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Effects of defoliation height on regrowth of timothy and meadow fescue in the generative and vegetative phases of growth

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Post-defoliation carbohydrate stores, leaf area and the number of active meristems are important factors affecting the subsequent regrowth of grasses. Defoliation height affects the magnitude of all these factors. Timothy (*Phleum pratense* L.) and meadow fescue (*Festuca pratensis* Huds.) are the two most common pasture species in Finland, but little is known about their response to defoliation height. In this study the effect of three defoliation heights, 3, 6 and 9 cm, on the regrowth rates of timothy and meadow fescue in both the generative (June–July) and vegetative (August) phases of growth were examined in two one-year experiment in year 2000 and 2001. In addition, the main post-defoliation parameters were measured and their contributions to regrowth were studied. In June–July 2000 the regrowth rates, kg dry matter ha^{-1} d^{-1}, of both species increased linearly by 19% by increasing the cutting height from 3 to 9 cm. In August 2000 the regrowth rates increased by 27% and the cumulative regrowth dry matter yield increased by 29%. In 2001 the defoliation height had no effect on the regrowth rates but the cumulative regrowth yield increased by 10% by increasing the cutting height. Meadow fescue produced 8–21% higher cumulative regrowth yields than timothy. In the reproductive phase, the regrowth rate of timothy is dependent on the population density of vegetative tillers but for meadow fescue population density did not have such importance. In vegetative phase there was no single factor essential for regrowth rates of either of the species.

Key words: carbohydrates, *Festuca pratensis*, fructans, leaf area index, pastures, *Phleum pratense,* tillering, water soluble carbohydrates

Introduction

In grazed plant communities the regrowth ability of individual plants is of crucial importance. Therefore numerous studies have been undertaken to identify plant responses to defoliation height and frequency as well as to disclose the key factors behind regrowth potential. Generally, four different factors have been identified as

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the main components affecting regrowth. These are the leaf area remaining after defoliation and its photosynthetic capacity (Parsons et al. 1988), stored carbohydrates (more commonly water soluble carbohydrates, WSC; Smith 1967, Davies 1988), stored nitrogen (vegetative storage proteins; Ourry et al. 1996), and the number and status of meristems (Richards and Caldwell 1985). It is logical that the relative importance of these factors is dependent on the plant species and environment as well as the grazing system involved. The most important effects of the grazing system on these four factors are defoliation height and frequency (Fulkerson and Donaghy 2001). Other management factors, such as fertilization, have a marked impact as well.

In a rotational grazing system the defoliation height is a direct consequence of the stocking rate or more precisely the herbage allowance (HA, kg dry matter per cow per day). The lower the HA, the closer the animal will graze the sward, thus leaving less leaf area and less dry matter (DM) per tiller and per m^2 (Virkajärvi et al. 2002). This affects also the carbohydrate pools (biomass x concentration in biomass) per tiller or per m^2, depending on the relative changes in biomass and carbohydrate concentration caused by defoliation height. If the tillers have already shifted to the generative growth phase, those meristems which are elevated above the defoliation height will be removed in defoliation. On the other hand if the animals leave an ample amount of plant material ungrazed, the subsequent regrowth may be rapid but the loss of herbage through senescence will be high and the herbage quality in the next harvest may be low (Parsons et al. 1988).

Although the research done on perennial ryegrass (*Lolium perenne* L.) has been extensive (Parsons et al. 1988, Fulkerson and Donaghy 2001), relatively little is known about the regrowth factors of timothy (*Phleum pratense* L.) and meadow fescue (*F. pratensis* Huds.), the two most important grass species on high latitudes. It is commonly known that these species differ in respect to regrowth potential and drought tolerance, but the difference in response to defoliation height and its morphological and physiological causes are not well known. Of the abovementioned four factors affecting regrowth rate, the residual leaf area, WSC reserves and number of active meristems are of major interest, since the relative N content and total N pools in residual herbage are predominantly determined by nitrogen fertilization, which in turn is largely determined by other, especially environmental reasons. In addition, both timothy and meadow fescue are known to accumulate fructans of different degrees of polymerization (Pollock and Jones 1979). The degree of polymerization may play an important role for regrowth potential as well. For example, according to Volaire and Gandoin (1996), increased death rates of cocksfoot (*Dactylis glomerata* L.) under drought have been associated particularly with a low proportion of high degree polymerization fructans.

Therefore, a field study was conducted to find out whether timothy and meadow fescue respond differently to defoliation height in regrowth potential. Furthermore, the importance of number of active meristems, residual leaf area, and WSC reserves including the degree of polymerization of fructans on a possible difference in regrowth was to be investigated.

Material and methods

Treatments and experimental design

The field experiment was carried out at the North Savo Research Station of MTT Agrifood Research Finland at Maaninka (63°10’N, 27°18’E) in 2000–2001. A split-plot design in four replicates was applied species (timothy cv. Tuukka or meadow fescue cv. Antti (2000) and Salten (2001)) on the main plots and defoliation height (3, 6 and 9 cm) on the sub plots. The size of the main plots was 12 m^2 and of the sub-plots 0.56 m^2. The experiment was first established on 20 July 1999 with seeding rates of 3000 for timothy and 1250 seeds m^{-2} for meadow fescue with

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Table 1. Defoliation dates and N fertilization rates during the experiments in years 2000 and 2001.

Cut	Date		N fertilization rate ($kg\ ha^{-1}$)		Observation and measurements
	2000	2001	2000	2001	
Pre-experimental	29 May	29 May	100[1)]	90[1)]	No measurements
1st cut	26 June	18 June	80	80	Pre- and post-defoliation measurements
2nd cut	18 July	11 July	50	50	Pre-defoliation and regrowth
3rd cut	8 August	2 August	50	50	Pre- and post-defoliation measurements
4th cut	29 August	30 August	–	–	Pre-defoliation and regrowth

1) Spring application 11 May 2000 and 10 May 2001.

row distances of 12.5 cm. The experiment was re-randomised and established again on 28 July 2000. Thus, the measurements were taken from first year swards in both years. The 0–40 cm soil profile consisted of fine sand (53%), silt (20%), clay (16%), and coarse sand (10%). According to soil analyses, the topsoil had a pH (H_2O) of 5.75, exchangeable K 77, and $P_{(AC)}$ 19 mg l^{-1} soil.

The plots were defoliated at a typical grazing stage of Finnish pastures, judged by the height and the phenological growth stage of the sward, which lead to five defoliations during the growing season, which is common in Finland (Table 1). During both years a pre-experimental defoliation was done late May by a Haldrup 1500 plot harvester to 7 cm stubble height without recording the yield. The sward was then allowed to reach grazing stage and the subsequent four defoliations per year were cut by shears. After the first and third regrowth cut the sward was observed for post-defoliation parameters (see below), and the regrowth rates until defoliations two and four were calculated. These two periods are referred to below as 'June–July' and 'August', respectively. The plots received annual fertilization of 270 and 280 kg ha^{-1} N in years 2000 and 2001, 16 kg ha^{-1} P and 88 and 162 kg K in years 2000 and 2001, respectively as compound fertilizer (Table 1).

Observations and measurements

Prior to each defoliation, sward height (SH) was measured at 4 points per plot. Tiller population density was assessed by counting the total number of tillers in two fixed 10 cm x 10 cm areas on each plot. Only tillers of the sown species were counted. The pre-defoliation leaf area index (LAI) of the canopy was measured *in situ* using a LICOR-2000 canopy analyser (LI-COR Inc., Lincoln, Nebraska, USA) at the same fixed areas as for the tillers. At each of these areas a small pit was dug to get the lens to ground level. The phenological stage of development was assessed from bulked samples of 5–40 tillers per replicate. The tillers were classified according to Simon and Park (1981) and the mean stage by count (MSC) was calculated. The numerical codes used in this study are as follows: 21 one elongated leaf sheat; 22 two elongated leaf sheats; 23 and so forth; 31 first node palpable at culm, 32 two nodes palpable at culm, 33 and so forth; 37 flag leaf just visible; 39 flag leaf ligule just visible, 45 boot swollen, 50 inflorescence 1–2 cm visible; 52 1/4 of inflorescence visible; 54 1/2 of inflorescence visible, 56 3/4 of inflorescence visible, 58 base of inflorescence just visible (Simon and Park 1981).

When defoliating the plots, a 0.75 x 0.75 metal frame was carefully placed in the sward so that it covered six seedling rows in each plot. The location of the plot was fixed by marking the corners of the frame in the ground with plastic sticks. The frame was adjustable to heights of 3, 6 and 9 cm as an aid to determine the right defoliation height. The herbage was weighted, and DM content was determined by drying (200 g) samples at 105°C for 24 h in a forced-air oven. Separate samples for chemical analyses (100 g) were dried at 60˚C for 40 h. The samples were analysed for organic matter content by ashing at 600˚C for 4 h and *in vitro* organic matter digestibility (IVOMD) using the NIR method (Boreal Plant Breeding, Jokioinen). The content of digestible organic matter in DM g kg^{-1} (D value) was calculated based on ash and IVOMD content.

After defoliation LAI was measured as described previously. The proportion of vegetative tillers was assessed by counting the number of vegetative tillers in the fixed areas 6–7 d after defoliation. The tillers were classified as vegetative (in previous defoliation) if they had a mark that they had been cut and they had continued growth after defoliation. The proportion of vegetative tillers was calculated as the ratio of the number of vegetative tillers after defoliation to the total number of tillers prior to defoliation. After the first and third defoliations the WSC status of the stubble was determined by taking two 5 cm x 20 cm representative samples of the plant material per plot. The samples were dug up, the main bulk of the soil was removed and the samples were stored immediately in an icebox and transported to the laboratory where they were stored at –23˚C. Later the samples were rinsed gently in cold water to remove the rest of the soil. The total number of tillers was counted. Since it would have been difficult to distinguish vegetative and generative tillers in the frozen samples, the proportion of vegetative tillers was assumed to be the same as in special countings in the fixed points. The samples were freeze-dried and ground to pass through a 1 mm sieve. After water extraction (30 min, 30˚C), WSC and high degree polymerisation fructans (HDPF, degree of polymerisation > 10) were analyzed by HPLC (Aminex HPX-42A strong cation exchange column in Ag^{2+} form; 300 mm x 7.8 mm;) at a column temperature of +30˚C and flow rate of 0.4 ml min^{-1} with an RI-detector. WSC pool per area (mg WSC m^{-2}) and per tiller (mg WSC $tiller^{-1}$) were calculated based on stubble DM (g m^{-2}, mg $tiller^{-2}$) and WSC content in DM.

The soil moisture content was measured at two points in the experimental area. At each point one gypsum block (Model 5201, Soilmoisture Equipment Corporation, Santa Barbara, Ca., USA) was located at a depth of 20 cm and one at a depth of 40 cm. The gypsum blocks showing plant available water as percentage of soil water holding capacity were read twice a week. Weather data were recorded at a meteorological station 300 m from the experimental field.

Statistical analyses

The data analysis was performed separately for June–July and August, since it has already been shown that generative (June–July) and vegetative (August) swards are fundamentally different in respect to regrowth (e.g. Davies 1988). The herbage mass (HM) yields of each defoliation and the sward properties were analysed by analysis of variance (SAS MIXED procedure, Littel et al. 1996). First the data were analysed including the effect of year and its interactions with species and defoliation height. This revealed that year, year x species, year x defoliation height or year x species x defoliation height had significant effects ($P < 0.05$) on most of the variables analysed (on total HM yield, pre-defoliation parameters, post-defoliation parameters and regrowth rate). Thus, the years were analysed separately.

Subsequently, the pre- and post-defoliation data as well as regrowth data for each year were analysed as a split plot design according to the following model:

$$y_{ijk} = \mu + Block_i + Species_j + E_{ij} + Height_k + Species_j \times Height_k + E_{ijk}$$

where: μ is the overall mean, block is the random effect of replicates, species is the fixed effect of species, and height is the fixed effect of defoliation height. E_{ij} is the main plot error term and E_{ijk} is the sub-plot error term. The linear and quadratic effects of defoliation height were analysed by contrast statements. The phenological stage (MSC) was treated as descriptive information and was not analysed by ANOVA.

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The relationship of post-defoliation variables and the subsequent regrowth rate were analysed by scatter plots and correlation analysis separately for June–July and August and for timothy and meadow fescue. Finally, the total HM yield was calculated as the sum of defoliations 1–4 and the regrowth HM yield as the sum of defoliations 2–4. Both were analysed with the split-plot model described above.

Results

The weather parameters and gypsum blocks showed that the seasons were different in terms of precipitation and soil moisture (Fig. 1). The summer of year 2000 was moist and the gypsum blocks showed that there was 90% of available soil moisture present throughout the growing season. On the contrary, the summer of year 2001 was dry, especially from the end of June onwards, and the gypsum blocks did not show a rise until the end of August. The differences in temperature, evaporation and radiation were much less. However, there were occasional light rains in July and early August in 2001 that favoured grass growth although they were too light to penetrate to the depth of the gypsum blocks.

Sward state prior to defoliation in June

Generally, the pre-defoliation SH ranged from 27 to 45 cm and LAI values 3.3–5.0. In June the defoliation height treatments had not yet been imposed, so the defoliation height had an effect only on the HM yield, which decreased in June 2000 and 2001 with increasing defoliation height (Table 2). Meadow fescue had a fairly similar distribution of development stages in 2000 and in 2001. Timothy had more advanced development stages than did meadow fescue, especially in 2001 (Fig. 2). In June 2000 the tiller densities of timothy and meadow fescue were similar,

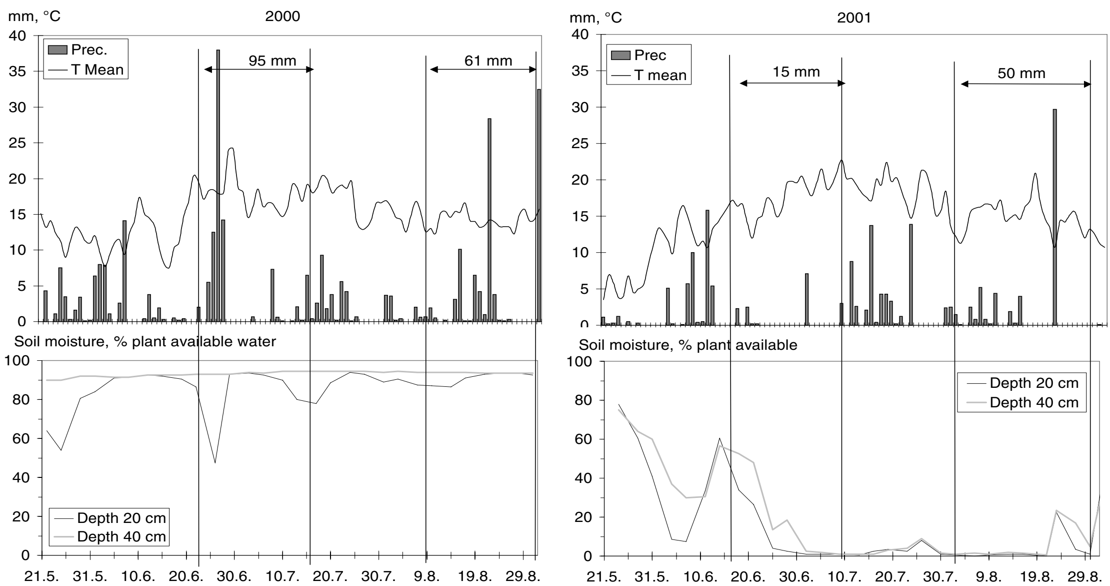

Fig. 1. Daily mean temperature (˚C), rainfall (mm) and soil moisture (% of plant available soil moisture) during experiment at Maaninka in 2000 and 2001. Horizontal arrows represent regrowth periods named generative and vegetative, respectively. The precipitation sum (mm) of each period is indicated above the arrows.

3880 m^{-2}. In contrast, in June 2001 timothy had a lower tiller density than meadow fescue (2930 vs. 4290 m^{-2}; SEM 226, P = 0.024).

Sward state prior to defoliation in August

At the third defoliation, in August, the defoliation height treatments had been imposed at two previous cuts. The HM yield was generally higher in 2001 than in 2000 (Table 2), but otherwise the differences between the years were small. Meadow fescue had 23% higher HM yield than timothy in 2000. In 2001 there was a species x defoliation height effect, which showed that timothy had the lower HM yield at a defoliation height of 3 cm whereas it had the higher HM yield at a defoliation height of 9 cm. The development stage distributions were fairly similar (Fig. 2) for both species in both years, although timothy had some tillers at more advanced development stages, whereas meadow fescue had not.

The effect of defoliation height was linearly positive for HM and tiller population density in 2000. In 2001 the effect was linearly positive for HM and LAI, but defoliation height had no effect on the tiller population density (Table 2).

Post-defoliation sward state in June

In June 2000 timothy tended to have the lower density of vegetative tillers. Otherwise the species did not differ from each other except the higher concentration of WSC and HDPF in timothy cut to 3 cm (Table 3, Fig. 3). On the contrary, in June 2001 the differences between species were prominent. Most striking was the low density of vegetative tillers in timothy as compared

Table 2. Herbage yield in June and August and tiller density in August in year 2000 and 2001 before the regrowth period as influenced by defoliation height (Height) to two species (SP) and their interaction (SP x Height).

	Timothy				Meadow fescue					P value			
	Cutting height, cm				Cutting height, cm					SP	Height[2)] L	Height[2)] Q	SP x Height
	3	6	9	Mean	3	6	9	Mean	SEM[1)]				
June													
Herbage yield, kg DM ha^{-1}													
26 June 2000	2740	2070	2070	2290	2650	2480	2210	2240	118	0.142	<0.001	0.108	0.057
18 June 2001	2850	2810	2300	2650	2550	2340	2220	2370	74	0.052	<0.001	0.032	0.006
August													
Herbage yield (kg DM ha^{-1})													
8 August 2000	1080	1340	1580	1340	1310	1670	1970	1650	65	0.001	<0.001	ns	ns
2 August 2001	2011	2278	2580	2290	2264	2375	2389	2343	79	ns	<0.001	ns	0.035
Tiller density m^{-2}													
8 August 2000	3360	4310	4920	4200	3590	4020	4590	4070	539	ns	0.013	ns	ns
2 August 2001	3940	4000	4190	4040	4510	4640	4330	4490	440	ns	ns	ns	ns

1) SEM = standard error of the mean
2) L = linear effect; Q = quadratic effect.
ns = P ≥ 0.20; DM = dry matter.
Least square means and P values from the analysis of variance.

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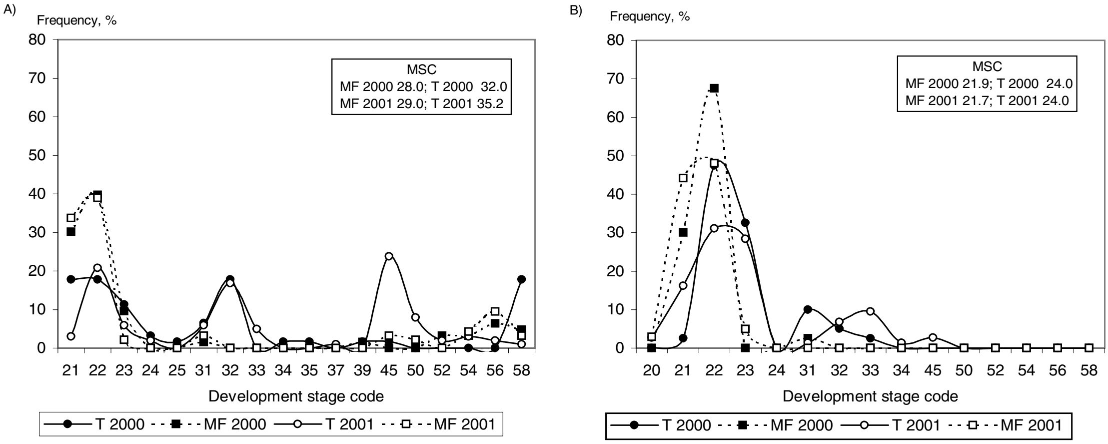

Fig. 2. Frequency distribution of stages of development in the beginning of the: a) generative regrowth period (June–July) and b) the vegetative growth period (August) in 2000 and 2001. T = timothy, MF = meadow fescue. Keys of development stages according to Simon and Park (1981; See text for details). MSC = mean stage by count.

with meadow fescue, and with the previous year. Timothy had the higher WSC concentration and tended to have the higher HDPF concentration. Since timothy also had bigger tillers (mg DM tiller^{-1}), the difference in WSC pool per tiller was even greater. Timothy tended to have a lower post-defoliation LAI than meadow fescue for June 2000 with cutting heights of 6 and 9 cm.

The residual LAI, tiller size and WSC pool per tiller increased with increasing defoliation

Table 3. Analysis of variance of post-defoliation sward parameters in June and August in two years at the beginning of regrowth period, respectively. Effects of species (SP) and cutting height (Height) and their interaction (SP x Height). Cf. Fig. 3.

	June			August		
	SP	Height[1)]	SP x Height	SP	Height[1)]	SP x Height
2000						
Vegetative tillers m^{-2}	0.070	0.092	0.104	ns	0.048	ns
Leaf area index	ns	<0.001	ns	0.014	<0.001	ns
WSC concentration(mg g^{-1} in DM)	ns	0.096	0.018	0.132	<0.001	ns
HDPF concentration (mg g^{-1} in DM)	ns	ns	0.023	0.126	<0.001	ns
Tiller size (mg DM tiller^{-1})	ns	<0.001	ns	ns	<0.001	ns
WSC pool (mg tiller^{-1})	ns	0.001	0.17	ns	<0.001	ns
2001						
Vegetative tillers m^{-2}	0.006	ns	ns	0.112	0.006	ns
Leaf area index	0.052	<0.001	0.023	ns	<0.001	ns
WSC concentration(mg g^{-1} in DM)	0.014	ns	0.085	0.019	0.030	0.105
HDPF concentration (mg g^{-1} in DM)	0.073	0.144	0.180	0.010	0.04	0.174
Tiller size (mg DM tiller^{-1})	0.011	<0.001	ns	ns	0.006	0.06
WSC pool (mg tiller^{-1})	0.018	0.021	ns	0.062	0.006	ns

1) Linear effect.
ns = P ≥ 0.20; WSC = water-soluble carbohydrates; DM = dry matter; HDPF = High degree of polymerization fructans.

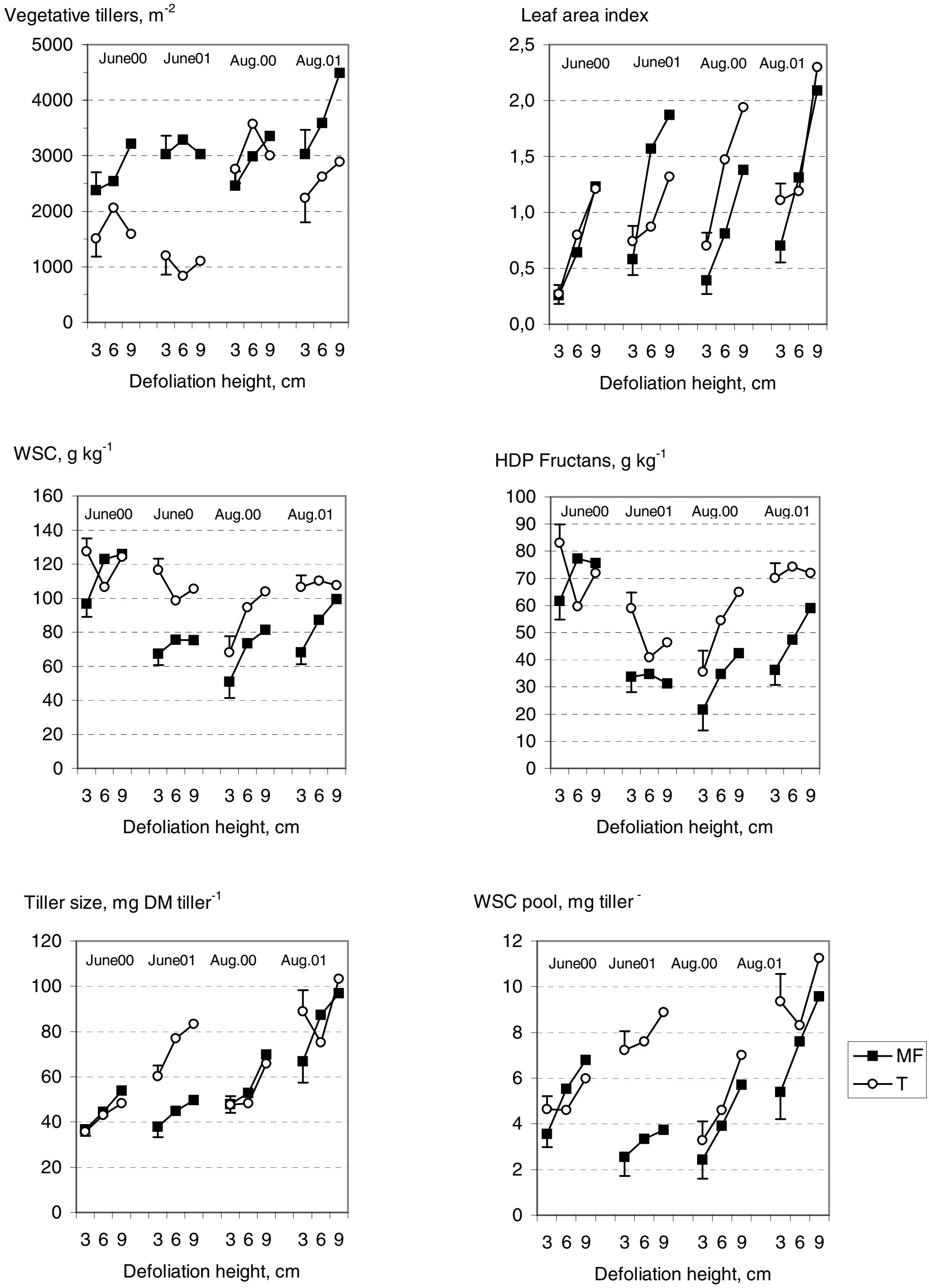

Fig. 3. Post defoliation parameters of two species as influenced by defoliation height for regrowth from June 26 to July 18 2000 and from June 18 to July 11 2001. T = timothy, MF = meadow fescue. Standard error of the mean is indicated at 3 cm cutting height recordings. See Table 3 for significance of effects.

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height in both years (Fig. 3). The defoliation height had no main effect on the WSC or HDPF concentration. Instead, there was a significant species x defoliation height interaction in June 2000 and a tendency to an interaction for WSC in June 2001. The reason for this was that in timothy the defoliation height of 6 cm produced the lowest WSC concentration whereas in meadow fescue the lowest WSC concentration was found with the 3 cm cut. The HDPF concentration was affected in almost the same manner.

Post-defoliation sward state in August

In general, the measured variables had higher values in August 2001 than in year 2000 except the density of vegetative tillers for timothy (Table 3, Fig. 3). Since the residual DM per tiller was higher in 2001 together with the WSC concentration, the greatest increase was in the WSC pool per tiller, which in August 2001 was almost twice as high as in August 2000.

The species did not differ systematically in regrowth traits in different years. In August 2000, timothy had a higher residual LAI than meadow fescue but not in August 2001. On the other hand, timothy had higher WSC and HDPF concentrations than meadow fescue in August 2001.

The effect of defoliation height was fairly similar in both years. It increased the density of vegetative tillers, residual LAI, WSC and HDPF concentrations, tiller size and WSC pool per tiller linearly in both years. No significant ($P < 0.05$) interactions between species and defoliation height were found although there was a tendency that the tiller size reacted differently in timothy and meadow fescue in 2001. The reason for this was the low DM per tiller in timothy that was cut at 6 cm.

Sward regrowth in June–July

There was a marked drop in the growth rate (kg DM ha^{-1} d^{-1}) of timothy in June–July 2001 as compared with June–July 2000. In contrast, the growth rate of meadow fescue was at the same level in both years (Table 4, Fig. 4). In other words, whereas there was no difference between the species in the growth rate in June–July 2000, the growth rate of timothy was only 63% of the growth rate of meadow fescue in June–July 2001. In June–July 2000, timothy had a higher LAI at the subsequent harvest compared to meadow fescue. The D value of regrowth was similar for both species.

Increasing the defoliation height increased the growth rate of both species by 19% linearly in June–July 2000. The increase in LAI was dependent on the species. In June–July 2001 defoliation height had no effect on the growth rate. The defoliation height had no effect on the D value, although it tended to decrease with increasing defoliation height in June–July 2001 in meadow fescue.

Sward regrowth in August

Both species reacted similarly to the difference between the years: the regrowth rates and D values were higher in August 2001 than in August 2000. Although there was no difference between the species in the growth rate, timothy had the higher LAI and D values in regrowth in both years.

Increasing defoliation height increased the growth rate in August 2000 by 27% for both species but not in August 2001. Increasing the defoliation height lowered the D value of meadow fescue in August 2000, while in August 2001 it decreased the D value systematically in both species.

Post-defoliation parameters and regrowth rate

The scatter plot and correlation analysis gave only restricted information concerning the factors explaining the regrowth rate since the post-defoliation variables were mostly highly correlated with each other. Also the variation in re-

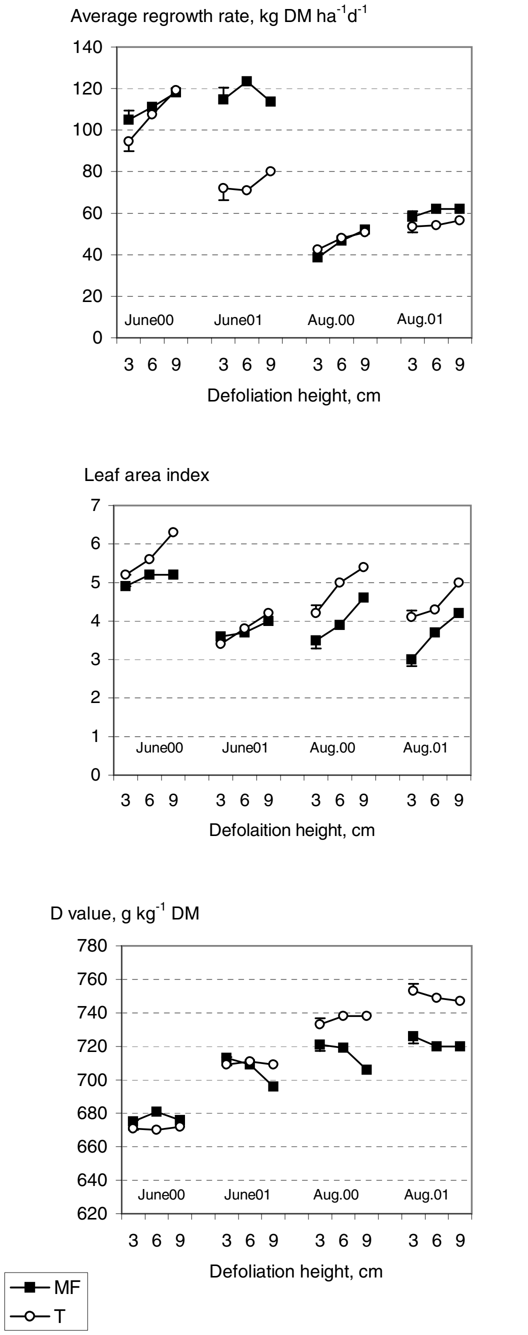

Fig. 4. Regrowth parameters of two species as influenced by defoliation height for regrowth from June 26 to July 18 2000 and from June 18 to July 11 2001. T = timothy, MF = meadow fescue. Standard error of the mean is indicated at 3 cm cutting height recordings. See Table 4 for significance of effects.

growth between the years 2000 and 2001 in June–July may obscure the true effects of the post-defoliation parameters. Thus, only few basic features could be discerned. First, a correlation was detected between the growth rate and the number of vegetative tillers in June–July for timothy. On the contrary, meadow fescue consistently had a high number and proportion of vegetative tillers, and no correlation with regrowth was found (Fig. 5). No other such a clear correlation was found between the explanatory variables and regrowth in June–July.

In August the situation was quite the opposite, since timothy and meadow fescue were then more similar in respect to regrowth factors than in June–July. Based on the scatter plots and correlation analysis there were no factors of outstanding importance. However, it is noteworthy that both the WSC and HDPF concentrations had a positive correlation with regrowth. In all, the variation and response of the HDPF concentration to the defoliation treatments were rather similar to the variation and response of the WSC concentration. The calculated WSC pools per tiller or per m^2 gave only a slight advantage compared to the WSC concentration when explaining the regrowth. In addition, the calculated WSC pool per tiller gave no advantage compared to tiller size alone.

Herbage mass production during the experiment

The measured HM production covers the experimental period (the sum of defoliations 1–4), but it is not equivalent to the annual production since the pre-experimental harvest is excluded. In general, the HM and digestible organic matter (DOM) production was higher in year 2001 than in 2000 (Table 5). Meadow fescue produced 7% more HM than timothy in 2000 and 10% more in 2001. In regrowth (the sum of defoliations 2–4) the differences between the species in HM yields were 8% and 21%, respectively. The differences in DOM yields were of the same magnitude.

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Table 4. Analysis of variance of sward regrowth parameters in June and August in two years as influenced by species (SP), cutting height (Height), and their interaction (SP x Height). Cf. Fig. 4.

	June-July			August		
	SP	Height[1)]	SP x Height	SP	Height[1)]	SP x Height
2000						
Leaf area index	0.026	0.002	0.088	0.019	<0.001	ns
D value (g kg^{-1} DM)	ns	ns	ns	0.007	0.196	0.045
Regrowth rate (kg DM ha^{-1} d^{-1})	ns	0.001	ns	ns	<0.001	ns
2001						
Leaf area index	ns	<0.001	0.022	0.019	<0.001	ns
D value (g kg^{-1} DM)	ns	0.058	0.153	0.005	0.025	ns
Regrowth rate (kg DM ha^{-1} d^{-1})	0.002	ns	ns	0.071	ns	ns

1) Linear effect.
ns = P ≥ 0.20; DM = dry matter.

Since there was no interaction between defoliation height and species, it can be concluded that HM yields during the experiment increased by 10% by increasing the defoliation height from 3 to 9 cm in 2000 but were not affected in year 2001. The HM yield in regrowth increased more, by 29% and 10%, respectively. The total and regrowth DOM yields increased correspondingly to the HM yields.

Discussion

Pre- and post-defoliation sward state

The mean pre-defoliation HM ranged from 1080 to 2850 kg DM ha^{-1} and pre-defoliation SH ranged from 27 to 45 cm during the experiment. The defoliation interval used in this experiment

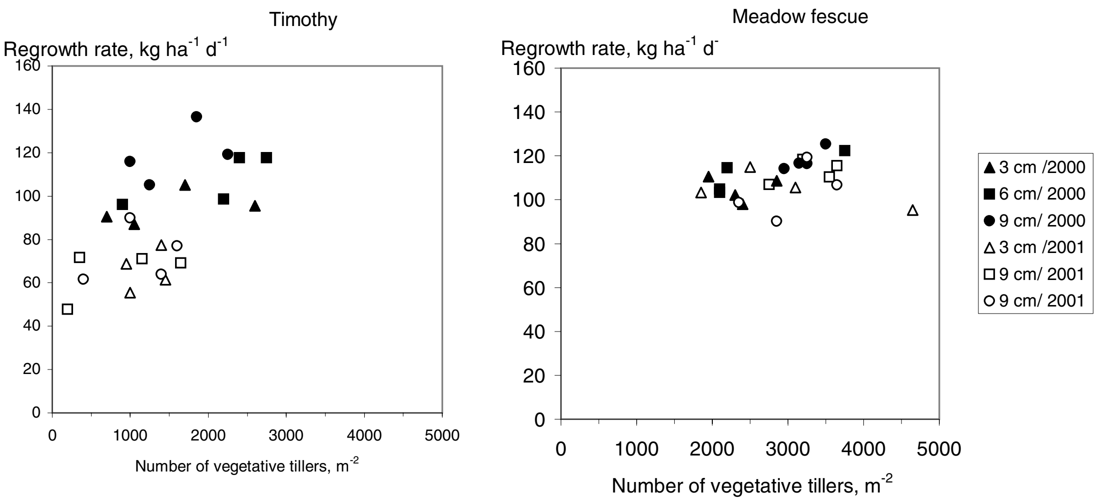

Fig. 5. Relationship between population density of vegetative tillers and average regrowth rate in the generative growth phase (June–July) of two species after defoliation to three stubble heights of first year ley in two years.

Table 5. Herbage and digestible organic matter (DOM) production during the experiment (cuts 1– 4) and in regrowths (cuts 2–4) as influenced by species (SP), cutting height (Height), and their interaction (SP x Height) in year 200 and 2001.

	Timothy				Meadow fescue					P value		
	Cutting height (cm)				Cutting height (cm)					SP	Height[2)]	SP x Height
	3	6	9	Mean	3	6	9	Mean	SEM[1)]			
2000												
Herbage yield (kg DM ha^{-1})	6880	6880	7440	7070	7150	7670	7970	7600	196	0.043	0.004	ns
– yield in regrowth (kg DM ha^{-1})	4140	4810	5370	4770	4500	5190	5770	5150	153	0.056	<0.001	ns
DOM yield (kg ha^{-1})	4680	4750	5120	4850	4910	5300	5480	5230	132	0.048	0.002	ns
– DOM yield in regrowth (kg ha^{-1})	2900	3370	3770	3350	3110	3600	3960	3560	107	0.091	<0.001	ns
2001												
Herbage yield (kg DM ha^{-1})	7870	8090	8140	8040	8860	9050	8730	8880	209	0.025	ns	ns
– yield in regrowth (kg DM ha^{-1})	5020	5280	5840	5380	6300	6710	6510	6510	195	0.009	0.012	0.117
DOM yield (kg ha^{-1})	5500	5640	5730	5620	6290	6400	6130	6270	150	0.018	ns	ns
– DOM yield in regrowth (kg ha^{-1})	3630	3810	4210	3880	4530	4770	4590	4630	135	0.009	0.025	0.071

1) SEM = standard error of the mean
2) linear effect
ns = P ≥ 0.20; DM = dry matter.
Least square means and P values from the analysis of variance.

was 21–28 days. These values can be regarded as typical for Finnish pastures (Virkajärvi et al. 2002). The sward was at a relatively mature stage in June, with a low proportion of vegetative tillers, but this is also typical of grass swards at high latitudes (Heide et al. 1985).

There was a striking difference between the species in the population density of vegetative tillers in June 2000 and even greater in June 2001. In June 2000 this difference between timothy and meadow fescue was solely due to the low proportion of vegetative tillers in timothy (0.56 in timothy vs. 0.78 in meadow fescue) since the total number of tillers was the same (Table 3). In June 2001, timothy had 32% lower total tiller density and moreover a lower proportion of vegetative tillers than meadow fescue (0.33 vs. 0.72, respectively). In addition, the low proportion of vegetative tillers is seen also in the development stage distribution (MSC; Fig. 2) where meadow fescue had a similar proportion of tillers in classes 21–22 (vegetative stage) in both years, whereas timothy had clearly fewer tillers in classes 21–22 in 2001 than in 2000.

There are two possible explanations for the lower number of vegetative tillers in timothy in 2000 compared with 2001. The first is the timing of the pre-experimental cut. In both years it took place on 29 May but in 2000 the temperature sum was 337°C (degree days since the beginning of the growing season, base temperature 0°C) and 282°C in 2001. According to Virkajärvi and Järvenranta (2001), at this time of the growing season the apices of primary tillers of meadow fescue are situated higher in the canopy than those of timothy especially in 2001. Most probably meadow fescue lost a substantial number of apices in both years in the pre-experimental

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cut but timothy only in the year 2000. Therefore meadow fescue had a higher proportion of vegetative tillers in the first experimental defoliation in both years and the difference was greater in 2001 than in 2000.

Another factor affecting the large observed species x year variation is that timothy has a single long day induction for flowering (Heide 1994). Therefore axillary tillers that emerged between the pre-experimental cut and the first cut may have switched to the generative growth phase due to the 19–20 h daylength at the experimental site. On the contrary, the axillary tillers of meadow fescue need vernalization or a period with short days before they are able to switch to the generative growth phase (Heide 1994) and therefore they remained vegetative (Fig. 2b).

A confounding factor affecting the large observed species x year variation may be the fact that the meadow fescue cultivar used was Antti in 2000 and Salten in 2001. However, based on official variety trials in Finland, Antti and Salten are similar in respect to HM production and their heading day differs by only 0.5 d (Kangas et al. 2001). Therefore it is unlikely that a major proportion of the observed species x year variation was caused by the replacement of Antti by Salten.

It is noteworthy that the tiller population density measured in August increased with increasing cutting height (Fig. 3). This is in contrast to perennial ryegrass (Grant et al. 1983) but similar to prairie grass (*Bromus willdenowii* Kunth.), which increased tiller population density when cut at 12 cm in comparison to the residual height of 6 cm (Xia et al. 1994). The observed low post-defoliation LAI values (minimum 0.3, maximum 2.3) support the findings since even with a defoliation height of 9 cm the LAI was generally well below 2 in June. As tillering rate generally slows down as soon as LAI reaches values of 3 (Simon and Lemaire 1987), it can be concluded that in this experiment shading was not restricting the initiation of new tillers after defoliation, not even with 9 cm defoliation treatment. Furthermore, the tiller population densities for timothy were $4200\ m^{-2}$ and $4040\ m^{-2}$ in August 2000 and 2001, and for meadow fescue $4070\ m^{-2}$ and $4490\ m^{-2}$, respectively. This indicates that timothy had to produce 180–210% more new tillers than meadow fescue between June and August, presuming that the death rates of the vegetative tillers were similar.

The WSC concentrations found were similar to those in other field studies on timothy and meadow fescue (Smith 1967, Virkajärvi et al. 2003). Timothy is shown to accumulate especially HDPF, degree of polymerization (DP) >10, whereas the amount of low DP fructans remains small (Spollen and Nelson 1988). In this study, timothy had a higher (46–57%) HDPF concentration than meadow fescue except in June 2000, but the difference was statistically significant ($P < 0.1$) only in 2001. One explanation of the small difference between the species is the fact that the accumulation of HDPF in timothy leaves is increased by temperature fluctuations or low night temperatures (Thorsteinsson et al. 2002). In the present experiment, such fluctuations were not observed in June or early August. In addition, the young development stage lowers the proportion of HDPF at least in timothy (Smith 1967).

Sward regrowth rate and annual herbage production

In this experiment, increasing the defoliation height increased the regrowth rates, as well as regrowth HM yields (yields 2 + 3 + 4), and even total HM yields (defoliations 1 + 2 + 3 + 4). Thus, the positive effect on regrowth yields was greater than the negative effect on the yield of the first defoliation. The increase was linear for both species in both years. This result is in contrast to the general concept regarding the effect of defoliation height on perennial ryegrass swards, for which a stubble height of 5 cm is considered as an optimum when the cutting interval is set to 3-leaf stages (Fulkerson and Donaghy 2001). The most probable explanation for this lies in the difference in the ability of the grass species to adapt to close defoliation. While perennial ryegrass is a grazing tolerant species, it has a good ability to compensate the reduced tiller height caused by close defoliation by increasing the tiller population density (e.g. Grant et al. 1983). The ability of timothy and meadow fescue to compensate in tiller size/density may be less than that of perennial ryegrass, at least under long day conditions, as an increase in defoliation height led to an increase in both tiller size and tiller population density of vegetative tillers in August in both years. Based on the results both species reacted to defoliation height more like prairie grass rather than perennial ryegrass in a temperate climate (Xia et al. 1994, Slack et al. 2000). The observed reduction in regrowth rate between 9 cm and 3 cm was less than the 30% reduction between 4 and 12 cm reported by Jäntti and Heinonen (1957) for meadow fescue or cocksfoot (*Dactylis glomerata* L). dominated swards in Southern Finland. Thus, it can not be excluded that a higher defoliation than 9 cm might have been beneficial in this study as well. Jäntti and Heinonen (1957) found no interaction with soil moisture and cutting heights of 4 and 12 cm. Instead a defoliation height of < 1 cm reduced the growth rate clearly more under dry conditions than in moist ones.

The most important difference in sward production between the years was the poor performance of timothy in June–July 2001 compared to both June–July 2000 and to meadow fescue in June–July 2001. There are two probable reasons for this. First, the observed drought (Fig. 1) and, second, the low number of vegetative tillers in June 2001 (Fig. 3). The amount of precipitation during the regrowth period in June–July 2001 was low (15 mm) compared to June–July 2000 (95 mm) or to August 2001 (50 mm). The amount of available soil water was also clearly lower (Fig. 1). It is noteworthy that the adverse effects of the drought were observed in timothy only and only in June–July 2001 and not in August 2001. One plausible explanation for this lies in the fact that in June–July 2001 there was almost no precipitation during the regrowth period, although there was about 40% available soil moisture left at 20 cm at the beginning of the period. The first abundant rain of > 5 mm took place 16 days after the defoliation. On the contrary, in August 2001, there were several rain showers ~ 5 mm immediately after defoliation, although they were so small that the water did not percolate to the depth of 20 cm and cause any increment in the resistance blocks. Since the yields and the growth rates in July–August (cuts 3 and 4) were higher in 2001 than in 2000, it is concluded that soil moisture measurements at a depth of 20 cm did not reflect the water status of the plants well in such conditions.

A reduction in tiller density is commonly observed in grass canopies under water stress. This is more related to a decrease in tiller emergence rather than to tiller death (Jones 1988). This phenomenon may have accelerated the effect of the low density of vegetative tillers in timothy in June–July 2001. Altogether, these factors led to changes in growth rate –33% in timothy and +6% in meadow fescue when comparing the regrowth rates of June–July 2000 and June–July 2001. As the effect of drought and the effect of low vegetative tiller density in timothy were confounded in this experiment, it is not possible to distinguish which one of the effects was of greater importance. However, the total HM yields were 14% and 17% higher in the dry summer of 2001 than in the moist summer of 2000 for timothy and meadow fescue, respectively, which is in contradiction to the low available soil moisture in 2001 compared to 2000.

Post-defoliation parameters and regrowth rate

The correlation analysis gives information on relations between the sward variables and the subsequent regrowth. Since defoliation height was the predominant factor affecting all the explanatory variables, the variables were mostly highly intercorrelated. Furthermore, the variation in regrowth between the years 2000 and

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2001 in June–July may weaken or strengthen the correlation depending on the variation in the explanatory variables between the years. Thus, the correlations found have to be considered with care and only few basic features can be discerned. However, the experiment was planned to simulate the defoliation performed by animals in field conditions, although neglecting the effects of treading, urine and faeces. Also the defoliation interval was fixed to simulate a typical pasture system in Central Finland, although it is well known that the defoliation height and the length of the regrowth period do generally interact (Parsons et al. 1988). Since typical grazing stages were achieved, the results are valid and of practical significance.

In June the generative tillers amounted to 0.44–0.67 of the total tiller population density of the timothy stand. These tillers lost their apices in defoliation. Defoliation height had no effect on the proportion of vegetative tillers observed after the defoliation in either of the years, which means that the lost apices were then on average situated higher than 9 cm above ground. Thus, a large part of the regrowth must have taken place by initiating new tillers from the axillary buds. This process is slower (Davies 1988), and it uses the WSC pools less effectively than regrowth directly from current meristems (Richards and Caldwell 1985). Therefore, a correlation was detected between the growth rate and the number of vegetative tillers in June–July for timothy. On the contrary, meadow fescue had a reasonably high number and proportion of vegetative tillers, thus no correlation with regrowth was found (Fig. 5). In the case of timothy, the results are similar to the findings of Bonesmo (2000), who also has shown that the proportion of non-elongated tillers was more important for the regrowth than the WSC concentration when regrowth after first cut at different phenological stages were compared. The latter had an effect only on the initial regrowth rate.

In August the situation was quite the opposite, since timothy and meadow fescue were then fundamentally more similar in respect to regrowth factors than in June–July. Secondly, the number or proportion of vegetative tillers did not correlate with regrowth. Due to intercorrelations and major differences in weather conditions between the years it cannot be concluded that any of the factors would have been of outmost importance for regrowth in August. Based on the scatter plots and correlation analysis it can be stated that the HDPF concentration did not explain the regrowth better than the WSC concentration. Actually, the correlation was positive for the percentage of HDPF of total WSC, which was not as expected (Spollen and Nelson 1988).

Conclusions

An increase in defoliation height from 3 to 9 cm increases the regrowth of timothy and meadow fescue similarly, but the regrowth capacity of meadow fescue is higher as such. Neither of the species had a tiller size/density compensation ability. The yearly variations in the post-defoliation canopy structure and in regrowth may be large. In the reproductive phase, the regrowth rate of timothy is dependent on the population density of vegetative tillers. Other factors play a minor role. For meadow fescue in reproductive phase population density of vegetative tillers did not have such importance. In August there was no single factor essential for regrowth rates of either of the species. The variation and response of the HDPF concentration to the cutting treatments did not explain the differences in the regrowth rate between the species.

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SELOSTUS

Leikkuukorkeuden vaikutus timotein ja nurminadan jälkikasvuun generatiivisessa ja vegetatiivisessa kasvuvaiheessa

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Nurmen jälkikasvun kannalta tärkeitä leikkuun jälkeisiä ominaisuuksia ovat aktiivisten kasvupisteiden määrä, jäljelle jäävä lehtiala ja hiilihydraattivarastot. Nurmen leikkuukorkeus vaikuttaa nurmen jälkikasvunopeuteen ja edellä mainittuihin ominaisuuksiin. Timotei ja nurminata ovat yleisimmät laidunkasvit Suomessa, mutta silti leikkuukorkeuden vaikutusta niiden jälkikasvuun ei ole tutkittu. Tässä tutkimuksessa verrattiin kolmen eri leikkuukorkeuden (3, 6 ja 9 cm) vaikutuksia timotein ja nurminadan jälkikasvunopeuteen generatiivisessa (kesä-heinäkuu) ja vegetatiivisessa vaiheessa (elokuu) vuosina 2000 ja 2001.

Leikkuukorkeuden nostaminen 3:sta 9:ään cm nosti timotein ja nurminadan jälkikasvunopeutta 19 % kesäkuussa ja 27 % elokuussa vuonna 2000. Vastaavasti kummankin kasvilajin kumuloituva jälkikasvusato suureni 29 % nostettaessa leikkuukorkeutta 3:sta 9:ään cm. Vuonna 2001 leikkuukorkeus ei vaikuttanut jälkikasvunopeuteen kesä- ja elokuussa, mutta kumuloituva jälkikasvusato nousi 10 %, kun leikkuukorkeutta nostettiin 3:sta 9:ään cm. Nurminata tuotti 7–10 % korkeammat kuiva-ainesadot ja 8–21 % korkeammat jälkikasvusadot kuin timotei. Mitä suurempi oli timotein niiton jälkeinen vegetatiivisten versojen tiheys kesäkuussa, sitä suurempi oli sen kasvunopeus niiton jälkeen. Nurminadalla vastaavaa ilmiötä ei havaittu. Elokuussa mikään yksittäinen tekijä ei selittänyt kasvunopeutta, vaan leikkuukorkeus vaikutti useiden ominaisuuksien kautta jälkikasvunopeuteen.