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THE BIOLOGY OF HORSEWEED [*Conyza canadensis* (L.) Cron.]

A Thesis Presented

by

MARILYN M. BEKECH

Submitted to the Graduate School of the
University of Massachusetts in partial fulfillment
of the requirements for the degree of

MASTER OF SCIENCE

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Department of Plant and Soil Sciences

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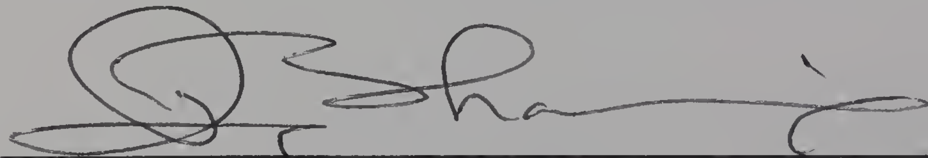
Approved as to style and content by:



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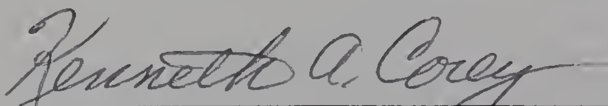

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Special thanks to my son, Phillip
for being a constant source of insight,
instigation, and inspiration
to get on with life.

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CHAPTER I

INTRODUCTION

Horseweed [Conya canadensis (L.) Cron.] is an annual or winter annual weed often found in newly abandoned fields and waste areas, where it occurs for a year or two before it is replaced by other species. Although horseweed occasionally infests grain fields, pastures, roadsides, nurseries and gardens, it has not been considered an agricultural problem in Massachusetts. However, in an experimental corn field which has been maintained for five years in no-till conditions at the University of Massachusetts Experiment Station in South Deerfield, horseweed is the dominant weed.

Changes in tillage practices often result in changes in the weed species composition of agricultural fields (Radesovich and Holt, 1986). Where conditions that favor annuals, such as disturbances of the soil every spring, have been replaced by other conditions that favor the long-term occupation of space, perennials dominate. The recent trend in agriculture toward reducing tillage as a means of reducing erosion,conserving soil moisture, and lowering costs constitutes a major change in the environment of agricultural weeds. Where no-tillage has replaced conventional tillage, a change from annual to perennial

weed species has often been noted (Hinkle, 1983; McCutchen and Hayse, 1983; Phillips and Phillips, 1984). These perennials may persist and may resist herbicides used for weed control.

In contrast, persistence of horseweed and other annuals depends on yearly seed production and on the continued availability of suitable sites for germination. Moreover, since seed production by annuals is usually proportional to the size of the plant, environmental effects on all stages of growth may also ultimately influence survival. Changes in environment may also change the allocation of plant biomass to root, stem, leaves, and reproductive organs and the timing of reproduction and seed germination.

In no-till systems, weeds are primarily controlled by application of herbicides. Any cultural measures that can either increase the effectiveness of herbicide treatments or decrease the frequency or rate of herbicide applications necessary for weed control contribute to the cost effectiveness of weed control programs.

Shading is one environmental factor that can be manipulated by cultural practices for the purpose of weed suppression in field crops. Planting date, row spacing, and crop variety can be selected to favor the rapid

establishment of a closed canopy (Staniforth and Wiese, 1985). Another useful environmental factor that can be manipulated in no-till fields is the amount of crop residue left on the surface after harvesting. Crop residues may lower soil temperature and provide a physical barrier that prevents the germination of weed seeds. The response of horseweed to shading and to crop residues may suggest measures that can be taken to minimize the severity of horseweed infestations and thus reduce the need for herbicide applications.

At the outset of this study, a small subpopulation of horseweed was observed consisting of plants with a distinctive inflorescence branching pattern which were shorter and flowered earlier than the rest of the popu lation. In studying the response of any species of plant to environmental factors, one usually assumes that the population being studied is genetically uniform or that variations in response can be attributed to environmental and not genetic factors. A study of the life cycle of horseweed at this site would be incomplete without noting the occurrence of this other type and determining if its distinctive morphology is genetically based, because a distinctive, genetically isolated subpopulation may require different control measures.

The overall objective of this study was to determine if certain aspects of the life cycle of horseweed, especially timing of germination and biomass partitioning in response to shading, may account for its sudden appearance and persistence in the no-till corn field studied. Specifically, the objectives were to compare the location and number of germinable seeds in no-till and conventionally tilled sites, to determine the timing of germination, the effect of residue cover on germination, the survival rate, and the effect of population density and shading on biomass partitioning.

CHAPTER II

LITERATURE REVIEW

A. Germination

Seasonal periodicity of germination may be an important consideration in any weed control program. Both environmental and endogenous factors may affect weed seed germination rates. Seeds of most agricultural weeds are heteroblastic, in that a single plant produces seeds which vary in germinability (Bewley and Black, 1978; Harper, 1977). Some factors that affect heteroblasty include daylength (Cumming, 1963), temperature (Taylorson and Hendricks, 1972), light quality and intensity (Wooley and Stoller, 1978; Fenner, 1980), and physiology of the parent plant during seed maturation (Kigel and Gibley, 1987). One or more of these factors may determine whether horseweed seeds germinate in the fall or the spring. It is not known what role most of these factors play in the dormancy of horseweed seeds, or if indeed there is any true dormancy of horseweed seeds other than that imposed by the environment. Gorske et al. (1977) found that germination of horseweed was not affected by light intensity or quality, so differences in shading do not account for seasonal variations in the germination rate. But they did not explain their figure of only 43% germination in both light and dark. Regehr and Bazzaz (1979) obtained

a germination rate of 25% in a growth chamber one week after collection, but only 6.5% in the field under normal growing conditions. Their percentage of germination in the field was based on their estimate of the number of seeds present on the soil surface and the subsequent number of plants observed. On the other hand, Palmblad (1968) obtained a germination rate of 100% on moist filter paper after seeds had been stored at room temperature. Whatever innate or induced dormancy factors account for these variations in germination rate may explain why peak germinations of horseweed occur in both fall and spring.

In no-till cropping systems, weeds are controlled by preemergence herbicides, which kill weeds as they germinate, and postemergence herbicides which kill weeds that germinated sometime prior to application, so the timing of germination may be very important in determining the proper herbicide combination to apply (Bhowmik et al., 1985; Bellinder and Wilson, 1983; Hagood and Davis, 1986). Residues from previous crops and weeds which are left in the field can suppress the germination and emergence of weed species. The date of peak germination may be delayed and the total number of seeds that germinate may be reduced by this method (Bewley and Black, 1978; Phillips and Phillips, 1984). Since horseweed is apparently adapted

for colonizing open ground (Cronquist, 1980), the amount of residue covering the soil may affect the amount and timing of horseweed germination.

B. Biomass Partitioning

Horseweed may gain an advantage over other annual weeds and spring planted crops by germination in the fall and overwintering in the rosette stage. It has been suggested that growth of horseweed and other winter annuals continues throughout the winter whenever conditions permit (Regehr and Bazzaz, 1975). Horseweed rosettes observed during the winter were found to photosynthesize at lower temperatures and light intensities than those observed in summer by Regehr and Bazzaz (1979), who suggest that this ability may allow horseweed and other winter annuals not only to survive but also to actually accumulate reserves during the winter.

Horseweed seeds that germinate in the spring produce plants that only briefly pass through the rosette stage of growth. In late spring, the stems of both fall and spring germinated plants elongate, producing a single vegetative shoot that typically grows to a height of 1 to 1.5 meters. Numerous flower heads 2 to 3 mm wide by 4 to 5 mm long are produced on a long, loosely branched inflorescence (Cronquist, 1980). It is not known what

environmental or endogenous factors control stem elongation or the initiation of flowers, or what minimum length of time is required for a plant to complete its life cycle. Tn any case, both fall and early spring germination allow horseweed to capture space and thus prevent the germination of other weed seeds, especially thosr annual weeds that germinate in late spring (Parrish and Bazzaz, 1977).

Both density dependent mortality and plasticity of growth often regulate the vegetative and reproductive output of an annual plant population. At higher densities, fewer individuals may survive long enough to produce seeds, and those that do survive may be constrained by the limited space available to produce fewer flowers and seeds than plants growing with more space. Over a wide range of densities, many annual plants exhibit plasticity of growth, expanding to fill the space available. As a result, total biomass and seed production per unit area tend to remain constant over a wide range of densities (Harper, 1977). Yoda et al. (1957) found that horseweed sown at the rate of 1-2 x 10^7 seeds/m^2 on scanty, infertile soil germinated 122,400 seedlings/m^2, but the population declined over a 9 month period to about 1060 plants/m^2, so that the adult, reproducing population represented only 1% of the seedling population. They also found that adding increasing

amounts of N:P:K fertilizer to a sequence of plots resulted in more self-thinning and therefore fewer but larger individual plants in the plots with higher fertility.

Most studies on the effects of intraspecific density on plant biomass partitioning have concentrated on the effects that can be observed at very high densities (Harper, 1977; Yoda et al., 1957; Palmblad, 1967; Weller, 1987). However, for the purpose of the present study it is also useful to examine the plasticity of horseweed at lower desities, and to determine the density at which a decrease in the number of plants represents an actual reduction on total biomass or seed production per unit area (Radesovich and Holt, 1984).

Most annual weeds are ruderal species, that is, they are adapted for taking advantage of disturbances that produce temporarily open ground (Duke, 1984; Radesovich and Holt, 1984). In response to most types of stress, ruderal species usually sustain reproductive growth at the expense of curtailing cegetative growth and even death (Harper, 1977; Grime, 1981). But in response to stress induced by shading, ruderal species invest more resources in stem growth, even at the expense of delaying reproduction or of ultimately producing fewer seeds. They may also transfer carbohydrates from lower leaves

to higher, younger leaves (Grime, 1981, Palmblad, 1968). presumably this is an adaptive response that in an open field environment allows the plant to penetrate the canopy of surrounding vegetation and thereby escape the shade. In a greenhouse study, Palmblad (1968) found that horseweed deed production per 37 cm pot was reduced in response to high density because some individuals remained vegetative. The effect of shading on growth and particularly on reducing the reproductive potential of horseweed may be a response that could be exploited for controlling horseweed infestations.

The relationship between monocarpy and senescence iis well documented (Noonden, 1980; Woolhouse, 1983). Monocarpic plants are those that reproduce only once during their life cycle and then die soon afterwards. All annual plants are monocarpic. But senescence of leaves is not necessarily related to reproduction. During the vegetative phase, shading can stimulate the process of leaf senescence. A distinctive type of canopy development, a rapidly ascending monolayer, in which older, lower leaves senesce when shaded by newer, higher leaves, is characteristic of dense stands of herbaceous vegetation (Grime, 1981). However, once seed production has begun, senescence of leaves may be accelerated as resources are preferentially allocated to reproductive parts. The

number of flowers and seeds produced may be directly proportional to the number of functioning leaves present at the onset of seed production.

the growth and development of species that colonize open ground are affected by interspecific and intraspecific competition, especially competition for light (Duke, 1984, Tremmel and Peterson, 1983; Smith, 1982). As carbohydrate partitioning changes in response to changes in plant density or shading, seed production per plant may be directly related to the density of plants or the amount of shading received by individual plants (Harper, 1977, Grime, 1981).

C. Genetic Isolation

The persistence of two or more biotypes in one location usually requires some mechanism of genetic isolation. *C. canadensis* has not been reported to be apomictic, although apomixis is not umcommon in the closely related genus, *Erigeron* (Hancock, 1977; MacDonald, 1927). Parrish and Bazzaz (1979) observed that although horseweed flowers were frequently visited by a number of potential pollinators, flowers that were covered with gauze to prevent cross fertilization produced 75% as many seeds as untreated horseweed flowers, and concluded therefor that *C. canadensis* is autogamous. It is possible for a

diploid species to become homozygous in a few generations by repeated self fertilization (Hancock, 1977; Briggs and Walters, 1984. Hancock (1977) found that plants pn populations of horseweed in abandoned fields in Ohio were almost exclusively monomorphic for four enzyme systems that he examined, indicating homoztgous populations. It seems likely, therefore, that morphologically distinctive subpopulations of horseweed may represent separate genetic strains.

CHAPTER III

MATERIALS AND METHODS

During 1985, the experimental site was planted to corn, but corn plants were cut at ground level and removed from the experimental plots. Fertilizer was applied as a broadcast during land preparation at the rate of 504 kg/ha of 5-8-12 N:P:K and in bands at planting time at the rate of 252 kg/ha of 10-29-10 N:P:K. During 1986, no crop was planted at the site, and no fertilizer was applied.

A. Germination

1. Distribution of Germinable Seeds in Soil

Ten soil cores were taken from the no-till site and 10 from the adjacent conventional-till field in May by inserting a 7.4 cm diameter soil corer to a depth of approximately 14 cm. Cores were separated in the field into samples representing the top 2 cm, 2 to 4 cm, 4 to 8 cm and deeper than 8 cm. These samples were spread in 1 cm layers on top of 10 cm diameter pots filled with a 1:1 mixture of soil and sand, and watered daily. Seedling emergence was recorded over a period of four weeks.

2. Periodicity of Germination

The number of seedlings present in 10 randomly placed 400 cm^2 quadrates was recorded every 2 weeks. All vegetation was removed after each counting.

3. Effects of Residue on Germination

Ten 0.2 x 0.2 m quadrates were placed in areas of the field covered with approximately 6 kg (dry weight) of corn and weed residues. Horseweed seedlings emerged in each quadrate were counted at 2 week intervals from April to the beginning of July.

B. Effects of Population Density on Biomass Partitioning

1. Naturally Occurring Densities

Ten 0.2 x 0.2 quadrates were placed in areas of dense horseweed seedling populations in a completely randomized design, and the number of surviving plants in each quadtate was counted every 2 weeks. After 12 weeks, when all leaves below the inflorescences had senesced, total dry weight, inflorescence dry weight, and dry weight of dead leaves and stems were measured and the number of surviving plants/m^2, total dry weight/m^2, and number of seeds/plant were calculated.

2. Established Densities

During the first week of June, 1985, five 0.4 x 0.4m plots were established in fertilized and non-fertilized areas. On this date plants were already taller and plant density was lower within the fertilized rows. Horseweed densities of 10, 50, 150, and 300 plants/m^2 were established between fertilized rows and densities of 10, 50, 100, and 200 plants/m^2 were established in the fertilized

rows. Densities were established by removing as many of the largest and smallest plants as necessary to achieve relatively uniform populations of the designated densities. The experiment was replicated four times in a randomized complete block design. Average plant height for 4 randomly selected plants in each plot was recorded every 2 weeks and the number of branches and flower heads was counted after 10 weeks, when all the leaves below the inflorescences had senesced.

During the last week of May, 1986, horseweed densities of 100, 200, 300, and 400 plants/m^2 were established in 1 x 1 m plots. The experiment was replicated four times in a randomized complete block design. Densities were maintained by hand thinning. At two week intervals 5 plants/plot were collected and separated into roots, stems, live leaves, dead leaves, and inflorescences. Samples were dried for 48 hours at 70° C and weighed. The number of seeds/plant was estimated by multilpying the average number of seeds/flower for 10 heads on each plant by the number of heads/plant for 5 plants in each plot.

C. <u>Effects of Shading on Biomass Partitioning</u>

When horseweed plants were still in the rosette stage, 2 x 2 m plots were covered with layers of nylon netting initially at a height of 50 cm, to produce shade levels of

66, 45, and 25% of full sunlight. Light intensity was measured with a photometer (LI-1888 integrating quantum photometer/radiometer) at 1500 $E/m^2/s$ at midday in July. All plots were thinned to 200 plants/m^2. Control plots were left uncovered. Samples were taken from a 1 x 1 m subplot at the center of each plot to avoid differences in light intensity aroung the edges of the plots. The experiment was replicated four times in a randomized complete block design. Procedures for collecting, drying and taking measurements of samples were the same as for the density experiments, part B.2.

D. Genetic Isolation and Autogamous Seed Production

Seeds from the earlier flowering type were collected before the later flowering type began flowering. Seeds from the later flowering type were collected from an area without the earlier flowering type. Sixteen plants of each type were grown in the greenhouse from each set of seeds. Growth was measured in terms of plant height, leaf number and leaf length and width. The number of branches, flower buds, open flowers and seeds per plant were counted. Measurements were recorded at 2 week intervals for 8 weks and weekly thereafter. Individual plants were grown in 10 cm pots, watered daily, and fertilixed with equal applications of 10-10-10 N:P:K fertilizer solution at 4 and 8 weeks. The arrangement of pots was

completely random, and was re-randomized each time measurements were taken.

In the field, 10 unopened flower heads on each of 10 plants were covered with gauze. Seeds/head were counted for the 10 covered and 10 uncovered heads on each plant.

CHAPTER IV

RESULTS

A. Germination

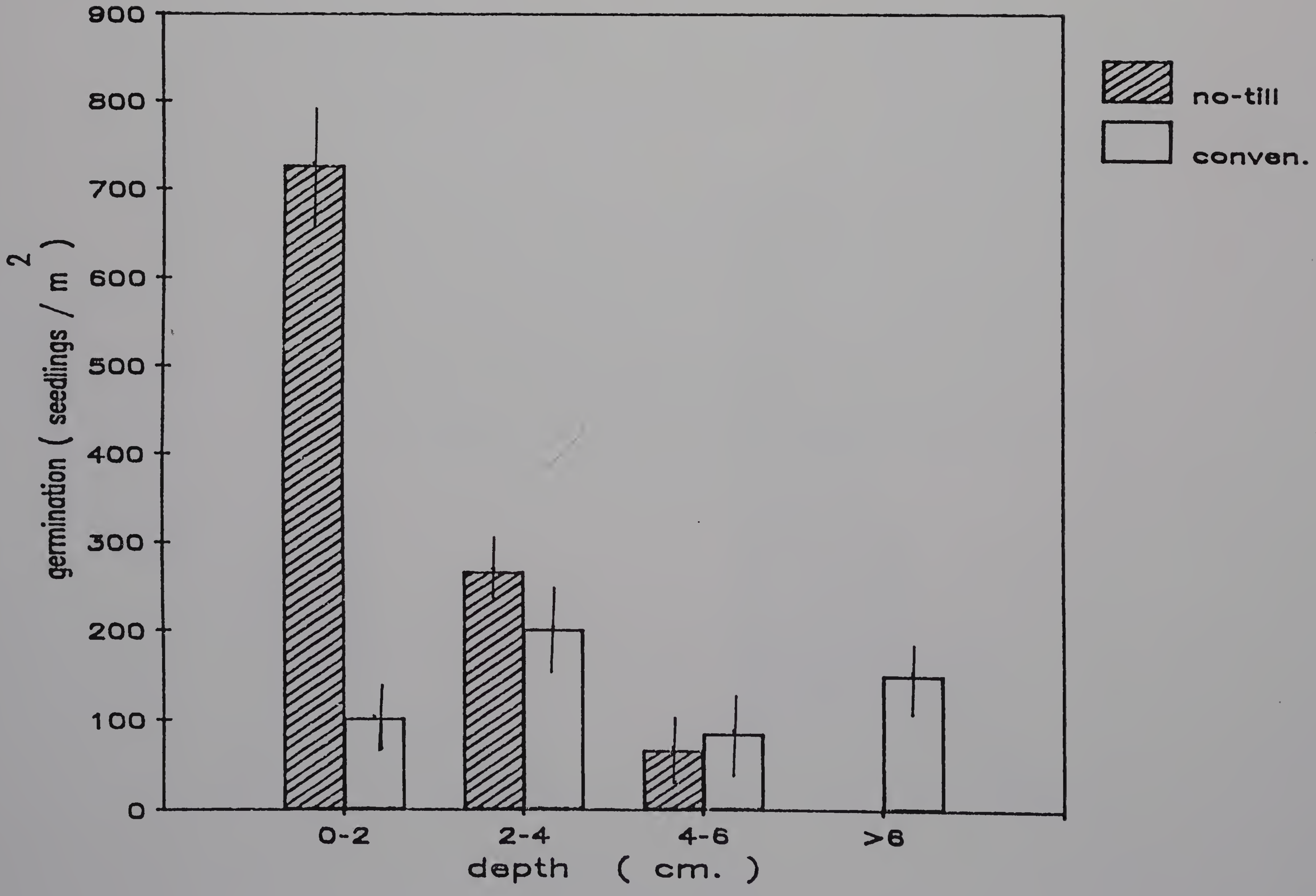
In soil from the no-till site, 80% of germinable horseweed seeds were in the top 2 cm of soil, and no germinable horseweed seeds were below 6 cm. Cores from the tilled site had fewer horseweed seeds, more or less evenly distributed through all layers (Figure 1).

Peak germinations occurred in late August to early September and in May, with some germination throughout the summer except during the middle of July (Figure 2). Residue cover delayed spring germination by four weeks and reduced total germination to only 20% of the uncovered plots (Figure 2).

B. Effects of Population Density on Biomass Partitioning

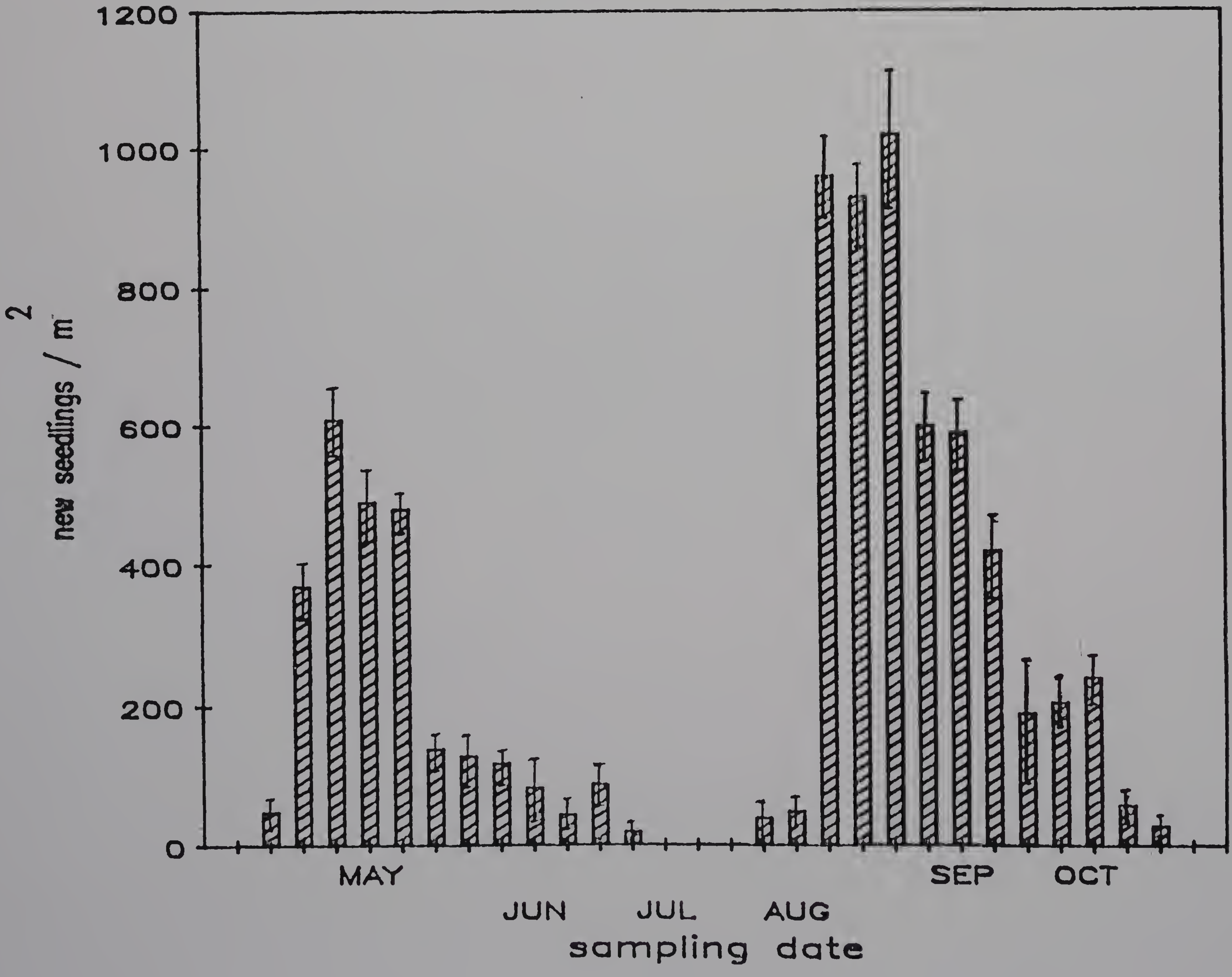
In 1985, plants in the fertilized plots grew taller and produced more branches and flowers than plants in the non-fertilized plots at all densities, but density did not affect the height of plants within fertilized or non-fertilized plots (Figure 4). The number of branches per plant decreased as density increased in both fertilized and non-fertilized plots (Figure 4), as did the number of seeds per plant (Figure 5). The number of seeds/m^2 increased to a maximum of 2×10^7 at 150 plants/m^2

Figure 1. Number of germinable horseweed seeds at four depths in adjacent no-till and conventional-till sites. Bars indicate standard deviations.



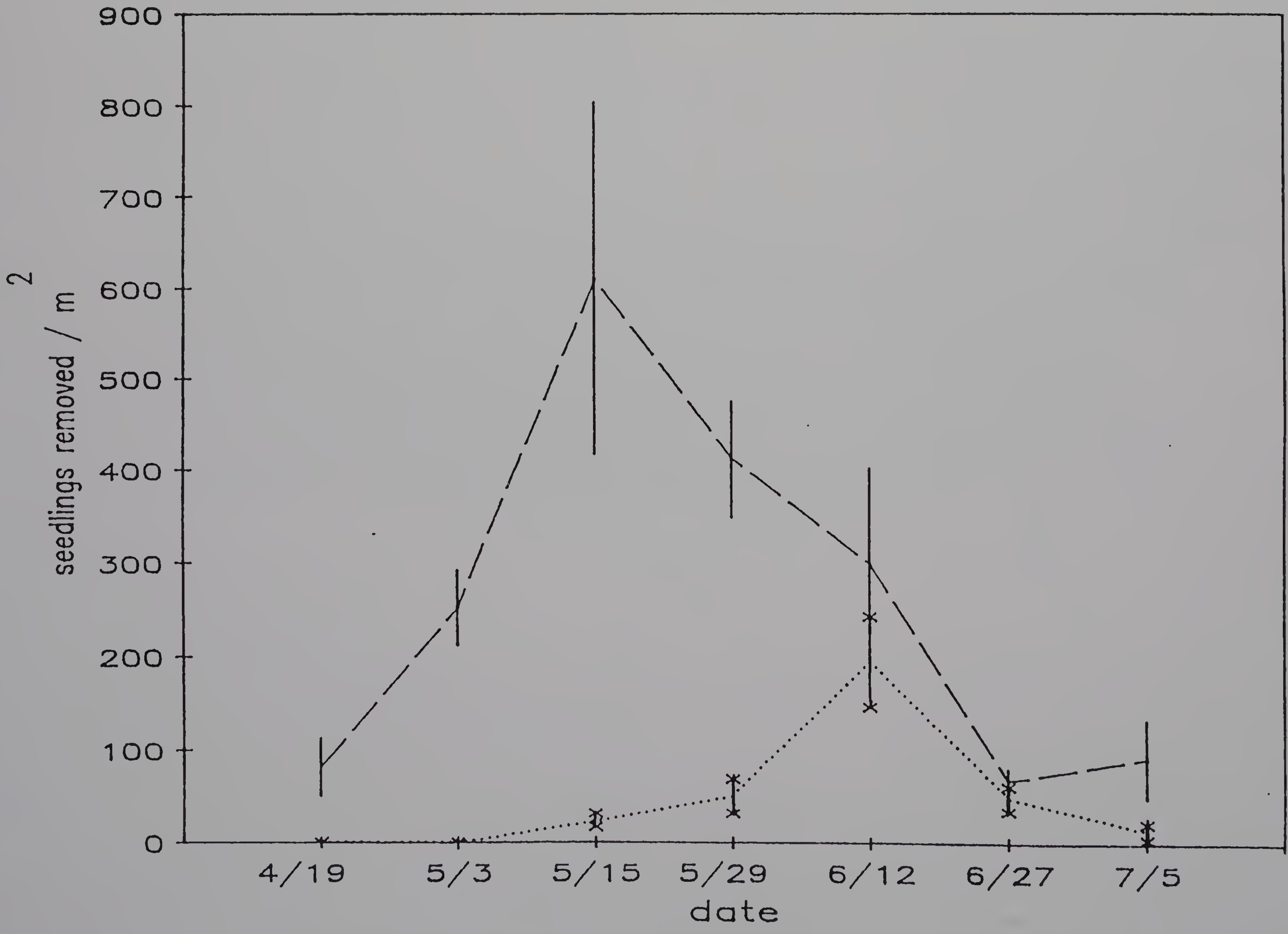
900
800
700
600
500
400
300
200
100
0
germination (seedlings / m 2)
no-till
conven.
0-2
2-4
4-6
>6
depth (cm.)

Figure 2. Number of horseweed seedlings/m^2 counted and removed at two week intervals from a fallow no-till corn field. Bars indicate standard deviations.



new seedlings / m^2
1200
1000
800
600
400
200
0
MAY
JUN
JUL
AUG
SEP
OCT
sampling date

Figure 3. Spring germination of horseweed with and without residue cover. Seedlings were counted and removed every two weeks. Dashed line = residue covered (approximatey 6 kg/ha dry weight of crop and weed residues). Dotted line = uncovered. Bars represent standard deviations.



seedlings removed / m 2
900
800
700
600
500
400
300
200
100
0
4/19
5/3
5/15
5/29
6/12
6/27
7/5
date

Figure 4. Effect of horseweed density on height and number of branches in fertilized and "non-fertilized" bands in a no-till corn field. Fertilizer was applied during land preparation as a broadcast at the rate of 504 kg/ha of 5-8-12 (N-P-K) and at planting time in bands at the rate of 252 kg/ha of 10-29-10 (N-P-K).

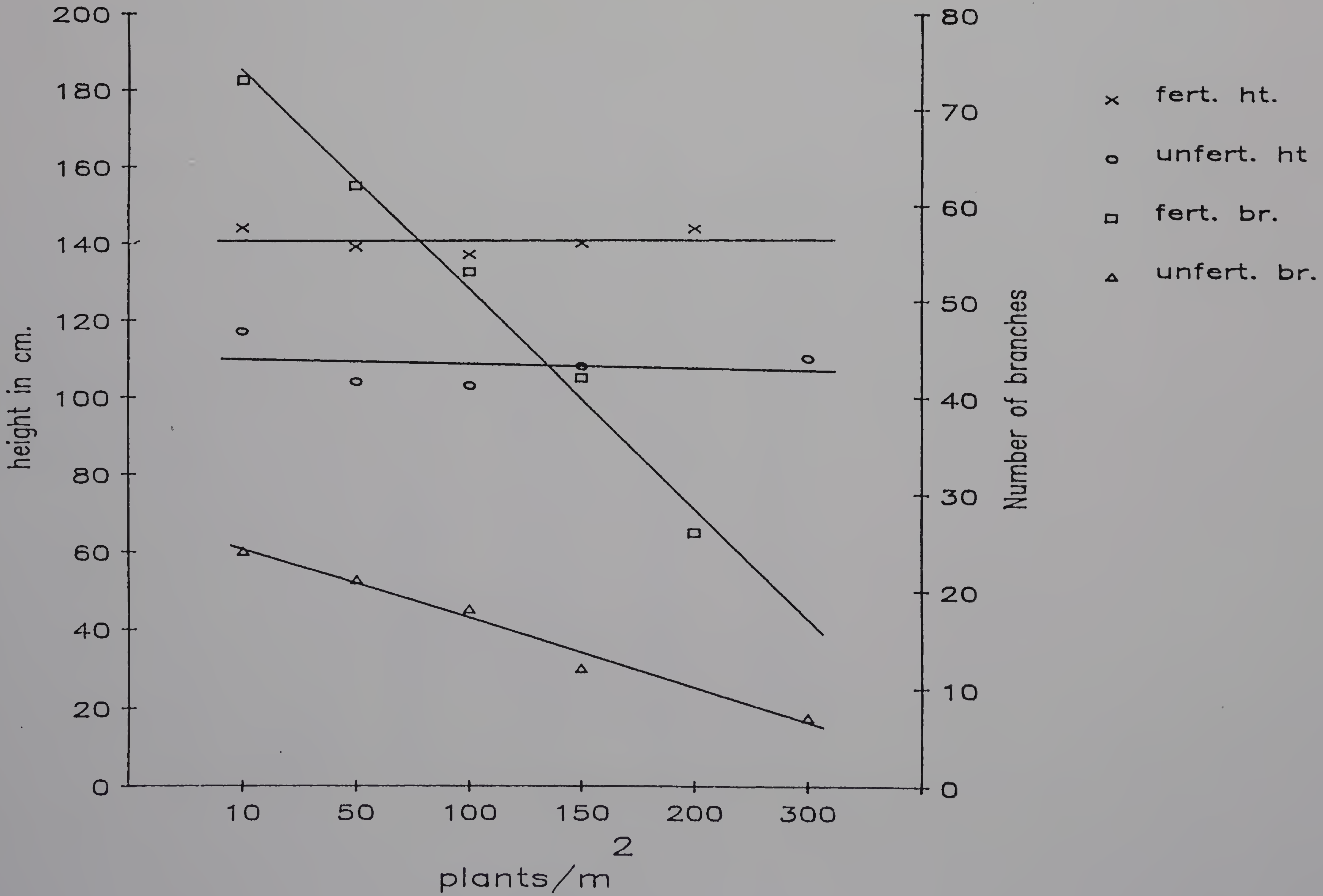
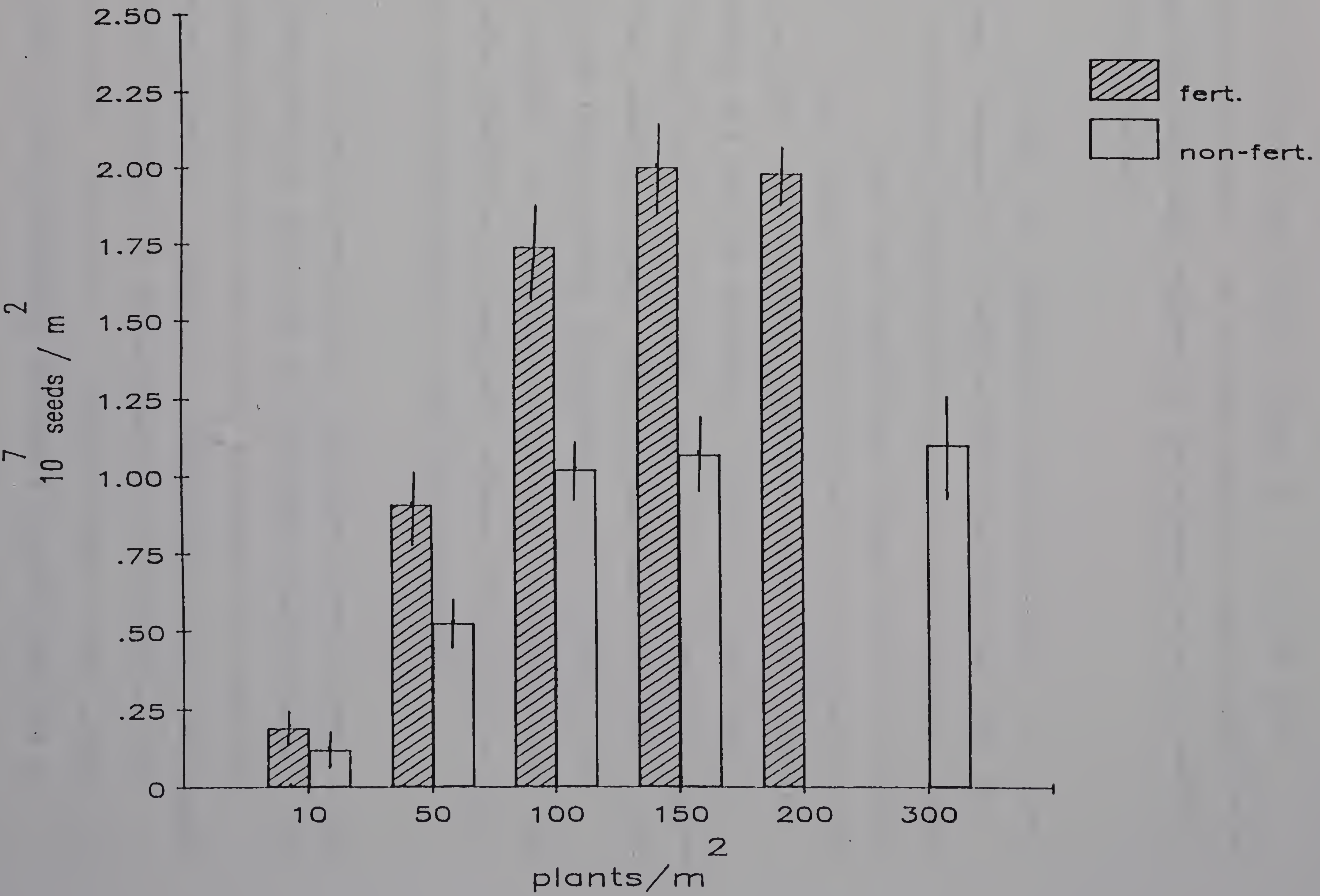

height in cm.
200
180
160
140
120
100
80
60
40
20
0
Number of branches
80
70
60
50
40
30
20
10
0
10
50
100
150
200
300
plants/m 2
x fert. ht.
o unfert. ht
□ fert. br.
△ unfert. br.

Figure 5. Effect of horseweed density on seed production/m^2 in fertilized and "non-fertilized" bands in a no-till corn field. Fertilizer was applied during land preparation as a broadcast at the rate of 504 kg/ha of 5-8-12 N:P:K and at planting time in bands at the rate of 252 kg/ha of 10-29-19 N:P:K. Bars indicate standard deviations.

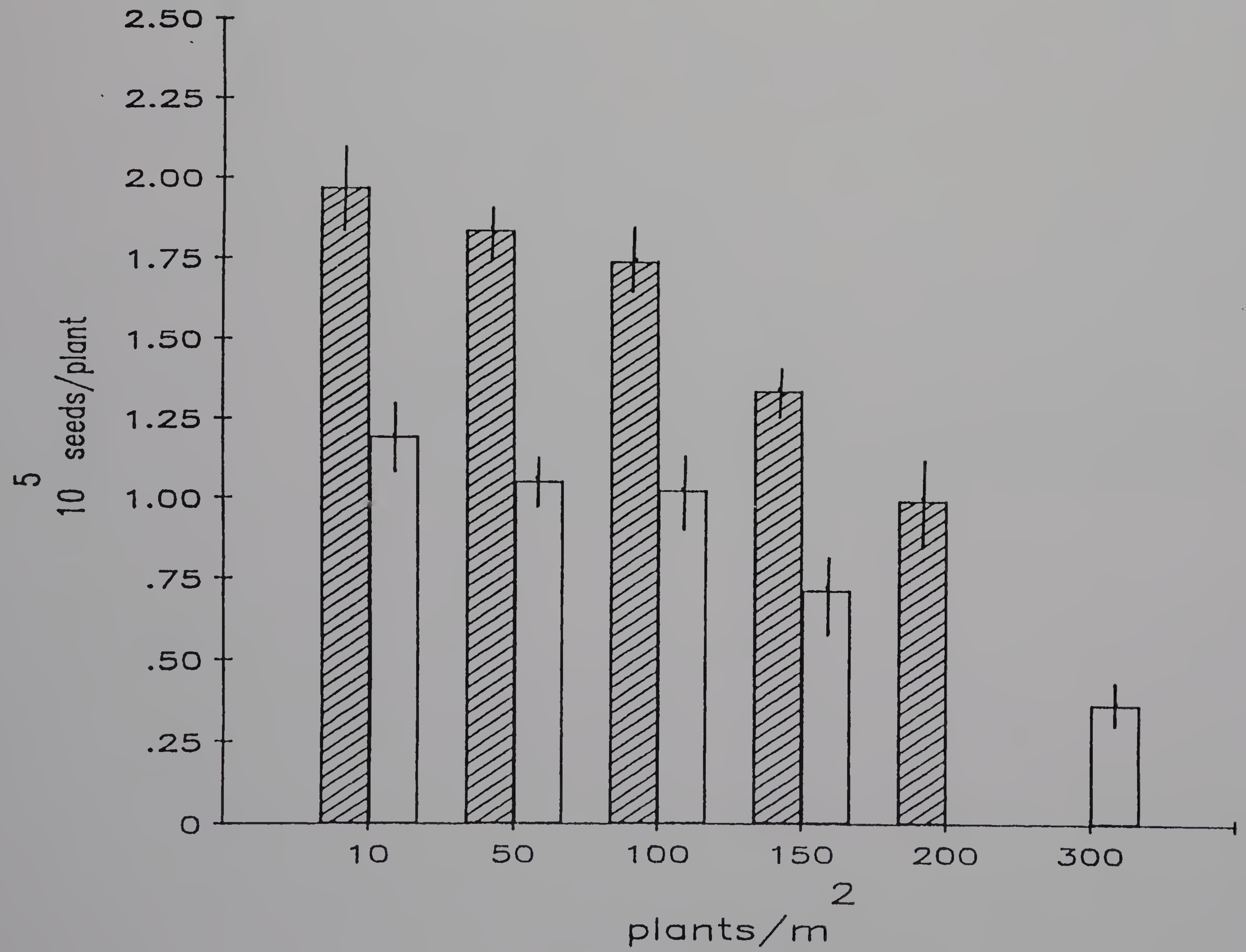

fert.
non-fert.
7 2
10 seeds / m
2.50
2.25
2.00
1.75
1.50
1.25
1.00
.75
.50
.25
0
10
50
100
150
200
300
2
plants/m

in the fertilized plots (Figure 6). In the non-fertilized plots, the maximum amount of seed production/m^2 may not have been reached at the highest density sampled, 300 plants/m^2.

In 1986, the "naturally occurring density" of horse-weed increased to a peak of 5960 plants/m^2 and then de-clined to an average of 587 plants/m^2 at flowering (Fig-ure 7). Total dry weight/plant ranged from 7.31 g/plant at a final density of 400 plants/m^2 to 3.9 g/plant at 750 plants/m^2, but total dry weight/m^2 did not vary signifi-cantly and was not related to initial or final density. Plants in plots with higher densities at flowering produced fewer seeds per plant. The average number of seeds/plant varied from 31,000 at 400 plants/m^2 to 14,000 at 750 plants/m^2, but because of variations in plant density, the total production of seeds/m^2, between 10-12 million, did not vary significantly (data not presented).

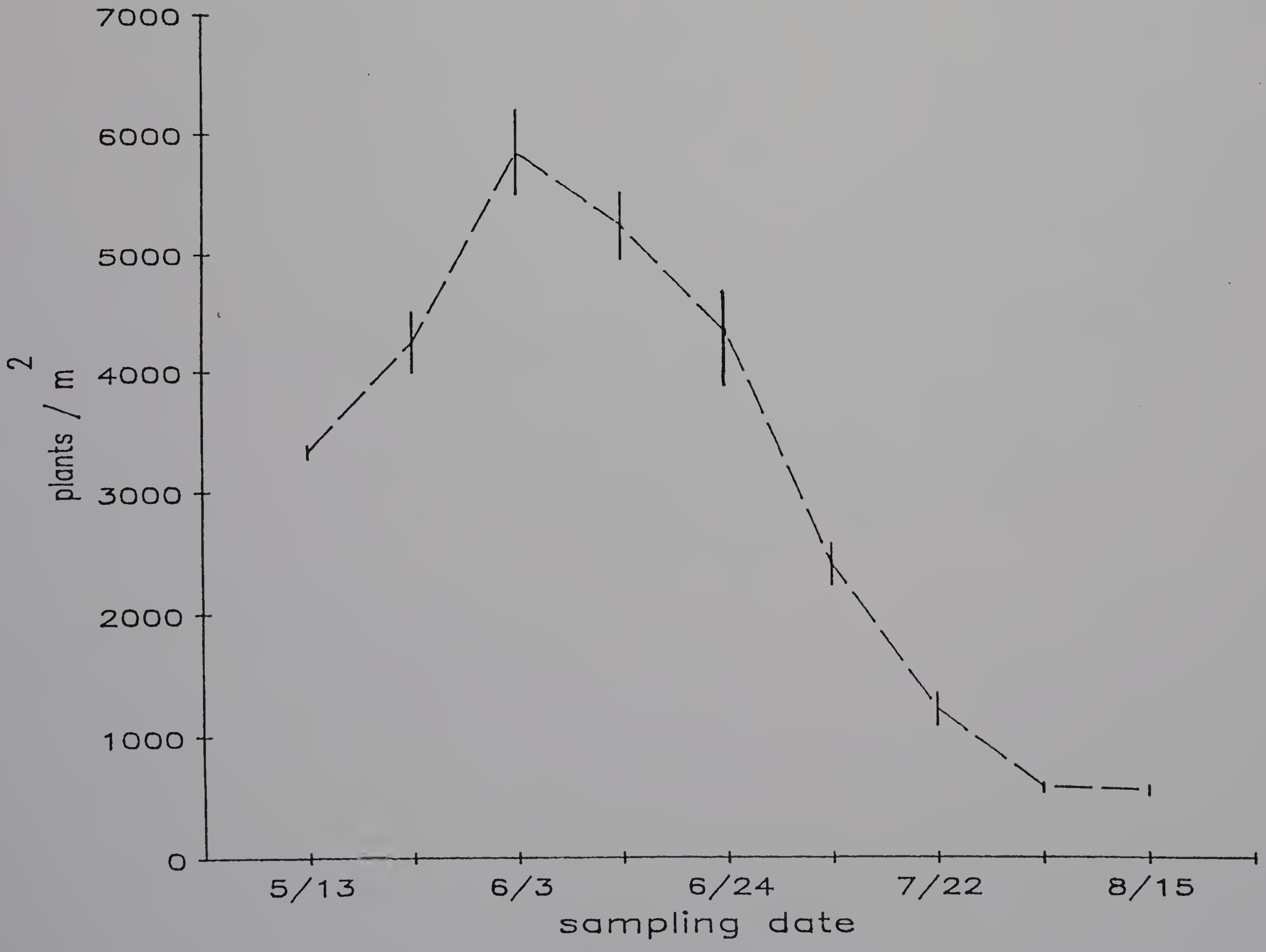
In the thinned plots, individual plant biomass at 400 plants/m^2 was about 25% of individual plant biomass at 100 plants/m^2 but the final total biomass/m^2 did not vary significantly (Figure 8). Seed production/m^2 decreased from 16,000,000 at 100 plants/m^2 to 8,500,500 at 400 plants/m^2 (Figure 9). The percentage of dry weight allo-cated to inflorescences decreased twofold from 27% to

Figure 6. Effects of horseweed density on seed production per plant in fertilized and "non-fertilized" bands in a no-till corn field. Fertilizer was applied during land preparation as a broadcast at the rate of 504 kg/ha of 5-8-12 (N-P-K) and at planting time in bands at the rate of 252 kg/ha of 10-29-10 (N-P-K). Corn plants were removed from sample areas. Bars indicate standard deviations.



fert.
non-fert.
10^5 seeds/plant
2.50
2.25
2.00
1.75
1.50
1.25
1.00
.75
.50
.25
0
10
50
100
150
200
300
plants/m^2

Figure 7. Naturally occurring densities of horseweed in a fallow no-till corn field. Bars indicate standard deviations.



7000
6000
5000
4000
3000
2000
1000
0
plants / m 2
5/13
6/3
6/24
7/22
8/15
sampling date

Figure 8. Effect of horseweed density on total dry weight/m^2.

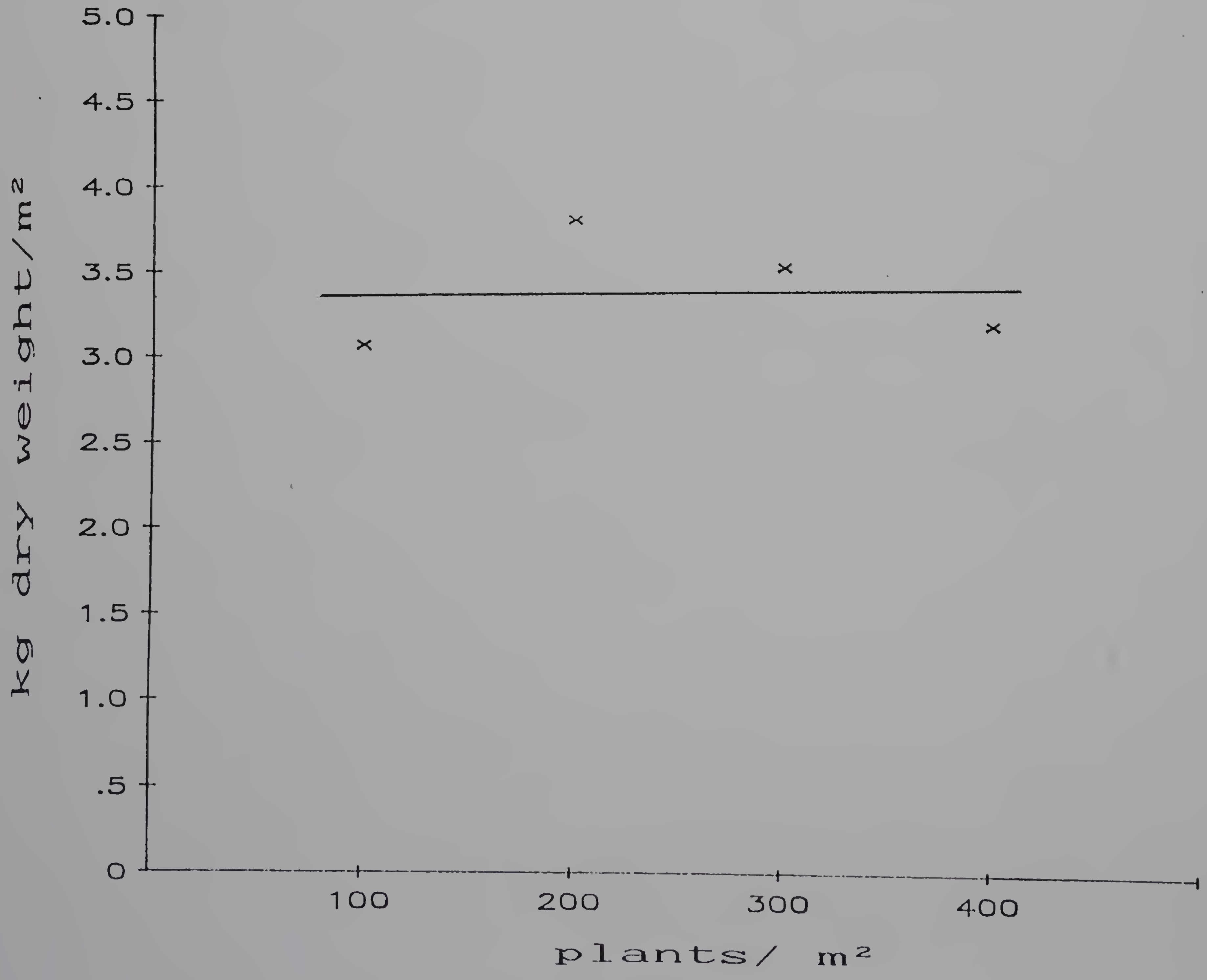
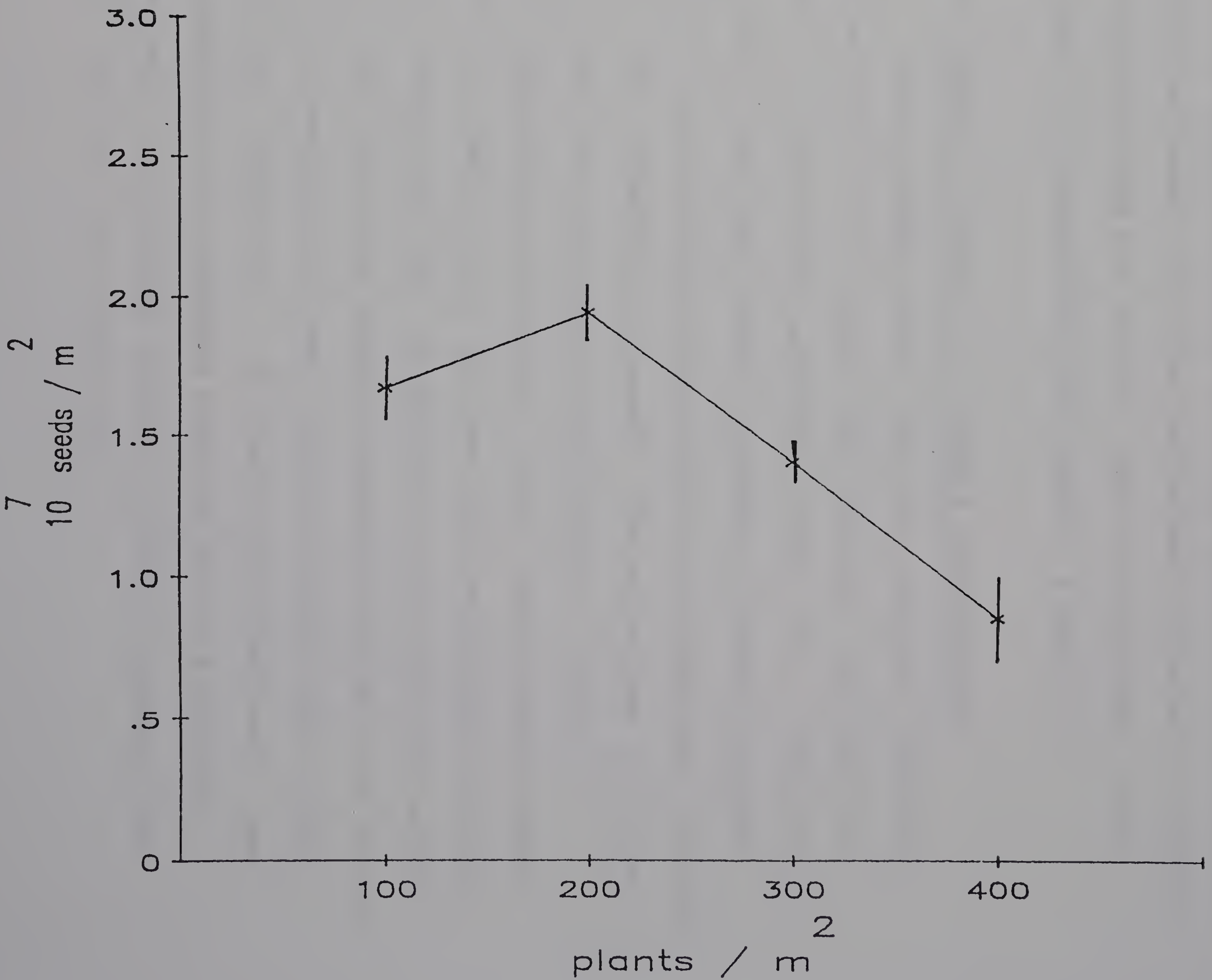

kg dry weight/m²
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
.5
0
100
200
300
400
plants/ m²

Figure 9. Effect of horseweed density on seed production/m^2. Bars indicate standard deviations.


3.0
2.5
2.0
1.5
1.0
.5
0
10^7 seeds / m^2
100
200
300
400
plants / m^2

12% while the percentage allocated to stems increased from 50.7 to 57.8% (Figure 10). Although the percentage of dry weight allocated to living leaves decreased as density increased, the total percentage allocated to leaves increased from 8.5 to 14.3, due to an increase in the amount of accumulated dead leaves (Figure 11).

C. <u>Effects of Shading on Biomass Partitioning</u>

Tn the shaded plots, total dry weight/m^2 increased from 0.44 to 3.53 kg as light intensity increased from 25% to 100% of full sunlight (Figure 12). The percentage of total dry weight allocated to stems decreased while the percentage allocated to inflorescences increased as light intensity increased. The percentage allocated to roots did not change significantly (Figure 13). The percentage allocated to living leaves was the same for all shade levels, but the total percentage allocated to leaves over time, as measured by the total dry weight of dead and living leaves, decreased from 18 to 9% due to less senescence of lower leaves at higher light intensities (Figure 14). As shade levels decreased, seed production/ m^2 increased from 680,000 to 19,000,000 seeds/m^2, and average height of plants increased from 91.7 to 191.7 cm (Figure 16).

Figure 10. Percent of total dry weight of horseweed allocated to stems, roots, and inflorescences after growing for 12 weeks at four densities. Densities were established when plants were in the rosette stage.

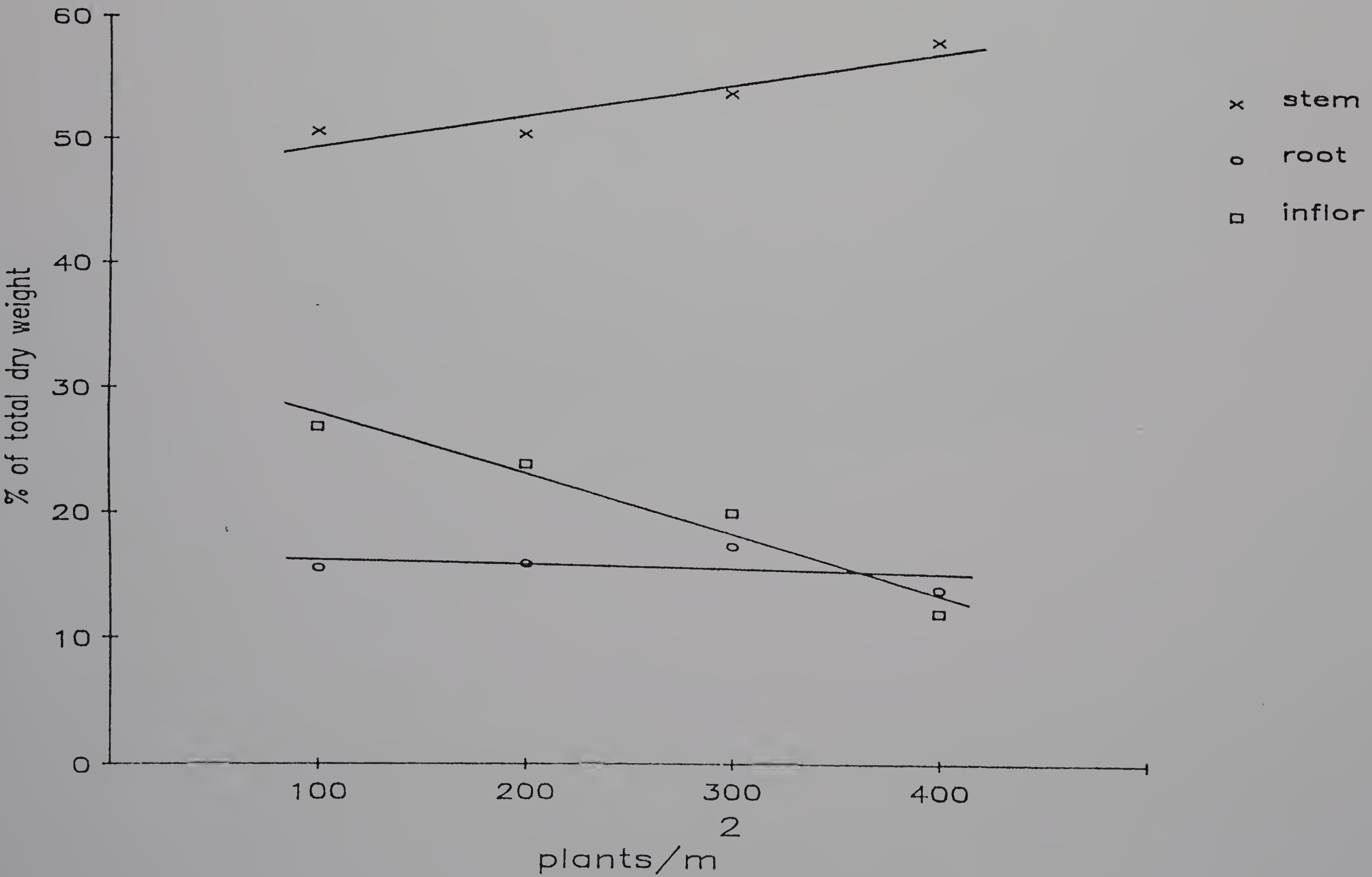
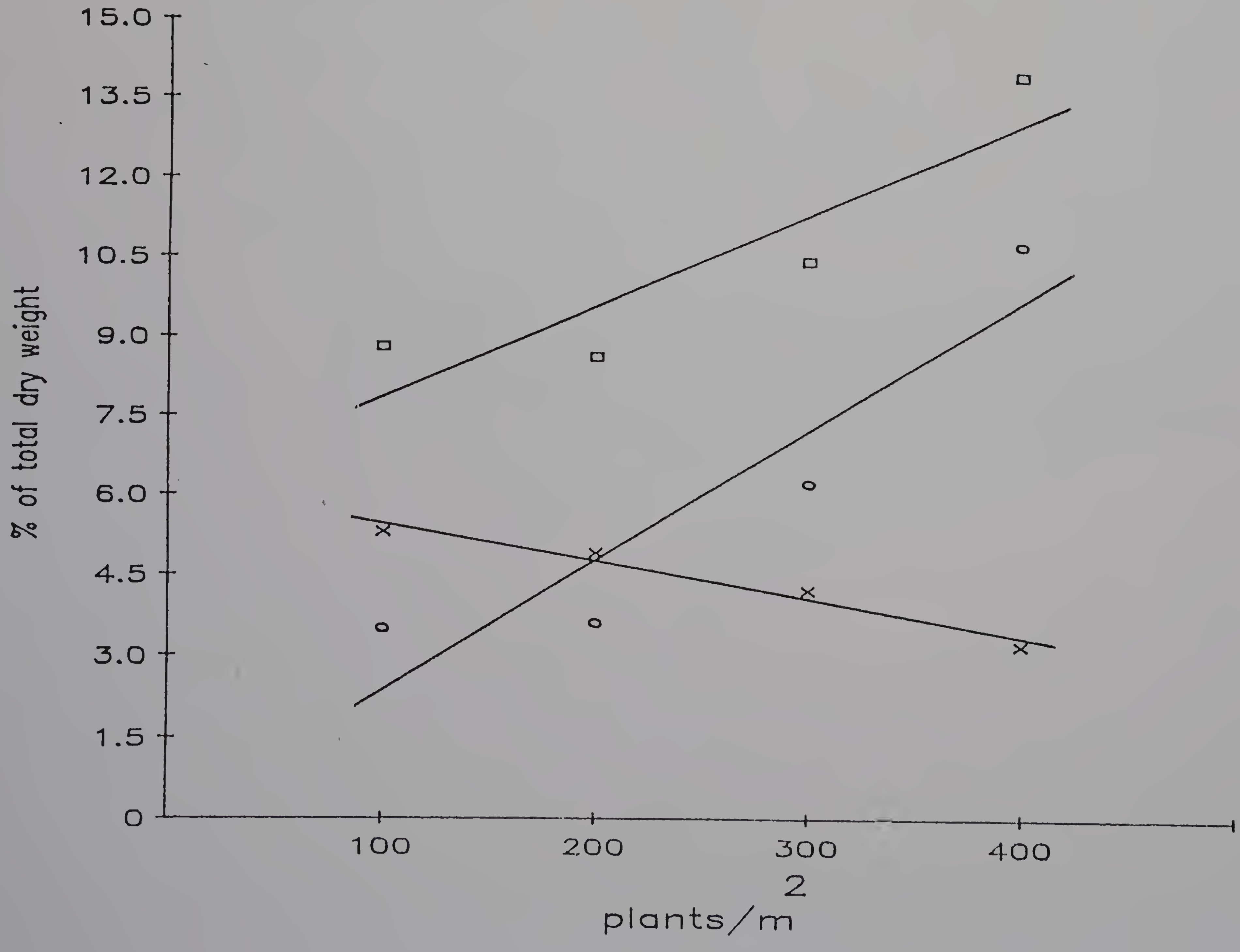

% of total dry weight
60
50
40
30
20
10
0
100
200
300
400
plants/m
2
x stem
o root
□ inflor

Figure 11. Percent of total dry weight of horseweed allocated to live, dead, and total leaves after growing for 12 weeks at four densities. Densities were established while plants were in the rosette stage.



× live
o dead
□ total
% of total dry weight
15.0
13.5
12.0
10.5
9.0
7.5
6.0
4.5
3.0
1.5
0
100
200
300
400
plants/m 2

Figure 12. Effect of shading on horseweed dry weight/m^2. Horseweed density was maintained at 200 plants/m^2. Shade levels were established while plants were in the rosette stage.

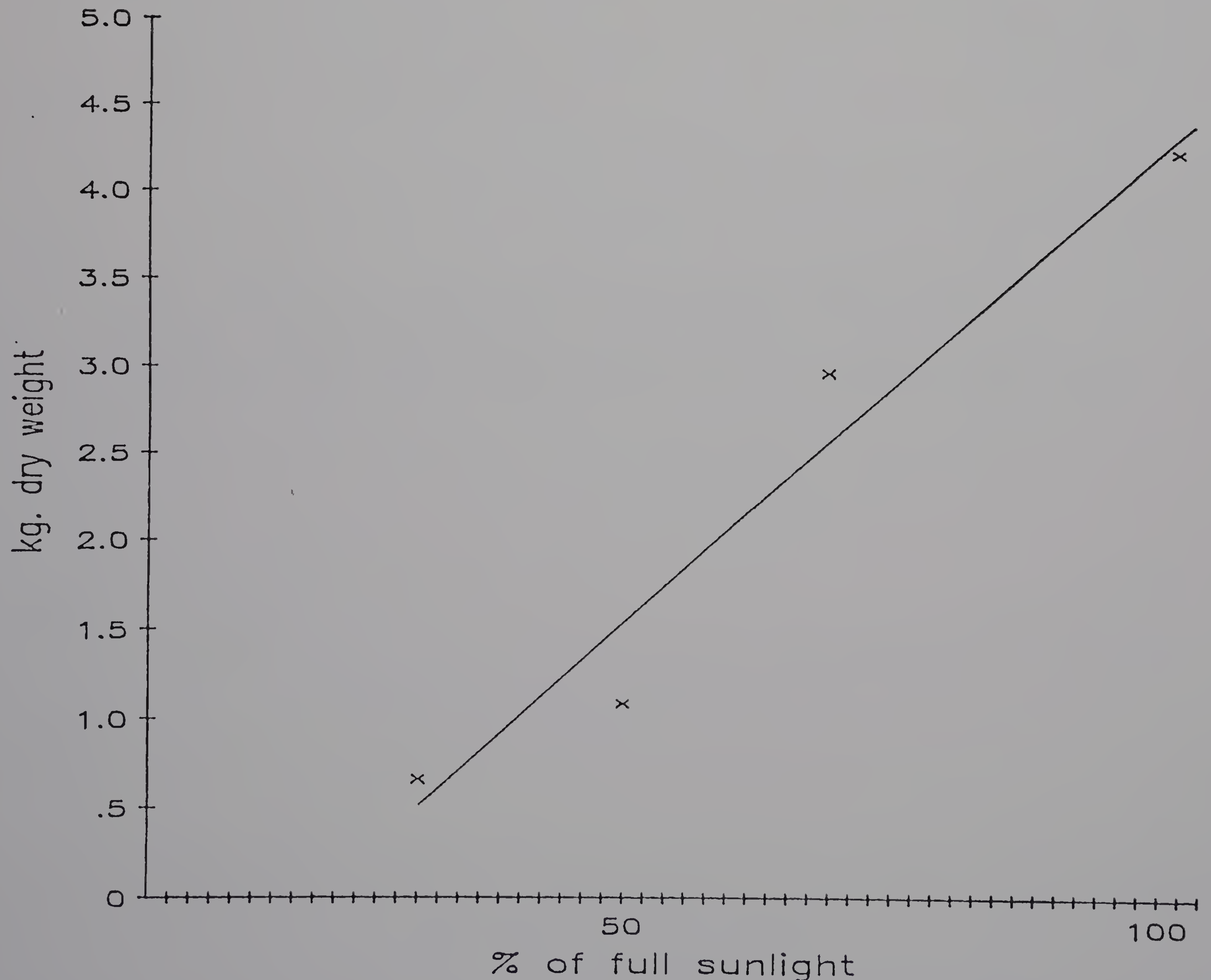
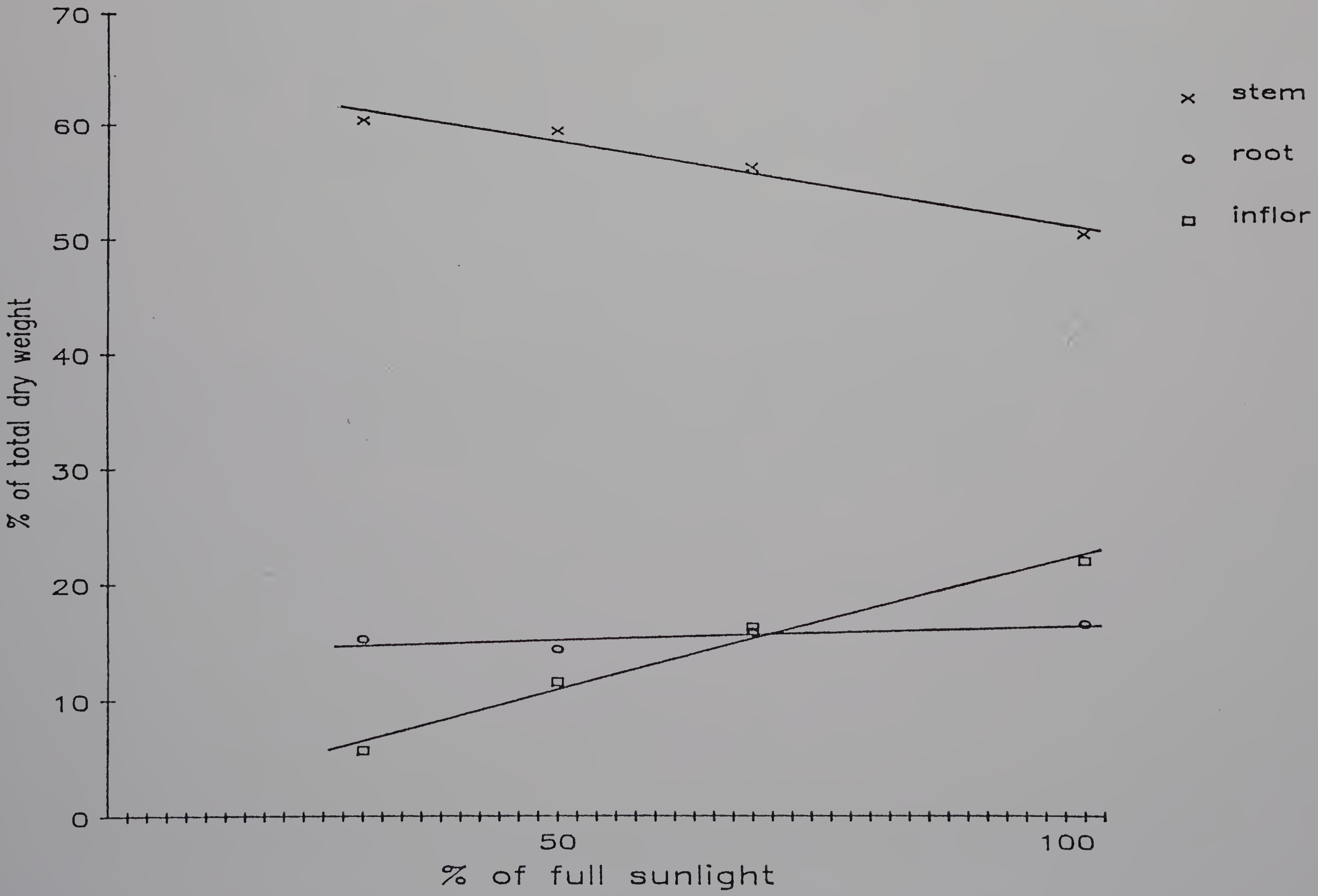
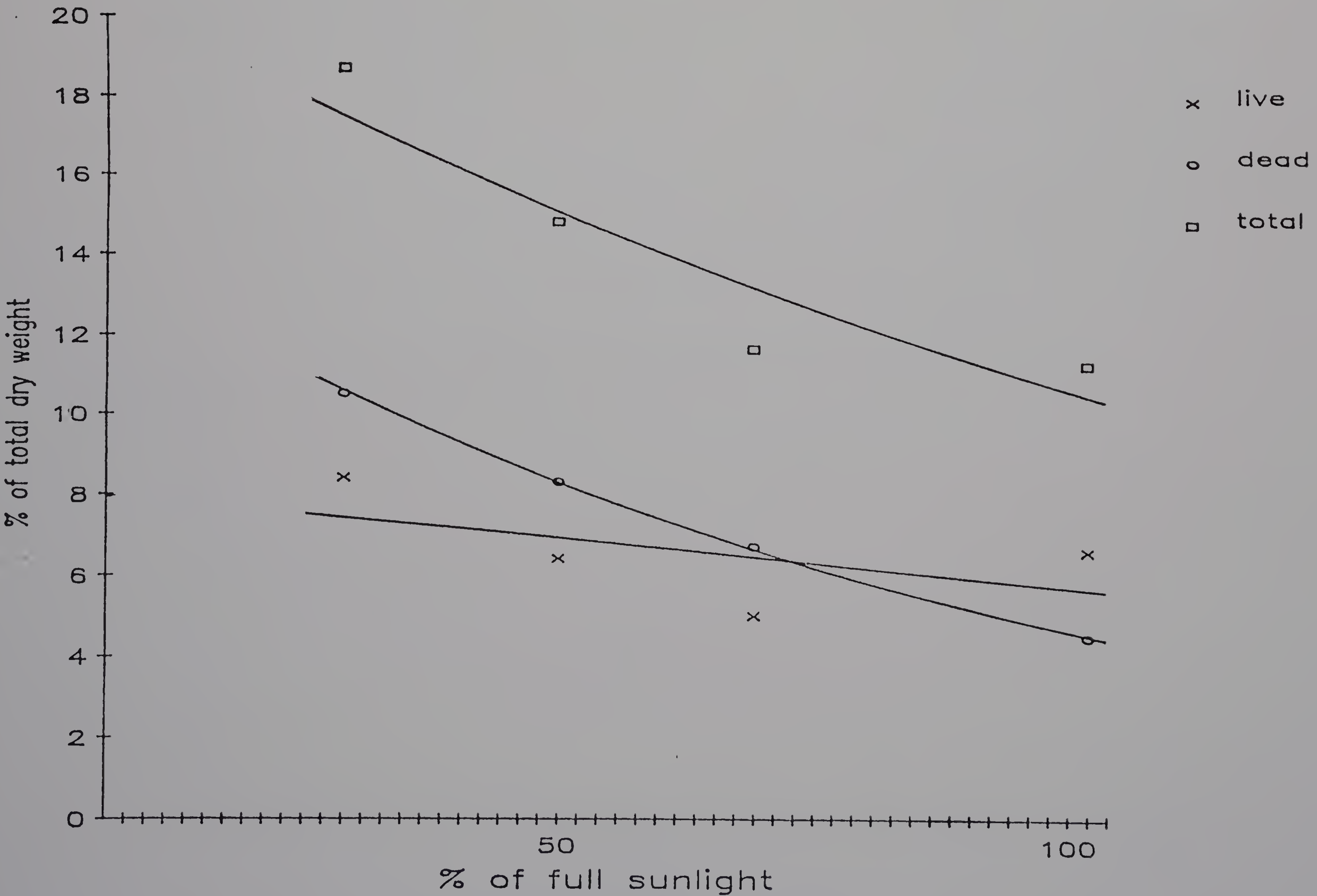

kg. dry weight
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
.5
0
50
100
% of full sunlight

Figure 13. Percent of total dry weight of horseweed allocated to stems, roots, and inflorescences after 10 weeks of shading. Horseweed density was maintained at 200 plants/m^2. Shade levels were established while plants were in the rosette stage.



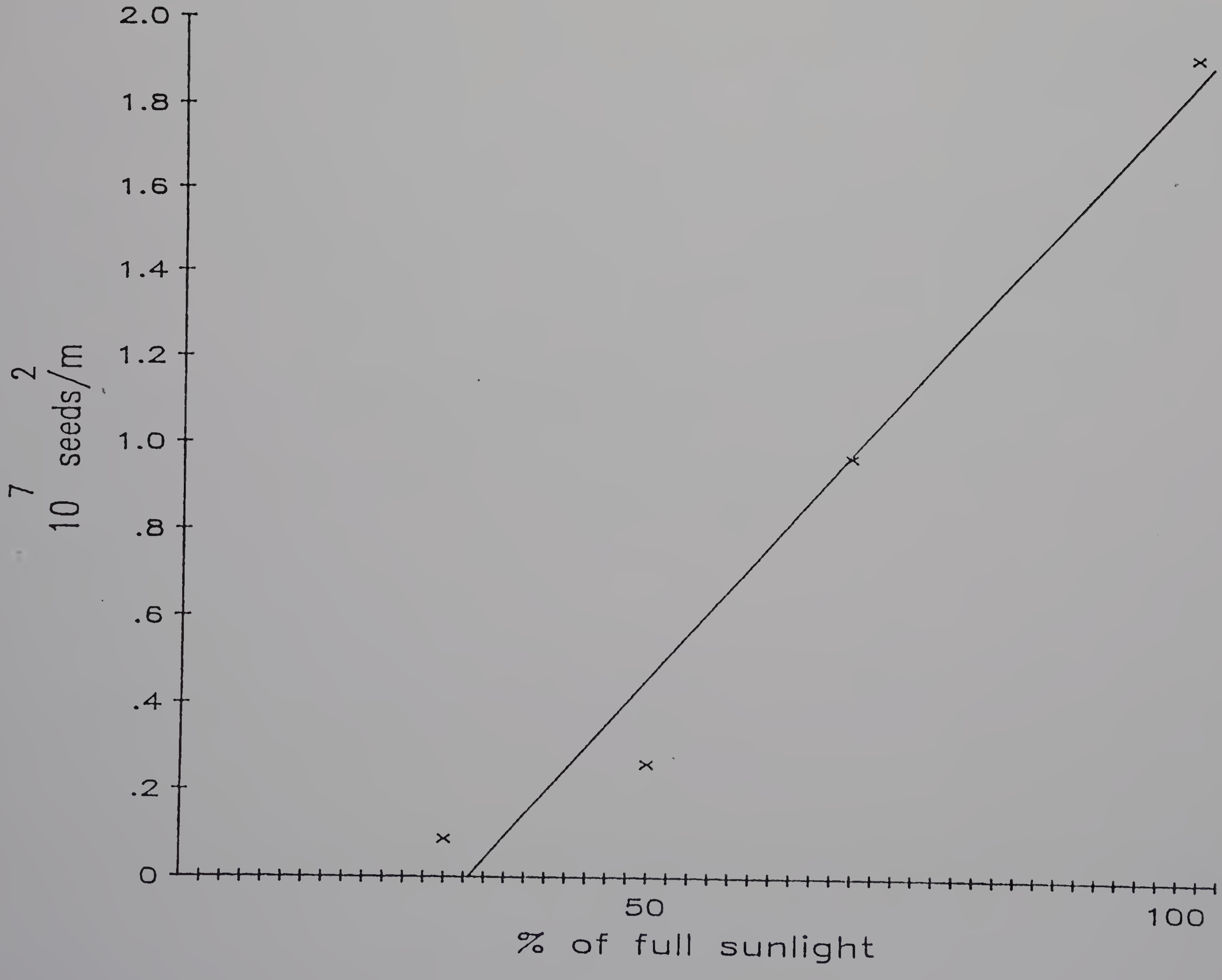
% of total dry weight
70
60
50
40
30
20
10
0
50
100
% of full sunlight
x stem
o root
□ inflor

Figure 14. Percent of total dry weight of horseweed allocated to live, dead, and total leaves after 10 weeks of shading. Horseweed density was maintained at 200 plants/m^2. Shade levels were established while plants were in the rosette stage.



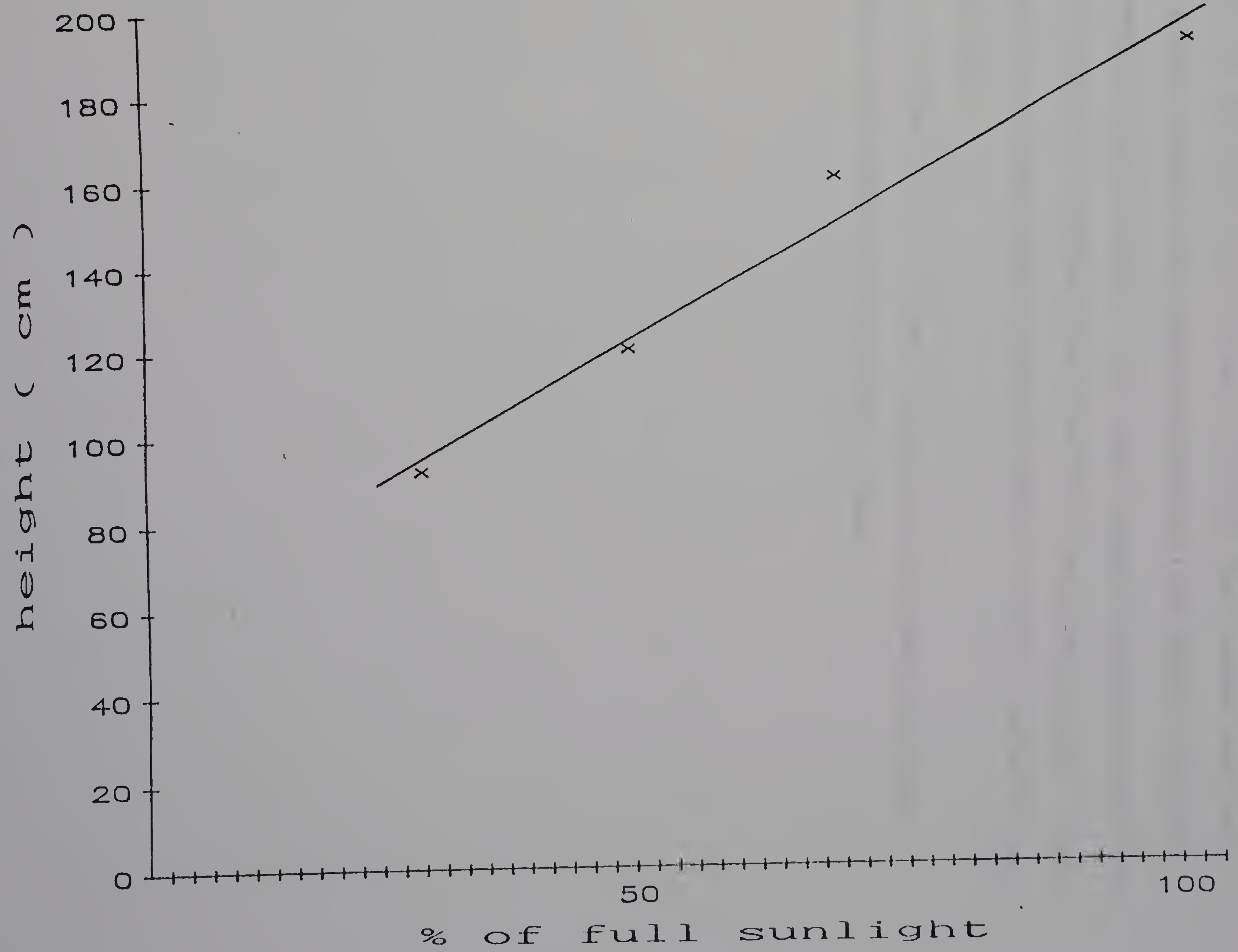
20
18
16
14
12
10
8
6
4
2
0
% of total dry weight
50
100
% of full sunlight
x live
o dead
□ total

Figure 15. Effect of shading on horseweed seed production/m^2.



2.0
1.8
1.6
1.4
1.2
1.0
.8
.6
.4
.2
0
7 2
10 seeds/m
50
100
% of full sunlight

Figure 16. Effect of shading on final height of horseweed.



height (cm)
200
180
160
140
120
100
80
60
40
20
0
50
100
% of full sunlight

D. Genetic Isolation and Autogamous Seed Production

In the greenhouse, flower buds appeared four weeks earlier and the first flowers opened four weeks earlier on plants grown from seeds collected from short, earlier flowering type plants. The stems began elongating earlier but reached a shorter final height than plants grown from seeds collected from the more common, taller, later flowering type.

In the field, flowers covered with gauze produced 75% as many seeds as uncovered flowers.

CHAPTER V

DISCUSSION

A. Effects of Population Density and Shading on Biomass Partitioning

In 1985, horseweed plants growing in the fertilizer bands were already larger and taller than those between bands when densities were established during the second week of June. For this reason, sampling plots were arranged to include only plants growing within or between the fertilizer bands. Before hand thinning, the average density was 251 plants/m^2 in the fertilizer bands and up to 772 plants/m^2 between them. This observation seems to agree with the finding of Yoda et al. (1957) that density dependent mortality is higher in more fertile sites. The addition of fertilizer promotes faster growth and results in fewer, larger plants. However, rates of germination and subsequent mortality were not recorded prior to setting up the present experiment. In 1986, when corn was not planted nor fertilizer applied at the site, seedling density was much higher, over 5000 seedlings/m^2, when densities were established during the first week in June. Densities comparable to early June 1985 were not achieved by self-thinning until late July. In addition to the lack of fertilizer, other factors, including later than normal spring germination, may have contributed to the comparatively late self thinning during this year.

At higher plant densities, intraspecific competition causes density dependent mortality, while at lower densities, individual plants expand to fill more space. therefore, one might expect both total dry weight and seed production per unit ares to remain fairly constant over a wide range of densities due to density dependent mortality and plasticity of growth (Harper, 1977, Weller 1987). But while total dry weight was not significantly affected at the established or the "naturally occurring" densities, this was not the case for seed production at the higher densities.

As expected, plants in the fertilized plots grew taller and had more branches, flowers and seeds than plants in the "non-fertilized" plots. Within each fertilizer treatment, the number of branches and flowers per plant decreased as density increased, but in terms of total seed production per unit area, the increased number of plants per unit area more than compensated for the smaller size of individual inflorescences. As a result, maximum seed production occurres at 150 plants/ m^2 in the fertilized plots, and 300 plants/m^2 in the "non-fertilized" plots.

At the higher densities, the number of seeds/m^2 decreased from a maximum of 2.2×10^7 seeds/m^2 to only 8.5×10^6 at 400 plants/m^2. At 100 plants/m^2, only

1.6 x 10 seeds/m^2 were produced, but apparently this lower seed production was due to the fact that the growth pattern of individual plants was not plastic enough to fill all the available space. Increasing the density from 200 to 400 plants/m^2 resulted in no significant change in total dry weight, but a decrease from 26 to 11% in the percentage of dry weight allocated to inflorescences and a corresponding decrease in seed production per unit area. The higher inflorescence dry weight at lower densities was apparently largely due to more extensive branching as plants filled in the increased space available.

It should be noted that the term "total dry weight" as used here includes dead and senescent leaves. Due to the continual senescence of lower leaves, the amount and percentage of total biomass allocated to leaves during the life cycle of horseweed is considerably greater than the amount or percentage being allocated to living, functioning leaves, especially in the mature plant. Apparently horseweed responds to increasing plant density by accelerating the rate of leaf turnover and increasing the percentage of dry weight allocated to stems. However, the total dry weight per plant decreased such that the increase in the percentage of dry weight allocated to stems did not affect the average height of plants.

The trend toward lower seed production at higher established densities described above was also observed in the self-thinning plots, where the average final density was 570 plants/m^2. Only 2.5 x 10 seeds/m^2, or 10% of the maximum seed production in the hand thinned plots, were produced. In most of these "natural density" plots, three or four large plants accounted for the majority of seeds produced, whereas in the hand thinned plots, plants tended to be more uniform in size.

It is not clear why seed production was lower in self-thinning "natural" densities than in densities estableshed by hand thinning, while at the same time total biomass per unit area was not significantly different. Possibyl, higher seed production/m^2 in hand-thinned is related to the time period during which individual plants are shaded by neighboring plants. In the hand-thinned plots, plants grew essentially without competition for light during their earlier stages of growth, until individuals had grown large enough to shade each other. But in the "naturally occuring" densities, a large proportion of the available space was always used, leading to an earlier occurrance of competition for light than in the hand-thinned plaot. As shorter plants died, the survivors maintained an ascending monolayer of leaves; the lower portions of all surviving plants were always in the shade and did

not produce inflorescence branches. If horseweed plants use materials translocated from leaves for reproductive growth, as suggested by the rapid senescence of all leaves below the inflorescence soon after flowering begins, then continual leaf senescence in response to shading may limit seed production directly.

The pattern of leaf senescence in resopnse to shading may also affect seed production indirectly by limiting branching. Horseweed flowers develop first at the shoot apex and then in successively lower leaf axils, but only in the axils of living leaves. Senescence of leaves begins at the base of the plant and proceeds upward, and is accelerated by shading. When the lower portion of the stem is shaded by surrounding vegetation, the lower leaves and axillary buds die, and the length of the stem that can be used to produce the inflorescence is correspondingly reduced. Therefore, establishing a density of, for example, 500 plants/m^2 early in the plants' life cycle may not decrease seed production as much as allowing plants to reduce their own density to that level over time by mutual shading.

The total dry weight/m^2 in the self-thinned plots, including senescent and dead leaves, was not significantly different from that in the hand thinned plots, but seed

production was greatly reduced because many of these plants died without producing seeds. When considered in combination, the results in the handthinned and self-thinned plots suggest that in fields highly infested with horseweed, where seedling and rosette populations may be as dense as 5000 plants/m^2, eliminating 95% of the seedling population (leaving 250 plants/m^2) could actually result in an increase in seed production unless the surviving horseweed is soon shaded by the crop canopy.

The resopnse of horseweed to shading shows that decreasing light intensity limits overall growth while disproportionately limiting reproductive growth. Although space remained available, plants did not expand to fill all of it at lower light levels. Even a decrease to 66% of full sunlight resulted in a significant reduction in total dry weight, percentage of dry weight allocated to inflorescences, and seed production. At 25% of full sunlight, total dry weight was 12% and seed production was only 4% of that of plants grown in full sunlight. All individuals at all light intensities tested produced some seeds. But it is likely that higher levels of shade, especially during earlier stages of growth and development, could eliminate seed production altogether, because plants would die before flowering, as did many of the smaller plants in the "naturally occurring" densities.

In a greenhouse experiment, Palmblad (1968) found that horseweed seed production was reduced in response to high density because some plants that were shaded by others remained vegetative. While the total reduction in seed production was less than twofold over a 200 fold range of densities, nevertheless this tendency to remain vegetative contradicts the generalization that most anual weeds respond to stress by quickly changing to reproductive growth. Similarly, Grime (1981) also noted that while water stress and mineral nutrient stress caused the annual grass Poa annua L. to allocate more dry weight to reproductive growth, shading caused a decrease in the percentage of dry weight allocated to inflorescences.

The tendency to remain vegetative while shaded by other plants may be advantageous in the early stages of succession in an abandoned field, where an increase in height brings the top of the plant above the surrounding vegetation, but it is useless if the surrounding vegetation remains taller, as in a corn field, or if the growing season is short. Although horseweed can overwinter as a rosette, once the stem has begun to elongate, the exposed shoot does not survive extreme cold, and only rosettes are found in early spring. The longer a plant remains vegetative, the shorter the time available available for seed production becomes.

However, differences in the time of flower initiation were not observed in this experiment. The increased proportion of dry weight allocated to shoot growth corresponded to increased senescence of lower leaves. Although flower initiation apparently occurred at the same time in all shade levels, more of the lower leaves had died on plants growing in less light, so they had fewer viable nodes at which to initiate inflorescence branches. Surprisingly, the increase in proportion of dry weight allocated to stems did not result in an increase in average plant height as shade increased. Instead, although the overall trend was to allocate agreater percentage of total dry weight to stems as shading increased, the total dry weight decreased so much that height also actually decreased as shade level increased.

B. Adaptiveness of Horseweed Life Cycle to No-till Environment

To understand why horseweed persists as a problem weed in no-till crops, it is useful to consider why it is not a problem in conventional-till crops. The number and location of seeds present in the soil and the significance of this number are different in conventional and no-till fields. Weeds that have evolved adaptations for surviving in conventional-till environments usually produce large numbers of seeds, which fall directly to the

ground, and some portion of which are dormant (Taylorson and Hendricks, 1972; Cumming, 1983). Dormancy of some portion of seeds insures that all seeds will not germinate at the same time. The survival value of partial dormancy is that any weed control measures taken at a particular time can not affect those seeds that have not yet germinated. Often such seeds can remain buried in the soil for years and then germinate when they are brought to the surface (Wooley and Stoller, 1978; Taylorson and Hendricks, 1972). The ability to survive in soil does not confer the same advantage in no-till conditions, where seeds sre much less likely to get buried. A more adaptive survival mechanism in this environment might be to germinate as many seeds as possible and thereby cover as much ground as possible in order to prevent other species germinating. This appears to be the germination pattern of horseweed, not because it has quickly developed adaptations to the relatively new environment of no-till fields, but because these newly created conditions closely resemble the natural environment to which it was already adapted.

Another key factor in the persistence of horseweed in no-till sites may be the timing of its germination. Horseweed seeds can germinate either in the fall or in the spring. Fall germinated plants complete their life cycle as winter annuals. They overwinter as rosettes, resume

growing as soon as conditions permit, flower the following summer and die while conditions are still favorable for the germination and early growth of the next generation. Spring plowing and secondary tillage for seed bed preparation effectively eliminate fall and early spring germinated horseweed during its vegetative stage. If seeds buried in the soil are brought to the surface, they may germinate in the spring after plowing and complete their life cycle as summer annuals. However, horseweed grows poorly even in slightly shaded conditions. At 25% of full sunlight, both the total dry weight and the percentage of dry weight allocated to reproductive structures are greatly reduced. Significant reductions occur even at higher light levels. Seedlings that germinate at the same time as a fast growing crop such as corn will have less than 25% of full sunlight available to them soon after germination, and therefore will produce few seeds. Depending on such factors as row spacing and planting density, sunlight may be reduced between 92 and 97% in corn fields (Knake, 1972). It should be noted also that in conventional-till fields, spring germinated horseweed must compete with other spring germinated weeds for light.

Under no-till conditions, on the other hand, horseweed plants that germinate in the fall and perhaps even early in the spring, are sufficiently large and have accumulated

sufficient reserves by late spring to be able to compete successfully with spring germinated weeds, as well as corn and other crops. If a cover crop is planted, horseweed seeds may germinate before planting and may continue to germinate even after the cover crop establishes a clesed canopy, since germination of horseweed is not inhibited by shade. If the cover crop is harvested in the spring, horseweed plants may either be undamaged because they are still in the very short rosette stage, or, if the stems have begun to elongate and are tall enough so that the tops are cut off, they may begin new growth from the axillary buds. If the cover crop is killed by herbicide in the spring, the survival rate of horseweed may depend on the herbicide used. The rosette arrangement of the leaves tends to protect the lower portions of the plant from contact herbicides such as paraquat (1,1'-dimethyl-4,4'-bipyridinium ion. A systemic herbicide such as glyphosate [N-(phosphonomethyl)glycine] is more effective against horseweed than paraquat (Hagood and Davis 1986). The choice of herbicide for residual weed control in no-till management may also affect the survival rate of horseweed. For example, atrazine (6-chloro-N-ethyl-N-(1-methylethyl)-1,3,5-triazine-2,4-diamine] resistant populations of horseweed have been found in fields repeatedly treated with atrazine, which is widely used for pre-emergence weed control in corn (Lehohoczki et al. 1984).

In its more typical habitat, such as abandoned fields or waste areas, horseweed would most likely be replaced in a few years by perennial weed species (Rehger and Bazzaz, 1979; Tremmel and Peterson, 1983). Once these become established, there is very little space for horseweed or any other weed to germinate, and too much shade for seedlings to grow if they did germinate. But in agricultural environments, efforts are continually being made to eradicate any and all weed species present. While the ideal aim of weed control programs is 100% elimination of all weeds, the practical goal is usually the reduction of weed populations to a level that is economically acceptable. A control rate of 80-95% usually reduces weed competition to the economic threshold, the point at which the cost of applying more herbicide would be greater than the benefit obtained by a slight increase in crop yield. In no-till crops, application of herbicides is the primary method of weed control. Both "knockdown" and residual herbicides are applied prior to planting the crop, to kill weeds already present as well as new seedlings as they emerge. In addition to killing seedlings, herbicide applications greatly reduce the lifespan of perennials that may have survived applications of the previous year, thus the perennials are never able to replace horseweed as they would in abandoned or untreated fields. Although the soil is not disturbed, the conditions of plant-free, open soil

are repeatedly recreated in the no-till field. If these conditions are present in the fall when airborne horseweed seeds are being disseminated, the chances of renewing the horseweed population are high.

Like most successful annual weeds, horseweed produces a prodigious number of seeds, as many as 200,000 per plant in well fertilized soil. But unlike the seeds of many common agricultural weeds, which fall to the ground close to the parent plant, horseweed seeds can be transported long distances by air (Rehger and Bazzaz 1979). A single surviving plant may give rise to infestations over a wide area, especially wherever residues are not covering the soil surface.

In no-till fields where crop and weed residues are left in place, probably all weed species are suppressed, and horseweed is no exception. Far fewer plants are able to grow in such residues than on open ground, partly because of the lower temperature in residue covered soil, but mainly because of the physical barrier imposed by the residues (Staniforth and Wiese 1985, Phillips and Phillips 1984). For the most part, weed and crop residues had been routinely removed during harvesting from the site studied. But in certain untreated areas, where corn was so stunted that it was not considered worth harvesting,

weeds and corn were cut down together and residues were left in place. The number of seedlings present before the residues were in place was not counted, but seeds were observed on the soil surface before the corn was harvested. The 80% reduction of horseweed in these areas suggests that leaving residues in place on the soil surface would help suppress horseweed infestations. Perhaps even more importantly, residues delayed spring germination of horseweed by four weeks, and apparently suppressed fall germination altogether. Under these conditions, an early variety of corn may be able to establish a closed canopy before horseweed plants have grown large enough to compete with corn and so impact on corn production.

C. Significance of a Genetically Isolated Subpopulation

It was initially assumed that the horseweed population at the site studied had a more or less uniform distribution if genotypes. Observations in 1985 indicated the possible existence of two distinct types of *Conyza canadensis*. An area approximately 3 x 2 m contained a subpopulation of horseweed that differed in several gross characteristics from plants in the rest of the field. Plants in this subpopulation were shorter, had less extensive branching, fewer and narrower leaves, and fewer flower heads than the more common type. They began flowering ten days earlier than the earliest of the surrounding

individuals, and had set seed before the other type began flowering. Plants grown from seeds collected from the two types of plants had the same characteristics as their parent plant. Since it is likely that a high percentage of horseweeds are produced by self-fertilization, and moreover since the earlier flowering of the shorter type prevents it from crossing with the taller type, these two types may remain largely genetically isolated.

While the presence of a small population of a morphologically distinctive type of horseweed did not affect the results of the rest of the experiments, which involved only the predominant type, it is worthwhile to note its presence, particularly since it is able to reproduce autogamously and remain genetically isolated. But whether or not this type of horseweed would respond any differently to the the treatments used in this work or whether or not any different measures would be required to control it in corn fields has not been studied.

CHAPTER VI

SUMMARY

The persistence of horseweed in no-till corn may be attributed to the maintainance of periodically plant-free, open, undisturbed soil, the very conditions to which horseweed is best adapted. Spring tillage, which kills horseweed while it is still in the vegetative stage in conventional-till corn, is absent in no-till, allowing fall germinated horseweed to compete successfully with spring germinated weeds and corn. Herbicide treatments used for weed control on no-till corn rarely eradicate 100% of the weeds present, but they do suppress the growth of horseweed and other weeds that would replace it otherwise. However, a single surviving plant, which may produce as many as 200,000 airborne seeds, represents a potentially serious infestation in no-till corn fields. Weed and crop residues delay germination and reduce total germination and may be used as part of a control program for horseweed. At the site studied, horseweed exhibited density dependent mortality at naturally occurring densities. Maximum plant densities were higher in less fertile soil. At lower established densities, total dry weight/m² remained constant, but it declined at 100 plants/m² because plants lacked the plasticity to fill all the available space. Seed production/m² declined slightly but

significantly in densities of 300 and 400 plants/m^2, probably because of mutual shading. Higher levels of shading reduced both the total dry weight/m^2 and the percentage of dry weight allocated to seed production. The absence of horseweed from conventional-till corn can be attributed to the interruption of the horseweed winter annual life cycle by spring plowing while the plant is still vegetative, and to the suppression of its growth and seed production in the shade.

Table 1. Statistical Analysis of Dry Weight Partitioning of Horseweed in Response to Population Density

Dependent Variable	Coefficient	Pr F
% live leaf dry weight	linear	0.0041
% dead leaf dry weight	linear	0.0406
% total leaf dry weight	linear	0.0056
% stem dry weight	linear	0.0299
% root dry weight	linear	0.4411
% inflorescence dry weight	linear	0.0321
total dry weight/plant	linear	0.0014
height	linear	0.0010

Table 2. Statistical Analysis of Dry Weight Partitioning of Horseweed in Response to Shade

Dependent Variable	Coefficient	Pr F
% live leaf dry weight	linear	0.0239
% dead leaf dry weight	linear	0.0340
	quadratic	0.0007
% total leaf dry weight	linear	0.0025
	quadratic	0.0197
% stem dry weight	linear	0.0014
% root dry weight	linear	0.0795
% inflorescence dry weight	linear	0.0001
total dry weight/plant	linear	0.0001
height	linear	0.0001

BIBLIOGRAPHY

Abrahamson, W.B. and M.D. Gadgil. 1973. Growth and reproductive effort in goldenrods (Solidago, Compositae). Am. Nat. 107: 651-661.

Bellinder, R.R. and H.P. Wilson. 1983. Comparison of several non-selective herbicides on reduced tillage systems. Proc. Northeast. Weed Sci. Soc. 37: 20-26.

Bewley, J.D. and M. Black. 1978. Physiology and Biochemistry of Seeds in Relation to Germination, Development, and Growth. Springer-Verlag, New York. pp. 34-70.

Bhowmik, P.C., S. Podmayer and E.N. McGlew. 1985. Effects of four tillage systems on herbicide performances in corn production. Proc. Northeast. Weed Sci. Soc. 39: 69.

Cronquist, A. 1980 Vascular Flora of the Southeastern United States. University of North Carolina Press. Chapel Hill, NC. p. 734.

Cumming, B.G. 1963. The dependence of germination on photoperiod, light quality, and temperature in Chenopodium sp. Can. J. Bot. 41: 1211-1220.

Duke, S.O. 1984. Weed Physioligy Vol. 1: Reproduction and Ecophysiology. CRC Press Inc. New York. pp. 49-56.

Fenner, M. 1980. The inhibition of germination of Bidens pilosa seeds by leaf canopy in some natural vegetation types. New Phytol. 84: 95-101.

Gadgil, M.D. and O.T. Solbrig. 1972. The concept of r- and K- selection: evidence from wild flowers and some theoretical considerations. Am. Nat. 106: 14-31.

Gorski, T., K. Gorska and J. Rybicke. 1977. Studies on the germination of seeds under leaf canopy. Flora 166: 249-259.

Grime, J.P. 1981. Plant strategies in shade. in Plants and the Daylight Spectrum. H. Smith, ed. Academic Press, New York. pp. 159-186.

Hancock, J.F., Jr. 1977. the relationship of genetic polymorphism and ecological amplitude in successional species of Erigeron. Bull Torrey Bot. Club 104: 279-281.

Hagood, E.S. and P.H. Davis. 1986. Horseweed control in no-till corn and soybeans. Proc. Northeast. Weed Sci. Soc. 40: 26.

Harper, J.L. 1977. Population Biology of Plants. Academic Press, New York. pp. 62-71.

Hichman, J.C. 1975. Environmental unpredictability and plastic energy allocation strategies in the annual Polygonum canadense (Polygonaceae). J. of Ecol. 63: 689-701.

Hill, T.A. 1977. The Biology of Weeds. Camelot Press Ltd. Southampton, England. pp. 99-112.

Hinkle, M.K. 1983. Problems with conservation tillage J. Soil and Water Cons. 38: 201-206.

Kigel, J.A., S. Gigley and M. Negbi. 1979. Seed germination in Amaranthus retroflexus as affected by the photoperiod and age during flower induction of the parent plants. J. Exp. Bot. 30: 997-1002.

Knake, E.L. 1972. Effect of shade on giant foxtail. Weed Sci. 20: 34-42.

Lehoczki, E., G. Laskay, E. Polos and J. Mikulas. 1984. Resistance to triazine herbicides in horseweed (Conyza canadensis). Weed Sci. 32: 669-675.

MacDonald, C.C. 1927. A study of seed development in three species of Erigeron with a special reference to apogamy. Bull. torrey Bot. Club 55: 479-496.

McCutchen, T.C. and R.M. Hayse 1983. Control of horseweed, cocklebur and smartweed in no-till soybeans. Proc. Southern Weed Sci. Soc. 36: 53.

Noonden, L.D. 1980. Senescence in the whole plant. in Senescence in Plants. K.V. Smith, ed. Crc Press, Boca Raton, FL, pp.45-53.

Palmblad, I.G. 1968. Competition in experimental populations of weeds with emphasis on the regulation of population size. Ecol. 49: 26-34.

Parrish, R.R. and F.A. Bazzaz. 1979. Differences in population niche relationships in early and late successional plant communities. Ecol. 60: 597-610.

Phillips, R.E. and S.H. Phillips. 1984. No Tillage Agriculture Principles and Practices. Van Nostrand and Reinhold Co., New York. pp128-131.

Radesovich, M. and J. Holt. 1984. Weed Ecology: Implications for Vegetational Management. John Wiley and Sons. New York. 295 pp.

Raynal, D.J. and F.A. Bazzaz. 1975. Interference of winter annuals with Ambrosia artemiliifolia in early successional fields. Ecol. 53: 35-49.

Regehr, D.L. and F.A. Bazzaz. 1979. The population dynamics of Erigeron canadensis, a successional winter annual. J. of Ecol. 67: 923-933.

Roberts, M.A. and P.M. Feast. 1973. Emergence and longevity of seeds of annual weeds in cultivated and undisturbed soil. J. of Appl. Ecol. 10: 133-143.

Ross, M.A. and C.A. Lembi. 1985. Applied Weed Science Burgess Publishing Co., Minneapolis. pp. 255-258.

Schmidt, J., D.W. Erdhardt and M. Cheo. 1986. Light dependent dominance and suppression in experimental radish populations. Ecol. 67: 1502-1507.

Smith, H. 1982. Light quality, photoreception, and plant strategy. Ann. Rev. Plant Physiol. 33: 481-518.

Staniforth, D.W. and A.F. Wiese. 1985. Weed biology and its relationship to weed control in limited-tillage systems. in Weed Control in Limited Tillage Systems. A.F. Wiese, ed. Weed Sci. Soc. of Am. Champaign, IL. pp. 15-25.

Taylorson, R.B. and S.B. Hendricks. 1972. Interactions of light and temperature on seed germination. Plant Physiol. 49: 127-134.

Tremmel, D.C. and K.M. Peterson. 1983. Competitive subordination of a Piedmont old field successional dominant by an introduced species. Amer. J. Bot. 70: 1125-1132.

Weller, D.E. 1987. A reevaluation of the -3/2 power rule of plant self-thinning. Ecol. Monogr. 57: 32-43.

Wilson, H.P., R.R. Bellinder and T.E. Hines. 1984. Herbicide programs in no-till soybeans. Proc. Northeast. Weed Sci. Soc. 38: 39.

Wooley, J.T. and E.W. Stoller. 1978. Light penetration and light-induced seed germination in soil. Plant Physiol. 2: 597-600.

Woolhouse, H.W. 1983. Hormonal control of senescence allied to reproduction in plants. in Beltsville Symposia in Agricultural Research 6: Strategies of Plant Reproduction. Allenheld, Osmun and Co. Totowa, NJ. pp.174-186.

Yoda, K. T. Kira H. Ogawa and K. Hozumi. 1957. Self thinning in overcrowded pure stands under cultivated and natural conditions. J. Biol. Osaka Cy. Univ. 14. cited in Harper, J.L. Population Biology of Plants Academic Press, New York. pp. 231-234.