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Identifying causes of low persistence of perennial ryegrass (*Lolium perenne*) dairy pasture using the Basic Grassland model (BASGRA)

Modelling persistence of perennial ryegrass

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Abstract

Recent years have seen a decline in herbage production and tiller populations in New Zealand's perennial ryegrass (*Lolium perenne*) dairy pastures. One hypothesis is that modern genotypes are less suited to the warmer, drier weather experienced under changing climate patterns. In this study, a combination of long-term trial data (2011-2017) and a process-based pasture model (BASGRA) was used to explore the causes and possible mitigation of the observed production and population loss at three sites (dryland sites in Northland and Waikato, and an irrigated site in Canterbury). Bayesian calibration was used to identify the model parameter sets that were consistent with the trial data, and to identify differences in plant morphology and responses between sites. The model successfully simulated the observed differences in tiller numbers between the dryland sites, where populations declined rapidly, and the irrigated site where populations were maintained at high density. Analysis of the model calibrations along with preliminary scenario simulations suggest that increased tiller mortality associated with drought was the main cause of persistence failure at the dryland sites, and that decreasing grazing pressure or breeding for tolerance to higher temperatures would not be a successful strategy to prevent this.

Keywords

perennial ryegrass (*Lolium perenne*), tiller population, water stress, grazing, Bayesian calibration

1 Introduction

The replacement of older pastures with a new perennial grass sward is a common practice in temperate grassland management. In New Zealand, dairy pastures mostly consist of a dominant perennial ryegrass component (*Lolium perenne* L.) combined with white clover (*Trifolium repens* L.) that contributes typically less than 20% of total annual yield (Tozer et al., 2014). The expectation behind pasture replacement on these farms is that the new sward will out-yield the old pasture and that this yield advantage will be sustained for several years so that there is a net positive economic return to the farm business. Often, however, the yield advantage is not sustained (e.g., Hopkins et al. 1990), leading to the conclusion that the new sward has failed to persist. In this case, ‘persistence’ is defined as the persistence of the yield advantage (Parsons et al. 2011). Persistence failure may arise from yield decline of the newly-sown sward over time with no, or minimal, change in population density (genotypic or phenotypic differentiation, Snaydon 1978), or reduction of population density to the point where size/density compensation (Chapman and Lemaire 1993; Matthew et al. 2000) can no longer sustain canopy cover, competitive dominance and herbage accumulation (Parsons et al. 2011).

Persistence failure undermines the profitability of pasture-based livestock production by reducing feed supply (in turn reducing animal production and/or increasing feed costs) and increasing pasture management costs due to more-frequent pasture replacement (Brazendale et al. 2011). Soil cultivation associated with reseeding also increases the risk of nutrient losses to the environment (Betteridge et al. 2011) and depletes soil carbon (Rutledge et al. 2017). Despite these concerns, neither the trajectory of persistence failure nor the causes have been clearly established (Lee et al. 2017).

The second pathway, population density decline, is frequently reported (Tozer et al. 2011a, 2014), especially where environmental conditions are marginal or turn unfavourable for the sown species (Chapman et al. 2011). This pathway is the basis for measures such as ground cover scores to assess sward productivity (Camlin and Stewart 1976) and to compare the persistence of grass cultivars (e.g. in perennial ryegrass; Cashman et al. 2014; O'Donovan et al. 2016). An important implicit assumption is that the rate of perennial grass tiller mortality exceeds the rate of tiller replacement (dominantly through clonal reproduction and site filling rates, Davies 1976) such that the population of perennial grass tillers cannot be sustained and herbage production declines (Camlin and Stewart 1978).

Identifying the causes and effects of density decline is complicated by the multitude of factors, and their interactions, that are involved in tiller mortality and/or tiller initiation (Tozer et al. 2017). Most of these factors are highly variable in space and time, posing further challenges for the design and interpretation of empirical field studies investigating the critical processes.

A complementary approach to understanding the causes of low persistence is process-based computer modelling. The majority of grass pasture models (e.g. Thornley and Cannell 1997; Li et al. 2011) focus on simulating the physiological processes driving canopy development, light interception and net herbage production, and do not include simulation of tiller population dynamics that are relevant for understanding persistence (Höglind et al. 2001). The BASic GRAssland model (BASGRA) is one of the few to explicitly include sward population dynamics. Originally called LINGRA, and developed in the Netherlands for perennial ryegrass (Schapendonk et al. 1998), later evolution was based in Norway (Höglind et al. 2001, 2016), focused on timothy (*Phleum pratense* L.) (Höglind et al. 2001), and extended the model to simulate multiple years (Höglind et al. 2016). Applications of the model have included production of perennial ryegrass under climate change (Rodriguez et al., 1999), leaf and tiller population dynamics in timothy (Höglind et al. 2001; Van Oijen et al. 2005), factors affecting overwintering survival of timothy in Nordic countries (Höglind et al. 2016), and growth of timothy and false oat-grass (*Arrhenatherum elatius* L.) in different climates (Hjelkrem et al. 2017). Use of the model to analyse causes of perennial ryegrass persistence failure in long term data sets, and identification of potential plant breeding or management solutions, represents a novel and ambitious extension to application of the model.

The objective of the current study, therefore, was to develop the capability of the BASGRA model to simulate primary production and tiller population dynamics in perennial ryegrass-based dairy pastures. In order to represent environments imposing contrasting levels of growth stresses on the grass populations, the model was calibrated to observations from dryland warm-temperate and irrigated cool-temperate regions of New Zealand (Lee et al. 2018). The higher-level objective was to develop a tool which could be used to propose management interventions and plant breeding objectives to mitigate against population density decline, based on underlying eco-physiological processes operating at the individual tiller and population levels.

2 Materials and Methods

2.1 Model History

BASGRA is a computer model for simulating grassland plant physiology, morphology and yield. The first version of the model was called LINGRA and was developed in Wageningen by Schapendonk and colleagues (Bouman et al. 1996; Schapendonk et al. 1998). LINGRA simulated only the growing season in mid-high latitudes of the northern hemisphere. To enable analysis of climate change impacts, the effects of CO_2 and temperature on the light-use efficiency of the sward were included (Rodriguez et al. 1999). Most of the further development of the model took place in Norway at Planteforsk, Saerheim (now NIBIO). Whereas the Wageningen version of the model was mainly used for perennial ryegrass, the model was changed in Norway to allow simulation of timothy. For that purpose, tillering was simulated in greater detail, distinguishing elongating from non-elongating tillers (Höglind et al. 2001; Van Oijen et al. 2005). Algorithms for winter processes were developed by Thorsen and colleagues (Thorsen et al. 2010; Thorsen & Höglind 2010). More recently, the model code was translated into FORTRAN, and the 'summer' and 'winter' processes were linked together, producing the year-round model now called BASGRA (Höglind et al. 2016). Model set up, calibration and analysis is performed in R (R Core Team 2014). The version described in this paper, BASGRA_NZ, is based on the 2014 version of BASGRA.

2.2 Model Development

The 2014 version of BASGRA simulates many processes, including soil water stress, carbon assimilation, allocation, and reserves, leaf area expansion, shading effects on tiller birth and death, phenological development, photoperiod effects on reproduction, and cutting. It also includes comprehensive treatment of snow and ice effects, although these were not needed in the current study.

Several modifications and developments were made to the model to represent grazed perennial ryegrass pastures in New Zealand better. Model modifications included refinement of the soil water and root growth sub-models. This defined an effective soil water content which linked plant water stress to root depth and mass. New model functionality included a vernalisation sub-model (based on the STICS model, Brisson et al. 2008), a basal area sub-model, a root depth sub-model, leaf and tiller death due to drought, a grazing sub-model, and a litter disappearance sub-model (based on Woodward 2001). The new sub-models were developed as simple response equations, in keeping with the design of BASGRA where sward structure and processes are represented on a daily and area-average basis to match the resolution of field data collected in long term pasture studies.

The following sections describe the new model logic that was developed for the current study. Model equations are presented as difference equations, as is typical in computer simulation models such as this one.

2.2.1 Vernalisation

Vernalisation of ryegrass tillers requires extended exposure to cold through winter, after which reproductive development is possible. Vernalisation was handled simply in previous versions of BASGRA (Höglind et al. 2016) since it is not an important process in timothy.

In the current model (BASGRA_NZ), the accumulation of "cold days" (VERND, d) is calculated from average daily soil surface temperature (TSURF, $^{\circ}$C) following the approach of Brisson et al. (2008), as

$$\mathrm{VERND}(t+1) = \mathrm{VERND}(t) + \max(0.0, 1.0 - ((\mathrm{TSURF}(t) - \mathrm{TVERN}) / 7.5) ** 2)$$

where TVERN ($^{\circ}$C) is the calibrated optimal vernalisation temperature (around 5 $^{\circ}$C) and ** is the power operator in FORTRAN. VERND is scaled between parameters representing minimum and full vernalisation (TVERNDMN and TVERND respectively) to give the cumulative vernalisation by day t as,

$$CVERN(t+1) = \max(0.0, (VERND(t+1) - TVERNDMN)/(TVERND - TVERNDMN))$$

The daily change in the proportion of vegetative tillers that are vernalised (VERN, till $till^{-1}$) is then calculated as,

$$VERN(t+1) = \min(1.0, VERN(t) + CVERN(t+1) - CVERN(t) - VERN(t) * GTILV(t) / TILV(t+1))$$

where TILV(t+1) is the number of vegetative tillers at the end of day t and GTILV(t) is the number of new vegetative tillers produced on day t. This formulation allows VERN to decline during the reproductive season as new, unvernalised vegetative tillers are formed. The equation is not strictly correct as it allows vernalisation of all tillers prior to CVERN reaching 1, even those that are very young, but nevertheless works well for our purpose.

2.2.2 Basal Area

The BASGRA model is designed to simulate grass monocultures. In our study, ryegrass was planted as a mixture with white clover, and invasive weeds were also important at our dryland sites, so that the ryegrass fraction was sometimes quite low, particularly in summer. To account for the effects of other species in a simple way, the area occupied by ryegrass (BASAL, $m^2\ m^{-2}$) was included as an additional model variable. The non-ryegrass area (1 – BASAL) was assumed to be occupied by bare soil and/or other species, and to have the same soil water content as the area under ryegrass. Ryegrass basal area was used to scale several plant processes that were density-dependent, particularly light capture, and rooting depth. The evolution of basal area was modelled in a notional way, as a moving-average response to leaf area index (LAI, $m^2\ m^{-2}$),

$$BASAL(t+1) = BASAL(t) * (1 - ABASAL) + \min(1.0, LAI(t+1) / KBASAL) * ABASAL$$

where the parameter KBASAL ($m^2\ m^{-2}$) represents the LAI at canopy closure and ABASAL is a moving average smoothing parameter. The conceptual model is that a "steady state" basal area is associated with a given LAI (i.e. min(1.0, LAI / KBASAL)) and the actual basal area will move towards this relatively slowly (with responsiveness controlled by ABASAL). This allowed the ryegrass basal area to shrink or expand as tiller numbers declined or increased.

2.2.3 Root Depth and Soil Water

Previous versions of BASGRA assumed that root depth (ROOTD, m) could only increase through time to a maximum (ROOTDM, m). Root depth was also not linked to root mass (CRT, gC m^{-2}). In the current model, root depth was linked to root mass as,

$$\mathrm{ROOTD}(t) = \mathrm{ROOTDM} * \mathrm{CRT}(t)/\mathrm{BASAL}(t) \,/\, (\mathrm{CRT}(t)/\mathrm{BASAL}(t) + \mathrm{KCRT})$$

where KCRT (gC m^{-2}) is a calibrated curvature parameter. ROOTD was then used to relate plant effective soil water content (WCL, -) to actual soil water content (WCLM, -), as,

$$\mathrm{WCL}(t) = \mathrm{WCAD} + (\mathrm{WCLM}(t) - \mathrm{WCAD}) * ((\mathrm{ROOTD}(t) - \mathrm{FDEPTH}) \,/\, (\mathrm{ROOTDM} - \mathrm{FDEPTH}))$$

where FDEPTH is the depth of frozen soil (m) (always zero in our study) and WCAD is the water content of air dry soil. A rapidly wetted soil surface layer (WALS, mm) was also added to the calculation of WCLM, as recommended by Woodward et al. (2001), to represent better both soil moisture and pasture response following rainfall in otherwise dry periods.

2.2.4 Leaf and Tiller Death

Previous applications of BASGRA considered only mild water stress (only affecting evapotranspiration, tillering, photosynthesis and growth), but not severe water stress (which would additionally affect tiller and leaf survival). Since the study sites used for model calibration (Lee et al. 2018) experienced severe droughts on several occasions, relative leaf and tiller death rate due to water stress (RDRW, d^{-1}) was introduced into the model as,

$$\mathrm{RDRW}(t) = \max(0, \mathrm{RDRWMAX} * (1 – \mathrm{TRANRF}(t) \,/\, \mathrm{TRANRFCR}))$$

where RDRWMAX (d^{-1}) is the maximum death rate and TRANRFCR (-) is the critical value of TRANRF (the transpiration realisation factor) below which leaf and tiller death due to drought occurs.

2.2.5 Grazing

The severity of defoliation due to grazing by dairy cows varies seasonally and with grazing management. The defoliation sub-model was modified to use user-supplied leaf defoliation fraction (HARVFR, -) on each grazing day. Defoliation of reproductive stem was then calculated as,

$$\mathrm{HARVFRST}(t) = \mathrm{HARVFR}(t) ** (1 - \mathrm{HAGERE})$$

where HAGERE (-) is a calibrated parameter that expresses the increased fraction of stem removed. The power operator ensures that HARVFRST remains between zero and one. Removal of dead material was similarly calculated as HARVFR(t) * HARVFRD, where HARVFRD (-) is the relative fraction of dead material harvested. A collateral death rate due to harvest (RDRHARV, d^{-1}) was also calculated, as

RDRHARV(t) = RDRHARVMAX * HARVFR(t)

where RDRHARVMAX (d^{-1}) is a calibrated maximum death rate parameter, and applied to leaf area index (LAI), leaf mass (CLV), carbon reserve mass (CRES), vegetative tillers (TILV) and generative tillers (TILG1) at each grazing.

In addition to these changes, the model logic was modified to consider harvesting to occur instantaneously at the beginning of each day (the method of "operator splitting"). This allowed the plant process models to be simplified, since growth-harvest interaction terms could be removed.

Secondary effects of defoliation events were not modelled, such as changes in root mass, root leakage and root sloughing which can impact root depth and water usage. The resulting change in rhizosphere chemistry (exudates fueling microbial and invertebrate decomposers) may, in turn, influence litter decomposition (Medina-Roldán and Bardgett, 2011).

2.2.6 Litter Disappearance

Dead material (litter) can comprise a significant portion of temperate summer pastures (e.g. Woodward 2001), and so is commonly included in measurements of pasture mass and composition. However, modelling the accumulation and turnover of dead material has not previously been a focus of BASGRA. A litter disappearance sub-model was added following the approach of Woodward (2001). This calculates the relative litter disappearance rate (RDLVD, d^{-1}) as the sum of microbial decomposition (DECOMP, d^{-1}) and removal (ingestion, burial) by earthworms (WORMS, d^{-1}), both calculated as soil water- and temperature-dependent rates, i.e.,

RDLVD(t) = DECOMP(t) + WORMS(t)

The rate of microbial decomposition was calculated following Andrén et al. (Andrén and Paustian, 1987; Andrén *et al.*, 1989, 1992, 1993), as

DECOMP(t) = DELD * DTEMP(t) * DWATER(t)

DTEMP(t) = if(DAVTMP(t) > 0, 2.0 ** ((DAVTMP(t) - 20.0) / 10.0), 0)

DWATER(t) = if(RAIN(t) > 0, 1.0, max(0.0, min(1.0, log(-7580.0 / PSIS(t)) / log(-7580.0 / (-10.0)))))

where DAVTMP (°C) is the daily average temperature, RAIN (mm d^{-1}) is the daily rainfall, PSIS (kPa) is the soil water tension, and DELD (d^{-1}) is a calibrated parameter. Based on the data of Wardle et al. (1994), DELD is expected to be around 0.0148 d^{-1} for naturally senescent perennial ryegrass–white clover litter. Soil water tension PSIS (kPa) was calculated from soil moisture content WCLM relative to wilting point WCWP and field capacity WCFC using the equations in Woodward et al. (2001), as

PSIS(t) = -PSIA * (WCLM(t) ** (-PSIB))

PSIA = 20.0 / (WCFC ** (-PSIB))

PSIB = -log(1500.0 / 20.0) / log(WCWP / WCFC)

The rate of litter removal by earthworms (WORMS) was assumed to be the product of the biomass of earthworms near the soil surface (EBIOMASS g m^{-2}) (Baker et al., 1992) and temperature and moisture dependent factors, as described in Daniel (1991):

WORMS(t) = DELE * EBIOMASS(t) * CT(t) * CP(t)

EBIOMASS(t) = max(0.0, min(1.0, 5.0 * WCLM(t) / BD - 1.0)) * EBIOMAX

CT(t) = if(DAVTMP(t) < 20, 0.515 * (20.0 - DAVTMP(t)) ** 1.84 * exp(-0.297 * (20.0 - DAVTMP(t))) / 2.345, 0.0)

CP(t) = if(PSIS(t) < -12.3, 0.549 * (-PSIS(t)) ** 0.793 * exp(0.113 * PSIS(t)), 1.0)

Baker et al. (1992) observed a peak number of *Aporrectodea* species earthworms near the soil surface of around 655 m^{-2} in South Australia. Based on the data of Martin (1978) and Fraser *et al*. (1996), numbers in New Zealand were assumed to be similar, with an average biomass of 0.2 g $worm^{-1}$ (i.e., 131 g m^{-2}). Based on Daniel (1991), the calibrated parameter DELE is expected to be around 0.0005 m^2 g^{-1} d^{-1}, which corresponds to 0.066 d^{-2} when multiplied by worm biomass.

With these changes, the model was able to simulate the dynamics of ryegrass physiology and morphology observed in a long-term grazing trial.

2.3 Trial Overview

The Seeding Rate Trial (see Lee et al. 2018 for details) was designed to examine the effects of seeding rate (6, 12, 18, 24 or 30 kg ha^{-1}) on the persistence of perennial ryegrass tiller populations of four cultivars (Grasslands Nui, Commando, Alto and Halo) when mixed with white clover in grazed dairy pastures in New Zealand. As described by Lee et al. (2018), the experimental sites (Fig. 1) were located at Fonterra's Jordan Valley Farm in Northland (-35.612, 174.262; 96 m.a.s.l.), DairyNZ's Scott Farm in the Waikato (-37.772, 175.378; 40 m.a.s.l.) and the Lincoln University Research Dairy Farm in Canterbury (-43.638, 172.462; 10 m.a.s.l.). The soil types at the three sites, respectively, were Wairua clay, Matangi silt loam, and Wakanui silt loam over a mottled sandy loam phase. These are classified as an Orthic Gley, a Typic Sandy Gley, and a Mottled Immature Pallic soil, respectively (Hewitt, 1998). Both the Northland and Waikato sites were dryland while the Canterbury site was irrigated (as standard for dairy farms in each region), with irrigation water applications of 232, 287, 194, 400 and 430 mm/year during years one to five after sowing. Nitrogen (N) fertiliser was also applied as urea at all sites, spread over two to nine applications per year. This resulted in total annual applications of 105, 146 and 238 kg N/ha/year at the Northland, Waikato and Canterbury sites, respectively, averaged over the five years. Each seeding rate by cultivar combination was replicated 5 times (blocks) at each site, and the trial ran for five years from 2011 to 2016. Plots were rotationally grazed by dairy cows at all sites, when mean pre-graze pasture mass reached 2500–3500 kg DM/ha above ground level. All plots at a site were grazed at the same time. This resulted in between 9 and 12 harvests per year. Site environmental inputs over the five years of the trial (2011-2016) plus the additional year simulated (2016-2017) are summarised in Table I.

Although the results of the trial indicated that persistence differences were not related to seeding rate or cultivar (Lee et al. 2018), persistence differences were observed between sites, making this a useful data set for the purpose of studying the mechanisms leading to decline of ryegrass tiller population. In the current study we focused on the data from the Alto cultivar sown at 18 kg ha^{-1}. Alto is typical of modern genotypes, and the 18 kg ha^{-1} treatment was most intensively sampled, and sampled for a longer time period in three blocks at each site.

(Figure 1 near here)

(Table I near here)

2.4 Data Collected

Beginning in 2011, a wide variety of measurements were collected regularly at each site, including climate, soil, plant, endophyte, and invertebrate analysis (see Lee et al. 2018 for details). Herbage above-ground biomass on the day before grazing (kg DM ha^{-1}) was measured by cutting to between 4.0 and 5.5 cm above ground level. Separate herbage samples were taken at the same time (cut above 4.0 cm) and analysed for botanical composition (fraction by dry weight of perennial ryegrass leaf, perennial ryegrass stem, annual ryegrass, other grass, white clover, weed, and dead material). Perennial ryegrass tiller density (tillers m^{-2}) was counted in randomly placed quadrats in spring and in summer of the 2011-2012 season, and once every autumn thereafter. In addition, calibrated rising plate meter estimates were made of pre-grazing and post-grazing herbage mass; this data was used to estimate the proportion of herbage removed at each grazing and the herbage mass below the 4.0 cm sampling height.

Although soil nutrient status was assessed for each replicate, and supplemented with applications of fertiliser where necessary (Lee et al., 2018), soil water content was not routinely measured as part of the trial. Soil water content was measured on five occasions during January-April 2017 at the Waikato site. Soil water data for Northland from September 2015 onwards were obtained from the NIWA Cliflo weather database (Agent 40980, -35.744, 174.329; 12 m.a.s.l.). The range of this data was very narrow (24.0 to 34.4%), which may be explained by the higher clay content of these soils, or may indicate a problem with the data. At Canterbury, soil water content was measured from May 2014 onwards as part of a separate trial that received the same irrigation.

Full plant botanical composition data from a screen-house trial by Tozer et al. (2017) were used to estimate the proportion of ryegrass leaf (including pseudostem), stem and dead material below cutting height to calculate the mass of each fraction to ground level. Data from McNally et al. (2014) were used to estimate the approximate mass of root relative to shoot, and give root mass values within the range of 2000-4000 kg DM ha^{-1} observed by Matthew (1996). Mass fractions were converted to carbon equivalents (gC m^{-2}) as described in BASGRA (2014) for comparison with the model state variables (see below). The fraction of ryegrass relative to other species in the green portion of the herbage samples was taken as a proxy for basal area for the purpose of model calibration. These "auxiliary" data for root mass and basal area are very helpful for model calibration but are highly uncertain due to being based on simplistic assumptions. This uncertainty is incorporated by attaching a relatively large standard error to these "data". It would be valuable to obtain direct measurements of these variables in future experiments, perhaps quarterly.

Assumed standard errors were 30 gC m^{-2} for ryegrass leaf, 10 gC m^{-2} for ryegrass stem, 20 gC m^{-2} for dead ryegrass leaf and stem, 60 gC m^{-2} for ryegrass root, 2000 m^{-2} for ryegrass tiller density, 20% for ryegrass basal area, and 10% for soil moisture. The standard errors represent uncertainty in the measurement of the observations and the model inputs, as well as model structural uncertainty, and therefore cannot be objectively estimated. The suitability of the assumed standard errors is checked *a posteriori* by examining the scatter of the residuals.

2.5 Bayesian Calibration

The BASGRA model code includes a Markov Chain Monte Carlo (MCMC) algorithm for Bayesian parameter estimation. The MCMC algorithm stochastically searches the model parameter space to identify the locus of parameter sets that is consistent with the calibration data and the given prior parameter distributions. By incorporating uncertainty, Bayesian parameter estimation avoids overfitting to the calibration data, and provides an estimate of the uncertainty of the inferred parameter values and of any subsequent model predictions. In the current project, the MCMC algorithm was upgraded to the popular $DREAM_{ZS}$ algorithm of ter Braak and Vrugt (2008), as implemented in the BayesianTools 0.1.5 package of Hartig et al. (2018) in R. This algorithm is highly efficient and the package also includes several useful diagnostic tools.

In Bayesian calibration, the searched parameter space is preconditioned by defining the prior distribution of the parameters. Prior parameter ranges were defined as independent beta distributions, specified by minimum, maximum and mode values, as well as a shape parameter. These were based on literature reviews of ryegrass studies (see Schapendonk et al., 1998; Rodriguez et al., 1999).

The likelihood of the observed data for a given parameter set was calculated using the probability distribution suggested by Sivia and Skilling (2006), which is much less sensitive to outliers than a Gaussian distribution, and assuming independent errors (c.f. Schoups and Vrugt 2010).

The model was calibrated against the basal area, leaf C, stem C, dead C, root C, tiller density, and soil water data from the Northland, Waikato and Canterbury sites simultaneously. Plant parameter values used (e.g. Rubisco content) were the same across all sites, whereas soil parameter values (e.g. soil bulk density) were varied between sites. The prior distributions of the calibration parameters are shown in Fig. 4, below. Latitude, weather, irrigation and grazing information (proportion of leaf harvested) were provided as site-specific inputs.

Using BayesianTools, three independent $DREAM_{ZS}$ chains were run in parallel (each containing three internal chains) in increments of 10000 samples, until the Gelman-Rubin MCMC convergence statistic (Gelman and Rubin 1992) was below 1.2 for all parameters. The last 10000 samples from each of the 9 chains were then combined and taken as the posterior distribution. The *maximum a posteriori* (MAP) parameter set was also recorded, which is the parameter set corresponding to the mode of the posterior, and can be thought of as the parameter set giving the best fit to the data and the prior.

Convergence of the calibration required 40000 iterations on each chain, with approximately 583000 runs of BASGRA in total. Using 3 parallel cores on a desktop PC (Intel Core i7 at 3.4 GHz), this took 12.2 minutes in real time.

(Table II near here)

2.6 Scenario Simulations

Following calibration, the model was used to explore options for improving pasture persistence at the Northland and Waikato sites. This was done by predicting pasture dynamics at these two sites under new, hypothetical management scenarios, based on parameter sets drawn from the posterior parameter distribution. The design of these scenarios was guided by the results of the model calibration phase, and so will be described later in this article (following the calibration results).

3 Results

3.1 Calibration to Data

The result of Bayesian calibration is the posterior distribution of model parameter sets and associated model predictions that is consistent with the sample data. In theory, the data-model residuals should then obey the assumed standard error distribution; otherwise this could indicate that the model is inappropriate. Fig. 2 presents the calibrated model predictions against the data for the three sites. The dark and light shading indicate the 90% credible interval of the model predictions due to parameter uncertainty and total uncertainty respectively. Total uncertainty includes uncertainty about error in the model inputs, model structure, and data measurement. The observations (shown as dots) are expected to lie within this band 90% of the time, in a random fashion (e.g., without autocorrelation).

To check this, Fig. 3 shows the scatter of the observed data relative to the median model predictions and uncertainty bands at the time of sampling. These confirm that the residuals lie within the uncertainty bands approximately 90% of the time.

(Figure 2 near here)

The calibrated model predictions generally matched the sample data well. Basal area predictions followed the auxiliary data values and mimicked the declines in ryegrass fraction observed at Northland and Waikato, while ryegrass fraction remained high at the irrigated Canterbury site.

Ryegrass leaf, stem and dead mass were also matched reasonably well across the sites. Because these data were based on botanical samples collected when pasture mass was at its highest, prior to grazing. These data points appear to be biased towards the higher value range of the model uncertainty bands in Fig. 2. To check for model bias the observed data were plotted against the median posterior model prediction at the time of sampling. The resulting visualisation (Fig. 3) shows that the predictions are not greatly biased. The exception to this could be the predictions of dead material which appear to under-predict dead mass at Northland. This may be due to the Northland weather and soil moisture data being inappropriate, as these were from a different site. We have already noted the unusually narrow range of the Northland soil moisture data (see Fig. 2). This highlights the need for site-specific weather, soil type, and soil moisture data when modelling pasture, which are not always needed (and hence not collected) for empirical field trials.

The auxiliary root data were also well matched. While these data are not of direct interest, root data provides a mass balance check for assimilate partitioning within the model, and so greatly assists with achieving a realistic model calibration.

Tiller density predictions were strongly seasonal, with net tiller production in the winter followed by net tiller death in the summer. Predictions generally matched the data very well, although the seasonal pattern was not able to be confirmed, since observations were only made once a year after the first trial year. The model only simulates the effects of temperature, moisture and shading on tiller numbers; factors such as invasive species, disease, insect pests were not modelled, but are known to be significantly different between sites (Lee et al., 2018). Again, more frequent (e.g. quarterly) tiller density data would have been highly valuable, especially considering the plant population focus of the experimental data. Nevertheless, the model successfully differentiated the low, declining tiller number at the Northland and Waikato dryland sites (probably associated with a loss in ryegrass basal area), from the consistently high tiller density at the irrigated Canterbury site. This suggests that differences in tiller populations between sites were due to environmental drivers, given that the plant "genetic" parameters were identical across all three sites. Potential drivers could be weather, irrigation, and grazing inputs, that were different across the sites, and calibrated site-specific soil parameters.

(Figure 3 near here)

3.2 Inferred Parameter Values

The direct outcome of calibration is the locus of model parameter values that are consistent with the observed data (the "posterior distribution"). The prior parameter distribution functions as a preliminary "observation" of the parameters, and inference (calibration) based on the observed sample data then provides additional indirect information on the parameter distribution. Comparison of the prior and posterior parameter distribution shows which parameter values (or combinations) can be inferred from the observation data and which cannot.

A list of calibrated parameters is given in Table II, and their marginal prior and posterior distributions are shown in Fig. 4. The figure also indicates the parameter values corresponding to the *maximum a priori* (MAP) parameter set. In the context of the Bayesian calibration, the MAP is the "most likely" parameter set (i.e., the mode of the posterior distribution). The MAP parameters tend to be relatively sensitive to the priors, the sample data, and the model, especially when the posterior is flat or multi-modal, whereas the full posterior distribution tends to be much more robust. For this reason, it is preferable to consider the median and credible intervals of the posterior, as shown in Fig. 2 and Fig. 5.

Fig. 4 does not show the correlations between the parameters. Although the MCMC procedure yields the full joint posterior probability distribution of the parameters, and parameter correlations were checked for convergence, comprehensive analysis of parameter correlations is not reported here.

(Figure 4 near here)

The most interesting parameters in Fig. 4 are those with a narrow posterior distribution, such as FWCFC at all three sites (the relative saturation of soil at field capacity), KBASAL (the LAI above which basal area tends to 1), and RUBISC (the rubisco content of the upper leaves). This means that considering the observation data allowed those parameters' values to be identified to within a narrow range. For example, the KBASAL parameter was determined as being around 3.5, and the RUBISC parameter (associated with photosynthesis) was identified as having a value between 2 and 4.

Previously Rodriguez et al. (1999) suggested values for RUBISC = 2.7, YG = 0.64, and TCRES = 2, which closely match the median values inferred from our data. Conversely, their suggested values of PHY = 100 and FSLAMIN = 0.5 were both slightly lower than the median values inferred from our data, although within the range of uncertainty. The earlier paper of Schapendonk et al. (1998) had suggested values of LAICR = 4.0, KLAI = 0.6 and FSMAX = 0.693, which were respectively 10% higher, 25% lower and 20% higher than the median values in our study, but generally within the range of uncertainty (KLAI = 0.6 was on the edge).

Parameters with similar prior and posterior distributions were not informed by the data, e.g., COCRESMX (the maximum concentration of carbon reserves in above-ground biomass), DAYLB (the daylength at which conversion of vegetative tillers to generative starts to increase) and TRANCO (the sensitivity of restricted transpiration to potential transpiration). This means that the model predictions of the observed variables are insensitive to those parameters. Accurate estimates of these parameters require additional information, probably measurement of variables not included in the calibration data. For example, van Oijen and Hoglind (2016) included soluble carbon reserves (RES), total herbage dry mass (DM), leaf extension rate of generative tiller (LERG), number of leaves on generative tiller (NELLVG), leaf appearance rate (RLEAF), specific leaf area (SLA), and fraction of generative tillers (FRTILG) in their calibration of BASGRA. This allowed them to accurately infer values for COCRESMX and DAYLB for one of their cultivars (cv. Grindstad), although TRANCO remained uncertain.

3.3 Predictions with Uncertainty

The posterior parameter distribution can also be used to generate other model predictions for which we do not have data. The uncertainty in these predictions may be small or large, depending on the related parameters. For example, several other model outputs of interest were predicted in Fig. 5. These were number of elongating tillers, leaf area index, cumulative ryegrass yield (i.e. harvested), soluble carbon reserves, tiller size, and proportion of tillers vernalised. The fraction of leaf harvested at each grazing (a model input) is also shown for reference. The uncertainty of variables closely associated with the measurements (i.e. Fig. 2) was generally small (e.g. LAI), whereas the uncertainty of variables for which there was no direct observation was high (e.g. carbon reserves, vernalisation fraction).

(Figure 5 near here)

Elongating tiller numbers increased going south from Northland to Waikato to Canterbury, in line with the increase in proportion of tillers vernalised. This is explained by the cold winter temperature requirement for vernalisation of ryegrass tillers. Warmer winters at Northland were predicted to result in incomplete vernalisation in most years (Fig. 5). While less stem formation may seem advantageous for increasing summer pasture quality (Litherland et al. 2002), the warmer climate in Northland and Waikato also permits invasion of less desirable grass and broadleaf species (Tozer et al. 2011b), which are not simulated in the model.

Leaf area index remained high at Canterbury, supported by the irrigation and higher tiller density at that site. Leaf area index dropped almost to zero during late summer in drought years at Northland (2013) and Waikato (2013, 2014) and also in later years, primarily due to loss in tiller numbers (Fig. 2) rather than tiller size (Fig. 5). Recovery of tiller numbers was slow in drought years (e.g. Northland 2013), consequently delaying recovery of leaf mass compared with non-drought years (e.g. Northland 2016) (Fig. 2). This explains why pasture models that don't consider tiller dynamics may tend to overestimate growth recovery after drought (e.g., Li et al., 2011; Hurtado-Uria et al., 2010, 2013).

Interestingly, soluble carbon reserves were often lower at Canterbury compared with the dryland sites. It appears that maintaining high leaf area during summer presents higher demands for assimilate than can be met, causing growth to be limited by photosynthesis at this time.

3.4 Scenario Predictions

As well as allowing deeper analysis of the historical trial data, the calibrated model can be used to simulate hypothetical scenarios or management options, e.g., to mitigate pasture persistence failure. Scenario simulations were carried out to determine which site or management differences could explain the observed poor persistence at Northland and Waikato sites compared with the Canterbury site. Since the model plant parameters were the same across all sites, the main differences were irrigation, grazing management (timing and severity) and climate (particularly temperature). In order to assess the importance of these factors, the Northland and Waikato trials were re-simulated as if they had received the Canterbury water (CW), Canterbury grazing (CG) or Canterbury temperature (CT) inputs: CW includes summer irrigation, CG includes a rest from grazing over the winter period, and CT is several degrees cooler than the other sites.

Fig. 6 and Fig. 7 show the predicted changes in pasture persistence at the Northland and Waikato sites, respectively, under CW, CG or CT. The results were consistent across both sites, with the model predicting that only improved water supply (CW) would translate into improved pasture persistence, i.e., maintained basal area, LAI, yield and tiller numbers. In particular, irrigation prevented drought-related tiller death in summer. Neither a simulated break in winter grazing (CG), nor a reduction in temperature (CT), was predicted to improve persistence.

(Figure 6 near here)

(Figure 7 near here)

4 Discussion

4.1 Causes of Low Persistence

The model successfully simulated the differences in evolution of tiller density and above-ground biomass between the dryland sites at Northland and Waikato and the irrigated site at Canterbury (Fig. 2). At all sites, tiller numbers were predicted to peak in late spring, decline rapidly through summer to a minimum in autumn, and then gradually recover through winter and spring. Although seasonal tiller data were not available to validate this prediction, these patterns generally match those described by Matthew et al. (2000) and Matthew and Sackville-Hamilton (2011), who noted high tiller turnover in summer, followed by rapid growth in autumn to reach peak density in winter.

Tiller losses during the critical summer period can be ascribed to several processes. The elongation and subsequent decapitation of reproductive tillers, for example, was common to all sites. Tiller numbers may also be reduced due to shading when LAI increases in reproductive swards, although this process probably played a minor part in the current study due to frequent grazing.

At the Northland and Waikato sites, significant tiller losses were associated with droughts (Fig. 2). Poirier et al. (2012) found that droughts have a relatively greater impact on grass populations (cocksfoot (*Dactylis glomerata* L.) and tall fescue (*Festuca arundinacea* Schreb.) in their study) compared with heat waves in which water availability is maintained. In the current trial, drought was also associated with secondary increases in invasive plant and pest species (Lee et al. 2018), which may have further contributed to tiller mortality. For example, volunteer weeds or unsown species, including poa (*Poa annua* L.), summer-active C4 annuals (e.g. dallisgrass (*Paspalum dilatatum* Poir.), hairy crabgrass (*Digitaria sanguinalis* L.) and broadleaf species such as dandelion (*Taraxacum officinale* L.), smooth hawksbeard (*Crepis capillaris* L.), narrow-leaved plantain (*Plantago lanceolata* L.) and broad-leaved dock (*Rumex obtusifolius* L.) were present at all sites, particularly the Northland and Waikato sites. Pests, including clover root weevil (*Sitona obsoletus*, formerly S. *lepidus*) and root-knot nematodes (*Meloidogyne* spp.) at Northland, grass grub (*Costelytra zealandica*) and black beetle (*Heteronychus arator*) at Waikato, and clover root weevil (*Sitona obsoletus*) at Canterbury, may also have had a significant impact. Although these secondary stressors are not explicitly represented in the model, their impact is likely to have been incorporated through calibration of the leaf and tiller death parameters RDRWMAX and TRANRFCR (Section 2.2.4).

Regardless of the causes of persistence failure, it is of interest to explore a range of options for mitigating these effects. In the current paper this was done using preliminary scenario simulations substituting the Canterbury site inputs (rainfall plus irrigation, grazing, temperature) into the Northland and Waikato runs, to determine which factor was most beneficial to ryegrass persistence. This , confirmed that irrigation would be most effective in preventing persistence failure at these sites. In contrast, using Canterbury's grazing intensity and frequency was predicted to give no improvements in tiller populations at Northland or Waikato. Applying Canterbury temperatures at Northland and Waikato was also predicted to give no improvement to tiller populations at the drylands sites. This could indicate that breeding perennial ryegrass cultivars for increased temperature tolerance would similarly fail to prevent persistence failure.

4.2 Value of Modelling

Perennial plant communities are complex, costly to measure and difficult to model. Even when planted as monocultures or bi-cultures, plant populations and species composition may rapidly change in response to weather, defoliation, manure, fertilisation, irrigation, pests and diseases. Additionally, the research sites chosen for study may differ in multiple aspects (weather, soil, topography, management), which are themselves not easy to characterise. This means that long-term, multi-site data sets such as used here are relatively rare, limited to research settings, and also very rich. They are also quite difficult to work with: all these differences are reasons to use process-based modelling.

The BASGRA model was designed to simulate the dynamics of grass monocultures (perennial ryegrass and timothy, in particular) over successive years and under repeated defoliation. Soil and plant processes are represented at levels of detail (daily time step, spatial averages) that align with commonly available weather information and pasture sampling methods. Even at this level of detail many plant processes are poorly quantified. Photosynthesis, for example, has been thoroughly studied and is able to be represented in some detail (van Oijen et al. 2004). In contrast, there is little scientific information available with which to model shrinkage of basal area in response to stress, and so only a crude sub-model is presently possible, whose parameters must be calibrated.

The value of a process-based model, even if highly simplified, lies in its ability to encapsulate a broad range scientific information within its equations and parameters, beyond what is measured within each experiment. Calibrating the model with data from the experiment (Fig. 2), in principle then allows the observed data to be used to inform the model parameters, reducing their uncertainty (Fig. 4). The model can then be used to make predictions of variables or scenarios which have not been measured, and to explore hypotheses for improved understanding and management. Despite the richness of the current data set, it has weaknesses with respect to the low frequency of tiller density information, lack of information on the areal coverage of ryegrass relative to other plant species, limited detailed information on soil moisture, and dates and amount of irrigation and fertilisation. Root data were also not available. Thus, crude assumptions were made to estimate levels of plant matter below the sampling height and below the ground to complete the plant tissue mass balance.

Fortunately, compared with non-Bayesian least-squares fitting approaches, the MCMC approach used here is relatively robust to the accuracy of the data; by defining an expected probability distribution for the residuals it is less prone to overfitting (a problem where the model parameters are overly determined by the particular calibration data set). This comes at a computational cost however, and MCMC calibration is only practical for fast models such as BASGRA.

5 Conclusion

Comparison of the calibrated model with the experimental data provided a basis for exploring the mechanisms responsible for observed differences in the longevity of tiller populations. The results indicated that the poor persistence of ryegrass populations in two dryland North Island sites, Northland and Waikato, was due to increased tiller mortality in response to drought, possibly including associated effects such as invasive weed and pest species. Preliminary scenario simulations suggested that irrigation would have prevented persistence failure at these sites, but that reducing grazing frequency pressure, or breeding plants for greater temperature tolerance, would be unlikely to be successful in preventing this.

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Conflict of Interest Statement

The authors whose names are listed immediately below certify that they have NO affiliations with or involvement in any organization or entity with any financial interest (such as honoraria; educational grants; participation in speakers' bureaus; membership, employment, consultancies, stock ownership, or other equity interest; and expert testimony or patent-licensing arrangements), or non-financial interest (such as personal or professional relationships, affiliations, knowledge or beliefs) in the subject matter or materials discussed in this manuscript.

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FIGURES

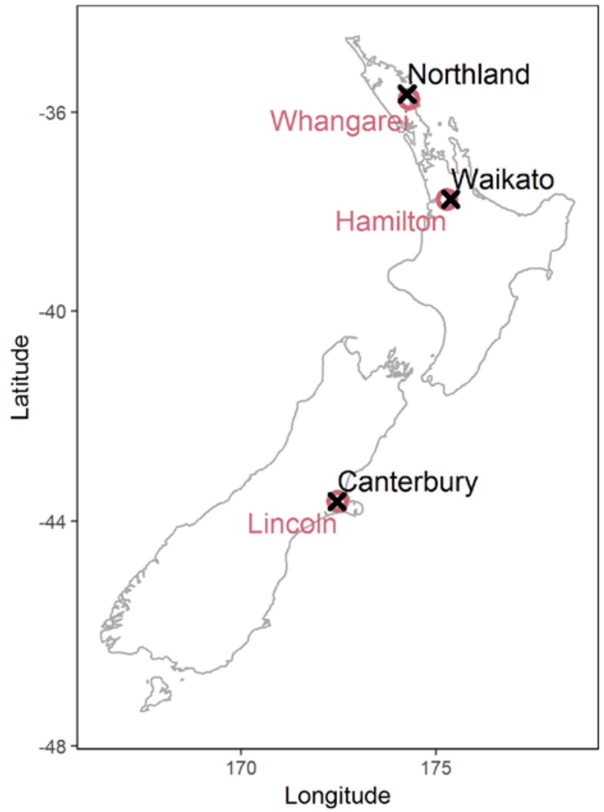
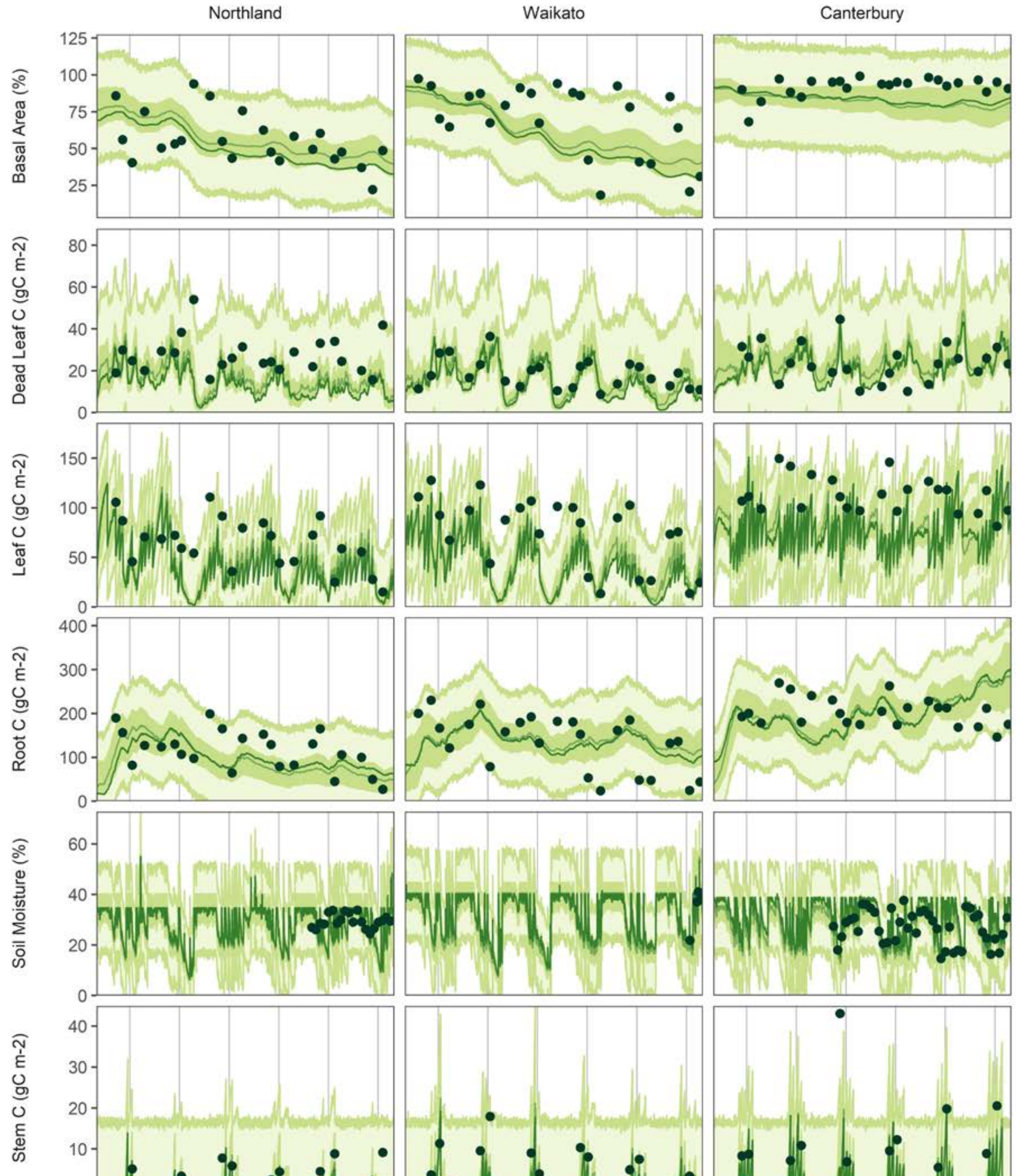


Fig. 1. Trial site locations (crosses) and nearby towns (circles).



Northland
Waikato
Canterbury
Basal Area (%)
Dead Leaf C (gC m-2)
Leaf C (gC m-2)
Root C (gC m-2)
Soil Moisture (%)
Stem C (gC m-2)

Fig. 2. Model predictions compared with calibration data. The 90% credible interval of model predictions are shown as dark and light shaded areas, representing parameter uncertainty and total uncertainty respectively. The median and *maximum a posteriori* (MAP) model predictions are shown as light and dark lines respectively. Observations are shown as dots.

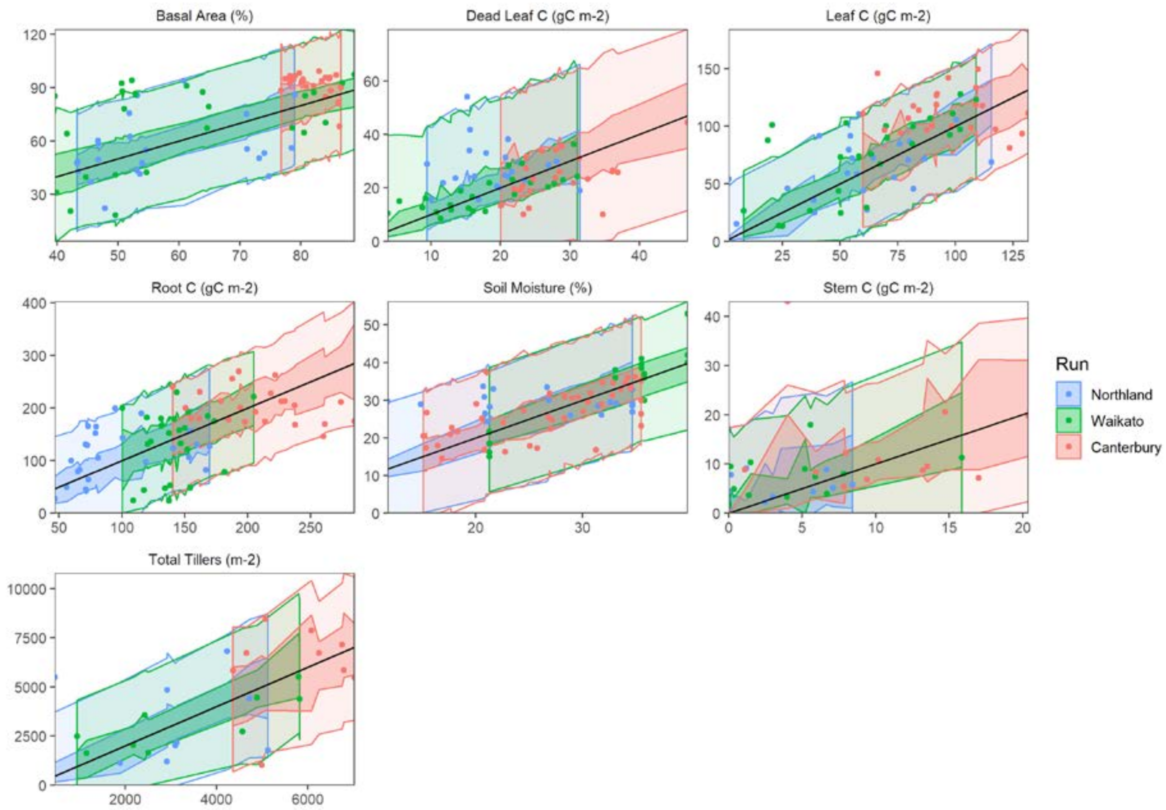


Fig. 3. Scatter of sample data relative to model predictions. The x-axis in each sub-plot is the median model prediction value, and the y-axis shows the sample data values and the model prediction bands (with the median 1:1 line shown in black, and the 90% credible intervals of parameter uncertainty and total uncertainty shown as dark and light shading respectively).

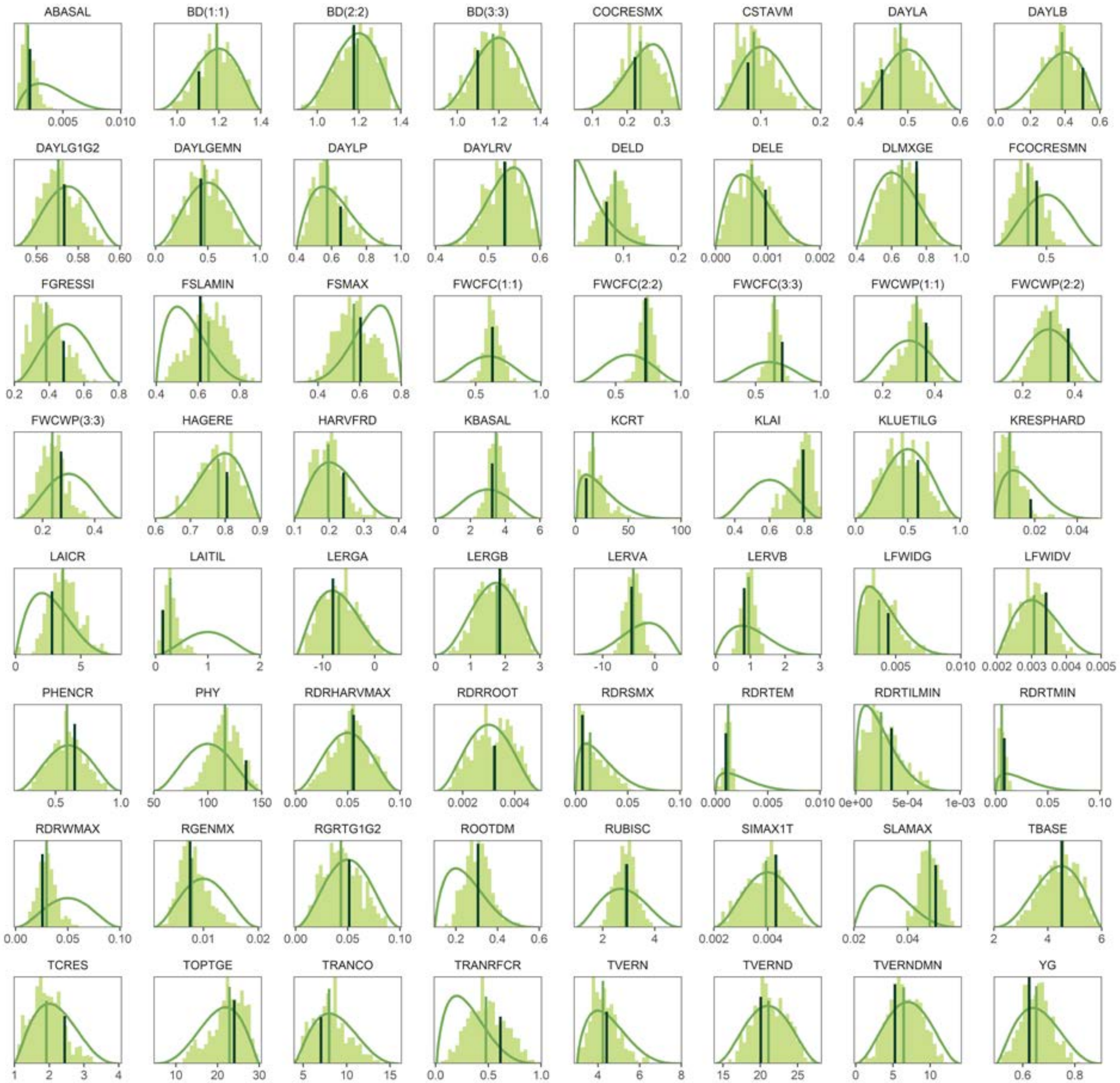
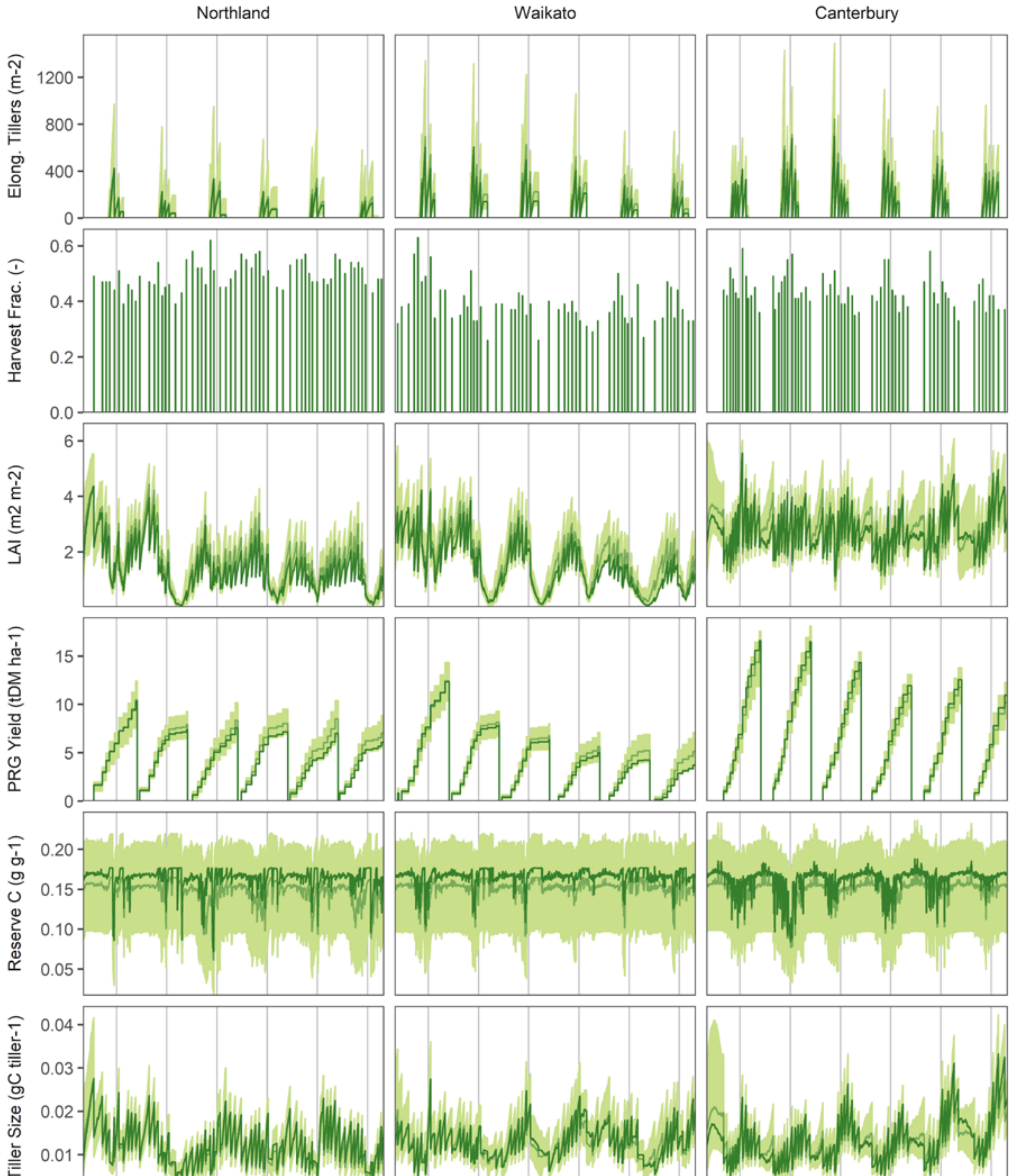

ABASAL
0.005 0.010
BD(1:1)
1.0 1.2 1.4
BD(2:2)
1.0 1.2 1.4
BD(3:3)
1.0 1.2 1.4
COCRESMX
0.1 0.2 0.3
CSTAVM
0.1 0.2
DAYLA
0.4 0.5 0.6
DAYLB
0.0 0.2 0.4 0.6
DAYLG1G2
0.56 0.58 0.60
DAYLGEMN
0.0 0.5 1.0
DAYLP
0.4 0.6 0.8 1.0
DAYLRV
0.4 0.5 0.6
DELD
0.1 0.2
DELE
0.000 0.001 0.002
DLMXGE
0.4 0.6 0.8 1.0
FCOCRESMN
0.5
FGRESSI
0.2 0.4 0.6 0.8
FSLAMIN
0.4 0.6 0.8
FSMAX
0.4 0.6 0.8
FWCFC(1:1)
0.5 1.0
FWCFC(2:2)
0.5 1.0
FWCFC(3:3)
0.5 1.0
FWCWP(1:1)
0.2 0.4
FWCWP(2:2)
0.2 0.4
FWCWP(3:3)
0.2 0.4
HAGERE
0.6 0.7 0.8 0.9
HARVFRD
0.1 0.2 0.3 0.4
KBASAL
0 2 4 6
KCRT
0 50 100
KLAI
0.4 0.6 0.8
KLUETILG
0.0 0.5 1.0
KRESPHARD
0.02 0.04
LAICR
0 5
LAITIL
0 1 2
LERGA
-10 0
LERGB
0 1 2 3
LERVA
-10 0
LERVB
0 1 2 3
LFWIDG
0.005 0.010
LFWIDV
0.002 0.003 0.004 0.005
PHENCR
0.5 1.0
PHY
50 100 150
RDRHARVMAX
0.00 0.05 0.10
RDRROOT
0.002 0.004
RDRSMX
0.00 0.05 0.10
RDRTEM
0.000 0.005 0.010
RDRTILMIN
0e+00 5e-04 1e-03
RDRTMIN
0.00 0.05 0.10
RDRWMAX
0.00 0.05 0.10
RGENMX
0.01 0.02
RGRTG1G2
0.00 0.05 0.10
ROOTDM
0.2 0.4 0.6
RUBISC
2 4
SIMAX1T
0.002 0.004
SLAMAX
0.02 0.04
TBASE
2 4 6
TCRES
1 2 3 4
TOPTGE
10 20 30
TRANCO
5 10 15
TRANRFCR
0.0 0.5 1.0
TVERN
4 6 8
TVERND
15 20 25
TVERNDMN
0 5 10
YG
0.6 0.8

Fig. 4. Calibrated parameter values (prior distributions as solid curves, posterior distributions as shaded histograms, and median and *maximum a posteriori* (MAP) values as light and dark line segments). Brackets, e.g. "(1:1)", indicate a parameter value for a particular site (1 = Northland, 2 = Waikato, 3 = Canterbury). Parameter descriptions are given in Table II. Initial condition parameters are not shown.



Northland
Waikato
Canterbury
Elong. Tillers (m-2)
Harvest Frac. (-)
LAI (m2 m-2)
PRG Yield (tDM ha-1)
Reserve C (g g-1)
Tiller Size (gC tiller-1)

Fig. 5. Model predictions of additional outputs. The 90% credible interval of model predictions are shown as dark and light shaded areas, representing parameter uncertainty and total uncertainty respectively. The median and *maximum a posteriori* (MAP) model predictions are shown as light and dark lines respectively.

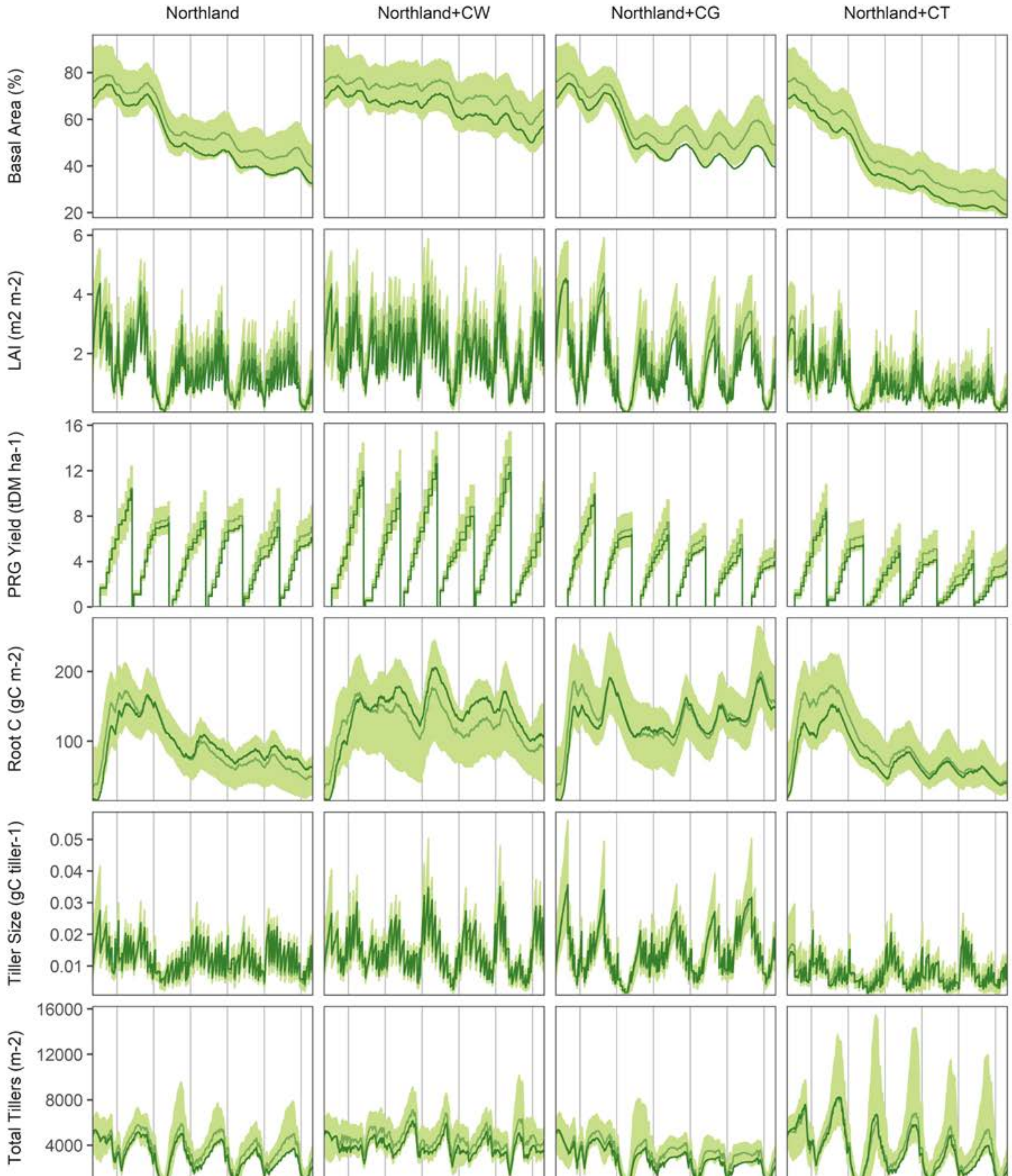
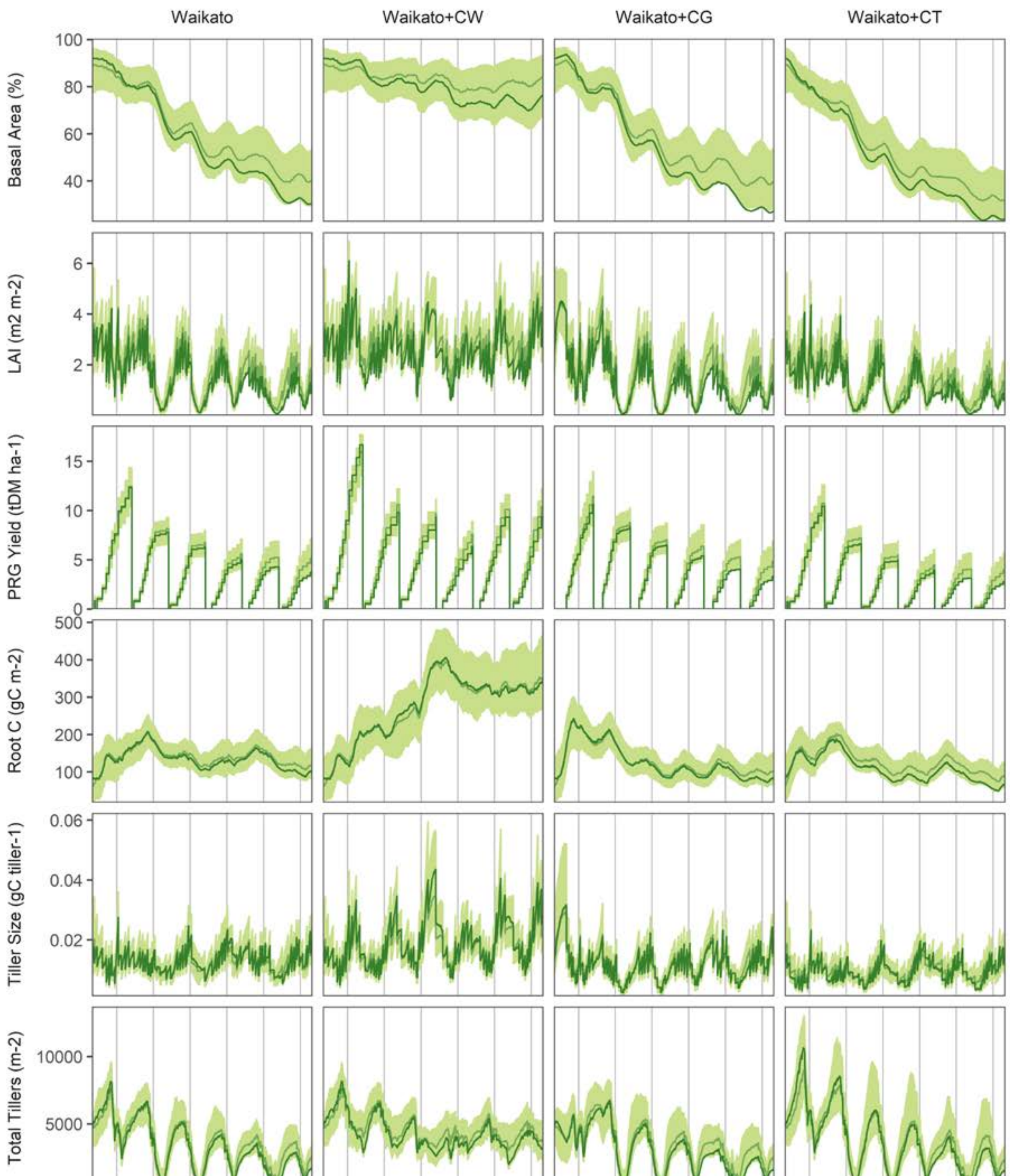

Northland
Northland+CW
Northland+CG
Northland+CT
Basal Area (%)
LAI (m2 m-2)
PRG Yield (tDM ha-1)
Root C (gC m-2)
Tiller Size (gC tiller-1)
Total Tillers (m-2)

Fig. 6. Predictions of pasture performance at the Northland site under alternative management scenarios (CW = Canterbury Water, CG = Canterbury Grazing, CT = Canterbury Temperature). The 90% credible intervals of model prediction are shown as shaded areas (representing parameter uncertainty). The median and *maximum a posteriori* (MAP) model predictions are shown as light and dark lines respectively



Waikato
Waikato+CW
Waikato+CG
Waikato+CT
Basal Area (%)
LAI (m2 m-2)
PRG Yield (tDM ha-1)
Root C (gC m-2)
Tiller Size (gC tiller-1)
Total Tillers (m-2)

Fig. 7. Predictions of pasture performance at the Waikato site under alternative management scenarios (CW = Canterbury Water, CG = Canterbury Grazing, CT = Canterbury Temperature). The 90% credible intervals of model prediction are shown as shaded areas (representing parameter uncertainty). The median and *maximum a posteriori* (MAP) model predictions are shown as light and dark lines respectively

TABLES

Table I. Summary of site environmental parameters over the five years of the trial (2011-2016) plus the additional year simulated (2016-2017): latitude (°), mean daily minimum and maximum temperature (°C), mean annual rainfall, irrigation and potential evapotranspiration (PET) (mm), and mean annual nitrogen fertiliser (kgN ha^{-1}).

Site	Latitude	Min. Temp.	Max. Temp.	Rainfall	Irrigation	PET	Nitrogen
Northland	-35.612	11.7	19.7	1343		940	105
Waikato	-37.772	9.2	19.4	1120		902	146
Canterbury	-43.638	6.8	17.2	589	332	819	238

Table II. List of calibration parameters. Site specific parameters are indicated with an asterisk (*).

Parameter	Mode	Units	Description
ABASAL	0.003	d^{-1}	Basal area response rate
BD*	1.2	$g\ ml^{-1}$	Bulk density of soil
COCRESMX	0.275	$g\ g^{-1}$	Maximum concentration of soluble C reserves
CSTAVM	0.1	$gC\ tiller^{-1}$	Maximum stem mass of elongating tillers
DAYLA	0.5	$d\ d^{-1}$	Day length above which growth is prioritised over storage
DAYLB	0.4	$d\ d^{-1}$	Day length below which phenological stage is reset to zero
DAYLG1G2	0.575	$d\ d^{-1}$	Day length above which generative tillers can start elongating
DAYLGEMN	0.5	-	Minimum daylength growth effect DAYLGE
DAYLP	0.55	$d\ d^{-1}$	Day length below which phenological development slows down
DAYLRV	0.55	$d\ d^{-1}$	Day length at which vernalisation is reset
DELD	0.0148	d^{-1}	Litter disappearance rate due to decomposition
DELE	0.0005	d^{-1}	Litter disappearance rate due to earthworms
DLMXGE	0.6	$d\ d^{-1}$	Day length below which DAYLGE becomes less than 1
FCOCRESMN	0.5	-	Minimum concentration of soluble C reserves as fraction of COCRESMX
FGRESSI	0.5	-	CRES sink strength factor
FSLAMIN	0.5	-	Minimum SLA of new leaves as a fraction of maximum possible SLA (must be < 1)
FSMAX	0.7	-	Maximum ratio of tiller and leaf appearance (must be < 1)
FWCFC*	0.6	$m^3\ m^{-3}$	Relative saturation at field capacity
FWCWP*	0.3	$m^3\ m^{-3}$	Relative saturation at wilting point
HAGERE	0.8	-	Parameter for proportion of stem harvested
HARVFRD	0.2	-	Relative harvest fraction of CLVD
KBASAL	3	$m^2\ m^{-2}$	Reference LAI for calcuation of BASAL

KCRT	10	gC m^{-2}	Root mass at which ROOTD is 67% of ROOTDM
KLAI	0.6	m^2 m^{-2} leaf	PAR extinction coefficient
KLUETILG	0.5	-	LUE-increase with phenology
KRESPHARD	0.01	gC gC^{-1} $°C^{-1}$	Carbohydrate requirement of hardening
LAICR	2.0	m^2 leaf m^{-2}	LAI above which shading induces leaf senescence
LAITIL	1.0	m^2 m^{-2} leaf	LAI above which site filling declines
LERGA	-8.21	°C	Leaf elongation intercept generative
LERGB	1.75	mm d^{-1} $°C^{-1}$	Leaf elongation slope generative
LERVA	-1.13	°C	Leaf elongation intercept vegetative
LERVB	0.75	mm d^{-1} $°C^{-1}$	Leaf elongation slope vegetative
LFWIDG	0.003	m	Leaf width on elongating tillers
LFWIDV	0.003	m	Leaf width on non-elongating tillers
PHENCR	0.6	-	Phenological stage above which elongation and appearance of leaves on elongating tillers decreases
PHY	100	°C d	Phyllochron
RDRHARVMAX	0.05	d^{-1}	Maximum tiller death rate due to harvest
RDRROOT	0.003	d^{-1}	Relatuive death rate of root mass
RDRSMX	0.01	d^{-1}	Maximum relative death rate due to shading
RDRTEM	0.001	d^{-1} $°C^{-1}$	Proportionality of leaf senescence with temperature
RDRTILMIN	0.0001	d^{-1}	Background tiller death rate
RDRTMIN	0.01	d^{-1}	Minimum relative death rate of foliage
RDRWMAX	0.05	d^{-1}	Maximum death rate due to water stress
RGENMX	0.01	d^{-1}	Maximum relative rate of tillers becoming elongating tillers
RGRTG1G2	0.05	d^{-1}	Relative rate of TILG1 becoming TILG2

ROOTDM	0.2	m	Maximum value rooting depth
RUBISC	2.7	g m^{-2} leaf	Rubisco content of upper leaves
SIMAX1T	0.004	gC $tiller^{-1}$ d^{-1}	Sink strength of small elongating tillers
SLAMAX	0.03	m^{2} leaf gC^{-1}	Maximum SLA of new leaves (Note unusual units!)
TBASE	4.5	°C	Minimum temperature for leaf elongation
TCRES	2	d	Time constant of mobilisation of reserves
TOPTGE	22	°C	Optimum temperature for vegetative tillers to become generative
TRANCO	8	mm d^{-1} g^{-1} m^{2}	Transpiration effect of PET
TRANRFCR	0.2	-	Critical transpiration factor below which leaf death occurs
TVERN	4	°C	Optimum vernalisation temperature
TVERND	21	d	Days of cold after which vernalisation completed
TVERNDMN	7	d	Minimum vernalisation days
YG	0.64	gC gC^{-1}	Growth yield per unit expended carbohydrate