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Process-based simulation of growth and overwintering of grassland using the BASGRA model

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Abstract

Process-based models (PBM) for simulation of weather dependent grass growth can assist farmers and plant breeders in addressing the challenges of climate change by simulating alternative roads of adaptation. They can also provide management decision support under current conditions. A drawback of existing grass models is that they do not take into account the effect of winter stresses, limiting their use for full-year simulations in areas where winter survival is a key factor for yield security. Here, we present a novel full-year PBM for grassland named BASGRA. It was developed by combining the LINGRA grassland model (Van Oijen et al. 2005) with models for cold hardening and soil physical winter processes. We present the model and show how it was parameterized for timothy (*Phleum pratense* L.), the most important forage grass in Scandinavia and parts of North America and Asia. Uniquely, BASGRA simulates the processes taking place in the sward during the transition from summer to winter, including growth cessation and gradual cold hardening, and functions for simulating plant injury due to low temperatures, snow and ice affecting regrowth in spring. For the calibration, we used detailed data from five different locations in Norway, covering a wide range of agroclimatic regions, day lengths (latitudes from 59° to 70° N) and soil conditions. The total dataset included 11 variables, notably above-ground dry matter, leaf area index, tiller density, content of C reserves, and frost tolerance. All data were used in the calibration. When BASGRA was run with the maximum a-posteriori (MAP) parameter vector from the single, Bayesian calibration, nearly all measured variables were simulated to an overall normalized root mean squared error (NRMSE) < 0.5. For many site x experiment combinations, NRMSE was < 0.3. The temporal dynamics were captured well for most variables, as evaluated by comparing simulated time courses vs. data for the individual sites. The results may suggest that BASGRA is a reasonably robust model, allowing for simulation of growth and several important underlying processes with acceptable accuracy for a range of agroclimatic conditions. However, the robustness of the model needs to be tested further using independent data from a wide range of growing conditions. Finally we show an example of application of the model, comparing overwintering risks in two climatically different sites, and discuss future model applications. Further development work should include improved simulation of the dynamics of C reserves, and validation of winter tiller dynamics against independent data.

Keywords: Cold hardening, Frost injury, *Phleum pratense* L., Process-based modelling, Winter survival, Yield

1 Introduction

1.1 Grasslands and climate change

Grasslands constitute the most important source of energy and nutrients for grazing animals in large regions of the world. In temperate and boreal regions, where low temperatures restrict or prevent growth during winter, grasslands are also extremely important for the production of conserved forage for winter feeding of cattle, sheep, goats and horses. Grass-based dairy and meat production constitute the economic backbone of agriculture in Northern Europe including Norway. Timothy (*Phleum pratense* L.) is the most important forage grass in Scandinavia and parts of North America and Asia where winter survival is critical. Compared to perennial ryegrass (*Lolium perenne* L.), which is grown in areas with milder winter conditions, timothy is more tolerant to most winter stresses (Höglind et al, 2010). However, weather driven inter-annual variation in grass yields may lead to substantial variation in the economic output of forage based livestock production even in systems where timothy is the dominant grass species.

Grassland productivity is expected to be affected by climate change (Tubiello et al. 2007; Jing et al. 2014). The changes may be detrimental or, especially at high latitudes, beneficial. However, there is still large uncertainty with respect to grassland productivity in Northern Europe under future climate conditions (Höglind et al. 2013). There is a lack of knowledge especially about the impact of weather conditions late in the growing season and during the winter on the inter-survival of the tillers, and thus the regrowth and yield of the sward. Increases in temperature variability may lead to warm spells that interrupt winter hardening and make the plants more sensitive to subsequent frost (Bélanger et al. 2002, Rapacz et al. 2014). The survival rate will not depend on the winter climate alone, but also on the state of the sward itself during the transition from growing season to winter, which in turn is affected by the environmental conditions during the growing season, sward genotype and management. Farmers can adapt to climate change by choosing different grass species or cultivars and by adjusting management practices such as fertilizer application strategies and timing of harvests. Plant breeders can contribute to the adaptation of climate change by breeding grasses that grow well under expected conditions.

1.2 Strengths and weaknesses of existing grassland models

Process-based models for weather dependent grass growth can assist farmers and plant breeders in the process of adaptation to climate change by simulating different adaptation options. These models can also be used to investigate different management options such as the prediction of the optimal harvest time for use in tactical planning at farm level under current conditions (Bonesmo and Belanger, 2002). A number of process-based grassland models for cold temperate climate conditions including LINGRA (Schapendonk et al. 1998; Höglind et al. 2001; Van Oijen et al. 2005a), the Hurley pasture model (Thornley and Cannell 1997), PaSIM (Riedo et al. 1998), CATIMO (Bonesmo and Bélanger, 2002), and STICS (Jégo et al. 2013) are available for use in this type of studies. A common feature for all the available grassland models is that they simulate the accumulation of biomass as dependent on temperature and the availability of light and water. Many models also simulate the effect of nutrient availability on grass growth and quality (e.g. Bonesmo and Bélager, 2002; Jégo et al. 2013). However, nearly all the existing grassland models for temperate climate conditions focus exclusively on the spring and summer growing season. Hence they cannot be used for predicting winter survival, which limits their usefulness for predicting grassland productivity in regions where winter survival is critical. An exception is the PaSIM model (Riedo et al. 1998) that simulates snow cover dynamics and the effect of snow cover on the temperature around the plant. However, this model does not simulate ice-cover and does not take into account the effects of cold stress, limiting its usefulness to winter conditions that constitute no risk to tiller survival.

1.3 Development of the new model BASGRA

Here, we present a full-year model for grassland growth named Basic Grassland Model (BASGRA), and parameterise it for timothy. It was developed by combining the LINGRA grassland model as used for summer growth of timothy (Van Oijen et al. 2005a) with the model for cold hardening and dehardening in grasses developed by Thorsen and Höglind (2010), and the SnowFrostIce model for soil physical winter processes in grasslands (Thorsen et al. 2010) with some modifications of the original models and some additional functions to handle the transition between summer and winter. Growth in BASGRA is modelled as dependent on source-sink relationships, which affect the dynamics of tiller density and leaf area in a similar way as in its forerunner LINGRA. Modifications of the original model include additional control functions for tillering, leaf appearance and leaf elongation, and a new algorithm for carbon allocation. Other novel aspects of the BASGRA model are:

- full-year simulation with different links between sward management, weather, day length, soil physics and plant ecophysiology,
- mechanistic simulation of the processes taking place in the sward during the transition from summer to winter including growth, cessation, the build-up of carbon reserves and the gradual frost hardening of the plants,
- comprehensive representation of winter damage processes related to low temperatures, short days with low irradiation, snow- and ice-covered fields
- mechanistic simulation of the resumption of growth in spring,
- inclusion of a third tiller category: non-elongated generative tillers.

For each of the models that were combined to form BASGRA, similar design principles were followed. Model structure was intended to allow simulation of the behaviour of the grass-soil system in different growing environments, with different possible disturbances. Moreover, we intended to simulate both short- and long-term responses to disturbances, so state variables needed to be included that determine a sward's capacity to regrow, such as carbohydrate reserves and tiller density. These objectives led to a fairly long list of model processes, as outlined above, and as described in detail in section 2. At the same time, the intention was to keep model structure as simple as possible, such that it would be possible to collect sufficient data for model parameterisation and for testing at the level of the represented processes. Where possible, parameter-sparse process representations were chosen, e.g. a canopy light-use efficiency (LUE) approach rather than a leaf photosynthesis model, but with LUE not treated as a constant to allow for sward responses to changes in the availability of water and CO_2.

1.4 Aims and outline of the remainder of this paper.

The major aim of this paper is to present the BASGRA model and show how it was parameterized. A second aim is to show an example of model application, and to discuss the scope for future applications. We first present, in Section 2, the details of the model structure.

The focus is on features that are unique to BASGRA, and that have not been presented in detail before. We then show in Section 3 how the model was parameterised, with emphasis on parameters not usually part of grassland models. In Section 4, we show an example application of the model to multi-year simulation of timothy growth at two sites in Norway. The paper is concluded with a discussion of the modelling approach and an outlook of future applications.

2 Model structure

2.1 Model overview

The grassland model BASGRA is a mechanistic model for simulating the year-round dynamics of tillers, leaves, roots and reserves. The model simulates the response of the sward to soil conditions, cutting, day length, and the weather including winter stresses. The model operates at a daily time step and contains 23 state variables and 71 initial constants and other parameters.

The three main features that characterize plant growth in BASGRA are: (1) simulation of source-sink relations where the source consists both of current photosynthesis and remobilisation of reserves, (2) simulation of leaf area dynamics and tillering for vegetative and generative tillers; and (3) cold hardening and the effect of physical winter stress factors on tiller survival and plant growth. Inputs to the model are daily values of radiation, temperature, rain, humidity and wind. The soil is characterised by a soil water retention curve, initial soil water content and soil temperature. In addition to the water balance, the depth of snow and ice on the soil surface as well as the temperature at the soil surface and the depth of frost in the soil are simulated.

Photosynthesis is sensitive to light intensity, temperature, day length, CO_2 concentration and water availability. Carbon from photosynthesis and remobilised reserves is allocated between sinks according to a system of changing sink priorities and changing sink strengths. Sink strengths are determined by the dynamics of leaves and stems and the acclimation to low temperature. The major occasional disturbance during the growing season is removal of tillers and leaves by cutting, with subsequent regrowth of the sward. Regrowth rate after cutting depends on the phenological stage at which cutting take place and on the strengths of sources and sinks. Damage by frost and by anaerobic conditions under ice accelerates senescence depending on the degree to which the plants are hardened. BASGRA is a one-dimensional model in that it keeps track of the height of snow cover and the depth to which the soil is frozen and roots are grown. The model does not simulate nitrogen relations or plant disease impact.

BASGRA is implemented in open source software; Fortran and R. The model version presented here, BASGRA 2014, is achieved online at http://dx.doi.org/10.5281/zenodo.27867 from where full code, including for Bayesian calibration, can be downloaded as a zip-file (Van Oijen et al., 2015). The zip-file also contains a comprehensive User Guide (including lists of parameters and variables with names and units, and conceptual diagrams of the model) and all the necessary files to run the model for default conditions (for cultivar Grindstad grown at Særheim in Norway) or to apply Bayesian calibration to the model parameters (one example using observations of Grindstad grown at Særheim). The User Guide also explains the history of the model.

In the following sections, we describe the major functions of BASGRA in more detail, with focus on the functions that are unique for the BASGRA model, and how it differs from its three predecessors, the LINGRA model for summer growth of timothy (Höglind et al. 2001; Van Oijen et al. 2005a), the model for cold hardening in timothy (Thorsen and Höglind, 2010), and the SnowFrostIce model for physical soil processes during the winter (Thorsen et al. 2010).

2.2 Soil processes and links to plant processes

The soil module of BASGRA combines the soil-water balance model for non-frozen summer conditions used in LINGRA (Höglind et al. 2001) with the SnowFrostIce model that simulates freezing and thawing in the soil (Thorsen et al. 2010). Both models have been described in detail in the cited works; their major features are summarized below.

Soil water and above-ground non plant bound water in the form of snow and ice in BASGRA is characterized by eight state variables. Two are spatial variables, representing snow cover height and soil frost depth. The remaining six state variables represent the mass of water in different phases (liquid, snow, ice) and locations (above- and belowground). During the growing season, all water states, except for the state variable representing the mass of liquid water in the soil, tend to be zero. BASGRA then acts as a model with a single soil layer between surface and rooting depth. Water is added to the soil pool by rain and irrigation, and by root growth leading to exploration of deeper soil. Water is lost from the soil through drainage, runoff, evaporation and transpiration by plants. Water availability to plants is determined by rooting depth and the amount of plant available water in that zone.

The form of precipitation is determined by a threshold temperature. Below the threshold, precipitation falls as snow, adding to the state variables representing mass of snow per unit ground area and the height of the snow pack. If the soil surface temperature falls below the freezing point, soil water will start freezing from the top. This is captured by a state variable for the mass of ice in the soil and a state variable for the depth of the ice layer. Once frost depth exceeds a threshold of 0.2 m, it is assumed that liquid water no longer infiltrate the soil according to (Iwata et al. 2008) and a surface pool of water is formed. The surface pool is subject to freezing and thawing, and thus requires two state variables to represent the different phases: liquid (water) and solid (ice) soil surface water. The rate of snow melt is calculated using a degree–day temperature index K (mm $°C^{-1}$ day^{-1}), which is described by a sinusoidal curve with a minimum in mid-winter and a maximum in mid-summer to incorporate the seasonal variation in incoming radiation that influences snow-melt in addition to temperature (Thorsen et al. 2010).

The central organs of overwintering grass plants that determine sward survival are the apices of the tillers. The apices of the overwintering (non-elongated) tillers are placed close to the soil surface during winter, and thus sensitive to the micro-climatic conditions in this environment. In BASGRA, the temperature at the soil surface is calculated as a function of the atmospheric temperature, snow depth and soil frost depth. In the absence of snow or ice, the soil surface temperature equals that of the atmosphere. The soil surface temperature below a cold insulating snow cover is expressed as a function of snow cover depth, whereas the impact of soil frost depth on soil surface temperature is described by more complex functions (Thorsen et al. 2010).

Effect of soil water on plant processes is mediated by the transpiration realisation factor TRANRF (Höglind et al. 2001). This intermediate variable is calculated as a function of soil water content, soil water retention characteristics, and plant transpirational demand. TRANRF has a value of one when soil water content is at field capacity. It starts to fall when water decreases below a critical level between field capacity and the wilting point, and it reaches zero at the wilting point. Several processes are directly proportional to TRANRF, including transpiration rate. Other processes that are affected are described in the following sections.

2.3 Light interception, photosynthesis and allocation of carbon

Light interception in BASGRA is modelled by Beer's law with a constant light extinction coefficient operating on the leaf area index (LAI) (Höglind et al. 2001). However, in contrast to LINGRA, the effect of snow cover on the availability of light is also taken into account. Thus, when the ground is snow covered, a constant light extinction coefficient (KSNOW) for snow operates in BASGRA, reducing the amount of light received by the plant canopy.

The rate of photosynthesis is modelled as the product of intercepted radiation and photosynthetic light-use efficiency (LUEMXQ), which is a function of CO_2, temperature, light intensity and Rubisco concentration of upper leaves (Rodriguez et al. 1999, Höglind et al. 2001). LUEMXQ accounts for carbon lost to maintenance respiration, but not growth respiration. So the calculated photosynthesis rate is gross photosynthesis minus maintenance respiration. LUEMXQ starts decreasing linearly when temperature drops below one degree Celsius until it becomes zero at minus four degrees according to observations made by Höglind et al. (2011). The latter is an important improvement compared to LINGRA which overestimated photosynthesis at low temperature (ibid.). Photosynthesis is also sensitive to drought and decreases with TRANRF.

BASGRA operates with five sinks: the processes of cold hardening, replenishment of the reserves pool, leaf growth, stem growth, and root growth. Sink strengths are defined as the rate at which these processes would proceed with no source limitation. The hardening process has top priority, so its demand is met in full if source strength is large enough, irrespective of the four other sinks. Root growth has lowest priority and depends on carbon unused by other sinks. The strength priority between reserves on the one hand, and leaves and stems on the other hand changes with day length. When day lengths are shorter than a cultivar-specific threshold, reserves have higher priority than stems and leaves, with the opposite during the rest of the year. Leaves and stems have equal priority so they receive carbon according to their sink strengths. For comparison, in LINGRA leaves have top priority irrespective of season.

The sink strength associated with the growth of leaves is calculated as potential leaf area growth (largely determined by temperature, but see also below) divided by specific leaf area (SLA). The SLA of new leaf growth decreases linearly with reserve content. The sink strength associated with the stem growth of elongating tillers decreases linearly with their biomass. The sink strength related to growth of leaves and stems is also drought sensitive, decreasing linearly with TRANRF. All these sink strength calculations are done in the same way as in LINGRA (Van Oijen et al. 2005a). The sink strength associated with cold hardening, which is unique feature of BASGRA, is expressed through the parameter KRESPHARD (g C g^{-1} C $°C^{-1}$) which is defined as the amount of C reserves needed to decrease the frost tolerance temperature (LT50, see below) per gram of foliage by one degree Celsius. The C reserves pool is defined as the carbon fraction of the water soluble carbohydrates in the plant.

2.4 Leaf area development

BASGRA distinguishes two leaf categories; leaves on vegetative and generative tillers (Höglind et al. 2001). Leaf appearance rate depends on temperature, at a constant phyllochron, but slows down under drought, short day length, and when the sward becomes dominated by generative tillers at an advanced phenological stage. Potential growth rate of leaf area is proportional to the product of the tiller density, the number of elongating leaves per tiller, a constant leaf width and a temperature-dependent leaf elongation rate. All four factors in that product differ between vegetative and generative tillers, so the calculation is done separately for the two categories and then summed to give the potential growth of the total leaf area on all tillers. Leaf elongation rates increase linearly with temperature, based on relationships determined by Peacock (1976) and observations at Saerheim in south-western Norway (Höglind et al. 2005). The effect of day length on leaf elongation is governed by the intermediate variable DAYLGE, with short days restricting leaf elongation equally on both tiller categories. The sink strength related to growth of leaves and stems is also drought sensitive, decreasing linearly with TRANRF.

BASGRA contains one state variable, which represents the phenological stage of the elongating, generative tillers: PHEN. The value of PHEN increases at a rate that depends on temperature and day length (Höglind et al. 2013). PHEN is reset to zero after each cut. Advancing PHEN stage leads to reductions in leaf appearance rate (RLEAF) and in the number of elongating leaves for this tiller category to account for the terminal growth behaviour of the generative tiller where leaf elongation stops after the flag leaf has developed fully (Höglind et al, 2005). In contrast to the original LINGRA model, leaf appearance in BASGRA is insensitive to the content of C reserves, based on a previous study (Van Oijen et al. 2005a).

2.5 Tillering

BASGRA distinguishes three tiller categories: (1) vegetative tillers, (2) non-elongating generative tillers, and (3) elongating generative tillers. The non-elongating generative tiller category, which is new compared to the forerunner LINGRA, was added to make full-year simulations possible for genotypes that have dual requirement for generative development: first a requirement of low temperatures (vernalization) and then a requirement for long days (Heide, 1994). In BASGRA, vegetative tillers are formed at a rate that is proportional to leaf appearance rate, but site-filling (proportion of potential tiller sites that produce tillers) is reduced when LAI is high or C reserve content is low. This is new compared to LINGRA, where site filling is only linked to LAI (van Oijen et al. 2005a). Vegetative tillers then move to the generative tiller category at a rate that has a temperature optimum and a day-length dependency with fewer generative tillers being formed at short day lengths. The day length dependent fraction of vegetative tillers that moves to the generative tiller category (DAYLGE) is calculated as follows:

$$DAYLGE = (DAYL_t - DAYLB) / (DLMXGE - DAYLB); \; 0 \leq DAYLGE \leq 1 \qquad (1)$$

where $DAYL_t$ (d d^{-1}) is the fractional day length on day t, DAYLB (d d^{-1}) is the minimum day length for vegetative tillers becoming generative, DLMXGE (d d^{-1}) is the minimum day length for maximum generative tillering. The intermediate variable DAYLGE is also used for calculating other day length dependent processes as described in other parts of the text.

Generative tillers move from the non-elongating to the elongating tillers category at a constant daily rate as long as the day length is above the minimum day length required for this process (Höglind et al. 2001). For Scandinavian timothy cultivars, this day length typically varies between 14 and18 h (Heide 1982). For genotypes with a vernalization requirement, this transition from vegetative to non-elongating generative tillers only occurs after the vernalization requirement has been fulfilled. In the current model version, the vernalization requirement is simulated in a simplistic way using a threshold temperature. As soon as the temperature falls below the threshold value, the vernalization requirement is considered fulfilled and vegetative tillers start moving to the non-elongating generative tiller category. For genotypes without vernalization requirement, the vernalization requirement in the model can be “bypassed” by using a very high threshold temperature, e.g. 20 °C, allowing for generative tillers to be formed already in the summer of the establishment year. Conversely, for cultivars with a vernalization requirement, the formation of generative tillers may be inhibited until the winter in the establishment year by using a low threshold, e.g. 0 °C. In timothy, many cultivars, including Grindstad do not need to undergo vernalization to produce generative tillers. This is in contrast to perennial ryegrass and many other grass species where most cultivars require vernalization to initiate generative tillers.

2.6 Senescence of leaves and tillers

In BASGRA, the senescence rate of leaves and non-elongating vegetative and generative tillers increases with LAI. Leaves, but not tillers, also die faster at higher soil surface temperatures. Two other drivers of foliage death, frost and anaerobic conditions, are described in section 2.7. The different processes leading to senescence are non-additive, i.e. the total senescence rate is determined by the process for which the highest potential senescence rate is calculated on a given day. The model does not simulate senescence of elongating tillers or roots. However, cutting removes all elongating tillers, leaving a biomass fraction called stubble. This stubble dies at constant relative rate during the first 1-2 weeks after cutting, allowing for remobilization of the carbon reserves in the stubble and its reallocation to regrowing plant parts.

2.7 Cold hardening and impact of frost and ice encasement

Sensitivity to frost is measured by the state variable LT50, the "Lethal Temperature 50%", which is the temperature that would kill half the leaves and non-elongating tillers if the sward was subjected to a standardized freezing test (Höglind et al. 2010). The process whereby plants reduce LT50, i.e. increase their level of frost tolerance, is called hardening. Dehardening describes the loss of freezing tolerance due to triggering conditions, whereas rehardening describes the regaining of freezing tolerance after a period of dehardening conditions (Kalberer et al. 2006). The most important trigger of dehardening under field is mild weather conditions. However, plants may also deharden in response to other stress events like anoxia (Höglind et al. 2010). In BASGRA, dehardening is sensitive to temperature but not to anoxia.

BASGRA simulates LT50 by estimating rates of hardening (RATEH) and dehardening RATED). RATEH and RATED are simulated as dependent on the temperature at the soil surface as in Thorsen and Höglind (2010). In short, hardening proceeds are fastest when LT50 is high and temperatures low, and the opposite applies to dehardening. A function which describes the relationship between RATEH and the content of C reserves was introduced in BASGRA according to observations (Hanslin and Höglind, 2009). RATEH is treated as a potential hardening rate that can only be fully realized when the content of C reserves (CRES) is above a threshold value, below which RATEH is linearly reduced. Hardening is hampered when carbohydrate reserves drop below 20% of biomass, decreasing linearly to zero when reserves become fully depleted. This compares to observed reserve levels in early winter (December-January) of 13 % to 28 % of biomass for timothy cultivar Grindstad grown in Norway. The estimated LT50 value is then used to calculate a relative death rate due to low temperatures in the field. The fraction of leaves and tillers that survive for one day (RSRDAY) at the soil surface temperature Tsurf is calculated using a truncated logistic curve:

$$\text{RSRDAY} = \max\{\ 0.5,\ 1\ /\ [1 + \exp(\text{Tsurf}-\text{LT50}_t)]\ \} \qquad (2)$$

where LT50_t is the simulated LT50-value at time step *t*. The fraction of leaves and tillers that die during one day due to frost, i.e. the relative death rate due to frost (RDRFROST) is thus

$$\text{RDRFROST} = 1 - \text{RSRDAY} \qquad (3)$$

When a surface ice layer is simulated, it is assumed that the plants are encapsulated in ice. As a result, anaerobic conditions are created with the accumulation of by-products from anaerobic respiration to toxic levels (Andrews, 1996). This phenomenon, often referred to as ice-encasement, is a major cause of winter kill in perennial grasslands in regions with cold winters like Northern Eurasia and Canada (Gudleifsson and Larsen, 1993). We estimate the number of days with anaerobic conditions (TANAER) as the accumulated number of days with continuous ice cover, and the number of ice-encapsulation days required to kill 50% of the leaves and tillers is termed LD50. The LD50-value was related to the LT50-value based on observations for two timothy cultivars (Grindstad and Engmo) (Höglind et al. 2010) using linear regression:

$$\text{LD50} = \text{LDT50A} + \text{LDT50B} * \text{LT50} \qquad (4)$$

Using the estimated LD50 value from Eq (4), the relative death rate due to the number of days of ice encasement is derived as minus the normalized derivative of the curve for the fraction of surviving plants: Relative death rate = - (d fSurv / dt) / fSurv. By describing the survival curve as a logistic function of the number of ice-days (TANAER) with the inflection point LD50 calculated from Eq (4), the relative death rate due to ice encasement (RDRTOX) is estimated as:

$$\text{RDRTOX} = \text{KRDRANAER}\ /\ (1 + \exp[-\text{KRDRANAER}\ (\text{TANAER} - \text{LD50})]) \qquad (5)$$

where KRDRANAER (d^{-1}) is the maximum relative death rate due to anaerobic conditions.

2.8 Impact of cutting

Most plant processes are interrupted during days when a cutting takes place. In BASGRA, the cutting removes all elongating tillers, but no non-elongating tillers. All leaf area associated with elongating tillers, and all leaf area associated with non-elongating tillers above a threshold is removed by the cutting, as is the associated biomass and carbon reserves. A fixed fraction of the stem biomass becomes stubble, and the stubble dies in a relatively short time allowing for remobilisation of carbon reserves as described in section on senescence (2.6).

3 Model parameterisation

BASGRA was parameterized by means of Bayesian calibration as described by Van Oijen and Höglind (2016). Here, we give a brief overview of the calibration procedure together with additional results to those presented by Van Oijen and Höglind with special focus on simulated results and observations for the winter season and the transitions between summer and winter.

3.1. Data

A dataset consisting of observations of the timothy cultivar Grindstad from experiments carried out on five different locations in Norway was used to calibrate the model (Table 1). Short descriptions of the different experiments are given below. Details on Exp. 1 can be found in Höglind et al. (2006), on Exp. 2 in Höglind et al. (2010) and on Exp. 4 in Höglind et al. (2005). Exp. 3 contains previously unpublished material (Sunde, 1996).

Table 1. Sites with timothy experiments from which data were collected for calibration of the BASGRA model, and for which simulations were performed in the example of application.

Location	Experiments	Latitude	Longitude	Elevation (m)	Climatic means, 1995-2012	
					Temperature [1] (°C)	Precipitation (mm y^{-1})
Apelsvoll	3	60°70’ N	10°87’ E	255	4.8 (-6,6)	679
Fureneset	1	61°29’ N	5°04’ E	12	7.7 (1.9)	2280
Holt	1, 2	69°65’ N	18°90’ E	12	3.8 (-3.1)	966
Kvithamar	1, 2	63°49’ N	10°88’ E	28	6.0 (-2.8)	1007
Særheim	1, 2, 4	58°47’ N	5°41’ E	83	7.8 (1.0)	1430

[1] Numbers without brackets show the mean annual temperature; numbers within brackets show the mean temperature for the winter months December to February.

Exp. 1 was carried out at three locations: Fureneset, Holt, and Særheim (Table 1). The swards were established in May (Fureneset, Særheim) or June 2005 (Holt). Shoot dry weight, leaf area index (LAI), specific leaf area (SLA), tiller density, content of water soluble carbohydrates (WSC), and frost tolerance (LT50) were determined on five occasions from November 2005 to March 2006 at all three locations. In addition, tiller density and DM yield (total dry weight of herbage above a stubble height of 5 cm) was determined in June 2006.

Exp. 2 was carried out at three locations: Holt, Kvithamar and Særheim (Table 1). The swards were established in June 2005. From November 2006 to March 2007, on three occasions per location, shoot biomass, tiller density, WSC, and LT50 were determined. In addition, tiller density was determined at Særheim in June 2007. The swards were cut once (Holt) or twice in the growing season 2006, and twice (Holt) or three times in the growing season 2007, and the DM yield from each cut above a stubble of 5 cm was measured.

Exp. 3 was carried out at Apelsvoll (Table 1) in a sward established in May 1990. Sampling to determine WSC and LT50 was carried out on 13 occasions between August 1990 and April 1991.

Exp. 4 was carried out at Særheim (Table 1). There were two fields. The first field was established in 1999, with measurements taken in 2000. The other field was established in 2000, with measurements taken in 2001 and 2002. Two cutting regimes were compared in each field. From April to August each year, with sampling intervals of 7-14 days, shoot biomass, LAI, SLA, tiller density, WSC, leaf appearance rate, number of elongating leaves per tiller, and leaf elongation rate per actively growing leaf were determined.

All experimental locations were equipped with automatic weather stations, located within 500 m from the experimental field. For the calibration of the model, daily weather data for the individual sites, together with descriptions of the soils, were downloaded from the weather database of Norwegian Institute for Agricultural and Environmental Research (present name Norwegian Institute of Bioeconomy Research -NIBIO).

3.2 Bayesian calibration

Bayesian calibration of BASGRA consisted of three steps (Van Oijen et al. 2005b, 2013): (1) defining the prior distribution for the model's parameters, (2) defining the likelihood function for the model's parameters, (3) sampling from the 'posterior distribution' given by the normalised product of prior and likelihood. The posterior distribution expresses how the data have reduced our uncertainty about parameter values. Prior parameter ranges for individual parameters were derived from earlier literature studies (Höglind et al. 2001; Van Oijen et al. 2005a; Thorsen et al. 2010) where available, whereas wide ranges of plausible values were assumed otherwise. All plant parameters were treated as site-independent, whereas soil parameters were considered site-specific.

The likelihood function quantified the probability, for any given parameter vector, of the mismatch between the data and the model outputs induced by the parameter vector. The measurement error terms in the likelihood function followed the conventional assumption of independent Gaussians with variances that varied between variables and observations. The sample from the posterior distribution was generated by means of Markov chain Monte Carlo (MCMC) methods using the Metropolis algorithm (Metropolis et al. 1953; Van Oijen et al. 2005b). Chain length was 300,000 to ensure convergence for all parameters.

To quantify the mismatch between the data and the outputs from the calibrated model, we used the Normalised Root Mean Square Error (NRMSE), which is the square root of the mean squared difference between observations and outputs, divided by the mean of the observations. The extent to which model output accounted for variation in the data was also quantified by means of the square of Pearson's correlation coefficient (r^2).

3.3 Calibration results

The Bayesian calibration was carried out using data from five different sites on a total of ten different variables. Table 2 and 3 gives an overview of the behaviour of BASGRA for biomass, yield, C reserves, LAI, SLA, tiller density and LT50 when run with the MAP (*maximum a-posteriori*) parameter estimates from the Bayesian calibration. Using this parameter vector, nearly all variables were simulated to an overall NRMSE less than 0.5 (Table 2). In a third of the site x experiment combinations, NRMSE was below 0.3 (Table 3), and median NMRSE for the combined dataset was below 0.4 for nearly all variables (Table 2). For leaf appearance rate, leaf elongation rate, and elongating leaf density, respectively, NMRSE was 0.46, 0.53 and 0.70.

Table 2. Normalised Root Mean Square Errors (NRMSE) and squared Pearson's correlation coefficients (r^2) for the mismatch between simulations and the data when running BASGRA with the maximum a posteriori (MAP) parameter estimates from the Bayesian calibration.

	Mean of data for all sites	Mean of simulations for all sites	Mean NRMSE for the total dataset	Median NRMSE for the total dataset	r^2 for the total dataset
Aboveground DM ($g\ m^{-2}$)	309	282	0.39	0.37	0.93
Reserves (g g-1)	0.15	0.12	0.40	0.37	0.38
DM yield ($g\ m^{-2}$)	312	409	0.51	0.38	0.64
LAI ($m^{-2}\ m^{-2}$)	3.3	3.1	0.44	0.46	0.81
SLA ($m^{-2}\ g^{-1}$)	0.026	0.028	0.27	0.35	0.27
Tiller density (m^{-2})	2542	2307	0.41	0.34	0.48
LT50 (°C)	-14.9	-15.2	0.23	0.19	0.75

Table 3. NRMSE for the mismatch between simulations and data when running BASGRA with the MAP parameter estimates from the Bayesian calibration split on individual experimental sites and experiments. Abbreviations in column headers refer to site names and experiment numbers listed in Table 1 (ex. Ap1 = Apelsvoll Exp. 1). Sa4 denotes the combined data from the two experimental seasons and two harvest regimes of Exp. 4.

		Ap3	Fu1	Ho1	Ho2	Kv2	Sa1	Sa2	Sa4
Biomass ($g\ m^{-2}$)	Mean of data	-	162	27	24	92	24	52	384
	NRMSE	-	0.23	1.14	0.59	0.19	1.21	0.81	0.36
Reserves ($g\ g^{-1}$)	Mean of data	0.20	0.12	0.16	0.18	0.15	0.17	0.20	0.13
	NRMSE	0.43	0.13	0.54	0.44	0.71	0.26	0.37	0.37
Yield ($g\ m^{-2}$)	Mean of data	-	346	-	638	297	-	278	-
	NRMSE	-	0.34	-	0.45	0.35	-	0.41	-
LAI ($m^2\ m^{-2}$)	Mean of data	-	1.3	0.2	-	-	0.3	-	3.8
	NRMSE	-	0.27	0.65	-	-	2.67	-	0.41
SLA ($m^2\ g^{-1}$)	Mean of data	-	0.029	0.033	-	-	0.020	-	0.026
	NRMSE	-	0.31	0.32	-	-	0.23	-	0.26
Tiller density (m^{-2})	Mean of data	-	1866	694	1282	2987	1685	2385	2755
	NRMSE	-	0.32	0.34	1.06	0.18	0.22	0.52	0.40
LT50 (°C)	Mean of data	-12.8	-12.4	-14.9	-16.9	-20.0	-17.7	-14.7	-
	NRMSE	0.33	0.19	0.12	0.10	0.18	0.23	0.17	-

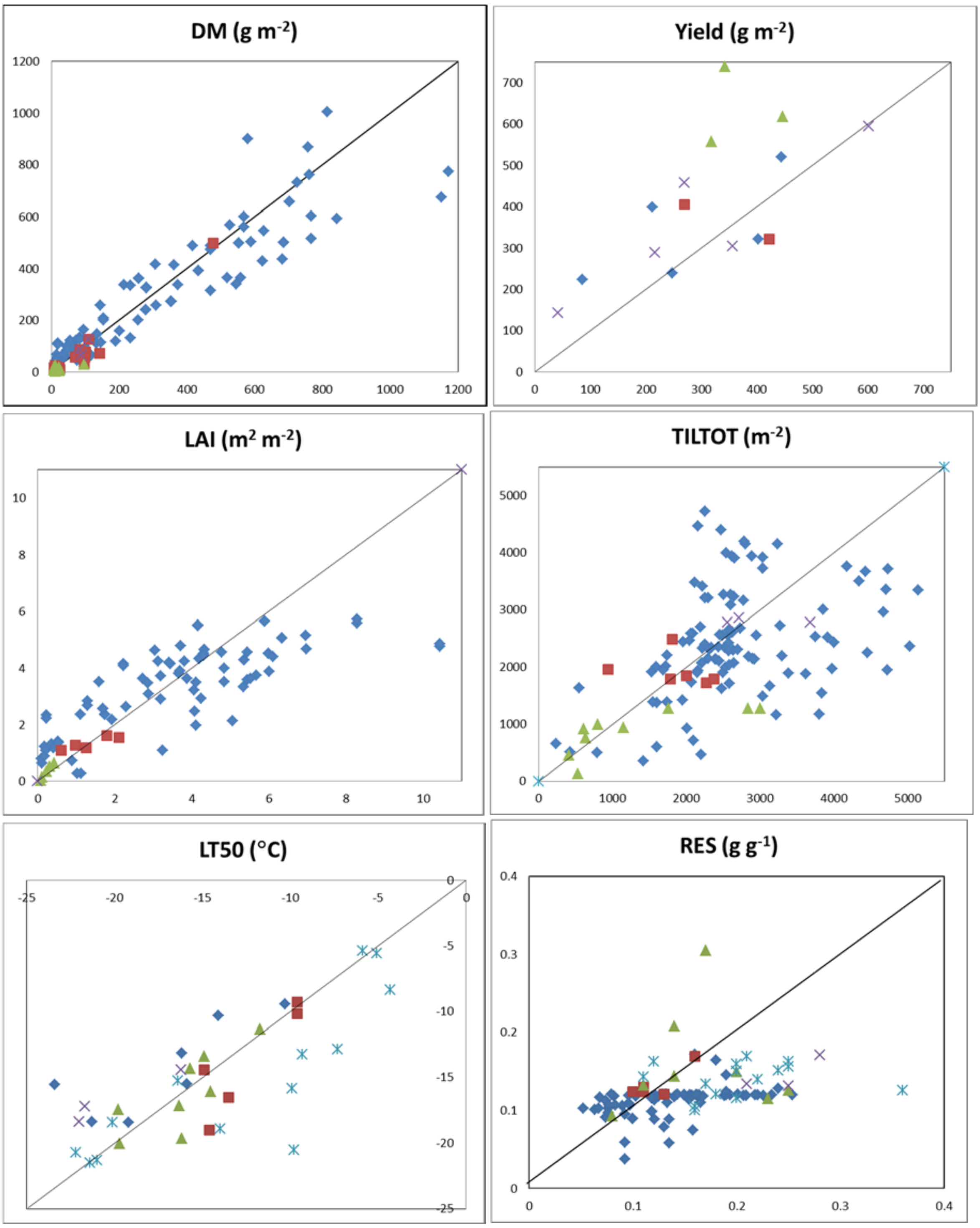

Figure 1. Collective scatterplots of measured (x-axis) versus simulated (y-axis) dry matter (DM), yield (Yield), leaf area index (LAI), tiller density (TILTOT), frost tolerance (LT50) and reserve content (RES) for timothy when running BASGRA with the MAP parameter estimates from the Bayesian calibration. Blue diamonds: Særheim; blue x-signs: Fureneset; light blue stars: Apelsvoll; green triangles: Holt; red squares: Kvithamar.

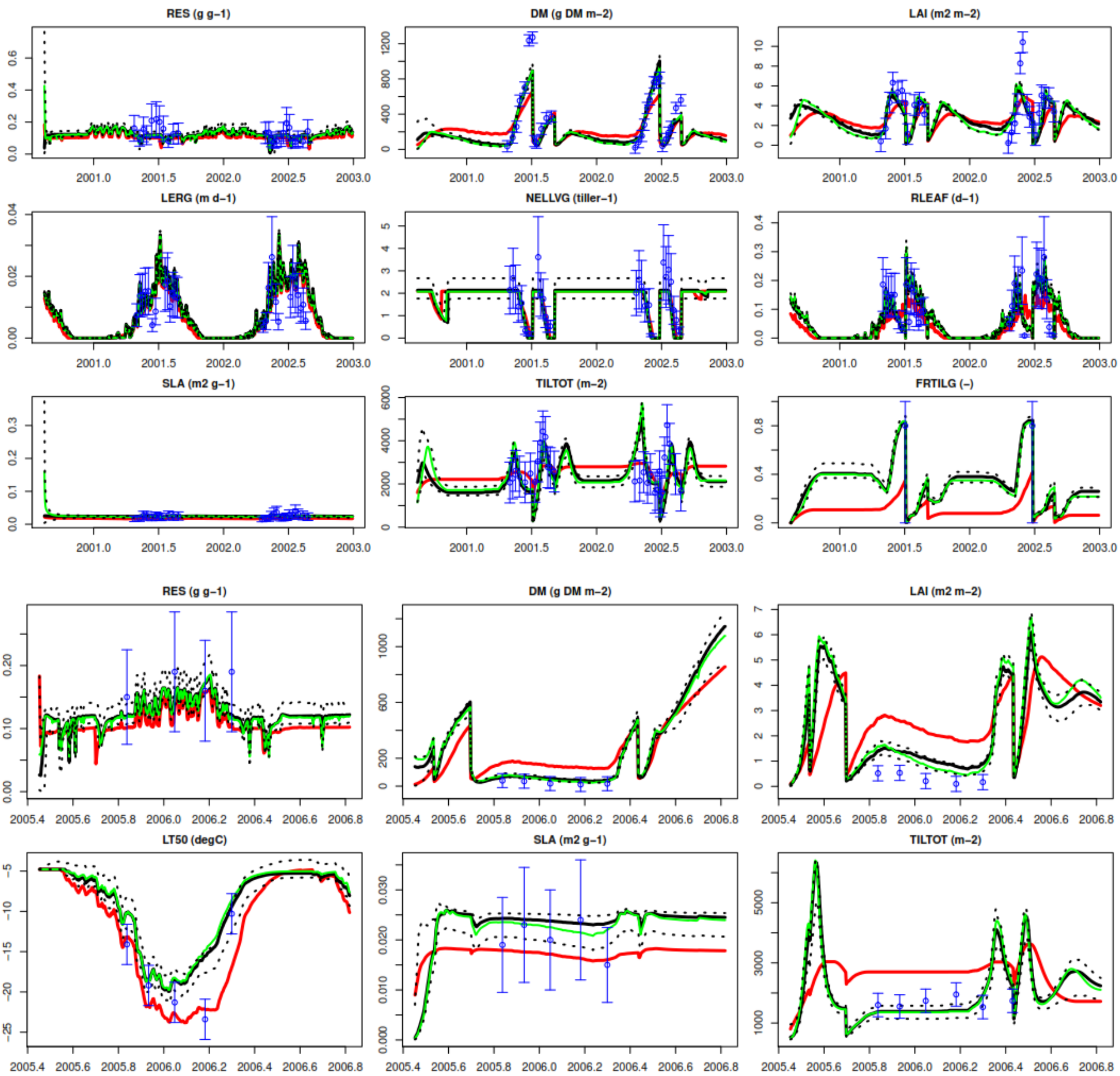

Figure 2. Results of Bayesian calibration, showing prior and posterior time series with a) the observations of the late cutting regime of Exp 4 carried out at Særheim in 2001-2002 (the nine uppermost graphs; this experiment included summer observations only), and b) all the observations of Exp 3 carried out at Særheim in 2005-2006 (lowermost six graphs; this experiment included winter observations only). Blue: observations ± standard deviation (SD). Red: model outputs for the mode of the prior distribution. Black: model outputs for the posterior mode ± SD: Green: model outputs for the parameter vector with highest likelihood. RES: reserve content, DM: dry matter, LAI: leaf area index, LERG: leaf elongation rate, NELLVG: number of elongating leaves per tiller, RLEAF: leaf appearance rate, SLA: specific leaf area, TILTOT: tiller density, FRTILG: fraction of tillers that is generative, LT50: frost tolerance.

Based on NRMSE, the model performed best for the variables LT50 followed by SLA and biomass, whereas in terms of r^2 it performed best for biomass followed by LAI and LT50 (Table

2). The scatterplots of measured and simulated values presented in Fig. 1 indicate a tendency to underestimate high biomass and LAI values. The simulated biomass yield was higher than the observed biomass yield for most of the observations. The scatterplots for tiller density and reserves show more extreme deviations between simulations and observations compared with those for biomass, yield, LAI and LT50.

Fig. 2 shows an example of the impact of the Bayesian calibration on the model behaviour for two experiments at the most data rich-site, Særheim. The temporal dynamics of the ten variables were in general well captured. This applies both for the summer and winter data. Corresponding graphs for the remaining experiments are presented as Supplementary material.

4 Model application: time courses of growth and underlying processes at two contrasting sites in Norway

We now show an example of application of BASGRA for the simulation of multiple consecutive years of timothy grass growth and underlying processes. This section is intended to highlight the capacity of the model to study overwintering processes and their linkages with preceding and following growing seasons. Simulations were performed for two sites in Norway, Holt and Særheim (Table 1). The northern location Holt is characterized by relatively harsh, unstable winter conditions, whereas Særheim generally has milder winter conditions (Table 1). At each site, simulations were performed for six three-year long grass rotations for the period 1995 to 2012. Two harvests per year were simulated, with harvest dates adjusted to local climate conditions (Höglind et al. 2013). BASGRA was re-initialized in the beginning of each growth cycle using the MAP values from the Bayesian calibration.

The 3-year cycles with the highest and lowest total dry matter yield for each site are shown in Fig. 3. According to agricultural insurance pay-out statistics, perennial grasslands survive most winters well in the region where Særheim is located (Rogaland county), whereas severe winter injury occurs every three to four years in the region where Holt is located (Troms county; Landbruksdirektoratet, https://www.slf.dep.no/no). The difference in winter conditions between the locations is also reflected in the simulation results. At Holt the winter survival varied considerable between years, and growth cycles. Notably a severe winter kill was simulated in the first winter of the 1999-2001 growth cycle, resulting in very poor total yield. This contrasts to Særheim, for which only minor differences in survival and yield between the growth cycles were simulated. Further examination of the results reveal that anoxic conditions due to a long period of ice encasement was the major cause of winter kill in the poor 3-year cycle at Holt. Figure 4a shows that one single event of prolonged anoxia and virtually no frost stress was simulated during the poor 3-year cycle at Holt. This contrast to the corresponding 3-year cycle at Særheim where virtually no winter stress of any type was simulated (Fig. 4b) although some very light frost stress is revealed if the graph is scaled up (not shown).

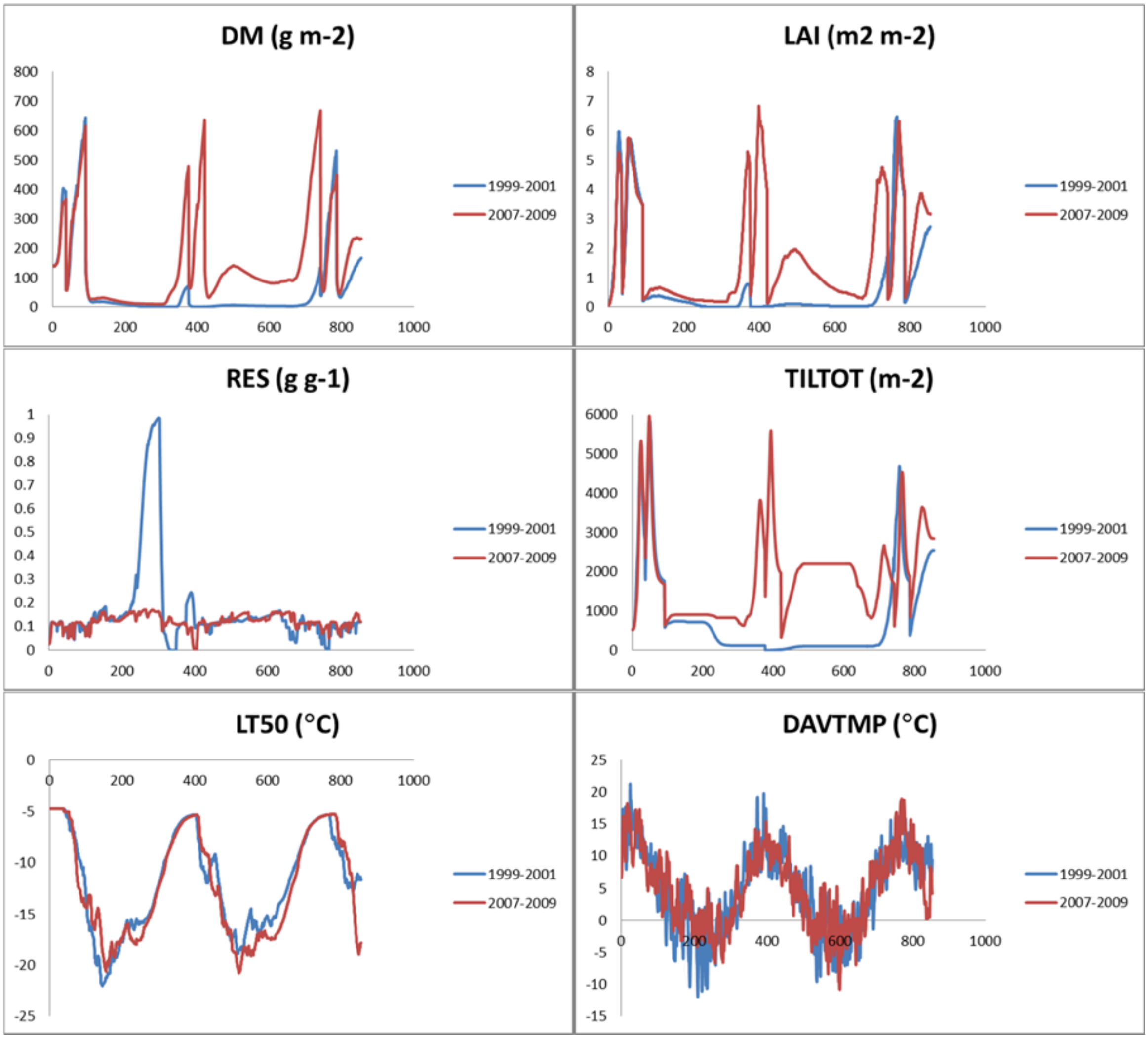

Figure 3a. Simulation results for timothy grown at Holt in the 3-year cycle with the highest (2007-2009) and lowest (1999-2001) total dry matter yield within the period 1995-2012. The x-axis shows the number of days since the start of simulation at sward establihment (19 June).

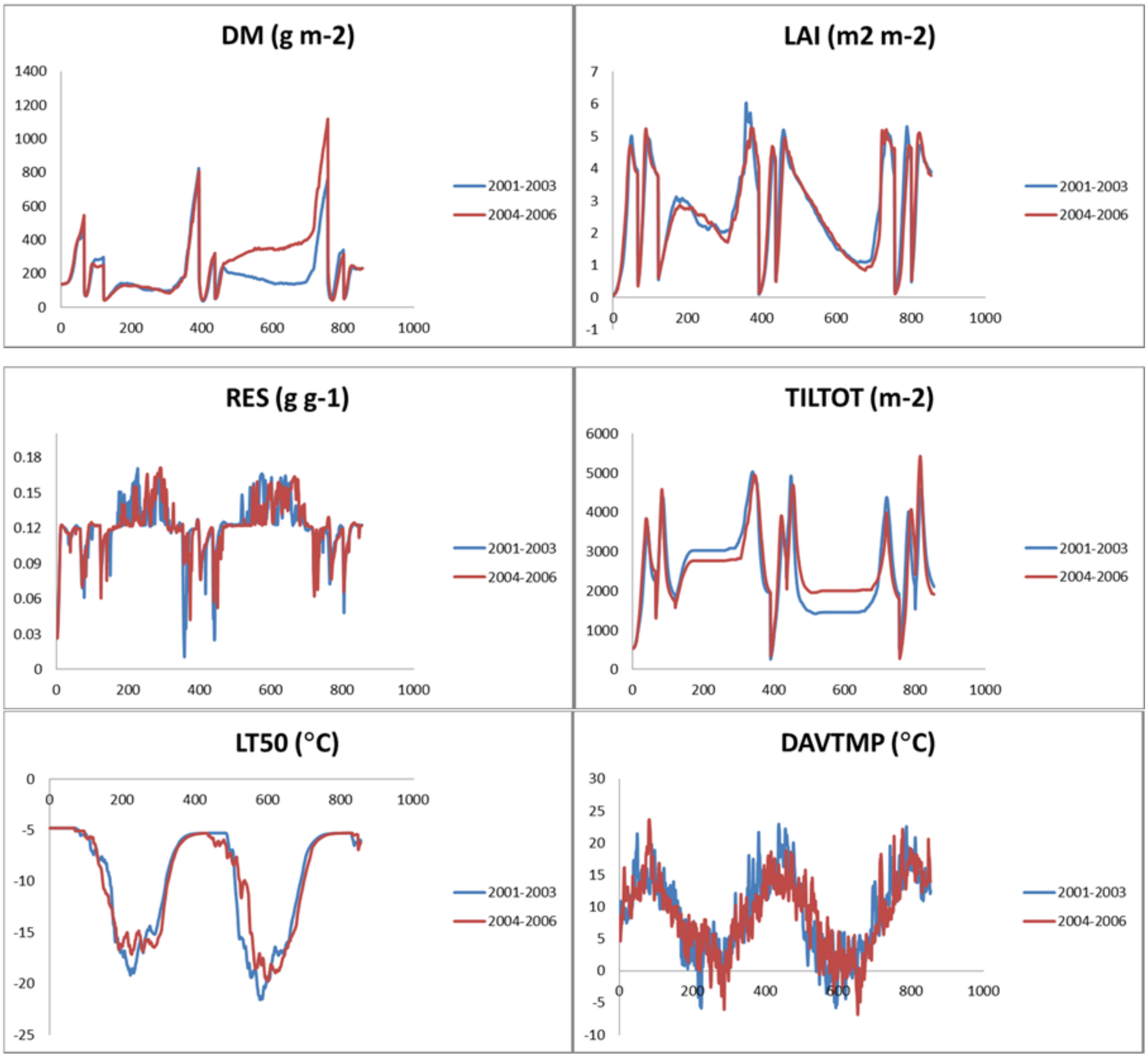

Figure 3b. Simulation results for timothy grown at Særheim in the 3-year cycle with the highest (2004-2006) and lowest (2001-2003) total dry matter yield within the period 1995-2012. The x-axis shows the number of days since the start of simulation at sward establishment (20 May).

A new feature of BASGRA compared with LINGRA is the additional tiller fraction representing generative, non-elongating tillers. The contribution of the different tiller categorises to the total tiller population and the relationship between them is exemplified in Fig. 5. At Holt, tillers mainly overwinter in the vegetative stage and the transition from vegetative to non-elongating generative tillers and further on to elongating tillers in spring is very quick. This contrasts to Særheim where both vegetative and non-elongating tillers survive, and where the transition between the non-elongating and elongating generative tillers starts earlier and takes more time, reflecting the more gradual increase in temperature and day-length at the southern location, as observed in controlled experiment with different temperature and day lengths (Heide 1982)

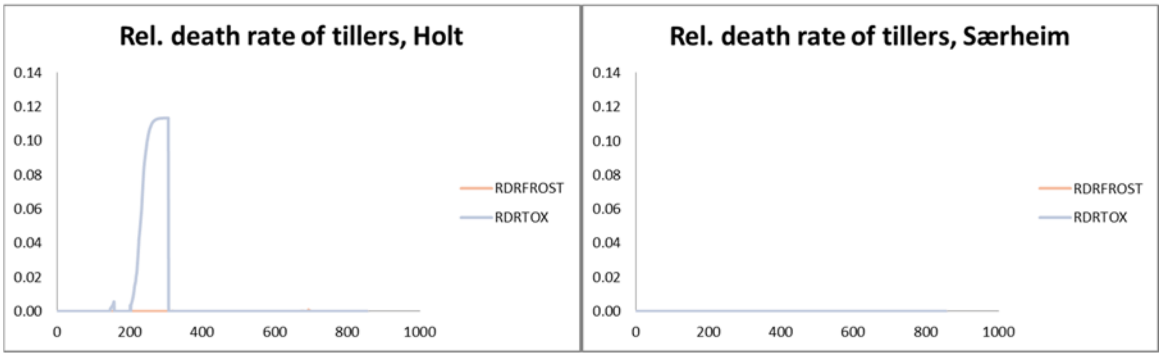

Figure 4. Simulated relative death rates of tillers due to frost (RDRFROST) and ice encasement (RDRTOX) stress at Holt 1999-2001 (left) and Særheim 2001-2003 (right). The x-axis shows the number of days since the start of simulation at sward establishment (19 June and 20 May, respectively).

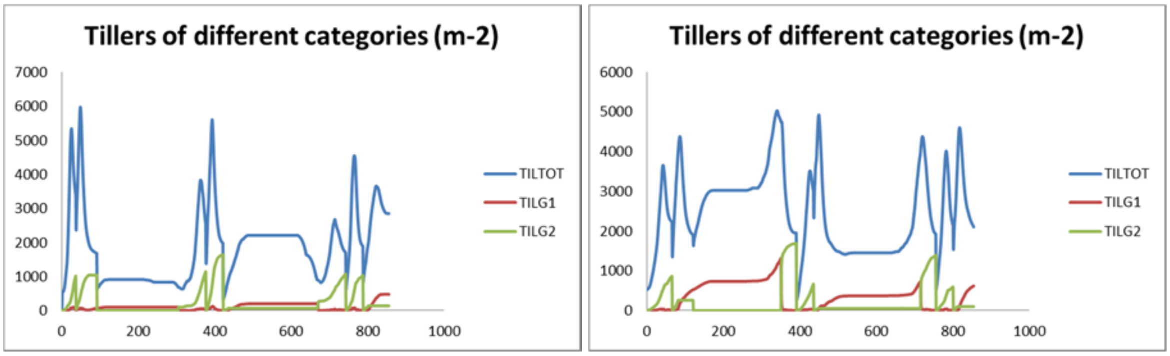

Figure 5. Simulated density of non-elongating(TILG1) and elongating (TILG2) generative tillers and total tillers (TILTOT) at Holt 2007-2009 (left) and Særheim 2004-2006 (right). The x-axis shows the number of days since the start of simulation at sward establishment (19 June and 20 May, respectively).

Fig. 6 presents normalized time courses for the average middle year of the six 3-year cycles that were simulated. These graphs illustrate the difference in growing conditions between the two sites, such as the longer growth season at Særheim, with earlier accumulation of biomass, leaf area development and tiller production and later cessation of these processes in autumn compared with Holt. These differences in spring and autumn growth between the two sites can, to a large extent, be explained by the differences in temperature and day-length conditions. Cold hardening is also controlled by temperature, as expressed in the faster development of simulated frost tolerance at the colder site compared with the warmer site Særheim. The faster simulated loss of frost tolerance (dehardening) in spring at Holt may at first look surprising given the lower mean winter temperature at this site. However, this site experienced repeated freeze/thaw events that, according to the simulation, lead to ice encasement and loss of C reserves in several of the winters, reducing the rehardening capacity of the sward more than at Særheim where C reserves were better maintained, as also observed in experiments at the two sites (Höglind et al. 2006, 2010).

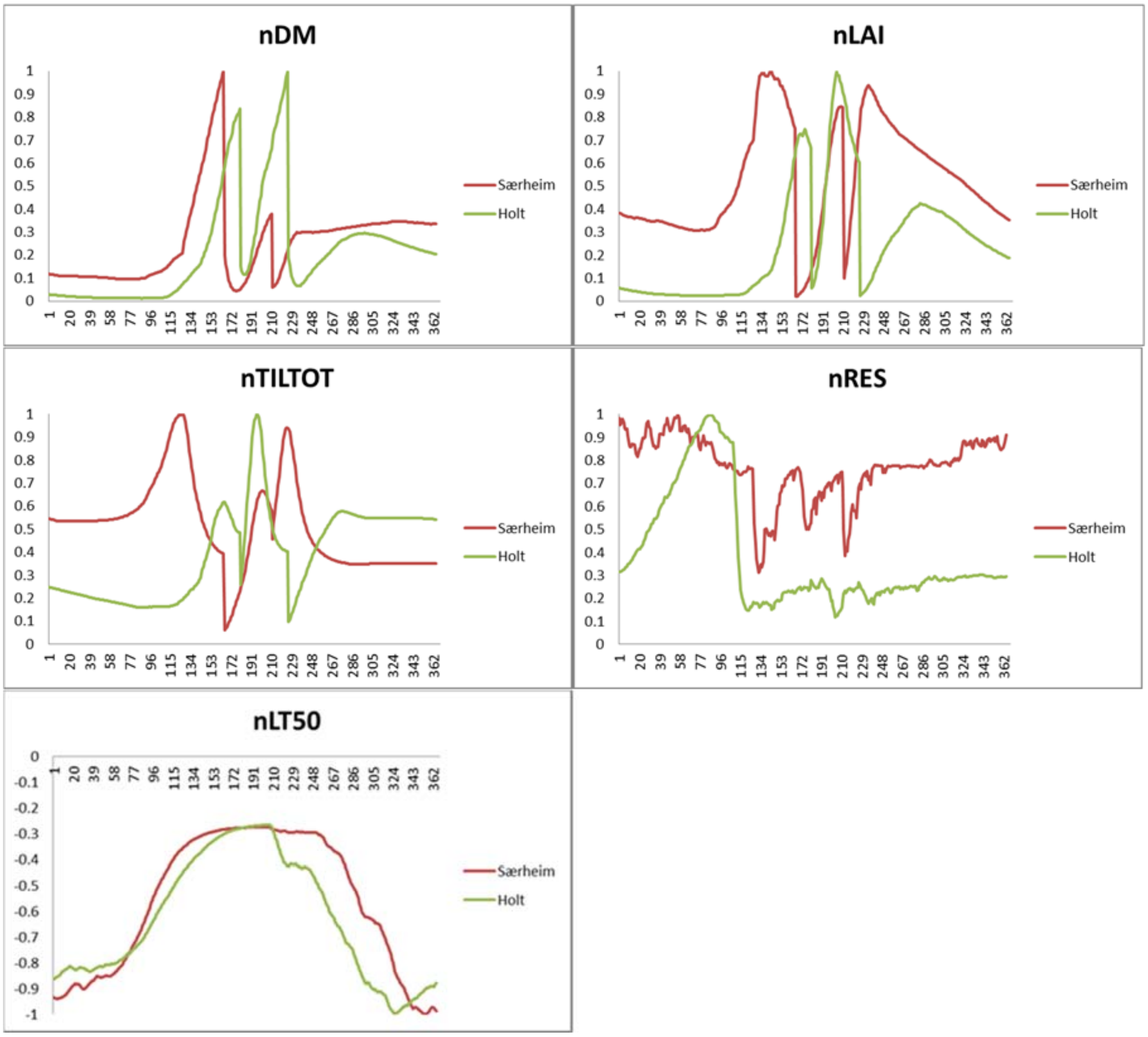

Figure 6. Normalized dry matter (nDM), leaf area index (nLAI), tiller density (nTILTOT), reserve content (nRES) and frost tolerance (nLT50) for the average second year of all the 3-year growth cycles that were simulated for timothy at locations Særheim and Holt (1995-1997, 1998-2000, 2001-2003, 2004-2006, 2007-2009, 2010-2012). All variables are expressed relative to the maximum value across the six cycles. The x-axis shows the day number of the year.

5 Discussion and outlook

5.1 Unique features of BASGRA

The BASGRA model is unique in several ways. Most important, it is the first process-based model for temperate grasslands that is able to simulate grass growth and survival for time series of full, consecutive years taking into account the ability of the plant to cold acclimate, and the effect of cold winter conditions on plant growth and survival. This was made possible by incorporating algorithms representing plant processes and control mechanisms which are usually not represented in grassland models. While any process-based model is a simplification of reality as it only includes the driving variables and physiological mechanisms that are considered the most important for the intended use of the model, it is important that it is based on current ecophysiological and agronomical knowledge. In the following, we discuss some of the central features of BASGRA in relation to current knowledge.

A novel important feature of BASGRA is the simulation of cold hardening as a function of temperature (Gay and Eagles, 1991; Fowler et al.1999), availability of reserves (Hanslin and Höglind, 2009), and time (Rapacz et al. 2014). For winter wheat, it has been shown that the ability to reharden after a mild episode is closely linked to the development stage of the tillers, with a reduction of the ability to reharden after the vernalization requirement has been fulfilled (Mahfoozi et al. 2001). In BASGRA, the ability to reharden is linearly decreased with time between mid-winter and spring. A more complex modelling approach including a link between vernalization and rehardening capacity did not give better simulations than the simpler approach used in the present model (Thorsen and Höglind, 2010). This fits well with recent observations indicating that vernalization and rehardening ability may not be as closely linked in forage grasses as in wheat (Seppänen et al. 2010; Rapacz et al. 2014). However, more research is needed before conclusions can be drawn on how rehardening capacity should ideally be modelled. There may be large but still unknown genetic variation in vernalization requirement and links between vernalization and rehardening capacity between timothy cultivars.

Short day length may stimulate hardening further under low temperatures as long as there is enough light for this energy demanding process (Rapacz et al. 2014). In BASGRA, we have incorporated an indirect effect of day length on cold hardening via the dependency of cold hardening on the content of carbohydrates, and the changed priority order for assimilates from growth to carbohydrate storage at short day lengths. There is also a direct control of short day length on leaf elongation in BASGRA, leading indirectly to a reduced demand of carbon for growth at short day lenghts. The data presented in this paper suggest that this approach works well. However, it should be noted that there are still many unresolved questions on how growth cessation in forage grasses is controlled, with multiple interacting factors including day length, temperature and genotype (Rapacz et al. 2014). When more knowledge becomes available, it will be possible to develop BASGRA further with respect to these processes and their controls.

Ice encasement tolerance in BASGRA is calculated using a simple approach where it is linearly related to frost tolerance, although these two tolerances do not share the same mechanisms (Höglind et al. 2010). A simple approach is also used for calculating ice encasement related mortality, where ice encasement exposure is purely a function of time. A more mechanistic approach could include an estimation of the accumulation of toxic compounds from anaerobic respiration in the plants (Bertrand et al. 2003) as a function of the availability of carbon reserves in the plants, the respiration rate of the encapsulated plant and soil biota, the volume of the ice encapsulated air space, and the rate of gas exchange with the surrounding atmosphere in case the ice is not fully impermeable (Andrews, 1996).

5.2 Calibration results

For the calibration we used detailed data on the growth and development of timothy grass swards and individual plants from five different locations in Norway, with up to five years of observations per site from either the summer or winter season or a combination of both seasons. The sites and years represent a wide range of climate and weather conditions as well as other environmental conditions like day length (latitudes from 59° to 70° N) and soil types (sandy to silty loams/clay loams). The total dataset included 11 variables, including biomass, LAI, tiller density, WSC content and LT50, with up to eight variables per site. The results of the calibration show that a single parameter vector, the MAP, suffices to simulate nearly all measured variables to a NRMSE of less than 0.5. This is in the same order of magnitude as the coefficient of variation of the data. For about a third of the site x experiment combinations, NRMSE was below 0.3, and median NMRSE for the combined dataset was below 0.4 for most variables.

The dataset from Exp. 4 was also used in a previous study (Van Oijen et al. 2005a) where the LINGRA model was evaluated. As LINGRA is the predecessor of BASGRA, it is interesting to note that the NMRSE and r^2 values obtained here for BASGRA using the data from Exp. 4, are at least as good as those obtained for LINGRA when only the summer season was taken into account. For many variables including biomass, BASGRA gave slightly lower NMRSE and higher r^2 values than LINGRA. This means that the changes introduced to turn the summer model LINGRA into the full-year model BASGRA, are a step forward not only in allowing for full-year simulations including winter processes, but also in simulating summer processes with increased precision.

The plots of simulated versus observed data presented in Figures 2 confirm that biomass, an output variable that is in many cases the one that is considered the most important, is simulated with good accuracy. However, harvested yield is generally overestimated. However, as biomass in general is satisfactorily simulated, this indicates that the harvested fraction of the aboveground biomass is systematically overestimated rather than dissatisfactory simulation of biomass. LAI and LT50 are also simulated with relatively good accuracy. Further, the temporal dynamics of these variables, as well as of several other variables were captured in a satisfactory way by the model, as evident from the time courses of simulated versus observed data presented in Figure 3 (Særheim x 2) and as Supplementary material (remaining experiments).

However, some variables, notably tiller density and reserve content are simulated with less accuracy, calling for model improvements with respect to the underlying processes influencing those variables. Such work would require more data, preferably from experiments with detailed measurements carried out throughout full life-cycles of three to four years, including observations in winter as well as summer on at least the 5-6 most central variables studied here. Currently, we have no clear answer to how to improve BASGRA with respect to simulation of tiller density and C reserves. The strong dependency of tillering on C reserves, and the mutual dependency of C reserves on the regrowth of tillers with photosynthetic tissue after a cut or stressful winter indicate that if the simulation of the processes governing one of these variables could be improved, the simulation of the processes governing the other might also be improved. Tiller density and C reserves are both sensitive to nitrogen availability (Höglind et al. 2001). The experiments from which the data used to calibrate our model were obtained had all received relatively high levels of nitrogen fertilizer, and we assumed non-nitrogen limiting growth conditions for all experiments. However, it cannot be excluded that nitrogen limited growth occurred occasionally in one or more of the experiment, for example in connection with dry soil conditions, which would affect tillering and C reserves in ways not accounted for in the model.

Taken together, the results of the comparison of simulations and observations may suggest that the BASGRA model is fairly robust, with an ability to simulate both the growth of the grass sward and important underlying processes with acceptable accuracy for a wide range of agroclimatic conditions without the need for site-specific parameterization, at least not for the range of geoclimatic variation considered here which included a wide latitudinal range.

However, we need to test the robustness of the model further by comparing the behaviour of BASGRA for sites in Norway with its behaviour for sites in other countries. Such work is underway for sites in Canada and Finland (Korhonen et al. in prep.).

5.3 Further validation

Parts of the BASGRA model have been validated before. The LINGRA model, parameterized for the same timothy cultivar as was used in the present study, i.e. Grindstad, was evaluated with respect to simulation of timothy dry matter yields over a wide range of agroclimatic conditions represented by seven locations in Iceland, Norway, Sweden and Finland (Persson et al. 2014). The frost tolerance model, parameterized for the Norwegian timothy cultivar Engmo, was validated with respect to simulation of LT50 using data from four Norwegian locations (Thorsen and Höglind, 2010). Finally, the SnowFrostIce model was validated for simulation of snow, ice cover and frost depth using independent observations from five Norwegian sites (Thorsen et al. 2010). A slightly modified version of SnowFrostIce was also validated with satisfactorily results with respect to simulation of snow cover dynamics in Canada (Jégo et al. 2014).

We used all the detailed data on Grindstad timothy growth and development during summer and winter seasons for the calibration that were available for this study, not leaving any independent data for validation. This choice was made to get a more robust calibration than what a smaller dataset would have made possible, the overall aim being to develop a model that would not need site-specific calibration for plant parameters. However, even though the simulations with the calibrated model described the calibration dataset with acceptable accuracy, a thorough validation of BASGRA against independent data should be performed when such data become available. There is specifically a need to validate the model for simulation of multiple consecutive years with variable overwintering conditions.

A possible approach for validation of BASGRA with respect to simulation of winter survival and subsequent growth under different climatic conditions would be to, as a starting point, use the same dataset that was used in the validation of the LINGRA model for summer growth (Persson et al. 2014). In the cited study, LINGRA was run for single summer seasons and locations using a common set of standard initial values for biomass, tiller density and LAI representing typical sward conditions in spring, with re-initialization of the model each spring. The model was evaluated by comparing observed and simulated dry matter yields from two to three harvests per year. To validate BASGRA, the model should not only be run for single growing seasons as in the cited study, but also continuously from establishment throughout the lifetime of the sward (generally three seasons) including winters. A rough test would be whether consecutive full-year simulations will give lower mismatch between observed and simulated yields compared to re-initializing the model each spring using standard initial values not accounting for possible differences in winter survival between locations and years.

5.4 Scope for application

A full year grassland model like BASGRA that takes into account cold hardening and the effect of winter conditions on plant growth and winter survival, can be applied in many types of studies, addressing various types of questions. In a recent paper, we discuss the possibility to use BASGRA for designing grass ideotypes for current climate conditions (Van Oijen and Höglind, 2016). This approach could also be applied to conditions of climate change. A number of climate change impact studies have been carried out using grassland models focusing on summer growth processes (Riedo et al. 1999; Höglind et al. 2013; Persson and Höglind, 2014; Jing et al. 2014). A natural extension of these studies would be to include the effect of the expected climate change on the winter survival of the grass sward and subsequent effects on yield.

BASGRA also has a great potential as a tool for tactical planning in relation to winter survival. Forecasts of winter injury could for example help seed suppliers to make sure that enough seed is available for reseeding in years with severe winter injury. In such years, seeds are commonly imported from regions with less winter injury. The sooner the seed supplier can have the right seed available in spring, the sooner the farmer can reseed, thus minimizing the non-productive time and increasing the yield potential of the sward. The example application presented in section 4 suggests that BASGRA may be suitable for such planning.

Finally, we note that BASGRA can be applied to other grassland species than timothy. This may include species such as perennial ryegrass (*Lolium perenne* L.) that are sown at greater density and have less winter tolerance and greater vernalization requirement than timothy. This would require changes in model initialisation and calibration but no changes in model structure.

5.5 Further development

BASGRA takes into account the effects of frost, snow and ice conditions on grass growth, development and winter survival. Frost and ice related winter injuries are especially common in high-latitude regions with coastal types of climate conditions typically characterized by variable snow conditions and relatively frequent episodes of freezing and thawing (Larsen, 1994). Such conditions are for example common along large parts of the Norwegian coast, where some of the most productive grasslands in this country are located. Frost and ice may also cause severe winter injury in inland areas with more stable snow conditions, especially in atypical years with less stable snow conditions. However, in inland regions, especially those which experience long and stable snow cover, fungal diseases are often a more common cause of winter injury than frost and ice encasement (Larsen, 1994).

Given the importance of fungal diseases for winter survival in certain agricultural regions, a natural further development of BASGRA would be to include functions for simulating the development of snow mould fungi on the plant, and the plants' response to snow mould infection. The strong interaction that exists between host and parasite for disease development and level of winter injury makes this a challenging task (Raspacz et al. 2014). However, the ability of BASGRA to simulate frost tolerance and snow cover is a good starting point as: (1) resistance to snow mould fungi and frost tolerance are often highly correlated (although frost tolerance and disease resistance may have different mechanisms) (Tronsmo, 1984), and (2) snow condition is an important factor controlling disease development (Matsumoto, 2009).

5.6 Conclusions and outlook

With BASGRA, we have taken an important step toward full-year simulations of timothy yield that take into account the major winter stress factors contributing to yield variability in Scandinavia and regions with similar conditions. The current version of BASGRA allows for simulation of cold hardening and dehardening and the effect of cold temperatures, snow and ice conditions on survival and yield. However, the effect of fungal diseases on winter survival is not yet accounted for, which would be needed to fully capture winter stress related yield variability in these regions. The comparison of simulations and observations for the 11 different variables in the calibration dataset indicate that BASGRA is a reasonably robust model with which the growth and important underlying processes in timothy swards can be simulated with acceptable accuracy for a fairly wide range of agroclimatic conditions. However, the robustness of the model needs to be tested further using independent data from different agroclimatic conditions and grass management regimes. BASGRA can also be parameterized for other species, and we are currently collecting calibration data for perennial ryegrass. Further work will include improvement of the model with respect to simulation of tillers and C reserves, incorporation of

N-dependent growth functions, and validation against independent data for the conditions for which it will be used.

6 Acknowledgments

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