Tiller Characteristics of Timothy and Tall Fescue in Relation to Herbage Mass Accumulation

Perttu Virkajärvi,* Kirsi Pakarinen, Maarit Hyrkäs, Mervi Seppänen, and Gilles Bélanger

ABSTRACT

Herbage dry matter (DM) yield of grasses is a function of the density and size of vegetative (VEG), generative (GEN), and elongating vegetative (ELONG) tillers. We determined the contribution of these three tiller types to DM yield accumulation along with their main morphological characteristics on three sampling dates during each of the primary growth and the regrowth of field-grown swards of timothy (*Phleum pratense* L.) and tall fescue (*Festuca arundinacea* Schreb.). Our results provide the first quantitative characterization of ELONG tillers, which contributed to timothy DM yield by up to 28% in primary growth and 58% in regrowth. In tall fescue, VEG tillers were dominant in primary growth and regrowth (74 to 100% of DM yield). The GEN tillers were dominant (67 to 74% of DM yield) in the primary growth of timothy while in the regrowth, VEG tillers were dominant early (84% of DM yield) but ELONG tillers represented 58% of DM yield later on. Timothy and tall fescue had similar rates of DM accumulation. The greater DM yield on all sampling times of the regrowth of tall fescue confirms a greater growth before the first sampling, most likely due to the greater proportion of VEG tillers. The GEN tillers were large with low leaf to weight ratio (LWR) and proportion of attached senesced material whereas VEG tillers were small with high LWR and large proportion of attached senesced material. The ELONG tillers were intermediate in size and LWR but they had a low proportion of attached senesced material.

P. Virkajärvi, K. Pakarinen, and M. Hyrkäs, MTT Agrifood Research Finland, Animal Production Research, Halolantie 31 A, FI-71750 Maaninka, Finland; M. Seppänen, Department of Agricultural Sciences, University of Helsinki, Latokartanonkaari 5, FI-00014 University of Helsinki, Finland; G. Bélanger, Soils and Crops Research and Development Centre, Agriculture and Agri-Food Canada, 2560 Hochelaga Blvd., Québec, QC, Canada G1V 2J3. Received 24 Jan. 2011. *Corresponding author (perttu.virkajarvi@mtt.fi).

Abbreviations: DM, dry matter; ELONG, elongating vegetative; GEN, generative; LWR, leaf to weight ratio; VEG, vegetative.

Tiller density and size determine the dry matter (DM) yield of forage grasses. Grass growth in spring begins with non-reproductive vegetative (VEG) tillers with an apex producing only leaf primodias (Moser and Jennings, 2007). Since the apex is located above nonelongated true stems near the soil surface, the short visible "stem" is actually a pseudostem formed of a leaf sheath tube. Transition to reproductive generative (GEN) tillers takes place when the apex starts to form flower primodias. This is accompanied by internode elongation and subsequent true stem formation, apex elevation, and a decrease in the leaf proportion (leaf to weight ratio [LWR]). In most grasses, the induction of flowering typically includes vernalization, a minimum accumulation of growing degree days, and a critical daylength or level of solar radiation (Moser and Jennings, 2007).

In a grass sward, some tillers remain at the VEG stage whereas others proceed to the GEN stage. This has several consequences. When the proportion of large GEN tillers or the total tiller density is high, smaller VEG tillers fail to compete for light, which results in accelerated senescence and accumulation of senesced leaf

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material. This impairs the nutritive value because senesced material has a low digestibility (Duru, 1997). Senescence also affects the C cycling in a grass community. Hence, understanding and quantifying leaf senescence is essential for process-based crop growth models (Woodward, 1998; Bonesmo and Bélanger, 2002; Romera et al., 2009). On the other hand, mowing or grazing of GEN tillers usually removes the elevated shoot apices and requires the establishment of new tillers (Woodward, 1998). This process is slower and needs more energy as compared to the regrowth of VEG tillers (Richards, 1993).

Stem formation contributes significantly to the accumulation of DM (Kuoppala et al., 2008). As stem elongation enables the presence of new leaves on the top of the canopy, it ensures a greater potential for photosynthesis of the developing leaves (Robson et al., 1988). The negative side of stem formation is that the digestibility of maturing stems decreases more rapidly than that of leaves during DM accumulation (Moser and Jennings, 2007). Stem formation is in general more substantial in spring growth than in the following regrowth due to the effects of vernalization and transition to the reproductive stage (Seppänen et al., 2010). The timing of stem elongation and flowering induction are in most cases connected to each other and therefore the requirements for flowering induction are probably important also for the initiation of stem elongation (Heide, 1994; Moser and Jennings, 2007)

Timothy (*Phleum pratense* L.) is the most important perennial forage grass grown for silage and hay production in Scandinavia (Höglind et al., 2005) and is also widely grown in other cool and humid regions in Europe, Asia, and North America (Bélanger et al., 2006). Timothy is adapted to short growing seasons and the long days of high latitudes and it flowers when the critical daylength is exceeded, even in regrowth (Heide, 1994; Casler and Kallenbach, 2007). Besides VEG and GEN tillers, timothy produces elongating vegetative (ELONG) tillers that are still either in vegetative or an aborted reproductive stage even though their apices are elevated from the soil surface following the development of true stems (Höglind et al., 2005; Seppänen et al., 2010). Tall fescue (*Festuca arundinacea* Schreb.) is economically the most important species within the *Festuca* genus (Casler and Kallenbach, 2007). The importance of tall fescue has increased during past years in Finland and Canada, mainly because of its good regrowth ability and drought tolerance. Whereas timothy does not require vernalization for flowering, a so-called double induction with vernalization followed by long days is necessary for the formation of flowering stems in tall fescue (Heide, 1994). Tall fescue is known to be more leafy than timothy but direct comparisons of those two species for their DM yield and morphological characteristics have never been reported.

Quantifying the contribution of tiller types to DM accumulation in forage grasses and determining their morphological characteristics is essential for the development of process-based base models of grass growth and nutritive value and for understanding the physiological basis of yield and nutritive value. Currently, there is little information on how the presence of different tiller types affects the DM accumulation in timothy and tall fescue. Because these species differ in flower induction requirements, we hypothesized that these two species differ in the contribution to DM yield of the different tiller types.

In this study, the objectives were to determine (i) the abundance of different tiller types in the primary growth and regrowth of timothy and tall fescue by considering both their proportion in the herbage DM and their density, (ii) the change in the proportion of tiller types with time or stage of development, and (iii) the main morphological characteristics of the tiller types.

MATERIALS AND METHODS

Establishment and Experimental Layout

The experiment was conducted on a Aquic Cryorthent, coarse-loamy soil at the Maaninka Research Station of MTT Agrifood Research Finland, Maaninka, Finland (63°08′ N, 27°19′ E) during the growing seasons of 2006 and 2007. For each of the primary growth and the regrowth, the experimental layout was a split-plot design with three replicates. Two species, timothy and tall fescue, were assigned as main plots and three sampling times (early, optimal, and late) as subplots. Individual plot size was 1.5 by 4.0 m. The experiment was established on 26 May 2005. Before sowing, the experimental area was fertilized with 55 kg N ha^{-1}, 13 kg P ha^{-1}, and 43 kg K ha^{-1}. Timothy (cv. Tammisto II) was sown with 3000 seeds m^{-2} (11.4 kg ha^{-1}) and tall fescue (cv. Retu) with 1000 seeds m^{-2} (29.7 kg ha^{-1}). Barley (*Hordeum vulgare* L. cv. Kunnari) was used as cover crop with a seeding rate of 350 seeds m^{-2} and it was harvested at the early dough stage on 28 July 2005 as whole crop silage.

In 2006 and 2007, the entire experimental area was fertilized in mid May with 90, 13.5, and 22.5 kg ha^{-1} and immediately after the first cut with 90, 0, and 31.5 kg ha^{-1} of N, P, and K, respectively. No irrigation or plant protection products were used. The early, optimal, and late sampling times during primary growth corresponded to developmental stages of booting, early heading, and full heading, respectively (Table 1). Sampling times were the same for both species because of similar phenological development. During regrowth, sampling times were 4, 6, and 8 wk after the first cut taken at the early heading stage of development. A cleansing cut of all plots was performed at the end of August 2006. Dates of fertilizer application and sampling with the corresponding cumulative growing degree days as well as the visual developmental stages of the sward at each sampling time are given in Table 1.

Measurements

Before each sampling, the developmental stage of the two species was determined according to the quantified scale of Simon and Park (1981) with the following values for some of the stages of

Table 1. Fertilizer application and sampling dates and corresponding cumulative growing degree days (GDD) (°C d; base temperature 0°C) in 2006 and 2007.

	2006				2007			
			Developmental stage†				Developmental stage†	
	Date	GDD (°C d)	Timothy	Tall fescue	Date	GDD (°C d)	Timothy	Tall fescue
Primary growth								
Onset of growth	27 Apr.	0			20 Apr.	0		
Spring fertilization	18 May	202			15 May	140		
Sampling 1	13 June	494	34	32	11 June	521	33	31
Sampling 2	20 June	625	56	54	18 June	608	58	56
Sampling 3	27 June	755	58	58	25 June	702	58	58
Regrowth								
Defoliation	16 June	0			18 June	0		
Fertilization	21 June	105			19 June	13		
Sampling 1	14 July	537	24	22	16 July	429	31	23
Sampling 2	27 July	739	33	22	30 July	661	34	23
Sampling 3	11 Aug.	988	34	22	13 Aug.	921	36	23

†Most advanced tillers. Scale: Simon and Park (1981).

development: 21, one elongated leaf sheath; 31, first node palpable at culm; 39, flag leaf ligule just visible; 45, boot swollen; 50, inflorescence 1 to 2 cm visible; and 58, base of inflorescence just visible. A subsample of the herbage was then cut at ground level from each plot using a 0.3 by 0.3 m quadrat. Cutting at ground level was chosen to obtain whole tillers. These subsamples were first fractionated into six categories: three tiller types (VEG, ELONG, and GEN), loose senesced material, loose living material, and species other than timothy or tall fescue. Tiller classification was based on the occurrence of nodes and inflorescences as follows: (i) VEG tillers: pseudostem instead of true stem, (ii) ELONG tillers: true stem with visible or palpable nodes but without the presence of an inflorescence, and (iii) GEN tillers: true stem with the presence of an inflorescence, either as emerged or still inside the flag leaf sheath. At each sampling time, approximately 20 ELONG tillers randomly selected from each subsample were dissected to determine the developmental stage of the apex by the scale introduced for perennial ryegrass (*Lolium perenne* L.) (Sweet et al., 1991). Whole tillers were divided into tiller types even if totally or partially senesced. Remaining loose timothy or tall fescue tissues were divided into loose senesced material and loose living material by dissecting the different tissues apart.

In the secondary fractionation of the subsamples, the number of the tillers of each tiller type was determined and the tillers were further divided into the following fractions: living leaf blades, stems (including leaf sheaths and pseudostem), inflorescences, and senesced tissues. Leaf blades were detached at their base of the true stems or the pseudostems. The senesced tissues were dissected at the intersection of green and senesced tissues. The tillers or tissues were considered senesced when they were severely chlorotic or dry. The fractions were dried in 60°C for 40 h and the respective DM weights were determined.

The DM weights of each tiller type were calculated by adding up the DM weights of the corresponding fractions. The average tiller weights (g DM tiller^{-1}) of each tiller type were calculated based on the total DM yield and the number of tillers of each tiller type. The proportion of living leaf blade (LWR) was calculated for each tiller type by dividing the living leaf blade DM yield of each tiller type with the total tiller DM yield. In calculating the LWR of herbage, the DM yield of loose senesced material and loose living material were included as well. The proportion of attached senesced material was calculated similarly. Tiller density (tillers m^{-2}) was calculated for each tiller type dividing the corresponding number of tillers by sample area (0.09 m^2). The total tiller density is the sum of all tiller types.

The herbage mass of each plot was determined by harvesting an area of 6 m^2 at a height of 7 cm with a Haldrup 1500 plot harvester (Haldrup, Løgtør, Denmark). The fresh weight of the forage was determined immediately and a sample of approximately 200 g was dried at 60°C for 40 h to determine the DM concentration.

Differences in temperatures between years were taken into account by using growing degree days (°C d) when presenting the results. We used 0°C as the base temperature for the calculation of growing degree days as suggested by Bonesmo and Bélanger (2002). Monthly mean temperatures, precipitation, and water balance (precipitation – pan evaporation; class A pan) of the growing seasons 2006 and 2007 are presented in Table 2.

Statistical Analyses

The data of the primary growth and the regrowth were each subjected to analyses of variance with the MIXED procedure of SAS (version 9.1; Littell et al., 1996). Statistical significance was postulated at $p \leq 0.05$. Replicates and production years were considered to be random effects while species, sampling times, and their interaction were considered fixed effects. It was evident that the data was not balanced since timothy contained tillers of each tiller type on each sampling time whereas tall fescue did not. In tall fescue, the regrowth consisted of VEG tillers only and the proportion of ELONG and GEN tillers was also low in the primary growth. Therefore, the comparison between species was done within each tiller type. Finally, the data was analyzed for total DM yield, total tiller density, LWR of total DM yield, and proportion of total senesced tissue. The model was the same as above.

RESULTS AND DISCUSSION

Herbage Dry Matter Accumulation

The herbage DM accumulation rate over the three sampling times, expressed as a function of cumulative growing degree

Table 2. Monthly mean values for temperature, precipitation, and water balance in the growing seasons of 2006 and 2007 at Maaninka and the 30-yr average (1971–2000) (Finnish Meteorological Institute, Helsinki, Finland).

	Daily mean temp (°C)			Precipitation (mm)			Water balance (mm)†		
	2006	2007	30-yr avg.	2006	2007	30-yr avg.	2006	2007	30-yr avg.
May	9.7	9.3	8.5	28.1	70.2	41.8	–67	–20	–57
June	15.7	14.4	14.3	35.4	36.7	65.6	–106	–93	–58
July	17.3	16.5	16.5	36.7	107.5	73.8	–147	+16	–49
August	17.1	16.4	14.0	29.4	49.0	83.8	–111	–39	+1
September	11.5	9.1	8.8	51.9	92.8	56.4	–4	+62	+20
May–Sept.	14.3	13.1	12.4	181.5	356.2	321.4	–435	–74	–144

†Precipitation – pan evaporation.

days (°C d), was almost linear ($R^2 > 0.95$) for both species during primary growth and regrowth (Fig. 1). Grass DM accumulation usually follows a sigmoid pattern (Robson et al., 1988), but this experiment focused on the linear phase of the growth curve when canopies are usually grazed or harvested (Bonesmo, 2000). The herbage DM accumulation rates during primary growth (0.0102 and 0.0110 Mg DM ha^{-1} °C d for timothy and tall fescue, respectively; average of 2 yr) were nearly twice those in the regrowth (0.0047 and 0.0050 Mg DM ha^{-1} °C d). Timothy and tall fescue did not differ for their herbage DM accumulation rates in primary growth and regrowth (no significant species × time interaction for DM yield, $p > 0.50$). In the regrowth, however, tall fescue had higher DM yield on all sampling times, suggesting that the difference in DM yield between the two species resulted from differences in growth before the first sampling of the regrowth.

The herbage DM accumulation rates in primary growth were slightly less than those reported by Bélanger and Richards (1997) (0.0132 Mg DM ha^{-1} °C d) and Bélanger et al. (2008) (0.0125 Mg DM ha^{-1} °C d) for timothy in eastern Canada but similar to those of timothy–meadow fescue (*Festuca pratensis* Huds.) mixtures in Finland reported by Pulli (1980) (0.0100 Mg DM ha^{-1} °C d) and Kuoppala et al. (2008) (0.0093 Mg DM ha^{-1} °C d). In the regrowth, however, the herbage DM accumulation rate of timothy (0.0046 Mg DM ha^{-1} °C d) was clearly lower than that reported by Bélanger and Richards (1997) (0.0079 Mg DM ha^{-1} °C d) or Höglind et al. (2005) (approximately 0.0095–0.0117 Mg DM ha^{-1} °C d)

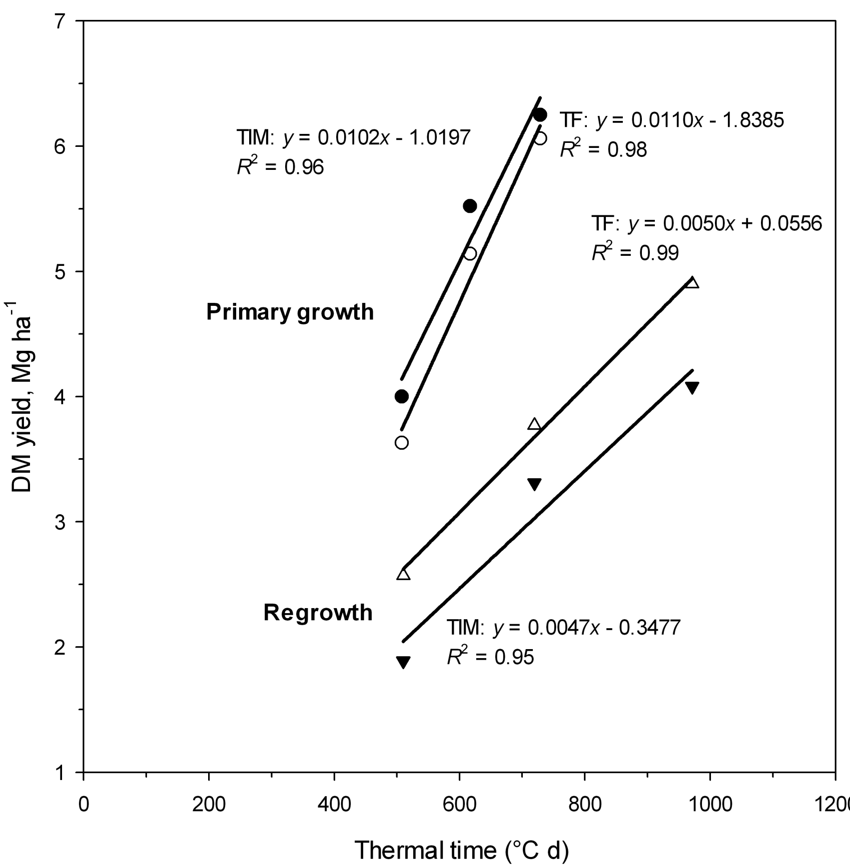

Figure 1. Dry matter (DM) yield accumulation in relation to thermal time expressed as cumulative growing degree days (base temperature of 0°C) for primary growth and regrowth of timothy (TIM) and tall fescue (TF). For regrowth, growing degree days were cumulated from the date of the first cut taken at the early heading stage of development. Values are average over 2 yr.

Table 3. Proportion of tiller types in herbage dry matter (DM) on three consecutive sampling times in primary growth and regrowth for timothy and tall fescue. Values are average over 2 yr.

			Sampling time			*p* values		
	Tiller type†	Species	1	2	3	Species	Time	Species × time
Primary growth	VEG	Timothy	0.03‡	0.02	0.01	<0.001	<0.001	0.48
		Tall Fescue	0.88	0.88	0.74			
	ELONG	Timothy	0.26	0.28	0.25	<0.001	0.80	0.47
		Tall Fescue	0.01	0.01	0.01			
	GEN	Timothy	0.67	0.70	0.74	<0.001	0.077	0.60
		Tall Fescue	0.10	0.11	0.24			
Regrowth	VEG	Timothy	0.84	0.44	0.30	–§	<0.001	–
		Tall Fescue	1.00	1.00	1.00			
	ELONG	Timothy	0.14	0.48	0.58	–	<0.001	–
		Tall Fescue	0.00	0.00	0.00			
	GEN	Timothy	0.00	0.03	0.11	–	0.002	–
		Tall Fescue	0.00	0.00	0.00			

†VEG, vegetative; ELONG, elongating vegetative; GEN, generative.

‡Values were square root transformed for analysis of variance and back transformed for biological interpretation.

§In regrowth, tall fescue had no ELONG or GEN tillers and therefore the ANOVA was performed for timothy only.

but again similar to or higher than those of timothy–meadow fescue mixtures in Finland (0.0015–0.0040 Mg DM ha^{-1} °C d [Pulli, 1980] and 0.0028 Mg DM ha^{-1} °C d [Kuoppala et al., 2008]). The lower herbage DM accumulation rates of timothy regrowth in Finland compared to that reported for eastern Canada or southern Norway could be at least partially related to a water stress. Irrigation was used by Bélanger and Richards (1997) in their study of the regrowth in eastern Canada and the monthly precipitation was around 100 mm after the first cut in the study in Norway (Höglind et al., 2005). In our study, however, precipitation and water balance during the regrowth leading to the second cut in 2006 were notably below the 30-yr average (Table 2).

Seasonal DM yields of timothy and tall fescue in our study are similar to those reported in other areas with short and cool growing seasons (Drapeau et al., 2007; Pelletier et al., 2010). In studies where both species were compared, their DM yields in first and second cut in the northern agricultural areas of eastern Canada (Pelletier et al., 2010) and their seasonal DM yield in New York (Cherney and Cherney, 2005) did not differ. Our results confirm that, in the primary growth, tall fescue and timothy have similar growth potentials under Finnish conditions. In the regrowth, however, tall fescue has a greater growth potential than timothy primarily because of a faster regrowth before the linear phase of growth. According to Cherney and Cherney (2005), although both species had similar seasonal DM yield, timothy produced a greater proportion of its DM yield in spring (66%) than tall fescue (55%), suggesting a greater growth potential of tall fescue in regrowth; this is in line with our results.

Contribution of Tiller Types and Their Leaf, Stem, and Inflorescence Fractions to Dry Matter Yield

In the primary growth, GEN tillers were predominant in timothy whereas VEG tillers were predominant in tall fescue (Table 3). By delaying the sampling time, the proportion of VEG tillers decreased slightly and the proportion of GEN tillers increased in both species. In the primary growth, ELONG tillers contributed for around 25% of the herbage DM yield of timothy but were nearly absent in tall fescue. In the regrowth, species differences in the proportion of tiller types and changes with time were more pronounced because tall fescue had only VEG tillers (Table 3). In contrast to tall fescue, all tiller types were present in the regrowth of timothy. There was a clear decrease in the proportion of VEG tillers with time along with a concomitant increase in the proportion of ELONG tillers and a slight increase in the proportion of GEN tillers.

The proportion of GEN tillers can be affected by N fertilization. Nitrogen fertilization increased the proportion of GEN tillers in the spring growth of tall fescue (Lafarge, 2006). In the regrowth of timothy, the proportion of GEN tillers increased from 10% with no N applied to 51% under nonlimiting N conditions (Bélanger and McQueen, 1998). In their study, however, Bélanger and McQueen (1998) did not differentiate between ELONG and GEN tillers. The combined proportion of ELONG and GEN tillers (51–69% on the last two sampling times) in the regrowth of our study is therefore comparable to that reported by Bélanger and McQueen (1998) for nonlimiting N conditions. The proportion of GEN tillers in the primary growth (10–24%) of tall fescue is consistent with values reported from other studies (5–15%) (Lafarge, 2006).

Nonflowering ELONG tillers with true stems were prominent in both primary growth and regrowth of timothy. The existence of this type of tillers in timothy has previously been reported (Langer, 1956; Höglind et al., 2005; Emoto and Ikeda, 2005). In most of those studies, however, stem apices were rarely dissected and the success of floral induction was not determined. In our study, most stem apices in ELONG tillers were in a reproductive

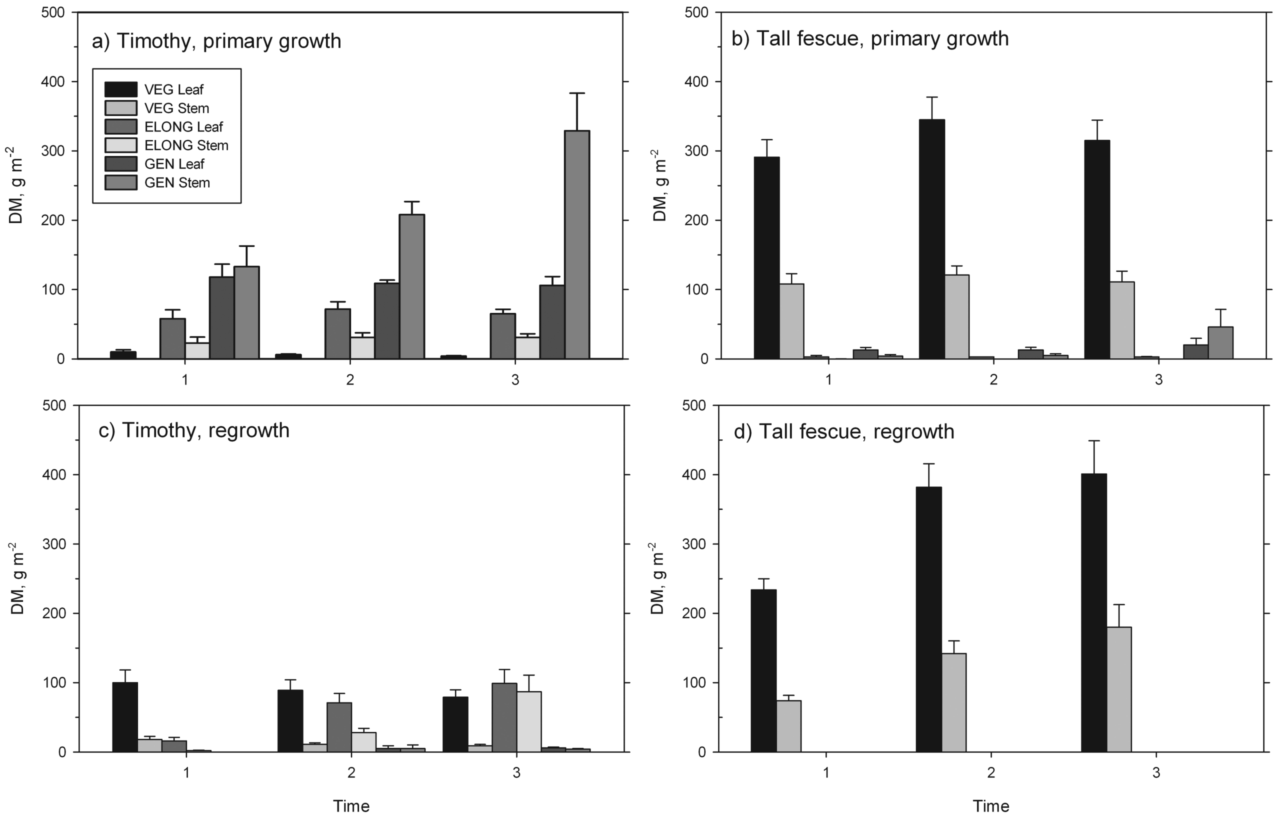

Figure 2. Contribution of different tiller types to dry matter (DM) yield of above ground biomass (cutting height of 0 cm) for primary growth and regrowth of timothy and tall fescue. Vertical bars indicate the standard error of the means. VEG, vegetative; ELONG, elongating vegetative; GEN, generative. Values are average over 2 yr.

stage during primary growth. This indicates a successful flowering inducement, although there was no production of actual inflorescences (Seppänen et al., 2010). Some ELONG tillers had vegetative apices in primary growth, especially when timothy was at the early heading stage of development. However, nearly all of the apices of the ELONG tillers were vegetative in the regrowth. Therefore, we propose that ELONG tillers of timothy are a distinct tiller type rather than a transition stage from VEG to GEN tillers. Furthermore, our results indicate that there are two types of ELONG tillers, one with apices in GEN nonflowering stage and one with apices in vegetative stage.

The contribution of living leaf blade and stem fractions (containing leaf sheaths) of the tiller types to DM yield is illustrated in Fig. 2. In the primary growth of timothy, the contribution of the stem fraction of GEN tillers to DM yield increased with time whereas the changes in other fractions were much smaller. In contrast to timothy, the DM yield of tall fescue was largely formed of leaf blades of VEG tillers along with the pseudostem fraction of the same tillers. The proportion of inflorescences in GEN tillers increased with time ($p < 0.001$) from 0.005 to 0.064 in timothy and from 0.004 to 0.032 in tall fescue (species × time interaction, $p < 0.001$; data not presented).

In the regrowth of timothy, there was a greater balance of all tiller types than in the primary growth. The contribution of the leaf blades of VEG tillers remained important despite the increased contribution of the leaf blades and stems of ELONG tillers with advancing timothy development. In tall fescue, most of the DM yield increase originated from the living leaf blades of VEG tillers, although the pseudostem fraction of VEG tillers also increased and made a significant contribution to DM yield. In regrowth, the proportion of inflorescence of GEN tillers in timothy remained insignificant ($p < 0.005$; data not presented).

Tiller Density and Tiller Weight Relationship

The weight and density of the different tiller types varied with species and sampling time (Fig. 3). In the primary growth, the density of VEG tillers of both species tended ($p = 0.079$) to decrease with time while the size of these tillers increased with time but only for tall fescue (species × time interaction, $p = 0.01$). Timothy had a lower density of VEG tillers ($p < 0.001$) and smaller VEG tillers ($p < 0.001$) than tall fescue. Timothy had a much greater density of ELONG tillers than tall fescue ($p < 0.001$) but the weight of the timothy ELONG tillers increased only moderately (33%) while the tall fescue ELONG tillers more than tripled in weight (species × time interaction, $p = 0.014$). In general, time had no effect on the density of ELONG or GEN tillers in either of the species ($p > 0.58$). The density of GEN tillers was greater in timothy than in tall fescue ($p < 0.001$). However, the GEN tillers of

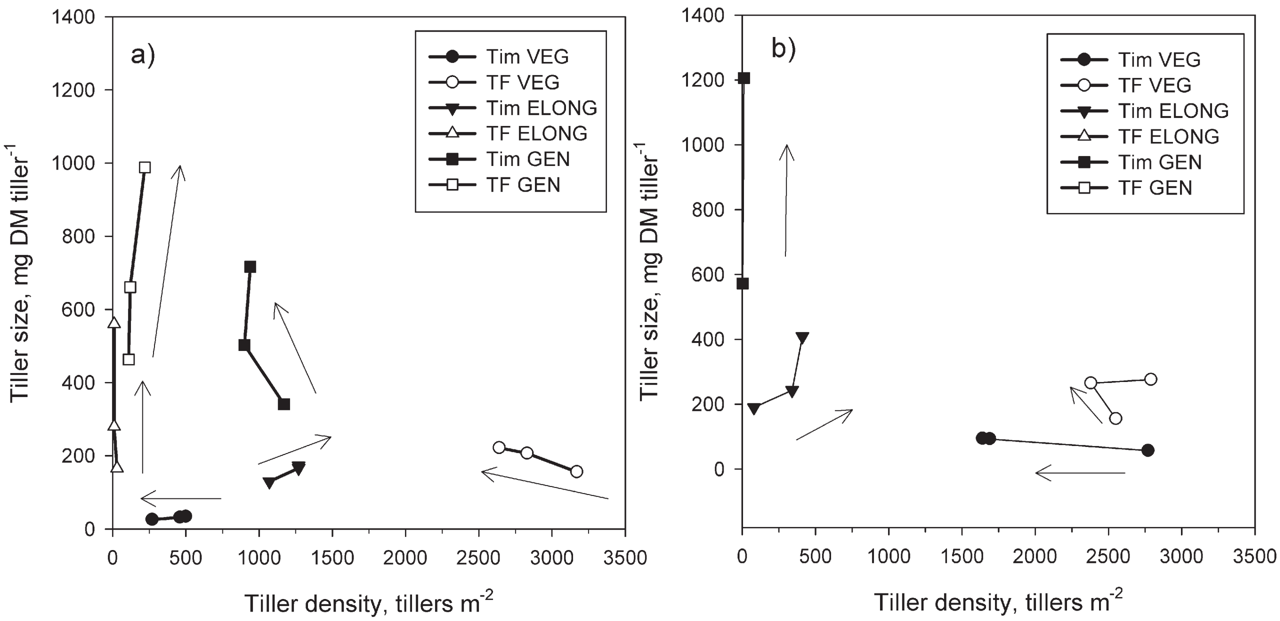

Figure 3. Relationship between tiller density and individual tiller weight for each tiller type in primary growth (a) and regrowth (b) of timothy (Tim) and tall fescue (TF). DM, dry matter; VEG, vegetative; ELONG, elongating vegetative; GEN, generative. Arrows indicate the effect of sampling time. Values are average over 2 yr.

tall fescue were larger than those of timothy ($p < 0.001$). The GEN tillers of both species more than doubled their weight with time ($p < 0.01$) but the increase was greater in tall fescue than in timothy (species × time interaction, $p = 0.03$). The previously described increase in DM yield of the primary growth of timothy was based mostly on the rapid growth of individual GEN tillers, especially their stem fraction. In tall fescue, the weight increase of individual VEG tillers (42%) more than offset the decrease in their density.

In the regrowth, the density of VEG tillers of timothy decreased with time whereas that of tall fescue remained nearly the same (species × time interaction, $p = 0.007$). The weight increase of individual VEG tillers of tall fescue (78%) was greater than that of timothy (63%, species × time interaction, $p = 0.034$). In timothy, the density of ELONG tillers tended to increase with time ($p = 0.09$) and the weight of individual tillers increased by 115% ($p < 0.001$). Few GEN tillers were present only at the second and third sampling times but their weight more than doubled in 2 wk ($p = 0.03$). In tall fescue, there were no ELONG or GEN tillers.

The total tiller density of timothy in the primary growth (2480–2740 tillers m^{-2}) was lower than that of tall fescue (2880–3310 tillers m^{-2}, $p = 0.04$). There was a slight tendency toward a decrease in total tiller density but the effect of time was not clear ($p = 0.20$). In the regrowth, there were no differences between species ($p = 0.78$) or sampling times ($p = 0.14$) as the total tiller densities varied from 2360 to 2940 tillers m^{-2} for timothy and from 2380 to 2790 tillers m^{-2} for tall fescue. The tiller density of timothy during spring growth varied between 1300 and 3500 tillers m^{-2} in eastern Canada and between 1600 and 3000 m^{-2} in southern Norway with a clear decrease in tiller density starting with the true stem development of GEN tillers (Bélanger, 1996, 1998; Höglind et al., 2005). The timothy tiller density observed in spring in our study conducted in Finland is therefore similar to those reported in other studies. Furthermore, the decrease in the density of VEG tillers suggests that the overall decrease in tiller density reported in eastern Canada is attributable mostly to the death of VEG tillers of timothy. In regrowth, both Bélanger (1998) and Höglind et al. (2005) reported timothy tiller density as high as 5000 tillers m^{-2}, values higher than those obtained in our study. A decrease in tiller density with time was also observed to start from 15 d (Bélanger, 1998) to 20 to 30 d (Höglind et al., 2005) following the defoliation. Our results confirm that the tiller density of timothy can decrease during the linear phase of growth in primary growth and regrowth, which is mostly due to the death of VEG tillers. It is clear that in the linear phase of growth, the priority is given to GEN and ELONG tillers. The generation of ELONG tillers can counterbalance the decrease in the total tiller density, especially in the regrowth. In perennial ryegrass, the number of tillers per plant declined by 50% during stem elongation (Colvill and Marshall, 1984) as a result of increasing competition for assimilates at flowering.

In contrast to timothy, the tiller density of tall fescue did not decrease so evidently in either the primary growth or the regrowth. To our knowledge, there are no reports of comparison of tall fescue and timothy in the same study for tillering characteristics. In a study conducted in the United States, the tiller density of tall fescue was around 2500 tillers m^{-2} (Zarrough et al., 1983) while in France, tiller densities between 2500 and 5000 tillers m^{-2} (Lafarge, 2006) were reported. These findings are in line with our results.

Table 4. Proportion of living leaf blade (leaf to weight ratio) of different tiller types and herbage on three consecutive sampling times in primary growth and regrowth for timothy and tall fescue. Values are average over 2 yr.

	Tiller type†	Species	Sampling time 1	2	3	SEM‡	*p* values Species	Time	Species × time
Primary growth	VEG	Timothy	0.56	0.46	0.59	0.032	0.028	0.41	0.023
		Tall Fescue	0.62	0.64	0.56				
	ELONG	Timothy	0.42§	0.35	0.30	–	0.169	0.420	0.066
		Tall Fescue	0.41	0.37	0.46				
	GEN	Timothy	0.33	0.22	0.16	0.030	0.090	<0.001	0.22
		Tall Fescue	0.28	0.23	0.07				
	Herbage	Timothy	0.31	0.24	0.18	0.032	<0.001	<0.001	0.034
		Tall Fescue	0.53	0.52	0.42				
Regrowth	VEG	Timothy	0.69	0.68	0.57	0.026	0.023	<0.001	0.059
		Tall Fescue	0.62	0.61	0.58				
	ELONG	Timothy	0.53	0.48	0.35	0.024	–¶	<0.001	–
		Tall Fescue	–	–	–				
	GEN	Timothy	–	0.23	0.13	0.030	–	0.056	–
		Tall Fescue	–	–	–				
	Herbage	Timothy	0.45	0.43	0.33	0.020	<0.001	0.008	0.005
		Tall Fescue	0.51	0.55	0.53				

†VEG, vegetative; ELONG, elongating vegetative; GEN, generative.

‡Standard error of the means for comparing sampling times.

§Values were square root transformed for analysis of variance and back transformed for biological interpretation.

¶In regrowth, tall fescue had no ELONG or GEN tillers and therefore the ANOVA was performed for timothy only.

Morphological Differences of Tillers of Timothy and Tall Fescue

In the primary growth, the LWR was the highest in VEG tillers of both species (Table 4). The LWR of VEG and GEN tillers of tall fescue was slightly greater than those of timothy, resulting in greater herbage LWR of tall fescue. The decrease in herbage LWR with time was faster in timothy than in tall fescue. The LWR of the different tiller types in our study represents the proportion of living leaf blades since the senesced leaf material was removed. The calculation of the herbage LWR, however, included loose living and loose senesced material. Consequently, the LWR of herbage is not the weighted mean of LWR of the tiller types.

In the regrowth, the LWR of VEG tillers was greater for timothy than for tall fescue (Table 4). The LWR decreased with time and this decrease tended to be greater in timothy than in tall fescue. The ELONG tillers of timothy had a greater LWR than the GEN tillers. In both tiller types, the LWR decreased with time. As for the primary growth, the herbage LWR of tall fescue was greater than that of timothy and it remained almost unchanged whereas that of timothy decreased with time.

In general, the observed values of herbage LWR were low for both primary growth and regrowth of the two species compared to those reported in earlier studies (Terry and Tilley, 1964; Bélanger and McQueen, 1998; Gustavsson and Martinsson, 2004; Kuoppala et al., 2008). This can be partly explained by the low sampling height (ground level), the exclusion of the senesced leaf blade from the leaf fraction, or the time period in our study focusing only on stages of development appropriate for silage harvesting. Especially timothy had a much lower herbage LWR in the regrowth (0.45–0.33) than previously reported in silage studies in Scandinavia (0.9–0.39) (Gustavsson and Martinsson, 2004; Kuoppala et al., 2008). The greater herbage LWR of tall fescue compared to timothy has often been reported but most studies were conducted only on the primary growth (Terry and Tilley, 1964; Morrison, 1980).

The two tiller types forming a true stem (ELONG and GEN) had distinctly different patterns. The ELONG tillers had a much greater LWR than the GEN tillers. This could be related to the smaller size of the ELONG tillers (Fig. 3). Also, the rate of decline in LWR in the primary growth was slower for ELONG tillers than for GEN tillers. The strong decrease in herbage LWR in timothy was a result of LWR changes in the dominating tiller types. In contrast, the domination of VEG tillers with a constant LWR restrained the changes in herbage LWR of tall fescue.

In addition to LWR, the proportion of senesced material can also affect the herbage nutritive value. In the primary growth, the VEG tillers of timothy had a greater proportion and GEN tillers had a smaller proportion of attached senesced material compared to tall fescue (Table 5). There were no differences between species in the proportion of attached senesced material in the ELONG tillers. Generally, the effect of sampling time was negligible or inconsistent. In the herbage, the proportion of the senesced material did not vary with species and time.

In the regrowth, the proportion of attached senesced material in VEG tillers was similar for both species but

Table 5. Proportion of attached senesced tissue of different tiller types and proportion of total senesced material (attached and loose senesced material) in herbage on three consecutive sampling times in primary growth and regrowth for timothy and tall fescue. Values are average over 2 yr.

	Tiller type†	Species	Time 1	Time 2	Time 3	SEM‡	*p* values Species	*p* values Time	*p* values Species × time
Primary growth	VEG	Timothy	0.18	0.32	0.17	0.027	0.005	0.063	0.002
		Tall Fescue	0.09	0.08	0.13				
	ELONG	Timothy	0.09	0.08	0.08	0.045	0.99	0.40	0.64
		Tall Fescue	0.11	0.05	0.09				
	GEN	Timothy	0.04	0.05	0.03	0.013	0.009	0.21	0.050
		Tall Fescue	0.10	0.05	0.10				
	Herbage	Timothy	0.18	0.14	0.12	0.019	0.112	0.54	0.130
		Tall Fescue	0.17	0.17	0.19				
Regrowth	VEG	Timothy	0.10	0.10	0.19	0.020	0.28	0.016	0.135
		Tall Fescue	0.15	0.14	0.16				
	ELONG	Timothy	0.01	0.02	0.04	0.010	–§	0.064	–
		Tall Fescue	–	–	–				
	GEN	Timothy	–	0.01	0.02	0.006	–	0.047	–
		Tall Fescue	–	–	–				
	Herbage	Timothy	0.36	0.22	0.25	0.029	0.23	0.002	0.49
		Tall Fescue	0.29	0.22	0.22				

†VEG, vegetative; ELONG, elongating vegetative; GEN, generative.

‡Standard error of the means for comparing sampling times.

§In regrowth, tall fescue had no ELONG or GEN tillers and therefore the ANOVA was performed for timothy only.

it increased with time (Table 5). The proportion of attached senesced material was negligible in ELONG and GEN tillers of timothy. In the herbage, the proportion of senesced material was greater in the regrowth than in the primary growth. The proportion of attached senesced material decreased for both species from the first to the second sampling time but remained unchanged on the third sampling time. This could be related to the generation of new ELONG tillers with a high proportion of living leaf blade in timothy and of new VEG tillers in tall fescue.

Although the physiology of leaf senescence is well established (Bélanger, 1996; Woodward, 1998; Virkajärvi and Järvenranta, 2001), the proportion of senesced material is seldom reported. The observed values in the primary growth (0.12–0.19) were slightly greater than those reported for timothy in the United Kingdom by Terry and Tilley (1964) (0.04–0.15) for approximately similar growth periods. With a typical stubble height for harvesting timothy–meadow fescue mixtures for silage in Finland, Kuoppala et al. (2008) reported proportions of senesced material to be about 0.01 in the primary growth but 0.06 to 0.12 in the regrowth. This difference between our observations in the regrowth (proportion of senesced material between 0.22 and 0.36) is largely explained by the lower sampling height (0 cm) in our study. Although the leaf life span is reported to be shorter for timothy (266–465 growing degree days) (Bélanger, 1996, 1998; Virkajärvi and Järvenranta, 2001) than for tall fescue (550 growing degree days) (Lemaire, 1988), the amount of senesced material was similar for both species. To our knowledge, there are no published values of the proportion of senesced material for different tiller types. The VEG tillers of timothy had a greater proportion of attached senesced tissue than ELONG or GEN tillers. This corresponds well with the observed decrease in the number of VEG tillers, which is probably the result of the leaf death and consequently tiller death. In tall fescue, there were no marked differences between tiller types.

Agronomic Implications

Both species had similar rates of DM accumulation during the linear phase of growth, even though the types of tiller present were different. Because a greater proportion of stem-containing tillers are known to result in increased radiation use efficiency (Robson et al., 1988), we might have expected a higher growth rate of timothy with its higher proportion of GEN and ELONG tillers than tall fescue. The slightly lower tiller density of timothy compared to that of tall fescue might have limited its growth rate but only in the primary growth since tiller densities of both species were similar in the regrowth. Another plausible reason for the similar growth rates despite differences in the proportion of tiller types lies in the size of VEG tillers of tall fescue that were 4.5 to 8.5 times larger in the primary growth and 2.7 to 3.0 times larger in the regrowth than those of timothy. According to Sugiyama et al. (1985), large tillers ensure the effective distribution of the incoming light energy within a tall fescue canopy, at least in vegetative swards. The results indicate that grass species with different types of tillers can achieve similar growth rates, highlighting the plasticity of grasses in achieving high yield. Because our study focused on the linear phase of growth, however, the implications of different tiller types on the initial growth in spring or following defoliation were not studied.

The difference in tiller types between the two species is also likely to affect the nutritive value. Several studies have shown the positive relationship between LWR and attributes of nutritive values such as digestibility and N concentration (Terry and Tilley, 1964; Kuoppala et al., 2008). The greater LWR of tall fescue, associated to a greater proportion of vegetative tillers, is likely to result in an improved nutritive compared to timothy. Furthermore, the proportion of senesced material especially in the regrowth can be so high that it may also affect the nutritive value (Romera et al., 2009).

Management practices can be used to manipulate the tiller type composition of the primary growth. The formation of true stem-containing tillers can be encouraged to some extent by sufficient fertilization with N and K (Langer, 1959) and by allowing the growth to continue well past the vegetative stages of development by lengthening the cutting intervals (Ito et al., 1997). This also applies to the regrowth as larger tillers and a greater proportion of elongating tillers will emerge if the tillers are in a more advanced stage of development at the time of defoliation of the primary growth (Höglind et al., 2005; Pakarinen et al., 2011). In addition, the choice of cultivars may affect the distribution of tiller types in both primary growth and regrowth of timothy (Virkajärvi et. al., 2010).

Following the defoliation in June, the initial regrowth of tall fescue was greater than that of timothy, most likely because of the large presence of vegetative tillers at the time of defoliation of tall fescue. These tillers can continue their growth despite the defoliation while, in timothy, the regrowth tiller population is mainly formed of new daughter tillers originating from basal apices of surviving tillers. In timothy, these tillers may develop right after (Ito et al., 1997) or even before the defoliation if the defoliation is delayed until the anthesis stage of development (Höglind et al., 2005).

CONCLUSIONS

The results presented in this paper represent the first quantitative characterization of ELONG tillers in timothy and tall fescue. The ELONG tillers are a distinct tiller type and they are not just a transition between VEG and GEN tillers. Although present in both species, ELONG tillers contributed significantly to herbage DM yield mostly in timothy with a contribution up to 28% in the primary growth and 58% in the regrowth.

A fundamental feature of timothy is the contribution of three tiller types to DM yield with a major contribution from stem-producing tillers (ELONG and GEN) in primary growth and regrowth. The GEN tillers were dominant in the primary growth whereas in the regrowth, the balance between VEG and ELONG tillers changed with time in favor of ELONG tillers. In contrast, VEG tillers were by far the main contributors to herbage DM yield in the primary growth and regrowth of tall fescue. As DM accumulation rates were similar for both species, these differences highlight the plasticity of grasses in achieving high yield.

The GEN tillers are characterized by their large size and their low LWR and amount of attached senesced material whereas VEG tillers are small and they have a high LWR and a large amount of attached senesced material. The ELONG tillers were intermediate in size and LWR but they have a low amount of attached senesced material.

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