

RESPONSES TO SIMULATED LEAF AND ROOT HERBIVORY BY A BIENNIAL, *TRAGOPOGON DUBIUS*¹

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Abstract. Removal of 25 or 75% of leaf or root tissue, and 25% of both, was used to simulate above- and belowground herbivory on *Tragopogon dubius*. Plants with 25% of their leaf tissue removed did not differ significantly from controls in total biomass; those with any root tissue trimmed produced significantly less biomass while the 75% leaf removal treatment was intermediate. A similar pattern was exhibited for plant mortality and flower production. Plants that had one or more flowers removed by herbivores grew significantly larger and produced significantly more flowers than plants that lost no flowers, regardless of treatment.

The greatest differences between treatments in nutrient allocation patterns occurred 1 d after manipulations were applied. Subsequently, differences between treatments moderated, and values tended to converge by 98 d postmanipulation, when the plants were harvested. Seeds had significantly higher nitrogen concentration levels than leaf or root tissue.

Key words: aboveground herbivory; belowground herbivory; growth; herbivory; mortality; nutrient allocation; pocket gopher; reproduction; simulated herbivory; *Tragopogon dubius*.

INTRODUCTION

Most plants are subjected to herbivory during some part of their life cycle (Crawley 1983). In some cases entire plants are consumed, or consumption may be tissue specific (e.g., leaves, stems, roots, flowers, or seeds). Because the investment of energy, structural material, and nutrients differ among plant parts (Mattson 1980, Caldwell et al. 1981), the impact of herbivory depends on the tissue(s) consumed. For example, removal of the flowering stalk may actually increase reproductive output in some plant species (Paige and Whitham 1987), but granivory obviously decreases the reproductive potential of the parent plant. Furthermore, the timing of herbivory is crucial. In the case of flowering stalk loss, the ability of a plant to compensate for herbivory depends on the size (i.e., age) of the plant at the time of flower loss (Maschinski and Whitham 1989).

As part of an evolutionary response to herbivory, plants may develop defensive chemicals in vulnerable tissues (Rhoades and Cates 1976). Inouye (1982) and van der Meijden et al. (1988) have suggested that an alternative strategy is compensatory regrowth following herbivory. This latter approach requires a reallocation of energy and constituents in the plant after consumption. Complex interactions between defense and compensation represent a continuum, and the precise processes and timing of responses vary signifi-

cantly among species, locations, and seasons (Paige and Whitham 1987, Maschinski and Whitham 1989).

Several categories of herbivory have received attention by investigators. Studies of leaf and stem herbivory, defoliation, and granivory (see Harper 1977, Brown et al. 1979, Crawley 1983 for overviews) have concentrated on the most obvious and easily analyzed tissues, while belowground plant parts have received significantly less attention (Detling et al. 1980, Lovett-Doust 1980, Reichman and Smith 1985, Andersen 1987, Reichman 1988, Seastedt et al. 1988, Brown and Gange 1989). Even less is known about how herbivory on one tissue affects the susceptibility of other tissues to consumption. Some authors have proposed an induced defense mechanism in which plants subjected to herbivory distribute chemical defenses in other tissues (Schultz 1988). Conversely, the specific reallocation patterns in response to consumption of one tissue type may actually make other tissues more vulnerable. For example, Seastedt (1985) and Seastedt et al. (1988) suggest that moderate levels of aboveground herbivory can cause a net allocation of carbon up from the roots to repair the damage. The remaining root tissue becomes relatively nitrogen-rich, thereby drawing the attention of belowground herbivores.

This study was undertaken to analyze the effects of simulated above- and belowground herbivory on the mortality, growth, flower production, and nutrient allocation patterns of *Tragopogon dubius*, a biennial composite. *T. dubius* spends its 1st yr as a low rosette; during its 2nd yr, if its root crown diameter is sufficiently large (Gross 1981), it sends up a long stem,

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which eventually produces 1–30 flowering stalks (but no more than 15 in the study reported herein). This widespread plant is a favored dietary item for pocket gophers (Behrend and Tester 1988). These large subterranean herbivores significantly affect the plant communities they inhabit via direct plant consumption and physical disturbance of the soil (Huntly and Inouye 1988). When pocket gophers (in this case, *Geomys bur-sarius*) encounter *T. dubius*, the rodents may consume 20–80% of the primary root, and the aboveground parts of the plant are susceptible to herbivory by several vertebrates (deer, squirrels, and rabbits), which bite off one or more flowering stalks (O. J. Reichman and S. C. Smith, *personal observations*). Thus, this system serves as a model for analyses of the impact and interactions of above- and belowground herbivory and the response of plants.

METHODS

We conducted a preliminary experiment to determine whether simulated root herbivory yields quantitatively different results than natural root herbivory by pocket gophers. We could not keep young *T. dubius* plants alive in our experimental arrangement over the winter, so we used red beans (*Castor* sp.) instead. In the summer of 1987, six seeds were planted in potting soil and vermiculite in 10 wooden troughs, 12 cm deep and wide. These troughs, which had hardware cloth bottoms through which roots could grow, were placed on top of similar troughs (with solid bottoms) filled with the same soil medium. After roots had penetrated to the bottom of the lower trough the upper trough was lifted off, with the roots extending down through the hardware cloth, and placed onto an empty lower trough.

A pocket gopher was then placed in the lower trough, which was partitioned to allow access to the roots of only three of the six plants; the protruding roots were quickly chewed off. The roots of the three other plants were trimmed with metal scissors. The upper trough was then replaced onto the initial lower trough filled with soil medium, and the plants were allowed to continue to grow for 3 wk, at which time they were harvested, dried, and weighed. This procedure was conducted 3 times, yielding 30 pairs of three-plant sets, each of which had been subjected to either gopher or scissor trimming. The biomass values for the three plants of each set were averaged (they represented repeated measures) and the 30 pairs of values were compared using a paired *t* test.

Subsequent field experiments with *T. dubius* were conducted at Cedar Creek Natural History Area (CCNHA), 45 km north of Minneapolis, Minnesota. Individual *T. dubius* plants were located within a 2-ha old field during late May 1987. Five simulated herbivory treatments were randomly imposed on plants that had uniform rosette sizes and had just begun to bolt; unmanipulated controls were also maintained (there were no statistical differences between rosette

diameters for those assigned to the five treatments and control; $F = 0.56$, $df = 5, 294$, $P > .50$). The five levels of herbivory included trimming 25 and 75% of the leaves (designated 25L and 75L, respectively), cropping 25 and 75% of the primary root (25R and 75R), and cutting 25% of both leaves and roots (25B). Leaf excision was done with scissors. Root trimming was conducted by placing a wood wedge the appropriate distance from the base of a plant, aligning a sharpened spade blade along the wedge surface, and shoving it into the ground until it severed the root. The appropriate wedge angle and distance from the plant base were determined after many trials using extra plants.

The treatments and controls were used to investigate two separate features of the target plants. One involved an analysis of plant biomass and production measures in relation to the treatments. Fifty plants were manipulated for each treatment and the controls; immediate postmanipulation losses reduced the number of each available for analysis during 1987 to 31–38. For these, the number of flowers produced, the number chewed off, the maximum height of each plant, and the date of death for those that died during the summer were recorded throughout the summer of 1987. Plants were harvested on 25 August (after most had stopped flowering), dried, and the biomasses of root and leaf tissues were recorded (leaf here refers to all aboveground tissues, including stems, except seeds). At the time of harvest most or all of the plants in the more severe treatments (those involving root trimming) were already dead.

Comparing all plants in each treatment, whether dead or alive at the time of harvest, integrates the effects of several treatment-generated factors (e.g., mortality, altered growth, and flower production rates). However, this also confounds analyses of the effect of each factor. To separate the effects of mortality, per se, from the other effects, comparisons between treatments of total biomass and number of flowers produced and missing utilized only those individuals alive at the earliest average date of death for any treatment (20 July, for individuals in treatment 25B). Only plants alive on 20 July (but harvested on 25 August; $n = 12–31$, depending on treatment) were used for analyses of biomass and flower production. A concurrent study on the phenology of *T. dubius* indicated that virtually all plants had stopped growing by 20 July (S. C. Smith, *personal observation*). The use of plants alive on this date provides a larger sample size for analysis (especially in treatments exhibiting nearly 100% mortality by the harvest date), while eliminating virtually all individuals whose early death and commensurate small size would have confounded the influences of mortality and the treatment effects.

Replicated goodness-of-fit tests were used to determine whether there were differences in mortality rates between the treatments. One-way ANOVA was used to detect whether differences existed between treat-

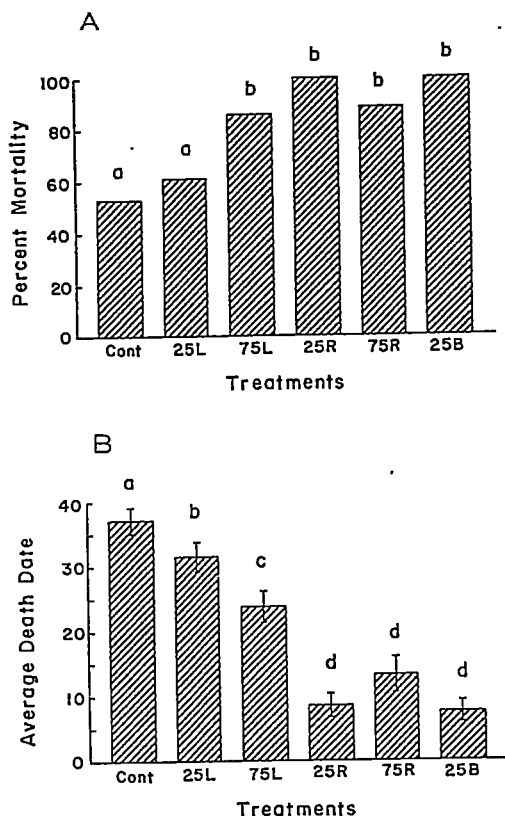


FIG. 1. The effect of treatments on percent mortality (A) and average date of death (B; average number of days plants in each treatment died after 13 July, the date of the first recorded death; the few plants that were still alive at harvest were assigned the maximum value [43]). Treatment codes indicate removal of, e.g., 25% of plant leaves (L), roots (R), or both (B). Bars (means) sharing letters are statistically indistinguishable, and vertical lines in graph B indicate ± 1 SE around the means. The number alive at the beginning of the season, from left to right, were 32, 31, 36, 39, 34, and 36.

ments in biomass, number of flowers (or capitula, for a composite) produced and percent missing (the latter using arcsine-transformed data), and maximum height. Variances among treatments were positively correlated with means (i.e., variances were not equal; $\chi^2 = 165.4$, $df = 30-38$). Therefore, the raw data were log transformed before analysis (Sokal and Rohlf 1981). Where differences between means were detected, Tukey-Kramer separation procedures were applied. A Wilcoxon signed-rank test was used to analyze differences in plant biomass and flower production between plants that were and were not eaten, and t tests, using arcsine-transformed data, were used to determine if the percent of flowers missing was different for plants that died before harvest and those that did not.

The second component of the investigation involved an analysis of leaf, root, and seed tissue for nitrogen and phosphorus concentration in relation to the treatment and time since the treatments were applied. No distinctive patterns for phosphorus concentration were

evident, so these results are not reported. Three plants were harvested from each treatment and the controls, four times during the summer (at 1, 34, 65, and 98 d from the imposition of the treatments; these plants came from a different set than those used for the biomass and production analyses). Three plants were also harvested prior to manipulation and served as the pre-manipulation samples for all treatments. All harvested plants were dried at 60°C for 5 d, and aboveground plant parts, roots, and seeds were weighed separately. Tissue from the harvested plants was used for nitrogen analysis with a Technicon Autoanalyzer II following tissue digestion by the Kjeldahl method. Two-way ANOVA (treatment \times sampling period) was used to determine if differences occurred between values (using arcsine-transformed percentages; variances were statistically indistinguishable), and Tukey-Kramer a posteriori separation procedures were employed to detect where differences occurred.

The simulated herbivory treatments were imposed on the same day for all aspects of the study, and the treatments were randomly assigned to individual plants within the field. It should be noted that the period during which the experiment was run was one of extreme drought in central Minnesota.

RESULTS

The average total and root biomasses for bean plants with roots trimmed by pocket gophers were 0.234 and 0.040 g, respectively, while for plants trimmed with scissors the equivalent values were 0.239 and 0.041 g. These values are not significantly different for the two types of root trimming ($t = 0.59$, $df = 29$, $P > .50$ for both total and root biomasses), suggesting that the simulated root herbivory we used would not yield quantitatively different results from actual root herbivory on this plant species by gophers.

The percent of *T. dubius* plants that had died by the time of harvest differed significantly among treatments ($G = 52.16$, $df = 5$, $P < .001$; Fig. 1A). Partitioning the heterogeneity revealed that mortality values in the control and 25L samples did not differ from each other but that both were significantly lower than those of the other treatments. All other treatments suffered high mortality, and none were significantly different from the others (Fig. 1). Furthermore, the average date of death (i.e., number of days past the date the first individual died, on 13 July) differed significantly, with individuals in controls, 25L, and 75L dying later, and all three treatments involving root trimming exhibiting early average death dates ($F = 31.9$, $df = 5$, 207 , $P < .001$; Fig. 1B).

There were significant differences in total, leaf, and root biomasses among the treatments ($F = 10.02$, 12.11 , 2.37 and $P < .001$, $.001$, and $.05$, respectively; all $df = 5$, 139). The patterns of values for total and leaf biomasses were very similar, exhibiting no statistical difference between the controls and 25L, significantly

less biomass for 75L, with 25R, 75R, and 25B significantly lower still (Fig. 2). The patterns of values for root biomass were not substantially different (Fig. 2). No statistical differences were found among controls, 25L, and 75L, all of which were significantly higher than 25R. Values for 75R and 25B were intermediate and not significantly different from either of the other two groups (Fig. 2).

These analyses included only those plants alive on 20 July (see *Methods*). Essentially identical patterns occur if all plants are included, regardless of date of death, although the actual average values for biomass are lower (especially for the more severe treatments, which include many individuals that died early while still small).

Total biomass was significantly correlated with leaf ($r = 0.99$) and root ($r = 0.69$) biomass, root crown diameter ($r = 0.45$), height ($r = 0.33$), and total number of flowers ($r = 0.86$; all $df = 144$, $P < .001$). Leaf biomass also was well correlated with other measures of plant production, but root biomass always exhibited a lower correlation coefficient when compared to the same variable.

The total number of flowers produced throughout the summer differed significantly among treatments ($F = 16.22$, $df = 5$, 139 , $P < .0001$; Fig. 3) in a pattern similar to that for total biomass. Specifically, the control plants produced the greatest number of flowers, and all treatments with any root trimmed produced the fewest (Fig. 3). Treatments with leaf tissue trimmed were intermediate.

Very little leaf herbivory was noted on mature *T. dubius* plants, but flowers were often chewed off by vertebrate herbivores (primarily deer). The 75R plants lost a significantly lower percentage of their flowers (3%; missing/produced ratio in Fig. 3) than the other

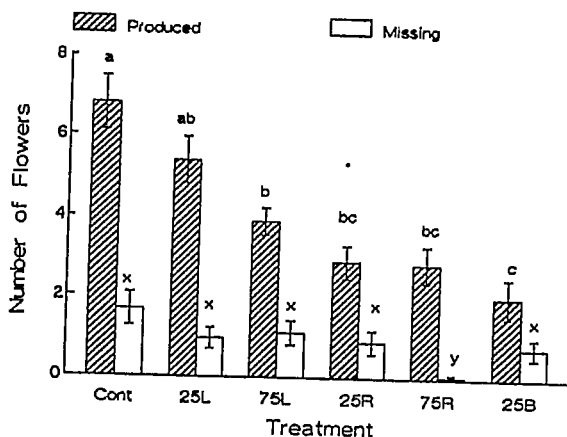


FIG. 3. The total number of flowers produced and missing (chewed off by herbivores) for the six treatments. Bars (means) sharing letters within either group are statistically indistinguishable; vertical lines indicate ± 1 SE. Samples sizes are as noted in Fig. 2 legend.

treatments, which were statistically indistinguishable from each other ($F = 4.01$, $df = 5$, 139 , $P < .005$).

An interesting pattern of total biomass and total number of flowers produced was exhibited by plants that had one or more flowers chewed off compared to those that lost no flowers (Fig. 4). Comparisons between these two categories within each treatment indicate that significant differences in total biomass occurred for the controls and for the two leaf-trimmed treatments (Fig. 4; all plants, regardless of date of death, were used, as comparisons are within and not between treatments; all plants produced at least one flower). More striking, all but the 75R treatment exhibited significant differences between the two categories in total number of flowers produced. In all cases, those plants missing one or more flowers were larger and produced more flowers than their counterparts without missing flowers. A Wilcoxon's signed-ranks test indicates that this is a significant difference across all treatments ($T = 0$, $P < .03$).

Few interpretable patterns were obvious in analyses of nitrogen concentration in leaf, root, and seed tissues following treatment (Figs. 5 and 6). In many cases, the most pronounced differences between treatments occurred shortly after manipulations were applied; subsequently, differences moderated and values tended to converge by the time of harvest (98 d postmanipulation).

The 25L and 25R treatments maintained significantly higher percent nitrogen levels in leaf tissue 1 d after manipulation than the other treatments ($F = 6.12$, $df = 4$, 14 , $P < .005$; Fig. 5). Subsequently, no statistical differences were found among treatments, although it is interesting to note that by 98 d all three treatments that involved root trimming were lower than those that had intact roots (Fig. 5). Values for percent nitrogen in the roots showed a wide range of variation among

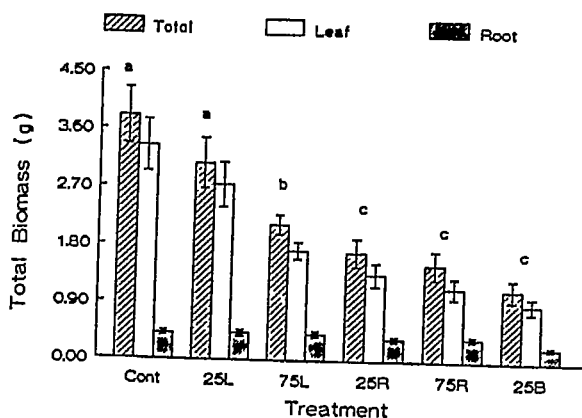


FIG. 2. Total, leaf, and root biomasses of plants in relation to treatments (codes as in Fig. 1). Vertical lines indicate ± 1 SE; bars (means) within each tissue group sharing letters are statistically indistinguishable (i.e., total and leaf biomasses exhibit identical patterns and no differences occurred between root samples). Sample sizes: Control = 31, 25L = 30, 75L = 30, 25R = 14, 75R = 17, and 25B = 12.

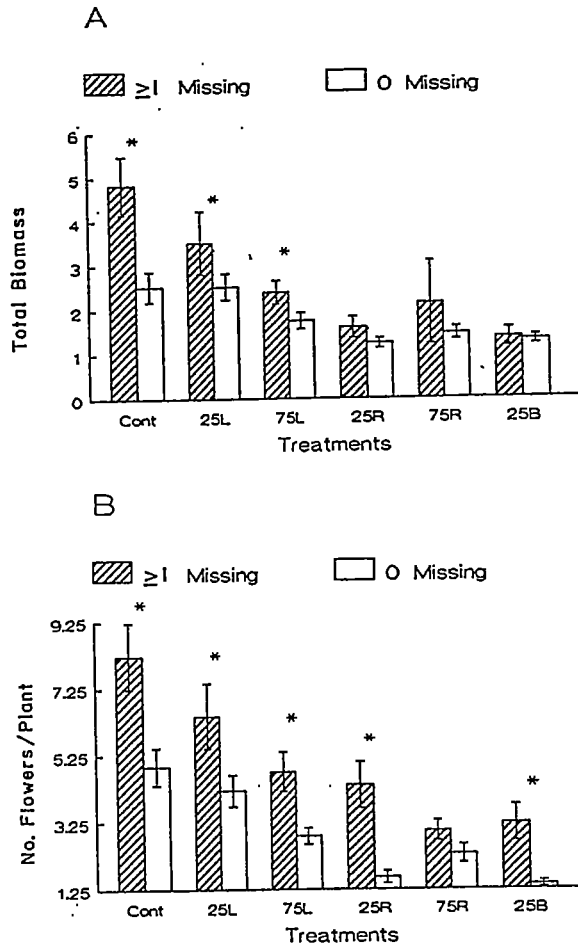


FIG. 4. Total biomass (A) and total number of flowers (B) produced for plants missing one or more flowers and those with all flowers intact. Bars give means; vertical lines show ± 1 SE. Asterisks indicate those pairs of values that are statistically distinct from each other. Sample sizes for each pair (>0 missing, 0 missing) in a treatment are Controls, 20, 12; 25L, 17, 14; 75L, 17, 19; 25R, 12, 27; 75R, 2, 32; and 25B, 13, 23.

treatments. Both treatments with 25% of their leaves trimmed (25L and 25B) showed high root nitrogen levels, while other treatments exhibited significantly lower values (Fig. 5). Percent nitrogen levels were approximately twice as high in seed tissues as in leaf or root tissues (Fig. 5). There were no distinguishable differences among treatments in percent nitrogen in the seeds until 98 d postmanipulation, when 75L and 75R treatments had relatively low values (Fig. 5).

The differences among treatments in total biomass (at the time plants were harvested) were very similar to those found in the first portion of this study (see Fig. 2). In addition, data in this portion of the study show the changes in biomass through time rather than just at the time of harvest (although sample sizes are small, two or three plants for each treatment each sampling period). When these values are applied to nitrogen con-

centration values (Fig. 5), the total nitrogen per tissue and per plant can be estimated. We could not calculate the total amount of nitrogen in seeds because not all seeds were harvested. This also means that values for total plant nitrogen content are inaccurate by the amount that would have been present in the total seed

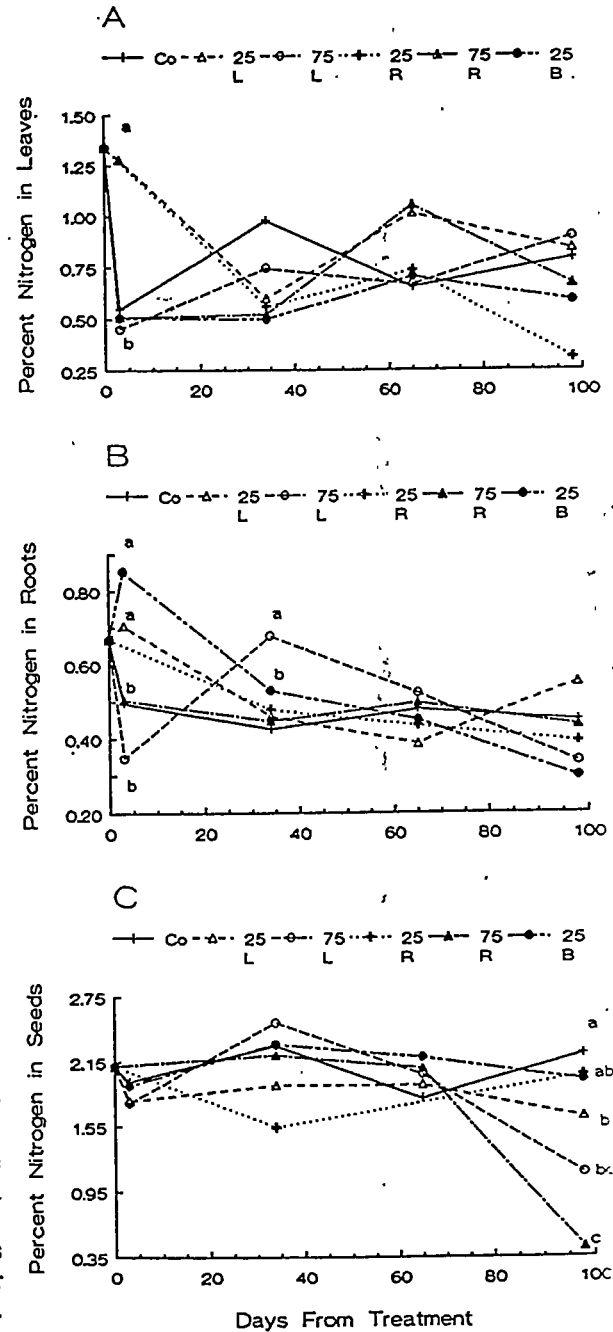


FIG. 5. Nitrogen concentration (% of dry mass) in leaf (A), root (B), and seed (C) tissue in relation to treatment and number of days postmanipulation. Letters indicate sampling periods during which statistical differences occurred. In those cases, values sharing letters are statistically indistinguishable

production (a relatively small biomass compared to the biomass of root and leaf tissue).

Immediately following the manipulations, total leaf nitrogen fell substantially in all treatments except 25L; subsequently, all treatments showed an erratic recovery (Fig. 6A). By 98 d postmanipulation, the controls had significantly higher total nitrogen levels in the leaves than any of the treatments, due primarily to their significantly larger size by this time (Fig. 6A). Total root nitrogen was highly variable among treatments immediately after manipulation, but values converged by 34 d postmanipulation (Fig. 6B). Subsequently, the values for controls rose and stayed relatively high compared to the treatments (Fig. 6B). Total plant nitrogen showed a very similar pattern (Fig. 6C).

DISCUSSION

Although some studies have shown differences in the effects of simulated and natural aboveground herbivory on plants (Dyer and Bokhari 1976, Capinera and Roltsch 1980, Havlickova 1982), our results using red bean plants and pocket gophers indicate that for these species there are no differences between simulated and natural root herbivory. We recognize that individual plant species may have idiosyncratic responses to herbivory, and that *Castor* is not a close relative of *T. dubius*. The results from red beans, however, indicate that there is no broadly overriding difference between simulated and actual root herbivory on plants, and therefore we assume that our mechanical root herbivory was an adequate simulation of actual root herbivory. Clearly, more thorough and meaningful analyses of this phenomenon could be undertaken.

Mortality figures indicated that the controls and 25L treatments did not differ significantly, and that both were substantially lower than the other treatments (Fig. 1). Thus, it appears that a modest loss of leaf tissue does not substantially increase mortality in *T. dubius*, while greater leaf loss and any form of root loss does reduce survivorship.

Patterns of total biomass suggest that root loss has a greater effect than leaf loss (Fig. 2). This is a complicated comparison, however, because the 25L and 25R treatments did not result in comparable absolute losses of tissue. Roots made up only $\approx 12\%$ of the total biomass (see controls in Fig. 2); thus, a 25% loss of root tissue represents a substantially smaller total tissue loss than in the 25L treatment. This, however, actually emphasizes the effect of root loss. For example, the loss of 0.101 g of root tissue (25% of root biomass for controls) yielded a 2.44-g reduction in total biomass (comparing controls to 25R), while a loss of 0.833 g of leaf tissue (25% of leaf biomass for controls) yielded a 2.06-g reduction in total biomass (controls vs. 25L). A comparison of the ratios of root or leaf tissue trimmed to the reduction in total biomass for the 25R and 25L treatments, respectively, reveals a 12-fold difference in gram-equivalent effect.

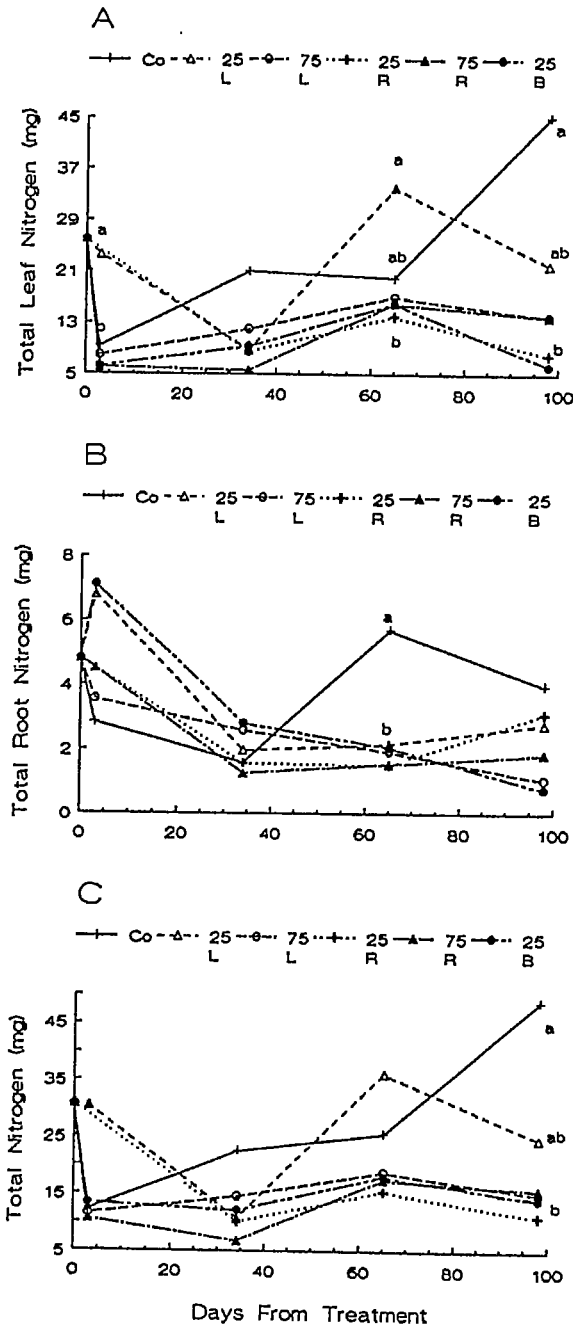


FIG. 6. Total nitrogen in leaf (A), root (B), and total plant (C; less nitrogen in seeds, which was omitted because not all seeds were harvested) in relation to treatment and days postmanipulation. Letters indicate sampling periods during which statistical differences occurred. In those cases, values sharing letters are statistically indistinguishable.

The disproportionate effect of root loss may be especially true for nutrient-poor soils such as those at CCNHA (Chapin 1980). Citing similar evidence, Detling et al. (1980) suggest that belowground herbivores may control primary production out of proportion to

their biomass or consumption rates. There was no overcompensation for leaf loss by *T. dubius*, as has been noted in other systems (Paige and Whitham 1987, Hendrix and Trapp 1989). Instead, the final difference in leaf biomass between the controls and the 25L treatments (a statistically insignificant difference) was 23.8%, essentially the same as the original loss of 25% of the leaf tissue. There was some compensation in the 75L treatments, which ended up with just 50% less leaf tissue in the final analysis. Thus, while neither leaf-trimmed treatment overcompensated, the 25L plants kept pace with the controls and the 75L treatments regained more tissue than they originally lost, on a percentage basis (Fig. 2).

The 25R treatments ended up with approximately the same deficit in the final samples (30% less root tissue than the controls), while the 75R plants ended up with only a 15% deficit. We cannot explain this peculiar pattern. Root loss, regardless of amount and whether coupled with leaf loss, yielded similar, substantial, reductions in total and leaf biomass (Fig. 2). The rather minimal deficit in root tissue in the root-trimmed treatments compared to the substantial reduction in leaf tissue suggests that plants losing root tissue repair that damage before increasing leaf production. This may be either an evolved response (i.e., an evolutionary strategy), or a simple result of resource acquisition patterns that initially involve the roots.

In summary, root loss had a greater effect on plant survivorship and biomass production than equivalent (by percent) leaf loss. When root tissue was lost, the plants tended to reduce that deficit before producing additional aboveground biomass (Fig. 2).

The effects of treatments on biomass translated into differences in the total number of flowers produced by plants (Fig. 3). Control plants produced the greatest number of flowers, while those treatments involving root trimming produced significantly fewer. The leaf-trimmed treatments were intermediate. Assuming that the total number of flowers produced is a measure of reproductive output (we were not able to collect all seeds produced), the various types of simulated herbivory had significant effects on the reproductive potential of *T. dubius*.

All of the treatments except 75R lost approximately the same number of flowers to herbivores (Fig. 3). However, because the treatments produced a different total number of flowers, the percent of flowers lost to herbivory varied substantially (the ratio of flowers missing to total produced in Fig. 3). It is unclear why the 75R plants lost so few flowers relative to the number produced (which was indistinguishable from the 75L, 25R, and 25B treatments; Fig. 3). The 75R plants were no shorter than the other plants, and so were no less apparent. They may have been less nutritious, but results from tissue samples indicate that the 75R plants had as much or more nitrogen in them as the other plants (Figs. 5 and 6).

Because of the pattern of branching and flower development at the terminus exhibited by *T. dubius* (which flowers indeterminately and sequentially), we were able to use the number of flowers missing as an index of the level of herbivory. One of the most interesting results of this study is that those plants that had one or more flowers chewed off eventually weighed more and produced more total flowers than those that were not missing any flowers (Fig. 4). We had not anticipated this pattern of increased plant mass and flower production, so we did not record when individual flowers were eaten and plant size at that time. Such data would allow us to determine whether the increased size and flower production was a result of herbivory, or whether plants that were already larger and had a greater number of conspicuous flowers were more apparent to consumers.

Circumstantial evidence, however, suggests that observed differences were induced by herbivores (Hendrix 1979, Paige and Whitham 1987). For example, the plants started out statistically indistinguishable in size and life stage (just beginning to bolt), they were all from a relatively uniform 2 ha area, and the conditions under which the plants were manipulated tended to make them fairly uniform in size. The plants with and without missing flowers were also statistically indistinguishable in height at the time of harvest, suggesting that plants with a higher mass were not taller, such that they might draw the attention of a vertebrate herbivore. Furthermore, phenology data from another experiment in the same field indicate that *T. dubius* plants that had rosette sizes statistically similar to those used in this experiment did not yield size (in this case height rather than mass) or flower number cohorts by the time plants in our treatments were harvested. This suggests that there were not groups with inherent differences as large as those we measured in relation to flower consumption patterns.

Finally, while the pattern was consistent across almost all treatments, the most significant effect was seen in the controls. These plants lived the longest, grew the largest, and exhibited the greatest difference between browsed and unbrowsed plants in flower production, revealing the strong influence of herbivores. Importantly, there was no difference among treatments in the percent of flowers browsed, suggesting that there were not inherent nutritional differences affecting herbivore choice or, presumably, plant growth and reproduction characteristics. While considerably more work needs to be done on this plant, the system appears to be appropriate for answering important questions about the effect of defoliation on plant reproductive success.

Only individuals alive on 20 July were included in the calculations for biomass and flower production. We also did calculations including all individuals, regardless of date of death. This approach yields an integrated measure of the effects of mortality, as mediated through early death, and of the effects of factors such as reduced

growth and flower production rates. The overall patterns are the same among treatments, although the absolute values are lower than those involving only plants that lived until late in the season.

Few consistent patterns emerge from an analysis of nitrogen allocation patterns in response to treatments. In general, the greatest effects were seen shortly after manipulation, and values tended to converge over time. There was a weak trend for root-trimmed treatments to have the lowest values for nitrogen by the end of sampling (98 d postmanipulation).

Comparisons among tissues reveal that seeds had approximately twice the nitrogen concentration of leaves and roots. Because there were so few statistically significant differences among treatments through time, values for total nitrogen tended to mimic values for total biomass, where significant differences did occur among treatments. Thus, controls eventually produced the highest nutrient concentrations, with those for the treatments arrayed significantly lower.

Sample sizes for nutrient analysis were small (2 or 3), which may have interfered with the statistical analyses. However, even where statistical differences did not occur there were no obvious trends, so this portion of the study produced equivocal results.

Tragopogon dubius, like most plants in natural settings, is subjected to myriad depredations. Large vertebrates consume substantial portions of its above- and belowground biomass, and there are, no doubt, numerous small herbivores that also prey on the plant. These influences, coupled with those associated with the competitive environment in which individual plants grow (O. J. Reichman, unpublished manuscript), generate a continuum of forces that operate over ecological and evolutionary time. Accordingly, plants have an array of complex responses, such as those exhibited by *T. dubius*. Maschinski and Whitham (1989) point out that as studies of compensation by plants in response to herbivore impacts become more sophisticated, consideration of complex microsite and temporal variables will be necessary to yield more accurate information about the relationships between the consumer and the consumed.

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