi* (Schmidt) Steiner & Bührer and *Meloidogyne* sp.

(d) *Higher plant parasites* — *Cuscuta* sp. have been found on *X. strumarium* in Texas (Anonymous 1960).

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ABDULRAHMAN, F. S. and WINSTEAD, J. E. 1977. Chlorophyll levels and leaf ultrastructure as ecotypic characters in *Xanthium strumarium* L. *Am. J. Bot.* **64**: 1177–1181.

AL-DABBAGH KHUDAIRI, S. Y. 1977. Ultrastructure of *Xanthium* leaf: Chloroplast variation in different cell types. *Bull. Biol. Res. Cent.* **9**: 3–15.

ALEX, J. F. and SWITZER, C. M. 1976. Ontario weeds. *Ont. Min. of Agric. and Food Publ.* 505. Ottawa, Ont. 200 pp.

ALEX, J. F., CAYOUILLE, R. and MULLIGAN, G. A. 1980. Common and botanical names of weeds in Canada. *Agric. Canada Res. Br. Publ.* 1397. Ottawa, Ont. 132 pp.

ANDERSON, J. M. and McWHORTER, C. G. 1976. The economics of common cocklebur control in soybean production. *Weed Sci.* **24**: 397–400.

ANONYMOUS. 1960. Index of plant diseases of the United States. *U.S. Agric. Handbk.* 165. 531 pp.

ANONYMOUS. 1973. The Noxious Weeds Act. Regulation N110-R1. Queen's Printer. Province of Manitoba, Winnipeg, Man.

ANONYMOUS. 1981. Guide to chemical weed control. *Ont. Min. of Agric. and Food Publ.* 75. Ottawa, Ont. 103 pp.

BARRENTINE, W. L. 1974. Common cocklebur competition in soybeans. *Weed Sci.* **22**: 600–603.

CAMPBELL, E. G. 1924. Nitrogen content of weeds *Bot. Gaz.* **79**: 103–115.

COLE, R. J., STUART, B. P., LANSDEN, J. A. and COX, R. H. 1980. Isolation and redefinition of the toxic agent from cocklebur (*Xanthium strumarium*). *J. Agric. Food Chem.* **28**: 1330–1332.

CONNERS, I. L. 1967. An annotated index of plant diseases in Canada. *Agric. Canada Res. Br. Publ.* 1251. Ottawa, Ont. 381 pp.

COOLEY, A. W. and SMITH, D. T. 1973. Germination and emergence of buffalobur, morning glory and cocklebur. *Texas Agric. Exp. Station, PR* 3197–3209: pp. 11–14

DARLINGTON, C. D. and WYLIE, A. P. 1955. Chromosome atlas of flowering plants. George Allan and Unwin, London. 519 pp.

DAVIS, R. G., WIESE, A. F. and PAFFORD, J. L. 1965. Root moisture extraction profiles of various weeds. *Weeds* **13** 98–100.

DAVIS, W. 1930. The development of dormancy in seeds of cocklebur (*Xanthium*). *Am. J. Bot.* **17**: 77–87.

EGLEY, G. H. and CHANDLER, J. M. 1978. Germination and viability of weed seeds after 2.5 years in a 50 year buried seed study. *Weed Sci.* **26**: 230–239.

ESASHI, Y., KOTAKI, K. and OHHARA, Y. 1976. Induction of cocklebur seed germination by anaerobiosis: A question about the "inhibitor hypothesis" of seed dormancy. *Planta* **129**: 109–112.

ESASHI, Y. and TSUKADA, Y. 1978. Thermoperiodism in cocklebur seed germination. *Plant Physiol.* **61**: 437–441.

GAUNT, J. K. and PLUMPTON, E. S. 1980. Photoperiodic control *in vivo* and *in vitro* of tocopherol oxidase in *Xanthium strumarium* L. *Biochem. soc. Trans.* **8**: 187–188.

HARE, J. D. and FUTUYMA, D. J. 1978. Different effects of variation of *Xanthium strumarium* L. (Compositae) on two insect seed predators. *Oecologia* **37**: 109–120.

HARE, J. D. 1980. Variation in fruit size and susceptibility to seed predation among and within populations of the cocklebur, *Xanthium strumarium* L. *Oecologia* **46**: 217–222.

HASAN, S. 1974. *Xanthium* rust as a possible biological control agent of Bathurst and noogoora burrs in Australia. *Proc. 3rd. Int. Symp. Biol. Control Weeds, Commonwealth. Inst. Biol. Control Misc. Publ.* **8**: 137–140.

HICKS, A. J. 1971. Systematic studies of *Xanthium* (Compositae: Ambrosiaceae); the cockleburs of Tazewell County, Illinois. Unpubl. Ph.D. thesis, University of Illinois, Champaign-Urbana, Ill. 60 pp.

HICKS, A. J. 1975. Apomixis in *Xanthium*. *Watsonia* **10**: 414–415.

HOLM, L. G., PLUNKNETT, D. L., PANCHO, J. V. and HERBERGER, J. P. 1977. The

- world's worst weeds. East-West Center Book. Univ. Press of Hawaii, Honolulu, Hawaii. 609 pp.
- HOLMGREN, P. K., KEVLEEN, W. and SCHOFIELD, E. K. 1981. Index herbariorum. Part I. The herbaria of the world. 7th ed. Regnum végétabile 106.
- KAUL, V. 1961. Water relations of *Xanthium strumarium* L. Sci. Cult. 27: 495-497.
- KAUL, V. 1965a. Physiological-ecology of *Xanthium strumarium* L. I. Seasonal morphological variants and distribution. Trop. Ecol. 6: 72-87.
- KAUL, V. 1965b. Physiological-ecology of *Xanthium strumarium* L. II. Physiology of seeds in relation to its distribution. J. Indian Bot. Soc. 44: 365-380.
- KAUL, V. 1965c. Physiological-ecology of *Xanthium strumarium* L. III. Effect of edaphic and biotic factors on growth and distribution. Proc. Nat. Acad. India 35: 203-216.
- KAUL, V. 1967. Physiological-ecology of *Xanthium strumarium* L. VI. Plasticity and distribution. J. Indian Bot. Soc. 46: 389-396.
- KAUL, V. 1968. Physiological-ecology of *Xanthium strumarium* L. V. Water relations. Trop. Ecol. 9: 88-102.
- KAUL, V. 1971. Physiological-ecology of *Xanthium strumarium* L. IV. Effect of climatic factors on growth and distribution. New Phytol. 70: 799-812.
- KING, L. J. 1966. Weeds of the world. Biology and control. Interscience Publ., New York. 526 pp.
- KINGSBURY, J. 1964. Poisonous plants of the United States and Canada. Prentice-Hall, Englewood Cliffs, New Jersey. 626 pp.
- LEONARD, M., KINET, J. M., BODSON, M., HAVELANGE, A., JACQARD, A. and BERNIER, G. 1981. Flowering in *Xanthium strumarium*. Initiation and development of female inflorescence and sex expression. Plant Physiol. 67: 1245-1249.
- LONGSTRETH, D. J. and KRAMER, P. J. 1980. Water relations during flower induction and anthesis. Bot. Gaz. 141: 69-72.
- LÖVE, D. and DANSEREAU, P. 1959. Biosystematic studies on *Xanthium*: Taxonomic appraisal and ecological status. Can. J. Bot. 37: 173-208.
- MAKSYMOWYCH, R. 1959. Quantitative analysis of leaf development in *Xanthium pennsylvanicum*. Am. J. Bot. 46: 635-644.
- MAKSMOWYCH, R. 1973. Analysis of leaf development. Cambridge University Press, Cambridge, U.K.
- MARTEN, G. C. and ANDERSON, R. N. 1975. Forage nutritive value and palatability of 12 common annual weeds. Crop Sci. 15: 821-827.
- McGLAMERY, M. D. and SLIFE, F. W. 1976. Corn herbicide performance at Urbana, Illinois in 1976. North Central Weed Control Conf.: 182 (Abstr.).
- McGLAMERY, M. D. and ZAJICEK, F. E. 1979. 1979 corn herbicide study at Brownstown, Illinois. North Central Weed Control Conf.: 185 (Abstr.).
- McMILLAN, C. 1973. Partial fertility of artificial hybrids between Asiatic and American cocklebur (*Xanthium strumarium* L.). Nature, Lond. 246: 151-153.
- McMILLAN, C. 1974. Experimental hybridization in *Xanthium strumarium* of American complexes with diverse photoperiodic adaptation. Can. J. Bot. 52: 849-859.
- McMILLAN, C. 1975a. Experimental hybridization of *Xanthium strumarium* (Compositae) from Asia and America. I. Responses of F<sub>1</sub> hybrids to photoperiod and temperature. Am. J. Bot. 62: 41-47.
- McMILLAN, C. 1975b. The *Xanthium strumarium* complexes in Australia. Aust. J. Bot. 23: 173-192.
- McMILLAN, C., MABRY, T. J. and CHAVEZ, P. I. 1976. Experimental hybridization of *Xanthium strumarium* (Compositae) from Asia and America. II. Sesquiterpene lactones of F<sub>1</sub> hybrids. Am. J. Bot. 63: 317-323.
- McWHORTER, C. G. and ANDERSON, J. M. 1976a. Effectiveness of metribuzin applied preemergence for economical control of common cocklebur in soybeans. Weed Sci. 24: 385-390.
- McWHORTER, C. G. and ANDERSON, J. M. 1976b. Bentazon applied postemergence for economical control of common cocklebur in soybeans. Weed Sci. 24: 391-396.
- McWHORTER, C. G. and HARTWIG, E. E. 1972. Competition of johnsongrass and cocklebur with six soybean varieties. Weed Sci. 20: 56-59.
- MILLSAUGH, C. F. and SHERFF, E. E. 1919. Revision of the North American species of *Xanthium*. Field Mus. Nat. Hist. Publ. Bot. Ser. 4: 9-49.
- MORAN, G. F. and MARSHALL, D. R. 1978. Allozyme uniformity within and variation be-

- tween races of the colonizing species *Xanthium strumarium* L. (noogoora burr). Aust. J. Biol. Sci. **31**: 283–291.
- NADEAU, L. H. 1961. Etude biosystematique sur le genre *Xanthium*. Unpubl. Ph.D. thesis, Université de Montréal, Québec.
- NEIDLE, E. K. 1939. Nitrogen nutrition in relation to photoperiodism in *Xanthium pensylvanicum*. Bot. Gaz. **100**: 607–618.
- OVERTON, J. R., HAYES, R. M., JEFFREY, L. S. and McCUTCHEM, T. C. 1979. Cocklebur control in soybeans with acifluorfen, bentazon and naptalam. Proc. South Weed Sci. Soc. **32**: 119.
- PORTER, N. G. and WAREING, P. F. 1974. The role of the oxygen permeability of the seed coat in the dormancy of seed in *Xanthium pensylvanicum* Wallr. J. Exp. Bot. **25**: 583–594.
- RASCHKE, K. R. 1976. How stomata resolve the dilemma of opposing priorities. Philos. Trans. R. Soc. Lond. **B273**: 551–560.
- RAY, P. M. and ALEXANDER, W. E. 1966. Photoperiodic adaptation to latitude in *Xanthium strumarium*. Am. J. Bot. **53**: 806–816.
- REED, C. F. and HUGHES, R. 1970. Selected weeds of the United States. U.S. Dep. Agric. Handbk. 366. 463 pp.
- REDDI, C. S., REDDI, E. U. B., BAI, A. J., RAJU, K. V. R. and REDDI, M. S. 1980. The ecology of anther dehiscence, pollen liberation and dispersal in *Xanthium strumarium* L. Indian J. Ecol. **7**: 171–181.
- SALISBURY, F. B. 1969. *Xanthium strumarium* L. Pages 14–61. in L. Evans, ed. The induction of flowering: some case histories. MacMillan, Melbourne. 488 pp.
- SALISBURY, F. B. 1981. Twilight effect: Initiating dark measurement in photoperiodism of *Xanthium*. Plant Physiol. **67**: 1230–1238.
- SATOH, S. and ESASHI, Y. 1978. Rhythmic behavior in germination of cocklebur seeds. Physiol. Plant **43**: 271–273.
- SATOH, S. and ESASHI, Y. 1980. D-Amino acid-stimulated ethylene production in seed tissues. Planta **149**: 64–68.
- SCOTT, H. D. and GEDDES, R. D. 1979. Plant water stress of soybean (*Glycine max*) and common cocklebur (*Xanthium pensylvanicum*): A comparison under field conditions. Weed Sci. **27**: 285–289.
- SHARKEY, T. D. and RASCHKE, K. 1981. Separation and measurement of direct and indirect effects of light on stomata. Plant Physiol. **68**: 33–40.
- STOLLER, E. W. and WAX, L. M. 1973. Periodicity of germination and emergence of some annual weeds. Weed Sci. **21**: 574–580.
- STOLLER, E. W. and WAX, L. M. 1974. Dormancy changes and fate of some annual weed seeds in the soil. Weed Sci. **22**: 151–155.
- SYMONS, J. L. 1926. Studies in the genus *Xanthium*. Bot. Gaz. **2**: 121–147.
- WALLACE, W. and PATE, J. S. 1967. Nitrate assimilation in higher plants with special reference to the cocklebur (*Xanthium pensylvanicum* Wallr.) Bot. Gaz. **31**: 213–228.
- WAPSHERE, A. J. 1974. An ecological study of an attempt at biological control of noogoora burr (*Xanthium strumarium*). Aust. J. Agric. Res. **25**: 275–292.
- WEAVER, S. 1980. Cocklebur control with metribuzin and bentazon. Res. Rep., Expert Committee on Weeds (East. Sect.), (Abstr.). 388.
- WILLS, G. D. 1976. Translocation of bentazon in soybeans and common cocklebur. Weed Sci. **24**: 536–540.