Research review

Timothy growth in Scandinavia: combining quantitative information and simulation modelling

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Summary

Timothy (Phleum pratense) is the most widely grown sown grass species for silage and hay production in the Nordic countries; it is also common in many other areas with a cold maritime climate. Research on timothy has identified many environmental factors and plant characteristics that determine timothy growth. However, much of the literature that analyses timothy growth presents only qualitative estimates of the importance of the different growth-determining factors. Here we present a review of quantitative information on timothy. Moreover, we analyse to what extent this quantitative information is sufficient to permit the construction of a simple process-based model of timothy growth. We then use such a model to identify the major growth-determining factors. Simulations with the model showed that the major processes to be elucidated in future research on timothy are tillering dynamics and the formation and loss of leaves from tillers. We conclude that a combination of literature review and analysis by means of simulation modelling, such as we attempted here, is an effective approach to identify and prioritize research goals.

Key words: Phleum pratense (timothy), grass yield, Scandinavia, literature review, process-based modelling, sensitivity analyses, climate, physiological characters.

Introduction

Timothy (Phleum pratense) is the most widely grown sown grass species for silage and hay production in the Nordic countries; it is also common in many other countries with a cold maritime climate, like Canada and the Baltic countries. Timothy is a winter hardy species. It is able to produce high yields of good quality under a wide range of environmental conditions, especially where perennial ryegrass (Lolium perenne), the most common forage grass in continental Europe and the British Isles, is less persistent because of low temperature in winter and early spring.

Research has identified many environmental factors and plant characteristics that determine timothy growth. However, much of the literature that analyses timothy growth presents only qualitative estimates of the importance of the different factors which determine growth, and few attempts have been made to integrate and analyse the existing knowledge in a mechanistic model. Here, we present a review of quantitative information on timothy. We use this information to assess the scope for building a process-based timothy growth model. Process-based models of timothy may eventually be useful for the definition of ideotypes for breeding for better grazing and drought tolerance, for agricultural decision support and for prediction of timothy yield in future warmer climates.

Mechanistic modelling of crop growth started in the 1960s. Various models for grass growth have been described for different purposes, as reviewed by Sheehy & Johnson (1988).
Most models simulate growth as a source-driven process, within limits determined by a statistical description of phenological processes. Such models have proven to be valuable tools for optimization of grassland management (Sheehy et al., 1980; Johnson & Thornley, 1983, 1985; Johnson & Parsons, 1985). In the early 1980s, models for grasslands were developed that simulated vegetative tiller dynamics as well as the carbon balance of the sward (Dayan et al., 1981; Coughenour et al., 1984), but accurate simulation of tiller dynamics proved difficult. More recent grass models have tended to ignore most typical morphological aspects of grasses, such as tillering, and focus on their physiology. Supplementary to this approach, a more mechanistic growth model for grass leaf tissue growth (Thorley, 1991) has become the basis of a recently published version of the ‘Hurley Pasture Model’ (Thorley & Cannell, 1997). This model describes the interaction between carbon and nitrogen in plant and soil under changing environmental conditions. Phenological processes such as tillering, however, are not simulated. In this approach, substrate transport and chemical conversion are the processes that determine allocation of carbon. Interactions of carbon fluxes with leaf appearance and tillering dynamics were accounted for in the pasture model LINGRA described by Schependonk et al. (1998). The global importance of grasslands in carbon sequestration has led in the 1990s to the development of a range of new grass models that attempted to give quantified predictions of climate change effects on grass production (Parrot et al., 1995; Chen et al., 1996; Thorley & Cannell, 1997; Hunt et al., 1998; Rodriguez et al., 1999). The predicted effects of climate change and elevated CO2 on grasslands differed strongly between the modelling studies. Parrot et al. (1995) found few significant increases (an average of grass production stimulation below 10% for 31 different modelled sites), whereas Cao & Woodward (1998) and Thorley & Cannell (1997) found increases of 30% or more. Clearly, the history of grassland modelling has not produced the definitive model yet.

In this paper, we analyse various quantitative aspects of timothy growth in detail and try to develop the simplest possible process-based model that incorporates the major characteristics of timothy. While realizing that any choice of model components is subjective, we postulate the following processes and feedbacks to be of major importance:

• Tiller dynamics, with consideration of differences between vegetative and generative tillers.
• Dynamically changing patterns of assimilate partitioning, both between shoot and root and between stems and leaves.
• The dependence of sward regrowth capability on the phenological stage at which it is cut.
• The dependence of sward regrowth rate on available sources and sinks, i.e. reserves, tillers and leaves.

We thus aim for a model that distinguishes reproductive and vegetative tillers, and stems and leaves. This opens possibilities for simulating not only herbage accumulation, but also feed quality development, since important factors like digestibility and fibre content are closely correlated to the leaf : stem ratio of the herbage harvested.

We restrict ourselves to the seasonal growth of timothy. We do not investigate the overwintering of the sward, which would require simulating the dynamics of tiller density and its phenology is more sensitive to photoperiod. The vegetative tiller apices of timothy are elevated higher than those of ryegrass and suffer higher mortality at cutting or grazing due to apex removal (Davies, 1988). Tilling starts later in timothy shoots (this tiller is in the axil of the third leaf) than in ryegrass. Generally the first leaf has to be fully emerged before any tillering is observed (Ryle, 1964). Moreover, in timothy a tiller generally does not develop until five leaves or more have appeared above its node of origin, whereas in ryegrass this number is only two. Thus, tiller density is typically lower in timothy than in ryegrass. The low tillering rate of timothy is part of the explanation for its comparatively slow rate of recovery after cutting.

A second important issue in the regrowth dynamics of most grasses is the strong relationship between regrowth rate and the phenological stage at which the sward is cut (Davies, 1988). Generally, regrowth rate declines with advancing phenological development, and for timothy this decline is especially large in the transition from the vegetative to the reproductive growth stages of jointing (the appearance of the first node) to early heading (Bonesmo & Skjelvåg, 1999). This phenomenon, which can largely be explained by the increased death rate of tillers (Bonesmo, 2000), has so far been ignored in grass models. However, this phenomenon is important for timothy as it is mainly grown for silage and hay, which means that the first cut is generally taken at relatively late stages of development, between early heading and anthesis, when the cut herbage consists largely of reproductive tillers (Langer, 1956). This is in contrast to cuts later in the season when vegetative tillers also make an important contribution to herbage yield. Vegetative tillers generally are less prone to decapitation of apex due to its lower position in the sward.

We have found no examples of mechanistic, process-based models of timothy grass. Torsell & Kornher (1983) have made a dynamic model of timothy that uses empirical indices to quantify the reduction of daily growth rate by suboptimal levels of light, temperature and water. The model, however, does not simulate the physiological processes underlying growth. It can therefore only be used for predicting yields in regions with climatic conditions and management practices that are similar to those for which the model has been calibrated. Gustavsson et al. (1995) developed a source-driven dynamic model for timothy based on the concept of light-use efficiency (Monteith, 1977) and weather indices (Torsell & Kornher, 1983) but this model does not account for processes that are related to tillering and leaf formation.

Mechanistic models developed for other grass species may not be applicable to timothy. Timothy differs in various respects from agricultural grassland species such as perennial ryegrass (L. perenne). Timothy has no requirement for vernalization;
carbohydrate status of tillers during the winter. Pests, weeds and diseases are not included in our overview as their effect on timothy growth is considered to be less than that of the abiotic environmental factors, with the possible exception of some fungal diseases. Also not discussed are soil toxicity and air pollution. These may be of local importance and may even be of generally increasing importance, but are less relevant in present-day Scandinavia. We concentrate on timothy genotypes in Scandinavian grass growing regions (which differ in photoperiod, light and temperature), with different levels of availability of water and nitrogen, and different management regimes.

Materials and Methods

Model structure

The model was developed by modifying LINTUL-GRASS; Light INT erception and Utilization Simulator GRASS (LINGRA) (Schapendonk et al., 1998; Rodriguez et al., 1999), a simple process-based model of vegetative growth of perennial ryegrass. In LINGRA, the daily growth rate is determined by the minimum of a sink and a source term. The sink term represents the potential growth rate of the plants, which depends on mean daily temperature, and can be modified by the effects of the availability of assimilates on tillering. Assimilate production depends on intercepted radiation, and a photosynthetic light-use efficiency (LUE) calculated as a function of CO$_2$, temperature, light intensity and the Rubisco concentration of upper leaves. The specific leaf area for newly grown leaves depends on the level of reserves.

In the present study we used the concepts described in these previous studies. In order to change the model from a ryegrass-specific application to a timothy-specific application, a literature survey was done to find appropriate parameter values. The new timothy model differs further from LINGRA in that it simulates the dynamics of both vegetative and generative tillers. Leaf appearance rate and formation of new vegetative tillers depend on reserve content. Site filling decreases at high leaf area index (LAI) because of the inhibitory effect of a low ratio of red:far-red light on bud emergence and (conversely) tiller death increases (Davies, 1988). Leaf death is also allowed to increase with shading in the model. The rate of formation of generative tillers is proportional to vegetative tiller density, and depends on temperature and day length. Sink strength of generative tillers decreases linearly with their size.

A schematic representation of the model is depicted in Fig. 1. The model has four weight state variables: leaves,

![Flow diagram of the timothy growth model.](image-url)
stems, roots (g biomass m$^{-2}$ ground area) and reserves (g CH$_2$O m$^{-2}$). There are two density state variables: vegetative and generative tillers (g m$^{-2}$); and one area state variable: LAI (m$^2$ leaf area m$^{-2}$ ground area). Light interception is modelled by Beer’s law with a constant light extinction coefficient. Assimilate production is calculated by multiplying light interception with a variable LUE that decreases with light intensity and follows an optimum curve with respect to temperature. The environmental sensitivity of LUE, explained in more detail by van Oijen & Ewert (1999) and Rodriguez et al. (1999), is based on the Farquhar et al. (1980) model for C$_3$ leaf photosynthesis, the Charles-Edwards (1982) semianalytical equation for upscaling from leaf to canopy photosynthesis, and on the Gifford (1995) observation of a constant daily ratio of respiration and photosynthesis. Leaves and stems have priority for biomass allocation, followed by the reserve pool, and finally the roots. Allocation thus follows a ‘cascade-method’: after the leaf-sink is fully supplied, there is overflow to the reserve pool, and when reserves are also at maximum, the roots grow on what is left. An overflow mechanism like this (with roots receiving the remainder of reserves after the rest of the plant has been supplied) was originally proposed by Troughton (1977) for grasses. Reserves can be remobilized with a time constant of 2 d.

Leaf elongation rate increases linearly with temperature. The function is differently parameterized for leaves on vegetative and generative tillers. Leaf width differs on vegetative and generative tillers, but is otherwise constant, so there is no temperature effect on leaf width. The specific leaf area (SLA) of newly grown leaves depends on the availability of reserves: when the reserve pool is at maximum, SLA is minimal, when the reserve pool decreases, SLA increases linearly towards a maximum. A single-layer water balance is included. Drought affects both source (LUE) and sink (formation of leaves and tillers and leaf expansion).

Our model has 28 parameters that characterize the physiological characteristics of timothy. Of these, 16 parameters already appeared in the original LINGRA model for perennial ryegrass. The 12 new parameters introduced for timothy quantify the formation rate of generative tillers, its sensitivity to environmental and plant factors, and the differences between vegetative and generative tillers in numbers of elongating leaves, leaf shape and elongation rate.

The source code of the model including a complete list of parameters will be sent by email upon request.

Experimental data used for model parameterisation

In a later section of this paper, we review the literature on timothy, focusing on quantitative information. This information is used to quantify the parameters in the model. However, it will become apparent that the literature contains insufficient data to parameterise our model completely, even though it is parameter-sparse compared with most other published grass models. Where insufficient data were available we quantified timothy-specific parameters for generative tillering by calibrating the model on timothy experiments carried out by Bonesmo (1999) and Bonesmo & Skjelvåg (1999). These experiments are described below.

Two field experiments were carried out with North-Norwegian timothy cv. ‘Bodin’ – one in 1993 in Vågønes (67°18’N, 14°29’E), and another in 1995 in Ås (59°40’N, 10°53’E). The accumulation of biomass was studied in the first year after establishment. Swards were supplied with optimal amounts of nitrogen (140 and 80 kg ha$^{-1}$ for the first and second growth cycles, respectively). They were not irrigated, but well provided with water except for a few occasions of mild drought. Total precipitation over the experimental period was 259 and 372 mm at Vågønes (2 May–11 September) and Ås (26 April–22 August), respectively. Average temperature/global radiation level at Vågønes and Ås was 10.7°C/14.7 MJ m$^{-2}$ and 13.1°C/18.4 MJ m$^{-2}$, respectively (Fig. 2).

There were five experimental treatments, differing in the phenological stage at which the swards were first cut: leaf stage; jointing; early heading; full heading; and anthesis. For each cutting treatment, regrowth was studied by sampling at five consecutive weeks after the sward had regained a height of 10–15 cm. Harvestable biomass was then determined as all biomass above a stubble height of 5 cm. Further details of the experiments are given by Bonesmo & Skjelvåg (1999).

Simulations

We carried out four types of simulation with the model:

- simulations of timothy growth for the conditions in the cutting-date experiments carried out by Bonesmo (1999) and Bonesmo & Skjelvåg (1999), described in the previous

Fig. 2 Time course of global radiation (dashed line) and temperature (solid line) in Ås (a) and Vågønes (b).
section. Simulations were run for both Norwegian sites and for each of the five treatments, which differed in cutting dates. The results of the 10 simulation runs were compared with the experimental results for each treatment.

The other three types of simulation only used the middle cutting date regimes from Bonesmo’s experiments, representing normal cutting practice for the two sites. For the southern, warmest site at Ås, one more regrowth period was simulated than had been included in the experiment, which had been ended somewhat prematurely in early July.

- Simulations with altered weather conditions. These simulations explored the effects of changes in radiation or temperature on timothy growth. For both sites, simulation runs were again based on the observed time course of weather, so variation between days was maintained, but with a specific change in radiation or temperature throughout the growing season. The simulated changes ranged from -25% to +25% for radiation and from -5 °C to +5 °C for temperature.
- Simulations for a general normalized sensitivity analysis. These simulations quantified the effect of small changes in 14 model parameters on yield, again both for Ås and Vågønes. The model parameters investigated in this sensitivity analysis did not appear in the original LINGRA model for perennial ryegrass or had different values there. To investigate model sensitivity to initial conditions, the initial values of vegetative tiller density and reserve pool size were included in the analysis as well. For each parameter, we defined the normalized sensitivity coefficient \( S_{yp} \) (or elasticity coefficient) as follows:

\[
S_{yp} = \frac{1}{Y_p} \frac{dY}{dp}
\]

(p, the default value of the parameter; and Y, cumulative yield at the end of the growing season.) \( S_{yp} \) was estimated from the change in simulated yield after a 1% change in the parameter. Parameter sensitivity depends on the growing environment, and our procedure accounts for this to some extent by providing two estimates of \( S_{yp} \), one for Ås and one for Vågønes. To assist in analysing the causes for the differences in \( S_{yp} \), we also report the sensitivity to the same parameter changes of three major yield determining factors: light-use efficiency, cumulative light interception over the whole growing season, and seasonal average tiller density (\( S_{\text{LUE}}, S_{\text{Itot}} = p \)). Simulations which explored the consequences for yield of reported variation in various timothy characters.

The literature review on timothy (presented in the next section) revealed significant variation for a number of parameters. To assess the importance of such parameter variability, simulations were run for Ås and Vågønes with the smallest and the highest parameter values found in the literature.

**Literature review on timothy**

We reviewed the literature on the physiological and morphological processes that underlie timothy productivity. Special attention was given to reports from the temperate to arctic transition zone of Norway, Sweden and Finland. We divided our literature review into four parts, each dealing with a group of related processes: light interception and utilisation; carbon partitioning; dynamics of leaf number and size; and tiller dynamics and phenology. The information acquired from the literature is used for model parameterisation, and results of the simulations using the model parameterised in this way will be given following the literature review.

**Light interception and utilisation**

Light interception per unit leaf area is largely determined by leaf angle distribution and leaf composition. Timothy is more planophile than perennial ryegrass because its leaves bend more easily when elongating. Planophil in itself would cause strong light extinction, but the effect is counteracted by the low light absorption capacity of individual timothy leaves. Timothy leaves are thinner and have lower chlorophyll content than Lolium leaves. The exponential light extinction coefficient in Swedish timothy varied between 0.44 and 0.63 (Kornher, 1971). The lower values reflect extinction coefficients in the young vegetative stage, the higher values correspond with the more planophile structure of the swards during the generative stage.

Light-use efficiency of grasses can be very high under low light conditions. Ryegrass growing under low light conditions in the glasshouse can produce dry matter with an efficiency of 5 g per MJ photosynthetically active radiation (Schapendonk et al., 1997). Such high efficiencies tend not to be achieved by timothy under field conditions, where it is often around 2 g MJ⁻¹ (Belanger & Richards, 1995). However, the typically long days with low average light intensity prevailing in Nordic countries may well cause relatively high LUE values.

Light utilisation in leaves is closely correlated with Rubisco content. Productive leaves contain high amounts of Rubisco and leaves that are limited in photosynthetic rates due to adverse conditions tend to have low amounts of Rubisco. No data on Rubisco content of timothy leaves were found in the literature. However, the amount of Rubisco tends to be closely correlated with the amount of leaf nitrogen (Evans, 1989), with about 30% of leaf nitrogen recoverable from the Rubisco fraction (Hikosaka & Terashima, 1995). The fraction is lower under conditions of low light or low nitrogen supply. We estimated timothy Rubisco content to vary from 2.1 to 2.9 g m⁻² leaf area, based on nitrogen contents of timothy leaves, and assuming a 30% investment of the available nitrogen in Rubisco (Table 1).

**Carbon partitioning**

Timothy partitioned between 0.21 and 0.30 of the dry matter to the roots in the pot experiment by Heide et al. (1985). Partitioning to roots decreased with increasing temperature and day-lengths. Partitioning of carbon to the root system starts when above ground sink-requirements and maximum
storage capacity have been satisfied. This approach works very well for a range of environmental conditions. For instance, low nitrogen conditions will lead to increased translocation of carbon to the roots because the sink activity of the shoot is limited by low leaf elongation rates. We have shown that the amount of carbon allocated to grass roots in spring is significantly higher than in summer due to the high source/sink ratio in spring (Schapendonk et al., 1997).

In grasses, carbon partitioning between plant organs and the storage pool is highly flexible. The survival strategy of grass swards depends on the alternation of storage and remobilization of carbohydrates. In timothy, carbohydrates are mainly stored in the swollen stem basis when there is a photosynthetic surplus (Kühbauch, 1974). The swollen stem basis is referred to as the haplocorm (Heide, 1982). From the haplocorm carbon is remobilized in times of assimilate shortage, which occurs mainly in early spring when there is little light or after cutting when the light interception is low. In addition to carbohydrates, vegetative storage proteins can be an important carbon source in defoliated plants; this has been demonstrated for several grassland species including perennial ryegrass (Volenec et al., 1996). However, carbon-nitrogen compounds may play a less significant role as a carbon source in timothy; shoot regrowth and mobilization of N reserves are poorly correlated in this species (Bakken et al., 1998).

The amount of fructans stored in the haplocorm fluctuates over the season, as shown for US conditions by Okajima & Smith (1964). There are no such time course data available for Scandinavian conditions. Breeders have acknowledged the importance of this storage component for a long time, and it is positively correlated with frost tolerance, resistance to snow mould fungi (Årsvoll & Larsen, 1977), over-wintering and early spring growth (Halling, 1988), and initial regrowth rate after a (severe) defoliation (Smith, 1974). The upper limit to the amount of stored carbohydrates is about 30% of the total above ground structural dry matter (Halling, 1988).

Dynamics of leaf number and size

The rate of leaf formation is one of the most important yield determining characteristics of a grass. Leaf formation not only provides the basis for light interception but it also generates the sinks through the formation of new sites for tiller buds (Chapman & Lemaire, 1993). Therefore, when leaf formation is slow, both sink and source activities will be reduced. Leaf formation rate in grasses is generally linearly related to temperature (Davies & Thomas, 1983). The time interval between successive leaves (phylochron) can thus be expressed in degree-days. Phylochron values of 70–101°Cd are reported for spring and summer canopies, respectively, of Canadian timothy (cv. ‘Champ’; Belanger, 1998). Leaf formation is also affected by nutrient availability. With no N applied, the rate of leaf formation in spring and summer was 61% and 67% of that obtained under nonlimiting N-conditions. High N

Table 1 Key growth determining characteristics of timothy, with values reported in the literature

<table>
<thead>
<tr>
<th>Process group</th>
<th>Equation</th>
<th>Range</th>
<th>Dimension</th>
</tr>
</thead>
<tbody>
<tr>
<td>Light interception and utilisation</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Extinction coefficient (K)</td>
<td></td>
<td>0.44–0.63</td>
<td>m² m⁻²</td>
</tr>
<tr>
<td>Rubisco content (RUBISC)</td>
<td></td>
<td>2.1–2.9</td>
<td>g m⁻²</td>
</tr>
<tr>
<td>Light-Use Efficiency (LUE)</td>
<td></td>
<td>1.6–5</td>
<td>g MJ⁻¹</td>
</tr>
<tr>
<td>Carbon partitioning</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum storage carbohydrate fraction (MXWSC)</td>
<td></td>
<td>0.3</td>
<td>g g⁻¹</td>
</tr>
<tr>
<td>Specific Leaf Area (SLA)</td>
<td></td>
<td>0.025–0.035</td>
<td>m² g⁻¹</td>
</tr>
<tr>
<td>Allocation to roots</td>
<td></td>
<td>0.21–0.30</td>
<td></td>
</tr>
<tr>
<td>Dynamics of leaf number and size</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phyllochron (PHY)</td>
<td></td>
<td>70°–101°Cd</td>
<td></td>
</tr>
<tr>
<td>Number of elongating leaves per tiller (NELL)</td>
<td></td>
<td>2.0–2.9</td>
<td></td>
</tr>
<tr>
<td>Leaf width (LFWID)</td>
<td></td>
<td>8 (vegetative); 10 (generative)</td>
<td>mm</td>
</tr>
<tr>
<td>Leaf elongation rate*</td>
<td></td>
<td>-0.76 + 0.52 T (vegetative); -11.5 + 2.66 T (generative)</td>
<td>mm d⁻¹</td>
</tr>
<tr>
<td>Tiller dynamics</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Optimum temperature for vegetative tillers to become generative (TOPTGE)</td>
<td></td>
<td>12 (Northern cultivar); 15–16 (Southern cultivar)</td>
<td>°C</td>
</tr>
</tbody>
</table>

The acronyms in brackets (K, RUBISC, etc.) refer to parameter names as used in the model. a(Kornher, 1971), b(Evans, 1989; Hikosaka & Terashima, 1995), c(Belanger & Richards, 1995), d(Schapendonk & de Vos, 1988), e(Halling, 1988), f(Solhaug, 1991), g(Heide et al., 1985), h(Belanger, 1998), i(Langer, 1954), j(Höglind, unpublished), k(Peacock, 1976), l(Heide, 1982). *Leaf elongation rate is given as a parameterized function of temperature (T; °C).
significantly increased the number of leaves at high temperature but not at low temperature (Ryle, 1964). Increasing the light intensity had no effect on the rate of leaf formation in timothy in a heated glasshouse (Langer, 1954).

Leaf elongation rate is mainly controlled by the same factors as leaf formation, that is temperature and N supply. However, leaf elongation is generally more sensitive to changes in the environment than leaf formation (Peacock, 1976; Belanger, 1998). In a British study, the rate of leaf elongation was linearly related to temperature, and the regression line was steeper in reproductive than in vegetative canopy (Peacock, 1976). With no N applied, the rate of leaf elongation in reproductive and vegetative canopies of Canadian timothy was approx. 40% of that obtained under limiting N-conditions (Belanger, 1998).

The overall rate of leaf elongation per tiller is the product of the number of simultaneously growing leaves and their average rate of elongation. The number of simultaneously growing leaves showed a variation ranging from 2.0 per tiller outdoors under UK winter conditions, to 2.9 and 2.7 in a heated glasshouse with and without additional light, respectively (Langer, 1954). Timothy normally carries between 4 and 6 living leaves per tiller (actively growing leaves and those with elongation completed) (Langer, 1956; Davies, 1979).

Leaf width changes with leaf number and phenological stage and it is sensitive to temperature and nutrient supply. In timothy in Canada, successive leaves on the main stem increased in width from 5 to 7 mm in spring, whereas in summer, leaf width was 6 mm irrespective of leaf position (Belanger, 1998). We observed average leaf widths of 10 and 8 mm in spring and summer canopies, respectively, of Norwegian cv. ‘Bodin’ at Særheim Research Station (lat. 58°46’ N). N-application had a small (< 2 mm) positive effect on leaf width increased in width from 5 to 7 mm in spring, whereas in summer, leaf width was 6 mm irrespective of leaf position (Belanger, 1998). Temperature and photoperiod both affect leaf width (Heide, 1982). At a high temperature (21°C), leaf width increased with increasing photoperiod (2 mm leaf width increase when photoperiod was increased from 8 to 24 h); however, the photoperiodic effect diminished with decreasing temperature. At short photoperiods (< 16 h) leaf width increased with decreasing temperature, but this temperature effect disappeared at long photoperiods.

The yield of timothy is very sensitive to the specific leaf area (SLA; m² leaf area g⁻¹), especially under frequent defoliation. A higher SLA means a lower investment of carbon to achieve a similar leaf area, which is particularly favourable when assimilates are scarce, for instance directly after cutting. SLA tends to fluctuate between limits of c. 0.025 and 0.035 m² g⁻¹, based on data provided by Solhaug (1991). In our model, the SLA of newly growing leaves varies inversely with reserve content between these two extreme values.

Tiller dynamics and phenology

Vegetative tillers arise from buds in the leaf axils, but tiller formation does not usually begin until the leaf above it is fully expanded, and new tillers only emerge from the axils of the third youngest leaf bud and onward (Ryle, 1964). Tillers generally do not appear in timothy until five leaves or more have been exerted above their node of origin. After 10 leaf appearance intervals, only 1–3 tillers were visible (Ryle, 1964). This means that the theoretical maximum value for site filling is lower in timothy than in perennial ryegrass. However, in the present version of the model we use the value for perennial ryegrass as a reference value (Neuteboom &antinga, 1989).

For spaced plants, tiller formation depends mainly on the phyllochron (which is highly sensitive to temperature) (Davies & Thomas, 1983). When the canopy grows dense, the decreased availability and spectral quality of light reduces tiller formation by increasing the phyllochron and by reducing site filling (perennial ryegrass experiment: Gautier et al., 1999). Defoliation to 5 cm stubble height reduced both the phyllochron and site filling (Gautier et al., 1999). Literature research revealed no attempts to separate environment and management effects on the phyllochron from those on site filling in timothy. The regulation of site filling in our model is therefore mainly based on what is known for perennial ryegrass (Schepenboom et al., 1998).

Literature research revealed little quantitative information on whole-season tiller dynamics in Scandinavian timothy. Langer et al. (1964) give a classic example of the seasonal trends of tiller emergence and senescence in timothy in the UK. Tiller production peaked in June, at about 500 tillers m⁻² wk⁻¹. Tiller death increased from about 100 tillers m⁻² wk⁻¹ in early April to > 700 tillers m⁻² wk⁻¹ in June. Tiller death started long before flowering (double ridge is about 10th of May and ear emergence is 40 d later) and continued after the ears were removed by mowing. Tiller death rates remain relatively high in timothy during June and July declining to a stable rate of 100 by the end of August, remaining stable in September and further declining to 0 by the end of December. Examples from Japan are given by Ito et al. (1997).

High mortality of vegetative tillers during stem elongation in perennial ryegrass has been associated with decreased export of assimilates from the flowering main shoots (Colvill & Marshall, 1984). It was concluded that the shading of these young tillers by the elongating main shoot was an important cause of deaths. Deposition of elevated apices is another important cause of tiller death. The proportion of tillers with their apices above cutting height rose from nil at leaf stage to 0.6 at heading in a pot experiment with Norwegian timothy (Bonepomo, 2000). In our model, tiller mortality is dependent both on internal shading (via LAI) and on the proportion of elevated apices (via phenological stage).

The flowering response of timothy varieties varies due to differences in the critical photoperiod for flower initiation (Heide, 1982). At a photoperiod of 12 h all plants remained as rosettes. There was a difference of two hours in critical photoperiod between Northern Norwegian cultivars and cultivars.
from Southern Norway. Moderate temperatures and high light intensity gave the most abundant flower induction (Heide, 1982). Plants exposed to photo-induction at successive stages after germination showed an increased flowering response to long photoperiods until the 5–7 leaf stage (Ryle, 1965). In the UK, Langer (1956) found that the ear-bearing capacity of tillers varied with their date of origin. The capacity reached 100% for December–January tillers; this was followed by a decline to 1.2% for July tillers, after which time newly formed tillers failed to produce a seed head. Wilson (1959), working in New Zealand, found a similar pattern. In our model, the formation of generative tillers from vegetative tillers follows a temperature and day-length dependent relative rate, derived through model optimization against data from Norwegian field experiments.

**Simulation results**

Simulations for the conditions in the cutting-date experiments

In the experiments, cumulative yield increased with advanced phenological stage, and the maximum yields of 1320 and 1550 g m\(^{-2}\) at Ås and Vågønes, respectively, were obtained in the treatment with a first cut at anthesis (Fig. 3). Simulated cumulative yields similarly increased with advanced phenological stage, but with maximum yield obtained after a first cut at a somewhat earlier stage of development: from early to late heading. The \(R^2\) value for the 10 pairs of simulated and measured yields was 0.75 (\(P < 0.05\)). Both experiments showed a similar pattern of measured biomass accumulation (Fig. 4a,b) with higher rates of accumulation in spring (first cutting) than in summer (latest cutting), and with a faster rate of recovery when the first cut was taken in the vegetative leaf stage rather than at later growth stages. The overall growth pattern was simulated well (Fig. 4c,d). LAI development (Fig. 5) followed a pattern similar to that of biomass, and while there was some leaf area remaining after the early first cut, virtually all leaf area was removed in the late first cut, when the majority of leaves had been elevated above cutting height on the reproductive tillers. Tiller density (Fig. 6) increased rapidly in early spring and after each cut, and it fell towards the end of each growth period. Phenological stage at cutting strongly influenced the proportion of decapitated tillers: 13–19% at leaf stage vs 88–91% at anthesis.

**Fig. 3** Measured (closed columns) and simulated (open columns) cumulative yields (sum of two harvests) in the five cutting treatments in Ås and Vågønes, respectively. Treatments numbers refer to different dates of first sward cut: 1, leaf stage; 2, jointing; 3, early heading; 4, full heading; 5, anthesis. Bars are 1 SE of the mean.

**Fig. 4** Time course of measured (a, b) and simulated (c, d) biomass accumulation in Ås (a, c) and Vågønes (b, d). Treatments numbers refer to different dates of first sward cut: 1, leaf stage; 2, jointing; 3, early heading; 4, full heading; 5, anthesis. Bars are 2 SE of the mean.
Simulations for the same experiments, but with altered weather conditions

Simulated yield in Ås was less sensitive to changes in radiation than in Vågønes where there was a strong decline in simulated yields when the radiation was reduced by > 20% (Fig. 7a). The simulated optimum radiation for yields at Ås and Vågønes were 5% higher and 20% lower, respectively, than the actual radiation levels. Simulated yield for Ås was moderately sensitive to deviations in temperature within −2 to +5 °C (Fig. 7b). The corresponding range for Vågønes was −3 to +3 °C. Temperatures beyond these values led to a dramatic fall in simulated yield. The temperatures that were identified by the model as being optimal for yield were, for both Ås and Vågønes, about the same as the present actual temperatures.

Simulations for a general normalised sensitivity analysis

The parameter sensitivity analysis showed that five of the 14 varied parameters had by far the strongest effect on yield: Rubisco content (RUBISC), the maximum size of the reserve pool (MXWSC), the phyllochron (PHY), the temperature at which the formation rate of generative tillers is maximal (TOPTGE), and the SLA (Table 2). For some parameters, there was an interaction with site, for example the light extinction coefficient was important at Ås but not at Vågønes, whereas the opposite was true for initial tiller density and the maximum relative rate at which vegetative tillers can become generative.

As yield by definition is the product of light interception and the efficiency of light use, reporting these values helps to identify the major causes of yield change. Most parameter changes affected yield mainly by affecting light use efficiency, whereas light interception was quite insensitive to parameter changes (Table 2). An exception to that finding is the ‘extinction coefficient’, which affected both attributes. Cumulative yield at the end of growing season was highly correlated with average light use efficiency ($R^2 = 0.93, P < 0.001$), but not with total light interception ($R^2 = 0.073, P = 0.713$). Moreover, yield was correlated with average tiller density ($R^2 = 0.38, P < 0.05$).

The normalised sensitivity analysis further identified four factors with comparatively large influence on tiller density:
leaf width and elongation rate, phyllochron, and SLA (Table 2). All four factors affect tillering indirectly, via effects on leaf dynamics.

The parameter changes generally affected tiller density more strongly than biomass accumulation. This was shown by the high average of the absolute value of the normalised sensitivity coefficient for tiller density ($S_{\text{stillers}}$) for the 14 parameters, which was 0.25, whereas that for yield ($S_{\text{Y,p}}$) was 0.14 (Table 2).

Simulations that explore the consequences for yield of reported variation in various timothy characters

Within the reported range of variation, the ‘Rubisco content’, ‘phyllochron’ and the ‘number of elongating leaves per tiller’ had a large influence on simulated yield, and this was irrespective of site (Table 3). For two other parameters, there was significant interaction with site. The ‘optimum temperature for the formation of generative tillers’ and the ‘base photoperiod for vegetative tillers becoming generative’ were only important for simulated yield at Ås. The model was not very sensitive to changes in the extinction coefficient. This is because any increase in light interception resulting from an increase in the extinction coefficient was counterbalanced by a reduction in light use efficiency.

Discussion

By contrast to perennial ryegrass, few quantitative data are available for timothy. Most studies go back to the 1950s and 1960s and they often involve cultivars that are not in practical use today. Notably, we found very few data from the Scandinavian countries. This was surprising as timothy is the dominating forage grass in this region. Leaf and tillering dynamics are processes that are especially poorly documented. Despite this drawback we derived sufficient information to formulate a mechanistic model based on morphological and physiological processes. A sound basis for this model was
The effects of reported variation in six model parameters on cumulative yield (\(\text{Yield}_{\text{cum}}\)), average light use efficiency (\(\text{LUE}_{\text{avg}}\)), total light interception (\(\text{PAR}_{\text{cum}}\)), and average tiller density (\(\text{Tillers}_{\text{avg}}\)). For both sites, the parameters are listed in decreasing order of their effect on cumulative yield.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Default value</th>
<th>Units</th>
<th>Tested value</th>
<th>(\text{Yield}_{\text{cum}}) (g m(^{-2}))</th>
<th>(\text{LUE}_{\text{avg}}) (g MJ(^{-1}))</th>
<th>(\text{PAR}_{\text{cum}}) (Wm(^{-2}))</th>
<th>(\text{Tillers}_{\text{avg}}) ((\delta) m(^{-2}))</th>
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<tr>
<td>Ås</td>
<td>Reference output</td>
<td>–569</td>
<td>1.67</td>
<td>1.93</td>
<td>869</td>
<td>2771</td>
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<tr>
<td>RUBISC</td>
<td>4.0</td>
<td>g m(^{-2})</td>
<td>2.1</td>
<td>–0.54</td>
<td>–0.52</td>
<td>–71</td>
<td>–569</td>
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<tr>
<td>PHY</td>
<td>70</td>
<td>°Cd</td>
<td>101</td>
<td>–0.19</td>
<td>–0.17</td>
<td>–29</td>
<td>–35</td>
</tr>
<tr>
<td>DAYLB</td>
<td>6</td>
<td>h d(^{-1})</td>
<td>15</td>
<td>–0.16</td>
<td>–0.23</td>
<td>18</td>
<td>550</td>
</tr>
<tr>
<td>TOPTGE</td>
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<td>h d(^{-1})</td>
<td>16.5</td>
<td>0.10</td>
<td>0.08</td>
<td>8</td>
<td>190</td>
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<tr>
<td>NELL</td>
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<td>–</td>
<td>2.0</td>
<td>0.06</td>
<td>0.00</td>
<td>–24</td>
<td>734</td>
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<tr>
<td>K</td>
<td>0.63</td>
<td>–</td>
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<td>0.03</td>
<td>0.24</td>
<td>–86</td>
<td>69</td>
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<tr>
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<td>1.94</td>
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<td>2561</td>
<td></td>
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<td>–0.41</td>
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<tr>
<td>PHY</td>
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<tr>
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<tr>
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<td>16.5</td>
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<tr>
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<tr>
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<td>h d(^{-1})</td>
<td>15</td>
<td>0.00</td>
<td>–0.03</td>
<td>7</td>
<td>179</td>
</tr>
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</table>

DAYLB, the minimum daylength at which generative tillers can be formed; K, extinction coefficient; RUBISC, rubisco content; LUE, light-use efficiency; PHY, phyllochron; NELL, number of elongating leaves per tiller; TOPTGE, optimum temperature for vegetative tillers to become generative.

Table 3
and analysis by means of simulation modelling, such as N-fertilization and defoliation intensity are especially quantified better how formation, development and loss of tillers of timothy where we presently rely on ryegrass data. We need to and the formation and loss of leaves from tillers. Primarily, Simulations with the model showed that the major processes parameterised the simple model first before considering more complex alternatives for the various algorithms in the model. We suggest that the best way forward is to attempt to cannot yet be parameterised and tested completely satisfactorily in itself because it does not clarify whether the major role of the tillers was to carry carbon source leaves or to provide a growth sink for carbon. In future work, we will attempt to use our model to clarify this question. Our model has already shown that the dynamics of tiller density itself may be strongly affected by changes in leaf properties, as the four parameters that affected this density the most were all 'leaf'-related parameters (leaf width and elongation rate, phyllochron, SLA). Our work has shown that there are still significant gaps in knowledge on timothy, such that a simple mechanistic model cannot yet be parameterised and tested completely satisfactorily. We suggest that the best way forward is to attempt to parameterise the simple model first before considering more complex alternatives for the various algorithms in the model. Simulations with the model showed that the major processes to be elucidated in future research are tillering dynamics and the formation and loss of leaves from tillers. Primarily, data are needed to fill in the gaps in the knowledge about timothy where we presently rely on ryegrass data. We need to quantify better how formation, development and loss of tillers and leaves depend on important environment and management factors. In this context, temperature, light availability, N-fertilisation and defoliation intensity are especially important factors. We conclude that a combination of literature review and analysis by means of simulation modelling, such as we attempted here for timothy growth in Scandinavia, is an effective approach to identify and prioritise research goals. Experiments to meet these goals are presently underway in Norwegian research stations.

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References


