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REGULAR ARTICLE

# Response of four temperate grasses to defoliation height and interval

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## ABSTRACT

Vegetative-stage meadow fescue [*Schedonorus pratensis* (Huds.) P. Beauv.], orchardgrass (*Dactylis glomerata* L.), reed canarygrass (*Phalaris arundinacea* L.), and quackgrass [*Elymus repens* (L.) Gould] tillers grown in the greenhouse were clipped to 5- or 10-cm height every 7, 14, 21, 28, or 35 days for two growth cycles and sampled after 7, 14, 21, or 28 days of regrowth. Grasses produced greater number of tillers, herbage dry weight, and root dry weight when defoliated to 10- compared to 5-cm height. Herbage and root dry weight of most grasses exhibited a quadratic increase in response to defoliation interval. The increase in herbage dry weight with increasing defoliation interval and regrowth time was due to an increase in average herbage dry weight per tiller in orchardgrass, but to an increase in number of tillers per plant in other grasses.

**Key Words**: *temperate grass; defoliation interval; defoliation height.*

## INTRODUCTION

The effects of defoliation on the growth of temperate grasses have been well-documented. Due to its widespread use and high nutritive value that is desirable for livestock production (Jung et al. 1996), ryegrass (*Lolium perenne* L.) response to defoliation has probably been studied more than in any other temperate grass. Ryegrass herbage yield decreases as the frequency of defoliation increases (Dale et al. 2008, Donaghy et al. 1997, Vinther 2006), and the detrimental effect of frequent defoliation on productivity and persistence is amplified as defoliation height is decreased (Fulkerson 1994; Fulkerson and Slack 1995). The effects of a shorter defoliation interval on above-ground growth have been attributed to reduced water soluble carbohydrate content of the stubble (Fulkerson and Slack 1995), N uptake and allocation to growing leaves (Lestienne et al. 2006), tiller production (Fulkerson 1994), and root growth (Vinther 2006).

Similar to ryegrass, increased herbage productivity is associated with increasing defoliation interval in tall fescue [*Lolium arundinaceum* (Schreb.) Darbysh.; Burns et al. 2002], orchardgrass and meadow fescue (Brink et al. 2010), reed canarygrass and smooth bromegrass (*Bromus inermis* Leyss.; Marten and Hovin 1980), and Kentucky bluegrass (*Poa pratensis* L.; Bryan et al. 2000). Response to defoliation height, however, is often specie-dependent. Brink et al. (2010) found that reducing the clipping height of tall fescue, meadow fescue, and orchardgrass from 10 to 5 cm increased annual yield of all three grasses over two years, but only orchardgrass exhibited a decline in persistence as a result of the shorter clipping height. In contrast, Volesky and Anderson (2007) reported that both productivity and persistence of irrigated orchardgrass, smooth bromegrass, creeping foxtail (*Alopecurus arundinaceus* Poir.), and meadow bromegrass (*Bromus riparius* Rhem.) declined as clipping height was reduced from 14 to 7 cm.

Although defoliation effects on temperate grass productivity are important, a better understanding of the mechanisms underlying these effects production responses in different grasses is needed. Cullen et al. (2006), for example, found that orchardgrass possessed greater defoliation tolerance than ryegrass, phalaris (*Phalaris aquatica* L.), and tall fescue due to a high leaf sheath:stem ratio, which permitted a sufficient level of photosynthesis to initiate regrowth after defoliation. Unlike the manner of defoliation (remove all herbage except one-half of one leaf every 3 to 4 d) imposed by Cullen et al. (2006), however, we sought to compare the responses of four temperate grasses typically utilized in North America to defoliation height and interval under representative grazing practices.

## MATERIALS AND METHODS

The experiment was conducted in a greenhouse at Madison, WI (43°4′31″N-89°25′6″W) beginning in October of 2007 and 2008 and ending the following February. Vegetative tillers (stage V3 to V4; Moore et al. 1991) of meadow fescue, orchardgrass, quackgrass, and reed canarygrass were dug to 20-cm depth in early September from rotationally-grazed pastures of the same species located near Prairie du Sac, WI (43°20′24″N-89°43′12″W) and placed intact with soil in plastic tubs (40 by 30 by 20 cm) in a greenhouse. In early October, single tillers of each grass having three collared leaves were washed until free of soil and roots were trimmed to 5-cm length. Tillers were then selected for uniformity and transplanted into Super Cell Cone-tainers (4-cm diameter, 21-cm length, 164 ml volume; Stuewe & Sons, Corvallis, OR) containing a 1:2:1 mixture by volume of commercial topsoil, washed sand, and Pro-Mix media (Premier Brands, Inc., New Rochelle, NY) that had been amended with 5.0 g Osmocote slow-release fertilizer (14-14-14; Scotts, Marysville, OH).

All tillers were clipped to a 10-cm height 21 d after transplanting. After reaching a mean height of 25 cm (longest extended leaf), tillers of each grass were clipped to either a 5- or 10-cm height. Tillers were then permitted to grow for 7, 14, 21, 28, or 35 d, and clipped again to either a 5- or 10-cm height. This cycle was repeated, with herbage harvested after each defoliation interval discarded. After the final clipping, tillers were permitted to grow for 7, 14, 21, or 28 d and then destructively sampled. At each destructive sampling, the number of tillers was counted, and each plant was dissected at soil level into herbage and roots. Root material was gently washed with water over a 2-mm screen until free of soil. Herbage and root material were dried for 48 h at 60ºC and weighed.

A split-split-plot arrangement of a randomized complete block design with six replicates was employed on the greenhouse bench with grass species as the whole plot, defoliation interval (7, 14, 21, 28, or 35 d) as the sub-plot, and a factorial combination of defoliation height (5 or 10 cm) and regrowth time before destructive sampling (7, 14, 21, and 28 d) as the sub-sub-plot. Cone-tainers were watered daily to field capacity after transplanting. Ambient light was supplemented from 700 to 1900 h with high-pressure sodium vapor lights that provided 208 W $m^{-2}$ measured 10 cm above the soil surface during a 12-h photoperiod. Average temperature of the greenhouse was 22.6º C during the day and 17.6º C during the night.

Data were subject to generalized linear models analysis assuming all treatment effects to be fixed, while replicates and all split-plot error terms were assumed to be random effects. Preliminary analyses indicated that there were no significant ($P \leq 0.05$) or biologically meaningful interactions of treatment effects with year, and the two years had homogeneous variances. Thus, the six replicates in each year were pooled to act as 12 replicates. Preliminary analysis also indicated strong evidence of interactions for grass species with all three management factors: defoliation interval, defoliation height, and regrowth time. Defoliation interval and regrowth time were partitioned into polynomial regression terms using contrasts (linear, quadratic, cubic, and residual for defoliation interval; linear, quadratic, and residual for regrowth time). All possible two- and three-factor interactions involving defoliation interval, regrowth time, and defoliation height were computed using contrasts (39 single-degree-of-freedom contrasts). Because the full model, including all 39 contrasts and their interactions with grass species, would not converge despite numerous attempts to alter the convergence criteria, the model with 39 fixed effects was run separately on each of the four species. The negative binomial distribution with the log link function was used for tiller number and the normal distribution was used for herbage and root mass using SAS Proc GLIMMIX (Gbur et al. 2012). Because many interaction effects may be significant but account for little meaningful variation, type I sums of squares (SS) for all sources of variation were used to compute the percentage of SS associated with each effect. Type I SS were computed in reverse using F-values and estimates of random effects for each portion of the split-plot analysis using the formula $SS_i = MS_e(F_i)$, where $SS_i$ = the type I SS for the $i^{th}$ fixed effect with 1 df, $MS_e$ = the error mean square for the correct portion of the split-plot analysis, and $F_i$ = the F-value for the $i^{th}$ fixed effect (Littel et al. 2002). Error mean squares for each portion of the split-plot analysis were constructed in a similar manner, using the residual covariance estimates and formulas for expected mean squares as described in Steel et al. (1997).

Main effects and interactions were deemed to have biological significance by a combination of $P$-value and contribution of the SS. If the $R^2$ for the linear term describing response to defoliation interval or regrowth time was 0.95 or greater, then all non-linear terms were ignored regardless of their significance. If the SS associated with a significant ($P \leq 0.05$) interaction accounted for less than 5% of the variation, the interaction was also ignored.

## RESULTS

### *NUMBER OF TILLERS*

The general linear models analysis indicated that the main effects of defoliation interval (linear term), defoliation height, and regrowth time (linear and quadratic term for all grasses except orchardgrass) accounted for approximately 96, 87, 92, and 84% of the treatment sums of squares for number of tillers of meadow fescue, orchardgrass, quackgrass, and reed canarygrass, respectively (Table 1). All cubic terms, as well as most two- and three-factor interactions were not significant ($P \leq 0.05$), and those that were significant usually accounted for less than 2% of the overall sums of squares for all treatment effects, and were not considered biologically important.

Table 1. Significance of (*P*-value) and sums of squares (SS) attributed to the main effects and all two- and three-factor interactions of defoliation interval, defoliation height, and regrowth time for number of tillers produced by four grasses.

| | Meadow fescue | | Orchardgrass | | Quackgrass | | Reed canarygrass | |
|---|---|---|---|---|---|---|---|---|
| | *P*-value | SS | *P*-value | SS | *P*-value | SS | *P*-value | SS |
| | | % | | % | | % | | % |
| Interval, linear (IL) | <0.0001 | 78.7 | <0.0001 | 75.8 | <0.0001 | 78.4 | <0.0001 | 66.6 |
| Interval, quadratic (IQ) | 0.3506 | 0.1 | 0.3246 | 0.4 | 0.0155 | 1.1 | 0.0248 | 0.9 |
| Interval, cubic (IC) | 0.6369 | 0.0 | 0.8877 | 0.0 | 0.5733 | 0.1 | 0.5641 | 0.1 |
| Interval, residual (IR) | 0.2639 | 0.1 | 0.2460 | 0.5 | 0.5224 | 0.1 | 0.3087 | 0.2 |
| Height (H) | <0.0001 | 5.2 | <0.0001 | 8.4 | <0.0001 | 8.1 | 0.0267 | 0.8 |
| Time, linear (TL) | <0.0001 | 11.4 | 0.0098 | 2.6 | <0.0001 | 4.2 | <0.0001 | 13.7 |
| Time, quadratic (TQ) | 0.0111 | 0.6 | 0.4442 | 0.2 | 0.0233 | 1.0 | 0.0001 | 2.6 |
| Time, residual (TR) | 0.9928 | 0.0 | 0.8310 | 0.0 | 0.0986 | 0.5 | 0.5648 | 0.1 |
| IL*H | 0.0003 | 1.2 | 0.2571 | 0.5 | 0.2416 | 0.3 | 0.0143 | 1.0 |
| IQ*H | 0.9102 | 0.0 | 0.3878 | 0.3 | 0.3416 | 0.2 | 0.2730 | 0.2 |
| IC*H | 0.6927 | 0.0 | 0.7076 | 0.1 | 0.0923 | 0.5 | 0.1443 | 0.4 |
| IR*H | 0.7975 | 0.0 | 0.9186 | 0.0 | 0.4726 | 0.1 | 0.5868 | 0.1 |
| TL*H | 0.0067 | 0.7 | 0.3768 | 0.3 | 0.5325 | 0.1 | <0.0001 | 3.5 |
| TQ*H | 0.4901 | 0.0 | 0.3294 | 0.4 | 0.0732 | 0.6 | 0.2403 | 0.2 |
| TR*H | 0.1969 | 0.2 | 0.4304 | 0.2 | 0.2970 | 0.2 | 0.0605 | 0.6 |
| IL*TL | 0.0988 | 0.3 | 0.1070 | 1.0 | 0.4483 | 0.1 | 0.0007 | 2.0 |
| IL*TQ | 0.2304 | 0.1 | 0.5013 | 0.2 | 0.7293 | 0.0 | 0.0028 | 1.5 |
| IL*TR | 0.4947 | 0.0 | 0.8117 | 0.0 | 0.2043 | 0.3 | 0.5956 | 0.0 |
| IQ*TL | 0.2658 | 0.1 | 0.7523 | 0.0 | 0.3567 | 0.2 | 0.2587 | 0.2 |
| IQ*TQ | 0.1910 | 0.2 | 0.0430 | 1.6 | 0.9176 | 0.0 | 0.2427 | 0.2 |
| IQ*TR | 0.4807 | 0.0 | 0.3262 | 0.4 | 0.4563 | 0.1 | 0.3145 | 0.2 |
| IC*TL | 0.9316 | 0.0 | 0.5577 | 0.1 | 0.3992 | 0.1 | 0.0612 | 0.6 |
| IC*TQ | 0.1412 | 0.2 | 0.0464 | 1.5 | 0.7632 | 0.0 | 0.6342 | 0.0 |
| IC*TR | 0.1803 | 0.2 | 0.9086 | 0.0 | 0.9574 | 0.0 | 0.6118 | 0.0 |
| IR*TL | 0.3556 | 0.1 | 0.3595 | 0.3 | 0.7098 | 0.0 | 0.0441 | 0.7 |
| IR*TQ | 0.5694 | 0.0 | 0.6122 | 0.1 | 0.9527 | 0.0 | 0.0449 | 0.7 |
| IR*TR | 0.8732 | 0.0 | 0.5468 | 0.1 | 0.0235 | 1.0 | 0.1127 | 0.4 |
| IL*TL*H | 0.5063 | 0.0 | 0.3402 | 0.4 | 0.6158 | 0.0 | 0.5985 | 0.0 |
| IL*TQ*H | 0.7110 | 0.0 | 0.0197 | 2.1 | 0.2146 | 0.3 | 0.8244 | 0.0 |
| IL*TR*H | 0.5329 | 0.0 | 0.4263 | 0.2 | 0.9442 | 0.0 | 0.0073 | 1.2 |
| IQ*TL*H | 0.5643 | 0.0 | 0.0667 | 1.3 | 0.6917 | 0.0 | 0.2875 | 0.2 |
| IQ*TQ*H | 0.7266 | 0.0 | 0.4335 | 0.2 | 0.2575 | 0.2 | 0.4472 | 0.1 |
| IQ*TR*H | 0.7469 | 0.0 | 0.7110 | 0.1 | 0.4853 | 0.1 | 0.1709 | 0.3 |
| IC*TL*H | 0.8561 | 0.0 | 0.7663 | 0.0 | 0.4213 | 0.1 | 0.2464 | 0.2 |
| IC*TQ*H | 0.2361 | 0.1 | 0.8731 | 0.0 | 0.9235 | 0.0 | 0.9449 | 0.0 |
| IC*TR*H | 0.9332 | 0.0 | 0.6429 | 0.1 | 0.6976 | 0.0 | 0.9906 | 0.0 |
| IR*TL*H | 0.2066 | 0.2 | 0.6928 | 0.1 | 0.0086 | 1.3 | 0.4447 | 0.1 |
| IR*TQ*H | 0.7404 | 0.0 | 0.9111 | 0.0 | 0.5123 | 0.1 | 0.9291 | 0.0 |
| IR*TR*H | 0.9487 | 0.0 | 0.3490 | 0.3 | 0.0707 | 0.6 | 0.6723 | 0.0 |

On a response scale (count), the effect of defoliation height on tiller production was similar to that measured in the field by Bell and Ritchie (1989) and Volesky and Anderson (2007); grasses defoliated to 5 cm compared to 10 cm produced fewer ($P \leq 0.05$) tillers across all defoliation intervals and regrowth times (Table 2). The general effect of defoliation is to disrupt photosynthesis and carbon transport (Chapman and Lemaire 1993), which leads to a decline in tiller production (Ferraro and Oesterheld 2002). Under rotational grazing of the same grasses tested here at similar maturity, however, Brink et al. (2013) found that reducing residual sward height from 8 cm to 2 cm reduced tiller density of only meadow fescue and quackgrass. The contrasting results suggest that the small but statistically significant ($P \leq 0.05$) effect of defoliation height on tiller number of orchardgrass and reed canarygrass (Table 2) observed here may not be biologically significant in field environments.

Table 2. Defoliation height effects on number of tillers, herbage dry weight, and root dry weight produced by four grasses (mean of five defoliation intervals and four regrowth times).

| Grass | Defoliation ht. | No. tillers | Herbage dry wt. | Root dry wt. |
|---|---|---|---|---|
| | | | ---------------- g ---------------- | |
| Meadow fescue | 5 | 13 | 0.71 | 0.38 |
| | 10 | 16 | 1.26 | 0.58 |
| Orchardgrass | 5 | 6 | 0.90 | 0.32 |
| | 10 | 7 | 1.68 | 0.49 |
| Quackgrass | 5 | 12 | 0.55 | 0.28 |
| | 10 | 15 | 0.99 | 0.41 |
| Reed canarygrass | 5 | 9 | 0.62 | 0.37 |
| | 10 | 10 | 1.11 | 0.56 |

Tiller production of all grasses increased on a response (count) scale with increasing defoliation interval (Fig. 1A; Table 3), as reported by Bell and Ritchie (1989) in prairie grass (*Bromus willdenowii* Kunth). In field environments, however, Brink et al. (2010; 2013) found that tiller density of meadow fescue and orchardgrass was greater when clipped or grazed more frequently. One explanation is that the shortest defoliation intervals employed here (7 days) imposed more stress on plants than those employed by Brink (2010, 2013; 20 to 25 days). Alternatively, the long defoliation interval employed by Brink et al. (2010, 2013; up to 65 days) resulted in fewer plants having more tillers per plant (Langer et al. 1964).

Number of tillers increased during regrowth (Fig. 1B; Table 3), exhibiting a linear (orchardgrass) or quadratic response (meadow fescue, quackgrass, reed canarygrass) to time. Tomlinson and O'Connor (2004) suggested that tiller recruitment is associated with resource availability; tillers are produced in response to increasing carbohydrate supply resulting from photosynthesis of new leaves produced after defoliation.

*HERBAGE DRY WEIGHT*

The general linear models analysis indicated that the main effects of defoliation interval (linear and quadratic term for all grasses except quackgrass), defoliation height, and regrowth time (linear term for all grasses excepted reed canarygrass) accounted for approximately 92, 93, 92, and 94% of the treatment sums of squares for herbage dry weight of meadow fescue, orchardgrass, quackgrass, and reed canarygrass, respectively (Table 4). All cubic terms and two- or three-factor interactions were not significant ($P \leq 0.05$), or were not considered biologically relevant due to low treatment SS (< 5%).

Defoliation height had a greater relative effect on herbage dry weight than on tiller number (Table 4) based on treatment SS. On a response scale, grasses produced nearly twofold more herbage when defoliated at a 10-cm compared with a 5-cm height (Table 2). Volesky and Anderson (2007) found that cutting height had a similar effect on annual yield of field-grown smooth bromegrass, orchardgrass, creeping foxtail, and meadow bromegrass; grasses cut at a greater sward height produced less herbage at each harvest than those cut lower, but were harvested more often over the growing season. In this study, the response of herbage dry weight to defoliation height was attributed more to an increase in average herbage dry weight per tiller (data not shown) than to the relatively small increase in number of tillers exhibited by each grass (Table 2).

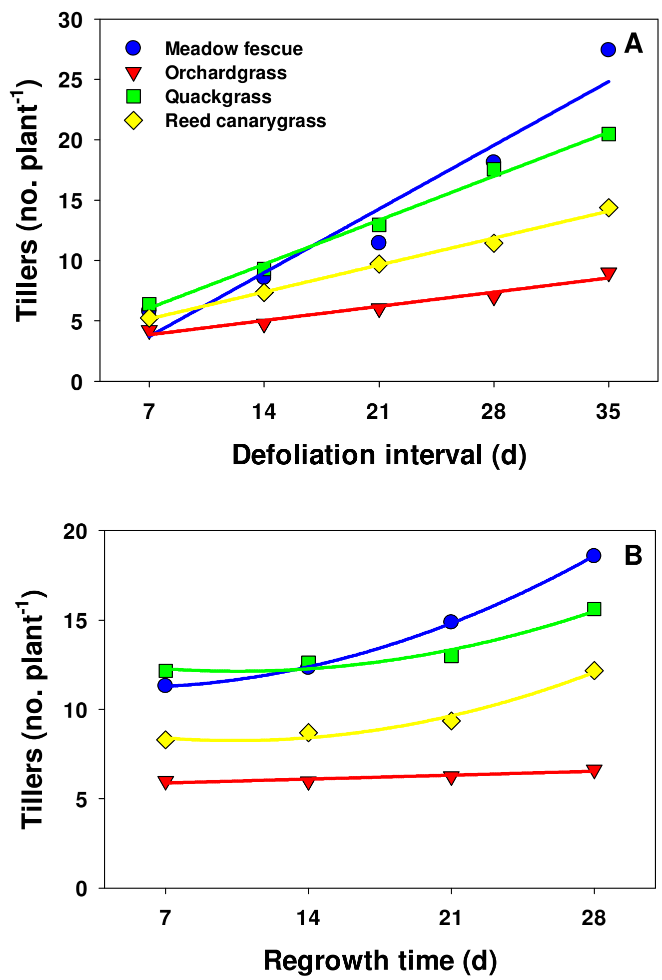


Figure 1.Number of tillers produced by four grasses subject to five defoliation intervals (A; mean of two defoliation heights and four regrowth times) and during four regrowth times (B; mean of two defoliation heights and five defoliation intervals).

Herbage dry weight of all grasses except quackgrass exhibited a quadratic response ($P < 0.0001$) to defoliation interval (Table 4), increasing as interval increased on a response scale (Fig 2A; Table 3). Volenec and Nelson (1983) attributed this response to defoliation interval in tall fescue to greater leaf elongation rate resulting from greater epidermal cell length and greater number of cells matured per day. This mechanism may have been responsible for the herbage dry weight increase of orchardgrass (Singer 2002) but not in the other grasses, which exhibited linear increases in number of tillers (Fig. 1A) and little or no increase in average dry weight per tiller with defoliation interval (data not shown).

Herbage dry weight of all grasses except reed canarygrass exhibited a linear response-scale increase with regrowth time ($P$ < 0.0001; Table 4). Similar to defoliation interval, the increase in herbage dry weight during regrowth (Fig. 2B, Table 3) was attributed primarily to increasing number of tillers in meadow fescue, quackgrass, and reed canarygrass and to increasing average herbage dry weight per tiller in orchardgrass.

Table 3. Regression equations relating number of tillers, herbage dry weight, and root dry weight of greenhouse-grown grasses with defoliation interval (I) and regrowth time (T).

| Trait | Grass | Defoliation interval | $R^2$ | Regrowth time | $R^2$ |
|---|---|---|---|---|---|
| No. of tillers | Meadow fescue | $Y = -1.6 + 0.75I$ | 0.93 | $Y = 11.5 - 0.13T + 0.014T^2$ | 0.99 |
| | Orchardgrass | $Y = 2.7 + 0.17I$ | 0.96 | $Y = 5.7 + 0.03T$ | 0.85 |
| | Quackgrass | $Y = 2.4 + 0.52I$ | 0.99 | $Y = 13.4 - 0.23T + 0.011T^2$ | 0.96 |
| | Reed canarygrass | $Y = 2.9 + 0.32I$ | 0.99 | $Y = 9.6 - 0.26T + 0.012T^2$ | 0.98 |
| Herbage dry wt. | Meadow fescue | $Y = 0.37 - 0.008I + 0.0014T^2$ | 0.99 | $Y = 0.32 + 0.038T$ | 0.98 |
| | Orchardgrass | $Y = 0.65 - 0.029I + 0.0023T^2$ | 0.99 | $Y = 0.52 + 0.044T$ | 0.97 |
| | Quackgrass | $Y = 0.11 + 0.031I$ | 0.98 | $Y = 0.33 + 0.025T$ | 0.96 |
| | Reed canarygrass | $Y = 0.44 - 0.006I + 0.0010T^2$ | 0.99 | $Y = 0.60 - 0.014I + 0.0014T^2$ | 0.99 |
| Root dry wt. | Meadow fescue | $Y = 0.26 - 0.016I + 0.0010T^2$ | 0.99 | $Y = 0.38 - 0.008I + 0.0006T^2$ | 0.99 |
| | Orchardgrass | $Y = 0.28 - 0.013I + 0.0007T^2$ | 0.99 | $Y = 0.36 - 0.006I + 0.0004T^2$ | 0.99 |
| | Quackgrass | $Y = 0.16 - 0.011I + 0.0008T^2$ | 0.99 | $Y = 0.33 - 0.011I + 0.0006T^2$ | 0.99 |
| | Reed canarygrass | $Y = 0.34 - 0.026I + 0.0012T^2$ | 0.99 | $Y = 0.53 - 0.032I + 0.0014T^2$ | 0.99 |

Table 4. Significance of ($P$-value) and sums of squares (SS) attributed to the main effects of defoliation interval, defoliation height, and regrowth time for herbage and root dry weight of four grasses.

| | Meadow fescue | | Orchardgrass | | Quackgrass | | Reed canarygrass | |
|---|---|---|---|---|---|---|---|---|
| | $P$-value | SS | $P$-value | SS | $P$-value | SS | $P$-value | SS |
| | | % | | % | | % | | % |
| **Herbage dry wt.** | | | | | | | | |
| Interval, linear | <.0001 | 55.7 | <.0001 | 55.6 | <.0001 | 48.1 | <.0001 | 45.1 |
| Interval, quadratic | <.0001 | 2.8 | <.0001 | 4.4 | 0.1544 | 0.2 | <.0001 | 2.3 |
| Interval, cubic | 0.0041 | 0.4 | 0.0132 | 0.3 | 0.5718 | 0.0 | 0.1901 | 0.1 |
| Interval, residual | 0.4646 | 0.0 | 0.2723 | 0.1 | 0.0147 | 0.7 | 0.1939 | 0.1 |
| Height | <.0001 | 15.8 | <.0001 | 18.8 | <.0001 | 24.4 | <.0001 | 19.6 |
| Time, linear | <.0001 | 18.1 | <.0001 | 14.3 | <.0001 | 19.6 | <.0001 | 25.5 |
| Time, quadratic | 0.0178 | 0.3 | 0.0026 | 0.4 | 0.0102 | 0.8 | <.0001 | 1.6 |
| Time, residual | 0.9942 | 0.0 | 0.4457 | 0.0 | 0.8140 | 0.0 | 0.1523 | 0.1 |
| **Root dry wt.** | | | | | | | | |
| Interval, linear | <.0001 | 64.8 | <.0001 | 62.8 | <.0001 | 69.3 | <.0001 | 58.4 |
| Interval, quadratic | <.0001 | 6.4 | <.0001 | 7.1 | <.0001 | 6.1 | <.0001 | 8.7 |
| Interval, cubic | 0.0013 | 0.6 | 0.0835 | 0.3 | 0.3439 | 0.1 | 0.0016 | 0.7 |
| Interval, residual | 0.7993 | 0.0 | 0.6245 | 0.0 | 0.9045 | 0.0 | 0.3032 | 0.1 |
| Height | <.0001 | 8.4 | <.0001 | 13.5 | <.0001 | 7.4 | <.0001 | 7.6 |
| Time, linear | <.0001 | 10.8 | <.0001 | 7.5 | <.0001 | 7.2 | <.0001 | 12.9 |
| Time, quadratic | 0.0002 | 0.8 | 0.0099 | 0.7 | 0.0078 | 1.2 | <.0001 | 3.7 |
| Time, residual | 0.6139 | 0.0 | 0.6358 | 0.0 | 0.5984 | 0.0 | 0.7945 | 0.0 |

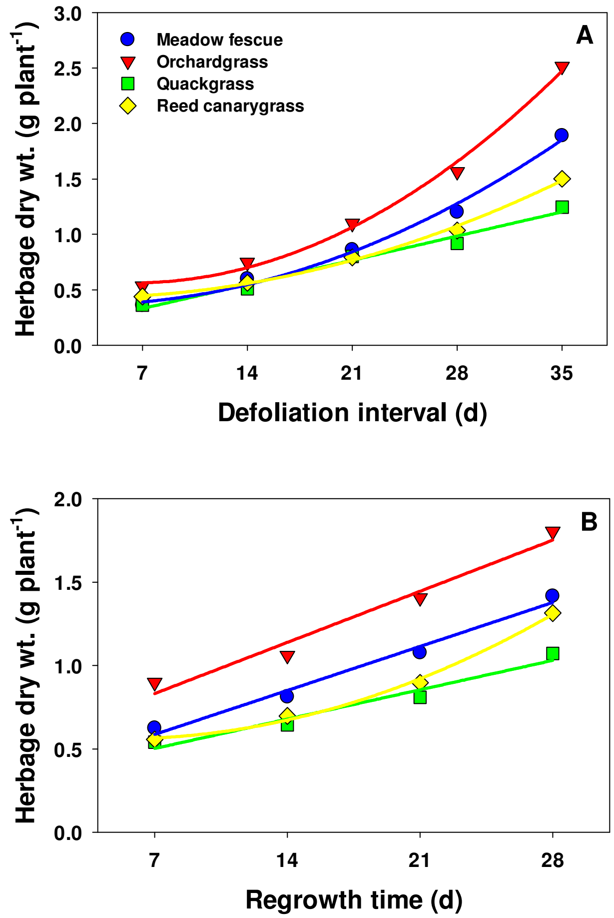


Figure 2. Herbage dry weight produced by four grasses subject to five defoliation intervals (A; mean of two defoliation heights and four regrowth times) and during four regrowth times (B; mean of two defoliation heights and five defoliation intervals).

*ROOT DRY WEIGHT*

General linear models analysis indicated that the main effects of defoliation interval (linear and quadratic term), defoliation height, and regrowth time (linear and quadratic term) accounted for approximately 91% of the treatment sums of squares for root dry weight of all grasses (Table 4). All cubic terms and two- or three-factor interactions accounted for less than 5% of treatment SS, and thus were not considered biologically important.

The effect of defoliation height on root dry weight was significant ($P < 0.0001$) in all grasses, but like tiller number, was less than its effect on herbage dry weight based on treatment SS (Table 4). Defoliation of each grass to a 5-cm height reduced ($P \leq 0.05$) root dry weight by approximately 50% on a response scale compared to 10-cm (Table 2). This effect has been observed in field environments (Richards 1984), and has important implications for sward management. Grazing or harvesting grasses to maintain adequate residual sward height will likely impart greater tolerance to stress such as limited soil water (Frank et al. 1996).

Root dry weight exhibited a quadratic response ($P \leq 0.0001$) to defoliation interval, and based on treatment SS, the response was greater than that measured in herbage dry weight (Table 4). The response-scale increase in root dry weight with increasing defoliation interval (Fig. 3A; Table 3) was a function of both increasing number of tillers (Fig. 2A) and average root dry weight per tiller (data not shown). Greater root growth following longer defoliation intervals may provide faster recovery from the negative effects of defoliation (Hodgkinson and Becking 1977), and the associated effects on nutrient (Lestienne et al. 2006) and water uptake (Frank et al. 1996).

Root dry weight of grasses also exhibited a quadratic response ($P \leq 0.001$) to regrowth time (Table 4), increasing as time of regrowth increased (Fig 3B; Table 3). Evans (1973) found that root elongation of ryegrass, orchardgrass, and timothy (*Phleum pratense* L.) declined from three to five days after defoliation but then increased in a manner similar to that measured here.

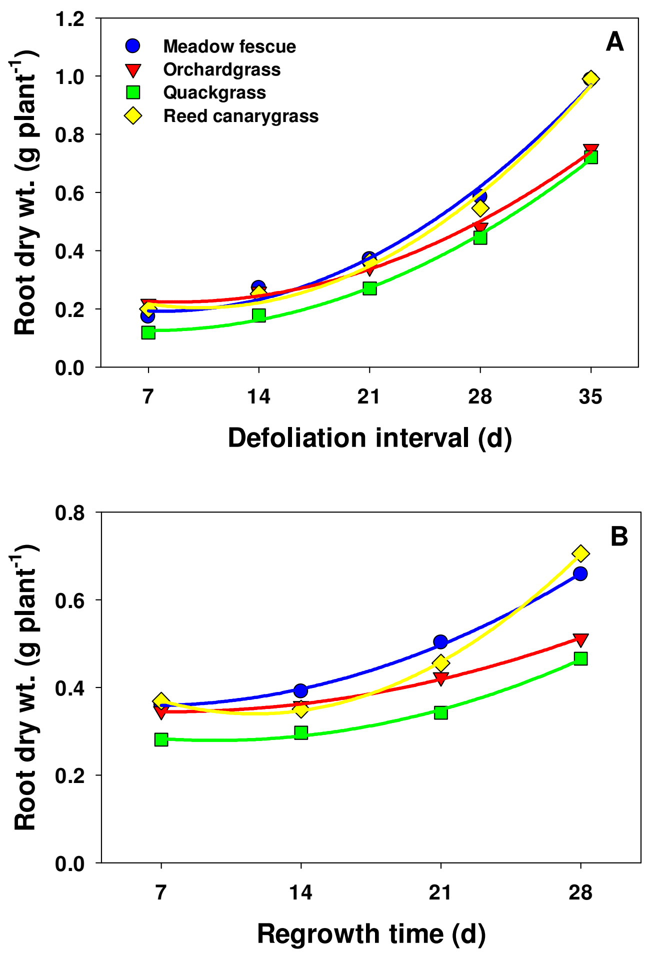


Figure 3. Root dry weight produced by four grasses subject to five defoliation intervals (A; mean of two defoliation heights and four regrowth times) and during four regrowth times (B; mean of two defoliation heights and five defoliation intervals).

## CONCLUSIONS

Grazed temperate grasslands are typically composed of several grass species which may have differing yield potential, growth habit, and sward structure. Unless a grass species possesses physical or chemical properties that inhibit herbivory, periodic defoliation will influence productivity and persistence. The four grass species used in this controlled experiment differ considerably in yield potential, growth habit (bunch and rhizomatous), and sward structure (herbage distribution throughout the canopy and leaf:stem ratio), but the pattern of their responses to height and interval of defoliation were essentially equivalent: productivity and potential persistence declined as defoliation height and interval were reduced. The mechanism by which species express this response may differ, however, such as the increase in herbage dry weight with increasing defoliation interval. In orchardgrass, this was attributed to an increase in herbage dry weight per tiller, but in the other grasses to an increase in the number of tillers. Our analysis also suggests that while interactions among these defoliation variables may be statistically significant, they are likely of little or no biological relevance in these grasses, with the possible exception of meadow fescue. Meadow fescue response to defoliation will require more detailed investigation in field environments to elucidate these effects.

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