AN ABSTRACT OF THE THESIS OF

Diane Henneberger for the degree of Master of Science in Entomology presented on December 17, 1986.
Title: Adequacy of Hand-Defoliation of Tansy Ragwort (*Senecio jacobaea* L.) as a Simulation of Defoliation by Cinnabar Moth (*Tyria jacobaeae* (L.))

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Peter B. McEvoy

Hand-defoliation was evaluated for its ability to simulate herbivory by cinnabar moth larvae, *Tyria jacobaeae* (L.) (Arctiidae) on the weed tansy ragwort, *Senecio jacobaea* L. (Asteraceae). The evaluation was done on a field population of flowering ragwort, for three different timings (early, middle, and late season) of damage.

In the insect-defoliation treatments third and fourth instar larvae were introduced to plots of ragwort and allowed to consume foliage and flower heads over a 12-day period. In the hand-defoliation treatments leaf laminae were stripped by hand from the petioles, and all floral material was picked off during a single day that corresponded with the end of the insect-defoliation period. Both hand- and insect-defoliation resulted in low (0-20%) survival rates similar to that of undefoliated plants. Larvae sometimes left small amounts of foliage and flower heads on the plants, but these did not affect the regrowth response of the plant. Both damage methods yielded similar effects on the amount of secondary (regrowth) foliage, the timing of reproduction, and the number of secondary capitula (flower heads). There were small but significant differences between the 2 methods in

the initial rates of regrowth, in stem and capitula height, and in biomass of stems. Extending the time period of hand-defoliation resulted in a stem height like that of insect-defoliated plants.

Where simulation of herbivory over a wider range in times of attack is desired, provision must be made for plant parts that escape damage in very early (e.g., basal leaves) and very late (e.g., mature capitula) times of attack. Observation of a natural population of cinnabar moth larvae revealed that the few larvae remaining late in the season may damage regrowth as it appears on some plants; repeated damage to regrowth could also be simulated by hand-defoliation.

Hand-defoliation was judged to be adequate in simulating the effects of cinnabar moth damage on parameters affecting the birth and death rates of ragwort. The tests comparing the defoliation methods were sufficiently sensitive to detect the effect of the timing of damage on the number of secondary capitula and amount of secondary foliage.

Adequacy of Hand-Defoliation of Tansy Ragwort (*Senecio jacobaea* L.) as a Simulation of Defoliation by Cinnabar moth (*Tyria jacobaeae* (L.))

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INTRODUCTION

Studies of the effects of insect herbivory on plants often simulate insect damage by cutting, clipping, punching holes, and inflicting other forms of artificial damage (e.g., Bowling 1978; Lee and Bazzaz 1980; Rockwood 1973). Rarely do such studies evaluate how well artificial methods simulate the effects of herbivores, or indicate how improvements in the simulation could be made. This study tested how well hand-defoliation mimics defoliation and defloration of tansy ragwort, *Senecio jacobaea* L. (Compositae) by cinnabar moth, *Tyria jacobaeae* (L.) (Arctiidae).

Simulated herbivory is easy to use and allows greater control in applying experimental treatments. It can be applied when natural insect populations are low or unpredictable (Capinera and Roltsch 1980). When replication of treatments in time or space is needed, simulated herbivory is often simpler than manipulating natural populations of insects or introducing artificial populations (Hare 1980, Poston et al. 1983). Treatments can be applied uniformly, since the intensity, timing, duration and placement of damage can be specified and controlled, and the amount of material removed can be quantified (Archer and Tieszen 1980). It may also be useful for treatments representing rare or extreme damage levels or for breaching particular portions of a plant's defense (Janzen 1979).

Simulated herbivory differs in a number of ways from the natural damage it attempts to mimic (Hare 1980, Jameson 1963, Kulman 1971, Poston et al. 1976, White

1973). Artificial damage may fail to duplicate the amount of material removed, the distribution of the damage in time or space, or other aspects such as a stimulatory effect of insect saliva (Dyer and Bokhari 1976, Detling and Dyer 1981) or fertilizing effects of frass (Mattson and Addy 1975).

A few experimental studies have compared the responses of plants to both simulated and insect defoliation. Damage to very young soybean plants by Mexican bean beetle, *Epilachna varivestis*, was simulated by both manual defoliation and application of the contact herbicide paraquat; 28 days later there were no significant differences in height or dry weight among plants defoliated by the 3 methods (Mellors et al 1984). Defoliation of blue grama grass *Bouteloua gracilis* by the grasshopper *Melanoplus sanguinipes* resulted in more tillering than when the grass was defoliated by clipping (Dyer and Bokhari 1976). Under conditions of severe defoliation, wheat seedlings defoliated by grasshoppers had lower rates of regrowth than those defoliated by clipping, but under conditions of lighter defoliation that pattern was reversed (Capinera and Roltsch 1980). In those two studies the discrepancies between plant response to grasshopper and artificial damage were tentatively attributed to the the effect of an unidentified factor in the insect saliva. There is evidence that the irregular damage by some lepidopteran larvae to soybean leaves may be better simulated by punching holes in leaves rather than by simply cutting leaflets. Punching holes yielded more realistic net photosynthesis rates of excised leaves than did cutting leaflets across the midrib (Poston et al. 1976). Punching also resulted in more realistic rates of water loss from excised leaves than did cutting off leaflets, possibly because it exposed amounts of cut leaf edge similar to that exposed by insect feeding (Hammond

and Pedigo 1981). On whole plants, however, the defoliation methods produced significant differences in water loss only during the first 16 hours after damage (Ostlie and Pedigo 1984). Thus, the effects of of the various methods on the long-term performance of soybean plants is unclear, even though the intended use of the methods was for fieldwork to estimate soybean yield under different defoliation intensities (Hammond and Pedigo 1982, Higgins et al. 1984).

The study reported here arose as part of an investigation of biological control of ragwort by the cinnabar moth. Ragwort is a biennial or short-lived perennial weed (Harper and Wood 1957). The plant is a native of Europe, and the cinnabar moth was imported from Europe to North America as a biological control agent. The larvae often totally strip ragwort plants of leaves and floral material, but the plant generally compensates by producing new foliage and flowers in the same growing season (Cameron 1935; Poole and Cairns 1940).

In field experiments examining the effects of the timing of defoliation on the regrowth of ragwort, McEvoy (in prep.) and Stimac (1977) defoliated ragwort plants by hand as a simulation of the defoliation by cinnabar moth larvae. By stripping all leaf laminae from the petioles, and removing all the floral material, they achieved a defoliation very similar in appearance to that done by cinnabar moth larvae, and they were able to uniformly defoliate plants on specified dates throughout the season. Regrowth responses such as reproduction and the biomass of regrowth were sensitive to as little as a two week difference in the timing of defoliation.

To determine whether regrowth of ragwort plants defoliated by hand is similar to that of plants defoliated by insects, I introduced populations of cinnabar larvae to field plots of ragwort plants to give

early-, mid-, and late-season defoliations, and defoliated plants by hand at 3 corresponding dates. Two additional treatments of simulated herbivory, in which the damage was extended over longer periods, were done to examine the effects of the duration and frequency of herbivory on the response of plants. I monitored the defoliation of another group of ragwort plants by a naturally occurring population of cinnabar larvae to compare the experience and response of plants undergoing the manipulated defoliations to those undergoing a natural defoliation. The plant responses compared among treatments were survivorship, quantity and timing of reproduction, stem height, height of release of dispersing seed, and biomass of plant parts.

LITERATURE REVIEW

Ragwort

Ragwort, *Senecio jacobaea* L. (Asteraceae) is a pasture weed of Eurasian origin (Harper and Wood 1957). In western North America it now ranges from northern California to British Columbia; the first record in North America was in 1913 from British Columbia (Isaacson 1971). The plant is toxic to cattle and horses because of pyrrolizidine alkaloids in its foliage and flowers (Muth 1968; Cheeke 1979). The cinnabar moth, *Tyria jacobaeae* (Arctiidae) was brought from France as a biological control agent and released in northern California in 1959 (Hawkes 1968) and in Oregon in 1960 (Isaacson 1971).

Ragwort is usually a biennial but may also behave as a short-lived perennial, particularly when damaged. After germination of seeds in the fall or spring the plant develops a low, vegetative rosette. The plant generally bolts and flowers in early summer of its second year but may remain a rosette for several years until it reaches the size required for bolting (van der Meijden and van der Waals-Kooi 1979). The bolting plant produces one to several flowering stalks; the stem branches toward the top to give a flat-topped corymb of yellow flower heads (capitula) (Poole and Cairns 1940). The number of capitula per plant varies widely (69-2489 capitula per plant), depending on growing conditions and number of flowering stalks (Cameron 1935). Central and marginal florets of the capitula yield fruits that differ in morphology, dispersal, dormancy, and germination characteristics (McEvoy 1984).

Ragwort can survive and regenerate after defoliation in a variety of ways (Cameron 1935; Poole and Cairns 1940). A plant prevented from flowering may become a

perennial and flower the following year. Alternatively, regrowth shoots from the root crown or from surviving parts of the primary shoot may regrow a smaller secondary crop of leaves and flowers in the same season as defoliation, drawing on carbohydrates stored in the roots (Otzen 1971). Plants commonly die after flowering, but Islam and Crawley (1983) observed a population in which more than half of the flowering plants, both defoliated and non-defoliated, survived the following winter. Small vegetative plants may regenerate from root buds, particularly on damaged rosettes (Poole and Cairns 1940; Harper and Wood 1957; Dempster and Lakhani 1979).

The response to defoliation varies with plant size, timing of damage, soil and climatic conditions, site, and other variables. Islam and Crawley (1983) found that large plants (>30 cm rosette diameter) produced four times as many seeds as did small plants (<20 cm rosette diameter) after complete defoliation. In that study the timing of the damage had little effect on the response of the plant, but in Oregon defoliation of plants at dates from May through August resulted in plant regrowth that declined steadily with delay in the defoliation date (McEvoy in prep). Cameron (1935) noted that cutting plants in an early flowering stage killed far fewer than did cutting after the first seed had set. In Oregon, the capacity of ragwort plants to compensate with regrowth following defoliation is positively correlated with the amount of moisture available to plants after defoliation (Cox and McEvoy 1983), and at Weeting Heath, England, Dempster and Lakhani (1979) found a positive correlation between the summer/autumn rainfall and the number of regenerative rosettes from rootbuds the following season. In that Weeting Heath population the lack of regrowth secondary shoots was attributed to the poor soil quality and small plant size (Dempster 1971). In Nova Scotia

early frosts may kill defoliated plants while they are still in a frost-sensitive stage, while milder conditions in British Columbia allow better regrowth and survival (Harris et al. 1976).

Cinnabar moth

The biology of the cinnabar is reviewed by Dempster (1982). The univoltine moths emerge in late spring from the overwintering pupae, mate, and lay eggs in clusters on the underside of basal leaves of the ragwort plants. The number of eggs per cluster varies with the year and population, averaging 30 to 40 (Dempster 1982, Isaacson 1973). Eggs hatch after about two weeks in the field. First instar larvae remain together on the underside of the leaf on which they hatched, and feed by skeletonizing that leaf. Later instars move to the top of the plant and consume the young leaves and floral material. Larvae disperse to other plants as the host plant is depleted but may leave a plant before all the foliage and flowers are removed (Isaacson 1971, van der Meijden 1976). Larvae frequently leave the plant to moult on surrounding vegetation (Dempster 1982). Each larva consumes nearly .45 g dry mass of plant material over its lifetime, and about 95% of that consumption occurs in the fourth and fifth instars (Isaacson 1971, Islam and Crawley 1983). The total larval period takes about a month.

Complete defoliation of ragwort plants by cinnabar larvae occurs in both native populations in Europe (England: Cameron 1935, Dempster 1971, Dempster and Lakhani 1979; Netherlands: van der Meijden 1971) and in introduced populations in Canada (Harris et al. 1975, Harris et al. 1976), California (Hawkes 1968, 1973), and Oregon (Isaacson 1973, Stimac 1977).

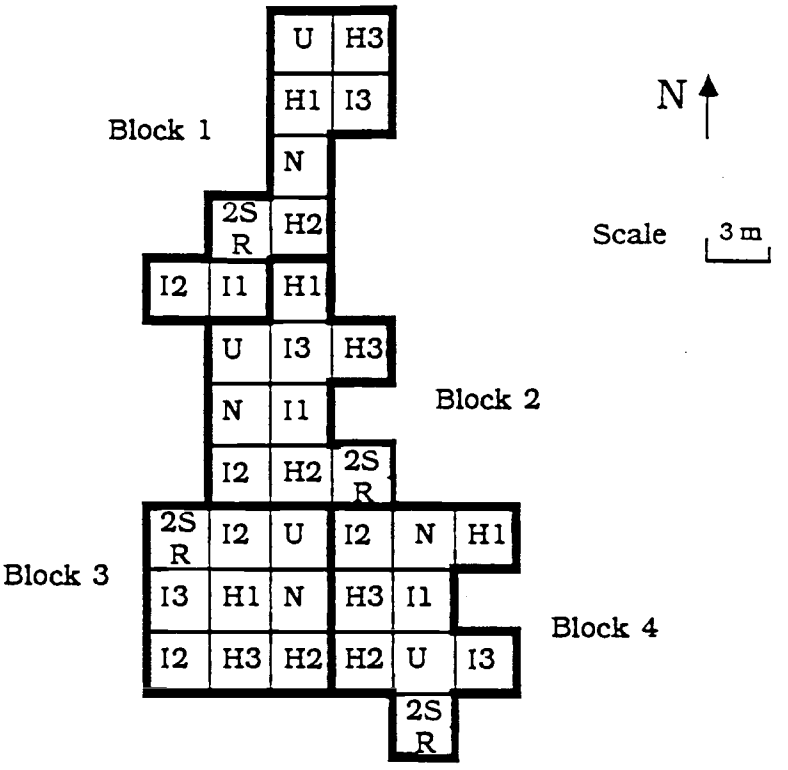
METHODS

Study area

The study was conducted in a weedy field on clay loam soil in the Wilson Game Farm, 10 km north of Corvallis in the Willamette Valley, Oregon. The area receives an average annual rainfall of 108.6 cm, with 76% falling during the 6 months from October to March, and 3% during the months of summer drought, July and August (Crane 1982). The temperature regime is characterized by moderate winter temperatures and hot summers, with summer maxima generally exceeding 38 C. The experimental area, a 40 x 25 m patch of *Senecio jacobaea*, *Cirsium arvense*, *Daucus carota*, *Vicia cracca* and other herbaceous plants, was surrounded by blackberry (*Rubus discolor*) and grasses. Ragwort was present at an average density of 7 flowering plants m^{-2}, 34 large (> 5 cm diameter) vegetative plants m^{-2}, and an undetermined number of small (< 5 cm diameter) vegetative plants. The cinnabar moth had defoliated much of the ragwort in the field the previous year (1979). Ragwort was rarely damaged by other herbivores, and other insects introduced into Oregon for biological control of ragwort (the ragwort flea beetle, *Longitarsus jacobaeae* (Waterhouse), and the ragwort seed fly, *Hylemya seneciella* (Meade)) were not observed at the site.

Treatments

The ragwort patch was gridded into 36 plots, each measuring 3 x 3 m, and each treatment was assigned to 4 plots in a randomized block design (Fig. 1). Blocking was based on a north-south gradient of plant height. In each plot, about 40 bolting, single-stemmed ragwort plants of medium height (25-55 cm in early June) were tagged with



Key to treatments

U	Undefoliated; protected from herbivory
I1	Insect-1; insect-defoliation, June 20-July 2
I2	Insect-2; insect-defoliation, July 4-July 15
I3	Insect-3; insect-defoliation, July 18-July 30
H1	Hand-1; hand-defoliation, July 2
H2	Hand-2; hand-defoliation, July 15
H3	Hand-3; hand-defoliation, July 30
2S	2-Stage hand-defoliation, July 9 and 15
R	Repeated hand-defoliation, July 9, 15, and 30. (This treatment was added to the study in mid-season, by re-defoliating a subset of plants in the 2-stage hand-defoliation treatment.)
N	Natural insect-defoliation; defoliation by resident moth population

Figure 1. Layout of field plots.

aluminum tags. Eggs and larva from the resident population of cinnabar moths were removed daily by hand from all but 4 of the plots. The following treatments were applied to the plots.

1) Protected from herbivory. I protected plants for the entire season by removing larvae by hand, in order to follow the development of undamaged plants,

2-4) Defoliation by introduced cinnabar moth larvae. I introduced cinnabar moth larvae at different times (June 20, July 4, or July 18) to achieve early-, mid- or late-season defoliations of plants (treatment names abbreviated as Insect-1, Insect-2, Insect-3). Each plot was fenced with 18 cm high aluminum lawn edging sunk about 2.5 cm into the ground with the exposed portion coated with a band of stickum. Leaf laminae on untagged ragwort plants were stripped from their petioles to eliminate alternative food for the larvae. The number of larvae to introduce and the duration of the feeding period were determined from previous field observations and lab feeding tests (Isaacson 1971, Pajutee 1980). I introduced late-third and early-fourth instar larvae, placing thirty larvae on each plant, and maintaining numbers of 10-15 larvae per plant after the first several days. I added or redistributed larvae to encourage the uniform and complete defoliation of all plants. Each defoliation period lasted 12 days, after which any remaining larvae were removed and the plants allowed to regrow undisturbed.

5-7) Defoliation by simulated herbivory. Early-, mid-, and late-season simulated herbivory treatments were timed to coincide with the end date of each of the insect-defoliation periods (treatment names abbreviated as Hand-1, Hand-2, Hand-3). On July 2, July 15 or July 30, plants in 4 plots were completely defoliated by stripping leaf laminae from the petioles, and removing all floral

material, as was done by McEvoy (in prep). Plants were then allowed to regrow undisturbed.

The six treatments described thus made up a 2-factor set, with 2 methods of defoliation (simulated and insect), and 3 timings of defoliation (early-, mid- and late-season).

8) Defoliation by two-stage simulated herbivory. The older cinnabar larvae usually consume the floral material and small leaves at the top of the ragwort plant and then feed on the lower leaves. To approximate this pattern, I hand-defoliated plants in two stages, removing all the floral material and the leaves from the upper 1/3 of each plant on July 9, then removing the remainder on July 15. I compared the responses of these plants with that of plants in the second insect-defoliation (July 4 to July 16) and the second hand-defoliation (July 16) described above.

9) Defoliation by repeated simulated herbivory. If plants regenerate new growth rapidly after defoliation, that regrowth may be at risk to consumption or damage by larvae still present. To test the effect of repeated defoliation, I randomly selected 48 plants which had already received the 2-stage hand-defoliation treatment, and on July 30 removed any regrowth produced in the previous 2 weeks.

10) Defoliation by resident cinnabar larvae. In 4 plots the cinnabar larvae hatching from eggs laid naturally within the plots were allowed to develop and defoliate the ragwort plants (treatment name abbreviated as Natural). Each plot was closed to migration by a fence as described earlier, but there was no other manipulation of the insect or plant population.

I estimated the approximate time of defoliation by recording at 2-week intervals for each tagged plant the number of hatched and unhatched cinnabar egg masses, the

number and instar of larvae, and degree of defoliation. The defoliation classes were (a) No defoliation (no sign of larval feeding on plant); (b) Light defoliation (less than 10% of plant defoliated); (c) Moderate defoliation (about 10-50% of the foliage and floral material consumed); (d) Heavy defoliation (50-90% of foliage and capitula consumed); (e) Total defoliation (95% or more of the foliage and capitula consumed). Lightly defoliated plants generally had one or two lower leaves skeletonized by young larvae, or less than 20% of the small upper leaves and capitula removed by older larvae. Moderate defoliation could include plants with all capitula consumed, if the majority of foliage remained. Heavily defoliated plants generally had lost virtually all their capitula, plus upper and middle leaves, but had some lower leaves remaining. The classes "heavy" and "total" were combined for analysis.

Sampling and measurements

Destructive samples were taken of the plants protected from herbivory (undefoliated plants) at 2-week intervals from June to October. Defoliated plants were sampled 4 weeks post-defoliation (July 30 for early-season defoliations, August 13 for mid-season defoliations, and August 27 for late-season defoliation; August 13 was chosen as the first sample for the natural defoliation plants). This staggered harvest schedule was then adjusted so that all treatments shared 3 late summer and autumn samples: August 27, September 24, and October 22. Additional information on the early regeneration of plants was gathered by sampling 3 treatments (Hand-1, Hand-2, and Insect-2) at 2 weeks post-defoliation. Samples of all treatments were also taken on December 10 and March 15 to evaluate plant survival.

Five plants were sampled on each date from each of the 4 plots for each treatment. Plants were excavated, brought back to the lab, and the soil was carefully washed off of the roots. Plants were classified as live or dead after examining their roots and cutting open the root crown. Floral capitula were counted and classified by the developmental stage described by McEvoy (in prep.): 3 immature stages (primordia, buds, flowers) and 2 mature stages (fruits, and dispersed capitula). The empty bracts of heads remain on the plant after achenes have dispersed. Primordia were subdivided into living and dead categories, since some died before further development. A developmental index was assigned each plant, equal to the mean stage of the capitula, where primordia = 1, bud = 2, flower = 3, fruit = 4, and dispersed = 5. The approximate height of the capitula above the ground was obtained by measuring the height of each axillary stem bearing capitula. For biomass measurements, plants were separated to roots, root crown, stem, axillary stems, capitula, and live and dead leaves, and dried for 72 hr at 70oC.

Analysis

I graphed the seasonal variation in most variables of plant response, and then compared treatments by ANOVA at 1 or 2 points in the trajectory (4 weeks post-defoliation or the end of the season). The measurements of the 5 plants subsampled from each plot were averaged to give a single value for each of the 4 replicate plots, which were the experimental units to which the treatments were applied. Transformations (logarithmic or arcsine) needed to stabilize the variances (F-max test, Sokal and Rohlf 1981) prior to ANOVA were done to those plot means.

The ANOVA had treatments and blocks as factors. Orthogonal contrasts within the set of 6 hand- and insect-

defoliation treatments were then used to test the effects of method of defoliation (hand or insect), date of defoliation (early, middle or late), and the interaction of method x date. I used the T-method (Tukey's honestly significant difference method) for unplanned comparisons (Sokal and Rohlf 1981) for test for differences among all treatments ($p < .05$).

The repeated hand-defoliation treatment and the natural insect-defoliation treatment were excluded from most of the ANOVA's and were compared non-statistically with the other treatments.

RESULTS

Timing of herbivory in relation to plant growth and development

Plants were bolting and flowering (Fig. 2) when defoliation occurred. In the 6 weeks spanning herbivory treatments, the flowering shoots elongated (Fig. 2D), capitula (flower heads) formed and bloomed (Fig. 2A), and biomass of live leaves declined (Fig. 2B) as the basal rosette leaves died.

Plant survivorship

Survivorship curves differed little among treatments (Fig. 3). Plants began dying in late August; 79% were dead by October 22, and most (94%) had died by December 10. The Hand-3 and 2-stage defoliation treatments each had 4/20 (20%) plants alive on December 10, indicating that plants possibly lived longer in those treatments. Of 88 plants recovered the following spring, only 1 (1.1%) (in the natural defoliation treatment) survived the winter (Table 1).

Plant reproduction

Primary capitula escaping herbivory. Hand-defoliation removed all capitula from the plants, whereas insect-defoliation sometimes left a portion of the capitula undamaged, or damaged but not consumed. The proportion of primary capitula escaping herbivory increased with delay in the timing of herbivory. Larvae consumed all of the capitula present during the first insect-defoliation and left an average of 0.8 and 5.6 capitula per plant in the second and third defoliation

Figure 2. Growth of ragwort plants protected from herbivory, in relation to the timing of defoliation treatments. All values are mean ± SE; n = 4 plots of 5 plants each. A) Total number of capitula per plant, with the proportion in stages: primordia (P), bud (B), flower (Fl), fruit (Fr), dispersed (Ds), and dead primordia (Dd). B) Biomass (g dry weight) per plant of live leaves and capitula. C) Biomass (g dry weight) per plant of main stem, axillary stems, and roots plus root crown. D) Main stem height (cm) and total height of plant (cm). E) Timing of the 3 insect-defoliation (12 day) treatments and the 3 hand-defoliation (1 day) treatments.

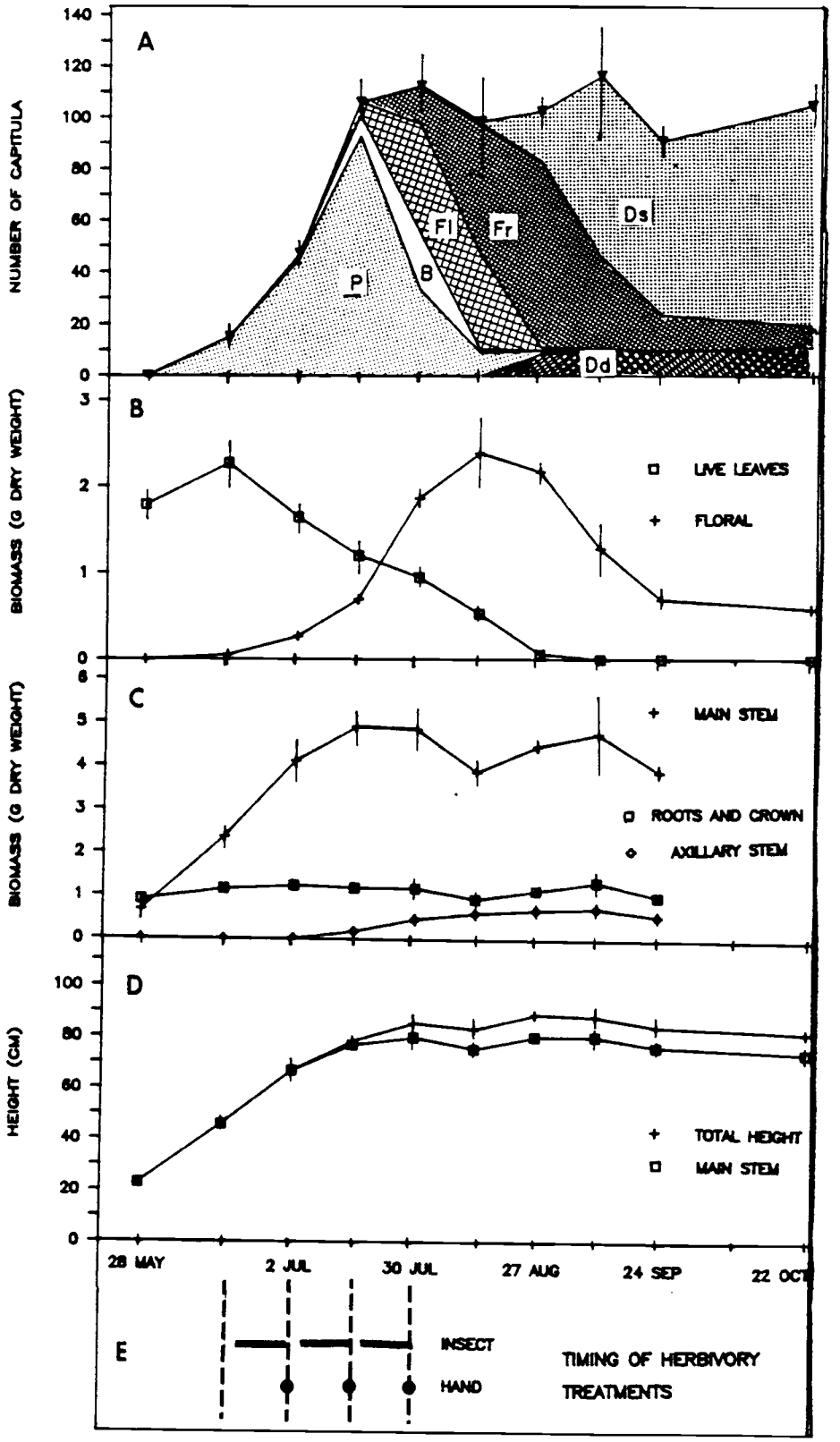

A
NUMBER OF CAPITULA
P
B
Fl
Fr
Ds
Dd
B
BIOMASS (G DRY WEIGHT)
LIVE LEAVES
FLORAL
C
BIOMASS (G DRY WEIGHT)
MAIN STEM
ROOTS AND CROWN
AXILLARY STEM
D
HEIGHT (CM)
TOTAL HEIGHT
MAIN STEM
28 MAY
2 JUL
30 JUL
27 AUG
24 SEP
22 OCT
E
INSECT
HAND
TIMING OF HERBIVORY TREATMENTS

Figure 2

Figure 3. Survivorship curves of ragwort subjected to various defoliation treatments. Points represent the number of live plants in each of four 5-plant samples at each date; curves are fit to the means of the 4 samples.

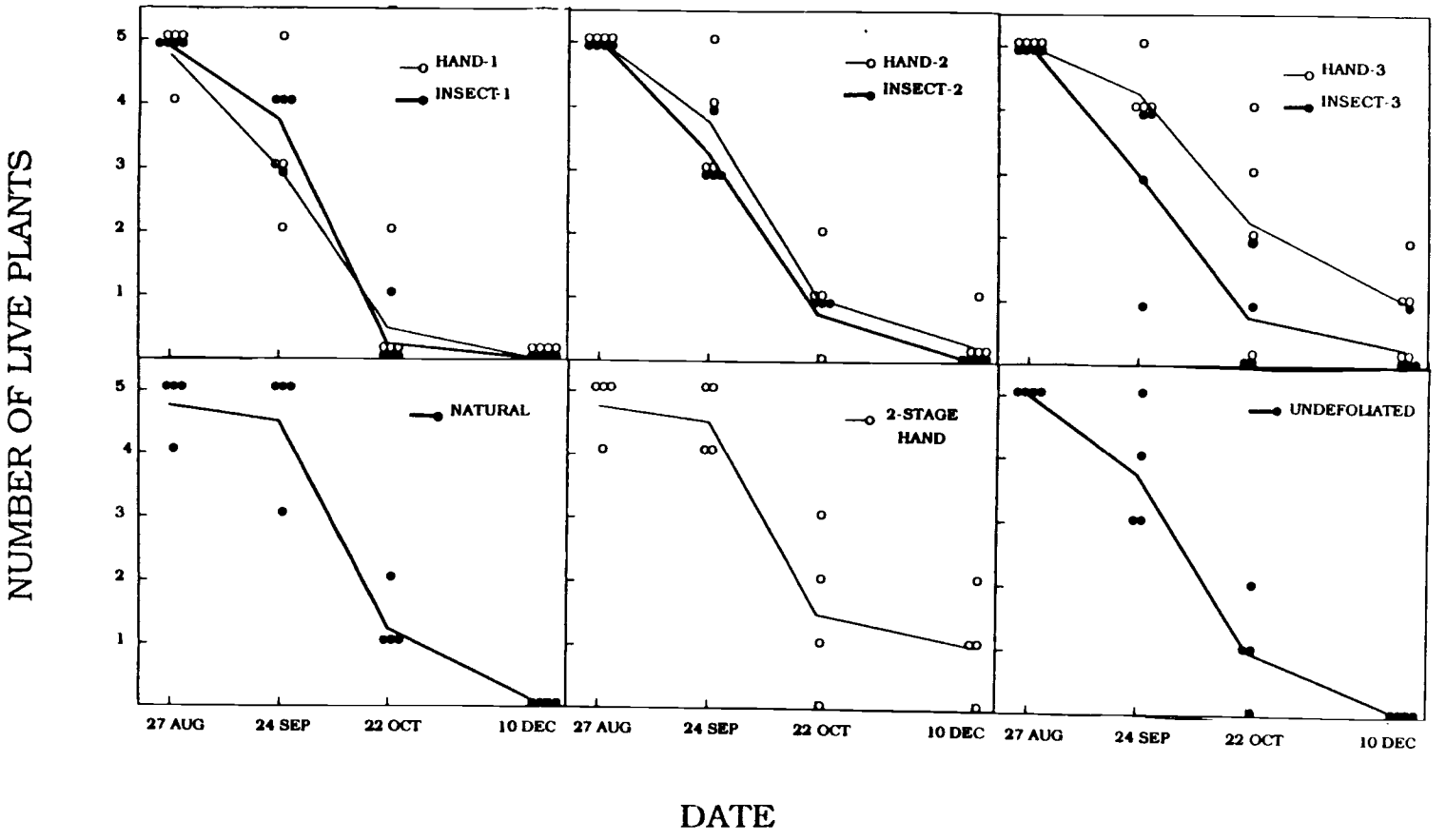

NUMBER OF LIVE PLANTS
HAND-1
INSECT-1
HAND-2
INSECT-2
HAND-3
INSECT-3
NATURAL
2-STAGE HAND
UNDEFOLIATED
5
4
3
2
1
27 AUG
24 SEP
22 OCT
10 DEC
DATE

Figure 3.

Table 1. Survival over winter by ragwort plants. Number of tagged plants located and alive on March 22, 1981.

Treatment	Number of plants located	Number of plants alive
Undefoliated	21	0
Insect-1	9	0
Hand-1	3	0
Insect-2	5	0
Hand-2	8	0
Insect-3	8	0
Hand-3	6	0
2-Stage	3	0
Natural	25	1

treatments. From 75-82% of these heads were damaged, leaving only .2 capitula undamaged per plant in the second treatment and 1.0 per plant in the third treatment. Feeding damage to the capitula ranged from light feeding on petals and involucral bracts to consumption of more than half a capitulum. Capitula in late flower and fruiting stages often were not damaged, suggesting that heads in those stages may be invulnerable to cinnabar moth.

Secondary capitula. A high proportion of plants (.75 to .98; Table 2) produced mature secondary capitula after defoliation, and the proportion did not vary significantly among defoliation treatments.

Regeneration began within 2 weeks after defoliation (Fig. 4), but plants produced, at best, less than half the number of capitula of undefoliated plants (Fig. 2). The number of secondary capitula per plant reached maximum levels 4 weeks after defoliation, then declined slightly as some primordia died and fell off the plant. Declines were significant (ANOVA, $p < .05$) in treatments Insect-2, Hand-2, Insect-3, and the 2-stage hand-defoliation. After achenes dispersed from mature heads, the empty bracts remained on the plant, giving a cumulative record of reproduction.

The date but not the method of damage affected the ultimate number of secondary capitula. Comparison of treatments at the end of the season (average of September and October harvests) showed no significant differences between hand- and insect-defoliation methods in the number of secondary capitula per plant (orthogonal contrasts, Table 3). Plants defoliated early by either method had more secondary capitula than those defoliated late (Table 3). However, comparison of treatments at 4 weeks after their respective defoliation dates showed the Hand-3 treatment to have significantly fewer capitula per plant

Table 2. Proportion of plants producing secondary fruits (mean of September and October samples). There were no significant differences among the 8 treatments in the ANOVA ($F(7,21) = 1.5919$; $p > .05$). Data were transformed by the arcsine transformation for analysis; means are shown back-transformed.

Treatment	Proportion
Insect-1	0.975
Hand-1	0.900
Insect-2	0.750
Hand-2	0.950
Insect-3	0.975
Hand-3	0.825
2-Stage Repeated [1]	0.975
	0.850
Natural [1]	0.870

[1] Treatment not included in the ANOVA

Figure 4. The number of secondary capitula per plant throughout the growing season, with the proportion of capitula in the age classes immature, mature, and dead primordia. Values are mean ± SE; n = 4 plots of 5 plants each. The number of both the primary capitula escaping herbivory and the secondary capitula are shown for the natural defoliation treatment, which was first sampled August 13.

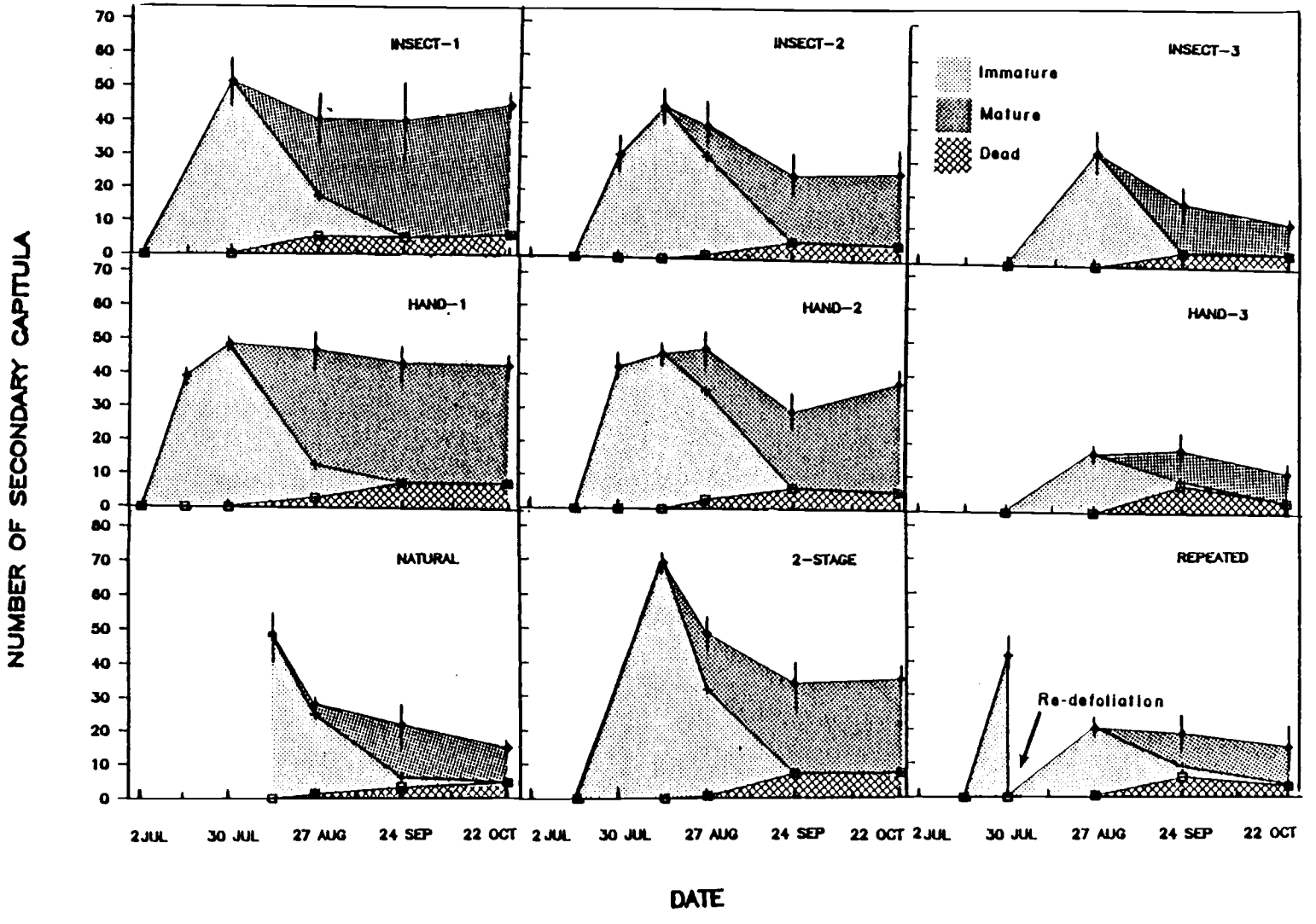

NUMBER OF SECONDARY CAPITULA
INSECT-1
INSECT-2
INSECT-3
HAND-1
HAND-2
HAND-3
NATURAL
2-STAGE
REPEATED
Immature
Mature
Dead
Re-defoliation
0
10
20
30
40
50
60
70
80
2 JUL
30 JUL
27 AUG
24 SEP
22 OCT
DATE

Figure 4.

Table 3. Number of capitula per plant at 4 weeks post-defoliation, and at the end of the season (mean of September and October harvests). For hand-defoliation treatments, the number of "escaped" capitula was estimated by the number of mature capitula at the time of defoliation. Within a column, means followed by the same letter are not significantly different ($p > .05$); T-method). Data were transformed by $\log_{10}(x + 1)$ for analysis; means are shown back-transformed.

Treatment	4 weeks post-defoliation	End of season (Sep. and Oct.)		
	Secondary capitula	Mature secondary capitula	All secondary capitula	Escaped primary plus secondary capitula
Insect-1	49.7 ab	35.3 a	41.1 a	41.1 a
Hand-1	47.4 ab	35.5 a	43.1 a	43.1 a
Insect-2	44.7 ab	20.1 ab	25.3 ab	26.1 abc
Hand-2	46.0 ab	27.2 a	32.9 a	32.9 ab
Insect-3	32.5 b	11.0 b	15.4 b	20.9 bc
Hand-3	17.4 c	9.0 b	14.8 b	18.1 c
2-Stage [1]	67.9 a	26.8 a	33.9 a	33.9 ab
Repeated [1]	19.6	10.7	16.2	16.2
Natural [1]	-	-	-	17.1
Orthogonal contrasts for set of 6 hand- and insect-defoliation treatments.				
Method	*	ns	ns	ns
Date	*	**	**	**
Method x date	*	ns	ns	ns

* $p < .05$
** $p < .01$
ns $p > .05$
[1] Treatment not included in the ANOVAs

than Insect-3. While rates of capitula production and loss may have varied among treatments in the short term, there appeared to be no significant variation in net production of capitula at the end of the season associated with method of herbivory.

The number of secondary capitula on plants in the 2-stage hand-defoliation treatment was not significantly different from any of the first and second defoliation treatments (Table 3). Plants subjected to repeated hand-defoliation lost 40 regrowth capitula per plant in the last application of damage on July 30, but by the end of the season had 16.2 capitula per plant, a number similar to that of plants defoliated for the first time on July 30 (14.8 capitula for Hand-3).

Total reproduction: primary plus secondary capitula. Since secondary reproduction accounted for nearly all of total reproduction, adding the primary heads that escaped insect attack or heads that matured prior to hand defoliation (3.2 heads per plant in Hand-3) did not alter the conclusions about the effects of treatments (Table 3).

Development of capitula. The developmental indices of plants at 4 weeks after defoliation were not significantly different among treatments except for Insect-3, which were significantly older than Hand-3, Hand-1, and Insect-1 (Table 4).

Fruiting curves. Cumulative fruiting curves (Fig. 5) show how the number of mature capitula per plant varied over time. I approximated the curves by discontinuous regression (ramp) functions (fitted by eye) and estimated several parameters. The intercept of the x-axis estimates the date of initial fruiting, the slope estimates the rate of fruiting, the fruiting time-50 estimates the date at which 50% of the capitula have matured, and the asymptote estimates the total number of fruiting heads matured by the average plant.

Table 4. Developmental index of capitula at 4 weeks after defoliation. Within a column, means followed by the same letter are not significantly different ($p > .05$; T-method).

Treatment	Developmental index
Insect-1	1.31 b
Hand-1	1.38 b
Insect-2	1.57 ab
Hand-2	1.58 ab
Insect-3	1.88 a
Hand-3	1.39 b
2 Stage[1]	1.56 ab
Repeated[1]	1.38

Orthogonal contrasts for set of 6 hand- and insect-defoliation treatments	
Method	*
Date	**
Method x Date	**

* $p < .05$
** $p < .01$

[1]Treatment not included in the ANOVA.

Figure 5. Number of mature capitula per plant over time for the various defoliation treatments. The discontinuous regression (ramp) functions approximating the curves were fit by eye. A single ramp was fit for each pair of hand- and insect-defoliation treatments.

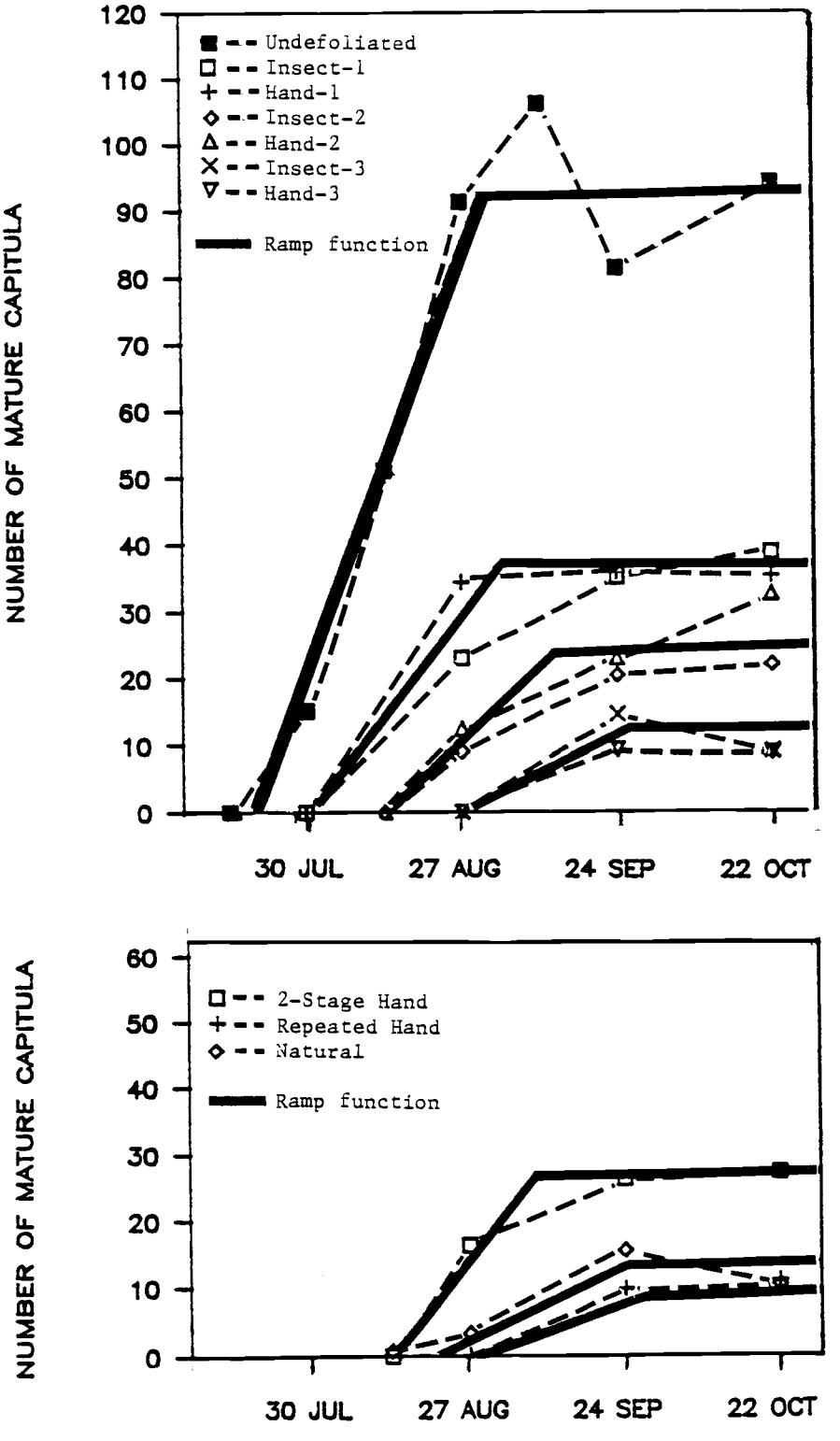

NUMBER OF MATURE CAPITULA
120
110
100
90
80
70
60
50
40
30
20
10
0
Undefoliated
Insect-1
Hand-1
Insect-2
Hand-2
Insect-3
Hand-3
Ramp function
30 JUL
27 AUG
24 SEP
22 OCT
NUMBER OF MATURE CAPITULA
60
50
40
30
20
10
0
2-Stage Hand
Repeated Hand
Natural
Ramp function
30 JUL
27 AUG
24 SEP
22 OCT

Figure 5.

Inspection of the curves reveals the following conclusions. Plants protected from herbivory produced fruits earlier and at faster rates than those subjected to herbivory. Among the herbivory treatments, curves for hand and insect methods were very similar, and delay in defoliation date resulted in later initiation and production of fruits, and lower fruiting rates (Fig. 5A). The rate and timing of fruit production in plants subjected to repeated hand defoliation was similar to that of plants in the third defoliation treatments.

Heights of stems and capitula

The main stems on protected plants reached maximum height in middle to late July (Fig. 2D). Axillary branches bearing flower heads elongated in early July and reached maximum extension in early August. Final plant height averaged 85 cm.

The earliest defoliations yielded plants with shorter main stems than the latest defoliations (Fig. 6; average of plants harvested in August, September and October), but there was a significant interaction of the effect of method and date of defoliation on stem height (orthogonal contrasts among the set of 6 hand- and insect-defoliation treatments, Table 5). Insect-defoliated plants were significantly shorter than hand-defoliated plants in the first 2 timings of defoliation, but there was no difference in height between Insect-3 and Hand-3 plants (Table 5). Plant height in the 2-stage hand-defoliation treatment was intermediate to the Insect-2 and Hand-2 plants, and not significantly different from either.

Comparison of the final main stem heights of defoliated plants (Table 5) with the stem growth curve of undefoliated plants (Fig. 2D) suggests that both hand- and insect-defoliation arrested stem elongation of bolting

Figure 6. Main stem height, total height of plant (average of August, September, and October samples) and mean capitula height (September samples). Values are mean ± SE, n =4 plots of 5 plants each. Treatment abbreviations: U = Undefoliated, I-1 = Insect-1, H-1 = Hand-1, I-2 = Insect-2, H-2 = Hand-2, I-3 = Insect-3, H-3 = Hand-3, 2S = 2-Stage Hand, R = Repeated Hand, N = Natural.

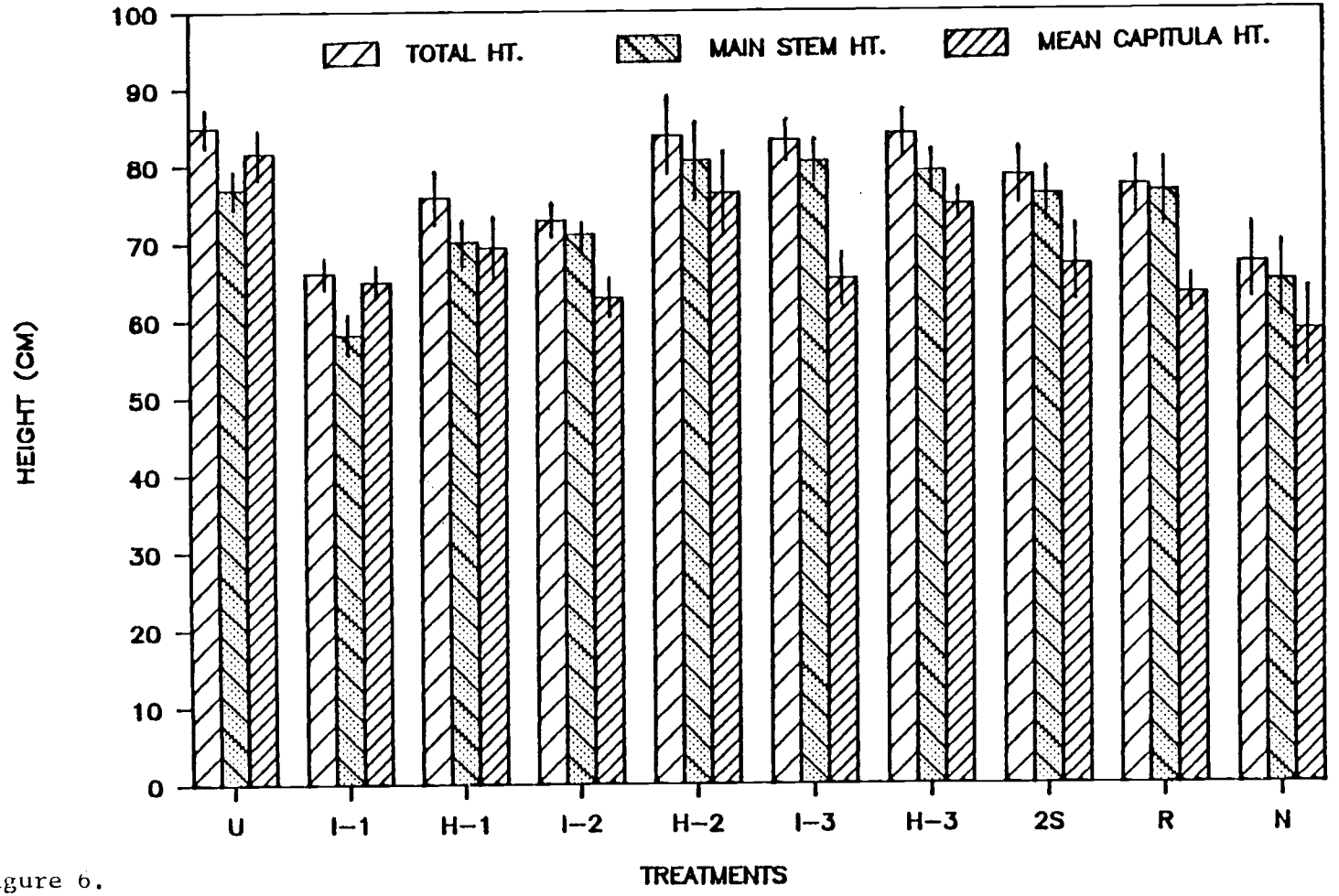

TOTAL HT.
MAIN STEM HT.
MEAN CAPITULA HT.
HEIGHT (CM)
100
90
80
70
60
50
40
30
20
10
0
U
I-1
H-1
I-2
H-2
I-3
H-3
2S
R
N
TREATMENTS

Figure 6.

Table 5. Height of main stem, height of total stem (mean of August, September, and October harvests), and mean height of capitula (September harvest) Within a column, means followed by the same letter are not significantly different (p > .05; T-method).

Treatment	Main stem (cm)	Total stem (cm)	Capitula (cm)
Undefoliated	76.9 abc	85.0 a	81.7 a
Insect-1	58.2 d	66.1 d	65.0 b
Hand-1	70.1 c	75.8 bc	69.3 ab
Insect-2	71.0 bc	72.8 cd	62.9 b
Hand-2	80.5 a	83.8 a	76.3 ab
Insect-3	80.3 a	83.1 ab	65.2 b
Hand-3	79.0 ab	84.0 a	74.7 ab
2-Stage Repeated [1]	76.0 abc 76.3	78.4 abc 77.1	67.1 ab 63.2
Natural[1]	64.8	67.2	58.5
Orthogonal contrasts for set of 6 hand- and insect-defoliation treatments.			
Method	**	**	**
Date	**	**	ns
Method x date	**	*	ns

* p < .05
** p < .01
ns p > .05

[1] Treatment not included in the ANOVAs.

plants at the time of damage. The damage in the insect-defoliation treatments apparently occurred about 5-7 days before the end of the 12-day defoliation periods (ie, earlier than the corresponding hand-defoliation). Damage occurring after stems had reached maximum height had no effect on height. Larvae did not shorten the main stem by eating it, as they sometimes do when food is scarce.

The total height of plants followed the pattern of main stem height. There was a significant interaction between the method and date of defoliation, and the Insect-1 and Insect-2 plants were shorter, respectively, than Hand-1 and Hand-2 plants (Table 5).

The average height of capitula was estimated for the September harvest, when initiation of capitula had ceased. The average height of capitula was lower for insect-defoliated plants as a group than for hand-defoliated plants (Fig. 6, Table 5), although the *a posteriori* test for comparison of means was not sensitive enough to detect significant differences between individual pairs of those means. Date of defoliation did not significantly affect the height of capitula.

Secondary capitula were produced on old defoliated branches, on new axillary branches initiated after defoliation, and rarely on regrowth shoots from the crown of the plant. In the earliest defoliation treatments, which occurred before much extension of branches, almost all regrowth was on new branches. In later defoliation treatments, short new branches were initiated below the existing ones. Regeneration on these new lower branches, rather on the old upper branches, was more common on insect-defoliated plants than on hand-defoliated ones, suggesting that insect damage may have caused greater damage to the upper branches or higher lateral buds.

Biomass of plant parts

Leaves and capitula on protected plants . On undefoliated plants the biomass of live leaves peaked around June 16 at 2.3 g per plant and then steadily declined as first basal (older) leaves and then higher (younger) leaves died (Fig. 2B). The biomass of floral material increased rapidly as capitula matured, peaked at 2.4 g on August 13 when about half the capitula were in the fruit stage, then declined as achenes dispersed from the heads.

Primary leaves escaping herbivory. Hand-defoliation removed leaf laminae and left only petioles, whereas larvae left petioles, bits of leaf lamina, and occasionally older leaves at the base of the plant. The number of lower leaves escaping herbivory varied with the timing of defoliation. In the Insect-1 defoliaion, 56% of the plants had such escapes (.8 leaves per plant escaping, averaged over all plants). In the Insect-2 defoliation, only 5% of the plants had live leaves remaining at the end of the defoliation period (.1 leaves escaping, averaged over all plants), and no live leaves remained at the end of the Insect-3 defoliation. The leaves escaping the first defoliation were basal leaves, which were often partially buried in the surrounding vegetation and beginning to turn yellow. The escaped leaves died within one or two weeks after defoliation. By the time of the later defoliation treatments, most of the basal leaves on the plants to be defoliated had died.

Comparison of treatments at 4 weeks after defoliation showed that insect-defoliated plants had greater mass of primary leaf tissue (petioles and leaves, all dead by that date) remaining on the plant than did hand-defoliated

Table 6. Mass (g dry weight) of primary petioles, primary leaves, and primary capitula that escaped herbivory, at 4 weeks post-defoliation. Within a column, means followed by the same letter are not significantly different ($p > .05$; T-method). Data were transformed by $\log_{10}(x + 1)$ for analysis; means are shown back-transformed. For stripped petioles, there were no significant differences between the 7 treatments in the ANOVA ($F(6,18) = .6838$; $p = .6650$).

Treatment	Stripped petioles	Live leaves	Dead leaves	Sum of leaves and petioles	Capitula
Insect-1	0.174	0.000	0.060	0.272 ab	0.000
Hand-1	0.140	-	-	0.161 b	-
Insect-2	0.191	0.000	0.029	0.268 ab	0.068
Hand-2	0.164	-	-	0.174 ab	-
Insect-3	0.230	0.000	0.145	0.421 a	0.170
Hand-3	0.114	-	-	0.142 b	-
2-Stage [1]	0.207	-	-	0.213 ab	-
Repeated [1]	0.295	-	-	0.306	-
Natural [1]	0.263	0.027	0.047	0.398	-

Orthogonal contrasts for set of 6 hand- and insect-defoliation treatments.

Method	**
Date	ns
Method x date	ns

** $p < .01$
ns $p > .05$

[1] Treatment not included in the ANOVA.

plants (Table 6); however, this difference is largely due to the fact that hand-defoliation had unrealistically removed leaf laminae from dead leaves as well as live. Larvae did occasionally leave ragged bits of leaf laminae along the petioles. In all treatments, the petioles and any remaining pieces of laminae died within a week of defoliation.

Secondary leaves and capitula. Comparison of treatments at the end of the season (September harvest) showed that the total biomass of leaves (live plus dead) declined with later defoliation date in both hand- and insect-defoliated plants (Table 7). There were no significant differences between the two methods. That pattern was not seen earlier in the season at 4 weeks after defoliation (the peak of live leaf biomass); Hand-3 plants had significantly less leaf biomass than Insect-3 plants at that time. Hand-3 plants apparently lagged behind Insect-3 plants in production of compensatory foliage, but net production by the end of the season was similar in both methods.

The peak in biomass of secondary capitula occurred around 6-8 weeks after defoliation. Treatments were compared at 4 weeks after defoliation, and showed an interaction of the date and method of defoliation on the biomass of secondary capitula (Table 7). Plants in the Hand-3 treatment had less biomass of capitula than plants in earlier defoliations, and there were no other signficant differences among the set of 6 hand- and insect-defoliation treatments.

Stem biomass. The biomass of the main stem was significantly affected by both the method and the date of defoliation (orthogonal contrasts for the set of 6 hand- and insect-defoliations, Table 8). The pattern is similar to that of the heights of the main stem (Table 5), since shorter stems tended to be lighter than the taller ones.

Table 7. Mass (g dry weight) of secondary leaves and capitula, at 4 weeks post-defoliation, and on September 24. Within a column, means followed by the same letter are not significantly different ($p > .05$); T-method). Data were transformed by $\log_{10}(x + 1)$ for analysis; means are shown back-transformed.

Treatment	Live leaves at 4 weeks	Live and dead leaves Sep. 24	Capitula at 4 weeks
Insect-1	0.169 a	0.154 a	0.370 b
Hand-1	0.194 a	0.118 a	0.434 ab
Insect-2	0.149 a	0.061 ab	0.415 ab
Hand-2	0.111 a	0.058 b	0.552 ab
Insect-3	0.037 b	0.023 b	0.317 bc
Hand-3	0.015 c	0.025 b	0.175 c
2-Stage [1]	0.218 a	0.059 ab	0.740 a
Repeated [1]	0.038	0.024	0.244
Natural [1]	0.123	0.037	0.652
Orthogonal contrasts for set of 6 hand- and insect-defoliation treatments.			
Method	*	ns	ns
Date	**	**	**
Method x date	*	ns	*

* $p < .05$
** $p < .01$
ns $p > .05$

[1] Treatment not included in ANOVAs.

Table 8. Mass (g dry weight) of main stem, axillary stem, and roots plus root crown (mean of August and September harvests). Within a column, means followed by the same letter are not significantly different ($p > .05$; T-method). Data were transformed by $\log_{10}(x + 1)$ for analysis; means are shown back-transformed. For roots and crown, there were no significant differences among the 8 treatments in the ANOVA ($F(7,21) = .77009$; $p = .6179$).

Treatment	Main stem	Axillary branches	Roots and crown
Undefoliated	4.235 a	0.620 a	1.090
Insect-1	2.798 b	0.387 ab	0.898
Hand-1	3.403 ab	0.384 ab	0.952
Insect-2	3.364 ab	0.274 b	0.907
Hand-2	4.466 a	0.438 ab	1.072
Insect-3	4.017 a	0.355 ab	1.022
Hand-3	4.404 a	0.582 a	0.978
2-Stage [1]	4.110 a	0.382 ab	1.090
Repeated [1]	4.275	0.307	1.204
Natural [1]	3.132	0.332	0.958

Orthogonal contrasts for the set of 6 hand- and insect-defoliation treatments.

Method	*	*
Date	*	ns
Method x date	ns	ns

* $p < .05$
ns $p > .05$

[1] Treatment not included in the ANOVAs.

Table 9. Number of nodes with secondary growth on September 24. There were no significant differences among the 7 treatments in the ANOVA ($F(6,8) = 1.4044$; $p = .2665$).

Treatment	Number of nodes
Insect-1	5.4
Hand-1	5.8
Insect-2	4.6
Hand-2	4.8
Insect-3	3.7
Hand-3	4.6
2-Stage	4.9
Repeated [1]	3.6
Natural [1]	3.8

[1] Treatment not included in the ANOVA

The biomass of axillary stems was significantly affected by the method but not the date of defoliation (Table 8). Hand-defoliation resulted in plants with greater biomass of branches that did insect-defoliation.

Roots and root crown. The biomass of combined roots and root crown ranged from averages of .898 to 1.204 g per plant (Table 8). There were no significant differences among the 8 treatments compared in the ANOVA.

Number of nodes with secondary growth

The average number of nodes with regrowth ranged from 3.7 to 5.8 per plant, but there were no significant differences between treatments (Table 9).

Defoliation of ragwort by resident larvae

Phenology and numbers of cinnabar moth. Eggs were observed on plants in the natural defoliation plots and in nearby fields from mid-May to mid-July. Sixty-eight percent of the egg masses found on June 25-26 on tagged plants in the natural defoliation plots had already hatched (Table 10). Only 2 unhatched egg masses were found at the next survey, July 10-11, and none on July 24-25. The earliest first instar larvae were seen on May 23, fourth instar larvae around June 15, and on August 13 only a few larvae remained in the plots.

The numbers of fourth and fifth instar larvae peaked between the June 25-26 and July 10-11 surveys of the plots. On June 25-26, most larvae on the tagged plants were in instars 1-3 (Table 11). By July 10-11 many had completed development or moved off the tagged plants, and the numbers of all instars on the plants were low (Table 11).

Table 10. Mean number of cinnabar moth egg masses per tagged ragwort plant in natural defoliation plots*, on June 25-26.

Plot	Proportion of plants with egg masses	Mean number of egg masses		
		Unhatched	Hatched	Total (SE)
1	0.35	0.2	0.4	0.6 (.9131)
2	0.29	0.1	0.2	0.3 (.3078)
3	0.59	0.4	0.6	0.9 (.9962)
4	0.37	0.1	0.3	0.4 (.1840)
$\bar{X}$	0.4	0.2	0.4	0.6

*49 plants per plot.

Table 11. Mean number of cinnabar moth larvae per tagged ragwort plant in the natural defoliation plots.

Date	Plot	Proportion of plants with larvae	Mean number of larvae per plant					
			I	II	III	IV	V	Total
June 25-26	1	0.91	6.8	4.6	3.2	1.0	0.1	15.8
	2	0.86	2.4	4.2	2.5	0.8	0.04	9.8
	3	0.94	4.3	12.0	7.0	2.8	0.02	26.1
	4	0.86	4.3	1.6	1.3	1.2	0.0	8.5
	$\bar{x}$	0.89	4.4	5.6	3.5	1.5	0.0	15.0
July 10-11	1	0.80	0.2	0.8	1.6	1.3	0.3	4.1
	2	0.80	0.1	0.7	1.3	1.1	0.6	3.8
	3	0.51	0.04	0.3	0.6	0.3	0.2	1.4
	4	0.88	0.1	0.5	2.2	1.2	0.3	4.3
	$\bar{x}$	0.74	0.9	0.6	1.4	1.0	0.4	3.4
July 24-25	1	0.28	0.0	0.02	0.18	0.12	0.08	0.4
	2	0.53	0.0	0.14	0.41	0.22	0.02	0.8
	3	0.24	0.0	0.04	0.02	0.14	0.06	0.3
	4	0.35	0.0	0.08	0.10	0.20	0.04	0.4
	$\bar{x}$	0.35	0.0	0.07	0.18	0.17	0.05	0.5
Aug. 13	1	0.12	0.0	0.0	0.0	0.10	0.02	0.1
	2	0.10	0.0	0.0	0.02	0.04	0.04	0.1
	3	0.29	0.0	0.0	0.02	0.20	0.26	0.5
	4	0.08	0.0	0.0	0.0	0.08	0.0	0.1
	$\bar{x}$	0.15	0.0	0.0	0.01	0.11	0.08	0.2

The average of 15 larvae per plant on June 25-26 (Table 11) was the maximum counted in the surveys, but this number may underestimate the peak levels of larvae feeding on the tagged plants between June 25 and July 10. Many egg masses were seen (but not counted) on the rosette plants in the plots, and larvae appeared to move from rosettes to the flowering plants as defoliation progressed.

Redistribution of larvae. More than half the plants received no egg masses but were defoliated by immigrant larvae. On June 25-26, only 40% of the plants had received egg masses (Table 10), but 89% of the plants had larvae on them, and 86% had feeding damage. The density of flowering plants and rosettes was high, and it was often possible for larvae to move between plants from leaf to leaf instead of leaving the plants and searching by ground. Plant-to-plant movement probably explains the observation of second instars and occasionally even first instars on plants with no egg masses.

Progression of defoliation. While 8.5% of the tagged plants were already defoliated by June 25-26, most of the defoliation occurred during the two weeks between June 25-26 and July 10-11 surveys (Fig. 7), when the number of fourth and fifth instars reached a maximum. By July 10-11, 67% of the plants had experienced either heavy or total defoliation, and no plants had escaped some amount of damage. By July 25, 96% of the plants were heavily defoliated (Fig. 8), and few larvae remained. Almost all the defoliated plants had new growth, at a mean of 4.4 nodes per plant. Larvae were seen feeding on this growth, which was damaged on 40% of the plants.

On August 13, the plants were vigorously regrowing. Larvae remained in very low numbers (an average of .2 per plant, Table 11); 60% of the plants had damage to new foliage and capitula.

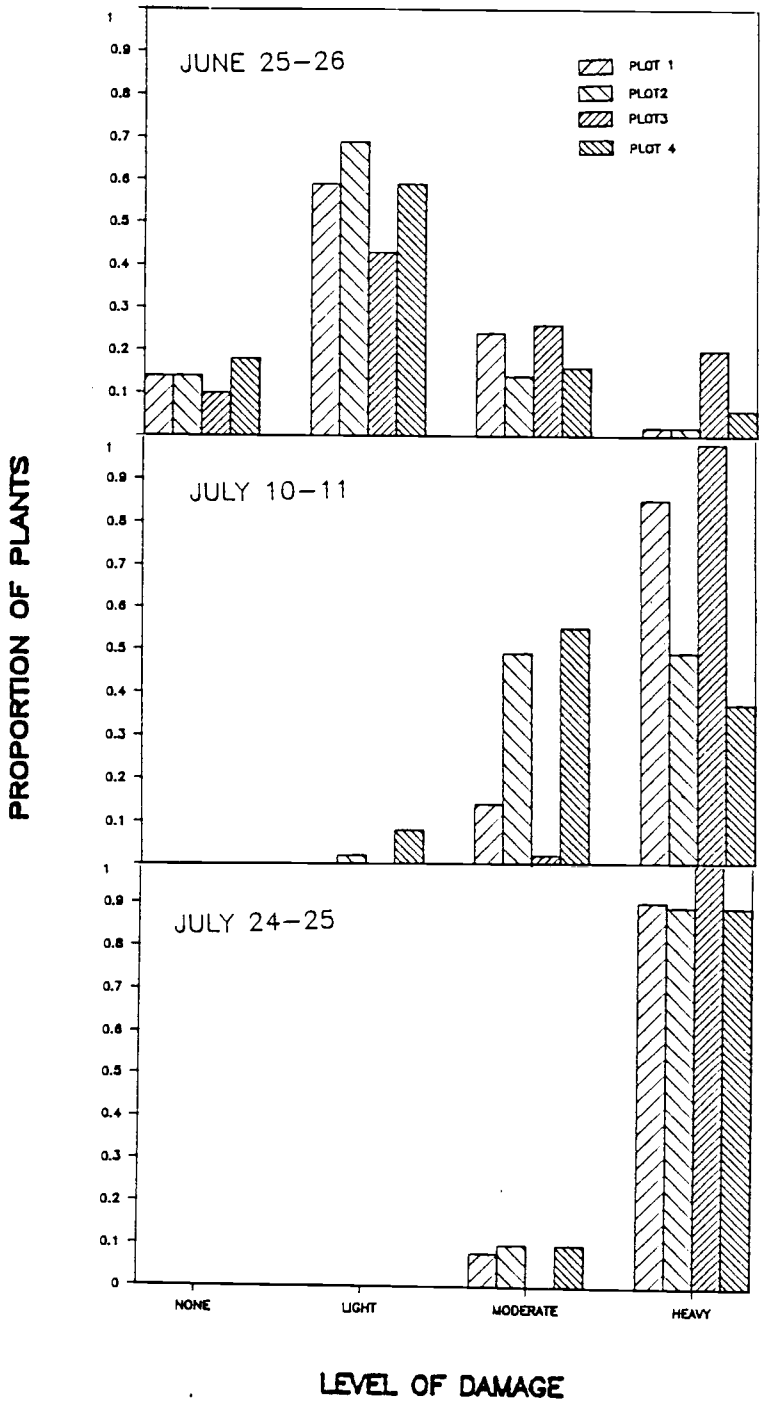


Figure 7. Progression of damage in the four natural defoliation plots. Proportion of plants with none, light, moderate, or heavy damage on 3 survey dates.

Comparison with other treatments. The timing of damage and the response of plants in natural defoliation plots did not correspond exactly to any one of the manipulated treatments. Defoliation of most plants in the natural defoliation plots was accomplished around the time of the first and second herbivory treatments. The average main stem height and the total height of the natural plots resembled those of the early defoliation plots (Fig. 6). The average height of capitula was most similar to insect-defoliation treatments (Fig. 6). The number of capitula per plant resembled that of the Hand-3, Insect-3, and Repeated hand-defoliation treatments (Table 3).

DISCUSSION

Adequacy of hand-defoliation

Artificial herbivory can be judged adequate if plants respond similarly to both insect damage and its mimic over an appropriate range of conditions. When responses differ, details in the pattern of insect damage (e.g., rate, frequency, selectivity of herbivory) may suggest changes that will improve the realism of a simple simulation. This study focused on responses important to the birth, death, and dispersal rates of a plant population: survivorship under field conditions, quantity and timing of reproduction, and the height of release of dispersing seed. It also examined the rate and biomass of regrowth, which may be important to vertebrate and invertebrate herbivores. Other evaluations of artificial damage have stressed physiological responses of individuals, including net photosynthesis (Poston et al. 1976), water loss (Hammond and Pedigo 1981; Ostlie and Pedigo 1984), or short-term changes in growth and development (Capinera and Roltsch 1980; Mellors et al. 1984). The responses examined in the present evaluation are those that are relevant to the understanding, prediction, and management of a weed population. Despite the crude simplicity of the hand-defoliation method, ragwort plants damaged by hand and by insect responded similarly over a range of defoliation dates. I discuss below responses of plants to insect- and hand-defoliation, and suggest some improvements in artificial defoliation method.

Hand- and insect-defoliated plants had similar patterns of survivorship and reproduction. Survivorship to the next year was very low in all treatments; only 6% of all plants survived to December 10, and only 1.1% to

the next March. The low survival rates resemble those observed in another Oregon population (McEvoy in prep.) but contrast with the survival of 75% of the plants in a population in England (Islam and Crawley 1983). The number of secondary capitula per plant declined with delay in defoliation date for both hand- and insect-defoliated plants, but only in insect-defoliated plants was later defoliation accompanied by an increase in escapes of maturing primary capitula. The primary capitula escaping insect herbivory in these treatments contributed little to the total of capitula under the conditions examined, but the number of escapes would probably have risen sharply with further delay in defoliation date. Two weeks after the last (July 30) defoliation treatment, almost half of the capitula on undamaged plants had matured. Over a wider range of timings, artificial herbivory could be improved by leaving mature capitula on the plants. Further study is required to determine (1) the precise stage at which capitula become invulnerable to consumption by different ages of larvae and (2) the contribution that damaged heads make to reproduction.

Hand-defoliation yielded patterns of capitula maturation that closely resembled those of insect-defoliated plants, with delay in defoliation resulting in delay in production of secondary fruits in both defoliation methods. A consequence of later maturation of regrowth achenes may be a shorter distance of achene dispersal; under certain conditions of site and surrounding vegetation, disk achenes dispersing early travelled farther than those dispersing later (McEvoy and Cox, in press).

The mean height of secondary capitula was lower on insect-defoliated plants than hand-defoliated plants because of lower main stem height and possibly greater damage to upper growing points. The height of release of

achenes from plants may affect the dispersal distance of achenes, but McEvoy and Cox (in press) found that differences of up to 150 cm in release height did not affect dispersal distance under climate and vegetation conditions similar to those at this site. The differences of up to 20 cm in mean height seen in this study are thus probably not significant to dispersal.

The net production of secondary leaves (measured as biomass of live and dead leaves at the end of the season) was similar for hand- and insect-defoliated plants, and declined with later defoliation date. The biomass of secondary leaves was small (up to .15 g per plant), but even small amounts of regrowth may be biologically significant as a food source to adult ragwort flea beetles (*Longitarsus jacobaeae* (Waterhouse)), which have been observed feeding on regrowth in late summer at a coastal site (P.B. McEvoy, personal communication).

The association of later timing of damage with reduced secondary growth is very similar to that seen at a nearby site in 2 different years (McEvoy, in prep.). In contrast, the timing of damage did not affect reproduction of ragwort plants at a site in England (Islam and Crawley 1983). In Oregon, timing may affect regrowth in part because of the summer drought, since the availability of moisture has been shown to affect compensatory growth (Cox and McEvoy 1983). Lack of growing points did not appear to be limiting, since there was no difference between treatments in the number of nodes with regrowth.

Regrowth of hand- and insect-defoliated plants reached similar levels by the end of the season, but rates of plant growth and development may have varied slightly with defoliation method within the growing season. Four weeks after defoliation, plants in the third insect-defoliation had greater biomass of secondary leaves, more secondary capitula, and a more advanced index of capitula

age than those in the third hand-defoliation. Those differences did not appear in the other insect vs hand comparisons. Small differences in initial growth and developmental rates associated with the two types of defoliation did not appear to yield net differences in secondary reproduction and foliage at the end of the season.

Some basal leaves escaped from larvae in the first insect-defoliation, but there was no association between such escapes and improved capacity of a plant to compensate for herbivory. In the absence of herbivory, the basal leaves die as bolting and flowering occur; thus most basal leaves were already dead by the time of the second and third defoliation. There was no evidence of an increased lifespan for leaves escaping damage; leaves and petioles that escaped consumption died soon after defoliation of the plants. This contrasts with turnips, in which older leaves escaping herbivory had prolonged life and contributed to the yield of the root (Taylor and Bardner 1968). In defoliations occurring much earlier, while ragwort's basal leaves are still vigorous, escaping leaves might survive longer and contribute to regrowth.

Both hand- and insect-damage arrested elongation of the bolting main stem. Insect-defoliated plants were shorter than hand-defoliated plants for the first 2 timings of damage, because insect damage to the stem preceeded hand-defoliation by 5-7 days. To better simulate insect damage, hand-defoliation could be applied at the midpoint of the insect-defoliation period, or applied gradually over an extended period. Stem height was the one variable for which the 2-stage defoliation gave a significant improvement over the Hand-2 defoliation.

Insect-defoliated plants had less biomass of axillary branches than did hand-defoliated ones. This could be due

both to a difference in the timing of damage to the growing branches and to possibly greater damage by insects to lateral buds.

I concluded that the two methods yielded similar effects on survivorship, quantity and timing of reproduction, and amount of compensatory foliage, but yielded minor differences in stem and capitula height, biomass of stems, and initial rates of compensatory growth. Where simulation of herbivory over a wider range in times of attack is desired, provision must be made for plant parts that escape damage in very early (e.g., basal leaves) and very late (e.g., mature capitula) times of attack.

Evaluation of defoliation by introduced larvae

The introduction of larvae to plots for insect-defoliation treatments was realistic in the numbers of larvae per plant and the timing and duration of defoliation, but was an artificial treatment in that plants were protected from further damage after the end of the defoliation period. In those treatments larvae were removed from plants after the end of the defoliation period, but in plots with natural insect populations, low numbers of larvae persisted into mid-August. In the latter plots I observed larvae feeding on regrowth tissue, which appeared on plants within 2 weeks after herbivory. Regrowth has been shown in laboratory feeding trials to support larval growth and development (Crawley and Nachapong 1984). The repeated damage may have reduced regrowth; the number of capitula per plant in the natural defoliation plots was lower than would have been predicted from the general timing of damage, and about one third of the capitula were damaged.

Ragwort continued to regenerate after damage to regrowth, as evidenced by plants subjected to repeated hand defoliation. In that treatment, the initial defoliation was complete on July 15, and regrowth was removed on July 30. Despite losing that growth, plants regenerated quantities of capitula and leaves similar to plants defoliated for the first time on July 30. Limited repeated damage apparently did not deplete ragwort's reserves. Regrowth could be predicted by the last date of attack.

Within a population plants defoliated early may thus suffer repeated damage to regrowth that appears while larvae are still present, and consequently may not respond in ways predicted by simple timing experiments that excude that feature. Repeated damage could also be included in both hand- and insect-defoliations to represent the experience of such plants.

Conclusions

Hand-defoliation adequately simulated the effects of a 12 day period of defoliation by cinnabar moth on the survival, compensatory regrowth and reproduction of ragwort, over three timings of damage. Where simulation of herbivory over wider range in times of attack is desired, provision must be made for plant parts that escape damage in very early (e.g., basal leaves) and very late (e.g. mature capitula) times of attack. Hand- and insect-defoliated plants differed in both stem height and mean height of capitula, but the small magnitude of the differences should have little influence on dispersal of seeds. Plants in both the hand- and insect-defoliation treatments were protected from damage to regrowth, but, to further increase realism, artificial defoliation could be

extended to include repeated attacks as sometimes occurs in the field.

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