BIOLOGY AND CONTROL OF COMMON MILKWEED (Asclepias syriaca)¹

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INTRODUCTION

From the earliest days, common milkweed's fragrant flowers, milky latex, and stringy roots attracted much attention (61). Common milkweed (Asclepias syriaca L. #3 ASCSY) is also known as cotton weed, silkweed, wild cotton, and asclepiade de Syrie (57). The milkweed family was named for the Greek God 'Asclepias'—the God of Medicine.

Common milkweed is a persistent, perennial broadleaf weed. This species has been of interest to agriculturists for many years because of its potential economic value as a new crop (7, 8, 74, 81) and its negative effects as a weed (21, 43, 76). Common milkweed and its related species are serious economic weed problems in crops in north-central states in the United States (75) and southern parts of Ontario and Quebec in Canada (21).

Various reports have been published on the biology (21, 81), physiology (36), floss characteristics (89, 119), utilization (61, 98, 119), and rubber-bearing potential of milkweed (82, 83, 84).

In 1943, Whiting (119) reviewed many uses of common milkweed including the use of floss as a substitute for kapok [silky fiber covering the seeds of the kapok tree (*Ceiba pentandra* L.)], the latex as a commercial rubber, and the seeds as a source of oil and meal. The potential for commercial use of common milkweed has been studied in France, Germany, the U.S.S.R., the United States, and Canada (98).

Common milkweed bast fiber can be used as a textile material and its stems as a raw material in the paper industry (74). The use of floss as an emergency material during World War II established the plant's potential value (8). Since then, the floss has repeatedly undergone scrutiny as a possible source of bast fiber. Recently, common milkweed's potential was reevaluated as a commercial fiber fill material in Canada (7).

In 1844, Schulz (96) in Germany first reported the presence of rubber in the latex. Milkweed latex has since been studied as a possible source of natural rubber.

Common milkweed flowers provide insects

with nectar. The entire group of tropical insects, the Danainae (26), including the familiar monarch (*Danaus plexippus* L.) and queen butterflies feed on common milkweed leaves, while other butterflies, bees, and insects use honey from flowers (68).

According to Gaertner (61), Louis Herbert, a Frenchman regarded as the first Canadian pharmacist, hoped that the milkweed plant would have medicinal value. It was used as an expectorant, against asthma, and as an emetic (tending to produce vomiting) and cathartic (purgative, laxative). Stille et al. (113) attributed its function as a diaphoretic (producing perspiration) in the forming stages of fevers to the slowing, lowering of the action of the heart. It is useful for treating acute rheumatism, bronchitis, pneumonia, and pleurisy. Common milkweed latex was suggested as dressing for wounds and superficial ulcers to promote cicatrization (healing).

Milkweed was also used for food first by Native Americans (56). The Chippewa used common milkweed flowers in a stew, while the Iroquois used the young sprouts and buds (8). Millspaugh (80) reported that housewives substituted it for asparagus. Common milkweed was considered as an unusual pot herb when its use was described by various naturalists (56, 60).

Moore's reference (85) to wine-making is the only one encountered, except for the experiment started by Gaertner in 1968. According to Gaertner (61), the wine product was drunk with impunity, and that 'the only effect produced was that of delight from the exotic aroma'.

HISTORY

Common milkweed seeds were among the first sent from New France to Paris by Louis Herbert (the Frenchman regarded as the first Canadian pharmacist) who was a farmer and settler in Stadacona (presently Quebec City, Canada) (61). Plants from these seeds were grown and later studied by Philip Cornut, a medical doctor and botanist. His treatise, Canadensium plantarum aliarumque nondum editarum Historia, published in 1635, is probably the first record on North American plants. Two of the present-day milkweeds, common milkweed and swamp milkweed (A. incarnata L.), are described.

According to Fernald (55), common milk-weed is native in eastern North America and is one of 20 species of Asclepiadaceae. It is

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³Letters following this symbol are a WSSA-approved code from Composite List of Weeds, Revised 1989. Available from WSSA, 309 West Clark Street, Champaign, IL 61820

⁴KOBA Consultants, Inc., Quebec, Canada. 1991. Personal communication: 'Evaluation of the milkweed fibre's potential use as a commercial fibre fill material'.

one of 13 species of Asclepias found in Canada (22).

DESCRIPTION

Species Characteristics. Common milkweed is a perennial broadleaf with creeping lateral rootstocks (Figure 1). It propagates both from seeds and root buds formed the previous year on either the crown or creeping rootstocks. It has simple stems up to 2 m high, usually several together from interacted root system. All plant parts contain a milky juice known as latex (21). However, Groh and Dore (65) stated that all organs of the plant except the roots contain latex.

Leaves are short stalked and smooth margined, and emerge in pairs on alternate sides of the stem. Mature leaves are 1 to 2.6 dm long and 0.4 to 1.8 dm broad with prominent veins. The upper surface is smooth and lower surfaces are covered with short white hairs and strong transverse nerves (1).

Flowers are formed in clusters (umbel) in the upper axils and tips of the stem. Individual flowers are on long, rather weak pedicels and are about 0.95 cm in diameter. Flowers are fragrant and purplish to pinkish but may vary in color from white to deep red. Corolla lobes are 6 to 9 mm long. Individual flowers contain two ovaries with five stigmatic areas. Pollen grains are in sacs (pollinia) which are set in pockets of the flattened filaments. Each stamen contains two pollinia.

Seed pods (follicles) are grey, slenderly ovoid, hairy, and covered with soft spiny projections 1 to 3 mm high. Pods are 7 to 10 cm long and about 2.5 cm across and split open along one side exposing many seeds. Seeds are brown, flat, and oval. They are 6 mm long and 5 mm wide with a tuft of silky hairs, known as comma.

Species Variations. Common milkweed is similar to showy milkweed (A. speciosa Torr.). Showy milkweed differs in leaf shape and flower stalks. Leaves are broad and oval to somewhat heart-shaped. Showy milkweed has densely wooly flower stalks with fewer and longer flowers. The flower has a long and lanceolate hood (three times as long as stamens) on the corolla as compared with common milkweed flowers (27).

Other similar plants with milky juice belong to *Apocynum* spp., known as dogbane. Dogbane flowers are small and bell-shaped. Fruits are very narrow with small slender seeds (59).

Seeds have a tuft of hairs similar to common milkweed seeds.

Ecotypes. Information on common milkweed ecotypes is limited. Stevens (111) found a milkweed form believed to be a hybrid near Dilworth, MN, about two miles east of Fargo, ND, where both common and showy milkweed were common in a field, and three distinct colonies of this form were observed. The flowers were intermediate between both species, both in size and number per cluster. The leaves were more nearly like those of common milkweed, and in this case were quite small and narrow (10.7 by 4.5 cm). In 1946, Moore (83) also found some plants that appeared to be natural hybrids between common milkweed and showy milkweed in experimental plots in which both species were growing. Moore (83) and Mulligan (86) reported chromosome counts of 2n = 22 for common milkweed.

There are many different types of pods among the wild stands of common milkweed growing in Michigan (105). Pods were found to vary in length and shape. The pod surfaces exhibited striking differences, ranging from smooth to spiny and sometimes very ridged. Sparrow (105) considered these different pod types to be genetic entities, not mere fluctuating characteristics due to environment.

DISTRIBUTION

The distribution of common milkweed in North America is limited to the region bounded by 35 and 50 degrees north latitude and 60 and 103 degrees west longitude (40, 124).

According to the Agricultural Research Service, United States Department of Agriculture, this species is spread throughout all the eastern half of the United States except states or parts of states along the Gulf coast (Figure 2). Evetts (43) reported that common milkweed is distributed in eastern North Dakota, eastern South Dakota, eastern Nebraska, eastern Kansas on the west, northwestern Oklahoma, northern Arkansas, northern Tennessee, northern North Carolina on the south, and the Atlantic Ocean on the east. The southern distribution is limited to Georgia and Oklahoma in the United States (124).

According to the Canadian Weed Survey (64), common milkweed was found in all provinces from Saskatchewan eastward with the exception of Prince Edward Island. The study of Canadian herbarium specimens of common milkweed by

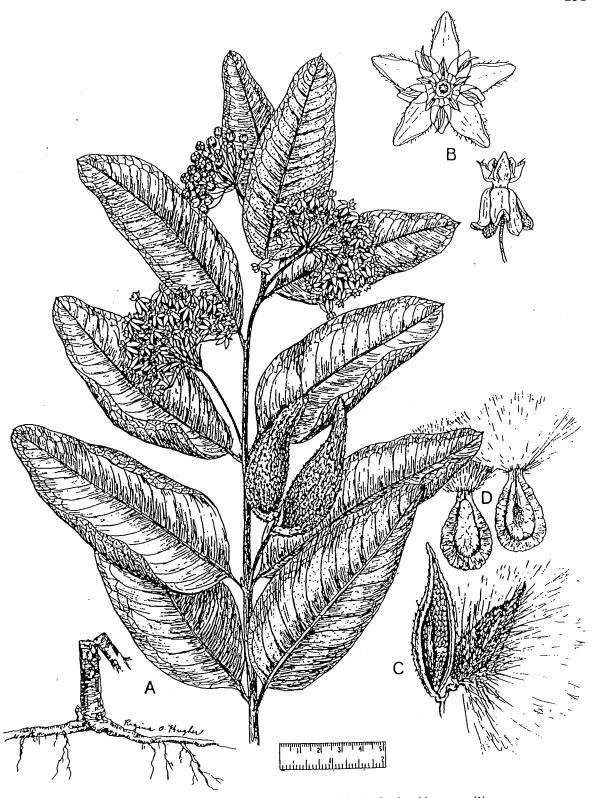


Figure 1. Common milkweed A. Root and stem; B. Flower; C. Follicle; D. Seeds with comma (1).

Bhowmik and Bandeen (21) revealed that this weed was found in all provinces from Manitoba eastward with the exception of Newfoundland, and the highest population was found in southern Ontario and Quebec.

HABITAT

Climatic Requirements. The distribution of common milkweed is limited by 18 and 32 C mean July temperatures in the North and South,

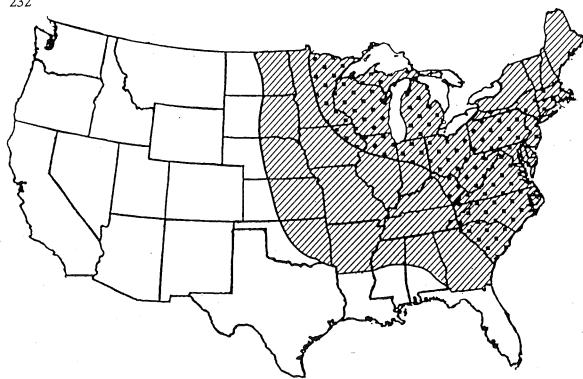


Figure 2. Distribution of Asclepias syriaca in United States (1).

respectively (40, 65, 124). Common milkweed growth is limited by a minimum of 50 cm rainfall during the three summer months; however, it is not limited by soil type, soil pH, or altitude, but grows well in fertile, moist soils (43).

Edaphic Requirements. Common milkweed is adapted to a wide range of edaphic and climatic conditions (34). Infestations may be found on soils of any textural group, but they are most prevalent on well-drained soils of loamy texture (65).

Groh (64) reported an alkaline preference of this species in eastern Canada. However, earlier studies indicated that common milkweed was abundant in acid soils in northern Michigan (116) and in soils with a pH range of 4 to 5 (107). Although seed germination of this species was reduced at 85.4 mM, seedlings tolerated salt concentrations up to 42.7 mM and pH ranging from 2 to 12 (44).

Sauer and Feir (95) found a significant positive correlation of 0.49, 0.48, and 0.43 between mean height of common milkweed and pH, magnesium, and calcium concentrations, respectively, in Missouri. Lack of boron limits the occurrence of milkweed in some soils in the United States (8).

Effects of nutrients. Common milkweed flour-

ishes in fertile soil with adequate moisture. Senecal and Benoit (97) investigated the effects of propagation method (direct seeding vs. transplanting) and fertilization on plant growth. After 5 wk, vegetative growth was not modified by seeding procedure, although transplanted seedlings had greater levels of N, K, and Mg, but lower levels of Ca. Leaf number, shoot and root dry weight, and levels of both Ca and Mg were greater for seedlings grown in larger (125 vs. 95 cm³) containers. Shoot dry weight, leaf area, and levels of N, P, and K of seedlings increased linearly with increased fertilization, while root dry weight and Mg level decreased linearly.

Effects of moisture. Common milkweed can grow over a wide range of soil moisture (81), although it is abundant in well-drained soils (64). Fully grown plants withstand drought well, but seedlings and young plants may easily be damaged by prolonged dry weather. Excessive moisture, however, is harmful.

Common milkweed can withstand moisture stress. In one study, 60% of common milkweed plants survived in 9% soil moisture, where the soil moisture in the upper 5 cm of soil was below the permanent wilting percentage (81). Plants produced shoots almost one-half the size of the plants at the higher level (52%) of soil moisture. Common milkweed growth increased

progressively as soil moisture level increased.

Common milkweed was more susceptible to moisture stress than kochia [Kochia scoparia (L.) Schrad.], sugarbeets (Beta vulgaris L.), and sorghum [Sorghum bicolor (L.) Moench.], and it was more tolerant than common sunflower (Helianthus annus L.), honeyvine milkweed [Ampelamus albidus (Nutt.) Britt.], and hemp dogbane (Apocynum cannabinum L.) (44).

Species Abundance. Common milkweed is found on roadsides, fence rows, railroads, right-of-ways, wastelands, and river basins of north-central and northeastern United States and Canada (21, 44, 76, 94). In Ontario, it was found in wooded areas (20%) and in cleared, grass, or marshlands (80%) (65). In Quebec, common milkweed grew in areas dominated by red top (Agrostis alba L.) and Kentucky bluegrass (Poa

pratensis L.) (41).

Recently, this species has become an increasingly troublesome weed in cultivated fields. Cornfields infested with common milkweed totaled 4.9 million ha in the north-central states (43). It also infested 2.7 million ha of soybeans [Glycine max (L.) Merr.], followed by smaller areas of small grains, pastures, roadsides, and sorghum. In 1980, common milkweed infested at least 10.5 million ha in the north-central states (76). The largest acreage infested was Iowa, followed by Nebraska and Wisconsin. The two crops with the largest infestation are corn (Zea mays L.) and soybeans in these states.

ECOLOGICAL ASPECTS

Seed germination is influenced by several factors, including temperature, moisture, light, dormancy requirements, substrates, seed size, and genetic makeup. Temperature, moisture, light, and dormancy requirements have been well documented for germination of common milkweed seeds (6, 9, 10, 42, 44, 54, 62, 64).

Seed Dormancy. Common milkweed seeds germinate poorly at maturity or a few days after collection in October (6, 17, 64). Intact seeds were innately dormant at maturity in October (6), although initial seed viability was 97% based on a tetrazolium (0.1% solution of 2,3,5-tetrazolium) test (44).

Common milkweed seeds require a 1-yr period of afterripening before they germinate moderately well (60 to 70%) (9, 64). Germination was poor (15 to 30%) immediately after collection at harvest and about 71% after 1 yr

of storage (64). Storing seeds at different temperatures (-12, 5, 21 C) did not improve germination for the first 3 to 4 mo of storage (9). However, germination peaked to 76% after 11 mo of storage at room temperature (21 C). There was 62% increase in seed germination 1 yr after burial in Nebraska compared with initial germination (30). Thus, seed dormancy become broken compared with seed germination of 11%. Initially, tetrazolium tests showed 94% seed viability.

Seed viability. Common milkweed seeds may remain viable for years in the soil. Seeds remained viable (32% germination) even after 9 yr of storage in glass jars (64), but seed viability declined sharply to about 8% after 7 yr when they were stored in paper envelopes, indicating the influence of oxygen (levels were not measured).

Crocker (39) reported that Shull (101) found common milkweed seeds, kept in an inundated soil at the freezing point, germinated after 4.25 yr. According to Cramer (35), common milkweed seeds will survive at least 3 yr in the soil and will germinate and develop normally between 14 and 35 C. However, normal viable seeds (54% germination) were destroyed when heated at 95 C for 15 min (66).

Methods of breaking seed dormancy. Intact seeds are innately dormant at maturity (6), but dormancy can be broken by various means. Seed treatments with concentrated sulfuric acid for 3 to 6 min, thiourea at 50 mM, or potassium nitrate at 25 mM (62) promoted seed germination. Plant growth hormones such as gibberellic acid at 29 to 115 μ M or kinetin (6-furfurylaminopurine) at 116 to 186 μ M (44) and kinetin at 0.1 mM or gibberellic acid at 0.3 mM (88) also promote seed germination.

Stratifying seeds in water at low temperature significantly increased germination (44, 69, 93) and the optimum time was found to be 7 to 28 d at 5 C (44). Baskin and Baskin (6) found stratification for a week effective in overcoming dormancy of some common milkweed seeds.

Oxygen plays a significant role in breaking common milkweed seed dormancy. Germination of seeds is 24% in air and 46% when incubation is in pure oxygen (62).

Seeds stratified in light and then incubated in darkness at 30/15 C germinated 75.3% (6). Seeds stratified in light or darkness for 2 and 3 wk and then incubated in light or darkness germinated 68% or more at thermoperiods of 35/20 and 32/15 C, but germinated to 20% or less at

20/10 C. Seeds stratified for 9 wk also germinated 70% or more at 20/10 C. This indicates the ability of common milkweed seeds to afterripen during winter months and germinate to a higher percentage at temperatures during late May to early June.

Seed Germination. The highest percent seed germination (59% average over all substrates) occurred with alternating 20 C (16 h), 30 C (8 h) temperatures (54). At a constant 30 C temperature, germination was lower (32% average) and much more variable among seeds from different populations. Germination was strongly correlated with seed source (population), temperature, and substrate type, and was poorly correlated with seed size. The maximum and minimum germinating temperatures were reported to be 35 C or 35 to 40 C and 15 C or 15 to 20 C, respectively (44).

Germination of common milkweed was significantly reduced in a 42.8 mM NaCl solution (44). The optimum pH for germination ranged from pH 4 to 8 and germination decreased below pH 4 or above pH 8 (44). Germination was not significantly affected by growing medium electrical conductivities below 7 mmho cm⁻¹ (38). Growth media at pH 2 significantly reduced germination percentage, hypocotyl length, and radicle length of common milkweed compared to pH 4 to 10.

Seedling Emergence. The time of seedling emergence and the factors for seedling growth can influence seedling competitiveness. Temperature significantly influenced seedling emergence of common milkweed (Figure 3). Maximum seedling emergence occurred at 27 C air temperature compared to 21 or 10 C. As the temperature increased, the time required for emergence decreased. In general, percent emergence decreased and emergence was delayed as the temperature decreased.

Population Dynamics. Common milkweed can disperse from roadsides and waste places into fertile cultivated lands. The subsequent spreading into cultivated lands may be related to the removal of annual weeds by the increased use of herbicides that do not control common milkweed. Thus, after seedling establishment either from seed or root fragment, patches expand in cultivated land and spreading occurs into adjacent areas (43).

Changing crop production practices have encouraged the spread and density of common milkweed infestations during the past two decades (47, 52). Farmers now rotate crops and cultivate less which provides more favorable conditions for seedling establishment, plant development, and subsequent spread. Also, the elimination of timely tillage allows common milkweed seedlings to become established permanently.

The common milkweed stand on Ontario roadsides ranged from 100 stalks per km in Lincoln County to about 1,863 stalks per km in Essex County (65). In fields, stands varied from 75 stalks per km in Lennox County to 10,954 stalks per km in Renfrew County. In southern Ontario fields, density varied from 11,819 to 88,226 stalks ha⁻¹ (21). Plant density varied from 1 to 3 plants per m² in east-central Missouri sites (95). In surveyed alfalfa (Medicago sativa L.) seed fields in Manitoba, the relative abundance of milkweed spp. was 0.2% with the occurrence of 0.3 plants per m² (63). A milkweed spp. frequency of 1.6% and a 0.3 plants per m² relative abundance in cereal and oilseed crops were also found in Manitoba (114).

GROWTH AND DEVELOPMENT

Phenology. Simard et al. (103) reported a detailed description of phenological stages of common milkweed. Common milkweed goes through nine stages to complete its life cycle (Table 1). These stages include shoot emergence, bud stage, umbel showing, first flowering, full bloom, flower senescence, small seed pod, mature seed pod, and ripe seed pod. At each stage, cumulative degree-days were calculated at base 4 C using the standard method, Trottier and Baskerville methods. The degree-days could be important in predicting seasonal development of this species.

The aerial shoots emerge in spring (April to May) from underground root buds as the weather becomes warmer. When there is sufficient foliage, surface root development becomes active. Root extension starts later in the year (July to August), but new shoots from newly formed roots do not reach the surface until the following spring (65). Root growth terminates during mid-August to mid-September when most shoots senesce.

Adventitious root buds are responsible for vegetative regeneration of new shoots. The buds arise either on the stem base near the soil surface or on lateral roots (17). Common milkweed seedlings become perennial within 21 d after germination because plants become capable of producing new shoots from buds (44). In other studies, seedlings become capable of pro-

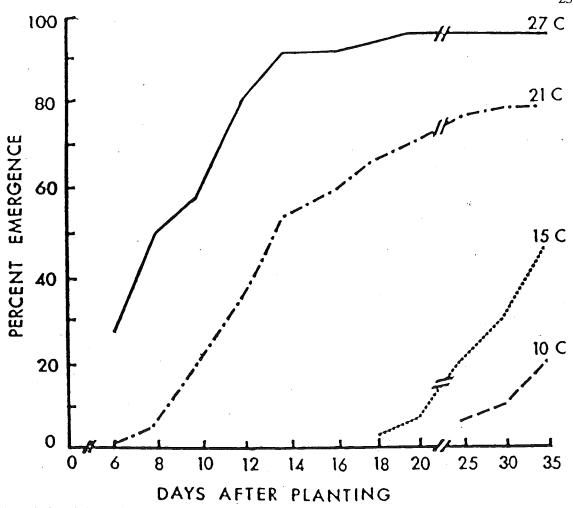


Figure 3. Cumulative total of emerged seedlings at different temperatures for a period of 35 d (10).

ducing new aerial shoots from root buds within 18 to 21 d after germination (17). The parent root survives for two or more growing seasons, depending on soil conditions and frequency of tillage practices. Most root buds remain viable throughout the severe winter months and sprout with the advent of spring weather.

Removal of topgrowth from 21-d-old seed-lings resulted in 28% resprouting of root buds (44). Sprouting activity increased as days from planting to clipping increased, and the number of days for resprouting decreased (20, 44).

Plants grown from seeds seldom flower until their second summer (17, 21, 74, 105). Also, newly developed shoots from the same root system normally flower during the next growing season. Flowering occurs in late June to July or early August depending on initial growth, weather, and location. Flowering in common milkweed does not occur before mid-June in Quebec (40).

Factors Affecting Growth. Milkweed grows

best in 30% to full sunlight, and thrives on sites unprotected from direct sunlight, even in dry, warm climate if it has plenty of available soil moisture (8). Berkman (8) suggested that a longer growing season in southern Michigan helps to some extent to offset unfavorable site conditions. In northern Michigan, where less than 100 d are available for food storage during the growing season, the effects of poor site conditions are more severe than in the southern part.

Effects of temperature and photoperiod. Common milkweed grows well at 27 C under a 16-h photoperiod (19). Sixty-day-old common milkweed seedlings produced as many as 52 buds on the root system at 27 C and a 16-h photoperiod. The rate of seedling growth decreased, producing small plants with narrow leaves, as temperature decreased to 15 C. Temperature and photoperiod interacted to influence root and shoot growth. Thus, dry matter accumulation progressively increased with each in-

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Table 1. Phenological stages of common milkweed and cumulative degree-days as calculated by three methods (4 C base) at L'Acadie Quebec in 1987 and 1988 (103).

			Cumulative degree-days			
Phenological				Methods		
stage	Year	Date	Standard	Trottier	Baskerville	
A. Shoot emergence	1987	April 15	77	107	92	
	1988	May 4	106	157	131	
B. Fully extended leaves	1987	April 25	180	213	197	
	1988	May 14	198	253	224	
C. First appearance of floral structure	1987	May 19	317	374	394	
	1988	May 24	312	367	338	
D. Floral buds well developed and first open flower	1987	June 15	707	764	734	
•	1988	June 15	597	653	623	
E. Full flowering	1987 1988	June 26 July 3	892 838	949 894	919 864	
F. Flower senescence	1987	July 1	972	1029	999	
	1988	July 7	912	968	938	
G. Small follicle (10 to 20 mm)	1987	July 6	1055	1112	1082	
	1988	July 11	1002	1058	1028	
H. Mature follicle (100 to 125 mm)	1987	August 20	1799	1856	1826	
·	1988	August 2	1766	1822	1792	
I. Follicle desiccation	1987	Sept. 25	2172	2232	2200	

crement of either temperature or photoperiod (13, 14).

Net photosynthesis for common milkweed was lower (16.2 μ mol m² sec⁻¹ of CO₂) in August than the rate (21.1 μ mol m² sec⁻¹) for butterfly milkweed (A. tuberosa L.) (73). However, the photosynthetic rate was higher in September for milkweed. Common milkweed also had lower water use efficiency (mol fixed/mol of water lost), maintained higher transpiration rates with lower stomatal diffusion resistance, and maintained much lower xylem water potentials (-8) than butterfly milkweed (-1.2 bars). The reduced rate of photosynthesis may explain the nature of competition between common milkweed and butterfly milkweed.

Origin and Development of Root Buds. Adventitious root buds of common milkweed originate in the pericycle at protoxylem poles and grow centrifugally towards the periphery of the root (92). Before emergence through the parent root surface, bud apices that will develop into vegetative shoots may be distinguished from

lateral root apices by their well-rounded shape and the presence of rudimentary leaf primordia. No root buds are initiated until after lateral roots have developed and some cambium activity had begun (92). Vascular connections from the buds to the stele of the parent root, or an associated lateral root, differentiate at an early stage of bud development.

Common milkweed is a successful weed largely because of its ability to propagate vegetatively by the development of adventitious root buds on underground roots (21). Root buds arise on the main root and upper lateral roots within 25 d of seedling establishment and are generally associated with the bases of lateral roots (17, 92).

Root Bud Development after Emergence. The development of adventitious root buds on an excised root segment, following emergence from the parent root, was characterized by node and internode development followed by internode expansion (108). Transverse sections of root buds reveal that bicollateral vascular bundles, as well

as leaf traces and gaps, are well developed in buds from 3-mo-old plants. Strands of xylem and phloem connect the parent root and root bud in both nongrowing and growing root buds.

Laticifer cells and latex development. Common milkweed has an extensive system of specialized cells that contain latex under positive pressure which are classified as nonarticulated branched laticifers (120). Although their function has not been determined, laticifers were suggested to function as an internal system for water regulation or as a site for sequestering secondary metabolites (23, 53).

The development of laticifer cells in common milkweed has been studied recently by Wilson and Mahlberg (120). The mature laticifer protoplast possesses a large central vacuole with an intact vacuolar membrane. Formation of this vacuole apparently results from dilation and subsequent enlargement of endoplasmatic reticulum and possibly in part by fusion of smaller vacuoles and limited cellular-lytic autophagy. Latex is produced in the cytoplasm and subsequently incorporated into the large central vacuole of laticifers. Rubber globules, the most prominent latex component, are surrounded by a membrane that does not have a normal trilaminate membrane structure. Globules are associated with an electron-dense fibrillar component in the vacuole. The white milky latex is composed of water containing dissolved or suspended minerals, salts, sugars, proteins, tannins, gums, resins, alkaloids, starch, and proteolytic enzymes (53). The function of latex in the plant is not clearly known but the most acceptable theory is that the latex contains metabolic byproducts and the latex canals serve as a secretory system (53).

. PHYSIOLOGICAL ASPECTS

Since the last review on common milkweed (21), research has focused on common milkweed physiology, especially the absorption, translocation, and metabolism of translocated herbicides.

Absorption, Translocation, and Metabolism. Earlier studies indicated that absorption of 2,4-D [(2,4-dichlorophenoxy)acetic acid] into the leaves of 45-d-old common milkweed seedlings was maintained up to 120 h after application (12). About 45% of the applied ¹⁴C-2,4-D was absorbed within the first 6 h, although little tracer was translocated at this time period. Translo-

cation of ¹⁴C-2,4-D occurred in the symplast and was basipetal. 2,4-D was rapidly metabolized (53%) and subsequently lost from the plant. Rapid metabolism of 2,4-D was later verified (126).

Differential absorption of glyphosate [N-(phosphonomethyl)glycine] and 2,4-D in common milkweed and hemp dogbane has been reported (126). Less glyphosate was absorbed than 2,4-D in both species but absorption of both herbicides was greater in common milkweed. Greater herbicide absorption by common milkweed than hemp dogbane was attributed to less epicuticular wax, less cuticle, lower contact angle of the herbicide spray, and the presence of more stomata and trichomes on the adaxial leaf surface.

In the same study of ¹⁴C-glyphosate absorption, translocation, and metabolism (126), only 23% of the applied ¹⁴C-glyphosate was recovered. Glyphosate translocated more rapidly than 2,4-D in common milkweed. More glyphosate than 2,4-D accumulated in areas of high meristematic and metabolic activity. There was no detectable metabolism of 2,4-D in hemp dogbane roots after 20 d, while 60% of the absorbed 2,4-D in common milkweed roots was metabolized.

Waldecker and Wyse (117) reported that latex samples taken from the abaxial leaf surface opposite to ¹⁴C-glyphosate-treated leaves and from petioles of treated leaves did not contain ¹⁴C. Thus they concluded that the laticifers in common milkweed do not accumulate glyphosate and therefore do not limit its transport in the plant.

The partial removal of the shoot and root prior to the application of ¹⁴C-glyphosate increased bud respiration and the concentration of ¹⁴C in the proximal root buds of common milkweed (118). Proximal root buds treated with 1 mM of 6-benzyl-aminopurine (BAP) for 6 d (3 d prior to application of ¹⁴C-glyphosate) contained seven times more ¹⁴C mg⁻¹ than root buds of BAP-untreated plants.

Root Reserves. The root reserves of common milkweed provide the long-term survival of the weed species, and the root reserves vary over the growing season (Figure 4). The percent carbohydrate of roots (samples to a depth of 1 m) of field-grown common milkweed declined from late May to June and reached a plateau (25%) in October after its sharp decline to about 10% in July (9, 16).

The distribution of total sugars varied between plant parts. The total sugar content in the

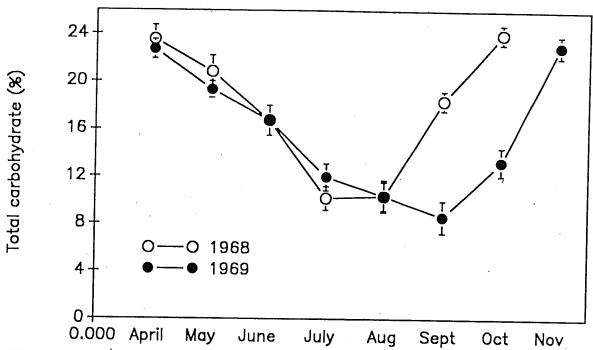


Figure 4. Distribution of total carbohydrate in common milkweed roots over time (9). Vertical bars represent standard error of the means.

stem base represented 17.4 to 23.2% of the total dry weight of this plant part (9). Sugars peaked in the stem base in July, followed by a slight reduction in August and September. The total reducing sugars (total glucose and fructose) in the rootstock of milkweed remained fairly constant throughout the growing season and ranged between 0.48 to 2.22% of the total dry weight (9). The nonreducing sugar (sucrose) contributed a major portion of the total sugars in common milkweed rootstocks (9). During June and July (the period of flower bud formation and fertilization), carbohydrate and nitrogenous materials migrated out of the root, leaf, and stem into the floral organs of the plant (62). This clearly demonstrates the source and sink relationship in common milkweed. The concept could be used in designing the application of translocated herbicides for perennial weed control.

Root Bud Dormancy. Although extensive root growth occurs during the first year, shoots from these roots do not emerge from the soil until the second year (21, 65). Bud growth is strongly inhibited by the parent shoot (21, 44, 69), but inhibition is unknown. Apical dominance, hormonal control, and root reserves could be responsible for adventitious root bud dormancy (21, 49). Root bud dormancy in common milk-

weed increased as the total sugar level in rootstocks increased in the fall (9, 15, 16).

According to Hsio and McIntyre (67), root bud growth increased within 24 h of the excision of the parent shoot. However, only a few of the measured buds continued to grow. The growth of most remaining buds became arrested within 48 h of their release from inhibition.

At low relative humidity (approximately 30 to 50%), the decapitated debudded stem, bearing only a single pair of leaves, promoted the early growth of the root buds but strongly inhibited their subsequent elongation and emergence as shoots (67). The mature stem (30 to 40 cm in height and with 20 to 30 pairs of leaves) itself, when completely defoliated, had low root and shoot production. At high relative humidity (93 to 100%), which reduced transpiration by approximately 50%, inhibition by mature shoots was either eliminated or greatly reduced, and the rate of shoot emergence and subsequent growth from root buds following the complete removal of the parent shoot were increased.

During the development of subterranean root buds on excised root segments, strands of xylem and phloem connect the parent root and root bud in both inhibited and noninhibited root buds (108). Thus, they concluded that retardation of growth of inhibited root buds in common

milkweed is not caused by anatomical constraints.

Competitive Effects. Common milkweed is not a good competitor in a cultivated land. Experiments at the Iowa Agricultural Experiment Station and the U.S. Department of Agriculture, at Beltsville, MD, have established that it is difficult for milkweed to compete with bluegrasses [Canada bluegrass (*Poa compressa* L.) and Kentucky bluegrass (*Poa pratensis* L.)] the first 2 yr after milkweed is planted (8).

Light competition (between foliage) did not reduce the height of common milkweed as much as soil competition (between root systems) (52). Common milkweed height was significantly reduced by light, soil, and full competition with green foxtail [Setaria viridis (L.) Beauv.], redroot pigweed (Amaranthus retroflexus L.), and sorghum (Moench 'RS-626'), where only green foxtail caused a significant reduction in height due to light competition. Common milkweed was a poor competitor with six annual weed species when light was a limiting factor (49).

Common milkweed can reduce crop yields, depending on the density of milkweed populations. Significant reductions in crop stand from common milkweed competition densities at 11,100 to 45,200 plants ha⁻¹ were observed for corn in 1977 and 1979 and for sorghum in 1976, 1977, and 1979 (Table 2). Reductions in stands ranged from 8 to 16% for sorghum, and 8 to 15% for corn. Soybean yield reductions from common milkweed competition ranged from 12 to 19% during the 4 yr of the study. Significant

reductions in sorghum yields occurred all years except 1977 and ranged from 4 to 29%. Corn yields were reduced slightly. In other studies, sorghum yield reductions increased in proportion to the density of common milkweed, with an average yield reduction of 21% at plant density of 5,000 to 50,000 plants ha⁻¹ (42, 47, 48).

Noncompetitive Effects. Noncompetitive allelopathic effects of common milkweed have been suggested to play a role in crop yield reductions (94, 127). Aqueous extracts from field-grown common milkweed leaves inhibited sorghum seedling growth (93). Wyrill and Burnside (127) showed in a stair-step pot experiment that leachate from both living and dead common milkweed plants reduced sorghum growth. Undiluted aqueous extracts of common milkweed shoot and root material significantly reduced germination, hypocotyl length, and radicle length of sorghum (38).

Wild oats (Avena fatua L.) have been reported to be inhibited by common milkweed (77). Water extracts of common milkweed stems suppressed normal germination of wild oats up through 5 d, after which some showed coleoptile elongation. By 13 d branched adventitious roots were evident but normal radicle growth was inhibited.

REPRODUCTION

Floral Biology. Insect-pollinated plants have great evolutionary diversity of their floral dis-

Table 2. Effects of common milkweed infestations compared with noninfested areas in corn, sorghum, and soybean fields on crop stand and yield during 1976 through 1979 in eastern Nebraska (38).

	Fields	Common milkweed population	Crop reductions from common milkweed competition ¹		
Crop	Year	observed	in infested areas	Stand	Yield
		no.	plants ha-1		%
Corn	1976	1	24900	8	10*
	1977	1	36600	15*	7
	1978	8	17900	8	2
	1979	6	11100	9*	2
Sorghum	1976	5	13600	16*	29*
J	1977	3	27800	8	4
	1978	6	35300	12*	21*
	1979	5	18700	10*	15*
Soybeans	1976	2	16200	•	12*
,	1977	3	32700	-	19*
	1978	7	45200	-	18*
	1979	5	26600	· . •	18*

¹Means within a crop followed by an asterisk (*) are significantly different compared to the noninfested area at the 5% level using a paired t-test.

plays (25). The flowers on a stem may be clustered in space and/or time, and flowering stalks may themselves be clumped in various ways and densities. The success of any floral display must be measured in terms of the number of viable offspring produced, which is likely to be a function of success in attracting effective pollinators. Common milkweed is no exception.

Common milkweed has an elaborate insect pollination system and is largely self-incompatible (84, 87, 124), although Stevens (110) reported some cases of self-pollination which may have resulted from experimental error. Insects pollinated from 14 to 80% of common milkweed flowers depending on the insect activity. The Hymenoptera, primarily wasps and bees, are largely responsible for pollination (41, 112). The Monarch butterfly (Danainae) has been reported to pollinate common milkweed (68), contradicting Doyon (41) who reported that the monarch butterfly was not a pollinator.

The duration of flowering varies from plant to plant, umbel to umbel (84), and clone to clone (115). Flowering progresses rapidly upwards from the lowest umbel. Moore (84) found that all flowers of an umbel usually opened within a period of 2 to 3 d. About 7 d elapsed between dates of full flowering of the lowest and the uppermost umbel of a stem of 4 to 6 inflorescences.

Three to 7 inflorescences per stalk of common milkweed and 8 to 128 flowers per inflorescence were observed in Ontario (21). A high percentage of flowers abscised 10 to 12 d after opening and only 2 to 4% of the flowers produced mature pods.

Some form of self-incompatibility was expected since nearly all selfed ovaries failed to form mature pods in common milkweed (69, 106). Differences between pollen donors in pod productivity support the hypothesis that pods are selectively produced in Asclepias. Bookman (25) found that approximately 70% of the ovaries in showy milkweed in eastern Washington fail to form mature pods, although insect pollinators had inserted sufficient numbers of pollinia into flowers. Moore (82, 84) found that about 50 to 75% of the enlarged ovaries of an umbel aborted.

The abortion of common milkweed flowers was observed by several authors (21, 82, 84), and it was suggested (24) that it might result from competition for food between endosperm and the adjacent material tissue of the ovule, the "somato-plastic sterility" of Brink and Cooper (82). Bookman (24) demonstrated that the cost (metabolic substances) entailed in ovary

production is actually small, 3% of the cost of mature pods for either N, P, K, Mg, H₂O, or total dry weight. Pod initiation and abortion is slightly more costly, one to five times that of ovary production for the same nutrients, H₂O, or total dry weight, despite the withdrawal of a large proportion of nutrients prior to abortion.

The number of pods matured by each inflorescence is limited and a minimum number of flowers appear to be necessary to ensure that pod production, within this limit, is maximized (121). Only 1 to 3% of the flowers produced a mature pod (82). About 80% of the flowers drop soon after flowering, showing no enlargement of the ovary, and many pods abort before maturity. Only 16% of fertilized ovaries ever produce a mature pod (84). Wilson and Rathcke (121) suggested that the balance between the high-cost (per fruit), low-risk strategy of producing small inflorescence for pod production and the low-cost (per set of pollinia), high-risk strategy of large inflorescences for increasing pollinia production is probably adaptive.

Although flowering periods vary annually for milkweed species (123), little is known of intraspecific variability in flowering among populations and individuals within a local area. Phenology varies within and between populations of swamp milkweed, eastern whorled milkweed (Asclepias verticillata L.), and common milkweed in Indiana (72). Swamp milkweed and eastern whorled milkweed flowered in July and August, and overlapped at least 30 d, whereas common milkweed typically flowered in June or early July. Despite such variability, the early-summer flowering of common milkweed is mostly asynchronous with mid-to late summer flowering of swamp milkweed and eastern whorled milkweed. This seasonal separation in flowering phenology enhanced strong physiological and partial mechanical barriers to interbreeding between common milkweed and the latter two species (70). Perhaps selection pressure for divergent flowering is greater in common milkweed, since it inhabits a wider variety of habitats and may be preferred by pollinators (71) because of the high sugar content per flower and volume of its nectar (104, 122).

The phenology of fruit maturation and seed release revealed greater synchrony in seed release, as well as longer periods for follicle maturation and dehiscence, for common milkweed compared to other *Asclepias* species (72). In common milkweed, fruits initiated early in the season retained their seeds longer than late-season fruits resulting in synchronous release in late autumn.

Seed Production and Maturation. One or both ovaries of a flower enlarge following successful pollination (84). Young seeds increase in size, particularly at the micropylar end, and in a plane that is approximately at right angles to the placental ridge to which the seed is attached (90).

Knowing the time interval between flowering and viable seed production would be important in preventing seed production and spread of any weed species. Common milkweed produced viable seeds 5 to 6 wk after flowering. A high percentage of seeds harvested 6 wk after flowering germinated (50). Seeds harvested 6 and 7 wk after flowering produced seedlings with significantly shorter radicles and hypocotyls than seeds harvested 8 wk after flowering. Seed weight was highly correlated with radicle and hypocotyl length (50).

Common milkweed in tobacco fields produced four to six pods per stalk, each with 150 to 425 seeds (19, 21). Moore (84) found an average of six pods per fertile stem. The 100-seed weight ranged from 42 mg (109) and 43 to 73 mg (19). Common milkweed at a density of 59,893 stalks ha⁻¹, each with an average of five pods and each pod with an average of 290 seeds, could produce as many as 86,844,850 seeds ha⁻¹ (21).

Floss Characteristics. For eight decades, common milkweed pods and floss have undergone scrutiny as a possible source of bast fibers. In 1947, Pearson (89) studied 156 pods representing 39 different pod types in Michigan. Floss length increased as pod length increased. Fiber width also increased as floss length increased. The number of fibers per tuft ranged from about 1,000 to 1,300 for most pod types.

The recent Canadian study indicates its renewed interest on potential use of milkweed fiber commercially. KOBA Consulting Farm⁴, in collaboration with Glanmar Mills in Canada, successfully developed various yarn and fabric samples from milkweed fiber. Milkweed fiber behaves as a cellulose fiber with much lower specific gravity than most cellulosic fiber.

Seed Dispersal. In general, wind plays a major role in dissemination of common milkweed seeds. Seed pods mature and split open in early fall (September to October) and the seeds are dispersed by wind, carried by the tufts of floss. Mature pods are found attached to dead stalks until late fall (November to December) and even in the following spring.

Vegetative Reproduction. Common milkweed

propagates vegetatively by a creeping root system. Seedlings produce buds on the main root close to the ground surface within a period of 18 to 21 d after emergence (17). Evetts and Burnside (44) found that 28% of the seedlings sprouted when the shoots of 21-d-old seedlings were removed.

The distribution of lateral roots and adventitious root buds on a common milkweed root system is presented in Figure 5. The maximum number of root buds was formed proximal to the root origin and the average number totaled 6.3 to 9.5 for the first 10 cm of root fragment. The number of buds varied from 2 to 4.5 per 10 cm root fragment beyond 30 cm from the point of origin. A considerable reduction in the number of buds was observed beyond 125 to 130 cm from the point of origin. The distribution of the lateral roots on the root system was variable in relation to the root length. The maximum number of lateral roots was formed over a distance of 80 to 120 cm from the point of origin.

In a clipping study to determine sprouting activity of common milkweed seedlings, the sprouting activity increased and the number of days required for sprouting decreased as days from planting to clipping increased (20, 44). The survival and regrowth of seedlings increased as seedlings developed additional leaf pairs. The number of sprouted buds ranged from 5 to 100% when the seedlings were clipped 2 to 3 cm and were 7.5 to 12 cm tall, respectively (20). Thus, sprouting does not occur in seedlings until they are clipped, indicating that apical dominance does play a role. After 4 yr of natural (undisturbed) establishment, one seedling produced as many as 56 stalks vegetatively and 94 seedlings in a 9-m² area (21).

Common milkweed roots usually grow to a depth of 100 to 120 cm (17). Numerous adventitious root buds appear throughout the root system, the majority remaining dormant (15, 62, 64) until conditions favor their growth. Root buds were most dormant in May (15). An average of 13.2% of the root fragments with a visible bud remained dormant in May compared to 52.2% in September. High temperature broke root dormancy. Thus, the root fragments collected in May to August and September sprouted to 80 to 95 and 67%, respectively, when they were incubated at 27 C. On the other hand, root fragments collected in May to July, sprouted 25 to 72% at 15 C. However, there was no sprouting in August and September at 15 C.

Size, length, and maturity of root fragments also played an important role in sprouting ac-

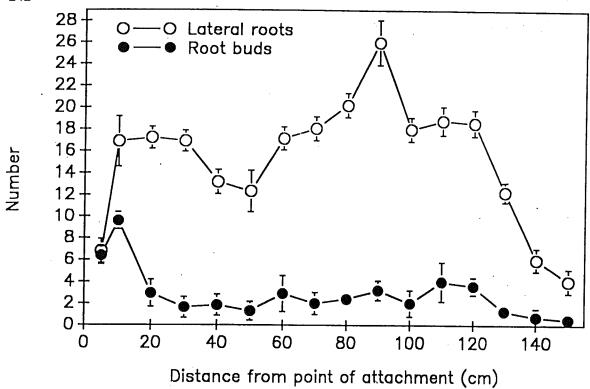


Figure 5. Distribution of lateral roots and adventitious root buds in relation to the point of attachment of common milkweed root (9). Vertical bars represent standard error of the means.

tivity in relation to the time needed for sprouting. Smaller root fragments required a longer time for sprouting (81). Root fragments 30 to 45 cm in length sprouted 90 to 100%, but shorter root fragments failed to sprout well (64). Only 36% of the root fragments 7.5 cm in length formed shoots reaching to or growing above the surface of the ground 3 mo after planting (81).

CONTROL METHODS

Cultural Control. Common milkweed is increasing most rapidly in dry land and cultivated fields. Infestations in sorghum fields in eastern and south-central Nebraska increased from 30 to 60% in 1969 and 1977, respectively (48). It is a relatively constant component along roads, railroads, and perennial grass areas, whereas it is decreasing under alfalfa (Medicago sativa L.) and winter wheat (Triticum aestivum L.).

A competitive crop or dense stands of annual weeds limit common milkweed seedling establishment (52). Seedlings become established more readily in row crops where annual weeds are controlled with herbicides that are ineffective on common milkweed and cultivation is reduced or eliminated (28).

According to Timmons (116), rotation to alfalfa was effective for eradicating or controlling

common milkweed in northern Michigan. The density of common milkweed, compared with that on an adjacent unmowed 'old sod,' was 7.1% for alfalfa 3 or more yr old, 54.2% for alfalfa 1 or 2 yr old, 62.9% for wild grass meadow, and 87.7% for red or 'Alsike' clover (Trifolium hybridum L.). The density of common milkweed in a row crop was 141.4% of that on an adjacent unmowed old sod.

Planting winter wheat into a common milk-weed-infested field can aid its control. Winter wheat establishes in the fall and initiates growth early in the spring so it is quite competitive. Established common milkweed stands can be eliminated with winter wheat and tillage for 5 consecutive years (28).

In general, crop rotations involving forage grasses or legumes, small grains, and irrigated corn help control common milkweed. These crops may restrict milkweed growth due to plant competition, or associated production practices may reduce the vigor of this weed.

Mechanical Control. A common milkweed patch or colony in the field is probably the result of the establishment of a single plant from a seed or root fragment following vegetative propagation. Cultivation chops the underground root system into small fragments and spreads

these fragments, leading to establishment of additional plants (19, 35, 81). Removal of stalks by clipping or mowing induces lateral root buds to sprout. Therefore, mechanical control such as clipping or cultivation can lead to the creation of a large colony of common milkweed plants, unless the tillage or mowing is repeated often enough to deplete stored carbohydrate reserves in the root system.

Seedbed preparation and row crop cultivation help control common milkweed. Growing oats (Avena sativa L.) or winter wheat provides a cropping system that can aid in common milkweed control (48). Also, intensive cultivation in the spring followed by cultivation at 3-wk intervals until seeding winter wheat can help control common milkweed.

As tillage is reduced, perennial weeds such as common milkweed increase (29). Tillages that repeatedly destroy the milkweed shoots help deplete its carbohydrate reserves from the root system. Undercutting with sweep tillage effectively controls this deep-rooted perennial (28). Deep fall plowing also exposes roots to drying and freezing conditions, and predisposes common milkweed to be winterkilled.

Chemical Control. Common milkweed seed-lings are controlled by the same soil-applied herbicides that control broadleaf weeds in corn, sorghum, and soybeans. Soil-applied herbicides include atrazine [6-chloro-N-ethyl-N'-(methylethyl)-1,3,5-triazine-2,4-diamine], EPTC (S-ethyl dipropylcarbamothioate), and metribuzin [4-amino-6-(1,1-dimethylethyl)-3-(methyl-thio)-1,2,4-triazin-5(4H)-one], or combinations thereof. (46, 125).

Control of common milkweed with herbicides is often variable and depends upon application, growth stage, and application timing, or environmental conditions at the time of application (11, 37). Satisfactory control (70% or better) of common milkweed was obtained with amitrole (1*H*-1,2,4-triazole-3-amine) or glyphosate application during the late-bud growth stage (45).

Postemergence treatments of 2,4-D did not satisfactorily control common milkweed shoots emerging from adventitious root buds. However, in growth chambers, 2,4-D at 0.8 to 1.2 kg ha⁻¹ restricted shoot growth and caused abnormalities and limited root bud formation on 10- to 25-d-old seedlings (18).

Common milkweed shoots can be controlled with 2,4-D, mecoprop $[(\pm)-2-(4-\text{chloro-}2-\text{methylphenoxy})$ propionic acid], MCPA [(4-chloro-2-methylphenoxy)acetic acid], dicamba

(3,6-dichloro-2-methoxybenzoic acid), or combinations of 2,4-D, MCPP, and dicamba without any appreciable effect on the root system (2, 9). Amitrole-T (a commercial formulation of amitrole and ammonium thiocyanate) at 1.1 to 2.2 kg ha⁻¹ controlled milkweed during the year of treatment, although about 5 to 10% regrowth occurred in the next growing season (2). In contrast, no regrowth of common milkweed in the following two growing seasons was observed when established plants were treated with amitrole-T at 4.5 kg ha⁻¹ (45).

Glyphosate, a postemergence translocated herbicide, effectively controlled common milkweed and other perennial weeds (3, 11, 31, 45, 48). Glyphosate at 2.2 to 3.5 kg ha⁻¹ in August and September 1971 killed all shoots of common milkweed in 1971 and allowed only 5 to 10% regrowth in the 1972 season (3, 45). Common milkweed treated with 2,4-D or dicamba regrew to the same extent the following year (4). In replicated studies, early application (June 25) of either glyphosate at 2.2 or 3.4 kg ha⁻¹ or amitrole-T at 1.1 or 2.2 kg ha⁻¹ controlled common milkweed more effectively the following year than late applications (July 30 or August 30) (4, 5).

The application timing of herbicides in relation to plant growth plays an important role in herbicide effectiveness. Glyphosate applied in June (early bud stage) reduced milkweed stands more effectively in the second year than did glyphosate applied in August (postflower stage) (Table 3). In contrast, satisfactory control (70% or better) was obtained with glyphosate at 2.2 kg ha⁻¹ applied at the early- or late-bud growth stage (Table 4). Amitrole at 4.5 kg ha⁻¹ controlled common milkweed better when applied at the later bud stage than when applied at the early-bud growth stage, whereas glyphosate applied at 1.1 kg ha⁻¹ controlled common milkweed equally well at both stages except in 1976.

Herbicide absorption and metabolism by plants could be a factor in controlling common milkweed. Limited absorption of glyphosate but not 2,4-D by hemp dogbane and metabolism of 2,4-D but not glyphosate by common milkweed were considered the primary factors involved in susceptibility differences of the two species (126).

Differential uptake of glyphosate between distal and proximal root buds on the intact root system of common milkweed has been attributed to proximal bud inhibition (117). Less ¹⁴C-glyphosate is concentrated in root buds proximal to the crown than in more distal buds, resulting in all subsequent shoot regrowth originating from root portions proximal to the

Treatment Rate		Time of application in 1973 ¹	Stand reduction ²		
	Rate		9-25-73	8-30-74	
	kg ha-1	-		7 ₀	
Glyphosate Glyphosate Amitrole Amitrole Glyphosate Glyphosate Amitrole Amitrole Glyphosate Glyphosate Glyphosate	2.2 3.4 1.1 2.2 2.2 3.4 1.1 2.2 2.2 3.4	Junc 25 Junc 25 Junc 25 Junc 25 July 26 July 26 July 26 July 26 August 30 August 30	100 a 96 a 100 a 100 a 100 a 95 a 92 a 78 ab 88 ab 81 ab 83 ab	6	
Amitrole Amitrole Untreated	1.1 2.2	August 30 August 30	64 b 65 b 0 c	60 b 70 b 10 c	

¹June 25 = early bud stage, July 26 = late bud to flowering stage, and August 30 = postflowering stage.

²Means within a column followed by the same letters are not significantly different at the 0.05 level according to Duncan's multiple range test.

Table 4. Influence of herbicide treatments on common milkweed stand 1 yr following postemergence applications in fallowed fields near Lincoln, NE, during 1976 and 1978 (37).

 						
		Con	trol 1	yr afte	r treatr	nent¹
		Common milkweed stages and treatment				
		Early	7 bud	I	ate bu	d
Herbicide	Rate	6/76	6/78	6/76	6/78	6/78
	kg ha-1			%_		
Untreated check		0	0	0	0	0
Amitrole	4.5	68	50	59	72	77
Glyphosate	1.1	67	66	49	75	73
Glyphosate	2.2	84	100	93	76	77
Glyphosate	4.5	88	57	100	57.	77
LSD _{0.05}		27	40	78	40	47

¹Average of 3 or 4 replications.

²Treatments were applied at two locations in 1976 and three locations in 1978.

crown tissue (117). Glyphosate transport into inhibited buds would not be restricted by rudimentary or incomplete vascular connections between the parent root and root bud, based on anatomical studies (108). Therefore, glyphosate would effectively control the root systems and root buds of treated common milkweed plants.

Dormant buds of common milkweed could be chemically stimulated to accumulate higher concentrations of translocated herbicides such as glyphosate. Waldecker and Wyse (118) suggested that proximal root buds can be stimulated to acquire lethal concentrations of glyphosate. Dormant root buds were stimulated by the addition of BAP (6-benzyl-aminopurine) and subsequently were killed by foliar application of glyphosate at 1.1 kg ha⁻¹ (118).

The enhancement of herbicidal toxicity by many surfactants has often been attributed to reduced surface tension and associated increases in leaf wettability and cuticle penetration. The addition of surfactants to glyphosate spray mixtures that already contain a surfactant (not disclosed) should be avoided, since no additional activity in glyphosate can be obtained (128). Ethoxylated stearyl ether and amine surfactants gave optimum effectiveness of hydrophile-lipophile balance (HLB) values of 15 to 16 and 19 to 20, respectively. Surfactants with a low HLB were usually less effective than those with a high HLB. The amine-containing surfactants were the most effective with increases in HLB and degree of ethoxylation.

Cationic surfactants were generally more effective than nonionic surfactants. These differences may be due to charge difference or to other factors such as HLB, chemical type, and molecular size. Contact angle was not related to surfactant enhancement of glyphosate (128).

Soil moisture may influence the chemical control of common milkweed. Low soil moisture levels have, in some cases, reduced the effectiveness of glyphosate by 20 to 35% (33, 79). Annual control of common milkweed with glyphosate is reduced when soil moisture is inadequate (less than 13%) (117). Water-stressed [13% (w/w) soil moisture] common milkweed plants treated with glyphosate at 1.1 kg ha⁻¹ produced shoot regrowth equal to untreated

plants, whereas shoot regrowth of nonstressed [25% (w/w) soil moisture] glyphosate-treated plants was only 6% of untreated plants.

Control with recirculating sprayer. Spot treatment with a translocated herbicide has become a more practical approach to weed control in recent years, especially with perennial weeds. Various innovations for the control of tallgrowing weed escapes have been developed (29). The recirculating sprayer (RCS) that utilizes a weed-to-crop height differential can be used selectively with a nonselective herbicide in shortstatured crops (78). Because common milkweed grows taller than soybeans or sorghum, glyphosate applied by RCS can control it without crop damage (31). Common milkweed control in soybeans varied considerably, but glyphosate at 1.1 to 4.5 kg ha⁻¹ applied through the RCS provided over 80% control (32). Retreatment during the subsequent years is essential, if near 100% control is desired 1 yr later.

Common milkweed control in noncrop areas. Control of established stands of common milkweed on noncrop land, or selective spraying in crop land, can be obtained with herbicides that are foliar applied to vigorous fall growth (2, 3, 4, 5, 51, 91) or during the bud stage in the spring (28). Glyphosate was most effective in common milkweed control 1 yr after the treatment, followed by amitrole, picloram (4-amino-3,5,6-trichloro-2-pyridinecarboxylic acid), dicamba, 2,4,5-T [(2,4,5-trichlorophenoxy)acetic acid], and 2,4-D (28). Picloram at 2.2 kg ha⁻¹ controlled common milkweed more than 90% 1 yr after treatment, while the combination of picloram and 2,4-D was not effec-(Table Fenac (2,3,6-5). trichlorobenzeneacetic acid), 2,4-D, 2,4- $DP[(\pm)-2-(2,4-dichlorophenoxy)$ propionic acid], and dicamba controlled common milkweed poorly.

For perennial weeds, topkill in the fall following a spring treatment is not a good indicator of the effectiveness of a herbicide. Control of common milkweed on the basis of stem counts taken in the fall about 4 mo after treatment was effective (81 to 99%) with all treatments (Table 6). However, the same treatments resulted in much lower control (27 to 88%) in the spring about 1 yr after treatment. Data reveals the importance of residual control of perennial weeds such as common milkweed 1 or 2 yr after application.

Biological Control. Insects and disease organ-

Table 5. Control of common milkweed in the spring 1 yr after treatment (average of three experiments) (58).

Herbicide	Rate	Control
	kg ha-1	_%_
Picloram	0.6	73
Picloram	1.1	88
Picloram	2.2	92
2,4-D + picloram	0.6 + 0.3	58
2,4-D + picloram	1.0 + 0.6	77
2,4-D + picloram	2.0 + 1.1	78
Dicamba	0.6	44
Dicamba	1.1	47
Dicamba	2.2	64
Fenac	1.1	37
Fenac	2.2	61
Fenac	4.5	61
2,4-D + dicamba	0.6 + 0.3	43
2,4-D + dicamba	1.1 + 0.6	40
2,4-D + dicamba	2.2 + 1.1	64
2,4-DP	1.1	18
2,4-DP	2.2	36
2,4-DP	4.4	40
2,4-D	1.1	10
2,4-D	2.2	33
2,4-D	4.4	. 29

Table 6. Apparent control of common milkweed in the fall of the year of treatment and in the spring 1 yr after treatment (58).

		Apparent conti	
Herbicide	Rate	Fall	Spring
	kg ha-1		%
Picloram	1.1	98	88
2,4-D + picloram	1.1 + 0.6	99	73
2,4-DP	2.2	84	50 '
Dicamba	1.1	88	, 29
2,4-D + dicamba	1.1 + 0.6	98	46
Fenac	2.2	88	52
2,4-D	2.2	81	27

isms attack common milkweed but can hardly be credited with any great reduction in plant density. Virus diseases result in a dense clumping of stems, together with yellowing or mottling and, finally, deforming of leaves, stems, and flowers.

Insects. A detailed study of insects found on common milkweed conducted by Dyon in 1960 (41) was reported in an earlier review by Bhowmik and Bandeen (21). Recently, Simard and Senecal (102) carried out an insect survey in two milkweed plantations in Quebec (Table 7). They found 140 insects belonging to six different orders, including 14 beneficial insects. Some of these insects could be explored for potential biological control of common milkweed.

Microorganisms and viruses. Limited infor-

Table 7. Inventory of beneficial and pest insects from a survey carried out on a 2-yr milkweed plantation at L'Acadie, Quebec in 1987 (102).

Species	Number insects collecte
	Conce
COLEOPTERA:	•
Cantharis rufa L.¹	2
Coccinella 7-punctata L.1	11
Coleonegilla maculata langi Timb¹	10
Diabrotica barberi S.&L.¹	12
Epitrix cucumeris Harris ²	2
Labidomera clivicollis Kby. ²	8
Photinus marginellus Lec. 1	1
Propylea 14-punctata L.1	4
Systena frontalis F. ²	11
Tetraopes tetrophthalmus Forst. ²	12
DIPTERA:	•
Bufofucilia silvarum Mg. ³	2
Coenosia tigrina Fab. ³	1
Delia olatura Mg. ³	1
Delia sp.3	1
Eristalis arbustorum L.¹ Eristalis dimidiata Wield.¹	1
	.1
Laphria thoracica Fab. ¹	
Pollenia sp. ³	3
Stratiomys normula Loew.1	1· 3
Syrphus torvus O.S.¹ HEMIPTERA:	3
Lygaeus kalmii Stal. ²	5
Lygus lineolaris P. de B. ²	3 10
Picromerus bidens L. ¹	4
Stenotus binotatus F. ²	3
HOMOPTERA:	3
	4
Cuerna sp. nymph²	•
Myzocallis asclepiadis Monell ² HYMENOPTERA:	10
Apis mellifera L. ¹	4
	4
Bombus perplexus Cresson ¹ Colletes kincaidii Cockerell ¹	1 1.
LEPIDOPTERA:	1
Choristoneura rosaceana Harris ²	2
Ctenucha virginica Esp. ²	2 1
Danaus plexippus L. ²	5
Tarachidia erastrioides Gn. ²	3 1
Turacinata erastriotaes On."	T

¹Beneficial insect; ²pest insect; ³insect with no impact.

mation has been reported on viruses or microorganisms that attack common milkweed since the last review by Bhowmik and Bandeen (21). The presence of flagella bacteria in the latex of common milkweed was reported in 1945 (65). The virus causing cucumber mosaic disease was reported to overwinter in common milkweed (75). Connors (34) also found aster yellow virus, Cellistephus virus 1, on common milkweed in Ontario. Limited efforts on the use of microorganisms or viruses for biological control have been made in the last 30 yr.

The most frequent disease of common milk-weed is caused by C. clavata (Ger) Cke. (41).

It is widespread in Ontario (34) and Quebec (41). Several parasitic fungi such as *Uromyces asclepiadis* Cke. and *Puccinia bartholomaei* Diet. *Phyllactinia guttata* Lev., *Erysiphe cichoracearum* DC. and *Glomerella fusarioides* Edgert., *Botrytis hypophylla* Ell. & Kell., *Septoria asclepiadis* Sacc., *Ascophyta asclepiadis* Ell. & Ev., *Fusarium roseum* Lk., *Cercospora asclepiadis* Ell., and *C. clavata* (Ger) Cke. attack common milkweed (99, 100).

Research Needs. It is apparent from this review that there is a lack of information on some important aspects of common milkweed biology. First, the mechanism of root bud dormancy of common milkweed is not well understood. To date, only observations have been made on root bud dormancy in relation to the size of root fragments, temperature, and carbohydrate reserve. Unfortunately, no detailed investigation has been made to determine the role of the above-mentioned factors. In addition, research efforts must be extended to identify the role of other factors such as auxins, carbohydrates, and environmental conditions.

There is an ambiguity in the terminology such as root buds vs. adventitious root buds and lateral roots vs. creeping roots. Also, the terminology on rootstocks, root fragments, root sections, and root system needs to be better defined and standardized for future research.

Since common milkweed is a perennial, encroachment of roots between the borders of adjacent plots in an experiment is unknown. It is important to restrict the spread between the adjacent plots for assessing the control of root system or for the control of any new growth. Therefore, methodology for establishing and conducting long-term control research on common milkweed should be developed. One needs to determine not only the first year control, but also monitor the residual control 1 or 2 yr following the treatment year.

Limited research information on the incidence or encroachment of common milkweed in no-till or reduced-tillage systems is available. Each cropping system deals with a specific tillage operation ranging from primary tillage, secondary tillage, or reduced tillage. Effects of tillage systems on the encroachment and persistence of common milkweed must be examined.

Biological control of common milkweed has potential as an area of future research. It is evident from the literature that various insect species feed on common milkweed. The life cycle and the specificity of these insects need to be explored for potential biological control of common milkweed.

There is also a need to develop methods for common milkweed control under integrated management systems. The interaction of mowing, cutting height, and residue from cover crops (including living mulch) on common milkweed population biology needs to be explored. Research efforts must continue for developing effective control of this species in various cropping systems in addition to corn, soybeans, small grains, and sorghum. Presently, economic analysis of any control strategies for common milkweed is practically nonexistent. Our research efforts must focus on economic analysis of common milkweed control if we are to make decisions on optimization of farm inputs for maximum crop yields.

CONCLUSION

Common milkweed is a perennial weed native to eastern North America. The first record on North American plants was reported in 1635. It is one of the 20 species of *Asclepiadaceae* found in the United States.

Common milkweed is a problem weed limited to the region bounded by 35 and 50 degrees N latitude and 60 and 103 degrees W longitude. It is spread throughout all the eastern half of the United States except states or part of states along the Gulf coast. Common milkweed is a problem weed in corn, sorghum, soybeans, and other crops. This species is also abundant on roadsides, fence rows, railroads, right-of-ways, and wastelands.

Common milkweed grows and reproduces rapidly at temperatures 20 to 27 C. Seedlings are capable of producing new aerial shoots from adventitious root buds within 21 d after germination. Each plant is capable of developing an extensive root system with adventitious root buds that may produce new shoots. One seedling is capable of producing as many as 56 stalks vegetatively and 94 seedlings in an undisturbed environment for a 4-yr period. Each plant can produce as many as 425 seeds in one growing season.

Common milkweed is not as competitive as other broadleaf weeds. However, it has potential to reduce crop yields as much as 10 to 30% in corn, soybeans, or sorghum. Water extracts of common milkweed can be allelopathic to some plants such as wild oats.

Common milkweed is still one of the difficult-to-control weeds in cropping systems. It is, however, easier to control in noncropping lands with a nonselective herbicide. The use of a recirculating sprayer with a nonselective herbicide in short-statured crops such as soybeans and small grains has been effective in controlling common milkweed. The most cost-effective control will result from an integrated program that utilizes crop rotation and spot treatment of the uncontrolled plants. This tenacious perennial weed will continue to be a problem weed in crop production as we reduce crop rotations and tillage practices. On the other hand, the search for potential use of common milkweed floss as a textile fiber will continue.

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