GROWTH AND DEVELOPMENT OF

HONEYVINE MILKWEED

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figure Page

INTRODUCTION

Each chapter of this dissertation is a separate and complete manuscript to be submitted to Weed Science for publication. The format of each manuscript conforms to the style of Weed Science.

PART I

GERMINATION AND DEVELOPMENT OF HONEYVINE MILKWEED (*Ampelamus albidus*)

Germination and Development of Honeyvine Milkweed (*Ampelamus albidus*)[1]

JOHN K. SOTERES and DON S. MURRAY[2]

Abstract. The ability of honeyvine milkweed [*Ampelamus albidus* (Nutt.) Britt.] to establish and develop from seed was studied in laboratory and field experiments. Optimum germination temperature was 30 C. Seed incubated at cooler temperatures and then transferred to 30 C germinated as well as seed originally incubated at 30 C. Germination was not affected at moisture stress levels between 0 and -4.6 bars, but was decreased at levels between -4.6 and -12.8 bars. The optimum pH range for germination was between 5 and 7. The greatest emergence of seedlings occurred at a depth of 0.5 cm with no emergence occurring at depths greater than 5 cm. Greater emergence was obtained in a loam than in a sandy loam at all planting depths except 0.5 cm. Field plots seeded on May 1 gave maximum seed production as compared to later seedling dates. Seed production decreased with each 2-week delay in planting. Planting dates of July 10 or later produced no seed. Seed germination was little affected by delayed planting through June 12. The following spring, regrowth was less vigorous from plants seeded on June 12 or later compared to regrowth from plants seeded earlier.

Additional index words. Weed biology, temperature, moisture stress, pH, soil type, depth of emergence, planting date.

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INTRODUCTION

Honeyvine milkweed is a perennial, herbaceous, vine which is a serious problem in many agronomic crops of southern, southwestern, and midwestern states. At this time, it is not a problem on large acreages in Oklahoma, but localized heavy infestations do occur on several sites (4). In areas where effective annual weed control is obtained, weed species shifts are occurring which appear frequently to include honeyvine milkweed. The occurrence of this weed has increased substantially over the past few years. Crop yield reductions have not been documented; however, the climbing nature of the plant causes harvesting problems with cotton strippers and peanut digger-inverters.

There are few reports available on the effects of environmental conditions on honeyvine milkweed seed germination (2, 3). Freshly harvested seed from Mississippi did not show any dormancy (6), and seed buried over winter in Illinois retained its capacity to germinate (2). Evetts and Burnside (3), reported that honeyvine milkweed seed germination occurred over a more restricted pH range than did common milkweed (*Asclepias sysiaca* L.). They further reported high levels of germination of honeyvine milkweed seed when salt concentrations were increased from 0 to 5,000 ppm.

Knowledge of seed production capabilities of perennial plants could help forecast the potential spread of a species into new areas. Some perennial species, such as common milkweed, do not flower and produce seed the first year (1). Keeley and Thullen (5), studying the influence of planting date on seed production of johnsongrass [*Sorghum halepense* (L.) Pers.], found that maximum production occurred with May 1 and June 1 planting dates. Production decreased with both earlier and

later planting dates. The maximum number of viable seed coincided with maximum seed production. Detailed studies of edaphic and climatic factors affecting germination, emergence, and development of honeyvine milkweed are necessary for predicting the potential spread of this weed into new areas, as well as aiding in the development of control or management procedures.

This paper describes experiments with honeyvine milkweed to determine the effect of (a) temperature, solution pH, and simulated moisture stress on seed germination and seedling development, (b) depth of seedling emergence as affected by soil type, and (c) planting date on establishment, phenological development, and seed production.

MATERIALS AND METHODS

Honeyvine milkweed seed used in all germination experiments were collected at locations in central Oklahoma in 1978 from mature, perennial plants. The coma, a tuft of hairlike structures on the seed, was removed and seed were stored at room temperature for 3 months prior to use. In most germination experiments, seed were placed between moistened, Whatman #2 filter papers in 10-cm diameter, plastic petri dishes. Preliminary experiments indicated that fungicide seed-treatment was not needed. A randomized block design was used in the incubators with four replications of 50 seed per petri dish, and all experiments were repeated. Unless otherwise noted, germination tests were conducted at 30 C in a dark incubator and seed were recorded as germinated when the emerging radicle was 2-mm long. Germination counts were taken at 2-day intervals over an incubation period of 8 days.

Temperature effects on germination. Germination was determined in

dark incubators set 15, 20, 25, 30 and 35 ± 1 C. The filter paper was moistened with 6 ml of distilled water. At the end of the 8-day incubation period, all petri dishes were transferred to the 30 C incubator and changes in germination were recorded at the end of an additional 8-day incubation period.

Simulated moisture stress. Aqueous solutions of polyethylene glycol[3] (PEG), having an average molecular weight of 6000, were prepared by dissolving appropriate amounts of PEG in distilled water to obtain osmotic potentials of -1.1, -2.7, -4.6, -6.3, -9.5, and -12.8 bars. Seed were moistened with 6 ml of the appropriate PEG solution and placed in a dark incubator at 30 C. Percent germination was determined at the end of the 8-day germination period and 10 germinated seed were selected at random from each replication and radicle lengths were measured.

Effects of pH on germination. Buffered solutions were prepared using 0.1 M potassium hydrogen phthalate in combination with either 0.1 M HCl or 0.1 M NaOH to obtain solution pH levels of 3, 4, 5, and 6. A 0.025 M borax solution in combination with 0.1 M HCl gave solutions with pH levels of 8 and 9. Unbuffered distilled water was used for pH 7. Petri dishes containing 50 seed were moistened with 6 ml of the appropriate pH solution. The use of buffered solutions for studying the influence of pH on germination has been described by Wilson (8).

Depth of emergence. Ten honeyvine milkweed seed were planted in a Norge loam (Thermic Paleustoll) and a Teller fine sandy loam (Udic Arg-

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[3]Polyethylene glycol was supplied as Carbo-Wax 6000, Union Carbide Corp.

iustoll) in 900-ml plastic cups at depths of 0.5, 1.5, 2.5, 5.0, 7.5, and 10.0 cm. Soils were initially moistened by subirrigation and then watered daily from the top. The experiment was conducted in a controlled environment chamber set at 28 ± 2 C with 12-h day. Emergence was recorded 40 days after planting.

Influence of planting date on seed production. Field studies were initiated in the spring of 1979 and 1980 to determine the influence of seed planting date on honeyvine milkweed establishment, development, and seed production. Seed were planted 2.5 cm deep in 2-m long rows in a Norge loam and watered daily until emergence. After emergence, plants were thinned to eight plants per plot. Seed were planted every 2 weeks from May 1 through July 24 in each year. Plots, single rows 2-m long, were arranged in a randomized block design with five replications. Data taken were as follows: (a) days from planting to emergence; (b) days from planting to flowering; (c) total pod production; (d) seed per pod; (e) total seed production; and (f) seed germination. Seed pods were harvested in November and total pod production was determined by counting all pods produced by the eight plants in a plot. Four pods were randomly selected from each replication and the number of seed per pod recorded. After storage at room temperature for 2 months, 30 seed were selected at random from four pods per replication for germination percentage determination at 30 C in a dark incubator. In the spring of 1980, plant height measurements were taken on the regrowth of plants seeded in 1979.

RESULTS AND DISCUSSION

Temperature effects on germination. The optimum germination tempera-

ture was 30 C with 86% germination (Figure 1). Germination decreased at temperatures above and below 30 C. No germination was noted at 15 C and only 6% of the seed germinated at 20 C. After the initial 8-day germination period, all seed were incubated for an additional 8 days at 30 C. Germination counts taken at the end of this second incubation period, indicated no injury to the seed associated with the 15, 20, or 25 C temperatures. Germination upon re-incubation was 87%, 85%, and 83% for 15, 20, and 25 C respectively. Seed incubated at 35 C showed no further increase in germination with a 30 C re-incubation, indicating that high temperatures may be lethal to honeyvine milkweed seed. This observation is in agreement with preliminary work conducted at Stonevill, MS, where a high temperature generated in field plots covered with clear polyethylene sheeting was responsible for a significant reduction in the number of viable seed of several weed species.[4]

Simulated moisture stress. There was a decrease in germination when the water potential of the germination medium was greater than -4.6 bars (Figure 2). Germination of 66% was recorded at the most severe simulated moisture stress of -12.8 bars as compared to over 90% when stress was -4.6 bars or less. This suggests less influence of moisture stress on honeyvine milkweed germination than was indicated by Evetts and Burnside (3); however, their simulated moisture stress was created by using mannitol solutions rather than PEG. They reported 99% germination at 0 bars of osmotic potential, and 78, 5, and 0% germination at osmotic potentials of -5.1, -9.1, and -11.1 bars, respectively. Thill

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[4]Anonymous. 1980. Weed control by solar energy. Weed Sci. Soc. Am., Newsl. 8(1):16.

et al.(7), suggested that PEG solutions were better germination media than mannitol solutions.

Radicle length decreased for each increment increase in moisture stress (Figure 2). The response of radicle growth to moisture stress was more pronounced than the response of germination. Honeyvine milkweed seed have the ability to imbibe water and initiate the germination process even under a stress of -12.8 bars (66% germination). However, seedling development is significantly retarded with a stress of only -4.6 bars (58% reduction in radicle length at -4.6 bars).

Effects of pH on germination. The optimum pH range for germination was between 5 and 7, where an average of 82% of the seed germinated (Figure 3). Germination decreased at pH levels outside this range, with germination percentages of 38 and 36% at pH 3 and 9, respectively. Evetts and Burnside (3), using unbuffered solutions containing HCl and NaOH, reported no significant differences in percent germination between pH 4 to 10.

Depth of emergence. Emergence of honeyvine milkweed seed decreased with increased planting depth in both soils (Table 1). No seedlings emerged with planting depths greater than 5 cm. Except for the values obtained with a 0.5-cm planting depth, significantly more emergence was observed in the loam as compared to the sandy loam. This could be attributed to the increased crusting of the soil surface found with the sandy loam. We did not observe a soil-volume change in pot cultures and therefore did not attribute the differences in emergence to soil composition. Coble and Slife (2), studying emergence of honeyvine milkweed from a clay loam, reported emergence with planting depths of 7.5 cm. These data indicate the importance of soil type on depth of

emergence in this species.

Influence of planting date on seed production. There were no significant differences in the response of honeyvine milkweed to planting date in either year; therefore, all responses except regrowth were averaged over both years. Maximum seed pod production was obtained with the earliest planting date (Table 2). Seed pod production decreased with each 2-week delay in planting with no pods being produced on plants seeded on or after July 10. The days after planting to emergence generally decreased with delay in planting date. Because plots were watered daily until emergence, the more rapid emergence with delay in planting was not due to differential soil moisture. Faster emergence could be related to warmer soil temperatures at later planting dates. For those plantings resulting in flower production, days to flowering after emergence decreased with delay in planting date. Flowering occurred from early August to early September, depending on planting date. These data suggest that while day length is critical to flowering, the physiological age of honeyvine milkweed is also a limiting factor.

No significant differences were found in the number of seed per pod or the percent germination for seed collected from the first four planting dates (Table 2). A reduction of seed/pod was noted for pods collected from the June 26 planting, and these seed did not germinate. The maximum number of seed produced per eight plants was approximately 18,500 from plants seeded May 1.

As an indication of regrowth vigor, height measurements were taken in May, 1980 from eight plants in each of the 1979 planted plots. Regrowth shoots emerged between April 10 and April 14, 1980, in all

plots planted in 1979. A reduction in regrowth height was observed with the later planting dates (Table 2). Honeyvine milkweed seeded in May or June has a more extensive root system and therefore produced more vigorous regrowth the following year. Further evidence of a more extensive root system with early plantings was the presence in September, 1979, of lateral shoots or daughter plants in plots seeded before July 10, 1979.

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TABLE I

INFLUENCE OF PLANTING DEPTH ON HONEYVINE MILKWEED SEEDLING EMERGENCE IN TWO SOIL TYPES

Planting depth	Soil type: Norge loam	Soil type: Teller fine sandy loam
(cm)	(%)	
0.5	84	84
1.5	70	53
2.5	63	23
3.5	53	17
5.0	34	1
7.5	0	0
10.0	0	0
Mean	38	22

Planting depth LSD (0.05)	12%
Soil type LSD (0.05)	12%
CV (%)	35

TABLE II

HONEVINE MILKWEED PHENOLOGICAL CHARACTERISTICS AND SEED POD PRODUCTION AS AFFECTED BY PLANTING DATE OF SEED[a]

Planting date	Planting to emergence	Emergence to flowering	Seed pods produced[b]	seeds/pod	Germination	Seed produced[b]	Regrowth height
	----------(days)----------		----------(no.)---------		(%)	(no.)	(cm)
May 1	14	82	127	146	65	18,500	22
15	10	77	106	155	68	16,400	22
29	9	71	44	139	61	6,100	28
June 12	13	68	23	140	63	3,200	15
26	10	61	0.4	103	0	40	16
July 10	9	-	0	-	-	0	11
24	6	-	0	-	-	0	9
LSD (0.05)	-	-	22	19	21	-	6
CV (%)	-	-	39	20	35	-	33

[a]All responses, except regrowth height, were averaged over two years data.

[b]Average of 8 plants per plot.

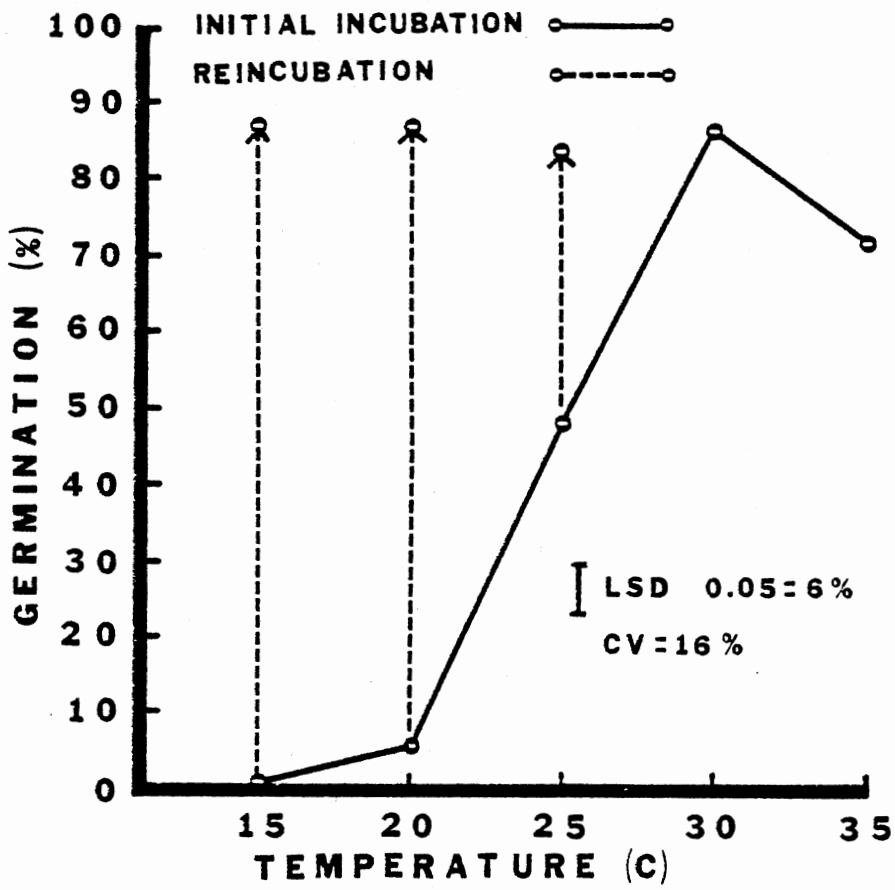

Figure 1. Influence of initial and reincubation temperatures on honeyvine milkweed seed germination.

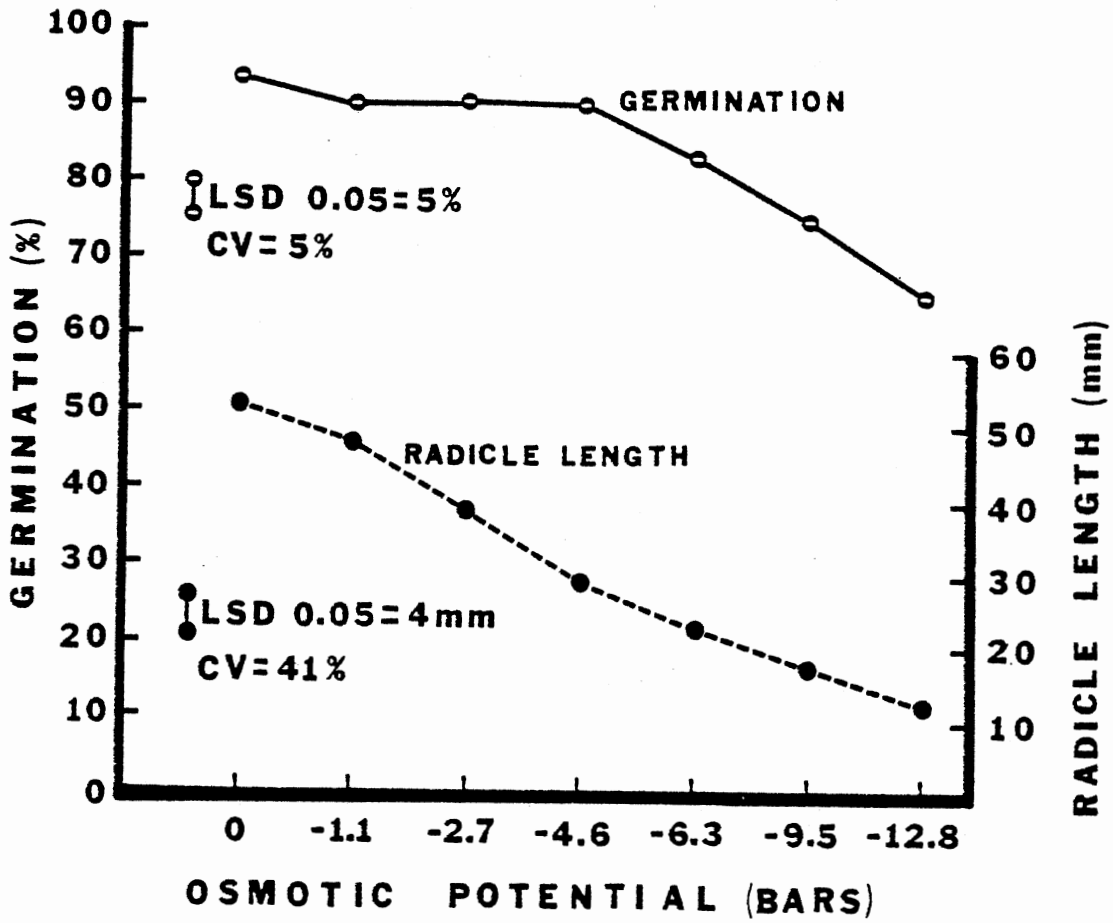

Figure 2. Germination and radicle growth response of honeyvine milkweed seed after 8 days exposure to various water potential levels.

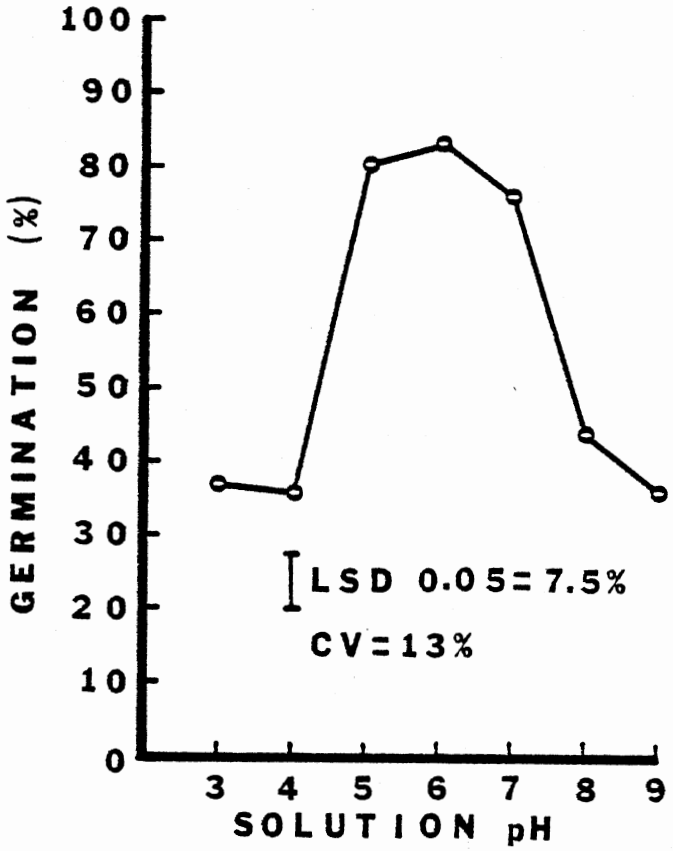

Figure 3. Influence of solution pH on honeyvine milkweed seed germination after 8 days.

PART II

ROOT DISTRIBUTION AND REPRODUCTIVE BIOLOGY OF HONEYVINE MILKWEED (*Ampelamus albidus*)

Root Distribution and Reproductive Biology of Honeyvine Milkweed (*Ampelamus albidus*)[1]

JOHN K. SOTERES and DON S. MURRAY[2]

Abstract. Laboratory and field experiments were conducted to define the root system of honeyvine milkweed [*Ampelamus albidus* (Nutt.) Britt.] and to study factors affecting the growth of new plants from rhizome fragments. The root system of a typical plant was composed of lateral roots radiating from a sparsely branched vertical tap root. Laterals tended to be concentrated in a boundary area between a loamy surface soil and a zone of clay accumulation; this being below the zone of cultivation. Vertical tap roots were found to a depth of 2-m, with sections collected at this depth and shallower demonstrating the ability to produce new plants. In laboratory studies, rhizome sections were killed by freezing for 2 h or by drying at either 20 or 30 C for 24 h. The optimum temperature for shoot development from rhizomes was between 20 and 30 C. Shoot emergence and growth from buried rhizome sections were not generally affected by depth of planting or length of rhizome. As many as 45 daughter shoots were produced from a single plant originating from seed and 27 daughter shoots from a planted rhizome section 131 days after planting. The maximum distance daughter shoots were observed from original plants was 111 cm.

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Additional index words. Weed biology, freezing, drying, space planting, root distribution, propogation from rhizomes.

INTRODUCTION

Honeyvine milkweed is a perennial vine and a serious problem in many agronomic crops of midwestern, southwestern, and southern states. Initial infestations are usually found in low, moist areas of cultivated fields and along fence rows. Once established, the weed is difficult to control through the use of either chemical or cultural methods and becomes a persistant problem.

The importance of honeyvine milkweed as a weed is related to its means of reproduction. The seed, which are light, with a silky tuft of hair at their apex, may be transported over great distances by the wind. The seed has a high germination capacity, and establishment appears to be easily accomplished (7). Honeyvine milkweed is also capable of vegetative reproduction from root and rhizome fragments. Roots and rhizomes have buds randomly arranged along their entire length. A new plant can develop from a fragment containing a single bud (2). Distribution within a field may be accomplished by the movement of these fragments during tillage operations.

A lack of agreement exist in the literature on the classification of various parts of the root system of honeyvine milkweed. Robinson (6), identified rhizome and root structures, but Coble and Slife (2), were unable to identify underground parts as rhizomes. However, in both papers, the location or depth that samples were collected was not specified. Frazier (3), mapped the root development of honeyvine milkweed seedlings at different growth stages and described the underground

system of a single plant as being composed of horizontal lateral roots radiating from a vertical tap root. Shoots emerged from buds located on what he described as "permanant lateral roots" which produce aerial stems and vertical underground stems which he termed "rhizomes". In preliminary research, we were unable to clearly identify vertical underground stem tissue as being a rhizome or root. However, for the purposes of this study we will use the terminology of Frazier for seedlings to describe the root system of established plants. Such a description for established plants growing under cultivated field conditions was not found in the literature. An objective of this research was to describe and map the root system of established plants. Studies determining the influence of various environmental factors on the regenerative ability of rhizome fragments and on the growth of plants arising from those fragments were also conducted.

MATERIALS AND METHODS

Root excavations. Three trenches were dug to a depth of 2-m in a cultivated field which had been infested with honeyvine milkweed for at least 10 years. The root system of 15 plants which had been exposed on the sides of these trenches, were observed and measurements taken. The soil in the study area was a Udic Argiustoll and consisted of a Teller sandy loam surface soil extending to 30 cm, a zone of clay accumulation between 30 and 100 cm, and a zone of loose sand below 1-m. The diameters of rhizomes, lateral roots, and tap roots were measured at depths to 2-m. Sections of tap root, 5-cm long, were collected at 30-cm intervals, from the 50 to 200 cm depths to determine their regenerative ability. Fifteen root sections per sampling depth were collected, taken

to the laboratory, and planted 2.5 cm deep in 6-cm deep flats containing a mixture of sand and peat. The flats were placed in a 30 C environmental control chamber with 12 h light and 12 h dark for 21 days. The criteria used to determine regenerative ability for this study and all others in this paper were the production of shoots from buds located on root and rhizome fragments.

Time required for bud formation. A field study was conducted to determine when viable buds were formed on tillage disturbed rhizomes. The, 30 by 30 m, study area was located adjacent to the root excavation site. The area was disked approximately 7.5 cm deep in May, 1980, and 15 rhizomes were collected from the top 15-cm of soil on six sample dates after disking. The six sample dates for rhizome collection were 17, 28, 40, 86, 131, and 274 days after disking. This corresponded to aerial growth stages of eight true leaves, 12 true leaves, 26 true leaves, flowering, seedpod formation, and winter kill or dormant stage, respectively. After collecting, rhizomes were wrapped in moistened paper and taken to the laboratory where each rhizome was cut into 5 c-m long sections and planted 2.5 cm deep in 6-cm deep flats containing a mixture of sand and peat. The flats were then placed in a greenhouse with 25 ± 3 C and 14 h days and 18 ± 3 C and 10 h nights. The total number of sections sprouting was recorded 21 days after planting.

Environmental factors affecting rhizome regenerative ability. Three seperate laboratory experiments were conducted to study the influence of temperatures between 15 and 35 C, drying, and freezing at -2 C on the regenerative ability of honeyvine milkweed rhizome sections. Prior to each experiment, rhizomes were randomly collected from the top 15 cm of soil from a field with an established infestation. Care was taken to

prevent drying after collection by keeping rhizomes wrapped in moistened paper until they were subjected to appropriate conditions. After collecting, rhizomes were cut into 5-cm long sections with each section having at least three prominant buds. All experiments were repeated and rhizomes were freshly collected from the same field before each experiment.

The influence of drying was studied by exposing rhizome sections to temperatures and relative humidities (RH) of 4 C with 40% RH, 20 C with 22% RH, and 30 C with 30% RH for 24, 48, 96, and 192 h. Rhizome sections were randomly arranged on open trays before being placed in dark incubators set for the appropriate temperatures and relative humidities. Fresh weights were taken before and after exposure. Six rhizome sections were removed at each time interval and weighted before planting. The sections were planted 4 cm deep in a Norge loam (Thermic Paleustoll) in 480-ml containers. A group of six rhizome sections, not incubated were planted immediately after being collected. The planted containers were arranged in a randomized complete block design in an 30 C environmental control chamber with 12 h light and 12 h dark. At the end of the 21-day growth period, shoot emergence was recorded.

The influence of freezing was studied by placing 5-cm long rhizome sections between moistened germination paper in 3 by 8 by 8 cm closed germination boxes and freezing for 2, 4, 6, 24, 48, and 96 h at -2 C. Two rhizome sections were placed in each germination box and the boxes were arranged in a randomized complete block design within the freezer. Three replicates were removed after each freezing period and allowed to thaw slowly, first at 10 C and then at 24 C, before being placed in a dark 30 C incubator. Rhizomes, treated in a similar manner but

not frozen, were immediately placed in the 30 C incubator. Shoot emergence was recorded 10 days after being placed in the 30 C incubator. Only shoots 2 mm or longer were counted.

The regenerative ability of rhizomes and growth of shoots exposed to above freezing temperatures was studied by placing rhizome sections between moistened germination paper in 3 by 8 by 8 cm germination boxes. Four boxes, of five rhizome sections per box, were arranged in a randomized complete block design within incubators set at constant temperatures of 15, 20, 25, 30, and 35 C. Rhizomes were incubated for 8 days. At the end of the incubation period, the number of rhizome sections sprouting, number of shoots per rhizome section, and the length of shoots were recorded. Only shoots 2 mm or longer were counted.

Influence of rhizome length and depth of planting on shoot emergence. Rhizomes were collected from the top 15 cm of soil and cut into 2.5, 5, 10, and 15 cm lengths. In 8-1 containers, two rhizomes of each length were planted 2.5, 5, 10, and 15 cm deep in a Norge loam. Fresh weights of rhizomes were recorded prior to planting. The rhizomes were initially watered by subirrigation and then surface watered every third day. The containers were arranged in a randomized complete block design in a 29 ± 1 C environmental control chamber with 12-h day and each treatment was replicated three times. The total number of rhizome sections which produced at least one aerial shoot was determined 45 days after planting. Days to emergence and shoot heights, 8 days after emergence, were also recorded. The experiment was repeated.

Lateral distribution of shoots. Seed and 10-cm long rhizome sections were planted in a field, free of honeyvine milkweed, on May 7, 1980. Seed were planted 2.5-cm depth and roots to 8-cm depth. Plantings were

spaced 4-m apart and arranged in a randomized complete block design with 4 replications. The number of daughter shoots produced by a single plant and the distance of daughter shoots from the original plant were determined 131 days after planting. Seed pod production for the original plants was also recorded.

RESULTS AND DISCUSSION

Root excavations. The root system of a typical honeyvine milkweed plant was prepared from composite observations taken from 15 excavated root systems (Figure 1). Vertical tap roots were traced to 200-cm, the maximum depth excavated, but evidence indicated that the roots extended further. Hitchcock and Clothier (4), also observed a tap root of honeyvine milkweed which extended to a depth of 215 cm. Tap roots were generally unbranched, but branching two or three times was occasionally observed, 50 to 70 cm below the soil surface. Buds were observed along the entire length of the 200 cm tap root. Lateral roots radiated from the tap roots, 20 to 30 cm below the soil surface. This depth corresponded to the boundary between the loamy surface soil and the zone of clay accumulation found in this soil profile. This depth was also well below the soil area which would be disturbed during tillage operations. Frazier (3) in describing the root system of 25 week old honeyvine milkweed plants growing in an undisturbed area, noted that several lateral roots appeared on the same side of tap roots at depths of 7 to 40 cm. Shoots emerged from all lateral roots regardless of depth. We did not find evidence of this occurring in established stands exposed to normal tillage practices. Only one lateral root radiated in a specific direction and all appeared to grow from the same general area on the

tap root. Tillage would have disturbed the shallower lateral root leaving only those below the disturbed zone intact. Associated with the lateral roots were a network of small fibrous roots, apparently functioning in nutrient and water uptake. Buds were not observed on these fibrous roots, and fibrous roots were not associated with tap roots below the junction of the lateral roots. We observed no evidence of two or more vertical tap roots being connected by lateral roots.

Rhizomes developed from buds located on lateral roots, and eventually gave rise to leafy shoots. Rhizomes also developed from the apical end of tap roots; this being above the junction of the lateral roots. These rhizomes, arising from either lateral or tap roots, are designated as primary rhizomes (Figure 1). In addition, it was observed that secondary rhizomes developed from buds located on primary rhizomes. This occurred when the primary rhizomes had been disturbed during disking but were still attached to the lateral roots.

Root diameters were measured as an indication of carbohydrate storage potential (Table 1). Studies on carbohydrate root reserves of horsenettle (Solanum carolinense L.) showed a close correlation between root weights and carbohydrate content (5). Lateral root diameters at the point where rhizomes emerged were larger than areas between rhizomes. Lateral roots were smaller in diameter than either rhizomes or tap roots. The average diameter of tap roots did not greatly change, as depth increased from 50 to 200 cm.

All tap root sections collected from 50 to 200 cm produced aerial shoots. Although other factors would be involved, this suggests that the root system of honeyvine milkweed has the potential of establishing

aerial shoots even after the destruction of a portion of the root system. Bakker and Gaessler (1), observed aeriel shoots of field bindweed (Convolvulus arvensis L.) arising from root stocks found at a depth of 1.5 m.

Time required for bud formation. Buds were not observed on rhizome surfaces and no shoots developed from the rhizome sections collected 40 days or less after disking (Table 2). Bud formation and subsequent shoot development was observed for rhizomes sampled 86 days or later after disking.

Environmental conditions affecting rhizome regenerative ability. Rhizomes of honeyvine milkweed are fleshy, brittle and lack a protective outer layer. This would suggest a vulnerability of the rhizome when exposed to environmental extremes. Rhizome sections frozen, in a moist environment, for 2 to 96 h, failed to produce shoots when thawed and transferred to the favorable temperature for shoot development of 30 C. The frozen rhizomes had decayed by the end of the 10 day, 30 C incubation period. The regenerative ability of rhizome sections dried for 24 h to 192 h at 5 C with 40% RH, 20 C with 22% RH, and 30 C with 30% RH, was also reduced. No shoots developed from rhizomes dried for 24 h or longer at 20 C (22% RH) and 30 C (30% RH). However, 75% of the rhizomes dried for 24 h at 5 C (40% RH) retained their ability to produce shoots but not when dried at this temperature for longer times. Rhizome weights were reduced by 34% when dried for 24 h at 5 C (40% RH). Rhizome weights were reduced more than 46% when dried for 48 h or longer at 5 C (40% RH) and 24 h or longer at 20 C (22% RH) and 30 C (30% RH). This suggests that rhizomes exposed on the soil surface for a relatively short time would have a reduced ability to produce shoots

and potentially develop into established plants.

The optimum temperature for shoot development from rhizomes was 20 and 30 C, with 100% sprouting at 30 C (Figure 2). No shoots developed from rhizomes incubated at 15 C and only 31% sprouted at 35 C. Rhizomes incubated at 20, 25, and 30 C, produced an average of 1.5 shoots per rhizome. However, observations from other studies have shown that one shoot will eventually dominate, with the others dying back. Multiple shoots were not observed on rhizomes incubated at 35 C. Shoot growth decreased at temperatures above and below 30 C (Figure 2). This suggests that high summer and cool spring temperatures may restrict honeyvine milkweed development from rhizomes.

Influence of rhizome length and depth of planting on shoot emergence. In general, as rhizome length increased, percent shoot emergence increased (Figure 3A). Shoot emergence from rhizome lengths of 2.5 and 5.0 cm showed a more dramatic response to depth of planting than did the longer lengths. Apparently with the 2.5 cm rhizomes planted at the 2.5 cm depth, soil moisture fluctuations caused erratic shoot emergence. Shoot emergence from rhizomes, 10 and 15 cm in length, did not show a variable response to depth of planting. Percent emergence, averaged over all depths and rhizome lengths, was 71%. This suggests that tillage would probably aid in the distribution of honeyvine milkweed.

Shoot heights were measured as an indication of the rate of plant growth. Within each planting depth, shoot heights generally increased as rhizome lengths increased (Figure 3B). This was especially apparent when rhizome lengths increased from 5 to 15 cm. As was observed for shoot emergence, shoot growth from each rhizome length was generally not affected by planting depth.

Lateral distribution of shoots. A single plant started from seed produced from 5 to 45 daughter shoots and a single plant started from a rhizome section produced from 3 to 27 daughter shoots (Table 3). The average number of daughter shoots produced from seed and rhizome was 16 and 13 shoots, respectively. The maximum distance daughter shoots were observed from the original plants (seed or rhizome) 131 days after planting was 111 cm. It was noted that shoots tended to radiate from the original plants in specific directions; an indication of lateral root distribution. No specific distances between shoots was indicated, as suggested by Robinson (6).

Honeyvine milkweed plants originating from either seed or rhizome have the ability to produce an appreciable quantity of seed during the first year of growth (Table 3). Plants originating from rhizomes produced slightly more seed than those started from seed.

Honeyvine milkweed has an extensive underground system of roots and rhizomes with the majority of this system located in the top soil horizon. This area is often subjected to frequent disturbances in cultivated fields, with rhizomes being fragmented and carried to virgin areas. As this work indicates, new populations may develop from these transported rhizomes. However, this is dependent upon the developmental stage of the rhizome as well as the exposure of rhizomes to various environmental conditions.

As was mentioned in the introduction, honeyvine milkweed is a persistant problem. This can be explained by the depth to which roots may penetrate and by their demonstrated regenerative ability. Therefore, control measures should be directed not only toward aerial shoot and

shallow root and rhizome control but also toward the control of these deep growing portions of the plant.

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TABLE I

HONEYVINE MILKWEED ROOT AND RHIZOME DIAMETERS

Depth below soil surface	Vegetative type	Diameter[a] mean	range
(cm)		--------(mm)	-------
10	rhizome	3.2	(3.0 to 3.5)
20 to 30	lateral root	2.6	(3.2 to 5.0)
60	vertical tap root	5.5	(4.0 to 8.0)
120	vertical tap root	5.1	(4.2 to 6.0)
200	vertical tap root	4.5	(3.0 to 6.0)

[a]Values are means of 15 observations

TABLE II

TIME REQUIRED AFTER DISKING FOR BUD FORMATION ON RHIZOMES

Days after disking	Aerial growth stage at sampling	Percent sprouting
		(%)
17	8 true leaves	0
28	12 true leaves	0
40	26 true leaves	0
86	blooming	100
131	pod formation	100
274	dormant	100

TABLE III

LATERAL DISTRIBUTION OF DAUGHTER SHOOTS FROM SINGLE PLANTINGS OF SEED OR RHIZOME SECTIONS

Original plant	Original plant number	Daughter shoots	Max. distance of daughter shoots from original plant	Seed production of original plant
		(no.)	(cm)	(no.)
Seed	1	45	111	43
	2	14	92	23
	3	8	98	14
	4	9	87	13
	5	5	69	12
Mean	-	16	91	21
Rhizome	1	27	91	54
	2	19	97	33
	3	9	86	27
	4	6	95	23
	5	3	57	15
Mean	-	13	85	30

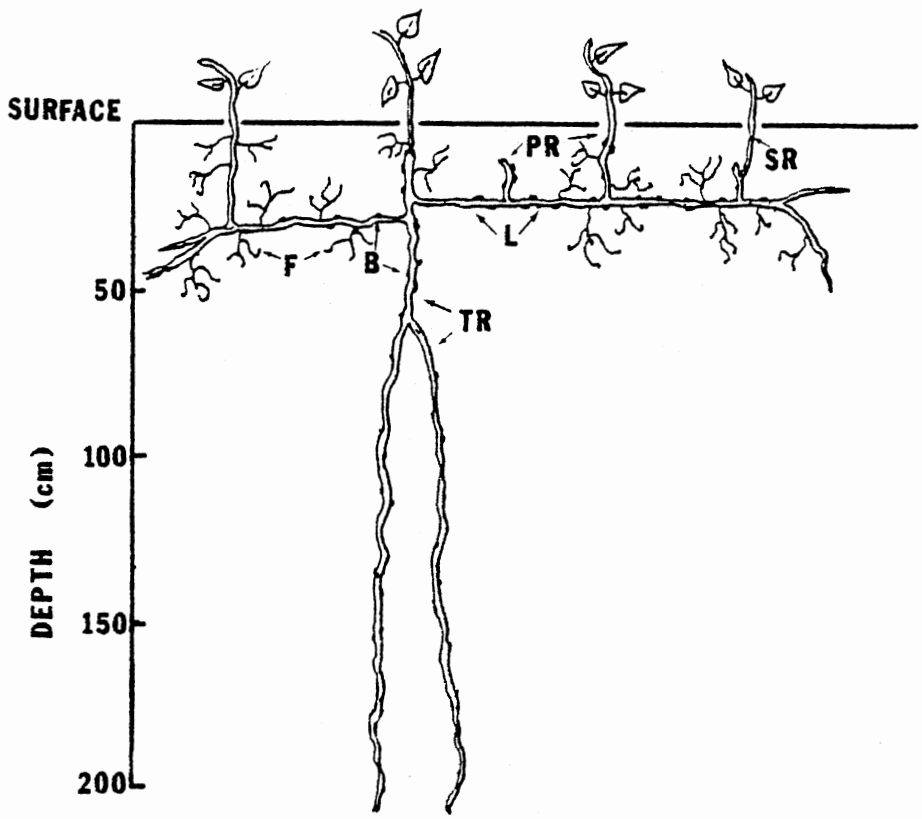

Figure 1. Typical root distribution of honeyvine milkweed as prepared from composite observations taken from roots excavated in a cultivated field site. TR, vertical tap root; L, lateral root; PR, primary rhizome; SR, secondary rhizome; B, buds; F, fibrous roots.

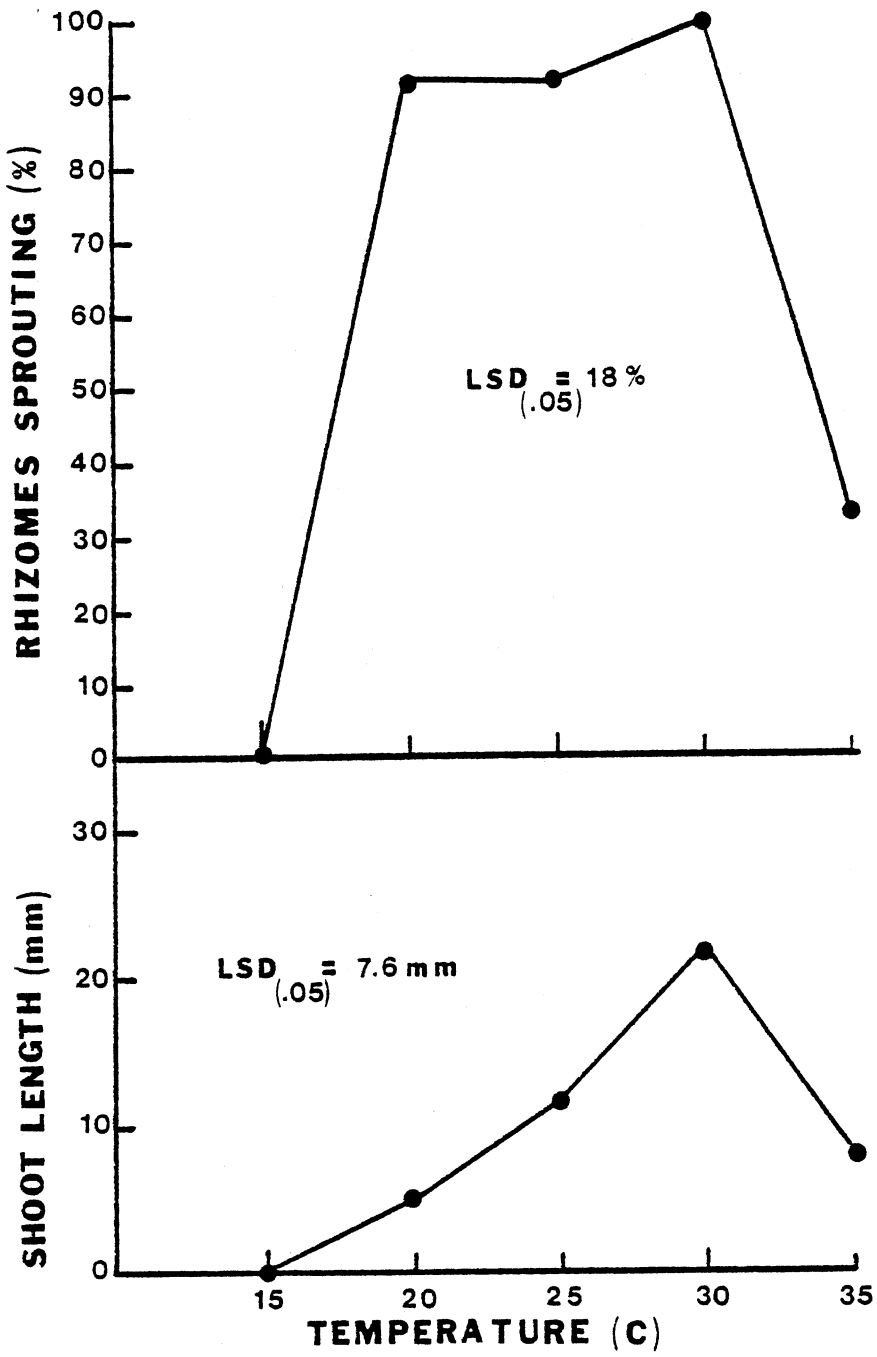

Figure 2. Effect of temperature on the regenerative ability of rhizome sections and subsequent shoot development.

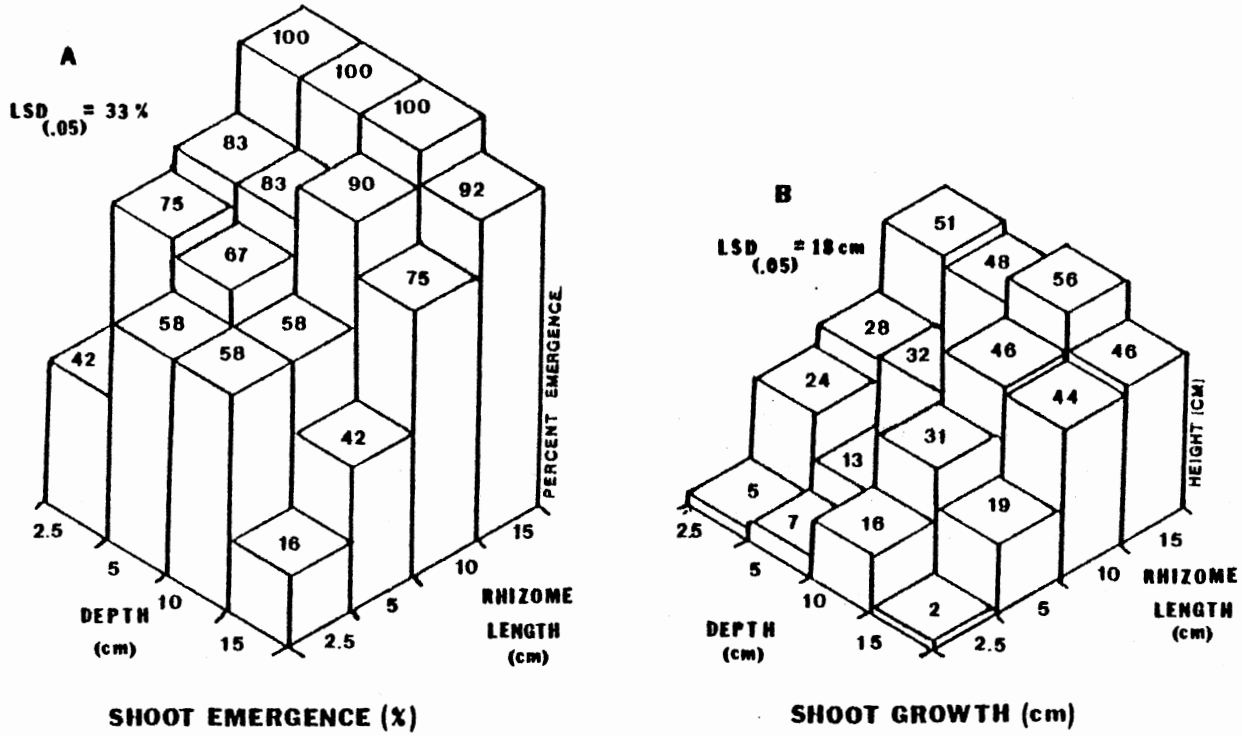

Figure 3. Influence of rhizome length and depth of planting on shoot emergence and growth. (A). Percent shoot emergence. Based upon total number of rhizome sections able to send up at least one shoot. (B). Aerial shoot growth recorded 8 days after each shoot emerged.

PART III

ADSORPTION OF 2,4-D, DICAMBA, AND GLYPHOSATE BY EXCISED HONEYVINE MILKWEED (*Ampelamus albidus*) LEAVES

Adsorption of 2,4-D, Dicamba, and Glyphosate by Excised Honeyvine Milkweed (*Ampelamus albidus*) Leaves[1]

JOHN K. SOTERES, DON S. MURRAY, and EDDIE BASLER[2]

Abstract. Absorption of the acid derivatives of 2,4-D [(2, 4-dichlorophenoxy) acetic acid] and dicamba [3, 6-dichloro-0-anisic acid] and the isopropylamine salt of glyphosate [N-(phosphonomethyl) glycine] by excised leaves of honeyvine milkweed [*Ampelamus albidus* (Nutt.) Britt.] was studied in relation to leaf position on the plant (terminal versus basal) and with versus without the spray additive SA-77[4-isopropenyl-1-methylcyclohexene]. Absorption of the three herbicides by terminal and basal leaves was increased with the addition of SA-77. However, SA-77 increased absorption into basal leaves more than into terminal leaves. SA-77 reduced surface tension and increased drying time of water droplets on adaxial leaf surfaces. The solution pH of the herbicides was reduced by SA-77. Scanning electron micrographs of adaxial leaf surfaces treated with SA-77 showed an alteration of epicular wax orientation. This disorientation resulted in areas with reduced wax cover and thus may have allowed easier penetration of the herbicides. Absorption of all three herbicides, without SA-77, was greater into terminal than into basal leaves. However, differential

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[1]Received for publication _____

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absorption between terminal and basal leaves was not apparent when SA-77 was added. Generally, no differences were observed in the absorption of 2,4-D and dicamba into leaves collected at different times. Glyphosate absorption was greater in terminal leaves collected after a period of adequate moisture than after a period of dry conditions.

Additional index words. Surfactant, additive, SA-77, leaf position, collection date, scanning electron micrographs, herbicide.

INTRODUCTION

Successful chemical control of weedy perennial species, such as honeyvine milkweed, often depends upon adequate herbicide penetration into aerial plant parts. Three herbicides expecially effective for the control of many perennial species are 2,4-D dicamba and glyphosate. The initial barrier to penetration of these foliar-applied herbicides is the lipophyllic epicuticular wax on leaf surfaces. Herbicide selectivity has been related to differences in thickness and chemical composition of this waxy layer (5, 9, 12). In addition, the quantity, composition, and orientation of the epicuticular waxes may vary with respect to leaf age and environmental conditions; and thus may influence chemical absorption (6, 7, 13, 15, 16, 17).

Surfactants are known to enhance the phytotoxicity of 2,4-D, dicamba, and glyphosate (1, 8, 19). Surfactants reduce the surface tension of the spray solution and thereby aid in absorption and phytotoxicity (18). However, increases in phytotoxicity have been associated with surfactant concentrations above those of maximum surface tension reduction (2, 14). Thus the possibility of mechanisms other than those which alter only the physical characteristics of the herbicide solution

may be suggested (3, 4, 13).

The spray additive, SA-77, is a new compound being promoted for use with herbicides. Preliminary field studies have shown that when SA-77 was used at concentrations greater than 1% v/v, increased glyphosate phytotoxicity was observed.[3] The objectives of this research were, (a) to examine the influence of SA-77 on the absorption of 2,4-D, dicamba, and glyphosate into excised leaves of honeyvine milkweed and (b) to determine the morphological responses of leaf surfaces to SA-77.

MATERIALS AND METHODS

Absorption procedure. Honeyvine milkweed leaves were collected from field grown plants on two different dates during the summer of 1980. The first collection date (Date 1) was July 29. Leaves collected on Date 1 were from well developed plants of approximately 50 true leaves that were under a moderate drought stress. Thirty days prior to Date 1, environmental conditions were hot and dry with average daily high and low temperatures of 37 and 25 C and 0.1 cm of rain recorded. The second sampling (Date 2) was made on August 28 when plants were flowering. During the eighteen days prior to Date 2, environmental conditions were slightly cooler with average daily high and low temperatures of 35 and 22 C and 8.7 cm of rain recorded. General conditions for growth were more favorable prior to Date 2 than prior to Date 1.

Terminal and basal leaves were collected at each collection date and were distinguishable not only by position but also by differences in

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[3]Chykaliuk, P. B., unpublished data.

size, texture, and color. Glossy, light green terminal leaves were collected from the top 2 cm of growth. The dull, dark green basal leaves were collected between 10 and 20 cm from the plant base. Dry weight of terminal and basal leaves averaged, 0.027 ± .009g and 0.146 ± .07g, respectively. After removal, leave petioles were immediately embedded into moistened tissue paper in 25 to 50 cm rectangular flats. The flats were covered with perforated clear polyethylene sheeting to prevent losses in leaf turgidity, and placed in a 25 C environmental control chamber with 12 h fluorescent light. Leaves were maintained in this environment for 2 h prior to herbicide treatment.

Herbicide solutions were prepared by adding appropriate amounts of ^{14}C-labeled 2,4-D acid, dicamba acid, and the isopropylamine salt of glyphosate to distilled water. The glyphosate solution also contained 0.03% of the surfactant, MON 0818. Specific activities were 10.10, 17.06, and 1.95 uC/uM for 2,4-D, dicamba, and glyphosate, respectively. SA-77 was added to half of each herbicide solution to give a SA-77 solution concentration of 5% v/v. Ten ul of each herbicide solution was applied in five 2-ul drops onto the adaxial surface of each leaf. Herbicide concentrations applied to each leaf were 1.61×10^{-4}, 9.4×10^{-5}, and 1.1×10^{-3} M of 2,4-D, dicamba, and glyphosate, respectively. After herbicide application, flats were covered with the polyethylene sheeting and placed in the 25 C environmental control chamber. At the end of 2 and 24 h exposure intervals, excess herbicide was removed from the leaf surfaces by rinsing the surfaces twice with 95% ethanol and then immersing the leaves in distilled water with agitation twice for 10 sec each. Leaves were blotted dry and immediately frozen before being freeze-dried. Absorption of ^{14}C-herbicide was

determined by combusting the leaf and petiole in a biological oxidizer and trapping the $^{14}CO_2$ released for liquid scintillation analysis. The data was analyzed as a factorial with treatments arranged in a randomized complete block design with eight replications.

Measurements of surface tension, drying time, and solution pH. The influence of SA-77 on surface tension was indirectly determined by measureing the diameters of equal volume droplets of distilled water and 5% v/v water solutions of SA-77 applied to adaxial leaf surfaces. Five 2-ml droplets of either water or water plus SA-77 were applied on opposite sides of the midribs of the three adaxial basal leaf surfaces. The leaves were placed under florescent lights and diameters were recorded prior to evaporation. The droplets having larger diameters were assumed to have lower surface tensions.

The influence of SA-77 upon the drying time of water droplets on adaxial leaf surfaces was studied. Leaves were spotted with 2-ul droplets of either distilled water or water plus SA-77 as described above. Elapsed time from application until the liquid film on the leaf surfaces were no longer visible was recorded.

The pH of 5% v/v SA-77 solution and solutions of SA-77 plus 2,4-D, dicamba, and glyphosate were determined using a standard pH electrode. Herbicide concentrations and formulations were the same as those used in the absorption experiments.

Leaf surface morphology. Scanning electron micrographs (SEM) were made of adaxial surfaces of terminal and basal leaves, treated and not treated with SA-77. Leaves were treated with 5% v/v SA-77 by applying 2-ul droplets on one-half of adaxial leaf surfaces. The leaves were maintained for 24 h in the manner described for the absorption experi-

ment. Portions of leaf from the treated and untreated areas were then prepared for the SEM by first fixing the tissue for 2 h in 2% osmuim tetroxide, mixed 1:1 with cacodylate buffer, and rinsing three times in distilled water. Samples were then dehydrated in an alcohol series and critical point dried before being coated with a 200-Å thick layer of gold/palladium in a Hummer II apparatus.

RESULTS AND DISCUSSION

Leaf absorption. Absorption of 2,4-D, with and without SA-77 was greater by leaves exposed for 24 h than leaves exposed for 2 h (Figure 1). Absorption of 2,4-D by both terminal and basal leaves was increased with the addition of SA-77, regardless of collection date or sampling time. After 24 h, SA-77, caused a greater increase in absorption into basal leaves than into terminal leaves, for both collection dates. Without SA-77, terminal leaves absorbed more 2,4-D than basal leaves at Date 1 but not at Date 2, after 24 h. When SA-77 was added, this difference between terminal and basal leaves was not observed. Under the environmental conditions of these experiments, date of collection was generally not observed to be important in the leaf absorption of 2,4-D. Environmental factors, such as temperature and available moisture, prior to treatment have been shown to influence the leaf absorption of herbicides (12).

Absorption of dicamba was greater by leaves exposed for 24 h than leaves exposed for 2 h (Figure 2). As observed for 2,4-D, collection date did not alter the absorption of dicamba after 24 h. SA-77 generally enhanced absorption of dicamba regardless of the date of collection or the exposure time. After 24 h, SA-77 increased dicamba absorption

into basal leaves more than into terminal leaves, for both collection dates. After 2 h, absorption in both terminal and basal leaves was increased with SA-77 for Date 1 but not for Date 2. After 24 h terminal leaves absorbed more dicamba, without SA-77, than basal leaves. With SA-77, terminal leaves absorbed slightly less dicamba than basal leaves. However, this was not apparent after 2 h, where absorption, with SA-77, was generally greater in terminal than in basal leaves.

Absorption of glyphosate increased as exposure time increased from 2 to 24 h (Figure 3). After 24 h, SA-77 increased absorption into basal leaves but did not influence absorption into terminal leaves, for both dates. Within each time interval, glyphosate absorption without SA-77, as influenced by leaf position, varied between the two collection dates. After 24 h, absorption was greater in terminal leaves than basal leaves on Date 2, but on Date 1 absorption was the same. After 2 h, absorption without SA-77, was also greater in terminal leaves than basal leaves on Date 2, but absorption was less in terminal than basal leaves on Date 1. More new growth occurred prior to leaf collection on Date 2 than prior to Date 1 because of the more favorable temperature and moisture conditions. Therefore, because of the more favorable growth conditions the epicuticular wax composition and orientation of terminal leaves collected on Date 2 may have been different from those collected on Date 1. This could have accounted for the differences observed.

The leaf absorption of 2,4-D dicamba, and glyphosate generally increased with the addition of SA-77, regardless of collection date. This trend was generally observed after 2 h, but was expecially apparent after 24 h. However, SA-77 did not appear to affect glyphosate absorption to the extent that it affected 2,4-D and dicamba absorption. This

may have resulted from the use of glyphosate solutions formulated with the surfactant, MON 0818, in addition to SA-77. Dicamba and 2,4-D did not have any additional surfactants. For these herbicides, SA-77 caused greater increases in absorption into basal leaves than into terminal leaves after exposure for 24 h.

Surface tension, drying time, and solution pH. Additives, such as SA-77 may alter absorption by various mechanisms. They may alter solution pH and thus affect absorption of ionic herbicides by influencing the proportion of charged to uncharged molecules in solution. SA-77, at 5% by volume, reduced the pH of distilled water and each of the herbicide solutions by approximately 2 pH units (Table 1). This lowering of solution pH would tend to increase the absorption of these herbicides. Additives may also reduce the surface tension and thus increase the area of contact between the herbicide and leaf surface. In addition, they may increase the drying time of the herbicide solution on the leaf surface. Positive responses to both of these factors would promote herbicide absorption (2). SA-77 increased the area of contact between the water droplets and leaf surface (Table 2). This suggests that SA-77 reduced the surface tension. Drying time was also increased with the addition of SA-77 (Table 2). In addition, it was observed that areas of leaf treated with SA-77 retained an orange residue after evaporation. These areas exhibited a water soaked appearance which was visible on the adaxial and abaxial leaf surfaces. This may indicate the eventual necrosis of the treated leaf tissue. Foy (3), reported that the phytotoxic effect of a surfactant he studied was initially seen as water soaked areas on leaves, followed by wilting.

Leaf surface morphology. Scanning electron micrographs, taken of

basal and terminal adaxial leaf surfaces which were treated or not treated with SA-77, showed a disorientation of the epicuticular waxes on the treated leaves (Figure 4). This disorientation resulted in leaf areas with less wax, thus possibly leaving exposed areas on the surface for easier herbicide penetration. High concentrations of surfactants and additives form aggreggates, termed micelles, which may consist of two to many molecules (11). Furmidge (5), suggested that micelle formation of several surfactants occurred at concentrations greater than 0.05% by volume. Once formation of micelles have occurred, the surfactant may solubilize or disorganize the surface waxes (5). This appears to be happening with SA-77.

Absorption, after 24 h, was generally greater in terminal leaves for all three herbicides without SA-77. This may be explained by the difference in orientation of epicuticular wax on basal and terminal leaves as pictured in Figures 4A and 4C. Wax on terminal leaves appear to be arranged into areas of dense wax deposition separated by less dense areas. These areas of reduced wax cover may provide sites of easier herbicide penetration. In contrast, wax deposition on basal leaves was more uniformly distributed with no obvious variability in wax density. Sargent and Blackman (10), demonstrated decreased absorption of 2,4-D with leaf maturation, i.e., terminal leaves absorbed more than basal. With the addition of SA-77, terminal leaves absorbed the same or slightly less of the three herbicides than basal leaves.

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TABLE I

INFLUENCE OF SA-77 ON SOLUTION pH

Herbicide	Without SA-77	With SA-77
	----------(pH)----------	
Distilled water	5.9	4.0
2, 4-D	5.7	3.8
Dicamba	5.8	3.9
Glyphosate	5.7	3.7

TABLE II

INFLUENCE OF SA-77 ON SURFACE TENSION

AND DRYING TIME OF WATER DROPLETS

Treatment	Surface tension		Drying time	
	Droplet diameter	Standard deviation	Time	Standard deviation
	--------(mm)---------		----(min)-----	
Distilled water	1.0	± 0.2	32	± 0.5
Water plus 5% SA-77	2.8	± 0.2	48	± 2.5

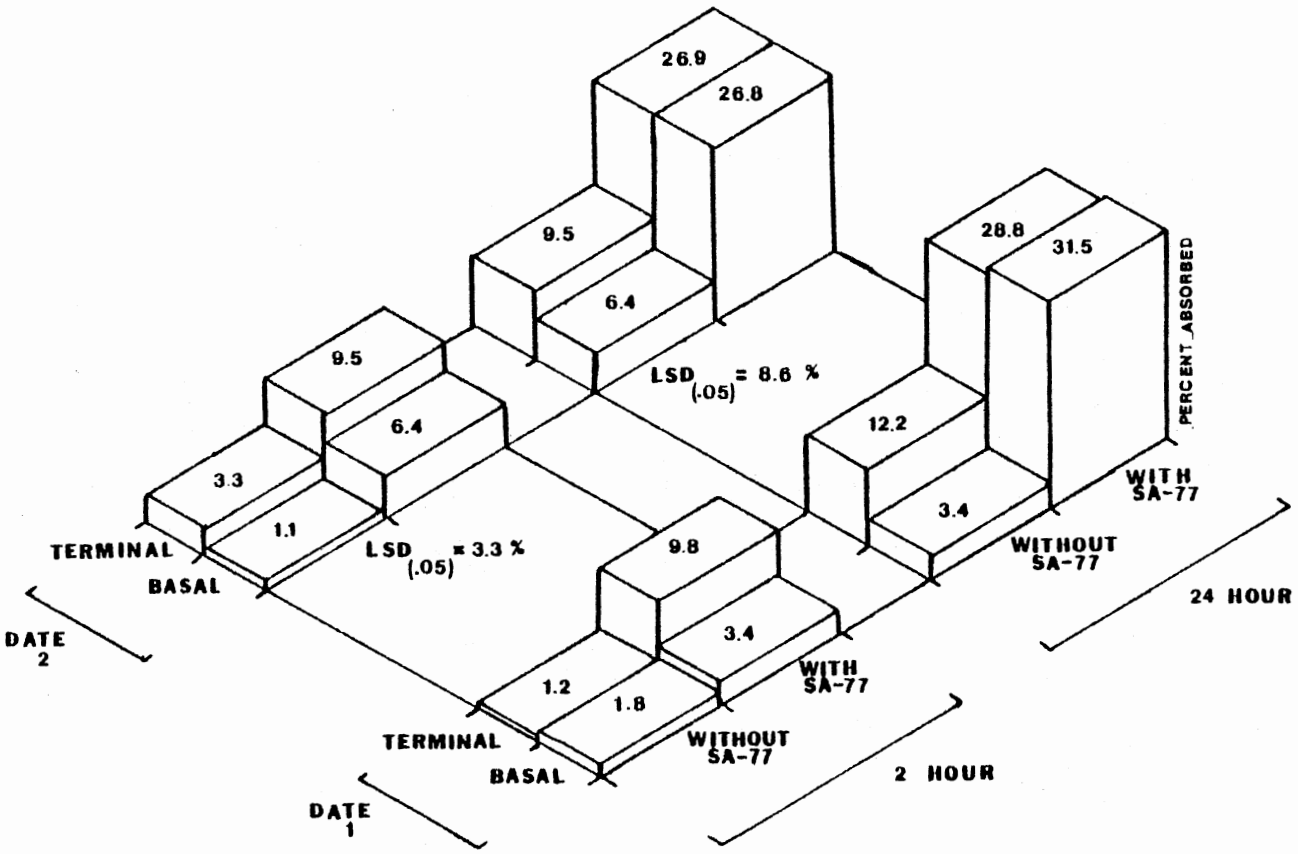

Figure 1. Percent 2,4-D absorbed into excised terminal and basal leaves of honeyvine milkweed. LSD values correspond to the factorial analysis of collection date, leaf position, and with or without SA-77, for each exposure time.

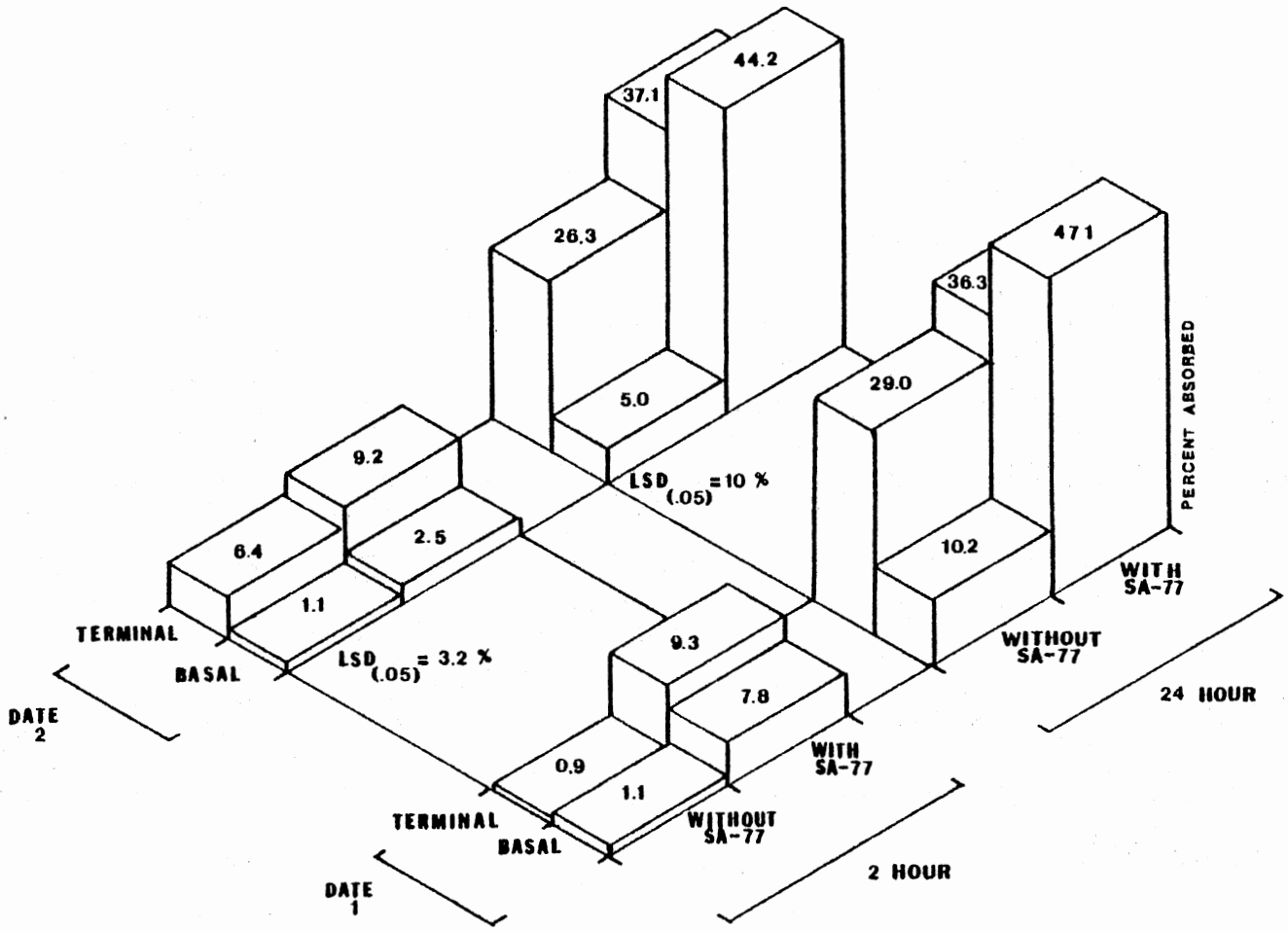

Figure 2. Percent dicamba absorbed into excised terminal and basal leaves of honeyvine milkweed. LSD values correspond to the factorial analysis of collection date, leaf position, and with or without SA-77 for each exposure time.

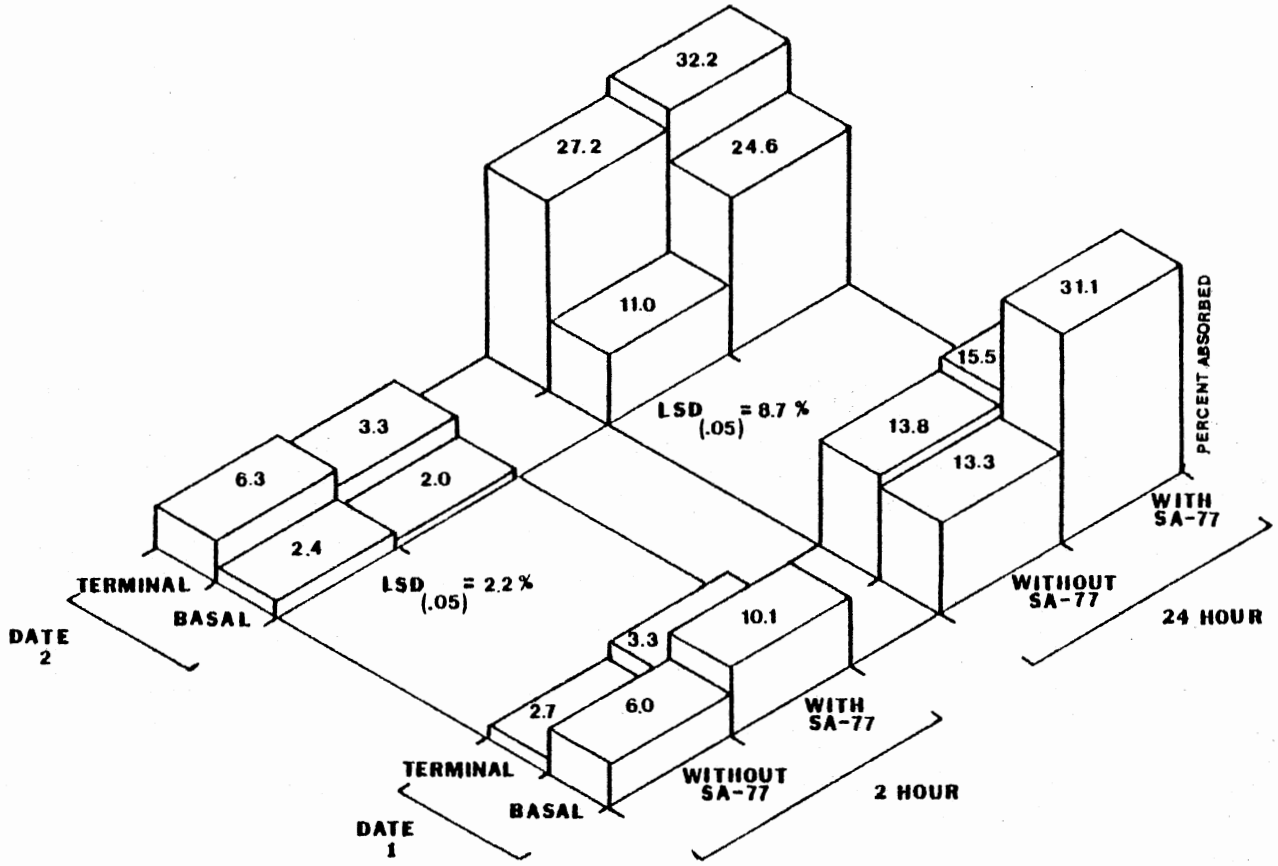

Figure 3. Percent glyphosate absorbed into excised terminal and basal leaves of honeyvine milkweed. LSD values correspond to the factorial analysis of collection date, leaf position, and with or without SA-77 for each exposure time.

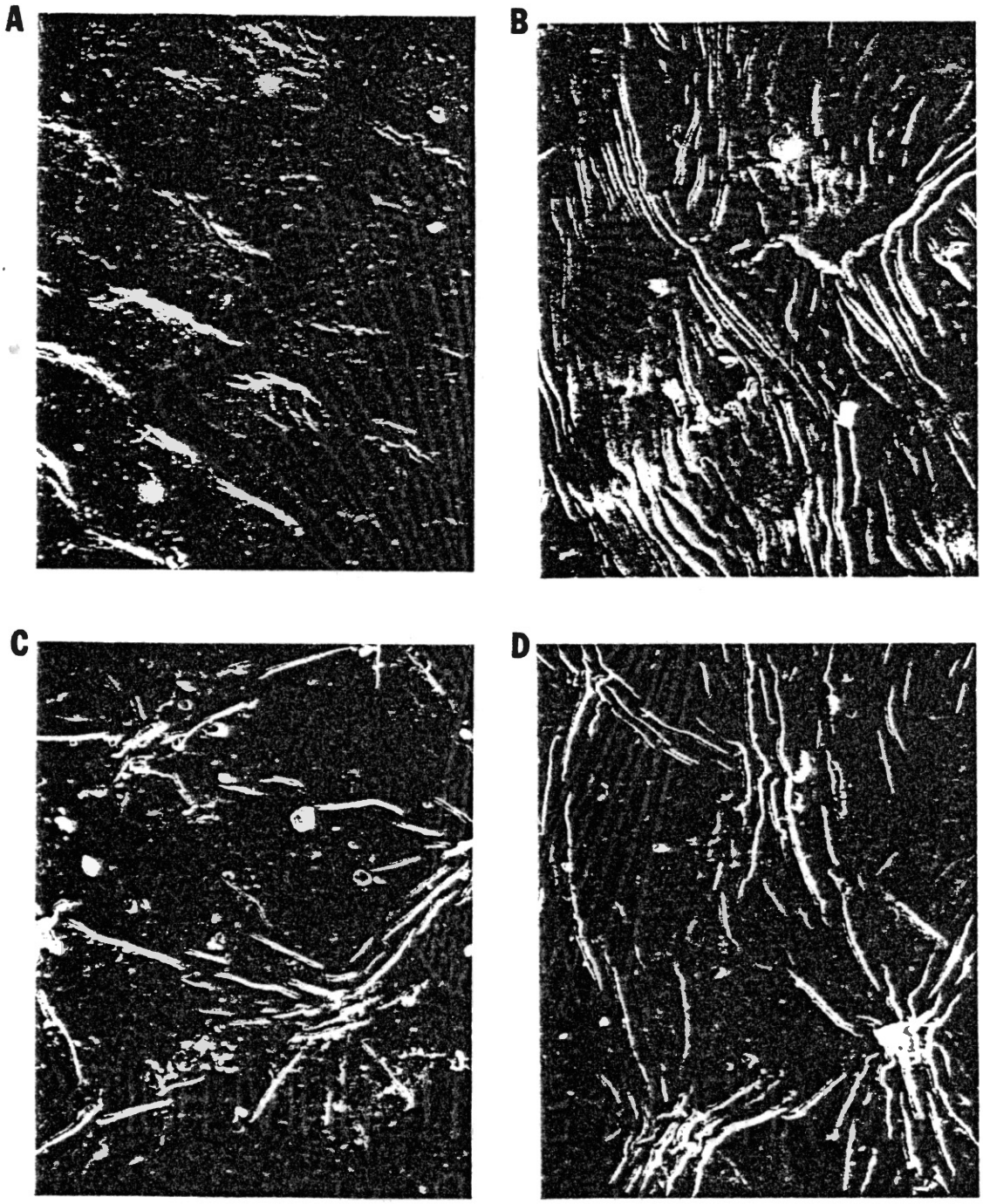

Figure 4. Scanning electron micrographs of adaxial leaf surfaces of honeyvine milkweed. (A). Terminal leaf, untreated; (B). Terminal leaf, treated with SA-77; (C). Basal leaf, untreated; (D). Basal leaf, treated with SA-77. Magnified 1500 X.

VITA[2]

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Doctor of Philosophy

Thesis: GROWTH AND DEVELOPMENT OF HONEYVINE MILKWEED

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