

Megacerus discoidus, A POTENTIAL BIOLOGICAL
CONTROL AGENT OF HEDGE BINDWEED IN
SOUTHWESTERN VIRGINIA

by

Ren Wang

Dissertation submitted to the Faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of
DOCTOR OF PHILOSOPHY
in
ENTOMCLOGY

APPROVED:

L. T. Kok, Chairman

R. L. Pienkowski

J. L. Eaton

E. C. Turner Jr.

K. K. Hatzios

May, 1985
Blacksburg, Virginia

2/2/86 MCR

Megacerus discoidus, A POTENTIAL BIOLOGICAL
CONTROL AGENT OF HEDGE BINDWEED
IN SOUTHWESTERN VIRGINIA

Ren Wang

Committee Chairman: Loke T. Kok

Entomology

(ABSTRACT)

Megacerus discoidus (Say)(Coleoptera: Bruchidae), a native North American seedfeeder, has 4 larval instars and one generation a year. Overwintering occurred in the 4th instar. Larvae fed on 40-50% of the seed content before diapause and the rest of the seed in the following spring. When more than one larvae attacked a seed, only one adult emerged because of cannibalism, which was most common among 2nd and 3rd instars. Adults oviposited mainly under the bracts of host seedpods. The life cycle of the beetle was well synchronized with the host phenology.

When diapause of the insect was experimentally terminated under 20°C and 28°C, there was increased mortality and prolonged adult emergence. No adult emergence occurred when infested seeds were maintained in the dark

under 10°C for 200 days. However, mortality of the larvae was significantly increased. Humidity and soil coverage of host seeds had no significant impact on the beetle mortality during diapause under field conditions.

Of 19 plant species tested, only hedge bindweed and wild sweet potato, Ipomoea pandurata, supported larval development to adults. Oviposition occurred only on seedpods of hedge bindweed and heavenly blue morningglory, Ipomoea tricolor. The latter did not support larval development.

An infestation rate of 5 M. discoidus eggs per seedpod of hedge bindweed in the field cages was achieved by releasing the adults at a relatively high adult/plant ratio (1.2 pairs/plant) plus inoculation of eggs on all seedpods in the cages. This resulted in a high rate (ca. 70%) of seed infestation, but did not destroy all of the seeds in the field cages. Release of lower number of adults led to lower seed infestation. Seed consumption did not cause any change in reproduction and vegetative growth of hedge bindweed. I consider the use of M. discoidus to be safe but it must be combined with other stress factors to achieve effective control.

ACKNOWLEDGEMENTS

First, I sincerely thank Dr. Loke T. Kok, my major advisor, whose wise advice has helped me solve the puzzles and avoid pit-falls throughout the past three and a half years of my study. His philosophy, encouragement, and sometimes, criticism, has certainly made me a better person, and, a more patient and accurate scientist. Appreciations also go to other members of my advisory committee, Drs. R. L. Pienkowski, J. L. Eaton, E. C. Turner Jr. and K. K. Hatzios, for their advice and editorial recommendations on my research and course work.

I am especially indebted to the Rockefeller Foundation, under whose generous fellowship, my long-cherished dream has come to reality, to Dr. Joseph R. Bookmyer of the Rockefeller Foundation, and to Drs. Clarence Gray III, Roger A. Teekell, P. Howard Massey Jr., and Bernard E. LaBerge of VPI&SU, each, in his own way, has made all this work possible.

Special thanks go to _____ for his technical assistance and advice on supplies and literature searches, to _____ and his wife _____, who have helped to make Blacksburg a much interesting place to stay, and to Thomas F. Wieboldt of the Herbarium, Dept. of Biology, VPI&SU, for identification of weed plants.

I deeply appreciate the company and help provided by my colleagues, , , and especially, . These names will always have a special place in my heart.

Finally, I wish to express my special thanks to , he and I have been sailing on the same boat for 5 years. Upon sharing our happiness, anguish, and ...homesickness, he, as a true friend, has helped me immeasurably to overcome the odds!

CONTENTS

ABSTRACT	II
ACKNOWLEDGEMENTS	IV

Chapter

	<u>page</u>
I. INTRODUCTION	1
II. BINDWEEDS AND THEIR BIOLOGICAL CONTROL	7
The Target Weeds	8
Taxonomy and distribution	8
Economic importance	10
Biology	12
Growth and development	12
Reproduction	15
Response to herbicides and cultural control	18
Biological control of bindweeds	19
Foliage feeders	21
Root and stem feeders	22
Seed feeders	23
III. LIFE HISTORY OF <u>MEGACERUS DISCOIDUS</u> (COLEOPTERA:BRUCHIDAE), A SEEDFEEDER OF HEDGE BINDWEED, IN SOUTHWESTERN VIRGINIA	26
Introduction	27
Materials and Methods	30
Life cycle	30
Synchronization with host	31
Results and Discussion	32
Life cycle	32
Synchronization with host	39
IV. INFLUENCE OF TEMPERATURE, HUMIDITY AND SOIL COVERAGE ON THE DIAPAUSE OF <u>MEGACERUS</u> <u>DISCOIDUS</u> (COLEOPTERA:BRUCHIDAE), A SEEDFEEDER OF HEDGE BINDWEED	44
Introduction	45
Materials and Methods	46
Effect of temperature on diapause of <u>M.</u> <u>discoidus</u>	46

Effect of temperature on mortality during diapause and post-diapause development of <u>M. discoidus</u>	47
Effects of humidity and soil coverage of the seeds on overwintering mortality of <u>M.</u> <u>discoidus</u>	48
Results and Discussion	49
Effect of temperature on diapause of <u>M.</u> <u>discoidus</u>	49
Effect of temperature on mortality during diapause and post-diapause development of <u>M. discoidus</u>	54
Effect of humidity and soil coverage of the seeds on overwintering mortality of <u>M.</u> <u>discoidus</u>	57
 V. HOST SPECIFICITY OF <u>MEGACERUS DISCOIDUS</u> (COLEOPTERA:BRUCHIDAE), A NATIVE SEEDFEEDER OF BINDWEEDS.	58
Introduction	59
Materials and Methods	61
Larval development tests	61
Oviposition tests	63
Results and Discussion	64
Larval development tests	64
Oviposition tests	65
 VI. IMPACT OF <u>MEGACERUS DISCOIDUS</u> (COLEOPTERA:BRUCHIDAE) ON GROWTH AND SEED PRODUCTION OF HEDGE BINDWEED	68
Introduction	69
Materials and Methods	70
Impact of <u>M. discoidus</u> on seed production	70
Hedge bindweed growth response to seed infestation	72
Results and Discussion	73
Impact of <u>M. discoidus</u> on seed production	73
Hedge bindweed growth response to seed infestation	76
 VII. SUMMARY AND CONCLUSIONS	79
 REFERENCES CITED	84
 VITA	93

LIST OF TABLES

<u>Table</u>	<u>page</u>
1. Insects and mites that have been evaluated for biological control of bindweeds	24
2. Duration of stages in the field and measurements of <u>M. discoidus</u>	33
3. Percent mortalities ($\bar{x}\pm S.D.$) of diapause and post-diapause stages of <u>M. discoidus</u>	55
4. Percent mortalities ($\bar{x}\pm S.D.$) of <u>M. discoidus</u> in response to seed coverage and high and low humidity.	56
5. Plant species used in the host specificity tests for <u>M. discoidus</u>	62
6. Summary of <u>M. discoidus</u> larval development tests.	66
7. Seedpod and seed formation of hedge bindweed in response to infestation by <u>M. discoidus</u> ($\bar{x}\pm S.D.$).	75
8. Responses in vegetative growth of hedge bindweed to infestation by <u>M. discoidus</u>	78

LIST OF FIGURES

<u>Figure</u>	<u>page</u>
1. Adults of <u>M. discoidus</u> (Say).	37
2. Percent of oviposition over <u>M. discoidus</u> female's life span.	38
3. Percent bloom of hedge bindweed in the Blacksburg area.	40
4. Synchronization of the life cycle of <u>M. discoidus</u> with its host phenology in Southwestern Virginia.	41
5. Percent adult emergence of <u>M. discoidus</u> from overwintering larvae in different treatments.	51
6. Percent emergence of male and female adults of <u>M.</u> <u>discoidus</u> from overwintering larvae maintained at 28°C.	53

Chapter I
INTRODUCTION

A weed is "a plant that originated under a natural environment and, in response to imposed and natural environments, evolved and continues to do so, as an interfering associate with our crops and activities" (Aldrich 1984). Man has been struggling with weeds since the beginning of agriculture. Traditionally, weed control falls into seven general categories: herbicidal, crop competition, crop rotation, biological, fire, mechanical, and hand labor (McWhorter and Shaw 1982). Biological weed control has the advantages of low cost, safety in the environment (such as no residues in the soil), simplicity of operation after establishment of the agent, and compatibility with other control measures. As a result, biological weed control has captivated increasing attention and research efforts in the last two decades. The majority of the weed biological control programs have involved insects, despite the increasing appreciation of microbial organisms as biological weed control agents. Insects can be used in two ways for biological control of weeds, (1) the classical method, i.e. exotic insects are introduced to control weeds of foreign origin, and (2) the manipulative method, i.e. to enhance and/or augment insects already existing on the target weed (Andres 1982). Among weed biocontrol programs, the classical method has been the most

successful. There have been few successful projects involving indigenous insects to control an introduced weed, although the importance and potential of utilizing such insects has been stressed (Andres 1982). The fundamental objective of modern integrated weed management (IWM) is the reduction, not the eradication, of the weed density to non-economic levels (Huffaker 1964). Thus, any factor which can exert a certain level of stress on the weed, without greatly diminishing the effects of other stress factors, may find its imperative role in an IWM program. Indigenous insect agents for biological weed control are often more readily obtainable than exotic ones and they are frequently well synchronized with the weed host. Unfortunately, the potential value of indigenous insects, when used alone or in combination with other native or introduced insects or microbial agents, has been inadequately studied. Consequently, the effects of these insects in suppressing weeds have been erroneously assumed as insignificant (Andres 1982).

In regard to selection of effective biological weed control agents, Harris (1973) summarized the characteristics of a promising agent by a scoring system, containing 12 criteria. According to this scoring system and recent developments in weed biological control (Wapshere 1980,

Pemberton and Andres 1980), effective biological weed control agents should (1) feed and complete development only on the target weed and/or closely allied weed species, (2) be able to cause effective destruction of the reproductive or dispersal organs of the weed, the plant tissues which are vital to the physiological or biological reaction processes, or the physical support of the weed without stimulating undesirable diversion of the physiology and growth of the infested host plants, (3) be well adapted to the ecoclimatic situations and synchronized with host phenology, so that it can establish and build up to massive populations on the host, and (4) have developed a minimum level of homeostatic relationship with the weed species. In practice, evaluation of an introduced biological control agent for a weed whose suitability for such a project has been verified, should include the following procedures (Kok 1974), (1) safety tests, (2) field establishment, (3) maintenance of cultures, and (4) assessment of efficacy of the agents in weed control. Although these procedures were established mainly for evaluating introduced insect agents, they should be generally suitable for indigenous species as well. Moreover, in evaluating indigenous insect species, factors which may diminish the insect population or diminish their effect on the weed should also be identified.

Hedge bindweed, Calystegia sepium (L.) Brown, and field bindweed, Convolvulus arvensis L., are two closely related weeds. Both are members of the family Convolvulaceae and are eurasian in origin. The suitability of these two weeds for biological control is verified by their important pest status in North America and in the world (Holm et al. 1977), their persistence against cultural and chemical control methods (Parrella 1977, Selleck 1978), and the richness of associated phytophagous insects (K. E. Erick, personal communication). Megacerus discoidus (Say) (Coleoptera: Bruchidae), a native North American seedfeeder, has been considered by Mohyuddin (1969a) as one of the most promising candidates for biological control of bindweeds. Mohyuddin (1969b) also briefly reported the occurrence of this beetle in Ontario, Canada. However, biological and ecological data on this insect are scarce and incomplete. Its host specificity and impact on host density and physiology are unknown. As pointed out by Rosenthal and Buckingham (1982), it is essential to obtain more information about this bruchid before any European seedfeeder is introduced into North America for bindweed biological control.

Thus, the purpose of my research was to obtain detailed biological information of M. discoidus. From 1982 to 1984, field and laboratory studies were conducted on M. discoidus

to (1) study its life history and behavior, and its synchronization with the host, (2) examine the influence of temperature , humidity, and soil coverage on its diapause, which appeared to be a vulnerable point in the insect life cycle to environmental factors based on preliminary observations, (3) test its host specificity, and (4) assess its impact on seed production of hedge bindweed and plant growth response to seed consumption. Hedge bindweed was used in the experiments, mainly because of its abundance in southwestern Virginia.

Chapter II
BINDWEEDS AND THEIR BIOLOGICAL CONTROL
- A Literature Review

2.1 THE TARGET WEEDS

Taxonomy and distribution

Field bindweed, Convolvulus arvensis L.:

This weed belongs to the tribe Convolvuleae (Tubiflorae: Convolvulaceae). It originated in Eurasia, and was introduced to North America as early as 1739 in Virginia (Wiese and Phillips 1976). It appeared in Pennsylvania in 1812, Maine in 1824, Kansas in 1877, and spread to all the Western states by 1900 (Whitesides 1979). The weed is currently distributed throughout the United States except the extreme southeast, parts of southern Texas, New Mexico and southern Arizona (Reed and Hughes 1970). In Canada, it was collected in Ontario in 1879, in Nova Scotia in 1883, and in British Columbia, Alberta and Manitoba in the 1980s, and is now present in the agricultural region of all provinces except New Foundland and Prince Edward Island (Weaver and Riley 1982). The weed has been found also in Europe, Asia, Egypt, Arabia, Mexico, South America, Syria, Palestine (Bakke 1939), and throughout Australia (Alcock 1974).

Hedge bindweed, Calystegia sepium (L.) Brown:

This species was erected by Linnaeus as Convolvulus sepium in 1753, and was revised to Calystegia sepium by

Brown in 1810 as he separated Calystegia from Convolvulus (Rickett and Stafleu 1960). This separation, however, has caused much debate and confusion. The majority of taxonomists has treated Calystegia and Convolvulus as distinct since Brown's revision, but others have questioned the distinction of the two groups and have continued to regard Calystegia as a section or synonym of Convolvulus (e.g. Fernald 1950). To resolve this dilemma, Lewis and Oliver (1965) concluded from their examination of male gametophyte and sporophyte characters of the species of Calystegia and Convolvulus that the differences between the two groups are so distinct that their separation into two genera should be confirmed. Since their study, there has been no other convincing argument opposing the status of these two genera, although misplacement of Calystegia sepium still occurs in both botanical and entomological documents related to this weed (Reed and Hughes 1970, Parrella 1977, Strausbaugh and Core 1978).

Hedge bindweed is native of Eurasia. There is no available record of its introduction into North America. The weed has been found throughout the Eastern half of U.S., extending as far west as Colorado and New Mexico; throughout parts of the Northwestern States; North into Southern Canada from Newfoundland to British Columbia, and in New Zealand (Reed and Hughes 1970), and South Australia (Alcock 1974).

Economic importance

Field bindweed has been considered as the 12th worst weed in the world with infestation records in 44 countries in 32 different crops (Holm et al 1977). It competes with crops for soil moisture, nutrients and, to some extent, light (Wiese and Phillips 1976), and causes yield losses ranging from insignificant to complete crop failure in nonirrigated areas of low average precipitation (Swan 1980). Yield loss from hedge bindweed or field bindweed infestation is difficult to assess, because these weeds often grow in patches, weed density changes quickly from year to year, and normal crop rotation sequences limit long-term studies (Messersmith 1980). Nevertheless, some data are available to illustrate the economic importance of bindweeds. It has been reported that heavy infestations by field bindweed can reduce yields of winter wheat by one-third, and yields of summer-growing crops by three-fourths (Phillips 1967). In the North central region and the southern Great Plains of this country, several million acres were infested by this weed in 1978 (Phillips 1978). In California, 2 million acres of crop land in 30 counties, representing 88.1% of the state's field crop acreage harvested during 1980 were infested by field bindweed, resulting in a total loss of about 25 million dollars (Rosenthal 1983a). In fruit

orchards, bindweeds cover bushes and small trees, increasing the time taken for pruning and picking. Fruit quality is also reduced; apples shaded by bindweeds do not develop their full color and are down-graded (Davison 1976). In California, 30.8% of the grape acreage was infested by field bindweed in 1980. Orchards of apples, pears, peaches, apricots, prunes, cherries, almonds, walnuts, avocados, and citrus were infested (Rosenthal 1983a).

Besides yield loss directly caused by field bindweed infestation, the weed also interferes with harvesting operations (Weaver and Riley 1982), provides a breeding site for insect pests attacking adjacent crops (Landis and Getzendaner 1947, Tamaki et al. 1975). It serves as an alternate host of viruses which cause potato X disease, tobacco streak, tomato spotted wilt, vaccinium false bottom (Holm et al. 1977) and alfalfa mosaic disease (Feldman and Gracia 1977). It is toxic to hogs (Muzik 1970).

No accurate data are available on infestation or economic loss caused by hedge bindweed, except that it has been reported as a serious pest of nurseries, crop land, and roadsides in the Eastern United States (Parrella 1977, Selleck 1979).

Biology

Growth and development

Morphological characteristics of field bindweed and hedge bindweed have been described by Fernald (1950), Weaver and Riley (1982), Swan (1980), Reed and Hughes (1970), Radford et al. (1968), and Strausbaugh and Core (1978). Characters that can be used to distinguish the two weed species in the field were summarized by Parrella (1977). The chromosome number of field bindweed has been commonly reported as $2n=48$ on European and Asian specimens, but as $2n=50$ by one report from U. S. specimens (Weaver and Riley 1982).

Extensive studies have been conducted on the field bindweed root system, which enables the weed to colonize new areas, to compete with crops for moisture and nutrients, and to persist despite frequent cultivation. The primary root is a taproot from which lateral roots develop adventitiously. The lateral roots produce endogenous buds, which generate rhizomes and shoots (Kennedy and Crafts 1931). After growing to a certain point, the lateral roots turn downwards; new shoots are produced near the downward turn and grow to the surface forming new plants (Frazier 1943, Swan 1980). Most rhizomes are produced up to 60 cm below the soil surface and vary in length from 2 to 60 cm or

more (Torrey 1958). When the field in which the weeds are growing is cultivated, the lateral roots tend to develop below the tilled area, while the vertical roots tend to grow below 60 cm (Swan 1980). Local spread of field bindweed depends largely on its lateral roots. The original plant can spread to 3.05 m in diameter with 25 or more shoots in one growing season (Best 1963), and to 5.48 m in two seasons (Swan 1980). The entire root system may cover an area up to 6 m in diameter and 9 m in depth (Holm et al. 1977). The extent of root development is often subject to environmental factors. In arid regions, root penetration may be limited by a permanently dry subsoil layer (Phillips 1978).

Colonization of hedge bindweed is through spread of aerial shoots, as well as development of rhizomes and underground lateral roots. In the fall, tips of those aerial shoots penetrate the soil to establish new plants. The ability to generate new plants from underground root fragments of hedge bindweed is even greater than in field bindweed (Davison 1976).

The weight of field bindweed roots has been estimated at over 3.17 tons per acre. About 12% of this weight is carbohydrate reserves (Bakke et al. 1939). When bindweed plants are dormant in winter (Guncan 1973), or subjected to extreme drought (Bybee et al. 1977), the food reserves in

the root stay stable until emergence or presence of favorable conditions, when the reserves are gradually depleted. The carbohydrate level shows a seasonal fluctuation. It was reported to be lowest in May due to early spring growth of the plant, and gradually reached the maximum in October or November, as nutrients were transported from leaves to roots during the growing season and converted to carbohydrate reserves (Barr 1940, Frazier 1943). Short-term variations in carbohydrate reserve level may be caused by flowering and seed set (Bybee et al. 1977).

In an excellent study on the regenerative capacity of field bindweed roots, Swan and Chancellor (1976) reported that regeneration occurred mainly from vertical roots. Creeping lateral roots were less important in root formation than previously assumed. They also noted that the greatest number of new roots were produced in May, and the least between November and March. Bonnett and Torrey (1965) examined root regeneration from a morphological point of view, and concluded that isolated root segments of field bindweed are capable of developing into new plants by forming both endogenous buds and roots. Roots are formed at the distal end of the segment while buds are formed anywhere along the axis. They indicated that this is due to movement of plant auxins from the proximal to the distal end of the segment.

Growth of shoots and morphological development of field bindweed varies from season to season, as well as with environmental conditions. The number of shoots formed from lateral root segments is greatest in early spring, resulting in the maximum total length of shoot per section in April (Swan and Chancellor 1976). It has been shown that soil moisture significantly affects root mass and weed density of field bindweed, and that wax content, shape and thickness of the cuticle are influenced by soil moisture, rubbing or scarification caused by wind-borne sand and dust particles, and shade (Meyer 1977). Also, variations in the development of vegetative organs of field bindweed, such as branch number, leaf size, plant weight etc., can occur in locations with different levels of soil moisture, as indicated by Rashed and Haderlie (1980).

Reproduction

The flowers of field bindweed last only one day, and are insect pollinated. Seed production by field bindweed is often influenced by environmental conditions. Seed set is favored in dry, sunny weather and in dry, calcareous habitats. In heavy, poorly drained soils and frequently cultivated land, the plant may fail to produce any seed (Brown and Porter 1942). The weed seldom sets seed during

the first year of growth, although flowers can occur within 6 wk after sprouting of field bindweed seeds in the greenhouse (Weaver and Riley 1982). Under field conditions, individual flowers may fail to set seed or to form mature seeds, and capsules which appear normal frequently contain no viable seed. Rate of fruit and flower abortion ranged from 4 to 40% (Brown and Porter 1942). Under favorable conditions, the number of seeds per capsule varies from one to four with an average of two (Brown and Porter 1942). However, an accurate estimate of seed production is very difficult. Wiese and Phillips (1976) estimated more than half a million bindweed seeds per acre in a wheat field, and 4.5 million seeds per acre in bindweed infested roadside ditches in Western Texas.

Seeds of bindweeds have a hard, impermeable seed coat (testa), which permits extension of seed life so that they are distributed in time as well as in space, and enables the weeds to infest crop lands long after flowering parent plants are controlled (Rolston 1978). The seed impermeability is affected by the morphological structure of the testa, by environmental factors such as relative humidity and temperature, light, and soil fertility, and by genetic variations (Rolston 1978). The seeds can be dispersed by water, by movement of crop seeds, by farm equipment (Jordan

and Jordan 1981), and by birds (Proctor 1968). Field bindweed seeds can remain viable while resisting the grinding action in the digestive tract of birds for up to 144 h. When buried in soil, seeds can remain dormant for many years and germinate when suitable environmental conditions are available (Timmons 1949). Stahler (1948) reported a 62% germination of field bindweed seeds after burial in the soil for 50 years.

The mean percent germination of freshly harvested seeds ranges from 5 to 25%, of impermeable seeds from 60 to 80% (Weaver and Riley 1982). Germination of impermeable seeds can be achieved by artificial scarification with concentrated sulphuric acid (1 h), absolute ethyl alcohol (20 h), or mechanical means. The latter, however, may damage the embryo of the seeds (Rolston 1978). Chilling of the seeds can improve germination by increased seed coat porosity caused by cell digestion. This structural change allows increased water and gas exchange through the seed coat and thus promotes germination (Jordan and Jordan 1982).

Field bindweed seedlings can be recognized by their notched basal leaves, which are absent in young shoots from established plants (Swan 1980). Damaged seedlings can regenerate from their root system, depending on their age and stage of development. Thus, all seedlings should be cultivated before they are a month old (Swan 1980).

In contrast, information on hedge bindweed biology has been scarce. This has been attributed to the relatively greater susceptibility of this weed to herbicides than that of field bindweed. Hence, research has been focused on field bindweed (Davison 1976).

Response to herbicides and cultural control

Considerable effort and resources have been placed on bindweed control since the beginning of this century when control measures were first recommended (Cox 1909, Bakke 1939, Cunningham 1958, Phillips 1967, Davison and Bailey 1974, and Weaver and Riley 1982). The most recently recommended herbicides for bindweed control are 2,4-D(amine salt), glyphosate, and dicamba (Swan 1982). Generally, seedlings and first-year plants can be sufficiently controlled by individual or combined postemergence applications of the above three herbicides (Weaver and Riley 1982). Older plants are very difficult to eradicate with chemical because of the vigorous regeneration of roots after destruction of the aerial portion of the plants (Weaver and Riley 1982)

Frequent tillage and competitive cropping have proven to be very effective in bindweed control. However, these methods require considerable labor and capital input. For

example, 14 to 20 tillage operations per year have been required (Wiese and Rea 1959). Cultivation and crop competition may effectively suppress vigorous shoot growth, but these methods can eliminate neither the roots nor seedlings emerged from the seed bank in the soil (Davison 1976). In response to this, research efforts have been increasingly oriented towards biological control of the weed.

2.2 BIOLOGICAL CONTROL OF BINDWEEDS

In an early attempt to search for biological control agents of bindweeds, Smith (1938) concluded that there was no important insect feeders on bindweed in Kansas. He also indicated the lack of insects feeding on the roots and stems, and the potential for introduction of such insects. Later, Frick (personal communication) compiled a list of about 430 insects and mites recorded from Convolvulus and related plants. In a list of "safe" insects which were recorded only from Convolvulus and/or Calystegia species, he named 5 species attacking seeds, 14 feeding on the foliage, 3 on stems, and 2 on roots. This demonstrated a rich resource of natural enemies of bindweeds. Mohyuddin (1969a) listed 125 insects and mites from Calystegia spp. and Convolvulus spp. found by him in Ontario, Canada and by

others in different parts of the world. Among these, he considered 13 as monophagous (confined to one plant genus) and 22 as stenophagous (feeding only on closely related plants). Baloch (1974) reported 34 species of insects, 2 species of mites and 1 species of fungi from Convolvulus spp. in Pakistan. Parrella and Kok (1975) examined 5 insect feeders on Convolvulus arvensis and Calystegia sepium for their potential in biological control of these weeds. Organisms collected from C. arvensis from Canada and the United States were also summarized by Weaver and Riley (1982) into a list of 28 insect species, 18 fungus, 2 nematodes, and 1 virus. More recently, a cooperative project was conducted by the University of California and USDA from 1970 to 1979 to explore for natural enemies of bindweeds in their native habitat, Mediterranean Europe. As a result, 139 species of phytophagous arthropods were collected from C. arvensis and its close relatives (Rosenthal and Buckingham 1982). Insects which have been evaluated for their value in biological control of bindweeds are listed in Table 1 The following is a brief discussion of these insects and those that have not been evaluated but are recommended for evaluation.

Foliage feeders

Galeruca rufa Germar, an European chrysomelid feeds only on plant species in the genera Convolvulus and Calystegia (Rosenthal and Carter 1977). Moderate populations of this insect can cause defoliation severe enough to reduce field bindweed flower production and kill seedlings (Rosenthal and Hostettler 1980). It has been considered by the above authors as a very promising biological control agent for field bindweed in the United States. A protozoan disease of this beetle caused by Nosema sp. (Rosenthal and Hostettler 1980) can be eliminated in the laboratory (Etzel et al. 1981).

A gall mite, Aceria convolvuli, has shown great potential as a biocontrol agent of field bindweed. It does not live or reproduce on sweet potato, Ipomoea batatas, an economically important crop in convolvulaceae, and is very damaging to field bindweed. Further tests on its host specificity are currently underway at the USDA, Biological Control of Weeds Laboratories in Albany, California (Rosenthal 1983b).

Another potential foliage feeder is Tyta luctuosa. This insect completes its development only on species of Convolvulus and Calystegia. However, its impact on bindweed populations still remains undetermined (Rosenthal 1978).

Tortoise-beetles, Cassida indicola, C. enervis, Aspidomorpha indica, Glyphocassis trilineata, Mettriona australica (Baloch 1977a), and Chelymorpha cassidea (Mohyuddin 1969b and Selleck 1979), a plume moth, Oidaematophorus monodactylus (Parrella and Kok 1978), and some other insects (Rosenthal and Buckingham 1982) (Table 1) can each defoliate field bindweed and/or hedge bindweed severely when their populations are high. However, their value in biological control is limited to areas where sweet potato is not grown commercially, because these beetles all feed on this plant. The leafminer, Bedellia somnulentella was excluded from biological control of bindweeds in U. S. because of similar reasons (Parrella and Kok 1977).

Root and stem feeders

The convolvulus flea beetle, Longitarsus pellucidus was found widespread and abundant in Europe by Rosenthal and Buckingham (1982). In Italy, the adults were found primarily on Convolvulus species and with only slight feeding on sweet potato observed (Rosenthal and Buckingham 1982). However, the screening study was incomplete due to failure of laboratory larval rearing (Rosenthal and Buckingham 1982). Menozzi (1931) reported that this insect attacks several wild and cultivated plants, which are mostly in the

convolvulaceae. It was recommended by Rosenthal and Buckingham (1982) for further study, because of the expected impact of a root-feeder on bindweeds.

Baloch (1977b) evaluated two insects feeding on stems and roots of bindweeds, Melanagromiza convolvuli and Noctuelia floralis in Pakistan. Unfortunately, both attack sweet potato, as well as some other species of Ipomoea which are common ornamental plants.

Seed feeders

Megacerus discoidus, a native North American seedfeeder, was considered by Mohyuddin (1969a) as one of the most promising candidates for biological control of bindweeds, because seeds of sweet potato are used neither for its reproduction nor for human consumption. This insect has been found on both field bindweed and hedge bindweed in Virginia (Parrella and Kok 1975). Considering the potential of this species and of another bruchid, Megacerus impiger for bindweed control in California, Rosenthal and Buckingham (1982) recommended both species for further study. Four European species of Spermophagus, especially S. sericeus have been found to be promising for introduction to North America for bindweed control (Rosenthal and Buckingham 1982).

Table 1. Insects and mites that have been evaluated
for biological control of bindweeds¹

Scientific name	Taxonomic status	Result of screening ²	References
Foliage Feeders			
<u>Galeruca rufa</u> Germar	Coleoptera:Chrysomelidae	P	Rosenthal and Carter 1977
<u>Hypocassida</u> <u>subferruginea</u> Schrank	" "	P	Rosenthal and <u>Buckingham 1982</u>
<u>Cassida indicola</u> Duv.	" "	L	Baloch 1977a
<u>Cassida enervis</u> Boh.	" "	L	Baloch 1977a
<u>Aspidomorpha</u> <u>indica</u> Boh.	" "	L	Baloch 1977a
<u>Glyphocassis</u> <u>trilineata</u> Hope	" "	L	Baloch 1977a
<u>Metriona</u> <u>australica</u> Boh.	" "	L	Baloch 1977a
<u>Chelymorpha</u> <u>cassidea</u> (Fab.)	" "	L	Mohyuddin 1969b
<u>Trachys punti-</u> <u>collis</u> var. <u>obscura</u> Obenberger	" :Buprestidae	L	Rosenthal and Buckingham 1982
<u>Tyta luctuosa</u> (Denis & Schiffermiller)	Lepidoptera:Noctuidae	P	Rosenthal 1978
<u>Hydrisis</u> <u>ornatalis</u> (Duponchel)	" :Pyralidae	L	Rosenthal and Buckingham 1982
<u>Chrysocrambus</u> <u>linetellus</u> (F.)	" "	L	Rosenthal and Buckingham 1982

(cont. on next page)

Table 1 (cont.)

Scientific name	Taxonomic status	Result of screening ²	References
<u>Brachmia</u> <u>triannulella</u> (Herrich-Schaffer)	" :Gelechiidae	L	Rosenthal and Buckingham 1982
<u>Oidaematophorus</u> <u>monodactylus</u> (L.)	" :Pterophoridae	L	Parrella and Kok 1977
<u>Bedellia</u> <u>somnulentella</u> (Zeller)	" :Lyonetiidae	L	Parrella and Kok 1977
<u>Aceria convolvuli</u> (Nalepa) Root and Stem Feeders	Acari:Eriophyidae	P	Rosenthal 1983b
<u>Longitarsus</u> <u>pellucidus</u> Foudr.	Coleoptera:Chrysomelidae	P	Rosenthal and Buckingham 1982
<u>Melanagromyza</u> <u>convolvuli</u> Spencer	Diptera:Agromyzidae	L	Baloch 1977b
<u>Noctuella</u> <u>floralis</u> Hb.	Lepidoptera:Pyralidae	L	Baloch 1977b
Seed Feeders			
<u>Spermophagus</u> <u>sericeus</u> (Geoffroy)	Coleoptera:Bruchidae	P	Rosenthal and Buckingham 1982

¹ Including species on which host specificity tests have been performed or are undertaken.

² P=Promising candidate, no feeding on sweet potato or other important crops.

L=Limited value to areas with no commercial production of sweet potato.

Chapter III

LIFE HISTORY OF MEGACERUS DISCOIDUS
(COLEOPTERA:BRUCHIDAE), A SEEDFEEDER OF HEDGE
BINDWEED, IN SOUTHWESTERN VIRGINIA

3.1 INTRODUCTION

Megacerus discoidus (Say) is a native North American seedfeeder of hedge bindweed, Calystegia sepium (L.) Brown, and field bindweed, Convolvulus arvensis L. (Bridwell 1929, Mohyuddin 1969a, Parrella and Kok 1975). It has been also reported in seeds of Ipomoea fastigiata and I. lepidophylla (leptophylla) (Teran and Kingsolver 1977), which are economically less important in the U.S.A.. Field bindweed is considered as the 12th worst weed in the world (Holm et al. 1977) and is a serious pest in Midwest and Western United States (Wilson 1978, Rosenthal 1983a). Closely related and biologically similar to field bindweed, hedge bindweed is more dominant in Eastern United States (Wang and Kok 1983). Both species produce vigorous foliage and reproduce by seeds and underground rhizomes. The seed has a very hard shell and is the primary means of dispersal (Parrella 1977).

M. discoidus was originally described by Say as Bruchus discoidus, but was referred to as Bruchus discoideus by several early workers (Bottimer 1968). Bridwell (1929) revised the species to Megacerus discoideus and was used as such by Mohyuddin (1969a), Parrella and Kok (1975), and Wang and Kok (1983). However, the species has also been referred to as Megacerus discoidus by Bottimer (1968) and Teran and

Kingsolver (1977). Other names of this insect in the literature are Bruchus discoidens (sic) (Dury 1879) and K.lytorhinus discoidii (Motschoulsky 1873). More recent literature has been consistent with the name Megacerus discoidus (Pfaffenberger et al. 1984) and it is so used in my dissertation.

M. discoidus has 4 larval instars and one generation a year (Mohyuddin 1969b, Wang and Kok 1983). It was considered by Mohyuddin (1969a) as the most promising biological control agent for the bindweeds. Rosenthal and Buckingham (1982) acknowledged the potential of this oligophagous species but also indicated the need for further knowledge of its biology and host range before any European seedfeeder can be considered for introduction for bindweed control in North America. Biological data on this species are sparse and incomplete. Pfaffenberger et al. (1984) described the 1st and 4th instars of M. discoidus on I. leptophylla (lepidophylla) and adults were described by Say (LeConte 1859) and Teran and Kingsolver (1977). Information on the pupal stage is lacking. A brief report of the occurrence of M. discoidus at Belleville, Ontario was given by Mohyuddin (1969b). Besides these accounts, little is known about the biology of this species. This chapter summarizes my studies on life cycle, larval and adult

behavior, reproductive characteristics and the synchronization with host of M. discoidus from 1982-84 in Southwestern Virginia.

3.2 MATERIALS AND METHODS

Life cycle

In 1982, seedpods of hedge bindweed were sampled throughout the growing season along the margins of a corn field in Blacksburg, Virginia. Thirty seedpods (3-4 seeds/pod) were collected at random twice a week from 5 to 29 July and on a weekly basis from 29 July to 14 October. The seedpods were examined for eggs and were dissected in the laboratory to determine duration of stages and parasitization of M. discoidus. Duration of the egg stage in the field was determined by the method of weighted means (Li 1964). The beginning of sampling was weighted by number of eggs found on the seedpods in each sample, and the summation of weighted durations of all samples was divided by total number of eggs found throughout the experiment. Forty to 70 larvae/pupae were found in the collected seeds from each sample. To determine the developmental stages of the larvae, head capsule width was measured, and the infested seeds were examined for exuviae. In the fall of 1983, field collected seeds were kept outdoors and groups were dissected every two days from 20 May to 28 June, 1984 to observe pupation and adult emergence under field conditions. Sufficient seeds were dissected to obtain 20 insects each time. Due to various numbers of each instar in

a sample, differences between the weighted mean duration of two consecutive stadia were calculated for each stage. The method of calculating weighted mean duration of each larval stage was similar to that used for the egg stage.

Reproduction of M. discoidus was studied in July-August, 1983. Newly emerged adults from field collected hedge bindweed seeds were caged on flowers and seedpods of hedge bindweed in the field at a rate of 1 pair/cage, replicated 12 times. The cages were made of organdy with screened top, cylindrical in shape, 10 cm long and 6 cm in diameter. They were tied on peduncles of either flowers or seedpods. The adults were transferred every 2 days and caged alternately on flowers and seedpods. Eggs on the seedpods and flowers were counted separately to determine ovipositional preference, but summed to calculate fecundity. The observation was continued until death of the adults to determine adult longevity.

Synchronization with host

During May to October, 1982, growth stages of hedge bindweed (germination, vegetative growth, blooming, seedpod formation, seed maturation, and plant senescence) were recorded every 3 days at 3 locations in the Blacksburg area. The bindweed grew on hedges along corn fields at each of the

sites, which are approximately 1.5-5 km apart. The phenology of hedge bindweed was compared to the developmental stages of M. discoidus. To study the synchronization of adult oviposition with host phenology, a sample of 20 bindweed stems was taken each time from each site. The stems were individually separated from leaf clusters and the percentage of blooming plants was calculated. Percentages of the seedpods with eggs in the life cycle study were compared with bindweed stages of development.

3.3 RESULTS AND DISCUSSION

Life cycle

Field developmental rates of M. discoidus and stage and instar measurements are summarized in Table 2. Other morphological characteristics and behavior of the various stages are as follows:

Egg. -Fresh eggs were smooth, slenderly oval in shape, and whitish to pale yellow in color. Eggs were usually laid singly under the loose bracts of the seedpods. If the bracts were too tightly overlapped, however, eggs were laid on the outside of the bracts. One to 5 eggs were usually found on the infested seedpods. The incubation period in the laboratory ($24^{\circ}\pm 2^{\circ}\text{C}$, 14 h photophase) was 7.2 ± 1.2 days (n=38).

Table 2. Duration of stages in the field and measurements of M. discoidus

Stage	Duration (days)	No. observed	$\bar{x} \pm S.D.$ in mm			No. observed
			Length	Greatest width	Head capsule width	
Egg	14.4	457	0.7 \pm .24	-	-	42
Larva-1st	11.0	121	0.7 \pm .15	-	0.14 \pm .01	30
-2nd	11.3	76	-	-	0.30 \pm .03	30
-3rd	12.9	104	-	-	0.43 \pm .03	30
-4th	296.7	49	3.5 \pm .17	-	0.63 \pm .04	20
Pupa ¹ -female	5.2	126	3.2 \pm .22	2.1 \pm .19	-	15
-male			3.2 \pm .32	2.1 \pm .24	-	15
Adult -female ²	16.7	213	3.2 \pm .09	1.9 \pm .09	-	15
-male ²	15.5	214	3.1 \pm .11	1.8 \pm .05	-	15

¹ Sex was not differentiated for duration.

² Quiescent stage only.

Larva. -Newly hatched larvae had a pale yellow body and a brownish head capsule partly hidden by the prothorax. Three pairs of thoracic legs were present in the 1st instar, but in the later instars legs were fleshy and vestigial. Larvae eclosed from the ventral side of the eggs, and newly eclosed larvae burrowed into the seeds within 24 h. Tunnels in the seedpods were near the site of egg deposition. While most seedpods of hedge bindweed contain 3-4 seeds per pod, the number and order in which the seeds were attacked by larvae varied. Larvae usually drilled into the seeds through the base. New larvae were able to burrow into seeds after the seed shells had begun to harden. Pfaffenberger et al. (1984) noted that larvae fed entirely on cotyledons of I. leptophylla seeds. We observed that the larvae destroyed all the inner parts of the seed of C. sepium. About 40-50% of the seed material was consumed before diapause; overwintered larvae fed on the rest of the seed in the following spring. The final (4th) instar underwent a facultative winter diapause, although a few 3rd instars were found throughout the winter and early spring. The larva excavated a pupation chamber by compressing the filiform feces onto the interior wall of the seed coat. A single larva consumed only one seed during development, but one seed could be attacked by several larvae. Cannibalism occurred mostly during the 2nd

and 3rd instars. This intraspecific competition ensured that only one larva completed development in a seed. Our data showed that 2 larvae were present in 31% of the seeds, and 3 larvae in 6% of the seeds at the beginning of the season.

Pupa -Body was milky white to pale yellow, oval shaped; eyes brown, reversely U-shaped, surrounding the antennal suture; ocelli absent; antennae transparent, scape attached to the eyes, pedicel and flagellum stuck on wings at the early stage of the development, but free from the body after about 3 days of pupation; mandibles pigmented, other mouthparts transparent; legs transparent, pro- and meso-legs visible, hind legs underneath the wings; wings transparent, distally attached on lateral side of the body. Head capsule exuviae of the final instar larvae were always attached on the epiproct of the pupae.

Adult -Fig. 1 shows several characteristics that can be used to distinguish this species. Detailed morphological descriptions were given by LeConte (1859) and Teran and Kingsolver (1977). A quiescent stage was noticed between pupation and adult emergence from the seeds, after the adults appeared to have completed morphological transformation from pupae. This period was slightly shorter in males than in the females (Table 2). Emergence of new adults from the seeds began in mid June and continued for

about 2 wk. Males emerged 2-4 days earlier than females. Adults were active diurnal fliers, visiting flowers of the hedge bindweed, resting in the bell-shaped corolla and probably feeding on the nectar and pollen. In the laboratory ($24^{\circ}\pm 2^{\circ}\text{C}$, 50-60% RH, and 16 h photophase), newly emerged adults survived for over 30 days on honey solution, sugar water, and brewers yeast plus honey solution, compared to 16 ± 2 days on water and 10 ± 3 days in starvation (5 pairs for each diet). However, none of these adults oviposited. Longevity of adult females and males in the field were 18 ± 7 (range 10-27) days and 11 ± 3 (range 6-20) days, respectively.

Mating was observed only in the laboratory, where adults were kept in a plastic jar. The female climbed on the wall of the jar, while the male hung upside down, holding her with his hind legs. In the field, M. discoidus had only one major oviposition peak, occurring 8 days after adult emergence (Fig. 2). The maximum oviposition period was less than a month. When adults were confined on flowers and seedpods of their host, 96.1% of the eggs were deposited on the seedpods, with only 3.9% on the flowers (n=232), indicating a strong ovipositional preference. Females laid an average of 23.1 ± 13.1 eggs (range 15-55).



Figure 1. Adults of *M. discoidus* (Say). A. Male. B. Female. Distinguishing characters: 1a: antennae pectinate in males; 1b: antennae serrate in females. 2: a large rufous spot on each elytron. 3: four black spots on the epiproct, 2 median ones round and 2 marginal ones triangular.

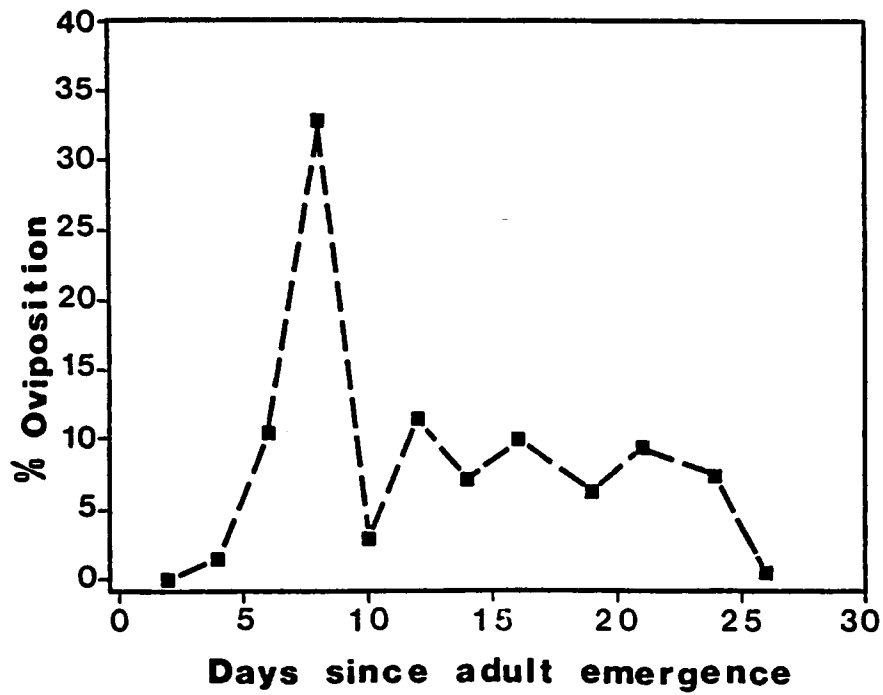


Figure 2: Percent of oviposition over M. discoidus female's life span

Synchronization with host

During 1982-84, hedge bindweed sprouted in late April to early May. Vigorous vegetative growth occurred from May to early June, at which time flower buds began to appear. Blooming peak occurred in mid July, although flowers could be found till early September. Most of the late blooms were found on young lateral shoots. Seed development began in mid July and was completed in about 50 days. Plants entered the senescent stage in early September. Despite some variations in the percentage of blooming plants (Fig. 3), the growth rate of hedge bindweed exhibited no significant difference among the 3 sites. Site 2, with the highest percentage and an intermediate time length of blooming hedge bindweed, was used to illustrate host-parasite synchronization.

In the field, the bruchid was in the 2nd and 3rd instars during August and early September, although a small portion of the 1st instars could be still found after late August (Fig. 4). The majority of the population reached the overwintering stage (4th instar) in early September, when host plants were in senescence. Larvae overwintered within the host seeds, most of which remained on the dried vine throughout the winter.

Good synchronization was found between adult emergence of M. discoidus and blooming of hedge bindweed, and between

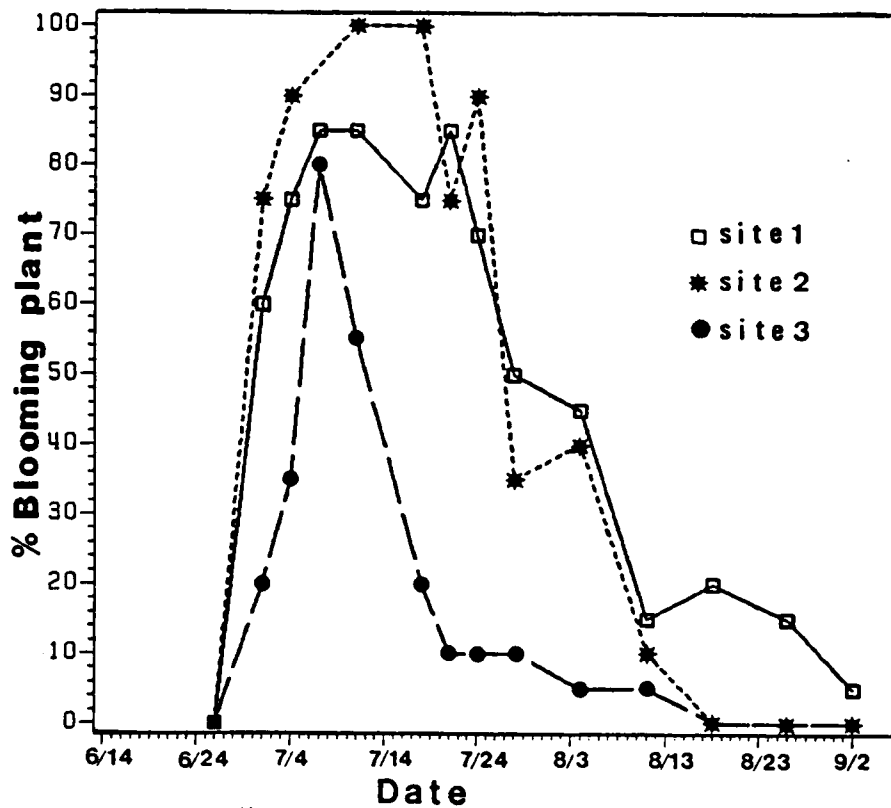


Figure 3: Percent bloom of hedge bindweed in the Blacksburg area.

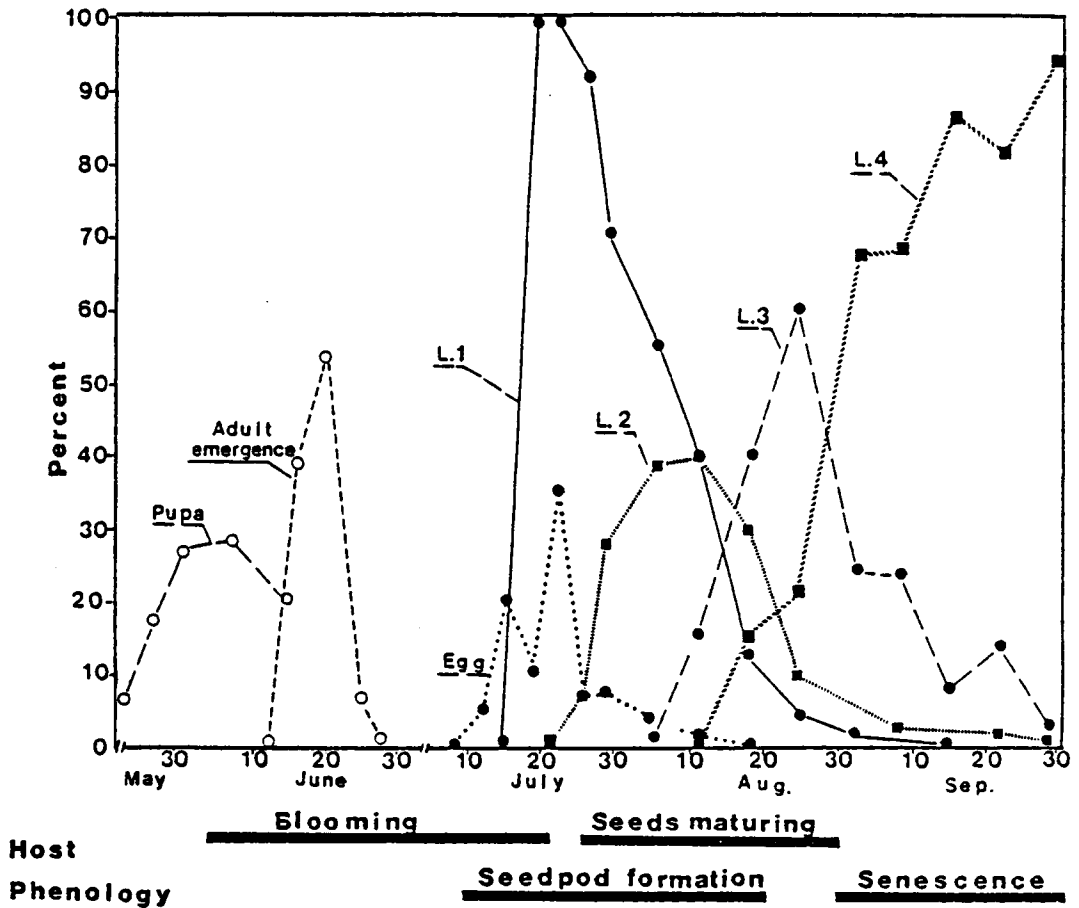


Figure 4: Synchronization of the life cycle of *M. discoidius* with its host phenology in Southwestern Virginia. (Eggs and larvae were observed in 1982. Egg: percent seedpods infested by *M. discoidius* eggs. L.1, L.2, L.3, and L.4: percent of each stage among total larvae sampled each time. Pupa and Adult emergence: percent pupae and adults emerged among total *M. discoidius* found in each observation in 1984).

oviposition and seedpod formation (Fig. 4). Adults emerged during June. Oviposition began shortly after the peak of adult emergence, as the percentage of blooming host plants increased. The peak of the seedpods with eggs occurred about two weeks after the peak bloom period of hedge bindweed, by which time, most of the seedpods had been formed. This observation is also consistent with the oviposition pattern of the females (Fig. 2). Good synchronization between the reproduction of a plant parasite and its host phenology is especially important for the success of the insect. Our study shows that M. discoidus seems to be very well synchronized with the development of the hedge bindweed in southwestern Virginia. Considering this and the high infestation rate of the hedge bindweed seeds by M. discoidus (38-68% in the 3 field sites in 1983) in the area, we think this bruchid is a very useful beneficial insect. This is especially significant because dispersal of hedge bindweed is primarily through the seeds.

Parasites

Two species of parasites were recovered from M. discoidus: an egg parasite, Uscana semifumipennis Girault (Hymenoptera: Trichogrammatidae), and an external larval parasite, Dinamus sp. (Hymenoptera: Pteromalidae). Parasitization was less than 3% and 3.5% by U.

semifumipennis and Dinamus sp., respectively. Both U. semifumipennis and members of the genus Dinamus are known to attack other species of Bruchidae (A. C. Hung, Beneficial Insect Introduction Lab, USDA - personal communication; Pajni and Jit 1979) and thus are not specific to M. discoidus.

Chapter IV

INFLUENCE OF TEMPERATURE, HUMIDITY AND SOIL
COVERAGE ON THE DIAPAUSE OF MEGACERUS DISCOIDUS
(COLEOPTERA:BRUCHIDAE), A SEEDFEEDER OF HEDGE
BINDWEED

4.1 INTRODUCTION

Hedge bindweed, Calystegia sepium (L.) Brown, and field bindweed, Convolvulus arvensis L.. Both are two perennial weeds, reproducing by seeds and underground rhizomes. Infestation by field bindweed is serious mainly in the Midwest and Western United states (Phillips 1978, Rosenthal 1983a), while hedge bindweed is a major weed in the Eastern part of the country (Parrella 1977). Megacerus discoidus (Coleoptera: Bruchidae), a native North American seedfeeder, has been considered as one of the most promising biological control agents of the bindweeds (Mohyuddin 1969a). It overwinters as the 4th instar inside host seeds (see chapter III) Hodek et al. (1981) reported on the roles of relative humidity, food, and ovipositional substrate on diapause duration and termination of Acanthoscelides obtectus (Coleoptera:Bruchidae), a seedfeeder of legumes. However, diapause, which is basic to the phenological adaptation and population dynamics of many insects (Tauber and Tauber 1976), is not well known in bruchids. Thus, environmental factors influencing the diapause of M. discoidus merit further study. This is especially important because of its potential for hedge bindweed control.

Weekly dissections of field collected hedge bindweed seeds in our preliminary studies have shown that over 90% of

M. discoidus larvae were in the 4th instar and had ceased feeding in early September, when host seeds matured. This chapter summarizes the results of our investigations on the effects of (1) temperature on the diapause of M. discoidus, (2) temperature on mortality during diapause (4th instar) and post-diapause (pupa and adult) development, and (3) humidity and soil coverage of infested hedge bindweed seeds on overwintering mortality under field conditions.

4.2 MATERIALS AND METHODS

Effect of temperature on diapause of M. discoidus

Mature hedge bindweed seeds were collected from the field to obtain overwintering M. discoidus during 3-9 September, 1982, and kept in the laboratory ($22\pm 2^{\circ}\text{C}$, 50-60% RH, 12 h photophase) for 10 days before testing. Several thousand seeds were randomly placed into 2 liter screened plastic jars, 250 seeds each, and subjected to 2 high and 3 low temperature treatments in growth chambers. The high temperature treatments ($20\pm 2^{\circ}\text{C}$ and $28\pm 2^{\circ}\text{C}$, 16 h photophase) were checked every 2 days for diapause termination, and continued until no adult emergence for 10 consecutive days. The low temperature treatments ($-4\pm 2^{\circ}\text{C}$, $4\pm 2^{\circ}\text{C}$, and $10\pm 2^{\circ}\text{C}$ in the absence of light) were carried out for 200 days before the seeds were transferred into a growth chamber maintained

at $24 \pm 2^\circ\text{C}$ and 16 h photophase. The seeds were also examined every 2 days for adult emergence. Use of long photophase (16 h) was to facilitate diapause termination of the insect at the higher temperatures, while absence of light was to favor diapause at the lower temperatures. A 60-70% RH was maintained by keeping jars of water in all the growth chambers. Each treatment was replicated 6 times. The adult emergence pattern in all the temperature treatments was compared with that under field conditions, where seeds collected from the same field sites in September, 1983 were kept outdoors in 5 replications (in jars as above) with 250 seeds per replicate. These were checked for adult emergence every 2 days from 12 to 28 June, 1984. Monthly temperature records for the control were obtained from the Field Weather Station at Prices Fork Research Center, Blacksburg. The complete randomization analysis (Zerbe 1979) was used to compare emergence rates by sex at 28°C , where the maximum number of adults was obtained.

Effect of temperature on mortality during diapause and post-diapause development of *M. discoidus*

The seeds in all the above temperature treatments were kept under their treatment conditions until June, 1983, to ensure complete post-diapause development of the insect. Seeds from which no adult emerged were dissected to record

the stage at which mortality occurred. Adult mortality refers to adults found dead in the seeds. We dissected 150 randomly selected seeds from each replicate of the high temperature treatments after emergence had ceased, while all seeds in the 3 low temperature treatments were dissected. A control was established by keeping seeds from the same source outdoors from September, 1982 to June, 1983. The control contained 4 replicates, 250 seeds each. Arcsine transformation was used for percent mortalities prior to the analysis of variance.

Effects of humidity and soil coverage of the seeds on overwintering mortality of *M. discoidus*

Overwintering *M. discoidus* were obtained from seeds kept outdoors after their collection. On 22 September, 1982, the seeds were randomly put into 4.5 liter paper cartons wrapped with plastic having a metal screen (0.6 cm mesh) cover on the top and a 5 cm screen hole (5 cm diameter) at the bottom for ventilation. The cartons, which were used in the following tests, were kept in wooden framed screen cages (90x90x60 cm) which had a plastic roof to prevent winter precipitation. The cages were surrounded by buildings from 3 sides for protection from the wind.

To test humidity as an influencing factor on mortality during the winter, the above cartons were placed in

individual holes dug in the ground (30 cm deep). To examine the fate of M. discoidus in seeds which fall to the ground and become covered by soil, the paper cartons were filled with a (1:2:2) mixture of perlite, vermiculite and sand. The seeds were buried in the mixture, about 40 mm from the surface. Results of these treatments were compared with the control which consisted of seeds placed on the ground in the cages without the soil mixture. Relative humidities were monitored once a month in the holes, as well as at the ground surface with a Psychron Model 566 psychrometer. All treatments and the control were replicated 3 times, with 250 seeds per replicate. In late June, 1983, 150 seeds per replicate were dissected and the mortalities recorded as in the previous experiments. Percent mortalities were transformed to arcsine for t test.

4.3 RESULTS AND DISCUSSION

Effect of temperature on diapause of M. discoidus

Larvae of M. discoidus, which were in diapause, resumed their development when temperature and day-length were again favorable. Adult emergence began 20 and 10 days after overwintering larvae were transferred to 20°C and 28°C, respectively (Fig. 5 A), indicating a much shorter post-diapause development of the larvae at 28°C than at 20°C.

Under natural conditions, there is about a 15 h daylength in June when the temperature is 20-28°C in this area. Thus, the 16 h photophase used in our high temperature treatments should have no significant difference from that in nature. Even if termination of diapause was induced by photoperiodic responses of the insect to a longer photophase (16 h) in the growth chambers than that in the natural environment, as in the case of many other insects (Beck 1980), temperature exerted a definite effect on the post-diapause development of M. discoidus. Compared to the adult emergence pattern under field conditions (Fig. 5B), however, the emergence occurred over a more prolonged period of time at both high temperatures (Fig. 5A).

No adult emergence was observed from seeds maintained under the three low temperatures for 200 days. This concurs with the expected effect of photoperiod and temperature on insect diapause-maintenance (Tauber and Tauber 1976, 1979). Unlike some insects where diapause intensity decreases as the course of diapause progresses (McLeod and Beck 1963, Beck 1980), no obvious change of diapause intensity was observed in our low temperature treatments, regardless of duration. This may be due largely to the absence of light. When seeds from the three low temperature treatments (-4°C, 4°C and 10°C) were transferred to 24°C and 16 h photophase,

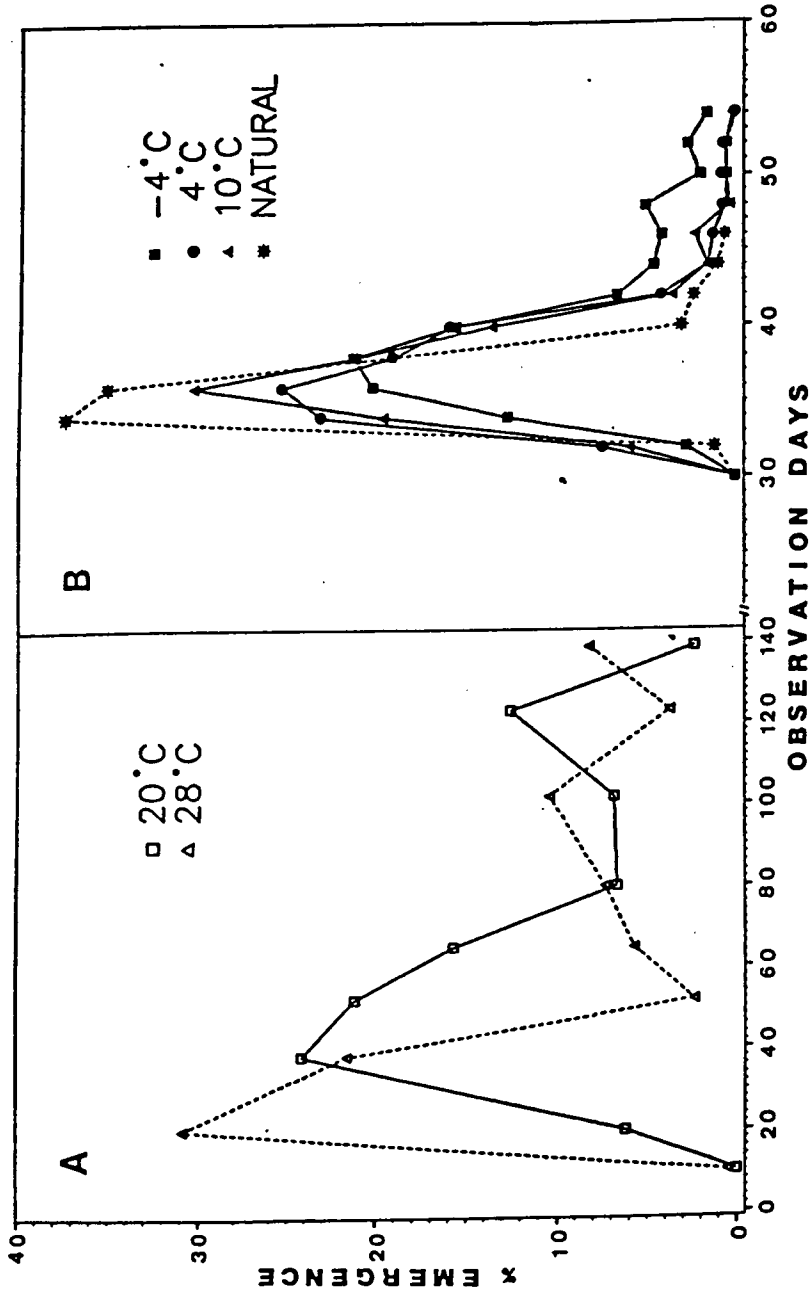


Figure 5: Percent adult emergence of *M. discoidius* from overwintering larvae in different treatments. (A) 20°C and 28°C (n=79.6±16.7 and 106.7±10.2 per replicate, respectively); (B) -4°C, 4°C, and 10°C for 200 days before being transferred to 24°C, 16h photophase, and field conditions (n=42.0±5.7, 95.8±6.8, 95.2±6.4 and 85.4±5.9 per replicate, respectively).

adult emergence occurred at almost the same time, with higher emergence peaks for higher temperatures during diapause (Fig. 5B). Adults subjected to a period of low temperatures (Fig. 5B) exhibited a more normal emergence pattern than those without such an experience (Fig. 5A).

M. discoidus exhibited a slightly different emergence pattern between sexes (Fig. 6). Randomization analysis ($F=0.97$, predetermined F level=0.05, $df=31$) showed that a significantly higher proportion of males versus females emerged ($33.4\pm 4.2\%$ and $27.7\pm 6.9\%$, respectively) in the first 20 days after seeds were placed at 28°C . However, duration of the emergence peak for the females was about 20 days longer than that of the males.

Since M. discoidus is distributed exclusively in North America where its host plants are not available for a second generation under natural conditions, an univoltine life cycle is essential for the insect to adapt to the host and the environment. M. discoidus adapts to host phenology through a larval winter diapause, while most univoltine legume feeding bruchids overwinter as adults (Southgate 1981).

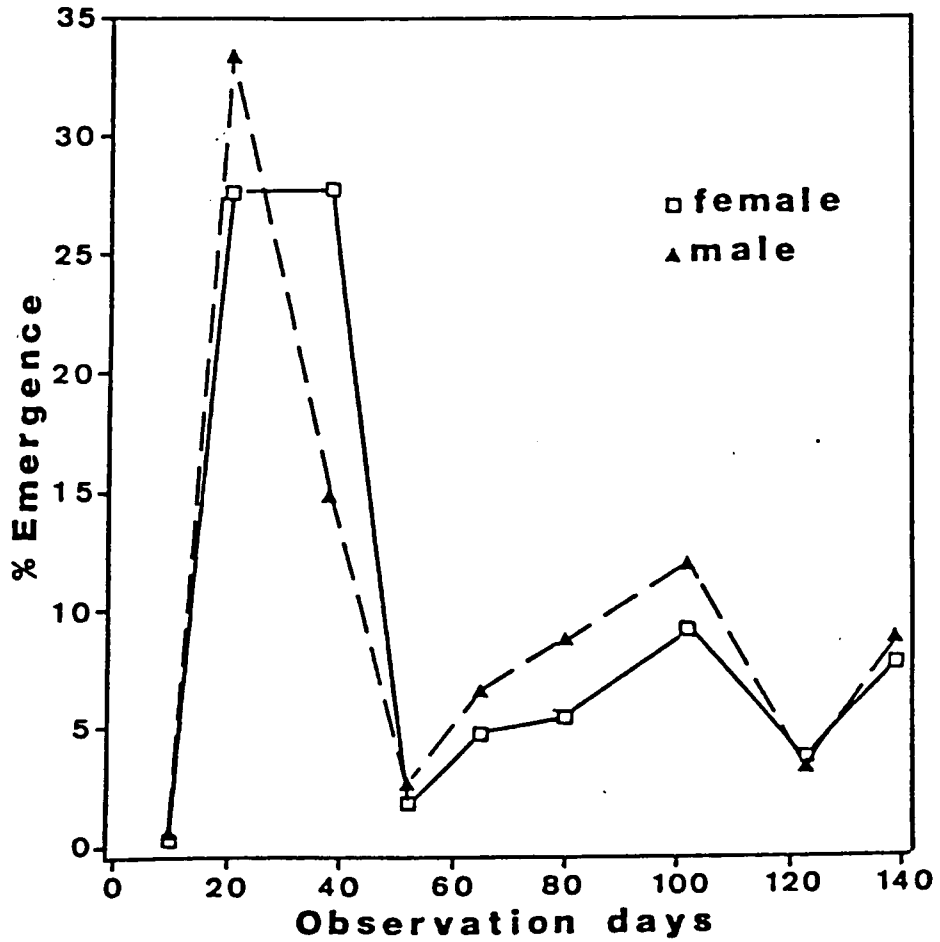


Figure 6: Percent emergence of male and female adults of *M. discoidus* from overwintering larvae maintained at 28°C.

Effect of temperature on mortality during diapause and post-diapause development of *M. discoidus*

About 73% of the seeds collected for the experiment were infested by *M. discoidus*. Mortality of the insect was high exceeding 20% under all observed conditions (Table 3). Temperature affected the various developmental stages differently. In the populations maintained at 20°C and 28°C, the significantly different total mortalities were directly related to differences in adult mortality; higher temperature appeared to be more favorable for survival of diapause-terminated populations. Adult mortalities under both temperatures were significantly higher than that of the control (monthly average temperature = $8.0 \pm 6.6^\circ\text{C}$, range of -16.9° to 31.7°C), indicating an adverse impact on adult survivorship when diapause was artificially terminated. This was also shown by the lower adult mortalities in the populations maintained under the 3 low temperatures before being transferred to 24°C. Diapause termination, however, did not impair pupal development. Larval mortality differed significantly between the populations (Table 3); it increased with decreasing diapausing temperature. The highest larval mortality ($62.5 \pm 4.1\%$) at -4°C suggests a profound effect of low temperature on mortalities of diapausing larvae. Thus, extended low temperatures during a cold winter could reduce the population of *M. discoidus* considerably.

Table 3. Percent mortalities ($\bar{x} \pm S.D.$) of diapause and post-diapause stages of M. discoidus.

Treatment grouping	Temperature (°C)	Total No. sampled	Mortality ¹			Total
			Larva	Pupa	Adult	
High temperature	28	510	8.3±4.3de	0.8±0.8b	24.3±5.2b	33.3±7.6d
	20	540	6.3±1.9e	2.1±1.4ab	43.7±5.3a	52.0±5.1b
Low temperature	10	875	19.0±3.0c	3.0±2.0a	6.5±2.9c	29.6±3.8d
	4	756	34.2±3.3b	3.0±1.4a	6.2±0.7c	43.5±4.5c
Control	-4	1097	62.5±4.1a	4.2±0.9a	4.0±2.1c	70.6±2.5a
	Natural conditions	322	10.9±4.2d	4.4±2.2a	5.2±2.4c	20.4±5.2e

¹ Percentages followed by the same letter within the same column are not significantly different (P=0.05, Duncan's (1955) multiple range test based on arcsine transformed percentage data).

Effect of humidity and soil coverage of the seeds on overwintering mortality of *M. discoidus*

No significant difference in mortality of *M. discoidus* was found between the treatments and the control, although some variation was apparent (Table 4); the control had the lowest mortality ($18.2 \pm 8.3\%$). Relative humidity of the environment was lower for the seeds in the control (20- 70%) than for those in the ground (46- 80%). However, neither humidity nor soil coverage of seeds had significant impact on overwintering mortalities of this insect. This is an adaptational advantage of the insect to its environment, because infested seeds of hedge bindweed are often dropped from the dried vines onto and covered by the soil.

Table 4. Percent mortalities ($\bar{X} \pm S.D$) of M. discoidus in response to seed coverage and high and low humidity

Treatment	Total No. of insects sampled	Mortality ¹ (%)			Total
		Larva	Pupa	Adult	
Seeds in soil mixture	182	19.6±18.0	3.2±1.0	13.5±9.6	36.3±16.4
Cages in ground (RH=46-80%)	313	5.3±3.8	2.7±2.3	11.9±3.7	19.9±6.5
Control (RH=20-70%)	229	8.0±6.7	2.8±3.7	7.3±3.7	18.2±8.3

¹ No significant difference was found between treatments and control by t test (P=0.05) based on arcsine transformed percentage data.

Chapter V

HOST SPECIFICITY OF MEGACERUS DISCOIDUS
(COLEOPTERA:BRUCHIDAE), A NATIVE SEEDFEEDER OF
BINDWEEDS.

5.1 INTRODUCTION

Hedge bindweed, Calystegia sepium (L.) Brown is a serious pest in corn fields, ornamental plantings and nurseries in the eastern United States. It reproduces from seeds and underground rhizomes, both of which are very tolerant of chemical and mechanical control. One of the most promising biological control agents of this weed, Megacerus discoidus, (Say) (Coleoptera:Bruchidae)(Mohyuddin 1969a), is a native North American seed feeder (Bridwell 1929). Rosenthal and Buckingham (1982) reported Spermophagus sericeus (Coleoptera:Bruchidae) as the most common seedfeeder of field bindweed, Convolvulus arvensis L., a noxious weed closely related to hedge bindweed in western Mediterranean Europe, where the two weeds originated. They also emphasized the need for further study of M. discoidus before introduction of S. sericeus into North America.

In southwestern Virginia, adults of M. discoidus occur from early June to September and feed on bindweed pollen and nectar (see chapter III). Eggs are usually laid under the bracts of the seedpods. Newly eclosed larvae burrow into the seeds and consume the entire seed contents. The 4th instar overwinters inside the host seed. This species belongs to the subgenus Megacerus (Teran and Kingsolver 1977), which has been reported exclusively associated with plants of the

tribe Convolvuleae (Center and Johnson 1976, Southgate 1979). Documented hosts of M. discoidus include Calystegia sepium, Convolvulus arvensis (Mohyuddin 1969b, Parrella 1977), Ipomoea fastigiata, and I. lepidophilla (Teran and Kingsolver 1977). According to Harris and Zwolfer (1968), phytophagous insects of a certain taxon which have been found associated with only a small group (genus or tribe) of hosts are often highly host specific, because their recorded host range demonstrates a failure of exploiting new hosts beyond those closely related plants. This, however, does not exclude the necessity of host specificity tests of a potential biological control agent, especially on those economically or ecologically important plants in the target country or region. The objectives of my study from 1982 to 1984 were to test oviposition and larval development by M. discoidus on a range of selected plant species.

5.2 MATERIALS AND METHODS

Larval development tests

Nineteen plant species representing 6 families were included in the test (Table 5); 18 were used in the larval development test and 12 for the oviposition test. The plants, either closely related species or important economic crops or ornamentals, were selected mainly to obtain information on the general host range of the insect. Emphasis was on members of the genus Ipomoea, since they have often been found susceptible to attack by organisms associated with the bindweeds (Rosenthal et al. 1983).

Eggs of M. discoidus were collected from seedpods of hedge bindweed in the field in Blacksburg, Virginia, during mid August, 1983 and 1984. They were inoculated on mature seeds or seedpods of the test plants with a camel's-hair brush at a rate of 2 eggs/seed(pod). These seeds were individually placed into vials (5 by 1.5 or 9 by 2.5 cm) sealed with cotton, and incubated in a rearing chamber maintained at $24^{\circ}\pm 2^{\circ}\text{C}$, 60-70% RH and 16 h photophase. They were checked daily until egg hatch; unhatched eggs were discarded. Thus, 10-52 larvae, depending on the availability of eggs, were tested on each plant species. Half of the infested seeds, unless the number of larvae tested was less

Table 5. Plant species used in the host specificity tests for M. discoidus

Family	Scientific name	Common name	Insect stage tested ¹
Convolvulaceae	<u>Calystegia sepium</u> (L.) Brown	Hedge bindweed	L,A
"	<u>C. spithameus</u> L.	Upright bindweed	A
"	<u>Ipomoea tricolor</u> Cav.	Heavenly blue morningglory	L,A
"	<u>Ipomoea purpurea</u> (L.) Roth	Tall morningglory	L,A
"	<u>Ipomoea coccinea</u> L.	Red morningglory	L
"	<u>Ipomoea lacunosa</u> L.	Small flowered morningglory	L
"	<u>Ipomoea hederacea</u> (L.) Jacq.	Ivy-leaved morningglory	L
"	<u>Ipomoea pandurata</u> (L.) G. F. W. Mey	Wild sweet potato	L
Gramineae	<u>Avena sativa</u> L.	Oat	L,A
"	<u>Zea mays</u> L.	Corn	L,A
"	<u>Sorghum bicolor</u> (L.)	Sorghum	L,A
Cruciferae	<u>Raphanus sativus</u> L.	Radish	L,A
Asteraceae	<u>Helianthus annuus</u> L.	Common sunflower	L,A
Leguminosae	<u>Phaseolus vulgaris</u> L.	Kidney bean	L,A
"	<u>Phaseolus aureus</u> L.	Mung bean	L
"	<u>Phaseolus limensis</u> var. <u>limenanus</u> Bailey	Bush bean	L
"	<u>Glycine max</u> (L.) Merr.	Soybean	L
Solanaceae	<u>Nicotiana tabacum</u> L.	Tobacco	L,A
"	<u>Solanum carolinense</u> L.	Horsenettle	L,A

¹L=larva, A=adult

than 20, were dissected 8-10 days after egg hatch to determine the survival of earlier stages; the rest of the seeds were observed for adult emergence, or dissected 50 days after egg hatch, to record the maximum developmental stage reached. For the species with less than 20 larvae tested, all seeds were dissected 50 days after egg hatch unless adult emergence had already occurred. Larval head capsule width was measured to determine larval instars.

Oviposition tests

Twelve plant species (Table 5) used for this test were grown from seeds in small field plots such that the test plant phenology was in synchrony with M. discoidus activity. M. discoidus were obtained from hedge bindweed seeds collected from the field in Blacksburg during late September, 1982 and 1983 for tests conducted in 1983 and 1984, respectively. The seeds were kept outdoors over the winter before being transferred to growth chambers at 20°C or 28°C, 60-70% RH, and 16 h photophase, about 7-10 days prior to the field test. The seeds were checked daily and newly emerged adults were immediately sexed, provided with water and held at 15±2°C, to prevent mating and excessive activity. Within 3 days after emergence, they were caged at a rate of one pair per cage on seedpods or fruit heads of

the test plants in the field. One or two flowers of the plants were included in the cage as adult food source. Cages for most plant species were made of organdy with metal screen (0.6 cm mesh) on the top, and tied to seedpods or fruit heads of the plant. Size and shape of the cages, however, were modified for each plant species, to prevent adults from escaping while allowing normal ventilation. The plants were examined for oviposition before and at 5, 10, and 15 days after adults were introduced. Any egg found at each examination was recorded and removed. Twelve to 27 pairs of adults, depending on their availability, were tested on each host species. Hedge bindweed was used as the control host.

5.3 RESULTS AND DISCUSSION

Larval development tests

On the plant species tested, development to the adult stage occurred only on hedge bindweed and wild sweet potato (Table 6), a weedy plant in waste areas and roadsides. Larvae also developed to the 4th instar (but did not pupate) on red morningglory, small flowered morningglory, and ivy-leaved morningglory, which are weeds in waste areas and crop fields. Failure to pupate was probably due to the insufficient seed content of these plants, as pointed out by

Southgate (1979) in host-plant relationships of Bruchidae. Only two insects reached 2nd instar in seeds of heavenly blue morningglory (Table 6), a commonly cultivated ornamental plant. Some tunneling of testa by newly eclosed larvae occurred on all other test plants, but the larvae died before any further feeding on the seed. The efficient tunneling observed in all larvae suggests an inherent behavior of the insect, as newly eclosed larvae could even burrow through the bottom of plastic vials. These results indicate that the hosts of M. discoidus in the genus Ipomoea are limited to weedy species.

Oviposition tests

The oviposition test was confined to selected hosts in which the blooming period was well synchronized with the adult appearance of M. discoidus. Although 90% of the females survived for more than 15 days on all test species, oviposition occurred only on hedge bindweed (control) and heavenly blue morningglory (eggs per female= 19.3 ± 14.8 and 1.3 ± 0.6 ; n=12 and 13 females, respectively). Females began to oviposit on hedge bindweed within 5 days after caging. Compared to hedge bindweed, the minimal oviposition on morningglory implies that it is unlikely to be selected for oviposition under natural conditions. This was confirmed by

Table 6. Summary of *M. discoidus* larval development tests

Plant name	No. insects tested ¹	Extent of damage ²	% Reaching (stage) ³				
			2nd inst.	3rd inst.	4th inst.	pupa	adult
Hedge bindweed	52	F	92.3	96.2	92.3	92.3	61.5
Heavenly blue morningglory	52	F	1.9	0			
Tall morningglory	21	T	0				
Red morningglory	10	F	-	-	40.0	0	
Small flowered morningglory	10	F	-	-	50.0	0	
Wild sweet-potato	37	F	80.9	43.8	43.8	37.5	18.8
Ivy-leaved morningglory	10	F	-	-	30.0	0	
Oat	52	T	0				
Corn	52	T	0				
Sorghum	52	T	0				
Radish	52	T	0				
Common sunflower	52	T	0				
Kidney bean	52	T	0				
Mung bean	52	T	0				
Bush bean	52	T	0				
Soybean	20	T	0				
Tobacco	20	T	0				
Horsenettle	11	T	0				

¹No. infested seeds dissected.

²F=Feeding of seed content; T=tunneling of testa, but no feeding of seed content.

³ In host species with more than 20 insects tested, percentages reaching 2nd instar were based on No. seeds dissected 8-10 days after egg hatch; percentages reaching further stages were based on No. seeds dissected 50 days after egg hatch.

a survey in the same field plot, where more than 100 naturally occurring flowers and seedpods of heavenly blue morningglory were examined. No eggs of M. discoidus were found, whereas many eggs were discovered on nearby hedge bindweed seedpods.

In summary, among the 19 host species tested, wild sweet potato was the only other possible host of M. discoidus besides the known hosts of the insect. Field bindweed was not included in this test, because it is a serious weed throughout the world and is a known host of M. discoidus. Sweet potato, Ipomoea batatas (L.) Lam was also excluded from the test, because its seed, which is seldom produced in cultivated fields, is neither important for reproduction nor is it used by man (Mohyuddin 1969a). Thus, M. discoidus is safe to use for biological control of bindweeds. Its narrow host range should be more desirable than a strictly monophagous seed feeder, since it helps to reduce host-parasite homeostasis and enables the insect to maintain itself on closely related weed species in areas where its primary host is not present (Harris 1973). The extent to which M. discoidus is used, however, will depend upon the impact of natural beetle populations on bindweed density, or on our ability to manipulate M. discoidus populations, which remain to be determined.

Chapter VI

IMPACT OF MEGACERUS DISCOIDUS
(COLEOPTERA:BRUCHIDAE) ON GROWTH AND SEED
PRODUCTION OF HEDGE BINDWEED

6.1 INTRODUCTION

Hedge bindweed, Calystegia sepium (L.)Brown, and field bindweed, Convolvulus arvensis L. (Tubifloreae: Convolvulaceae) are two serious pests in the United States (Rosenthal and Buckingham 1982). They compete with crops for light by their vigorous foliage and climbing habit, and for soil moisture and nutrients by their deep and perennial root systems (Weaver and Riley 1982). Reproduction is through underground rhizomes and seeds. The seed has hardened testa and is the major means of dispersal (Jordan and Jordan 1982). Megacerus discoidus (Say), a native North American seedfeeder, has been considered as one of the most promising candidates for biological control of bindweeds (Mohyuddin 1969a, Rosenthal and Buckingham 1982). Having studied the biology and host range of this insect (see chapter III and V), the next step in weed biological control (Kok 1974) is to assess the impact of this insect on density and growth of bindweeds.

Harris (1973) stressed that a successful weed biocontrol agent should exert its attack at the most vulnerable developmental stage of the host. Infestation of unimportant tissues by a phytophagous insect may exclude it as a candidate for biological weed control (Pemberton and Andres 1980). On the other hand, feeding on certain parts of

a weed by a biological control agent should cause no physiological changes in the plant such that growth of other organs of the weed will be stimulated. Such changes have been described by Bidwell (1979). According to Maddox (1980) and Cartwright (1983), these physiological changes could offset the effects of biological control agents. Such interactions need to be taken into account in evaluation of a biological weed control agent. However, this may not be the case here, because M. discoidus larvae feed exclusively on the seed content (endosperm/embryo) of bindweeds. But because of the potential value of this insect for bindweed control, I investigated the hedge bindweed growth response to seed consumption, as well as the impact of M. discoidus on seed production of the weed.

6.2 MATERIALS AND METHODS

Impact of M. discoidus on seed production

Several thousand hedge bindweed seeds were collected from the field in late September, 1983 to obtain M. discoidus. The seeds were caged outdoors until May, 1984, when they were moved to a rearing room maintained at $18 \pm 2^\circ\text{C}$ and 12 h photophase to delay adult emergence. They were subsequently placed in a rearing chamber ($26 \pm 2^\circ\text{C}$ and 16 h photophase), beginning in early June at 5-day intervals so

that adult emergence of M. discoidus was synchronized with the phenology of hedge bindweed in the field. Newly emerged adults were immediately sexed, moved to the rearing room, and fed with 10% sugar solution for 1-3 days before introduction into field cages at two field sites, approximately 3 km apart in Blacksburg, Virginia, where hedge bindweed grew on fences along corn fields. When hedge bindweed was in peak bloom (late June—Site I, early July—Site II), the plants at each site were randomly grouped and confined in cages of aluminum screen (0.6 cm mesh), about 2 m long, 1.5-1.7 m high (ca. 10 cm above the plants), and 50-70 cm wide which enclosed plants on both sides of the fence. The cages were temporarily closed with staples and the bottom edges were buried in soil until July 16, when the plants reached peak seedpod formation. This served to inhibit natural infestation of the weed by M. discoidus. One day before beetles were introduced into the cages, number of plants in each cage was counted. Hedge bindweed plants were randomly collected from fences adjacent to the cages to calculate mean number of seedpods per plant. At Site I, 2 to 3 days-old adults were released into the cages on 20 July, 1984, at a rate of 50 pairs per cage (ca. 1.2 pairs per plant). To ensure infestation of 5-6 eggs/seedpod, field collected M. discoidus eggs were inoculated with a

camel's-hair brush on all seedpods in the cages 10 days after the adult release. The cages were closed after each release. A control was established by caging plants with no release of adults. At Site II, adults were released into each cage at rates of one pair per three plants (0.3 pairs/plant) and one pair per ten plants (0.1 pairs/plant), respectively. All treatments at both sites were replicated three times. On 10 August, 1984, a second release of 2 to 3 days-old adults into the same cages was conducted using the same beetle:plant ratio as the first release for each treatment, to ensure exposure of newly formed seedpods to the adults.

Between 6 and 15 October, 1984, at plant senescence, all cages were removed and matured seedpods collected from each cage. The number of seedpods per plant was determined and all seeds were dissected in the laboratory to obtain infestation rates. Percent seed infestation was transformed to arcsin for analysis of variance.

Hedge bindweed growth response to seed infestation

At the above field sites, 10-15 hedge bindweed plants were randomly sampled before release of M. discoidus. Stem diameter at 1 cm above ground was measured with a caliper and number of lateral branches of each sampled plant was

counted. When the cages were removed and plants harvested on October, stem width and number of branches per plant in the treated and control cages were compared with those sampled at the beginning of the season. To overcome abnormality of counted data for analysis of variance, number of branches per plant was transformed to square root. All the foliage of hedge bindweed was collected, dried at 70°C for 60 h, and weighed.

6.3 RESULTS AND DISCUSSION

Impact of *M. discoidus* on seed production

At field site I, the release of a relatively high proportion of adults plus egg inoculation resulted in a significantly higher rate of seed infestation ($70.9 \pm 4.5\%$) than that in the control ($38.8 \pm 18.6\%$) (Table 7). This shows that with a high level of infestation, seed production of hedge bindweed can be significantly reduced by *M. discoidus*, which is important in suppressing the weed population and diminishing its dispersal. However, seeds were not all eliminated, because not all seeds in a pod were attacked, even though beetle eggs exceeded the number of seeds in a pod early in the season. Maddox (1980), in reporting a significant increase in floral counts of puncturevine attacked by a seed weevil, *Microlarinus lareynii*, indicated

that it was due to interference with the vegetative growth of the plant by the weevil. In bindweeds, similar physiological changes in the plant caused by insect damage could occur as vertical roots often generate shoots (Swan and Chancellor 1976), which can set seedpods even late in the season. Nevertheless, formation of seedpods and seeds of hedge bindweed was not interrupted by M. discoidus in this experiment, because the number of seedpods and seeds per plant was not significantly different between the treatment and control (Table 7). It has been reported that seedpods of field bindweed which appeared to be normal often contain no viable seeds, and seeds that set early in the season may fail to mature (Weaver and Riley 1982). This explains the significant difference between number of seedpods per plant sampled at the beginning of the season and that when plants were senescent in the treated plants and control.

At field site II, however, release of adults did not increase the seed infestation significantly (Table 7). The low infestation rate at this site was not the result of adult mortality, because living female adults were observed in the cages 10 days after their release. It was likely due to the low beetle:plant ratio, inadequate mating or oviposition, because no egg inoculation was made at this site. Number of seedpods or seeds per plant between the

Table 7. Seedpod and seed formation of hedge bindweed in response to infestation by M. discoidus ($\bar{x} \pm s.d.$)¹

Treatment	No. plants observed /cage	% seed infested	No. seedpods /plant	No. seeds /plant
Site I				
Pre-release sample ²	12	-	8.6±6.7 a	-
Adult & egg added	44±4	70.9±4.5 a	4.3±1.8 b	8.7±4.7 a
Control	34±16	38.8±18.6 b	3.3±1 b	6.6±2.1 ab
Site II				
Pre-release sample ²	15	-	8.3±4.4 a	-
Release adult (1 pair/3 plants)	59±7	13.1±3.4 c	3.4±0.8 b	5.7±1.6 ab
Release adult (1 pair/10 plants)	76±15	11.4±3.8 c	2.0±0.4 b	3.0±0.6 b
Control	46±14	19.1±7.4 c	2.2±1.4 b	3.0±2.0 b

¹ Means with the same letter in a column are not significantly different, Duncan's (1955) multiple range test (P=0.05); Analysis of variance based on arcsine transformed percentage data.

² Samples were taken from plants outside experimental cages.

treatments and the control at Site II was also not significantly different. Thus, for any observable impact, M. discoidus has to be in sufficiently high levels to ensure adequate infestation of the seeds.

Hedge bindweed growth response to seed infestation

The number of lateral branches of hedge bindweed is significantly different between treated cages and the control at both field sites (Table 8). However, since insect attack at site I was related to an increase in number of lateral branches per plant, while at site II, it was related to a decrease; the actual effect of insect attack is uncertain. The seed infestation rate was not significantly different between treatments and the control at Site II. These indicate that the difference in lateral branch numbers is likely a reflection of growth pattern variation of the weed, as described by Weaver and Riley (1982), rather than the influence by M. discoidus.

Plant stem diameter showed no significant difference between the treatment and control at Site I (Table 8). The difference at Site II was apparently due to plant growth variation. Foliage dry weight, which is often a better indication of vegetative growth than stem width or branch number, showed no significant differences at either site

(Table 8). These results disproved the previous assumption that vegetative growth of hedge bindweed might be stimulated by destruction of the seed content.

In summary, feeding by M. discoidus destroyed the seeds but did not cause any undesirable side effect on the growth of hedge bindweed. Higher seed infestation occurred when the beetle/plant ratio was increased, suggesting that inundative release of this insect could greatly reduce the number of seeds produced by the weed, and effectively suppress the density and dispersal of the weed. However, effective control of hedge bindweed may require the combined use of M. discoidus with other stress factors, because it attacks only the seeds and not all seeds in a seedpod are destroyed.

Table 8. Responses in vegetative growth of hedge bindweed to infestation by *M. discoidus*¹

Treatment	No. plants sampled /cage	No. branches /plant(x±s.d.)	Stem diam. (mm)	Plant dry weight(g)
Site I				
Pre-release sample ²	12	4.3±2.6b	3.4±0.6bc	-
adult & egg added	44±4	6.4±3.5a	3.3±0.4bc	2.3±0.9a
Control	34±16	3.8±1.7bc	2.9±0.5c	3.6±2.0a
Site II				
Pre-release sample ²	15	1.6±0.7d	3.5±0.6b	-
Release adult (1 pair:3 plants)	59±7	2.8±2.7cd	3.5±1.0b	4.3±1.0a
Release adult (1 pair:10 plants)	76±15	2.6±2.0cd	2.9±0.9c	4.1±0.5a
Control	46±14	4.2±2.5b	4.4±0.5a	4.9±3.2a

¹ Means with the same letter in a column are not significantly different, Duncan's (1955) multiple range test (P=0.05).

² Samples were taken from plants outside the experimental cages.

Chapter VII
SUMMARY AND CONCLUSIONS

The biology of Megacerus discoidus (Say) was studied in southwestern Virginia from 1982 to 1984. The beetle has 4 larval instars, one generation a year, and overwinters as a fourth instar inside the host seed. Each larva consumed about 40-50% of the seed content before diapause and the rest of the seed the following spring. Although several larvae could infest a seed, only one successfully completed its development within a seed. Cannibalism was most common among 2nd and 3rd instars. Adults emerged in mid to late June; they are active diurnal fliers. The females usually oviposited under the bracts of the host seedpods and occasionally on flowers. There was only one peak of oviposition activity which lasted about one month. Good synchronization was observed between the life cycle of the insect and the phenology of hedge bindweed. An egg parasite, Uscana semifumipennis Girault (Trichogrammatidae), and an external larval parasite, Dinamus sp. (Pteromalidae), were found.

Diapause of M. discoidus was experimentally terminated, and adults began to emerge within 20 and 10 days after overwintering larvae were transferred to 20°C and 28°C respectively (16 h photophase, 60-70% RH). Artificial termination of diapause, however, increased mortality and prolonged the emergence period of adult beetles. Diapause

continued for 200 days when the larvae were kept below 10°C in the absence of light. Subsequent development of these overwintered larvae showed that larval mortality was significantly increased by low temperature during diapause. Humidity and soil coverage of the hedge bindweed seeds had no significant impact on mortality of M. discoidus in diapause under field conditions.

Larval development and adult oviposition tests were conducted to determine host specificity of M. discoidus. Hedge bindweed and wild sweet potato, Ipomoea pandurata (L.) G. F. W. Mey, were the only species of 18 plants tested that supported larval development to the adult stage. Larvae reached the fourth instar on three other Ipomoea species, I. coccinea L. (red morningglory), I. hederacea (L.) Jacq. (ivy-leaved morningglory), and I. lacunosa L. (small flowered morningglory). These 3 Ipomoea species were not suitable hosts of M. discoidus because of their small-sized seeds. Larvae did not feed on economically important ornamentals and crop plants tested. Females oviposited only on hedge bindweed and heavenly blue morningglory, I. tricolor Cav.; the latter did not support larval development. The risk of the beetle attacking economically and ecologically important plants in the eastern U.S.A. is very small.

A high rate ($70.9 \pm 4.5\%$) of seed infestation of hedge bindweed was obtained by releasing a relatively high proportion of M. discoidus adults per plant (1.2 pair per plant) plus egg inoculation in field cages. Complete elimination of the seeds by releasing the beetles, however, would probably not occur because not all the seeds in a pod were attacked even though the pod had more beetle eggs than number of seeds. Release of a lower number of adults (0.3 pairs/plant or 0.1 pairs/plant) led to a low seed infestation rate. Seedpod and seed formation of infested weed plants were not influenced by seed consumption. In addition, the high seed infestation rate apparently did not cause any change in vegetative growth of infested plants. Thus, effective reduction of seed production of hedge bindweed and suppression of the weed dispersal by M. discoidus can only be achieved at high insect/plant ratios.

Perennial weeds commonly have alternative reproductive organs, such as seeds, rhizomes, and other types of perennating parts. Thus, complete biological control of these weeds can hardly be achieved by using an insect which causes damage limited to the seeds. However, this does not imply that effects of individual biological control agents should be neglected. Research efforts should be directed to continued investigation of phytophagous arthropods which

damage bindweeds. Such efforts may lead to harmonious use of multiple stress factors in an integrated management program of the weeds. In this respect, it will be essential to evaluate the impact of these stress factors individually and collectively, and the response of the host to these factors. Previous research on this subject has been mostly limited to descriptive analysis. Utilization of other methods, such as radiotracer techniques, in quantitatively assessing the impact of insect feeding and plant response should be explored. This will provide a basis for more efficient selection and use of effective biological weed control agents. Considering that sweet potato, Ipomoea batatas, and some ornamental plants in the genus Ipomoea are often subjected to attack by insects associated with bindweeds, conflicting interests will still be the major taboo in search of biological control agents for bindweeds (Andres 1980). Thus, benefits derived from using some stenophagous insects to control bindweeds should be more reasonably weighed against the economical and ecological value of those plant species. Moreover, more intensive studies are needed on searching and evaluating microbial agents for bindweed control, because these organisms offer great promise even though such studies have not been conducted.

REFERENCES CITED

- Alcock, C. R. 1974. Field bindweed or *Convolvulus* - A guide to identification and control. *J. Agric.* 77:141-144.
- Aldrich, R. J. 1984. Weed crop ecology-Principles in weed management. Breton Publishers. A Division of Wasworth, Inc., N. Scituate, Massachusetts.
- Andres, L. A. 1980. Conflicting interests and the biological control of weeds. Proc. 5th Int. Symp. Biol. Control Weeds. Brisbane, Australia. pp. 11-20.
- Andres, L. A. 1982. Integrating weed biological control agents into a pest-management program. *Weed Sci.* 30 (supplement):25-30.
- Bakke, A. L. 1939. Experiments on the control of European bindweed (*Convolvulus arvensis* L.). pp. 365-440 In Iowa State College Agric. Exp. Stn. Res. Bull. No. 259
- Bakke, A. L., W. G. Gaessler, and W. E. Loomis. 1939. Relation of root reserves to control of European bindweed, *Convolvulus arvensis* L. Iowa Agric. Exp. Sta. Res. Bull. 254:113-114.
- Baloch, G. M. 1974. Phytophagous organisms associated with bindweeds, *convolvulus* spp. in Pakistan. Tech. Bull. Commonw. Inst. Biol. Control. 17:29-36.
- Baloch, G. M. 1977a. Tortoise-beetles (Chrysomelidae:Cassidinae) associated with field bindweed, *Convolvulus arvensis* L. in Pakistan. Tech. Bull. commonw. Inst. Biol. control. 18:131-144.
- Baloch, G. M. 1977b. Insects as biological Control agents of field bindweed, *Convolvulus arvensis*. PANS 23:58-64.
- Barr, C. G. 1940. Organic reserves in the roots of field bindweed. *J. Agric. Res.* 60:391-414.
- Beck, S. D. 1980. Insect photoperiodism. 2nd ed. Academic Press, New York.
- Best, K. F. 1963. Note on the extent of lateral spread of field bindweed. *Can. J. Plant Sci.* 43:230-232.

- Bidwell, R. G. S. 1979. Plant Physiology, 2nd ed. Macmillan Publishing Co., Inc. New York.
- Bottimer, L. J. 1968. Notes on Bruchidae North of Mexico with a list of world genera. Can. Entomol. 100:1009-1049.
- Bridwell, J. C. 1929. Description of a Bruchid immigrant into Hawaii breeding in the seeds of Convolvulaceae (Coleoptera). Proc. Entomol. Soc. Wash. 31:112-114.
- Bonnett, Jr., H. T. and J. G. Torrey. 1965. Chemical control of organ formation in root segments of Convolvulus cultured in vitro. Plant Physiol. 40:1228-36.
- Brown, E. O. and R. H. Porter. 1942. The viability and germination of seeds of Convolvulus arvensis L. and other perennial weeds. Agric. Exp. Stn. Iowa State College Res. Bull. 294
- Bybee, T. A., C. G. Messersmith, and D. R. Gigax. 1977. Root carbohydrate reserves in leafy spurge, Canada thistle, and field bindweed. Proc. N. Central Weed Control Conference 33:22-23.
- Cartwright, B. O. 1983. Response of Carduus thistles to three biological control agents. Ph.D. dissertation, Virginia Polytechnic Institute and State University, Blacksburg.
- Center, T. D. and C. D. Johnson. 1976. Host plants and parasites of some Arizona seed-feeding insects. Ann. Entomol. Soc. Am. 69:195-201.
- Cox, H. R. 1909. The eradication of bindweed - or wild morningglory. USDA Farmer's Bull. No. 368.
- Cunningham, T. S. 1958. Bindweed control in Oklahoma. OK. State Univ. Ext. Circ. E-668.
- Davison, J. G. and J. A. Bailey. 1974. The response of Convolvulus arvensis (bindweed) to 2,4-D, MCPA, MCPB, Dichlorprop, Mecoprop, 2,4,5,-T, Dicamba, and Glyphosate at various doses and application dates. Proc. 12th British Weed Control Conference 2:641-648.
- Davison, J. G. 1976. Control of the bindweeds Convolvulus arvensis and Calystegia sepium in fruit crops. Pestic. Sci. 7:429-435.

- Duncan, D. B. 1955. Multiple range and multiple F tests. *Biometrics* 11:1-41.
- Dury, C. 1879. List of the Coleoptera observed in the vicinity of Cincinnati. *J. Cincinn. Soc. Nat. Hist.* 2:162-178.
- Etzel, L. K., S. O. Levinson, and L. A. Andres. 1981. Elimination of *Nosema* in *Galeruca rufa*, a potential biological control agent for field bindweed. *Environ. Entomol.* 10:143-146.
- Feldman, J. M. and O. Gracia. 1977. Studies of weed plants as sources of viruses V. Occurrence of alfalfa mosaic virus on origanum crops and on some weeds in Argentina. *Phytopathologische Zeitschrift* 90:87-90.
- Fernald, M. H. 1950. Gray's manual of botany. 8th ed. Am. Book Co., New York.
- Frazier, J. C. 1943. Amount, distribution and seasonal trend of certain organic reserves in the root system of field bindweed, *Convolvulus arvensis* L. *Plant Physiol.* 18:167-184.
- Guncan, A. 1973. Carbohydrate reserves of *Sonchus arvensis* rhizomes during a vegetative season and comparison with *Convolvulus arvensis* L. *Int. Symp. over Fytofarmacie en Fytiatrie part I. Mededetinger Fakulteit Landbouwwetenschappen Gent.* 38:1011-1017.
- Harris, P. 1973. The selection of effective agents for the biological control of weeds. *Can. Entomol.* 105:1495-1503.
- Harris, P. and H. Zwolfer. 1968. Screening of phytophagous insects for biological control of weeds. *Can. Entomol.* 100:295-303.
- Hodek, I., A. Bonet, and M. Hodkova. 1981. Some ecological factors affecting diapause in adults of *Acanthoscelides obtectus* from mexican mountains. *Series Entomol.* 19:43-55.
- Holm, L. G., K. L. Plunknett, J. V. Pancho, and J. P. Herberger. 1977. The world's worst weeds. East-West Center Book, Univ. Press of Hawaii, Honolulu, Hawaii.

- Huffaker, C. B. 1964. Fundamentals of biological weed control. pp. 631- 649 In P. DeBach (ed.), Biological control of insect pests and weeds. Chapman and Hall LTD, London.
- Jordan, L. S. and J. L. Jordan. 1981. Field bindweed (Convolvulus arvensis) seed germination. Proc. North Central Weed Control Conference 35:151-152.
- Jordan, L. S. and J. L. Jordan. 1982. Effects of Pre-chilling on Convolvulus arvensis L. seed coat and germination. Ann. Bot. 49:421-423.
- Kennedy, P. B. and A. S. Crafts. 1931. The anatomy of Convolvulus arvensis, wild morning-glory or field bindweed. Hilgardia 5(18)591-622.
- Kok, L. T. 1974. Principles and methodology of biological weed control. FAO Plant Protection Bull. 22(4):77-81.
- Landis, B. J. and C. W. Getzendaner. 1947. Aleyroides spiraeoides infesting potatoes. Sci. Notes 40:567.
- LeConte, J. L. 1859. The complete writings of Thomas Say on the entomology of North America. vol. II. Bailliere Bros., New York. 814 pp.
- Lewis, W. H. and R. L. Oliver. 1965. Realignment of Calystegia and Convolvulus (Convolvulaceae). Ann. Missouri Bot. Garden 52:217-222.
- Li, J. C. R. 1964. P.195 in Statistical inference I.. Edwards Brothers. Inc., Ann Arbor, Michigan, 658pp.
- Maddox, D. M. 1980. Seed and stem weevils of puncturevine: a comparative study of impact, interaction, and insect strategy. Proc. 5th Int. Symp. Biol. Control Weeds, Brisbane, Australia.
- McLeod, D. G. R., and S. D. Beck. 1963. Photoperiodic termination of diapause in an insect. Biol. Bull. 124:84-96.
- McWhorter, C. G. and W. C. Shaw. 1982. Research needs for integrated weed management systems. Weed Sci. 30(supplement):40-45.
- Menzio, C. 1931. Damage caused by insects to sugar-beet in Italy during the year 1931. L'Ind. Saccarif. Ital. XXIV, No. 12.

- Messersmith, C. G. 1980. Economics of perennial weed control. Proc. N. Central Weed Control Conference 35:51 (abstr.).
- Meyer, L. J. 1977. The influence of environment on growth and control of field bindweed. Proc. N. Central Weed Control Conference 33:141-142.
- Mohyuddin, A. I. 1969a. Insects from Calystegia spp. and Convolvulus spp.. Tech. Bull. Commonw. Inst. Biol. Control. 11:93-104.
- Mohyuddin, A. I. 1969b. The biology and host spectrum of some stenophagous insects found on Convolvulus and Calystegia spp. at Belleville, Ontario. Tech. Bull. Commonw. Inst. Biol. Control. 12:131-146.
- Motschoulsky, V. 1873. Enumeration des nouvelles especes de coleopteres rappedtes de ses voyages. Bull. Soc. Nat. Mosc. 46:203-252.
- Muzik, T. J. 1970. Weed biology and control. McGraw Hill Book Co., New York.
- Pajni, H. R. and S. Jit. 1979. Some observations on the biology of Callosobruchus analis (Fabr.) (Bruchidae: Coleoptera). Research Bull. Panjab Univ., Science. India. 27:141-146.
- Parrella, M. P. 1977. Oidaematophorus monodactylus (L.) and Bedellia somnulentella (Zeller): two potential biological control agents of hedge bindweed in southwestern Virginia. MS Thesis. VPI&SU, Blacksburg, Virginia.
- Parrella, M. and L. T. Kok. 1975. Bindweeds and their potential for biological control. Va. J. Sci. 26:44 (abstr.).
- Parrella, M. P. and L. T. Kok. 1977. The development and reproduction of Bedellia somnulentella on hedge bindweed and sweet potato. Ann. Entomol. Soc. Am. 70:925-928.
- Parrella, M. P. and L. T. Kok. 1978. Oidaematophorus monodactylus: oviposition and development on sweet potato and inundative releases on hedge bindweed. Environ. Entomol. 7:803-806.

- Pemberton, R. and L. Andres. 1980. Insect feeding effects on host plant tissues, physiology and survival; the impact of Coleophora parthenica Meyrick on Salsola iberica Et Pau.. pp. 355 in Abstr. 16th Int. Congress Entomol., Kyoto, Japan.
- Pfaffenberger, G. S., S. M. DeL'Argentier, and A. L. Teran. 1984. Morphological descriptions and biological and phylogenetic discussions of four species of Megacerus larvae (Coleoptera: Bruchidae). The Coleopterists Bull. 38:1-26.
- Phillips, W. M. 1967. Field bindweed and its control. Leaflet No. 496, USDA.
- Phillips, W. M. 1978. Field bindweed: the weed and the problem. Proc. North Central Weed Control Conference 33:140-141.
- Proctor, V. W. 1968. Long-distance dispersal of seeds by retention in digestive tract of birds. Science 160:321-322.
- Radford, A. E., H. E. Ahles, and C. R. Bell. 1968. Manual of the vascular flora of the Carolinas. Univ. N. Carolina Press.
- Rashed, M. H. and L. C. Haderlie. 1980. The relationship between anatomical and physiological aspects of field bindweed under water stress conditions. Proc. N. Central Weed Control Conference 35:26(abstr.).
- Reed, C. F. and R. Hughes. 1970. Selected weeds of the United States. USDA-ARS Agric. Handbook No. 366.
- Rickett, H. W. and F. A. Stafleu. 1960. Nomina generica conservanda et reficienda spermatophytorum IV. Taxon 9:67-86.
- Rolston, M. P. 1978. Water impermeable seed dormancy. Bot. Rev. 44:365-39
- Rosenthal, S. S. 1978. Host specificity of Tyta Luctuosa (Lep.:Noctuidae), an insect associated with Convolvulus arvensis (Convolvulaceae). Entomophaga 23:367-370.
- Rosenthal, S. S. 1983a. Field bindweed in California D Extent and cost of infestation. Calif. Agri. 37:16-17.

- Rosenthal, S. S. 1983b. Current status and potential for biological control of field bindweed, Convolvulus arvensis, with Aceria convolvuli. pp 57-60 In Biological control of pests by mites. M. A. Hoy, G. L. Cunningham and L. Knutson (ed.) Proc. Conference April 5-7, 1982, Univ. Calif. Berkeley. Special Publ. 3304. Agric. Exp. Stn. Div. Agric. Natural Resources, Univ. Calif.
- Rosenthal, S. S. and J. Carter. 1977. Host specificity and biology of Galeruca rufa, a potential biological control agent for field bindweed. Environ. Entomol. 6:155-158.
- Rosenthal, S. S. and H. Hostettler. 1980. Galeruca rufa (Col.:Chrysomelidae) seasonal life history and the effect of its defoliation on its host plant, Convolvulus arvensis (Convolvulaceae). Entomophaga 25:383-390.
- Rosenthal, S. S. and G. R. Buckingham. 1982. Natural enemies of Convolvulus arvensis in western Mediterranean Europe. Hilgardia 5(2):1-19.
- Rosenthal, S. S., L. A. Andres, C. B. Huffaker. 1983. Field bindweed in California D The outlook for biological control. Calif. Agri. 37(9):18 and 22.
- Schlising, R. A. 1980. Seed destruction of California morning glories(Convolvulaceae:Calystegia) by bruchid beetles. Madrono 27:1-16.
- Selleck, G. W. 1978. Biological control of perennial bindweeds with argus tortoise beetle. Proc. 1978 British Crop Protection Conference -Weeds. pp. 499-502.
- Selleck, G. W. 1979. Biological control of hedge bindweed on long Island. Proc. Northeastern Weed Sci. Soc. 33:114-118.
- Smith, R. C. 1938. A preliminary report on the insects attacking bindweed with special reference to Kansas. Trans. Kansas Acad. Sci. 41:183-191.
- Southgate, B. J. 1979. Biology of the Bruchidae. Ann. Rev. Entomol. 24: 449-473.
- Southgate, B. J. 1981. Univoltine and multivoltine cycles -their significance. Series Entomol. 19:17-22.
- Stahler, L. M. 1948. Shade and moisture factors in competition between selected crops and field bindweed, Convolvulus arvensis. J. Am. Soc. Agron. 49:490-502.

- Strausbaugh, P. D. and E. L. Core. 1978. Flora of West Virginia. Seneca Book, Inc., Grantsville, West Virginia.
- Swan, D. G. 1980. Field bindweed, Convolvulus arvensis L. College of Agric. Res. Cent. Bull. 0888, Washington State Univ. 8 pp.
- Swan, D. G. 1982. Long-term field bindweed (Convolvulus arvensis) control in two cropping systems. Weed Sci. 30:476-480.
- Swan, D. G. and R. J. Chancellor. 1976. Regenerative capacity of field bindweed roots. Weed Sci. 24:306-308.
- Tamaki, G., H. R. Moffitt, and J. E. Turner. 1975. The influence of perennial weeds on the abundance of the Redbacked Cutworm on asparagus. Environ. Entomol. 4:274-276.
- Tauber, M. J. and C. A. Tauber. 1976. Insect seasonality: diapause maintenance, termination, and postdiapause development. Ann. Rev. Entomol. 21:81-107.
- Tauber, M. J. and C. A. Tauber. 1979. Inheritance of photoperiodic responses controlling diapause. Bull. Entomol. Soc. Am. 25:125-128.
- Teran, A. L. and J. M. Kingsolver. 1977. Revision del genero Megacerus (Coleoptera: Bruchidae). Opera Lilloana 25, Tucuman, Argentina, 287 pp.
- Timmons, F. L. 1949. Duration of viability of bindweed seed under field conditions and experimental results in the control of bindweed seedlings. Agron. J. 41:130-133.
- Torrey, J. G. 1958. Endogenous bud and root formation by isolated roots of Convolvulus grown in vitro. Plant Physiol. 33:258-263.
- Waddington, k. D. 1976. Foraging patterns of Halicid-bees at flowers of Convolvulus arvensis. Psyche 83:112-119.
- Wang, R. and L. T. Kok. 1983. Synchronization of Megacerus discoideus with the hedge bindweed, Calystegia sepium in southwestern Virginia. Va. J. Sci. 34:109 (abstr.).
- Wapshere, A. J. 1980. Recent thoughts on exploration and discovery for biological control of weeds. Proc. 5th Int. Symp. Biol. control Weeds. Brisbane, Australia. pp. 75-79.

- Weaver, S. E. and W. R. Riley. 1982. The biology of Canadian weeds. 53. Convolvulus arvensis L.. Can. J. Plant Sci. 62:461-472.
- Whitesides, R. E. 1979. Field bindweed: A growth stage indexing system and its relation to control with glyphosate. Ph.D. dissertation, Oregon State Univ. Corvallis.
- Wiese, A. F. and W. M. Phillips. 1976. field bindweed. Weeds Today. 7(1): 22-23.
- Wiese, A. F. and H. E. Rea. 1959. Bindweed (Convolvulus arvensis L.) control and seedling emergence as affected by tillage, 2,4-D, and competitive crops. Agron. J. 51:672-675.
- Wilson, R. G. 1978. Field bindweed control in western Nebraska. Proc. North Central Weed Control Conference. 33:142-144.
- Zerbe, G. O. 1979. Randomization analysis of the completely randomized design extended to growth and response curve. J. Am. Stat. Assoc. 74:215-221.

**The two page vita has been
removed from the scanned
document. Page 1 of 2**

**The two page vita has been
removed from the scanned
document. Page 2 of 2**