THE ORIGIN AND ITS EFFECT ON GROWING HABITS OF THE REGROWTH TILLERS OF TIMOTHY AND TALL FESCUE IN FINLAND

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Abstract: The regrowth of timothy and tall fescue were compared to reveal the origin of different tiller types developing into the regrowth canopy, the recovery potential of different primary growth tiller types after the cut and the effect of primary growth tiller type and developmental stages on regrowth habits. Experiments were conducted during 2006-2009 in Maaninka, Eastern Finland. Tiller type or the final developmental stage of the regrowth tillers in timothy or tall fescue were not determined by the type of tiller in the primary growth, with the exception of generative tillers in the regrowth of timothy originating only from primary growth generative tillers. Thus, tiller type is not an inherited feature of one individual plant and either environmental factors or tiller characteristics determine the final type of the tiller in the regrowth. Recovery potential of different tiller types was contrasting between the species: in timothy, highly developed tillers during the primary growth were had the best survival capacity after cut, but in tall fescue it was the opposite. For obtaining large and rapidly growing tillers into the regrowth, primary growth tillers at advanced elongating vegetative (seven nodes) or early generative stage (before the full emerge of the inflorescence from the flag leaf sheath) in timothy and large vegetative (four leaves) or early generative (inflorescence swollen inside the flag leaf) in tall fescue were the most optimal.

Key words: timothy, tall fescue, regrowth, tiller type, tiller feature.

INTRODUCTION

Harvesting the summer regrowth is an important part of grass silage production in Scandinavia, where only two or three cuts per growing season can be taken. Timothy and different fescues, namely meadow fescue and tall fescue, are the most common forage grasses for silage production in Finland, and their growth habits on the tiller level in the regrowth differ greatly. Especially timothy (Phleum pratense L.) and tall fescue (Festuca arundinacea Schreb.) are two contrasting species.

According to visual observations, the regrowth canopy of timothy can consist of three tiller types: vegetative (VEG; containing only leaves and leaf sheaths), elongating vegetative (ELONG; containing true stem and leaves) and generative (GEN; containing true stem, leaves and an inflorescence). On the contrary, tall fescue produces mostly VEG tillers and only few tillers contain true stem in the regrowth. In grasses, there are two alternative means to produce tillers for the regrowth: either continue the growth despite the tiller has been cut if the apex has not been destroyed by the cut, or to form new tiller from the buds nearby the ground level if the primary growth tiller has been seriously damaged in the cut. Tiller type distribution and size in the canopy determine the actual yield of the regrowth sward: in timothy both VEG and ELONG are important in biomass production, while in tall fescue VEG tillers are dominating [1].

If a high regrowth yield with a good feeding value is desired, the tillers should tolerate the cut and recover from it quickly creating a dense canopy, have high rates in tiller length growth, leaf appearance and leaf length growth, resulting in a high total tiller size and abundant amount of living leaf tissue per tiller. In cross-pollinated grass species like timothy or tall fescue, tillers in a sward of a single cultivar are not genetically identical but a population with varying genetical information. Thus, there is variation in the growing habits of individual plants. The developmental stage of tillers during the primary growth cut is supposed to affect the sequential development of regrowth tillers, but only little information is available on which features of the regrowth are determined by the tiller type or developmental stage of the tillers in primary growth.

Our aim in the present study was to compare the regrowth of timothy and tall fescue and reveal: a) the origin of different tiller types developing into the regrowth canopy and the recovery potential of different primary
growth tiller types after the cut; b) the effect of primary growth tiller type and developmental stages on regrowth habits. This was done by examining individually marked tillers of timothy and tall fescue after the primary growth cut during four growing seasons in the Nordic climate conditions in Maaninka, Finland.

MATERIALS AND METHODS

The study was conducted during four growing seasons (2006-2009) at MTT Agrifood Research Finland (at present, Natural Resources Institute Finland (Luke)), Maaninka Research Station (68°08´N, 27°19´E). For the studies during growing seasons 2006-2008, the experimental field was established in 2005 and for growing season 2009 in 2008 on fine sand in three replicates by sowing with timothy (cv. Tammisto II) and tall fescue (cv. Retu). During 2006-2009, both experimental fields were cut for the primary harvest before the end of June each year and the second cut was performed in the end of August of each year in order to mimic the standard farming practices of the area. Both experimental fields were fertilized for the primary growth in mid May using 90 kg ha⁻¹ of N and for the regrowth immediately after the first cut with using 90 kg ha⁻¹ of N. P and K were given according to the soil fertility and typical farming practice of the area. No irrigation or plant protection products were used on either of the field experiments. The data for growing conditions were recorded daily (temperature, precipitation). The effective temperature sum above 0 ºC during regrowth was calculated using the date of the primary growth cut as a zero point.

For tiller measurements, randomly chosen individual main tillers were marked prior to primary growth cut. Tillers were visually determined for the developmental stage and divided into three tiller types as follows:

- VEG. Stages 20-29 according to Simon and Park (SP) [2]; i.e. containing only leaves and leaf sheaths and the number of fully emerged leaves given by the second digit in the SP stage
- ELONG. SP 31-38; tillers containing true stem and leaves and the number of nodes given by the second digit of the SP stage
- GEN. In this study stages SP 45 or higher; tillers containing true stem, leaves and an inflorescence either inside the flag leaf (SP 45) or emerging (SP 50 or higher)

This way, the effect of the developmental stage of the tiller in the primary growth could be taken into account, when measuring the development of tillers in the regrowth. Regrowth tillers were observed visually and measured for SP stage, tiller and leaf appearance, growth and senescence during the regrowth phase approximately once a week (for 6 to 8 weeks and for 8 to 10 times per growing season, depending on the year) until the timepoint of typical regrowth harvest time.

During the regrowth periods of four years, some marked tillers were injured by herbivores or by observational work. In cases where the inclusion of these tillers would distort the results, these tillers were excluded from the data. Results from all years were used and data was not separated by the years, because we did not intend to test the effect of years but merely the effect of developmental stage over the years. To compare timothy to tall fescue, the data was always separated for species.

Recovery potential of tillers was calculated separately for each tiller type class of primary growth using the highest observed SP stage during the regrowth for each tiller, including tillers that did not grow after the primary growth cut. All other parameters were calculated excluding the tillers that had no regrowth. Growth rate of total tiller height (mm ºCd⁻¹) and leaf appearance rate (LAR; mm ºCd⁻¹ tiller⁻¹) were calculated by dividing the weekly growth or the number of new emerging leaves by the number of accumulated degree days (above 0 ºC) during the past observational interval. Values for LAR were multiplied by 100 for the clarity of results. Total leaf length per tiller (mm tiller⁻¹) and senesced leaf length per tiller (mm tiller⁻¹) were calculated by adding up the respective values of all leaves inside each tiller. After the weekly observations were calculated, the growth parameters were firstly averaged separately for each tiller to gain a set of independent values for measurements. Secondly, the tiller averages were averaged for the SP stages of the respective primary growth tillers (PG tiller) separately for each tiller type.

RESULTS AND DISCUSSION

We aimed to mark the same amount of primary growth tillers in each tiller type class to obtain a solid dataset, but due to natural differences in the primary growth habits of these species, this was not possible (Table 1). In the primary growth of timothy, all three tiller types were present, but the proportion of VEG main tillers was rather small. In the primary growth of tall fescue, ELONG tillers were almost absent as only three such tillers were found and marked over the four year period of tiller observations. As the number of tillers per
tiller type class do not present the actual tiller type distribution in the primary growth canopy, our results in this paper do not describe the actual tiller type distribution in the regrowth, but the a) origin of different tiller types developing into the regrowth canopy; b) the effect of primary growth tiller type to regrowth habits. Nevertheless, the distribution, size and longevity (i.e. the tiller life span over the regrowth period) of the tillers determine the effect of different tiller types on the formation of both yield and feeding quality. The actual distribution and potential of biomass production of these tiller types in the same field experiment has been evaluated by Virkajärvi et al. [1] and the feeding value by Pakarinen et al. [3].

**The origin of different tiller types in the regrowth**

During the summer regrowth the canopies of timothy consisted of all three tiller types: VEG (developmental stages 20-29 according to Simon and Park (SP) [2], ELONG (SP 31-38, respectively) and GEN (SP 45 or higher, respectively) (Table 1). On the contrary, tall fescue produced mostly VEG tillers and only few tillers contain true stem in the regrowth. In both species, tillers that ended up as VEG in the regrowth originated from all primary growth tiller types. There was no difference inside the species in the average developmental stage (i.e. number of leaves) of VEG tillers originating from different primary growth tiller types, but in timothy there was on average 3 living leaves per tiller (SP 23) and in tall fescue 2 leaves (SP 22).

<table>
<thead>
<tr>
<th>Tiller type in the primary growth</th>
<th>Tiller type in the summer regrowth</th>
<th>Timothy</th>
<th>Tall fescue</th>
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<td>Developmental stage (SP) in the regrowth</td>
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<td>Average</td>
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<td>PG-VEG</td>
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<td>PG-ELONG</td>
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<td>PG-GEN</td>
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In timothy, also ELONG tillers in regrowth originated from all primary growth tiller types, but in tall fescue the only ELONG tiller observed originated from an ELONG primary growth tiller. In timothy the most developed ELONG tillers (SP 35) originated from primary growth VEG tillers and the less developed from primary growth GEN tillers (SP 33). The size (above ground weight or height) of the primary growth tillers producing ELONG tillers in the regrowth did not explain this. It is possible, that the large ELONG tillers in the regrowth originating from VEG tillers, have started their apical transition from VEG to ELONG or GEN before the primary growth cut, but the actual stem elongation was realized after the cut during regrowth.
GEN tillers in the regrowth of timothy originated only from GEN primary growth tillers and were almost flowering in the end of the observation period (SP 59-60). As a long-day grass species, timothy does not obligatorily need a new vernalization for reflowering [5]. In Maaninka, Finland, the day length during the regrowth period was between 15-19.5 h during the experimental years, which is enough for timothy to obtain the induction for flowering. Another explanation for the appearance of GEN tillers into the regrowth canopy is the movement of molecular flowering inducers to other tillers in the same plant through the basal tissues, which has been shown to happen in some grasses [4]. However, there was no clear correlation between the type of primary growth tiller and the type of regrowth tiller in the same plant (data not shown), mostly because most of the tillers in the regrowth reached only VEG stages. This points out that the tiller type is not – at least not fully – a genetic trait or inherited feature in either of the species, and that other factors must affect strongly on the final type of the tiller in the regrowth.

Recovery potential after the primary growth cut
There was a clear difference between the species in the recovery potential of different primary growth tiller types after primary cut. In timothy, only half of all primary growth VEG tillers were able to regrow, while two-thirds of ELONG and nearly all GEN primary growth tillers were able to produce tillers in the summer regrowth (Table 1). In tall fescue, this was quite the opposite, as nearly all primary growth VEG tillers regrew and only a quarter of primary growth GEN tillers formed regrowth tillers. The difference between the two species is due to their different strategies in the onset of regrowth: in tall fescue, most primary growth VEG tillers just continued with their leaf growth despite the cut, but in the primary growth of timothy VEG tillers were very small and were apparently fatally injured in the cut [6].

Primary growth ELONG and GEN tillers have to produce their regrowth through new tillers from side buds near the ground level, and in this process it is essential for the tiller to have good reserves of carbohydrate in the remaining stubble and root [7]. In timothy, this is leads to a solid regrowth canopy after a lag phase during the initiation of visual regrowth and the recovery potential seems to be higher on more developed primary growth tillers. In tall fescue these new sidetillers tend to suffer from shading of the already steadily regrowing leaves (of primary growth VEG tillers) and are not as successful as the ones in timothy.

Growth habits of the regrowth tillers originating from different primary growth tiller types
Regrowth of tillers is suspected to be more vigorous, if the concerned primary growth tiller has reached higher developmental stages, produced larger leaf number and leaf area and thus has more ample reserves of carbohydrates in the stubble [7]. In our study, this effect was in some cases seen when the data was divided firstly according to the tiller type of primary growth (in the case of tall fescue, only VEG and GEN tillers were present in the primary growth in sufficient number) and secondly according to the SP stage.

In timothy, there were no clear differences along the increase of SP stage inside any tiller type group, but the total leaf length and the amount of senesced leaf tissue per tiller tended to be smaller, when the SP stage of primary growth ELONG tillers was increasing until SP stage 35 (Figures 1C and 1D). Even though the regrowth parameters of primary growth GEN tillers of timothy were usually the highest, SP stage 45 during the primary growth of timothy seemed to produce smaller and more slowly growing tillers than SP stages 52 or 56 (Fig. 1A-D). From primary growth GEN tiller group, SP stage 52 (generative, inflorescence starting to emerge from the flag leaf sheath) and from primary growth VEG and ELONG groups, the SP stages 25 (vegetative with 5 leaves) and 37 (elongating with 7 nodes) seemed to produce the fastest growing and largest tillers into the regrowth, respectively, but the differences were not significant due to the small number or tillers and high variation.

An increase in the SP stage inside the primary cut VEG tiller group might increase the growth rate and total tiller length in the regrowth of tall fescue, but reduce the same parameters inside the GEN tiller group, but the differences were not significant due to large variation (Fig. 1A and 1C). Increased SP stage did not affect leaf appearance rate (LAR) or leaf senescence in tall fescue (Fig. 1B and D). In tall fescue, the primary growth tiller type (VEG or GEN) did not affect the growth rate or LAR, but the primary growth GEN tiller type produced a smaller amount of total leaf tissue and senesced leaf per tiller in the regrowth (Figures 1C and 1D). For obtaining large and vital tillers into the regrowth of tall fescue, primary growth VEG tillers, especially SP 24 (vegetative with four leaves) were the most optimal (Fig. 1A and 1c). From more advanced primary growth tillers, SP 45 (early generative, inflorescence swollen inside the flag leaf) produced fast growing regrowth tillers, but not large tiller size (Fig. 1A-C).
Figures 1A, 1B, 1C and 1D. The effect of developmental stage (according to Simon and Park, 1981) of the tiller in the primary growth (PG) on A) growth rate of total tiller height (mm °Cd⁻¹); B) leaf appearance rate (LARx100, leaves °Cd⁻¹ tiller⁻¹x100); C) total leaf length per tiller (mm tiller⁻¹); D) senesced leaf length per tiller (mm tiller⁻¹) inside each tiller type of timothy (TIM) and tall fescue (TF). VEG = vegetative, ELONG = elongating vegetative, GEN = generative. Given values are averages of tillers during the – 8 weeks of regrowth for tillers produced by certain SP stages in PG tiller types; error bars show standard error of the mean (SEM); number of tillers (n) is given below the SP stage.

In the primary growth ELONG tillers, advanced SP stages mean that tillers have more nodes and internodes in the true stem but the number of leaves to emerge has not been fixed. In the GEN tillers, advanced SP stages
The formation of highly fibrous tissue for the stem – or the formation of an inflorescence – is biologically a costly sink for the tiller, which means less photosynthetic products are channelled and accumulated as storage carbohydrates or proteins into the root system and stubble. Thus, the reduction in the regrowth potential for the aftermath cut of these more developed primary growth tillers is probably due to the scarcity of reserved carbohydrates that should be available for the initiation of regrowth right after the cut.

CONCLUSIONS

Tiller type and developmental stage during the primary growth affected strongly on the recovery potential after the cut and on growth habits of the regrowth tillers in the same plant of timothy and tall fescue. Tiller type in the same plant was not a constant feature, and other factors determine the final type of the tiller in the regrowth.

For the formation of large and rapidly growing tillers into the regrowth, highly advanced elongating vegetative (timothy), early generative (in both species) or large vegetative (in tall fescue) primary growth tillers were the most optimal. Lower vegetative or more advanced generative developmental stages lead to lower growth rates and smaller amount of leaf tissue per regrowth tiller, which is probably due the level and sufficiency of photosynthesized carbohydrates during the time of the primary growth cut.

REFERENCES