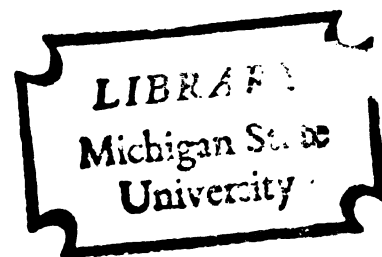


A LIFE HISTORY STUDY OF WHITE COCKLE
(*Lychnis alba* Mill.)
AND SOME COMPETITIVE EFFECTS IN
ALFALFA (*Medicago Sativa* L.)

Thesis for the Degree of Ph. D.
MICHIGAN STATE UNIVERSITY
JOHN O. PEARSON
1969



This is to certify that the

thesis entitled

A Life History Study of White Cockle (Lychnis alba Mill.)
and Some Competitive Effects in Alfalfa (Medicago sativa L.)

presented by

John O. Pearson

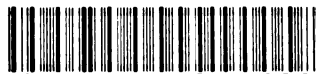
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ABSTRACT

A LIFE HISTORY STUDY OF WHITE COCKLE (Lychnis alba Mill.)
AND SOME COMPETITIVE EFFECTS IN ALFALFA (Medicago sativa L.)

By

John O. Pearson

White cockle has been a troublesome weed for many years in new seedings and established stands of alfalfa. In six Northeastern and North Central states, white cockle is one of the worst weeds in pastures and hay crops and infestations are still increasing. Studies concerning the life history of white cockle were carried out to provide information for weed control practices and experimentation involving the plant. Growth and development under various photoperiods and temperatures, male and female plant comparisons, the reproductive potential by asexual and sexual means and requirements for seed germination were the life history aspects of the study. Associated growth of white cockle and 'vernal' alfalfa was investigated to gain an understanding of some aspects of the nature of competition between the two species.

White cockle was found to be indeterminate in response to photoperiod. Plants grown under 8, 16, and 24 hours of light required an average of 70, 39, and 20 days

to flower, respectively. The growth of white cockle was observed under three temperatures, 12.8, 23.9, and 29.4 C, and it was found that 23.9 C was the most favorable.

In the field female plants were found to be slightly larger than male. However, in the greenhouse there was no size difference between the sexes of plants harvested at either the same physiological or chronological age.

White cockle had no stolons or rhizomes and vegetative reproduction is mainly by the growth of crown buds. Crown-root segments are susceptible to drying on the soil surface. New shoots are capable of emerging from segments buried as deep as 38 cm and from segments with only 1 cm of root remaining.

The spread of white cockle was observed to be mainly by seed. Ninety-seven per cent of white cockle plants in a new alfalfa seeding originated from seed. Very few additional seeds germinated after the initial flush of white cockle seedlings produced within two weeks.

White cockle plants sampled in mid-July had a seed production potential of about 24,200. Capsules were found to mature and open in about five weeks after pollination; however, seeds were viable two to three weeks after pollination. Mature seeds germinated immediately after harvest. Light facilitated the germination of white cockle seed. Photoperiod and light intensity had no effect on germination. Germination responses to 12.8, 18.3, 23.9, 29.4, and 35.0 C showed 23.9 and 29.4 C to be the most conducive.

White cockle seedlings were capable of emerging from a depth of 5 cm in a sandy clay loam and sandy loam but not in a clay loam or silt loam. Alfalfa emerged before white cockle at all temperatures so it does not owe its competitive position relative to alfalfa to an earlier emergence.

Greenhouse studies showed that the yield at the first cutting of alfalfa was considerably reduced by competition from white cockle and that the reduction in yield decreased in subsequent cuttings. Competition between roots or tops alone reduced alfalfa growth as much as when both roots and tops were in contact.

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INTRODUCTION

For many years floras, manuals, and weed studies have stated the presence of white cockle as a weed in new seedings and established stands of grasses and legumes. In 1909 Clark and Fletcher (16) described white cockle as a problem in grain crops and meadows. Remedies at that time for suppressing the weed were described as summer fallow, rotations including cultivated crops and mowing to prevent seed production. In the main, recommendations for controlling white cockle have not changed since then. In 1953 Buchholtz and Briggs (13) listed white cockle as one of the twenty-four worst weeds in Wisconsin and commented that there was no satisfactory means of control in pastures. Recently the United States Department of Agriculture (75) reported that in Connecticut, Massachusetts, Michigan, Minnesota, New Hampshire and Wisconsin, white cockle is one of the five worst weeds in pastures and hay crops and infestations are still increasing.

The purpose of this study was to further the understanding of the biology and ecology of white cockle to permit a more intelligent approach to its control. Literature concerning life history aspects of white cockle is fragmentary and limited, particularly in relation to weed control,

and more information is needed. Growth and development studies under various photoperiods and temperature regimes, male and female plant comparisons, the reproductive potential by asexual means and requirements for seed germination were the general areas investigated in regard to the life history. Some aspects of the nature of white cockle growth and competition with alfalfa were also studied.

LITERATURE REVIEW

Life History of White Cockle

Nomenclature

The scientific name of white cockle which is used most extensively is Lychnis alba Mill. Synonyms of L. alba, which occur mostly in European literature, are L. vespertina Sibth. (11), Melandrium album Gark (38), and M. pratense Roehl (47). White cockle is the common name of the species accepted by the Weed Science Society of America (73). There are also numerous other common names that have been assigned to this weed, among them, white campion, white robin, bachelor's buttons, and evening lychnis.

Descriptions

The morphological description of white cockle is in general agreement by most botanists (2), (11), (22), (34), (38), (48), (71). Generally authors agree that the species is dioecious; however, Britton and Brown (11) state that white cockle is often dioecious implying that it is not always so. Discrepancies in description of white cockle concerning the life cycle of the plant do exist. The life cycle is usually classified as either biennial, short-lived perennial, perennial or, rarely as annual. Only Baker (2)

and Gleason and Conquist (38) have referred to white cockle as an annual. Baker states that it can behave as a summer annual if germination is in spring or early summer, but if it is later in the season, the plant may behave as a biennial. He also reports it will bloom for more than one season and in cultivation it lives for at least three years.

Another difference is that many manuals do not state the presence of any modified stems; however, some report that the species possesses rootstocks (61), (79), or stolons (2). Reproduction is said to be largely by seed (79).

Origin and distribution

White cockle originated in the Mediterranean Region (3) and was introduced to North America from Europe by means of impure clover seed and rubbish from grain-ships added to the ballast heaps in Philadelphia (50). The rapid spread of the species through the sowing of impure clover and alfalfa seed is documented in most floras. In 1911 Beal (4) reported that white cockle was becoming common in the lower peninsula of Michigan. According to the literature (11), (38), (61), white cockle now occupies much of Northern United States and southern Canada. The distribution of the weed in the western hemisphere is strongly correlated with the spread of agriculture and other human operations, never being found far away from scenes of human activity.

White cockle is found in many field crops especially in new legume seedings, in lawns, fallow fields before woody

plant dominance, along roadsides, and around buildings. Baker (2) says that the plant often occupies large areas but never forms a continuous cover. Most authors state that white cockle is a weed in arable fields especially in cereals, forage grasses and legumes. Brenchly (9) states that white cockle is particularly adapted to grow among smother crops and is generally found in clover. Baker, however, says that the species is a "sun-lover" and considerable light intensity is necessary during all seasons. In regard to the soil habitats, white cockle seems to prefer chalky or calcareous soils (2), (60), but this relationship is probably due to soil preference of crops with which white cockle is associated. In Michigan it can be found on most arable soils.

Growth characteristics

Literature concerning the growth and development of white cockle is fragmentary and limited, the works of Baker (2) and Anderson (1) being the most detailed. Baker records that the rosette of leaves formed at the end of the plant's first season contains more leaves if flowering has not already taken place. In such cases the rosette is formed partly from the outer leaves of the stolons which are formed in the axils. The stolons referred to by Baker may be prostrate lateral stems developing from basal buds. If flowering has taken place, the lowest leaves die away and the rosette consists only of the outer leaves of the stolons

developed at the bases of the flowering shoots. According to Baker there appears to be a considerable storage of sugars in the large roots of M. album which tends to offset the disadvantage of the small rosette. The actual amount of sugar was not stated.

In the British Isles (2) new leafy shoots usually appear in March when the leafy stolons begin to expand. A very few of the leaves at the lowest nodes form a sparse rosette while the over-wintering ground leaves shrivel. Generally, flowering occurred from May to October but it could begin earlier in the spring or persist longer in the fall depending on the local climate. White cockle was said to be a long day plant. Ripening and opening of the capsules occurred four to five weeks after flowering. The seeds appeared to be fully developed and dry about two days before dehiscence of the capsule.

Preliminary to herbicide trials, Anderson (1) made observations of the growth of white cockle in a one and a two year old field of alfalfa in Minnesota. It was found in both locations that lush spring growth of semi-erect rosette leaves was typical. Erect stems emerged from the rosette and by early summer, basal leaves which had formed the rosette had disappeared. Mature seed was produced in the third week of July. Regrowth of white cockle was from crown buds which gave rise to new growth in the fall. The stages of growth, recovery from cutting, and dormancy patterns of alfalfa and white cockle were found to be similar.

In Connecticut (78) it was found that established white cockle plants bloomed from June to November and that photoperiod had no effect on flowering. In Vermont (78) the growth of branch stems was initiated about May 1. Flowering began about June 1 and continued until late summer, with some occurring until frost. No rooting of branches was observed.

Estimates of the seed production by white cockle varies among different workers. Baker (2) found that the number of seeds per capsule varied from 48 to 359 and that 40 capsules may ripen on each plant but usually the number is about 20. Davis (24) recorded white cockle in a fallow corn field in southern lower Michigan averaged 157 capsules per plant and 355.3 seeds per capsule; thus yielding an average seed output of 55,782 seeds per plant. Workers in Vermont (78) noted that plants had an average of 140 flowers and 98 seeds per capsule which resulted in over 13,000 seeds per plant. Stevens (72) in North Dakota sampled average size white cockle plants with little competition and recorded only 8,440 seeds per plant.

The only studies of white cockle under controlled environmental conditions (5) found that seedling emergence was delayed only one day by reducing the temperature from 32.2 C to 12.8-15.8 C. However, the total seedling emergence of L. alba was highest at 15.6 and lowest when exposed to the 32.2 temperature. No information of the species' reaction to various photoperiods was given.

Seed investigations

In England Baker (2) germinated white cockle on moist filter paper and found germination to be only 10.7% after one month. He said that after shedding there is an initial period of dormancy which is less than one year. Germination was quicker with alternating temperatures (25 C and room temperature for 24 hours each) than at a constant 25 C or room temperature. He did not say how much germination increased after dormancy or with alternating temperatures. It was suspected that germination was assisted by light. Baker also reported that germination may take place at depths of at least 4 cm below soil-level, but a marked reduction in number of seedlings emerging occurs when seed is buried more than 1.0-1.5 cm.

Connecticut investigators (78) reported that seed germinated on moist filter paper immediately after collection showing no signs of dormancy. Davis (24) found that germination at 4, 10, and 20 C was 0, 13.3, and 60.0%, respectively, and was complete after two weeks. It is not known how soon after seed harvest the germination test was conducted.

Competition

One of the first recorded definitions of plant competition, according to Clements et al. (19), was made in 1920 when De Candolle stated that all the species of a given region or all the plants of a given place are in a state of

war with respect to each other. The effects of competition, however, have been known since man first began to cultivate crops and have challenged his ingenuity ever since.

In recent years the term "competition" has become a subject for discussion because of different preconceived notions of the subject (43). According to some workers (6) (43), competition, in its strict sense, occurs when plants of the same or different species utilize common resources which are limiting. If this definition is to be used, increasing recognition that interspecific interference among plants can also occur by the production of inhibitory or toxic compounds (called alleopathy) makes it necessary to separate interspecific interference into two components: competition and alleopathy. Early literature and much current literature do not make this distinction since the definitions which have been widely used, i.e., De Candolle's, describe competition as any hardship suffered by neighboring plants. Thus, the term competition can be used in a broad sense to mean the struggle for nutrients by plants and/or the production of interspecific inhibitors. It is in this way that competition is used in this thesis.

Extensive experimentation concerning interspecific competition was conducted in the early 1900's by Clements, Weaver, and Hanson (17) (18) (19) (20) and resulted in many concepts of competition which are still generally accepted. Actual competition was described as beginning only when one plant encroaches upon the space occupied by another and

occurs only when the plants that meet each other are on more or less "equal terms." This prompted Clements' primary law of competition which states that "competition is closest when individuals are most similar." Interference among the individuals studied resulted in a change in size, form, and arrangement and indicated that competition was a physical process which included such factors as water, humidity, light, and temperature.

Pavlychenko and Harrington in 1934 (65) showed that success in competition depends on readiness and uniformity of germination under adverse moisture conditions, the ability to develop a large assimilation surface in the early seedling stage, the possession of a large number of stomata and a root system with a large mass of fibrous roots close to the surface and main roots penetrating deeply. Cow cockle (Saponaris vaccaria L.), similar to and in the same family as white cockle, was found to be a serious competitor in flax; however, it was the least competitive of thirteen weeds studied in association with various crop species.

Donald (27) (28) (30) has made comprehensive studies concerning the nature of competition among crops and pasture plants which can be related to crop-weed interactions. He emphasized that if all competing crop plants are of similar stature, habit, vigor, and nutritional requirements, then each plant has comparable competitive ability and the outcome tends to produce a community of plants of nearly equal ecological and yield status. On the other hand, with an

association of two or more dissimilar species, one or more species will be partially or completely suppressed by the aggressor. Harper (43) stated, however, that suppression does not always take place since natural diversity exists everywhere.

Koyama and Kira (55) pointed out that even plants of the same species are not entirely equal in regard to morphology and vigor. They showed that populations of plants at low density showed normally distributed plant weight, and log normal distributions with the passage of time and with increases in density. Not only is there a forced sharing of limited resources with a compensating reduction in individual development, but a hierarchy develops among the individuals in the population. The hierarchy consists of a few large individuals and a high number of small individuals.

There are several reports in the literature of the effects of competition on the component parts of plants. Clements et al. (20) found that higher densities of sunflowers had less dry matter, smaller stems, fewer and smaller leaves, smaller flower heads, and fewer and smaller seeds. Harper and McNaughton (44) showed that plants of Papaver species reacted to density by a reduced chance of establishment and a plastic reduction of plant weight, capsule numbers, and seeds per capsule. Giant foxtail in corn (53) decreased the yields of grain, cobs, stalks, stalk diameter and ear weight of corn. In soybeans, weeds delayed crop maturity by one day, increased lodging and decreased height. Knake and

Slife (53) found a decrease in number of pods per plant and in straw weight of soybeans. Cruciferous weeds in competition with barley reduced the number of tillers, fertile shoots, and spike size (7).

Donald (30) studied the effects of varying density of Trifolium subterraneum L. and Lolium rigidum Gaud. on dry matter yields, flowering, and seed production. Seed production showed a peak at moderate densities and a progressive decline at higher densities. The greatest number of inflorescences was produced at densities exceeding those of maximum seed production. Although the most widely spaced plants had the greatest number of inflorescences and seeds per plant, they had smaller seeds and fewer seeds per inflorescence than did much denser swards. Dry matter reached a peak at moderate densities and leveled off at higher densities.

Factors involved in competition

Reduction in plant growth due to competition have been attributed to water, light, minerals, and carbon dioxide (17) (21) (54). Clements et al. (18) stated that the importance of each not only depends on the total amount available but also on the rate of demand and supply. The competition for these factors was described as a physical process and when the immediate supply of a single necessary factor falls below the combined demands of the plants, then competition begins.

Numerous articles and texts cite specific cases of the importance of single factors when they become limiting in competition. Fewer studies, however, have been made concerning the interaction of competition for light, water, and minerals by the use of specially designed greenhouse experiments which can partition the effects of each factor (29) (70). Donald (29) stated that limiting nutrients or water meant less leaf area and thus less interception of light, even though there was no competition for light. Similarly, the direct effect of competition for light was reduction of photosynthesis, while the indirect effect was an inefficiency to use a water or nutrient supply available without competition. Donald emphasized that when competition occurs, the overall effect is not a simple interaction between two or three factors but an interaction between two groups of factors which may lead to a marked "build-up" of effects.

Competition in alfalfa

According to Dunham (31), Fletchall in 1957 estimated that the annual losses from weeds in pastures in humid regions totaled about \$720 million. Klingman (51) stated that in general, for every pound of weeds grown in pastures, the production of more desirable forage plants is reduced by about an equal amount. This broad generalization varies with moisture content and the weed and pasture species involved. McCarty (58) reported that a June spraying of a

Nebraska pasture with 2, 4-dichlorophenoxyacetic acid (2,4-D) reduced broadleaved weeds by 1,535 pounds per acre and increased alfalfa yields by 1,260 lb/A. In an established field of alfalfa, (81) reducing the yield of downy brome grass (Bromus tectorum L.) by 1,223 lb/A increased alfalfa yields 1,459 lb/A. This was an increase of 119 pounds of alfalfa per 100 pounds reduction in downy brome grass.

Alfalfa germinates rapidly; however, in the seedling stage it grows slowly (59). When the water and nutrient supply is not a limiting factor, the dense canopy formed by fast-growing broadleaved weeds effectively excludes light and can cause poor establishment of alfalfa (8). Dry matter accumulation in alfalfa seedlings has been found to be essentially proportional to light intensity when grown under 750, 1500, and 3000 foot candles (14). Gist and Mott (37) showed that light and moisture are critical with alfalfa seedlings and that root growth may be affected more than top growth at low levels of light intensity and moisture.

Weed control has been a major problem in growing small seeded legumes such as alfalfa (8) (52). Alfalfa in the seedling stage is highly vulnerable to competition from annual species and considerable loss of high quality forage in new seedlings has resulted. Perennials may also interfere with establishment or may persist and increase later when the alfalfa becomes thinned. The problem is worsened in such perennial crops because of the limited opportunity

to control weeds by cultural means and the lack of effective postemergence herbicides.

Although alfalfa seedlings are vulnerable to weed competition, well-established alfalfa is known as a successful competitive or smother crop, capable of competing with weeds by excluding light or utilizing large quantities of water and mineral nutrients (21). Anderson, Hastings, and Kust (1) (45) have recently shown that reducing the density of white cockle with 2-chloro-4, 6-bisethylamino-1,3,5-triazine (simazine) did not increase alfalfa yields when compared to the check treatment. However, Buchholtz (12) reported that 1,2-dihydropyridazine-3, 6-dione (maleic hydrazide) increased alfalfa yields by 83 lb/A for every 100 pounds reduction of curled dock (Rumex crispus L.) and white cockle. It is not known what percentage of the weeds was white cockle. It appears that white cockle is not a very competitive plant in established stands of alfalfa; however, this may depend on weed and crop density. In a study of plant succession, Davis (25), correlating the percentage of plant cover with the size of an area open to colonization, also showed that after the initial flush of seedling growth, white cockle does not seem to be a very aggressive species.

Alleopathy

The literature pertaining to inhibitory or toxic excretions by higher plants has been surveyed by many workers (9) (41) (64). A number of cases have been reported of

effects of higher plants upon one another which can not be attributed to competition for water, light, and nutrients. According to Ohmen and Kommedahl (64), Molish first termed such interactions as alleopathy. Grummer (41) classified exudates formed by higher plants and toxic to other species as kolines.

The alleged inhibitions or stimulations of certain species on surrounding vegetation is questionable many times and difficult to attest; however, there is much evidence supporting the effects of alleopathy. The inhibitory effect of black walnut on neighboring plants is widely accepted (23). The absence of all or only some species around certain shrubs in California is another alleopathic phenomenon that is widely recognized (40) (62) (80). It has been known for many years that the yield of flax is greatly reduced when even a small percentage of flax-weed (Camelina alyssum Thell.) is growing among flax plants (42). Grummer and Beyer (42) using artificial rain showed the leaves of flax-weed to be the source of a potent plant inhibitor. The reductions in seed germination when seeds are sown in established sod suggest an interference interaction and in many cases (15) (68) (69) the evidence suggests the presence of alleopathic compounds that operate under field conditions. Quackgrass (Agropyron repens L.) residues in cultivated fields have been reported to contain compounds inhibitory to alfalfa and oats; however, Ohman and Kommedahl (64) linked

this effect to a high carbon/nitrogen ratio which resulted in a temporary deficiency of soil nitrogen.

METHODS AND MATERIALS

Growth and Development Studies

Photoperiod responses

The response of white cockle to photoperiod was investigated by placing eight 5-week old seedlings and six crown-root segments¹ in each of three controlled environment chambers. Photoperiods of 8-, 16-, and 24-hours were maintained in chambers under a constant temperature of 23.9 C. The seedlings were grown in 6-inch clay pots and the crown-root segments in flats containing a greenhouse soil mix consisting of two parts field soil, one part peat, and one part sand. All greenhouse soil mentioned hereafter was of the same mixture. The crown-root segments were dug from the field and trimmed leaving roots 15 cm long and stems 2 cm long. The plants remained in the chambers for 98 days. Flowering was designated as the time of appearance of the first flower. The height of plants at flowering was measured from the soil to the first flower.

¹The term crown-root segments is used throughout this thesis to denote crowns with roots which will produce new stems or shoots.

Temperature responses

Temperature effects on white cockle were studied by using controlled environment chambers at 12.8, 21.1, and 29.4 C with a day length of 14 hours. The selection of 29.4 C as the high temperature was based on earlier work by Behrens (5) who found that 32.2 C was detrimental to seedling emergence. Eight 10-day old plants in 6-inch clay pots containing potting soil were grown in each chamber for 52 days. The basal diameter and plant height were measured weekly. Plant height measurements were made when the stems of plants in the 21.1 C chamber began to elongate. The height of plants with elongated stems was measured by extending the elongated stems and the standing height of leaves was measured for plants still in the rosette form.

The influence of temperature of the time of sprout emergence from crown-root segments was determined in the same chambers. Six segments possessing roots about 2 cm in diameter immediately below the crown, roots 15 cm long, and stems 3 cm long were planted in flats and covered with approximately 2 to 3 cm of soil.

Male and female plant comparisons

Twenty-four 3-month old male and female plants, and 15 male and female plants at least 2 years old, were randomly selected from the field to study differences between male and female plants. Leaves and stems were separated, dried at 60 C and weighed.

White cockle was also grown in the greenhouse to observe the characteristics of male and female plants under more controlled conditions. Because of the differences in time of flowering among individual plants, observations were made at both the physiological and chronological age. Twenty-four plants were grown in clay pots and harvested at the same physiological age which was immediately after the first flower appeared. Leaf areas and dry weights of stems and leaves were determined for each sex. Leaf area was measured by tracing leaves under a sheet of acetate with a planimeter. Plant parts were dried at 85 C. Twelve female and eight male plants were used in the final comparison. In a second study 30 plants were harvested at the same chronological age (101 days). Leaves and stems of 10 male and nine female plants were separated, dried at 60 C, and weighed. The t-test for nonpaired observations was used for testing significance (56).

Sexual reproduction

The seed production potential of white cockle was determined by counting the number of seeds per capsule and the number of capsules and flowers per plant on 11-month old plants randomly selected in mid-July when the bulk of seed production occurs. Twenty-five capsules were used to determine the average number of seeds per capsule.

Vegetative reproduction

The possibility of white cockle spreading by rooting at the nodes of stems or stolons was investigated by layering the stems of potted plants in adjacent flats containing greenhouse soil. Three to four stems were placed in each flat and covered with a small amount of soil which was kept moist. In the field 150 established white cockle plants were observed for any such rooting from nodes under natural conditions and for the detection of rhizomes based on the presence of nodes and internodes.

Anatomical observations were also made to ascertain the presence or absence of rhizomes. Five plants selected with lateral roots arising very close to the crown on the main tap root were taken from the field. The classification of these structures as either roots or stems was made by examining the external morphology and the internal anatomy. Temporary mounts (39) of free hand sections were stained with a safranin stain and examined under a light microscope.

The vegetative reproductive potential of white cockle was observed by studying the effects of drying, size and depth of planting on the viability of crown-root segments. The effects of drying were observed by placing crown-root segments with roots about 2 cm in diameter and 15 cm long on dry barren soil in the field. Each day for 2 weeks, five segments were removed to the greenhouse where they were transplanted in flats of soil. The viability of the segments was determined by the presence of new shoots at the end of 2 months.

The reproductive potential of small crown-root segments was investigated by collecting segments with roots about 1 cm in diameter below the crown and trimming the roots to varying lengths of 1, 2, 4, and 6 cm. Eight segments were cut to the desired root length, randomized and planted in four flats filled with potting soil. The segments remained in the soil for 7 weeks and were observed for the production of new stems.

The effect of planting depth on reproduction by crown-root segments was studied by planting segments 15 cm long and 2 to 2.5 cm in diameter at depths of 13, 25, and 38 cm in soil in four large (43 cm diameter x 61 cm length) clay tiles. To provide adequate drainage, each tile was placed on two cement slabs and filled with 5 cm of sand. Emergence of new shoots was observed for 15 weeks. In the field, the depth of sprouting crown-root segments was

observed by carefully digging soil away from the emerging sprouts.

Seed Studies

Effects of temperature on germination

The effect of five temperatures on the germination of white cockle was studied in controlled environment chambers at 12.8, 18.3, 23.9, 29.4, and 35.0 C with a 14-hour photoperiod. Four Petri dishes with moist filter paper and containing 50 seeds each, were placed in each chamber. Germination was counted every 3 days for 3 weeks.

Effect of seed maturity on viability

Capsules in 12 different stages of maturity were collected in 1966 and 1967. The degree of maturity was indicated by the color of the capsule and the surrounding calyx. Four capsules representing each stage were sampled and 50 seeds from each were placed in Petri dishes containing moist No. 3 filter paper. The seeds were germinated at 30 C, with 12 hours of light at 2,314 lux. Germination of both years' lots of seed was begun 1 week after harvesting the seed in July 1967. Unless otherwise noted, all germination trials were conducted with 50 seeds in glass Petri dishes containing moist No. 3 filter paper for a period of 2 weeks at which time germination was complete.

Effects of light on germination

The effects of light versus dark, photoperiod and light intensity were investigated using four replications with 50 seeds in each. The light versus dark study was conducted in a chamber with a 12-hour photoperiod and a temperature of 30 C. Continuous dark conditions were achieved by individually wrapping half of the Petri dishes in black plastic while the remaining dishes were wrapped in clear plastic. The effects of photoperiodism on germination were studied in chambers at 23.9 C and 8, 16, or 24-hour day lengths. The germination period was 19 days.

The influence of light intensity was observed in a controlled environment chamber with a temperature of 30 C and a 16-hour photoperiod. Light intensities of 21,528, 10,764, 5,382, and 538 lux were maintained by placing the Petri dishes at various distances from the lights. The 538 lux treatment was achieved by placing several layers of cheesecloth over the Petri dishes. A second test concerning the interaction of light intensity and temperature was studied in a similar manner. Seeds at two light intensities, 16,146 and 1,615 lux, were subjected to 12.8, 23.9, and 35.0 C constant temperature environments. Each Petri dish was placed in a plastic bag to decrease the rate of water evaporation from the filter paper. The test was run for 3 weeks.

Emergence and seedling growth

The number of white cockle plants emerging from old plants or seed in a 1966 summer seeding of alfalfa was determined by counting seedlings and sprouts in four permanent .6 x .6 meter quadrats in 25 randomly located 15 x 25 cm quadrats. The exact history of the field was not known; however, the white cockle plants were at least 1 year old at the time of plowing. The exact density of white cockle prior to plowing was not determined but was estimated to have been about 10 or 15 plants per square meter. Counts were made 3 months after the August seeding of alfalfa and in the four permanent quadrats, counts were also made in the following spring. Five weeks after a May 1967 seeding of alfalfa the number of white cockle from seed and sprout origin were again measured using a 15 x 25 cm quadrat frame which was randomly tossed 25 times. In all studies concerning alfalfa the variety 'vernal' was used.

The time of white cockle emergence after planting was also measured over the entire growing season after a seeding of alfalfa. Twelve 10 x 30 cm quadrats were randomly placed in each of four replicated control plots which were part of a herbicide trial. The alfalfa was band seeded on May 13, 1968, and the quadrats were placed over the band. Counts of living white cockle plants were started on May 27 and repeated every 2 weeks until September 30. On July 31 the alfalfa was clipped and raked off. Since mortality was occurring as well as germination the counts yielded net change.

The relative time of emergence of white cockle and alfalfa was observed in the greenhouse, in controlled environment chambers, and in the field. In the field six 10 x 30 cm quadrats in addition to those mentioned above, were randomly placed in each of four replicated control plots which were part of a white cockle control study. The number of alfalfa and white cockle plants were counted every week for 8 weeks until the first frost. Weather data for the 1968 growing season are found in Table II of the Appendix. In the greenhouse and controlled environment chambers, 40 alfalfa and 40 white cockle seeds were planted in separate halves of one-pint plastic cups. The seeds were planted in a sandy loam soil and covered with 1 cm of soil. The soil surface was kept moist to prevent crusting. Four cups were placed in each of five different temperature regimes. Three constant temperatures were 13, 20, and 30 C. Alternating temperatures were maintained in a controlled environment chamber with 14 hours at 26 C and 10 hours at 15 C and in the greenhouse where the average maximum and minimum temperatures were 34.0 and 20.6 C, respectively. Emerging seedlings were counted and removed every 2 days for 2 weeks.

The emergence of white cockle from various soil depths was studied in the greenhouse using 25 seeds in 16-ounce cups. A preliminary study using a greenhouse soil mix showed emergence was possible from a depth of 2 inches, the highest percentage of germination being with seeds placed on the soil surface. Another study was conducted to

observe emergence capabilities of white cockle from four soil depths in four soil textures: clay loam, silt loam, sandy clay loam, and sandy loam. The mechanical analyses for these soils is in Table III of the Appendix. The seeds were planted at .6-, 1.3-, 2.5-, and 5.0-cm soil depths, always with 5 cm of soil below the seed. The cups were arranged in a completely randomized block design with four replications and were watered periodically to prevent crusting. The seedlings were counted and removed every 2 days for a duration of 26 days.

Competition Studies

Field experiments

To verify that white cockle competes with alfalfa in the first cutting growth, alfalfa planted on August 12, 1968, was harvested from plots with and without white cockle. White cockle was controlled with 3.4 kg/ha of ethyl N, n-dipropylthiolcarbamate (EPTC) which was applied and incorporated into the soil immediately before planting on August 12. Other weeds in the plots were negligible. Because of winter injury and failures in establishing stands, the alfalfa available for sampling was only 2 months old. The distribution of white cockle was not uniform and as a result, relatively small sample areas (1.1 square meters) were randomly selected within infested portions of the plots so that weed-free areas would not repress the effects of competition in other areas. The alfalfa and white cockle were

hand-separated and weighed. The plots were arranged in a completely randomized block design with four replications.

Competition between alfalfa and white cockle in the second crop growth was evaluated in a 1-year old stand of alfalfa. After one cutting of alfalfa was made the first year to remove annual weeds, ten 1.2x 3.6 meter plots were staked and half of the plots were hand-weeded to remove the white cockle. The plot layout was a completely randomized design. On June 14, 1968, of the second year the white cockle was harvested by hand and .9x 3.6 meter sample areas of alfalfa were harvested by machine and weighed. Sub-samples of the alfalfa were taken to determine the percentage of moisture. The average density of the white cockle in the infested plots was 8.6 plants per square meter.

Greenhouse experiments

1. Effects of white cockle density:

A competition study involving alfalfa and four densities of white cockle was initiated to observe the effects of density and to observe the pattern of competition in the second and third growth of the alfalfa. Alfalfa was seeded at a rate equal to 11.2 Kg/ha in 1-bushel metal baskets. The soil was a greenhouse mix with a pH 6.7 and had a nutrient status of 230 Kg/ha of phosphorus and 115 Kg/ha of potassium. In order to provide uniform plants, white cockle with one pair of true leaves about 1 cm long was transplanted into the baskets at the time the alfalfa

was seeded. The four densities were obtained by planting either zero, one, two, or four white cockle plants per basket which was equivalent to 0, 6.5, 13.0, and 27.0 plants per square meter. The soil was watered to field capacity at the first signs of wilting by the white cockle. A plastic shading material with 6% light transmission surrounding the baskets was used to contain the alfalfa within the bounds of the baskets. The shading was continually moved upwards so that it was always as high as the alfalfa. This kept the white cockle and alfalfa in contact and prevented lateral light from lessening the effects of competition. All three cuttings of alfalfa were made when the alfalfa was in the early bloom stage. The baskets were arranged in a randomized block design with five replications. Fluorescent lights were used for supplemental lighting in all competition experiments in the greenhouse. The day length was maintained at 15 hours when natural day length was shorter than 15 hours.

2. Modes of competition

The factors involved in competition such as light and nutrients were investigated by using a technique which was a modification of that used by Donald (29) and Schreiber (70). White cockle and alfalfa were grown in bushel baskets as previously described. By partitioning the above and below-ground portions of the baskets as shown in Figure 2, four types of competition were achieved: no competition, full competition, above-ground competition, and below-ground

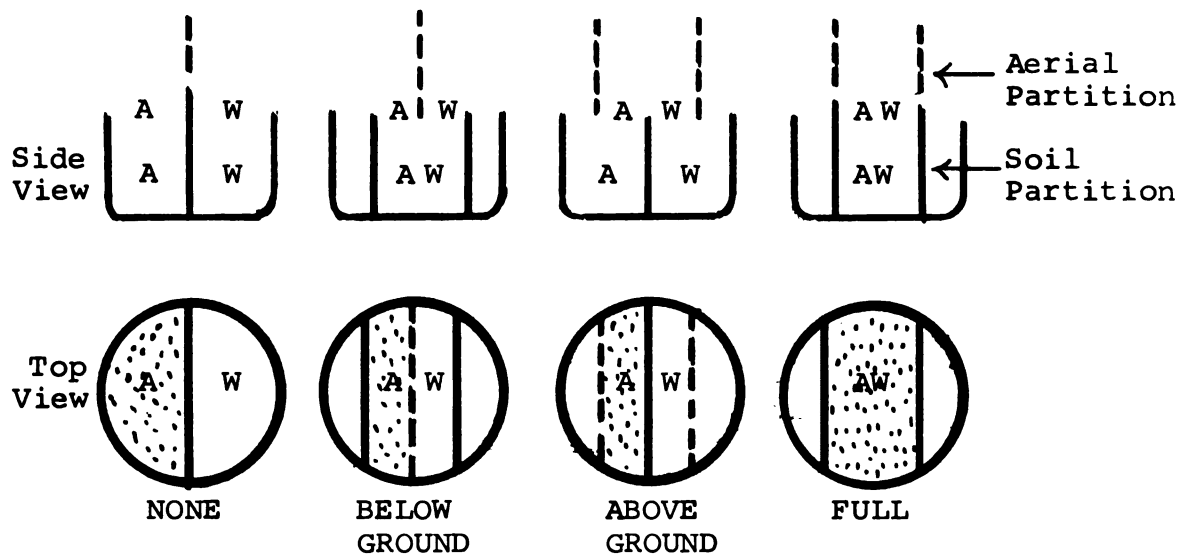


Figure 1. Diagrammatic view showing arrangements of partitions for studying various modes of competition. (A = alfalfa, W = white cockle.)

competition. The above-ground partitions were made by suspending plastic shading and the below-ground partitions were made by sealing plastic 1 mm thick to the metal baskets with caulking compound. No competition was maintained by growing white cockle and alfalfa in separate halves of the baskets so that there was no contact between the two species. Full competition involved both species growing together in the same compartment which was also equal to half the volume of the containers. Above-ground competition was achieved by growing the tops of the alfalfa and white cockle together and by separating the roots. Below-ground competition was just the opposite to above-ground competition in that the roots were allowed to grow together but tops were kept separate. In all cases, the area of the compartments where the plants were growing alone or together was equal to one-half of the total volume of the containers. Soil was carefully poured so that compartments of the same size would have equal amounts of soil. The soil had a pH of 7.0 and contained 50 Kg of phosphorus and 130 Kg of potassium per hectare. Three white cockle plants (equivalent to a density of 41 plants per square meter) were planted in each appropriate compartment. The height of alfalfa and white cockle was measured once a week between the first and second cuttings. The bushel baskets were arranged in a randomized block with four replications.

A second study concerning the factors in competition was conducted to more clearly define the comparative effects

of light, water, and mineral nutrient competition. This study was conducted in the same manner as the previous one except the below-ground competition treatments included two fertility and two moisture levels. The treatments were as follows:

<u>Mode of Competition</u>	<u>Fertility Level</u>	<u>Moisture Level</u>
None	Low	Low
Full	Low	Low
Above-ground	Low	Low
Below-ground	Low	Low
Below-ground	Low	High
Below-ground	High	Low
Below-ground	High	High

High fertility levels were obtained by inoculating the seed and adding phosphorus and potassium at the rate of 400 and 1344 Kg/ha. No additional nutrients or inoculant were added for the low fertility level. The soil was a greenhouse mix with a pH of 7.2 and contained 86 and 137 Kg/ha of phosphorus and potassium, respectively. High moisture levels were maintained by watering to field capacity twice weekly and low moisture levels were maintained by watering at the first signs of wilting by the white cockle which was 10 to 14 days. At the early bud stage of alfalfa, the tops and roots were harvested and dried at 105 C.

RESULTS AND DISCUSSION

Growth and Development Studies

Photoperiod responses

White cockle was found to have an indeterminate photoperiodic response. Results are shown in Table 1. At the end of 98 days all plants grown from seed at 16- and 24-hour day lengths had flowered; whereas, at the 8-hour day length only four of the eight plants had flowered. Sprouts from crown-root segments showed a similar response in that all flowered at the 16- and 24-hour day lengths but only two of the six flowered at the 8-hour photoperiod. Thus, plants grown from both sources have the same type of response to short and long day photoperiods.

The number of days required for flowering was significantly less for plants from both sources at the 24-hour day length. The time required for flowering for plants grown from seed decreased significantly as day length increased. There was more variation among the sprouts grown from crown-root segments within the same day lengths and statistically there was no difference in time needed for flowering between the 8- and 16-hour day lengths. However, the time required for sprouts to flower at the 24-hour day

Table 1. Response of white cockle from seed and crown-root segments to three photoperiods

Day Length (hrs.)	Percentage of Flowering Plants		Number of Days to Flowering		Height at Flowering (cm)	
	Seed	Crown-root	Seed	Crown-root	Seed	Crown-root
8	50.0	33.3	69.5a*	46.0a	52.5ab	28.0a
16	100.0	100.0	38.8b	34.3a	42.3b	45.7a
24	100.0	100.0	20.3c	18.7b	60.3a	50.0a

*Means in the same column followed by different letters are significantly different at the 5% level.

was significantly shorter. In all cases plant height at flowering was the same, except for plants grown from seed at the 16-hour day length which were significantly shorter than those at the 24-hour day length. The reason for this low value can not be correlated with day length. The indeterminate response of white cockle to photoperiods under controlled day lengths corresponds to its flowering habits in the field in that white cockle can be seen in flower from June until late fall when freezing weather prevails.

Temperature responses

A general response of white cockle to temperature was observed at 13, 21, and 29 C for 62 days. Data showing dry weight of tops, flowering behavior, and the time required for sprouts to emerge are shown in Table 2. Weekly averages and tests of significance for basal diameter and

Table 2. Response of white cockle to three temperatures

Temp. (C)	Dry Wt. of Tops (g)	No. of Days to Flowering	Ht. of Flowering (cm)	% Flowering Plants	Days Req. for Sprout Emergence
13	2.6 b*	---	---	0.0	29
21	7.1 a	46.8 a	55.8 a	75.0	14
29	5.2 ab	43.0 a	49.6 a	87.5	14

*Means in the same column followed by different letters are significantly different at the 5% level.

plant height are in Table I of the Appendix and are graphed in Figure 2.

Significant differences among the three temperatures did not appear until after 5 weeks. However, the height of white cockle increased most rapidly for the first 6 weeks at the 29 C temperature. At the end of 8 weeks fewer plants had flowered at the 21 C temperature and, as a result, stems were still elongating and the curve continued to show an increasing trend. After 8 weeks the average height of the plants at 13 C was only 10.1 cm which was significantly smaller than plants growing at 21 and 29 C.

The differences in basal diameter were not great and the only significant differences occurred between the third and fifth weeks of growth. At 3 weeks the basal diameter was greatest at 29 C but at 5 weeks the diameter was greatest at 21 C and continued so for the duration of the study. At the end of 8 weeks there were no significant differences

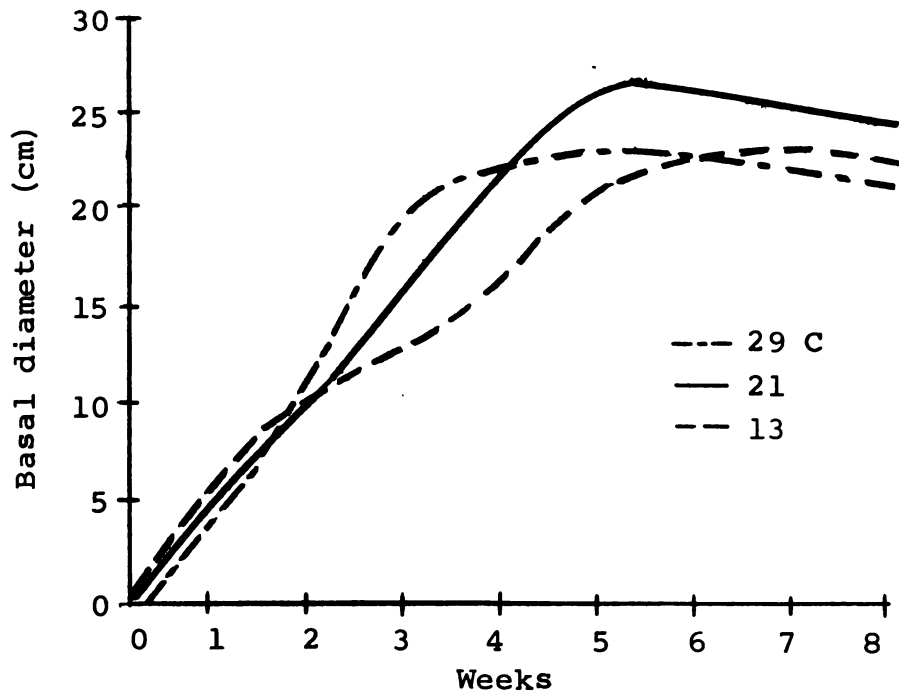
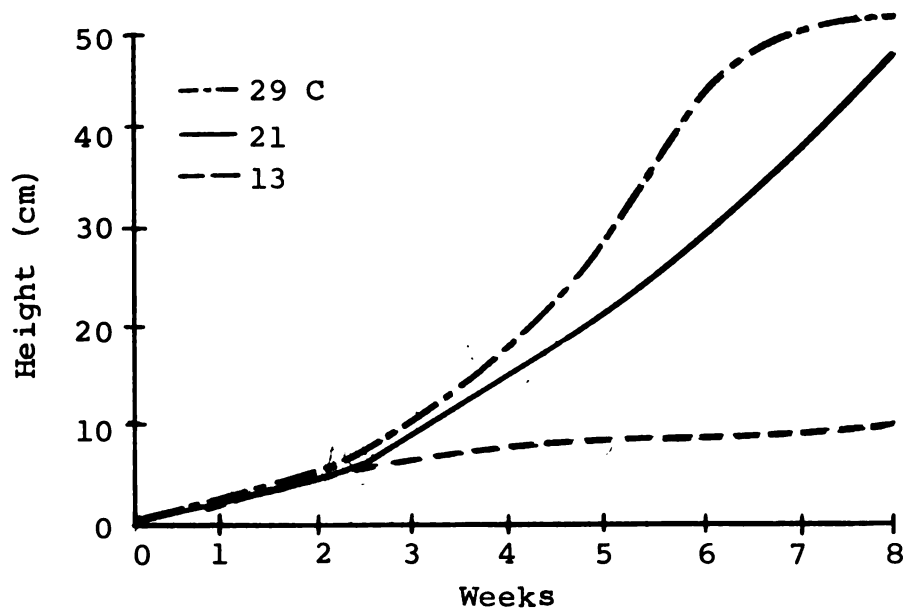


Figure 2. Effects of three temperatures on height and basal diameter of white cockle.

in basal diameter among the three temperatures. Once the plants began elongating and flowering, there was little increase in basal diameter at the 21 and 29 C temperatures. However, at 13 C the plants had not begun to elongate and in time the diameter of the rosettes equalled that at the other temperatures.

The growth of white cockle in terms of dry weight is shown in Table 2. Root weights were also measured but there were no significant differences due to temperature. Dry weight of top growth was greatest at 21 C but only significantly greater than the plants at 13 C. White cockle plants growing at 13 C did not flower and plants growing at 21 and 29 C flowered in an average of 47 and 43 days, respectively. There was no difference in height of plants between the 21 and 29 C temperatures at the time of flowering. Although differences in growth and development are slight between the 21 and 29 C temperatures, white cockle at 21 C was greener and less spindly than at 29 C, particularly in the last 2 to 3 weeks of the study. Plants growing at 29 C also had more of a purplish hue.

Male and female plant comparisons

The objective of comparing male and female plants was to determine if one sex might affect experimental results more than the other. There were no significant differences between male and female white cockle plants grown in the greenhouse in respect to dry weight, leaf area, and

the number of days required for flowering (Table 3). The leaf weights in Tables 3 and 4 also include flower structures. This is contrary to the findings of van Nigtevecht (63) who stated that female plants have, on the whole, larger stems and leaves than male plants. However, he did not say how much larger the plants were or if total leaf area were greater for female plants. The fact that no differences exist between male and female plants grown in the greenhouse means that studies conducted with relatively few plants will not be biased significantly by the presence of male or female plants in unequal numbers.

Table 3. Comparisons of male and female plants at the same physiological or chronological age

Same Physiological Age						
	Dry Weight (g)			Leaf Area (cm ²)	Height (cm)	Days to Flower
	Stems	Leaves	Total			
Male	1.87	.66	2.53	562.1	70.0	69.3
Female	1.44	.72	2.17	436.8	67.4	68.0
Same Chronological Age						
	Total Dry Weight (g)			Height (cm)	Days to Flower	
Male	6.99			74.7	70.2	
Female	8.19			78.7	68.4	

The correlations between the leaf, stem, and total dry weights and leaf area of plants cut at the same physiological age were .915 and .911, respectively. In another group of plants grown in the greenhouse, the correlation between the leaf weight and leaf area was .980. Thus, when leaf area of white cockle plants is not measured directly, top growth weight will be indicative of the leaf area which may be important in competition studies. Leaf area measurements, alone, may not always be true indices of the leaf area effective in competition, since white cockle plants in the rosette form, for example, may not compete as much in an alfalfa stand as plants with elongated stems.

The comparisons of male and female plants growing in the field are shown in Table 4. The leaf, stem, and total dry weights of 4-month old plants were higher for female plants. The dry weights of stem and leaf components of 2-year old male and female plants were not significantly different at the 5% level; however, they were significant at the 10% level. Apparently greater variation in the individual size of the 2-year old plants measured, accounts for the less significant differences in stem and leaf weight between male and female plants. When the total weight is considered for the 2-year old plants, female plants are significantly heavier than male plants. The proportion of males and females in dioecious plants is approximately equal in nature (26) (76) and in most instances the problem of unequal

Table 4. Average dry weight in grams of male and female plants growing in the field

	Three-month Old Plants			Two-year Old Plants		
	Stems	Leaves	Total	Stems	Leaves	Total
Male	1.65 b*	.92 b	2.57 b	3.77 a	1.58 a	5.35 b
Female	2.93 a	1.20 a	4.13 a	7.79 a	2.85 a	10.63 a

*Means in the same column followed by different letters are significantly different at the 5% level.

numbers of male or female plants in the field giving erroneous results would not exist.

Sexual reproduction

Eleven-month old plants sampled in mid-July showed that white cockle has an average of 66 flowers and capsules per plant. The average number of seeds per capsule was 367. Assuming all female flowers produce seed, white cockle would have an average seed production potential of 24,222 seeds per plant. When the indeterminate photoperiodic response of white cockle is considered, flower formation from June until November would account for even a higher seed production per plant. The number of seeds produced by a white cockle plant will vary with the age of the plant and the amount of intra- and interspecies competition. Based on work by Donald (28) and Harper and McNaughton (44) and others, plants growing in populations of low density will have more capsules than plants in crowded populations.

Vegetative reproduction

The attempts to force rooting of nodes by layering of stems in greenhouse soil failed to produce any positive results. Also, of the 150 observations made of white cockle growing in the East Lansing area, no evidence was found to suggest that white cockle spreads by means of stolons as Baker (2) suggested. No rhizomes were found in this survey.

Anatomical observations of lateral roots closest to the crown, which could possibly indicate rhizomes by position only, showed typical characteristics of roots and not stems. Primary xylem was noted in the center of the sections and formed a solid cylinder in the usual star-shaped form found in roots (32). The absence of pith and collateral bundles of vascular tissue which are found in white cockle stems also points out that these lateral structures were of root tissue. Externally, no nodes and internodes could be recognized on the lateral roots (46).

Thus, based on observations at East Lansing, white cockle does not possess any modified stems such as rhizomes and stolons which could aid in the spread of this plant as a weed. It has been observed, however, that vegetative reproduction of white cockle can be accomplished by the growth of numerous buds on crown tissue and occasionally from adventitious buds on roots. The spread of white cockle by vegetative means, then, is limited to mechanical movement of roots and crown-root segments.

The crown-root segments of white cockle are not very resistant to air-drying. Segments of substantial size exposed to drying on the soil surface were not viable after more than 2 days' exposure (Table 5). No rainfall occurred in this period and the average maximum and minimum temperatures were 28.6 and 14.3 C, respectively.

Table 5. Effects of length of drying in the field on viability of crown-root segments

Days Exposed	% of Segments Showing Regrowth	Temperature (C)	
		Max.	Min.
1	80	28	10
2	20	28	15
3	0	29	15
4	0	29	17
5	0	30	16
6	0	31	15
7	0	30	15

*Five segments used for each duration of exposure.

Exposure for 1 day did not injure the segments since four of the segments produced new shoots and the fifth appeared to be viable after removing it from the soil at the end of the study. After 2 days of exposure only one segment was still viable. This is merely an indication of the resistance of large crown-root segments to drying. Under natural conditions the size of the segments, the amount of soil covering them, temperature and rainfall, all could either increase or

decrease the longevity of crown-root segments uprooted in tillage operations.

In order to observe the reproductive potential of segments that may be cut but survive tillage operations, relatively small crown-root segments with roots only 1 cm in diameter were trimmed leaving roots of varying lengths. As shown in Table 6, crown-root segments with roots only 1 cm long were capable of producing new shoots; however, after 7 weeks only one shoot developed to the flowering stage. The number of viable shoots did increase with increasing root lengths. These small crown-root pieces, probably much smaller than most which survive plowing and seedbed preparation, are able to produce new plants under favorable conditions.

Table 6. Effect of root length on viability of crown-root segments*

Root Length (cm)	% Viable Segments	Number of Flowering Shoots
1	5	1
1	6	4
4	8	6
6	8	6

*Eight segments for each length were planted.

Another indication of the reproductive potential of crown-root segments was determined in the greenhouse by burying segments at three soil depths. Table 7 shows that

Table 7. Influence of planting depth on vegetative reproduction of crown-root segments* in the greenhouse

Depth (cm)	% of Segments Showing Regrowth		
	1 Month	2 Months	3 Months
13	7	8	8
25	0	5	7
38	0	1	2

*Eight segments were planted at each depth.

even when buried to a depth of 38 cm new shoots can emerge. Two of the eight shoots emerged from the 38 cm level by the end of 3 months. All segments at the 13 cm depth produced shoots and emerged earlier than shoots from the 38 cm depth. In the field, observations made 9 months after an August planting of alfalfa showed shoots emerging from an average depth of 9.9 cm.

The reproductive potential of crown-root segments appears to be very great unless the segments are exposed to drying conditions. However, 97% of white cockle plants in a seeding of alfalfa originate from seed. Thus, mechanical injury together with deep burial or drying conditions occurring during the preparation of a smooth seedbed probably account for this low percentage of sprouts from old crown-root segments.

Seed Studies

Effect of temperature on germination

Table 8 shows the effects of temperature on white cockle seed germination at the end of 3 weeks. Germination was essentially complete at the end of 15 days. The highest percentage and fastest rate of germination was found at the 24 and 29 C temperatures. The 13 and 35 C temperatures were the least conducive to germination of white cockle seed. Whenever possible, subsequent germination tests were conducted at 30 C because of the high germination percentage and the availability of a germination chamber at this temperature.

Table 8. Effect of temperature on white cockle seed germination after three weeks

	Temperature (C)				
	13	18	24	29	35
% Germination	8 d*	75 b	92 a	88 a	30 c

*Means in the same row followed by different letters are significantly different at the 5% level.

Effect of seed maturity on viability

Seed harvested from capsules in different stages of maturity germinated in varying amounts and not always in proportion to the apparent maturity of the capsules. Of

the 12 maturity stages sampled in 1966 and 1967, five with corresponding color characteristics are listed in Table 9. White succulent seeds from green capsules with a green calyx are capable of germinating. The high percentage of germination of seed from the more mature capsules indicates very little, if any, seed dormancy. Other investigators (78) have also found this; however, Baker (2) stated there was an initial period of dormancy less than 1 year.

Table 9. Effect of flower maturity on germination of white cockle seed

Calyx Color	Capsule Color	Seed Color	% Germination	
			1966 Seed	1967 Seed
Green	Green	White	2.0	0.0
50% Brown	Green	Light Brown	11.0	37.6
90% Brown	10% Brown	Light Brown	59.6	79.6
100% Brown	50% Brown	Light Brown	88.0	90.0
100% Brown	100% Brown	Brown-Gray	95.4	69.0

Based on observations made in the greenhouse with white cockle flowers, it takes 2 to 3 weeks after pollination for the calyx and capsule to begin to turn brown and 5 weeks for the capsules to reach full maturity. The important agronomical point is that white cockle seed is viable before capsules dehisce and if clipping is to be used as a means of reducing seed production, it must be done soon after flowering. This has also been found to be true with other weeds such as sow thistle (Sonchus arvensis), Canada

thistle (Cirsium arvense), and curly dock (Rumex crispus) (36) (51).

Effects of light on germination

In an initial germination test in an unlighted germinator, only 1.2% germination of white cockle seed was observed. Later tests in a lighted germinator showed that a higher germination percentage was possible. Results from a test involving Petri dishes wrapped with clear or black plastic showed that the omission of light allowed for only 5.5% germination and the exposure to light enhanced germination to 79.5%.

Photoperiod was found to have no significant influence on germination. Seed exposed to an 8, 16, and 24-hour photoperiod had a germination percentage of 54.6, 44.0, and 43.0, respectively. Isikawa and Mayer (49) and Koller (54) also reported that photoperiodism has an effect on seed germination similar to that of the flowering response.

Different light intensities ranging from 21,528 to 538 lux was found to have no significant effect on germination. Intensities of 21,528, 10,764, 5,382 and 538 lux at 30 C resulted in germination percentages between 74.4 and 82.4% with no significant differences among them. The effect of 16,146 and 1,615 lux was also studied at 13, 24, and 35 to detect any interactions that might exist between temperature and light intensity. On the average, there was no difference in germination between the two light

intensities (Table 10). As would be expected from previous work, germination was best at 24 C (see Table 8). An interaction did exist at 35 C where germination was significantly higher at the 1,615 lux light intensity. It is felt that this effect was due to a higher temperature at the high light intensity treatment. Although the air temperature surrounding the Petri dishes at both intensities was the same, Petri dishes at the 16,146 light intensity were always warmer to the touch. Thus, the lower germination percentage was probably due to injurious high temperatures caused by the absorption of radiant energy by the Petri dishes rather than an effect of light intensity.

Table 10. Effect of light intensity and temperature on germination of white cockle seed

Temperature (C)	Light Intensity (lux)	% Germination
13	16,146	8.0 d*
	1,615	5.0 d
24	16,146	92.4 a
	1,615	85.6 a
35	16,146	29.6 c
	1,615	50.4 b
Average Effects:		
13 C	- 6.4%	16,146 lux - 43.4% a
24	- 89.0	1,615 47.0% a
35	- 40.0	

*Means in the same column followed by different letters are significantly different at the 5% level.

Emergence and seedling growth
of white cockle

Following an August 1966 and May 1967 seeding of alfalfa on land heavily infested with white cockle, the number of new white cockle plants per M^2 averaged between 120 and 180. In both seedings 97.8% of all white cockle originated from seed. Even though the reproductive potential of crown-root segments is high under favorable conditions in the greenhouse, very few plants in the field survive the effects of plowing and seedbed preparation. This is desirable in terms of weed control since it is generally much easier to control weed seedlings rather than weeds growing from rhizomes, stolons, or crown-root segments.

The initial flush of white cockle that emerges soon after planting alfalfa is probably the most troublesome. It can be seen in Figures 3 and 4d that the majority of white cockle has appeared by the end of 4 weeks and very few seedlings appear after this time. In the observations made for the full growing season (Figure 3), only 11 new white cockle seedlings appeared after June 6 at which time there was a total of 700 in all quadrats. On the average, however, the number of plants decreased after June 6. The dip in the curve after clipping all top growth resulted from the failure to recognize living plants that later produced new growth.

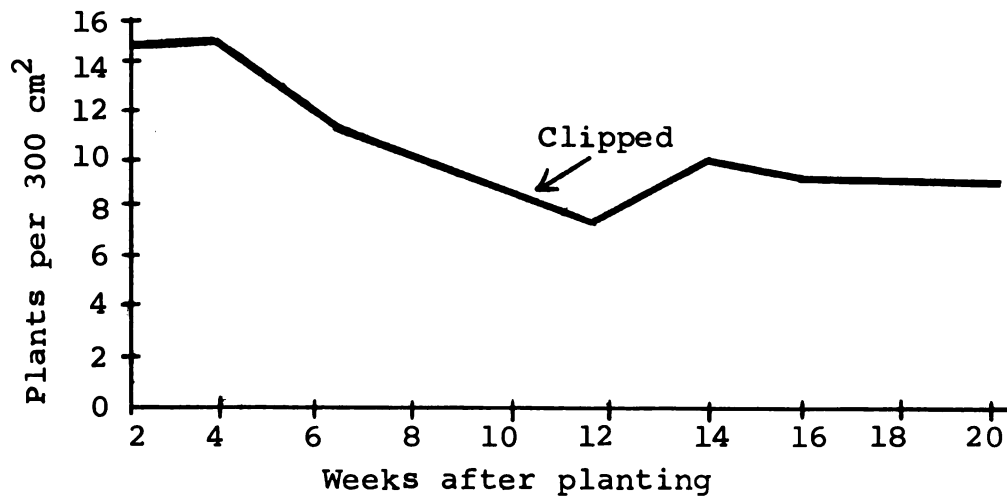


Figure 3. Survival of white cockle after a spring planting of alfalfa. Plots clipped on July 31, 1968.

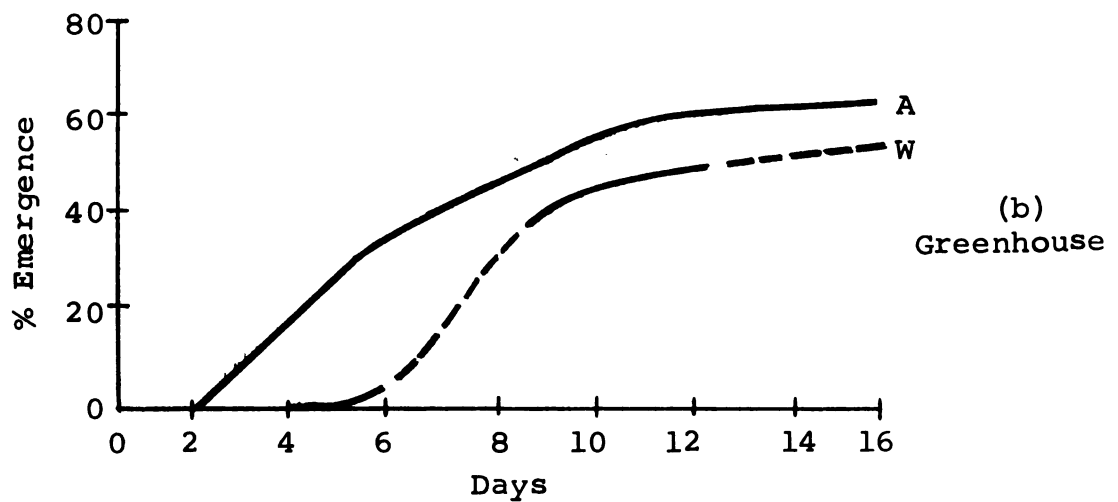
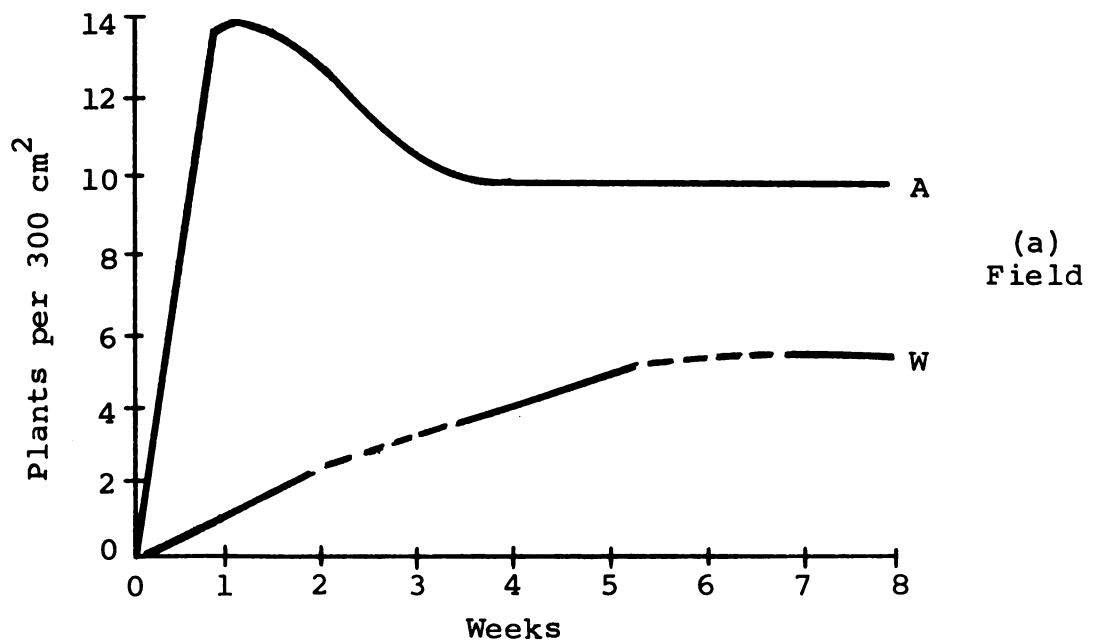


Figure 4. Survival in the field (a) and the relative time of emergence of alfalfa and white cockle in the greenhouse (b), and under four controlled temperature environments (c-f). (A=alfalfa, W= white cockle.)

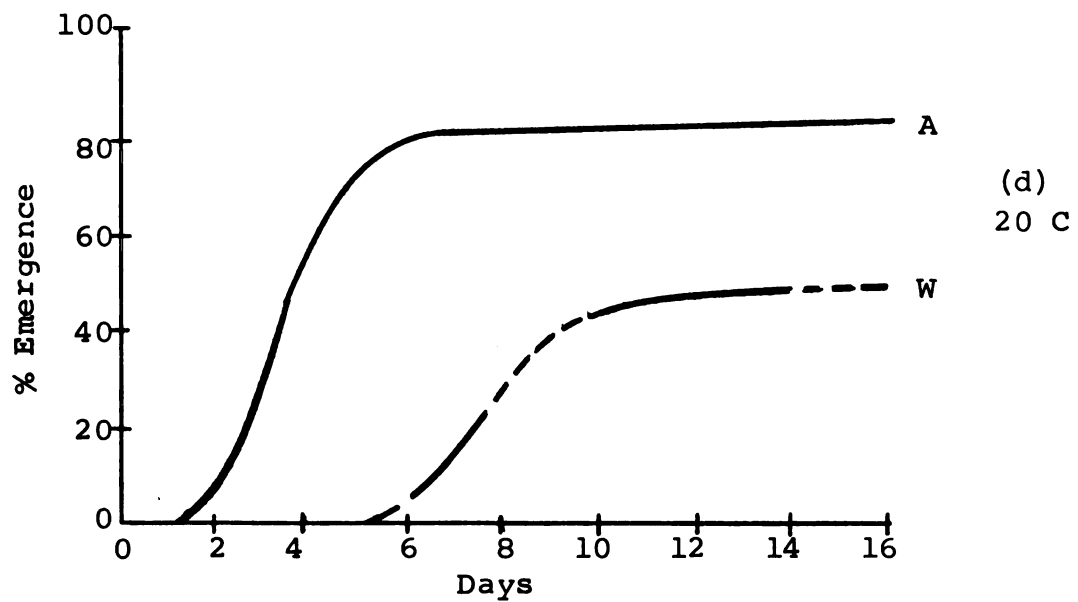
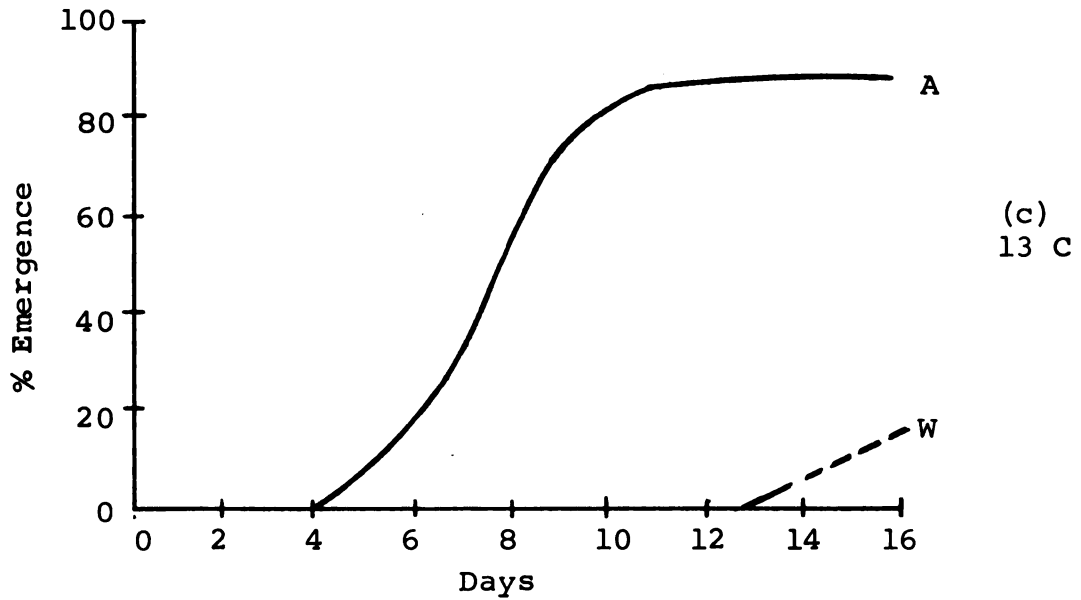


Figure 4--Continued. Survival in the field (a) and the relative time of emergence of alfalfa and white cockle in the greenhouse (b), and under four controlled temperature environments (c-f). (A = alfalfa, W = white cockle.)

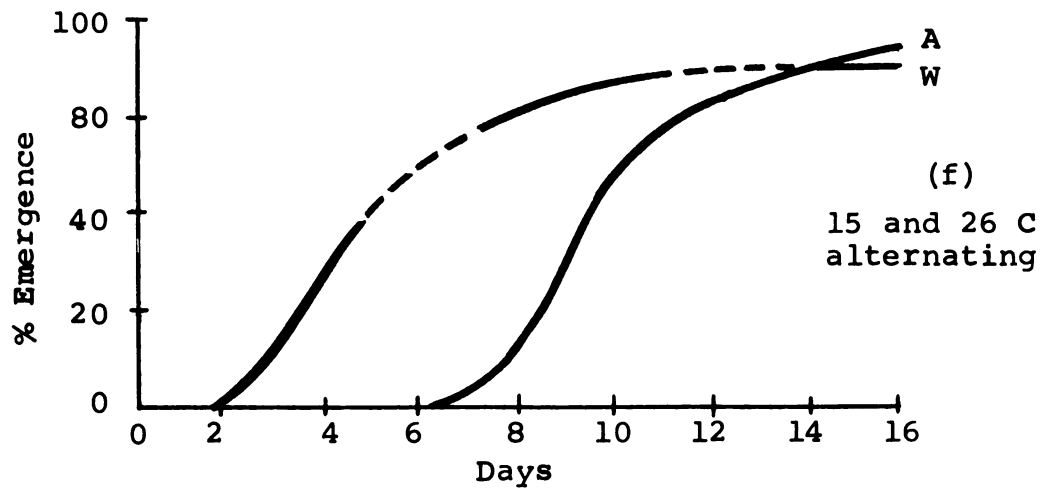
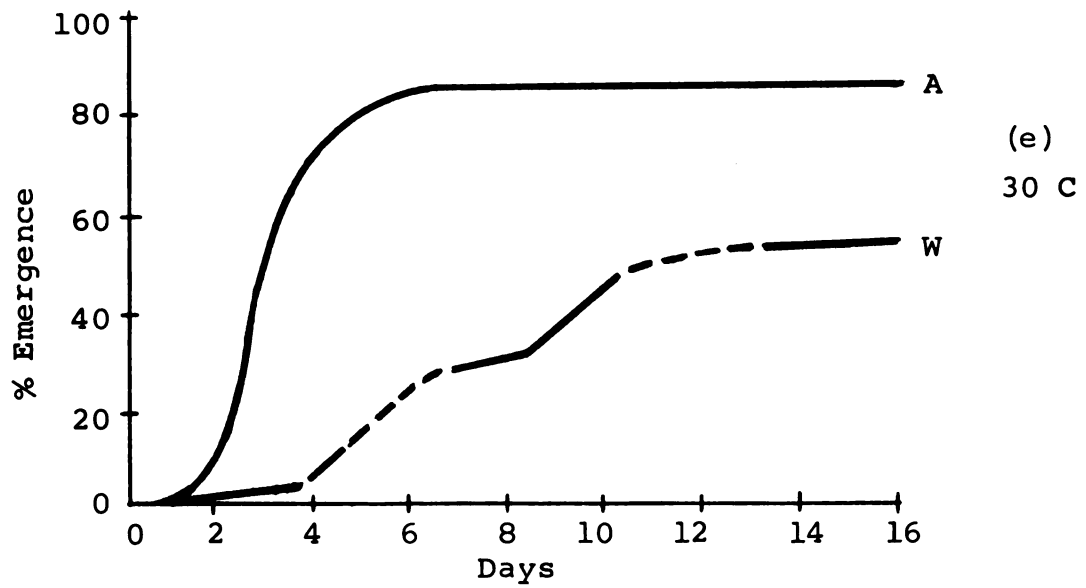


Figure 4--Continued. Survival in the field (a) and the relative time of emergence of alfalfa and white cockle in the greenhouse (b), and under four controlled temperature environments (c-f). (A = alfalfa, W = white cockle.)

It is evident from the graphs in Figure 4 that alfalfa emerges faster than white cockle. The interval of time between the maximum emergence of the two species is less under the alternating temperatures in the controlled environment chamber and in the greenhouse than with the constant temperatures of 13, 20, and 30 C. However, under fluctuating conditions in the field, maximum emergence of white cockle was much slower than alfalfa. This quicker emergence of alfalfa, which also had been observed in a previous field plantings, is a desirable crop-weed relationship. The faster emergence of alfalfa in the field may be partly due to the fact that alfalfa is seeded at a somewhat uniform depth near the soil surface, whereas, natural populations of white cockle seeds are present in the soil at various depths. The competitiveness of white cockle, then, is not due to an advantage attained by early seedling emergence but must result from other factors during vegetative growth.

The emergence of white cockle from various depths in soil of different textures is shown in Table 11. The highest emergence percentage was in the sandy loam soil and in the upper layers of all soils. There were no differences in percent emergence among the .6-, 1.3-, and 2.5-cm levels of seed placement. At the 5-cm level, emergence was significantly lower in all soils with no emergence occurring in the clay loam and silt loam soils. The emergence of white cockle from the lower depths helps explain the high percentage

Table 11. Effect of seed planting depth on emergence of white cockle in the greenhouse

Soil	Depth (cm)	Emergence (%)	
Sandy loam	0.6	39.0 a*	
	1.3	42.0 a	
	2.5	46.6 a	
	5.0	10.6 d	
Sandy clay loam	0.6	24.0 b	
	1.3	25.0 bc	
	2.5	22.0 bc	
	5.0	4.0 d	
Silt loam	0.6	6.0 d	
	1.3	12.0 cd	
	2.5	10.0 d	
	5.0	0.0 e	
Clay loam	0.6	8.6 d	
	1.3	6.6 d	
	2.5	2.0 d	
	5.0	0.0 e	
Soil Texture Averages		Depth of Planting Averages	
Soil	Emergence (%)	Depth (cm)	Emergence (%)
Sandy loam	27.6 a	0.6	19.4 a
Sandy clay loam	15.0 b	1.3	21.4 a
Silt loam	5.6 c	2.5	20.2 a
Clay loam	3.4 c	5.0	3.6 b

*Means in the same column followed by different letters are significantly different at the 5% level.

of white cockle plants originating from seed in the field. It also points out again that light is not absolutely necessary for the germination of white cockle seed since light cannot penetrate soil as deep as 5 cm (54).

Competition Studies

Field experiments

To confirm that white cockle is a competitor in first cutting growth of alfalfa, an early cutting of alfalfa was made on plots with varying infestations of white cockle. Plots with an average of 129 white cockle plants per M^2 yielded 645 kilograms of alfalfa dry matter per hectare; whereas, plots infested with only 14 white cockle plants per square meter as a result of an application EPTC at 3.4 Kg/ha yielded 1,691 Kg/ha (Table 12). Thus, white cockle comprising about 30% of the total forage reduced alfalfa yields by 62%. It was obvious from other observations in the field that the dense mat of white cockle present after seeding definitely interfered with alfalfa growth.

The benefits of low densities of white cockle can also be seen by noting that for every kilogram of white cockle eliminated, there was a gain of 3.9 kilograms of alfalfa. This is somewhat higher than the ratio stated by Klingman (51): for every pound of weeds grown in pastures, the production of more desirable plants is reduced by an equal amount. Perhaps this 1 to 3.9 ratio, white cockle to alfalfa, would have been narrower had the alfalfa been

Table 12. Effects of white cockle density on alfalfa and white cockle dry matter yields in kilograms per hectare in the field

White Cockle Plants/m ²	Alfalfa	White Cockle	Total Forage
129	645 b*	283 a	928 b
14	1,691 a	16 b	1,707 a

*Means in the same column followed by different letters are significantly different at the 5% level.

harvested at a more mature stage. White cockle may compete less with alfalfa at more advanced stages of growth.

A first cutting made on June 12, 1968 in a 1-year old stand of alfalfa showed that the reduction in alfalfa yields due to the presence of white cockle was not statistically significant. Alfalfa infested with 8.6 plants per m² yielded 6,630 kilograms of dry matter per hectare; whereas, alfalfa with no white cockle yielded 7,750 Kg/ha. This is similar to the results of Anderson (1), and Hastings and Kust (45) which showed that when white cockle at 20.5 plants per m² in an established stand of alfalfa was satisfactorily (60-100%) controlled, alfalfa yields were not increased. The competitive effects of white cockle are apparently much less in second and third cuttings of alfalfa. A question that remains to be answered is--what densities of white cockle remaining in alfalfa after the first cutting are yield-reducing and economical to control.

Greenhouse experiments

The effects of four densities of white cockle on yields of alfalfa for three cuttings are shown in Table 13. Yields of alfalfa decreased as the density of white cockle increased except that there was no difference in yields between 6.5 and 13.0 white cockle plants per square meter. Alfalfa yields with 27 white cockle plants per m² were reduced 46.3% when compared to alfalfa with no white cockle present. At the second cutting this same density lowered alfalfa dry matter by only 23%. Also in the second cutting the yields at the 13.0 density did not differ from those where no white cockle was present.

At the time of the third cutting, the amount of white cockle dry matter was very small compared to that of the first cutting and consequently, the competition between white cockle and alfalfa was nil. The decreasing competitiveness of white cockle following the first cutting can be seen more clearly in Figure 5. This helps explain why there was no increase in alfalfa yield when white cockle was hand-weeded from second cutting growth in the field or was controlled chemically with simazine (1) (45).

In the first study involving modes of white cockle competition, below-ground competition was found to be more severe than above-ground (Table 14). First cutting alfalfa growth was reduced 58% by below-ground competition but only 36 and 38% by above-ground and full competition, respectively.

Table 13. Influence of four densities of white cockle on yields of alfalfa and white cockle dry matter in grams per pot in the greenhouse

White Cockle Plants/M ²	1st Cutting			2nd Cutting			3rd Cutting		
	Alfalfa	Cockle	Total	Alfalfa	Cockle	Total	Alfalfa	Cockle	Total
0.0	14.9 a*	0.0 d	14.9 d	17.3 a	0.0 c	17.3 a	13.9 a	0.0 c	13.9 c
6.5	12.2 b	3.1 c	15.2 a	15.4 b	0.7 b	16.0 a	14.0 a	0.4 b	14.4 a
13.0	12.2 b	5.2 b	17.4 a	16.4 ab	0.7 b	17.1 a	14.1 a	0.5 b	14.8 a
27.0	8.0 c	10.9 a	18.9 a	13.3 c	2.3 a	15.6 a	13.7 a	1.4 a	15.1 a

*Means in the same column followed by different letters are significantly different at the 5% level.

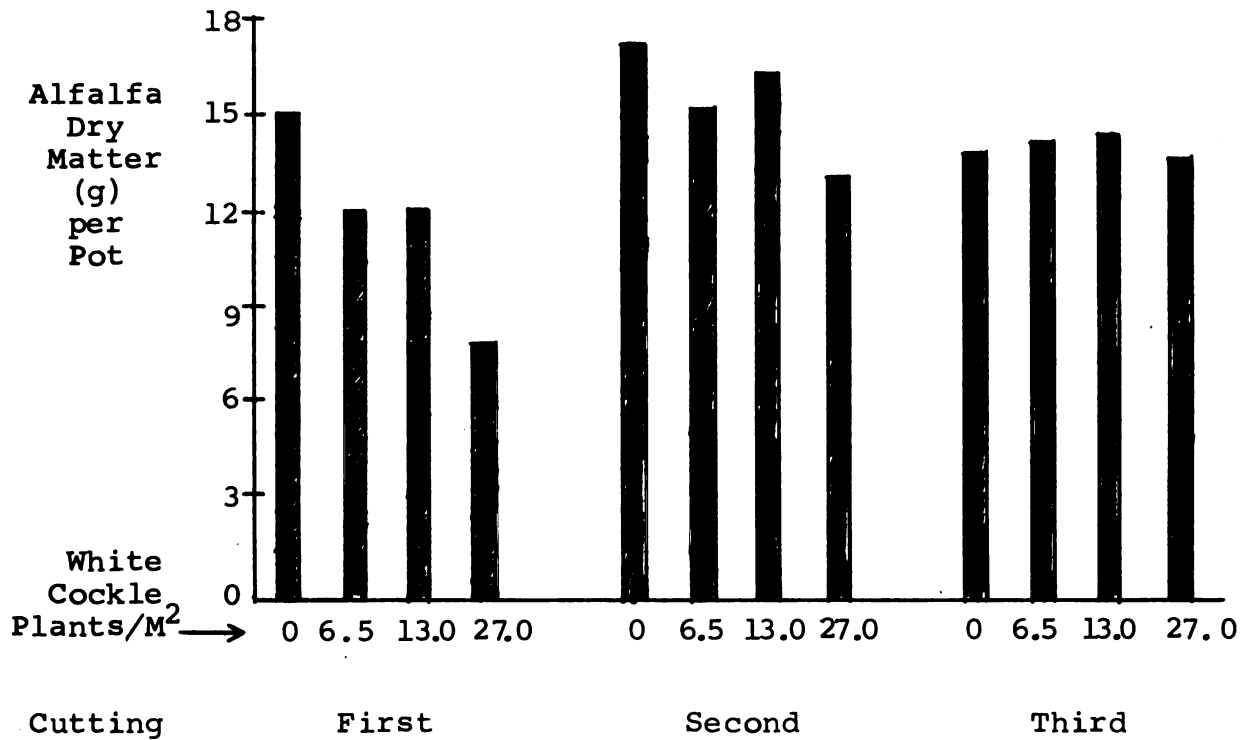


Figure 5. Effects of four densities of white cockle dry matter yields of alfalfa in the greenhouse.

Table 14. Effects on top growth of four modes of competition of top growth of alfalfa and white cockle

Mode of Competition	Dry Weight (g) per Pot			Height (cm)	
	Alfalfa	White Cockle	Total	Alfalfa	White Cockle
<u>1st Cutting:</u>					
None	5.8 a*	6.8 a	12.6 a	56.9 a	71.5 a
Below-ground	2.4 b	7.7 a	10.2 ab	45.0 b	73.0 a
Above-ground	3.7 b	4.6 a	8.4 b	57.1 a	70.0 a
Full	3.6 b	4.0 a	7.7 b	57.0 a	70.0 a
<u>2nd Cutting:</u>					
None	5.3 a	0.6 a	5.9 a	48.2 a	18.4 a
Below-ground	5.0 a	1.6 a	6.5 a	52.3 a	28.3 a
Above-ground	4.0 a	0.4 a	4.5 a	49.0 a	23.1 a
Full	4.6 a	0.6 a	5.2 a	49.0 a	27.5 a

*Means in the same column followed by different letters are significantly different at the 5% level.

The reason for competition below-ground being more severe than full competition may be a result of the branching habit of white cockle. In below-ground competition each species has a full unit of aerial portion but both species must share one unit of soil. Because white cockle stems spread more freely than alfalfa, it may take full advantage of the aerial space available to it. As a result, white cockle roots may develop more than when subject to full competition and thereby render below-ground competition more harsh than full competition. Donald (29) also stated that although there is competition for one or two factors, a remaining factor may be interacting and causing a "build-up" of effects.

At the second cutting there were no significant differences among the modes of competition. This may be partially explained by comparing the height of alfalfa and white cockle at the time of cutting (Table 14). In all cases alfalfa was taller than the white cockle which may give the alfalfa a competitive advantage by shading the white cockle. Figure 6 shows that alfalfa held this height advantage for the entire 5 weeks of regrowth. However, at the first cutting when competition was evident, white cockle was taller than the alfalfa for all modes of competition.

In the second study involving modes of competition (Table 15), it was found that below-ground competition under conditions of low fertility and moisture was equal to full competition and above-ground competition.

It was previously proposed that the strong below-ground competition was due to a large amount of white cockle root growth. In Table 15 it can be seen that white cockle had only 617 mg of roots in full competition and had 1,306 mg in below-ground competition under low fertility and moisture which is an increase of 112%. Comparing the same modes of competition, alfalfa root growth was also higher but only by 68%. The greater utilization of the aerial portion of the containers in below-ground competition can be seen by comparing the amounts of top growth in below-ground and full competition. The difference in white cockle top growth between the two modes of competition is not significant; however, it lacks significance by only one-tenth gram.

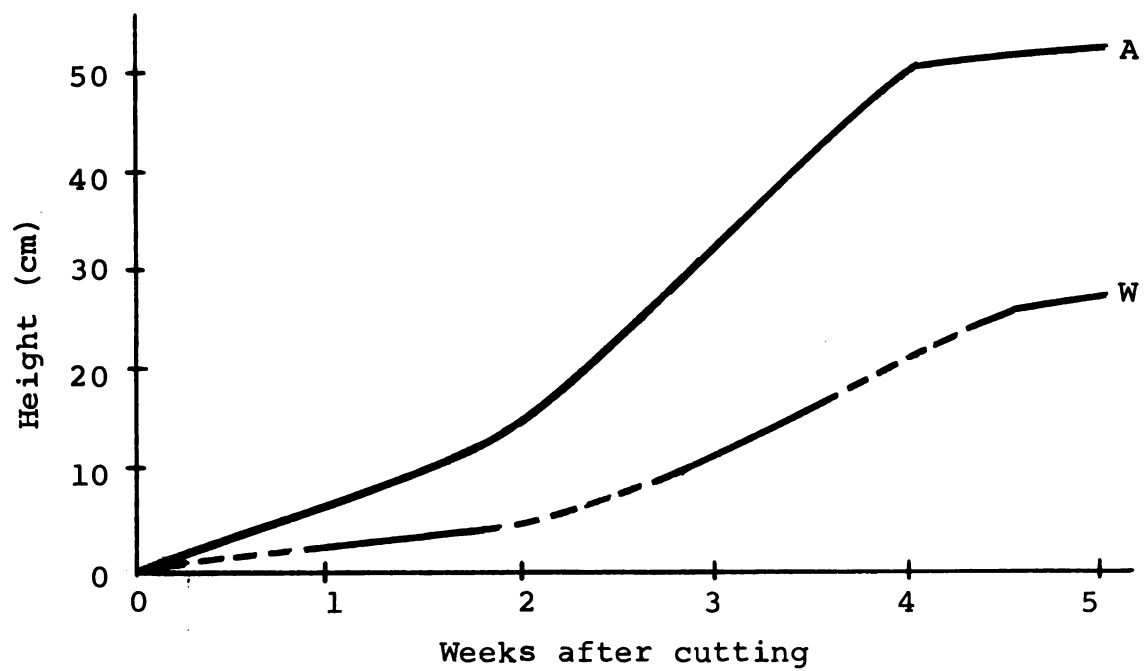


Figure 6. Regrowth of alfalfa and white cockle after first cutting. (A = alfalfa, W = white cockle.)

Table 15. Effects of four modes of competition, fertility levels, and moisture levels on dry weights of alfalfa and white cockle

Mode of Competition	Fertility Level	Moisture Level	Top Growth (g) per Pot			Roots (mg) per Pot		
			Alfalfa	Cockle	Total	Alfalfa	Cockle	Total
None	Low	Low	8.8 a*	11.6 a	20.5 a	959 bc	924 abc	1883 bc
Full	Low	Low	3.8 d	4.0 b	7.8 d	1040 bc	617 bc	1657 bc
Above-ground	Low	Low	4.4 cd	5.2 b	9.6 cd	586 c	411 c	996 c
Below-ground	Low	Low	4.2 cd	8.7 ab	12.9 bc	1752 a	1306 a	3058 a
Below-ground	Low	High	5.6 c	8.8 ab	14.5 b	1105 b	1070 a	2175 bc
Below-ground	High	Low	3.9 cd	5.4 b	9.2 cd	1076 b	1033 ab	2109 ab
Below-ground	High	High	7.2 b	8.4 ab	15.6 b	1164 b	1046 ab	2210 bc

*Means in the same column followed by different letters are significantly different at the 5% level.

This increased top growth probably is responsible for the corresponding increase in root growth involved in the below-ground competition. Studies by Schreiber (70) and Fabricus and Nalewaja (33) also showed below-ground competition to be the same and sometimes greater than full competition. Schreiber showed the root and top growth of pigweed in competition with wheat to be greater below-ground than in full competition.

As already stated, alfalfa root growth was also greater in below-ground competition with low fertility and moisture than in full competition. However, there was no corresponding increase in top growth. The higher amount of white cockle top growth may have resulted in an increase of root growth which thereby deprived alfalfa of water and nutrients. Greater amounts of root growth in soils with limiting amounts of water and nutrients than in soils with no limiting factors is well documented in the literature (77). It can be seen in Table 14 that with the high levels of fertility or moisture, alfalfa root growth was significantly less than with below-ground competition under low water and fertility conditions.

In Tables 14 and 15 data of individual and total weights do not indicate that the reductions in growth of alfalfa or white cockle resulted from effects of alleopathy. The techniques were not designed to separate effects of alleopathy and nutrient competition between roots and no

conclusions can be made in this respect. Most evidence supporting the effects of alleopathy is based on studies which show that water soluble inhibitors are leached or volatilized from the foilage (40) (62) (80). In the present study, however, alfalfa and white cockle were watered at ground level and separated by a porous shading material and consequently, the possibility that foliar leachates or volatile inhibitors had any significant effect is not very great.

SUMMARY AND CONCLUSIONS

Studies concerning the life history of white cockle were carried out to provide information which may aid in weed control practices and in any future experimentation involving white cockle. Growth and development under various photoperiods and temperatures, male and female plant comparisons, the reproductive potential by asexual and sexual means and requirements for seed germination were the life history aspects of the study. Associated growth of white cockle and alfalfa was investigated to gain an understanding of some aspects of the nature of competition between the two species.

The results of these investigations have provided the following conclusions:

1. White cockle was found to be indeterminate in response to photoperiod. Plants grown under 8, 16, and 24 hours of light required an average of 70, 39, and 20 days to flower, respectively.
2. There was little difference in time required for flowering and in size of plants grown at 29.4 and 23.9 C; however, white cockle plants were greener at 23.9 C. Plants grown at 12.8 C were smaller and did not flower at the end of 62 days.

3. In the field female plants were found to be slightly larger than male plants. However, in the greenhouse there was no difference between the sexes of plants harvested at either the same physiological or chronological age.

4. It was found that white cockle does not possess any stolons or rhizomes and that vegetative reproduction is mainly by the growth of crown buds.

5. Nearly all crown-root segments exposed to drying on the soil surface for more than one day were killed. New shoots emerged from crown-root segments buried as deep as 38 cm and from segments with only 1 cm of root remaining.

6. The spread of white cockle was observed to be mainly by seed. Ninety-seven per cent of white cockle plants in a new seeding originated from seed. Very few additional seeds germinated after the initial flush of seedlings produced within two weeks after a seeding.

7. White cockle plants sampled in mid-July had a seed production potential of about 24,200. Capsules were found to mature and open in about five weeks; however, seeds were viable two to three weeks after pollination. Mature seeds germinated immediately after harvest.

8. Light facilitated the germination of white cockle seed. Photoperiod and light intensity had no effect of germination. Germination responses to 12.8, 18.3, 23.9, 29.4, and 35.0 C showed 23.9 and 29.4 C to be the most conducive.

9. White cockle seedlings were capable of emerging from a depth of 5 cm in a sandy clay loam and sandy loam but not in a clay loam or silt loam.

10. Alfalfa always emerged before white cockle, thus rapid emergence is not a factor in the competition between white cockle and alfalfa.

11. Greenhouse studies showed white cockle competition to be most severe in alfalfa prior to the first cutting and to decrease in subsequent regrowth.

12. Competition between roots or tops alone inhibited alfalfa as much as full competition under low moisture and fertility conditions.

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APPENDIX

Table I. Weekly averages of basal diameter and height for white cockle temperature response study

Week	1	2	3	4	5	6	7	8
<u>Basal Diameter (cm)</u>								
13 C	6.9 a*	11.0 a	13.4 b	17.4 b	21.8 b	22.8 a	23.0 a	22.0 a
21	5.1 b	11.3 a	16.8 ab	23.5 a	26.7 a	26.2 a	25.2 a	24.6 a
29	5.3 b	12.9 a	21.1 a	22.2 a	23.3 ab	23.4 a	22.3 a	21.4 a
<u>Height (cm)</u>								
13 C	---	---	6.4 a	6.7 a	7.9 a	8.3 b	8.3 b	10.1 b
21	---	---	8.3 a	15.5 a	21.0 a	30.1 a	36.6 a	49.0 a
29	---	---	9.0 a	17.2 a	27.1 a	43.8 a	50.0 a	50.3 a

*Means in the same column followed by different letters are significantly different at the 5% level.

Table II. Monthly precipitation and average temperatures for 1968 at East Lansing, Michigan

	Precipitation (inches)	Temperature (F)
April	1.75	49.5
May	4.39	54.1
June	7.16	66.6
July	2.34	69.7
August	2.23	70.2
September	3.49	64.1

Table III. Mechanical analyses of soils used in seed depth study

	Sand (%)	Silt (%)	Clay (%)
Clay loam	45.12	24.84	30.04
Silt loam	26.56	52.26	21.18
Sandy clay loam	53.10	17.72	29.18
Sandy loam	71.84	8.48	19.68

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