Title: Modelling of lucerne (*Medicago sativa* L.) for livestock production in diverse environments.

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Highlights:

1. The GRAZPLAN model for lucerne was further developed and comprehensively validated
2. Changes in the overall representation of plant phenology ensured agreement between modelled and observed data for different genotypes types with varying winter activity
3. The model is suitable for use with the spectrum of different genotypes, climates, soils and farming systems based on lucerne in Australia.

Abstract

A number of models exist to predict lucerne (*Medicago sativa* L.) dry matter production; however most of these models do not adequately represent the ecophysiology of the species to predict daily growth rates across the range of environments in which it is grown. Since it was developed in the late 1990s the GRAZPLAN model has not been updated to reflect modern genotypes and has not been widely validated across the range of climates and farming systems in which lucerne is grown in modern times. Therefore the capacity of GRAZPLAN pasture growth model to predict lucerne growth and development was assessed. This was done by re-estimating values for some key parameters based on information in the scientific literature. The improved GRAZPLAN model was also assessed for its capacity to reflect differences in the growth and physiology of lucerne genotypes with different winter activity. Modifications were made to GRAZPLAN to improve its capacity to reflect changes in phenology due to environmental triggers such as short photoperiods, declining low temperatures, defoliation and water stress. Changes were also made to the parameter governing the effect of vapour pressure VPD on the biomass-transpiration ratio and therefore biomass accumulation. Other developments included the representation of root development and partitioning of canopy structure, notably the ratio of leaf to stem dry matter. Data from replicated field experiments across Australia were identified for the purpose of model validation. These data were broadly representative of the range of climate zones, soil types and farming systems in which lucerne is used for livestock grazing. Validation of predicted lucerne growth rates was comprehensive due to the plentiful data. Across a range of climate zones, soils and farming systems there was an overall improvement in the capacity to simulate the pasture dry matter production, with a reduction in the mean prediction error of 0.33 and the root mean square deviation of 9.6 kg/ha/d. Validation of other parts of the model was restricted however as information relating to plant roots, soil water, plant morphology and phenology were limited. This study has highlighted the predictive power, versatility and robust nature of GRAZPLAN to predict the growth, development and nutritive value of perennial species such as lucerne.

54 *Keywords*: Agroecosystems, grazing systems, farming systems, biophysical model, GRAZPLAN,
55 alfalfa

1 Introduction

Lucerne (or alfalfa, *Medicago sativa* L.) is the most widely grown perennial pasture legume in the world. In Australia, lucerne is used in a wide range of livestock and farming systems. It is grown in areas ranging from cool temperate to subtropical areas for both intensive and extensive agriculture in both dryland and irrigated settings. It is commonly grazed, or cut and conserved as hay or silage. It is also often integrated into crop-livestock systems as a ley phase in cropping rotations to control weeds and disease (Dalal *et al.* 2004), to augment soil nitrogen and carbon stocks (Angus and Peoples 2012), and to improve soil structure (Hanley *et al.* 1964) and water infiltration (McCallum *et al.* 2004). Lucerne is also grown in order to capitalise on summer rainfall to produce quality forage; it also alleviates waterlogging (McCallum *et al.* 2004) and de-waters the soil profile (e.g. Dolling 2001) making it an important tool in combating secondary soil salinity.

A wide range of germplasm options from different genotypes are available to match different combinations of farming systems, climate and soil type. Available genotypes vary in their winter growth activity (the inverse of which is known as fall dormancy) from winter inactive to highly winter active (Humphries *et al.* 2004). Farmers choose genotypes based on the desired availability of forage, persistence and tolerance to defoliation. Compared to regions in the northern hemisphere that experience extreme cold periods, the growing season of lucerne in Australian farming systems is commonly longer and stands may be defoliated more frequently, and most of the year round in many areas (Lodge 1991).

The exact nature of the physiological differences between lucerne genotypes with differing winter activity is not well understood. For example various authors have found that more winter-active genotypes do not initiate the inactivity (or dormancy) process as early as winter-inactive genotypes (Bula *et al.* 1956; Shih *et al.* 1967; Paquin and Pelletier 1980). Brown *et al.* (2005) suggested that the rate of leaf emergence also showed genotype dependency, possibly in relation to assimilate supply. However the actual differences in terms of ecophysiology such as the initiation or termination of

dormancy are not clear from the literature and the actual effects might be complicated by genotype by environment interactions.

In Australia, the proportion of land sown to lucerne is increasing (Donald *et al.* 2012) with expansion from 3.2 M ha in 2006 to 7.5 M ha considered realistic in the medium term (Robertson 2006). Mathematical modelling has an important role to achieve this expansion, because it offers the opportunity to understand the productivity of lucerne, especially in highly variable climates, and allows farmers and their advisors to confidently plan to maximise the benefits to farm operations with consideration of the business risks. These types of models need to be developed on sound principles, and thoroughly validated.

The ability to accurately predict responses in the growth and nutritive value of lucerne to environmental variations is of primary importance in modelling production from grazing systems (Brown *et al.* 2012). The responses of perennial forages such as lucerne to environmental conditions are, however, more challenging to predict than for annuals due to the activity of the perennial organs (Teixeira *et al.* 2009). In particular this involves the need to represent the dynamics of assimilate storage and mobilisation in the perennial reserve organs in response to environmental conditions (photoperiod and temperature) experienced by plants during the year (Teixeira *et al.* 2010); hence it is important to take a biophysical approach. The interactions between lucerne and its environment are complex (Christian 1977). Often interactions due to changing temperature, moisture stress, nutrient status and/or light, as well as the length of grazing period, influence plant phenology and physiology which in turn have an effect on lucerne biomass quantity and quality (Lodge 1991). The interactions among growing conditions, defoliation patterns and winter growth characteristics influence the relationship between flowering stage and the partitioning of assimilates. A number of attempts have been made to express dormancy in lucerne models (Fick 1984; Kanneganti *et al.* 1998; Moot *et al.* 2001; Chen *et al.* 2008; Teixeira *et al.* 2009; Pembleton *et al.* 2011), however while they were effective in replicating biomass dynamics for a given dataset they were not physiologically robust and therefore it is difficult to confidently

transfer the parameter sets across diverse combinations of climate and different farming systems in other locations. As in Australian farming systems defoliation through cutting or set stocking/rotational grazing can occur all year round, in predictive models there needs to be careful consideration of the links between plant physiology, phenology and the plant's environment.

Despite extensive research conducted worldwide contributing much to the collective knowledge of the ecophysiology of lucerne, the ability to accurately model lucerne plant physiology across the diverse spectrum of environments, and genotypes remains underdeveloped. Simulating the growth and development of lucerne which occurs largely as a result of dormancy and the ecophysiology of the lucerne plant (i.e. physiological responses to its environment) (Brown *et al.* 2005; Teixeira *et al.* 2009) are significant challenges and several areas remain elusive for modelling. These include accurately predicting lucerne phenology (such as the initiation of reproductive growth and flowering), particularly in autumn; and its acquisition and use of below-ground reserves; capturing differences between genotypes with different levels of winter activity; and predicting changes through the year in the nutritive value of lucerne. A number of models predict lucerne growth, such as CropSyst (Stöckle *et al.* 2003), APSIM (Robertson *et al.* 2002) and ALSIM (Fick 1984). These biophysical models of plant-soil-climate dynamics represent carbon assimilation, partitioning and utilization (Fick and Onstad 1988; Robertson *et al.* 2002) to simulate growth, development and N accumulation in response to temperature, photoperiod, soil water and N supply and were developed primarily for lucerne stands under cutting management. None of these models represent different genotypes, nor defoliations of lucerne stands by grazing animals which is the most common management system in Australia.

This study aimed to review and revise the lucerne parameter set for lucerne in the GRAZPLAN model of pasture growth (Moore *et al.* 1997) to improve its ability to predict growth rate; and validate the predictions of the model set against experimental data from different agro-ecological areas within Australia. In particular we attempted to model the differences in winter growth activity between genotypes; and to formally test the model in Mediterranean environments, with temperate and summer-

dominant rainfall. This required updating the model to better represent seasonal phenology, biomass partitioning, leaf:stem ratio, nutritive value *etc*. Previous versions of GRAZPLAN (and APSIM, Robertson *et al.* 2002) were based on the semi winter–active cultivar, Hunter River, which has been largely superseded by other options and so the model was updated to include the full range of genotypes available to farmers.

2 Materials and Methods

2.1 The GRAZPLAN model

The GRAZPLAN simulation model of grazed temperate grasslands (Moore *et al*. 1997) is a biomass-based, multi-species model that operates at a daily time step and that is designed to capture the dynamics of both perennial and annual plant species. The model includes equations for the phenological cycles of various classes of perennial and annual plants, including representation of reduced winter activity caused by cold conditions or by drought; capture of light, water and soil nutrients; assimilation and respiration; the allocation of net assimilate to the production of leaves, stems, roots and seeds, including the influence of phenological stage on allocation; relocation of below-ground reserves to new shoot growth; the dynamics of forage nutritive value; and the death, fall, decomposition and disappearance of dead biomass. It has been specifically designed to interact with a model of selectively grazing livestock (Freer et al., 1997). The GRAZPLAN models, and decision support tools based on it, are used widely within Australia for purposes of research (e.g. Cayley *et al.* 1998; Moore *et al.* 2014) and also in decision support for producers (Donnelly *et al.* 2002 and references therein; Warn *et al.* 2006). In this study, the GRAZPLAN grassland model has been used in conjunction with the APSIM soil water, soil nutrient cycling and surface residue models (Holzworth *et al.* 2014).

Defoliation by either grazing or cutting is represented in the GRAZPLAN model. Defoliation by cutting removes shoots above a nominated height; the relative distribution of leaf and stem over the height profile is modelled, so that cut herbage can contain a higher proportion of leaf than the stand as a whole.

Shoot biomass is divided into age cohorts of regularly decreasing dry matter digestibility (DMD) and the declines in digestibility of living leaves and stems due physiological senescence, and of dead herbage due to microbial decomposition, are modelled as functions of temperature and (for dead herbage) moisture status. Grazing is controlled by the animal module of GRAZPLAN (Freer et al. 1997). Briefly, all forage above a livestock-specific height is aggregated into 6 equally-spaced digestibility classes; animals are assumed to select higher digestibility classes preferentially over those of lower digestibility, and to be able to digest the latter more rapidly and so to consume more of them (Freer *et al.* 1997); and total consumption of forage in each digestibility class is allocated *pro rata* to the species and plant parts of which it is comprised (Moore *et al.* 1997).

2.2 Revision of the GRAZPLAN genotypic parameters for lucerne

2.2.1 Allocation of growth between roots, leaves and stems

Khaiti and Lemaire (1992) found that the seasonal variations in potential shoot production of lucerne were not determined by changes in the radiation use efficiency for the production of total biomass, but by the annual pattern of assimilate partitioning between roots and shoots. The seasonality in shoot production which is characteristic of lucerne – and which partly determines its pattern of forage supply – is therefore largely driven by differences in assimilation partitioning throughout the year. Teixeira *et al.* (2008) found that fractional partitioning of dry matter to roots increased from near zero in winter and early spring to more than 0.45 in autumn (i.e. the period of reduced shoot growth). The latter figure corresponds to a root:shoot ratio of approximately 0.8, so the parameter giving the "target" root:shoot ratio during vegetative growth was decreased to this value; the target ratio after flowering was set to 0.3.

Modelling experimental data sets in which leaf and stem biomass were separated highlighted that the original parameter set underestimated the leaf fraction. This is of importance as the leaf fraction is

arguably the single most important determinant of value for livestock production. This problem was addressed in the following ways:

- The parameters governing allocation to leaf as a proportion of shoot allocation during vegetative growth were increased to a fixed value of 0.80 (in the original parameter set, this value ranged between 0.25-0.70 depending on the degree of shading) based on the work of Teixeira et al. (2008) who found that the fractional partitioning of dry matter to roots increased from near zero in winter and early spring (reproductive growth) to more than 0.45 in autumn (i.e. the period of reduced activity). The latter figure corresponds to a root:shoot ratio of approximately 0.8,
- The parameters affecting the phenology (KV3, KV5, KV6), specifically the transition from vegetative to reproductive stages were taken from field data reported by Moot et al. (2001), Brown et al. (2005), Zahid (2009) and Teixeira et al. (2011). The canopy morphology profile of the sward was adjusted so that there would be a better representation of the sward in response to selective grazing. The upper layers of the sward have a higher proportion of leaf (Woodward and Sheehy 1979), so that samples of herbage obtained by cutting to heights above ground level have a higher proportion of leaf than the pre-cutting sward as a whole. Consequently, the "morphology" parameter K_{MO1}, which describes the variation of the leaf:shoot mass ratio with height, was fitted by least-squares minimisation to the data of Woodward and Sheehy (1979), resulting in a value of -0.30 (which implies that there is a height below which all herbage is composed of stem),
- Leaf:stem ratio in lucerne is reduced by high temperature (Carter and Sheaffer (1983). This effect is captured in the GRAZPLAN model through the link between phenology and allocation between stem and leaf: higher temperatures lead to more rapid initiation of reproductive growth and flowering, and assimilate is redirected from roots to stems during the reproductive phenological stage (see equation 36 of Moore et al. (1997).

Changes were also made to the parameter governing the effect of VPD on the biomass-transpiration ratio. This influences biomass accumulation under low CO_2 conditions when stomata are closed. The model was found to fit the experimental data better if the parameter setting the temperature above which photosynthesis proceeds at its maximum rate was increased to 18°C.

2.2.2 Extension of the rooting front

The rate at which the rooting front of a newly-sown lucerne stand develops (called the extraction front velocity or EFV) is important in determining the length of time a lucerne stand takes to exploit this soil water resource. In the GRAZPLAN model, the EFV is modelled as a function of soil bulk density, sand content, soil moisture content and thermal time. EFV increases with decreasing bulk density and with increasing sand content, both of which imply the presence of larger soil pores into which roots can penetrate.

Data presented by Dolling *et al.* (2005a) for 9 locations in Western Australia were used to estimate the parameters of the existing EFV sub-model, because only this data set included both a range of soil types and measurements of the soil attributes necessary to estimate EFV using the GRAZPLAN model equation. Rather than use the average EFVs over the whole soil profile presented by Dolling *et al.* (2005a), EFVs for the B horizons were estimated by linear regression of the data presented in their Figure 3. This was done to control the effects of soil moisture and temperature on EFV: the experimental conditions in the Dolling *et al.* experiment made it likely that there would always be soil moisture available at the base of the rooting front, and temperatures in the subsoils would not vary greatly from the long-term mean, allowing the measured EFVs in mm/d to be converted to the values in mm/°C.d that are predicted by the model equation.

The 4 parameters (K_{R2} to K_{R8}) for the effect of bulk density and sand content on EFV (Appendix A) were fitted to the measured EFVs by the method of least squares. Figure 1a compares the fitted and

estimated EFVs, and Figure 1b shows the fitted relationship between EFV and bulk density for soils with a range of sand contents. The RMSE was 0.41 mm/day for the Dolling et al. (2005a) data.

2.2.3 Representing different winter activity types

A period of reduced winter activity or sometimes referred to as "dormancy" is a distinctive characteristic of the annual growth cycle of lucerne. Reduced winter activity relates to a collection of processes that enable the plant to survive during the onset of stressful times of the year and that manifest as a slowing of shoots growth. For lucerne, during this period the plant continues active photosynthesis but transitions from partitioning assimilates and activity to below-ground rather than above-ground structures (Christian 1977). Lucerne genotypes can be rated for their winter activity according to the extent of shoot elongation in winter. Plants are cut at the end of autumn and their productivity, canopy height and leaf:stem ratio 4 weeks later are used to assign a winter activity rating. For the purposes of GRAZPLAN genotypes with rating between 1 and 11 have been classed into four groups: winter inactive (WI, activity rating 1-3), semi-winter active (SWA, rating 4-5), winter-active (rating 6-7) and highly winter active (8-11)(Humphries et al. 2004).

Attempts to parameterise the existing model for the initiation of reduced activity were unsuccessful, and so this part of the phenology submodel was re-specified. A lagged mean temperature is defined as:

$$T_{lag}(t) = T_{mean}/K_{V30} + T_{lag}(t\text{-}1) \times (1 - 1/K_{V30})$$

and the sward displays reduced activity whenever the following condition holds:

$$RAMP(\ T_{lag}, K_{V26}, K_{V27}\ ) + RAMP(\ DL, K_{V28}, K_{V29}\ ) \geq 1$$

The same equation controls both the start and end of the period of reduced activity. When reduced activity is no longer enforced, the phenological cycle recommences at the start of vegetative growth.

This submodel treats reduced activity as an enforced rather than induced partial dormancy, i.e. it ends shortly after environmental conditions become suitable for growth. This assumption is supported by the experimental evidence of McKenzie *et al.* (1988).

The equations describing the start and end of reduced winter activity were modified to use 5 new parameters (see Appendix A). The literature is unclear whether these triggers vary according to winter activity rating, but similar values have been concluded from experiments in different environments and with different genotypes (Major *et al.* 1991; Brown *et al.* 2005; Sim 2014). What is known, however, is that winter-inactive genotypes partition greater amounts of reserves to the taproot and consequently have a greater reduction in shoot growth than winter-active genotypes (Hodgson 1964; Teuber and Brick 1988). The modified GRAZPLAN model was therefore parameterised upon the premise that differences in dormancy of lucerne genotypes are best described as differences in the *intensity* of dormancy rather than differences in its *duration*.

The parameters of the new equation are taken to be the same for all genotypes, so that the simulated duration of reduced activity in a given environment will also be the same. (It was not possible to test this assumption using the available experimental datasets, but the available evidence provides little support for an alternative parameterization). Differences in winter activity classes are instead assumed to be due to two physiological differences:

- More winter-active genotypes undergo a relatively smaller reduction in meristematic function during the period of reduced winter activity (represented by K_{MR1}, the maximum relative growth rate of shoots during the "winter-inactive" phenological stage). This results in a lower root:shoot ratio during the winter, i.e. proportionately less investment of assimilate into the perennial organs, in more winter-active genotypes.
- More winter-active genotypes remobilize root reserves more rapidly into aboveground tissue when conditions are suitable, such as after defoliation and at the commencement of reproductive growth.

The parameter values describing these differences in winter activity were derived by trial-and-error calibration to the spring and summer experimental data sets, especially those with frequent defoliation (see K_{MR1}, K_{TL1}, K_{TL2} in Appendix A). It is possible that other factors may vary between genotypes such as the temperature and photoperiod triggers relating to the period of winter inactivity, however as yet these are not well enough defined experimentally to specify differentially in the model.

A complete listing of the GRAZPLAN parameter set for lucerne is given in Appendix A.

2.3 Selection of experimental data sets for testing

Because the GRAZPLAN models are applied across a wide range of environments, the first criterion for selection of the available databases for model validation was to obtain experimental datasets that gave reasonable coverage of this environmental diversity within the grazing regions of Australia. Datasets were therefore collated from around Australia, covering the range of climates, soil types and farming systems in which lucerne is used throughout the continent. Experiments covering longer spans of time were preferentially chosen because they allow the model to be tested against a greater range of temperature and moisture conditions. A range of datasets with desirable characteristics were sourced and a final set of 7 experiments was chosen based on the availability of adequate site characterisation in terms of soil properties and local meteorological conditions during the experiment, the length of record, whether shoot biomass accumulation was recorded at for least 10 intervals, the inclusion of a number of genotypes (differing in their winter activity) in the experiment, as well as the availability of data other than shoot production (*e.g.* chemical composition of the shoot material, leaf:shoot proportion, root data, soil water dynamics *etc.*). The locations of the selected experimental data sets are shown in Figure 1 and the experiments are summarised in Table 1.

2.4 Simulation of the experimental data sets

Simulations of each experiment were constructed using the GRAZPLAN pasture and livestock models (Freer *et al.* 1997; Moore *et al.* 1997) linked to the APSIM soil water and soil nutrient cycling models

(Holzworth *et al.* 2014) by using the AusFarm software (version 1.4.8). Weather data (precipitation, maximum and minimum air temperature, vapour pressure deficit, solar radiation) were obtained from official local (or onsite experimental) weather stations where possible; otherwise a Patched Point dataset for the closest climate station was extracted from the SILO data base (Jeffrey *et al.* 2001).

Soil physical and chemical attributes were taken from on-site measurements where available; otherwise soil attributes were acquired for the most suitable soils using detailed information in databases such as APSoil (Dalgliesh *et al.* 2009) based on advice from local experts. Soil attributes for the Forth and Cranbrook sites were taken from the modelling study of Ojeda et al. (2016), which also used the APSIM soil water balance model. Local soil data for some sites such as the Tamworth experiments in particular were limited, which introduces uncertainty into model predictions from the outset. Where not available from records or local experts, the maximum rooting depth of each species was set based on soil physical properties (*e.g.* bulk density).

Details of management practices such as sowing, fertiliser use, grazing, cutting and weed control were extracted from publications relating to each experiment (Table 1) and reproduced using the management-rule system available in AusFarm (Moore 2014). Where descriptions of management activities were incomplete, they were inferred based on the authors' and local experts' knowledge of the same or similar systems. Information on cutting heights and the durations and stocking densities in periods of grazing was frequently not reported.

The initial conditions of the soils at the time of sowing of the lucerne were not recorded for any of the experiments used for validation. In order to reduce this potentially large source of uncertainty in soil moisture, carbon and nitrogen pools, each simulation was run for a period prior to the commencement (i.e. sowing) of each experiment. In a number of cases the pre-experimental management of the sites was not fully reported; pre-experimental conditions for these experiments were modelled based on the

advice of local experts and typically a fallow period with regular weed control was simulated prior to sowing of the lucerne.

In order to realistically represent the experiments, simulations consisted of mixed swards rather than monocultures, even though the botanical composition, or total content of species other than lucerne, was only recorded or reported for a minority of sampling dates. In most cases this meant the inclusion of a winter grass, forb (such as a broadleaf weed) and sometimes (if reported) an annual legume and summer grass. All species except lucerne were sown in the simulations prior to the start of the fallow period.

The experiments were defoliated in various ways, following the management reported in the papers describing them. Defoliation techniques included grazing, cutting, others were grazed followed by cutting the residual biomass to a set height. Grazing or cutting activities were carried out using the corresponding events in the GRAZPLAN model. The dates of defoliation were defined in the datasets. Cutting events were modelled using the corresponding event in the GRAZPLAN model, with a best-available estimate of the cutting height used. Mown biomass was either removed from the plot or retained, as reported for each experiment. Grazing was often reported as 'crash grazing', i.e. sheep grazed the experimental plots at a high stocking density until herbage mass was reduced to a low level. This residual biomass was reported following estimates for experiments as a whole but not measured. In these experiments, the length of each modelled post-harvest grazing period depended on the availability of forage. In other cases the number of sheep was adjusted according to the pre-grazing biomass so that animals were on the plots for a set period of time.

In some of the experiments, the height to which biomass samples were cut was not the same as the height to which plots were subsequently mown. The actual sampling height was taken into account when recording biomass values for comparison with measured data, including the differentials in leaf

proportion in the sampled biomass and the un-sampled residual. Details of the phenology at defoliation were not often recorded or reported however.

For each data set and sampling interval, pasture growth rate (PGR, kg/ha/d) was calculated for the period from completion of cutting or grazing to the next herbage sampling date. This was denoted "actual" PGR. The modelled PGR for the same period was also calculated and the two values compared for each time interval.

3 Results

3.1 Simulation of experimental data sets

Model predictions for a selected winter activity class were compared against the corresponding data from each of the 7 experiments. A winter-active or highly winter-active genotype has been selected in each case as a reference as these genotypes are widely suited to Australian farming systems. Predictions are then are summarised over different seasons, for one genotype at each location compared to the experimental data (Figure 3) showing that the strength of the model predictions vary with season and with location.

Model predictions for lucerne stands at Forth and Cranbrook locations in Tasmania captured the seasonal patterns of pasture growth satisfactorily over the 6 site-years at these two locations, with root mean square deviations (RMSD) for PGR of 21 kg/ha/d at Forth and 16 kg/ha/d at Cranbrook. At both locations, the regression of actual PGR compared to modelled PGR was not significantly different from the 1:1 line. Overall, the model adequately reflected the high growth rates in summer. At both sites there was there was no consistent relationship between the residuals and seasonality. As these two locations there was no difference in the average prediction residuals between the four genotypes, but there were stronger R^2 for the SWA and WA genotypes.

At Hamilton the RMSD for PGR at 21 kg/ha/d was similar to the Tasmania sites, but with the model significantly over predicting daily PGR. The predictions were strongest for the SWA, followed by WA and then HWA. The model's predictions for the Hamilton dataset do not show systematic errors at particular seasons of year however were weaker for winter growth. Importantly the model successfully captures the high spring growth rates in the Hamilton data set. For the Cootamundra experiment there was only moderate (although statistically significant) agreement between actual and modelled PGR values, with a RMSD of 19 kg/ha/d. There was no distinguishable pattern in the model deviations due to seasonality.

Lucerne growth rates in Boschma experiment at Tamworth experiments were the best predicted with an RMSD of 13 kg/ha/d. The relationship between predicted and actual growth rates did not depart significantly from the 1:1 line overall, but autumn growth rates were over-predicted. While the GRAZPLAN model succeeded in representing periods of low lucerne growth and the subsequent recovery in the Lodge experiment, the quantitative performance of the model in this experiment was the poorest of the 7 data sets with a RMSD of 13 kg/ha/d but a low R^2 of 3% that was non-significant. As the soil properties of the Lodge experiment were unknown it has been omitted from further summaries of overall measures of model performance and further discussion.

The changes in lucerne growth rate over time were well predicted at the low rainfall site at Quarading with a RMSD of 5.9. The correlation between actual and predicted growth rates was moderately high (R^2 of 56.6%) and the relationship between actual and modelled growth rates was close to the 1:1 line with a slight under prediction overall. There was no apparent relationship between the time of year and the residuals in the model's predictions.

Figure 4 summarises the overall patterns of lucerne growth in the datasets from 6 locations/experiments and also the modelled patterns of growth rate over the same periods of time and calculated in the same way (i.e. allocating growth in each defoliation interval by assuming that the rate of growth over each

cutting interval was constant). While the model over- and under-predicts growth rates in each season, the only consistent bias in these average growth rates is a tendency for the model to over-predict autumn growth rates. In the other seasons, the model over-predicts for some experiments and under-predicts for others. When summarised across seasons and experiments, model captures most of the variation in the seasonal *patterns* of lucerne growth (data not shown). The model explains 84.5% of the variation across seasons and experiments, with an overall RMSD of only 9 kg/ha/d.

The capacity of the new parameter set to predict differences between winter activity was relatively modest. Overall, the new parameters were quite successful at describing the differences between the cultivars in the Tasmanian experiments, but predicted an advantage for winter-active genotypes at Tamworth that was not reflected in the experimental results. At Hamilton, the lower overall production of semi-winter active genotypes relative to highly winter active genotypes was correctly predicted (although underestimated) but the large measured difference between winter active and highly winter active genotypes was not captured by the model. Given the non-linear response between winter activity rating and total production in this experiment, it appears that some other factor not accounted for in the model – perhaps disease – may have influenced the production of the winter-active cultivar (SARDI 7).

3.2 Long-term behaviour of modelled lucerne stands

The new lucerne parameter set was used to simulate long-term patterns of growth rate in permanent, dryland lucerne monocultures grazed by sheep. This was done in order to assess the plausibility of the modelled growth over the long term. Eight cutting dates at regular intervals of 45 days were used, with the first cut on 1 September so that the winter cutting interval was slightly longer than the other seven. Simulations were run from 1 January 1970 and average growth rates for cutting intervals that ended in the 40 years from 1972-2011 were summarised.

Long-term average pasture growth in these plausibility-simulations was high (Figure 5), reflecting the lax grazing regime, lack of weed competition and the ready supply of N to the lucerne through biological

fixation. The main feature of the growth rate patterns presented in Figure 5, however, is the high variability in lucerne growth rates between years (except at Forth, even under dryland conditions).

The modelled median lucerne growth rates follow a similar seasonal pattern to the corresponding experimental datasets at Forth, Cootamundra and Tamworth. At Hamilton, however, the long-term simulation has a higher summer than spring growth rate, and at Quairading a permanent lucerne stand utilises any stored soil water within 3-4 years and is predicted to grow very little over summer thereafter, unlike the lucerne ley pastures in the Quairading experiment (Dolling *et al.* 2005b; Latta and Lyons 2006). This exhaustion of stored water reserves has previously been identified by various authors (e.g. Dolling *et al.* 2011).

4 Discussion

The model successfully predicts lucerne growth at locations where it grows and is grazed all year round. We have shown that using the new version of GRAZPLAN this is possible for a range of genotypes. The modelling approach used was contingent on phenology; although none of the datasets used contained records of plant phenology at a number of different stages during the experiments. However, the methods used mean that the tests of the new GRAZPLAN model parameters are particularly rigorous by the standards of grassland model validation studies. First, the model has been tested across a wide range of contrasting environments. Second, considerable effort has been made to base the soil descriptions and weather data on locally-measured values. Third, by using the management logic available in the AusFarm software, the actual experimental management has been mimicked as closely as possible, taking the individual features of each experiment into account. These have been effective to ensure the model is robust and can be used for grazing and cutting systems across a wide range of Australian conditions.

We have also increased the rigour of our validations by assessing the GRAZPLAN model's performance from its predictions of growth rate, rather than from predictions of harvested biomass. In

grazing experiments, biomass measurements are auto-correlated, and so it is easier to predict them to a given level of accuracy than it is for growth rates. In cutting trials such as those used here (i.e. locations at Hamilton, Tamworth and the 2 Tasmanian sites), the harvested biomass is the product of the average growth rate (which must be predicted by a model) and the interval between cuts (which is known in advance of the model run). If there is variation in the cutting intervals, therefore, the correlations between predicted and actual growth rate can be expected to be lower than those between predicted and actual yield.

4.1 Predictions of lucerne growth rate over short intervals

Mean prediction errors (MPE, i.e. the ratio of the RMSD to the mean value) of PGR ranged from 0.26 at Forth to 0.74 for the Cootamundra experiment. The average MPE across sites was 0.52. The same datasets were modelled using the original parameter sets. The original parameter set had two genotypes 'semi winter dormant' and 'winter active' which were used for the datasets of winter inactive and semi winter active, and winter active and highly winter active genotype respectively. When the same sites were modelled with the original parameter set, the average MPE across sites was 0.854; the new parameter set and dormancy equations resulted in a reduction of MPE at all of the locations and an overall improvement in RMSD of 9.6 kg/ha/d.

To place this into context, it is useful to compare it to other studies. One of the only multi-site studies involving lucerne was reported by Ojeda *et al.* (2016). We reinterpreted the production data from Figure 8 in Ojeda *et al.* (2016) and calculated the growth rates based on available dry matter above the reported 30 mm cutting height. Comparing the results for the winter-active genotype at the Cranbrook site, the MPEs were the same. For the high producing site at Forth our results had a lower MPE than those in Ojeda *et al.* (2016) for the winter dormant genotype reported – 0.30 compared to 0.44. Although the Tamworth and Hamilton locations had similar latitudes to those at Rafaela and Balcarce, because of the differences in rainfall and other factors, comparisons are not meaningful. Two further pasture model validation studies that addressed a comparable number of sites and predicted PGR rather than biomass were those conducted by Barrett *et al.* (2005) and Cullen *et al.* (2008). Barrett *et al.* (2005) used the

GrazeGro model to simulate perennial ryegrass pastures in cutting trials at five European locations; they included nine site-years (compared with 21 site-years in our analysis). Barrett *et al.* (2005) obtained mean prediction errors ranging from 0.20 to 0.76, with an overall MPE of 0.45. In the study by Cullen *et al.* (2008) across 10 sites (predominantly perennial ryegrass), the mean MPE of the EcoMod grassland model was 0.36.

While Barrett *et al.* (2005) and Cullen *et al.* (2008) were able to predict perennial ryegrass growth with MPEs lower than obtained in our lucerne modelling, in general they were representing much more productive environments. (The exception was the Forth site which was highly productive.) The mean measured PGR in Barrett *et al.* (2005) was 50 kg/ha/d, compared with 33 kg/ha/d across our 7 data sets. While the mean PGR in datasets of Cullen et al (2008) was 36 kg/ha/d, the productivity range across their sites was much smaller than in this study (their average total PGR ranged from 8.9 to 21.6 t/ha/year compared 4.5 t/ha in the Dolling data set to 25.7 t/ha/year in the Forth data set). Because relative measurement errors increase as yields decrease, MPE of any model can be expected to be higher in less-productive environments. Average PGR for the five southern Australian lucerne experiments was 43 kg/ha/d and the MPE over these experiments was 0.47, which is very close to the value obtained by Barrett *et al.* (2005). It also should be noted that the GrazeGro study used only data sets with established grasslands, unlike the present experiments, and that perennial ryegrass is the most intensively-researched grassland species.

In their validation of APSIM-Lucerne, Robertson *et al.* (2002) used a single experiment at Lawes, Queensland over 2 years. The MPE for pasture growth rate in that simulation was 0.48 (from analysis of their Figure 7). Because the Lawes experiment was irrigated and growth rates were high, this result is best compared with the MPE of 0.26 obtained here for Forth. Moot *et al.* (2015) improved the representation of a semi-winter active genotype in a cool temperate environment by calibrating APSIM to intensive measurements of above and below ground biomass. These changes improved the RMSD in their study from 53% to 38% for shoot biomass and 29% to 18% of the mean for roots. In their case

the site was irrigated and the soil had no physical or chemical impediments to plant growth (Sim 2014). Our results were not as favourable however our sites included settings and climates, many of which were challenging for plant growth and included factors (i.e. soil constraints) which might not represented in GRAZPLAN or APSIM.

In a number of the validation simulations, the early growth of the lucerne stand was not well simulated. Although this can be viewed as being of less importance over the life of the plant, lucerne is increasingly been assessed for its potential role in short term leys and is often undersown with a cover crop so it is important to correctly assess the early growth. Sim *et al.* (2015) reported that the regrowth phase consistently reached reproductive development faster than the seedling phase. Another reason for the disparity is that the GRAZPLAN model represents sowing according to the mass of seed sown, and assumes 100% seed viability. This assumption is likely to be inaccurate for lucerne. In the Quairading experiment, for example, 5 kg/ha of seed was sown; at a mean seed weight of 1.7 mg, this corresponds to nearly 300 seeds/m^2 sown, but only 38 plants/m^2 established. It may be necessary to redefine this in the model to specify sowing events in terms of the numbers of plants establishing, as in the APSIM crop growth models (including APSIM-Lucerne).

4.2 Predictions of lucerne growth rate patterns across sites and seasons

We are not aware of any other similar published evaluations of different genotypes of lucerne across different environments. Apart from the study by Ojeda *et al.* (2016) it is rare in literature that lucerne has been tested across such a range of diverse locations. In the present study the inclusion of the two lower-rainfall sites at Quairading and Cootamundra, and both winter and summer rainfall environments, means that a full evaluation of the sites where lucerne is grown has been carried out.

The performance of GRAZPLAN is encouraging when the effects of the environmental conditions are averaged over the long term and the time frame of comparisons is extended from single cutting intervals to entire seasons (i.e. 3 months; Figure 6). Nonetheless, there are some features of our results where the

558 model could do better. The general over-prediction of growth rates in autumn is presumably due to the
559 either the intensity of water limitation not being accurately modelled overall or an incomplete
560 description of the below ground assimilate partitioning.
561
562 Interestingly Cullen *et al.* (2008) found the highest deviations from predicted growth rates were in also
563 in autumn (and summer in their case). In reality in the Australian context, lucerne stands are commonly
564 used opportunistically, to maximise animal productivity, depending on rainfall and the feed supply from
565 other pastures (Lodge 1991). Therefore being able to confidently predict lucerne growth over short
566 intervals in warm environments where water supply is variable, as well as in crop-livestock farming
567 systems and in dry environments where access to soil water is important as these are where lucerne is
568 widely grown.
569
570 There is a tendency for the model to under-predict total lucerne production in maritime environments
571 (Forth, Hamilton) and to over-predict it in continental environments (Tamworth, Quairading). This may
572 be related to the term in the growth rate equation that limits growth due to stomatal closure under high
573 vapour pressure deficits. For consistency with APSIM crop growth models (so that they can be linked
574 with GRAZPLAN) VPD in the GRAZPLAN model is calculated from air temperature by assuming that
575 dew point temperature equals the minimum temperature (Bristow 1992). This assumption does not
576 hold in all environments (e.g. Tanner and Sinclair 1983) and it may be that a more accurate approach
577 to estimating VPDs would allow this error in the model to be corrected (Brown *et al.* 2012).
578
579 At some sites (e.g. Tamworth), the model over-predicted lucerne growth in the final year of the dataset
580 after a drought period. (A similar phenomenon can be seen in the results of Ojeda et al (2016).) It is
581 possible that plant disease, or reductions in plant density over and above self-thinning, were reducing
582 the measured growth rates in these experiments. Neither process is represented explicitly by either the
583 GRAZPLAN or the APSIM lucerne models; indeed the representation of stress-related plant deaths is
584 an area of weakness in all biophysical crop and grassland models.

585

586 **4.3 Seasonal growth patterns and differences between winter activity types**

587 The capacity of GRAZPLAN to predict differences between genotypes with differing winter activity
588 was relatively modest. In environments where lucerne grows all year phenology and reduced winter
589 activity cannot just be represented by simple functions for the accumulation of thermal time, and
590 genotype differences show up as differences in winter growth rather than in survival. Variation in, for
591 example the sequential emergence of leaves on the main stem between cultivars supports the notion that
592 differences in genotypes need to be considered when parameterising lucerne models (Moot *et al.* 2015).
593 We have implemented an approach to represent the dormancy of different lucerne genotypes based on
594 environmental triggers of photoperiod and temperature. This has also been attempted by Pembleton *et*
595 *al.* (2011) and Ojeda *et al.* (2016) however the approach we have used seems more robust across
596 different climates than locally calibrated values. More detailed studies on ecophysiology as it relates
597 to genotypes will improve these parameter values further. For example, which physiological
598 characteristics vary with genotype - such as to whether the temperature and photoperiod triggers relating
599 to the period of reduced winter activity - is largely unknown, as often modelling studies are conducted
600 on a limited number of genotypes in one location (e.g. Moot *et al.* 2015).

601

602 It has been suggested that in the case of cold acclimation, the specific rate of change in photoperiod
603 may be the critical factor for triggering the response rather than a specific photoperiod per se
604 (Castonguay *et al.* 2006). The assumptions embedded in the new parameterisation of the phenology of
605 lucerne, and in the responses of shoot growth and relocation to the period of reduced winter activity
606 represent a hypothesis about this physiological basis that could profitably be explicitly tested.

607

608 The model was found to fit the experimental data better if the parameter setting the temperature above
609 which photosynthesis proceeds at its maximum rate was increased to 18.0 °C from 15.0 °C (Brown *et*
610 *al.* 2006). This response was only detectable because the model was tested across environments with a

range of winter temperatures. This is a specific requirement that can be addressed by more rigorous testing through experimental work.

Overall, the new parameters were quite successful at describing the differences between the genotypes at the cool temperate locations in the Tasmanian experiments, but predicted an advantage for winter-active genotypes Tamworth that was not reflected in the experimental results (Figure 4). At Hamilton, the lower overall production of semi-winter active genotypes relative to highly winter active genotypes was correctly predicted (although underestimated), but the large measured difference between winter active and highly winter active genotypes was not captured by the model. Given the non-linear response between winter activity rating and total production in this experiment, it appears that other factors not accounted for in the model – namely poor establishment (Li *et al.* 2010) – have influenced the production of the winter-active cultivar (SARDI 7).

An area of uncertainty concerns the growth, development and functioning of lucerne roots. The model development for improved prediction of EFV is an initial step and the predictions can be rigorously assessed through experimental work in the field or in controlled environments. The EFV used in the currently modelling is derived from stands of mature plants. EFV may vary with plant maturity (Sim 2014) and the use of one number only as in our modelling may contribute to an underestimation of soil water extraction during the early stages of the plant's life. However to date, very few datasets are available to enable the development of widely applicable physiological principles for the inclusion into modelling frameworks. Additionally it is unclear if the EFV is genotype dependent, or is regulated more by the supply of assimilate than by meristematic activity (the latter is implicitly assumed by the temperature-dependent function used in the model).

4.4 Differences between winter activity types in lucerne

In this study we have successfully attempted to explicitly represent genotype differences, which is not a capability of most other lucerne models. This however is an area that requires further experimental

information before model development can continue. We were surprised to discover that, despite numerous chamber and glasshouse studies, the physiological basis of the environmental triggers for winter-activity differences in lucerne remains essentially unknown. The assumptions we have embedded in the new parameterisation of the phenology of lucerne, and in the responses of shoot growth and relocation to the period of reduced winter activity represent a hypothesis about this physiological basis that could profitably be explicitly tested. In particular, our hypothesis that winter activity expresses the intensity, rather than the duration, of the dormancy mechanism should be amenable to experimental investigation.

Our attempt to represent the differences between the winter-activity types was only partially successful. Our current model correctly predicts that winter-active genotypes will have higher production in southern Australia, but the apparent advantage of winter-inactive types in northern NSW (Tamworth experiments) was not reproduced. Examination of the winter-active *vs.* winter-inactive genotype comparison, however, suggests that the model *is* predicting a south-north gradient in the differential between genotypes, albeit a gradient of smaller magnitude than the experimental datasets suggest. We therefore conclude that although the set of parameters for different winter activity types of lucerne is satisfactory in the new version, that further work on this aspect of the lucerne model will be needed.

In general, comprehensive experiments investigating the interactions between genotype, different environments/climates and management have not been conducted for lucerne in Australia and therefore the interactions remain not well understood. If model testing and validation are to continue a number of key datasets are required. For the Australian context, in particular quantitative information data on the nutritive characteristics of the harvested forage is lacking. At the least this would include digestibility and crude protein for different genotypes, at different phenostages and at different levels of water stress. Most of the datasets used in the model development and validation only involved one component, for example above ground biomass. Datasets that include the simultaneously assessment of different parts of the model are extremely helpful. For example, herbage mass, soil water, phenology,

665 rooting depth and soil water gathered in a complimentary way would be incredibly valuable. A study
666 involving a range of genotypes, in a range of climate zones, for seedling and regrowth growth, across a
667 number of years, combined with this auxiliary data would be the definitive dataset. The datasets used
668 in this study did not contain root data which was a short coming. Datasets that enable better calibration
669 of the dynamics of the rooting front and changes in root respiration across seasons are other areas that
670 may potentially improve dynamics in above ground biomass (e.g. Moot *et al.* 2015). Root EFV can
671 vary throughout the life of the plant and better information could improve the accuracy of water supply
672 and demand especially during the early stages of growth (Sim 2014). Root turnover rate may also be
673 influenced by changes in photoperiod (Moot *et al.* 2015). More experimental information on both these
674 would help to better represent the seasonal changes in below underground biomass dynamics however
675 and it is unclear as to if there are differences between genotypes.
676

677 **5 Conclusion**

678 If lucerne is to be more widely adopted, it will be important that landholders maximise the benefits
679 (usually as a part of a diverse feedbase) to their livestock enterprises, as well as optimizing the benefits
680 and minimizing the costs of lucerne phases to subsequent crops. This study has improved the
681 representation of different lucerne genotypes in terms of important physiological processes that affect
682 phenology, transpiration, root development and biomass partitioning which in turn improve the
683 prediction of nutritive value and thereby livestock production potential. This study has quantified the
684 particular strengths of the re-parameterized GRAZPLAN model for predicting plant growth rates.
685 Weaknesses relate to differences in the ecophysiology between genotypes and transpiration in warm
686 and moist environments. The GRAZPLAN pasture growth model is robust and has been configured to
687 model lucerne, both in grazing and in mixed farming systems but there are a number of areas where the
688 performance of the model is known to be in need of improvement and with further testing against data
689 sets that contain information about the nutritive value of harvested herbage and below ground biomass
690 would be particularly useful.
691

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Appendix A

Table 1. GRAZPLAN pasture parameters for lucerne. Parameters in **bold** have their definition changed, or are new, since previously published in Moore et al. (1997). Previous (prev.) parameter values for lucerne are given in square brackets. NR = the parameter is not required to represent lucerne.

Parameter	Value	Units	Meaning
grass	FALSE		TRUE for grasses
legume	TRUE		TRUE for legumes
annual	FALSE		TRUE for annuals, FALSE for perennials
isc4	FALSE		TRUE if the species has the C_4 photosynthetic pathway
longday	FALSE		TRUE if long days required to induce reproductive growth
K_{V3j}	**1.0**	**ºC**	**Base temperature for degree-day computations [prev. 5.0]**
K_{V4j}	**NR**	**hr**	**Day length for commencement of reproductive growth [prev. 12.0]**
K_{V5j}	**350**	**ºd**	**Degree-day sum for commencement of reproductive growth [prev. not implemented]**
K_{V6j}	**600**	**ºd**	**Degree-day sum for commencement of flowering [2] [prev.: 100]**
K_{V7j}	**NR**	**d**	**Maximum length of flowering period**
K_{V8j}	**NR**	**d**	**Effect of soil moisture stress on flowering duration**
K_{V9j}	**NR**	**ºd**	**Degree-day sum beyond which the reproductive phenostage ends[3] [prev. 2900]**
K_{V10j}	**0.25**	**0-1**	**Value of the soil moisture growth-limiting factor that defines "drought" for the senescence calculations [3]**
K_{V15j}	**0.5**	**0-1**	**Reduction in the rate of development due to water stress in pre-flowering, reproductive plants [prev. 0]**
K_{V20j}	**15.0**	**d**	**Length of the drought period required to induce senescence (i.e. end reproductive growth) when DD(j)= KV9j [4]**
K_{V21j}	**NR**	**ºd**	**Value of DD(j) at which senescence occurs in the absence of drought[4] [prev. 5000]**
K_{V22j}	**0.0**	**0-1**	**Upper margin of phenology-sensitive horizon during vegetative growth[5]**
K_{V23j}	**1.0**	**0-1**	**Thermal time (as fraction of K(V,6)) for upper margin of phenology-sensitive horizon to reach top of sward [5]**
K_{V24j}	**0.5**	**0-1**	**Final lower boundary of phenology-sensitive horizon[5]**
K_{V25j}	**0.0**	**0-1**	**Height of removal for reset of phenology (as fraction of lower boundary of phenology-sensitive horizon)[5]**

Parameter	Value	Units	Meaning
K_{V26j}	**0.0**	**°C**	**Lagged mean temperature below which reduced winter activity always ensues[6]**
K_{V27j}	**13.0**	**°C**	**Lagged mean temperature above which dormancy is not promoted[6]**
K_{V28j}	**8.0**	**hour**	**Day length below which dormancy always ensues[7]**
K_{V29j}	**14.0**	**hour**	**Day length above which dormancy is not promoted[6]**
K_{V30j}	**5**	**day**	**Lag period for computing mean temperatures[6]**
K_{I1j}	0.0260	m^2/g	Reference specific leaf area (ratio of leaf area index to leaf weight)
K_{I2j}	**0.0040**	**m^2/g**	**Reference specific stem area[8] [prev. 0.0065]**
K_{I3j}	13.5	$MJ/m^2/d$	Curvature factor for effect of light on specific area
K_{I4j}	15	ºC	Temperature threshold for maximal specific area
K_{I5j}	0.6	0-1	Relative specific area at 0 ºC
K_{I6j}	0.12	-	Relative decrease in specific leaf area at twice reference (CO_2)
K_{I7j}	**0.80**	**0-1**	**Apparent light extinction coefficient under ungrazed conditions[9] [previously 0.5]**
K_{I8j}	**0.80**	**0-1**	**Apparent extinction coefficient under heavily grazed conditions[9] [previously 0.6]**
K_{I9j}	0.80	0-1	Apparent extinction coefficient of standing dead
K_{I10j}	1.00	0-1	Apparent extinction coefficient of litter
K_{WU1j}	0.35	0-1	Available soil water threshold for growth limitation
K_{WU2j}	1.0	0-1	Proportion of any transpiration deficit that can be recovered from moist layers
K_{WU5j}	150	s/m	Reference leaf stomatal resistance at 350 ppm CO_2
K_{WU6j}	0.5	-	Relative change in leaf stomatal resistance at 700 ppm CO_2
K_{RU1j}	2.35	g/MJ	Radiation use efficiency (gross assimilation) under reference conditions
K_{RU2j}	99.9	$MJ/m^2/hr$	Effect of radiation intensity on radiation use efficiency
K_{RU3j}	0.6	0-1	Relative photosynthetic efficiency of stems
K_{RU4j}	16.0	ppm	CO_2 compensation point at 0ºC
K_{RU5j}	35.0	Ppm	CO_2 compensation point at 20ºC
K_{RU6j}	55.0	ºC	Maximum temperature for CO_2 compensation function
K_{BT1j}	15.0	kPa g/kg	Biomass-transpiration coefficient
K_{T1j}	6.0	ºC	Mean daytime temperature for 5% of maximum gross assimilation rate (NB not mean temperature for day and night)
K_{T2j}	**18.0**	**ºC**	**Mean daytime temperature for 95% of maximum gross assimilation rate[8] [prev. 15.0]**
K_{W1j}	0.70	0-1	Transpiration ratio below which assimilation rate decreases
K_{WL1j}	0.85	0-1	WFPS threshold for waterlogging

Parameter	Value	Units	Meaning
K_{WL2j}	23.0	-	Curvature of growth limitation by waterlogging
$\boldsymbol{K_{MR1j}}^{*}$	**cvv**	**/d**	**Maximum relative growth rate of shoots during reduced winter activity[10]**
$\boldsymbol{K_{TL1j}}^{\dagger}$	**cvv**	**-**	**Threshold growth-limiting factor for translocation from belowground reserves [10] [prev. called $\underline{K_{U1j}}$]**
$\boldsymbol{K_{TL2j}}^{\ddagger}$	**cvv**	**/d**	**Relative rate of translocation from belowground reserves[9] [prev. called $\underline{K_{U2j}}$]**

Genotype	K_{MR1} (g/g/d)	K_{TL1} (g/g/d)	K_{TL2} (g/g/d)
Highly winter active	0.020	0.30	0.05
Winter active	0.010	0.30	0.04
Semi-winter active	0.005	0.40	0.03
Winter inactive	0.000	0.40	0.02

K_{RE1j}	0.3	g/g/d	Maintenance respiration rate at 10 ºC (g DM/g N/d)
K_{RE2j}	1.8	-	Q10 factor for maintenance respiration
K_{RE3j}	0.20	0-1	Reduction in maintenance respiration in summer- or winter-inactive plants[11] [prev. 1.0]
K_{RE4j}	0.25	g/g	Growth respiration rate
$\boldsymbol{K_{A1j}}$	**0.80**	**-**	**Target root:shoot ratio during vegetative growth[8] [prev. 1.2]**
$\boldsymbol{K_{A2j}}$	**0.30**	**-**	**Target root:shoot ratio during reproductive growth[8] [prev. 0.8]**
$\boldsymbol{K_{A4j}}$	**0.80**	**0-1**	**Maximum value of the ratio (leaf allocation):(shoot allocation)[8] [prev. 0.7]**
$\boldsymbol{K_{A5j}}$	**0.80**	**0-1**	**Minimum value of the ratio (leaf allocation):(shoot allocation)[8] [prev. 0.25]**
$\boldsymbol{K_{MO1j}}$	**-0.3**	**-**	**Parameter governing height distribution of leaves**
K_{R1j}	3000	mm	Maximum rooting depth under optimal soil conditions
$\boldsymbol{K_{R2j}}$	**0.65**	**mm/ºd**	**Maximum rate of root front extension[8] [prev. 2.0]**
K_{R3j}	0.0	ºC	Base temperature for root front extension
K_{R4j}	0.25	0-1	ASW below which root extension is reduced
$\boldsymbol{K_{R5j}}$	**1.95**	**Mg/m³**	**Threshold bulk density for reduced root extension in 100% sand[11] [prev. 1.4]**
$\boldsymbol{K_{R6j}}$	**-0.65**	**Mg/m³**	**Threshold bulk density for reduced root extension in 0% sand[11] [prev. 1.2]**
$\boldsymbol{K_{R7j}}$	**1.20**	**m³/Mg**	**Rate of decrease in root extension with increasing bulk density[11] [prev. 2.0]**
$\boldsymbol{K_{R8j}}$	**0.15**	**0-1**	**Minimum value of the bulk density effect on root extension[11] [prev. 0.1]**
K_{R9j}	85	m/g	Specific root length
K_{R10j}	0.00022	m	Average radius of effective roots
K_{D1j}	800	ºd	Thermal age at which death of shoots commences

Parameter	Value	Units	Meaning
K_{D2j}	0.005	/ºd	Background death rate of old shoots in seedlings & established plants
K_{D3j}	0.003	/ºd	Additional death rate of all shoots in senescing plants
K_{D4j}	**-4.0**	**ºC**	**Temperature for 5% mortality at the first frost (formerly K_{D2j})**
K_{D5j}	**-11.0**	**ºC**	**Temperature for 95% mortality at the first frost (formerly K_{D3j})**
K_{D6j}	**1.0**	**ºC**	**Frost-hardening factor (formerly K_{D4j})**
K_{D7j}	**-**	**0-1**	**Value of the seedling stress index at which seedling mortality commences (formerly K_{Z1j})**
K_{D8j}	**-**	**0-1**	**Value of the seedling stress index for 100% seedling mortality (formerly K_{Z2j})**
K_{DR2j}	0.0025	/d	Specific root loss rate at 10ºC
K_{DR3j}		g/g	Recovery rate of mass from dying roots
K_{DR4j}	1.5	-	Q10 for root aging and loss
$K_{F1,leaf,j}$	0.003	/d	Fall of standing dead: reference rate for leaf
$K_{F1,stem,j}$	0.001	/d	Fall of standing dead: reference rate for stem
K_{F2j}	40	-	Fall of standing dead: maximum relative effect of precipitation
K_{F3j}	10	/mm	Fall of standing dead: curvature of precipitation effect
K_{F4j}	30	/kg animal/d	Fall of standing dead: trampling effect
$K_{BR1j,leaf}$	0.10	/d	Background specific rate of breakdown of leaf litter
$K_{BR1j,stem}$	0.02	/d	Background specific rate of breakdown of stem litter
K_{BR2j}	10	-	Litter breakdown: trampling effect
K_{BR3j}	0.02	/d	Specific rate of incorporation under dry soil conditions
K_{BR4j}	0.05	/d	Specific rate of incorporation under wet soil conditions
$K_{Q1,leaf,j}$	**0.85**	**g/g**	**Average digestibility of newly-produced leaf [12] [prev. 0.8]**
$K_{Q2,leaf,j}$	**0.75**	**g/g**	**Minimum digestibility of green leaf during vegetative growth[12] [prev. 0.7]**
$K_{Q3,leaf,j}$	0.70	g/g	Minimum digestibility of green leaf during reproductive growth
K_{Q4j}	300	ºd	Thermal time during which green leaf maintains its digestibility
$K_{Q5,leaf,j}$	0.006	/ºd	Rate parameter for decline of DMD of green leaf
$K_{Q6,leaf,j}$	4	ºC	Base temperature for maturation- senescence of green tissue
$K_{Q1,stem,j}$	**0.85**	**g/g**	**Average digestibility of newly-produced stem[12] [prev. 0.8]**
$K_{Q2,stem,j}$	**0.70**	**g/g**	**Minimum digestibility of green stem during vegetative growth[12] [prev. 0.6]**
$K_{Q3,stem,j}$	0.45	g/g	Minimum digestibility of green stem during reproductive growth
$K_{Q5,stem,j}$	**0.002**	**/ºd**	**Rate parameter for decline of DMD of green stem[12] [prev. 0.004]**
K_{Q6j}	4.0	ºC	Base temperature for maturation & senescence of green tissue

Parameter	Value	Units	Meaning
K_{Y1j}	0.024	/d	Reference rate of microbial decomposition of digestible DM
K_{Y2j}	4.7	-	Factor for temperature response of decomposition
K_{Y3j}	32	ºC	Factor for temperature response of decomposition
K_{Y4j}	0.05	-	Minimum value of the moisture factor for standing dead
K_{Y5j}	7	g/g	Maximum moisture content of standing dead
K_{Y6j}	-0.2	-	ASW for 5% of maximum decomposition
K_{Y7j}	0.85	-	ASW for 95% of maximum decomposition
K_{Y8j}	0.125	0-1	Relative rate of decomposition of indigestible DM
$K_{NU1N,leaf,j}$	0.060	g/g	Maximum content of N in green leaf at maximum DMD
$K_{NU2N,leaf,j}$	0.030	g/g	Minimum content of N in green leaf at maximum DMD
$K_{NU3N,leaf,j}$	0.026	g/g	Minimum content of N in green leaf at midpoint DMD
$K_{NU4N,leaf,j}$	0.022	g/g	Minimum content of N in green leaf at minimum DMD
$K_{NU5,leaf,j}$	0.1	-	Relative decrease in leaf N content (per unit leaf area) at twice reference (CO_2)
$K_{NU1N,leaf,j}$	0.040	g/g	Maximum content of N in green stem at maximum DMD
$K_{NU2N,leaf,j}$	0.030	g/g	Minimum content of N in green stem at maximum DMD
$K_{NU3N,leaf,j}$	0.022	g/g	Minimum content of N in green stem at midpoint DMD
$K_{NU4N,leaf,j}$	0.015	g/g	Minimum content of N in green stem at minimum DMD
$K_{NU5,leaf,j}$	0.0	-	Relative decrease in stem N content (per unit mass) at twice reference (CO_2)
$K_{NU1N,root,j}$	0.015	g/g	Maximum content of N in live root
$K_{NU2N,root,j}$	0.015	g/g	Minimum content of N in live root
$K_{NU5,root,j}$	0.0	-	Relative decrease in root N content (per unit mass) at twice reference (CO_2)
K_{FX1j}	0.20	0-1	N-fixation: relative depth of nodulation
K_{FX2j}	0.15	0-1	N-fixation: nodulation at depth:nodulation at surface
K_{FX3j}	0.85	0-1	N-fixation: ASW for maximum fixation rate
K_{FX4j}	30	mg/l	N-fixation: solution NO_3 conc. for maximum fixation rate
K_{FX5j}	90	mg/l	N-fixation: solution NO_3 conc. for suppression of fixation
$K_{UE1,NO3,j}$	1.0	-	Uptake effectiveness parameter for nitrate
$K_{UE1,NH4,j}$	1.0	-	Uptake effectiveness parameter for ammonium
K_{RL1Nj}	0.33	/d	Relocation rate parameter for element *e* (*e*=N, P, S)
K_{AA1j}	1.2	mol/kg	Ash alkalinity of newly-grown leaves
K_{AA2j}	1.2	mol/kg	Ash alkalinity of newly-grown stems
K_{AA3j}	0.6	mol/kg	Ash alkalinity of newly-grown roots

Parameter	Value	Units	Meaning
K_{AA4j}	1.2	mol/kg	Ash alkalinity of newly-grown seeds
K_{AA5j}	4.5	-	pH below which no cation uptake takes place
K_{AA6j}	5.0	-	pH above which maximal cation uptake takes place
K_{HRj}	1.6	-	"Height ratio": also governs the size of the ungrazeable portion of the pasture
K_{SFj}	0.0	-	Parameter controlling the relationship between DMD and relative nutritive value

*Parameter K_{MR1} is the maximum relative growth rate of shoots during the reduced winter activity phenological stage; parameter $^{\dagger}K_{TL1}$ is the threshold value of growth-limiting factors above which translocation from below-ground reserves takes place; $^{\ddagger}K_{TL2}$ is the proportion of effective root mass that can be re-mobilized above ground in a single day if both environmental conditions are suitable and the current root:shoot ratio is above a target level set by the phenological stage. Paramaters with NI value are not implemented in the current version.

[1] adjusted following Moot *et al.* (2001) and Brown *et al.* (2005)
[2] fitted to data in Zahid (2009)
[3] based on reanalysis of data presented in Halim *et al.* (1989) and Hattendorf *et al.* (1988)
[4,5,6] from parameter fitting across all the datasets
[7] based on reanalysis of data presented in Schonhorst *et al.* (1957)
[8] based on Teixeira (2007)
[9,10] from parameter fitting across all the datasets
[11] based on reanalysis of data presented in Dolling *et al.* (2005a)
[12] fitted data based on Hayes *et al.* (2010) from Cootamundra

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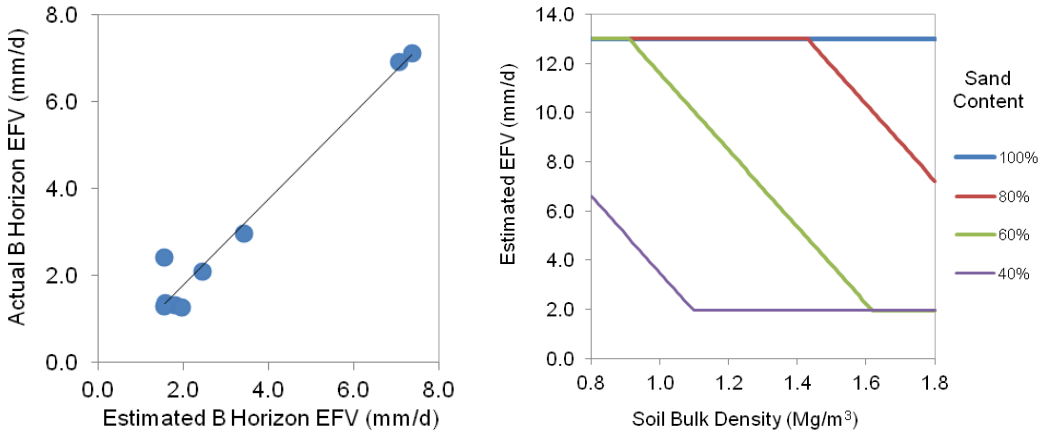

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874 Figure 1. (left) Observed vs fitted root extraction front velocities for B horizons in the data set of Dolling *et al.* (2005a). The
875 1:1 line is shown and the relationship is significant (R^2=0.97, p=0.02) (right) Fitted response of root extraction front velocity
876 to bulk density and sand content in the layer containing the current rooting depth, on a (summer) day where 20° C.d of thermal
877 time accrues.

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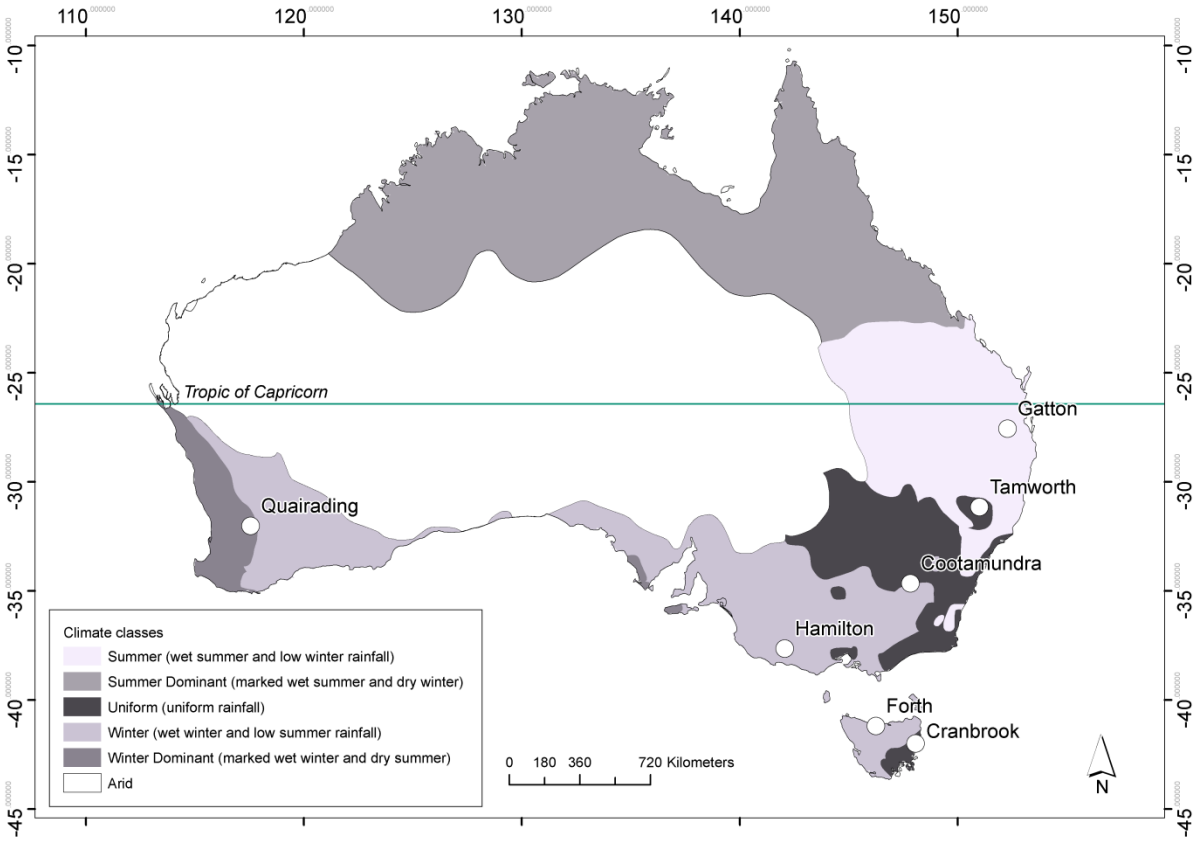

879

880 Figure 2. Locations of the experimental data sets that were used for testing and developing the lucerne parameter set for the
881 GRAZPLAN pasture model. Climate zonation is based on the season of highest rainfall in each area and use the median
882 annual rainfall (based on the 100 year period from 1900 to 1999) and seasonal incidence (the ratio of the median rainfall over
883 the period November to April to the period May to October) to identify these six major zones (Data source: Commonwealth
884 of Australia, Bureau of Meteorology 2005). Gatton was used in long-term simulations to examine patterns of growth.

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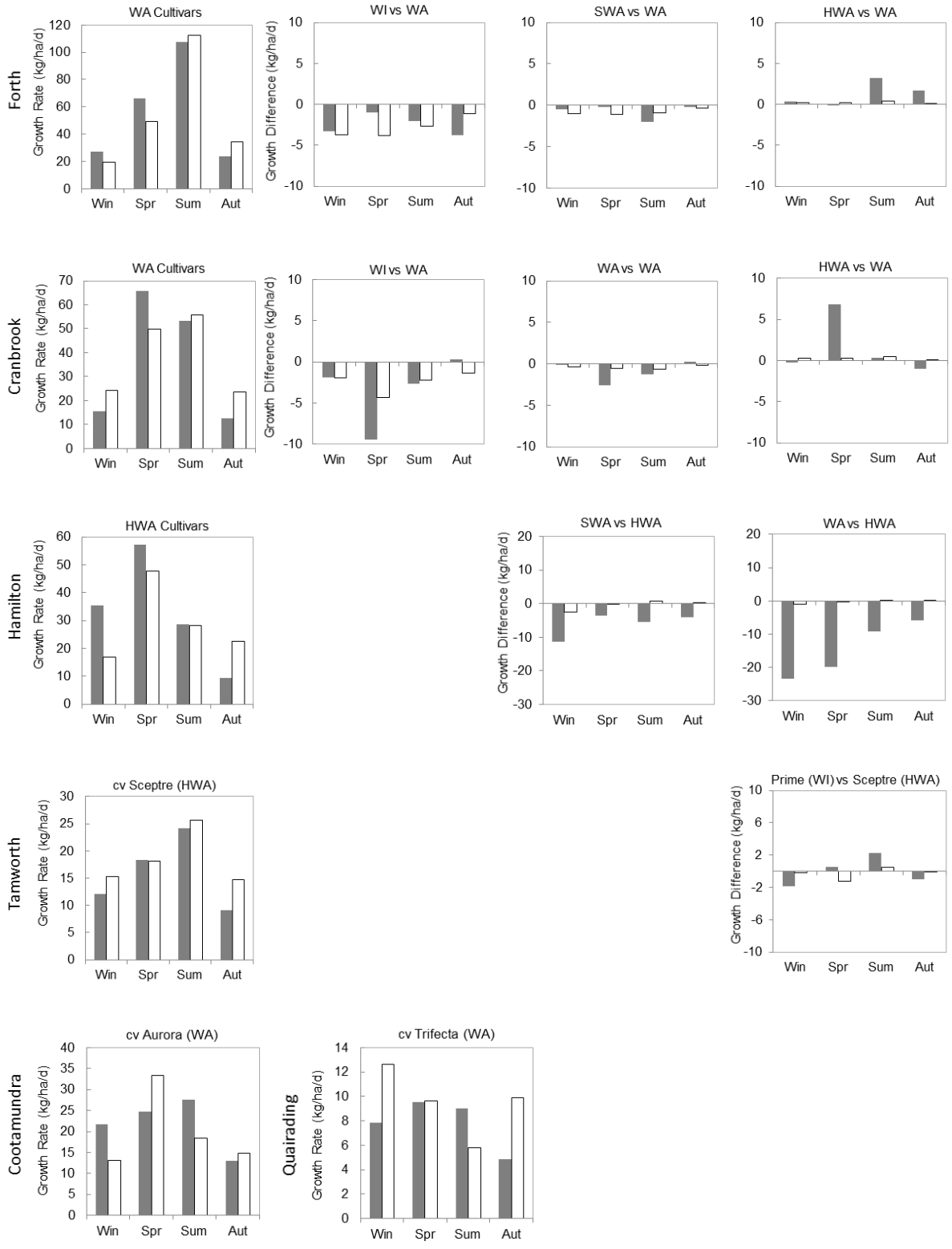
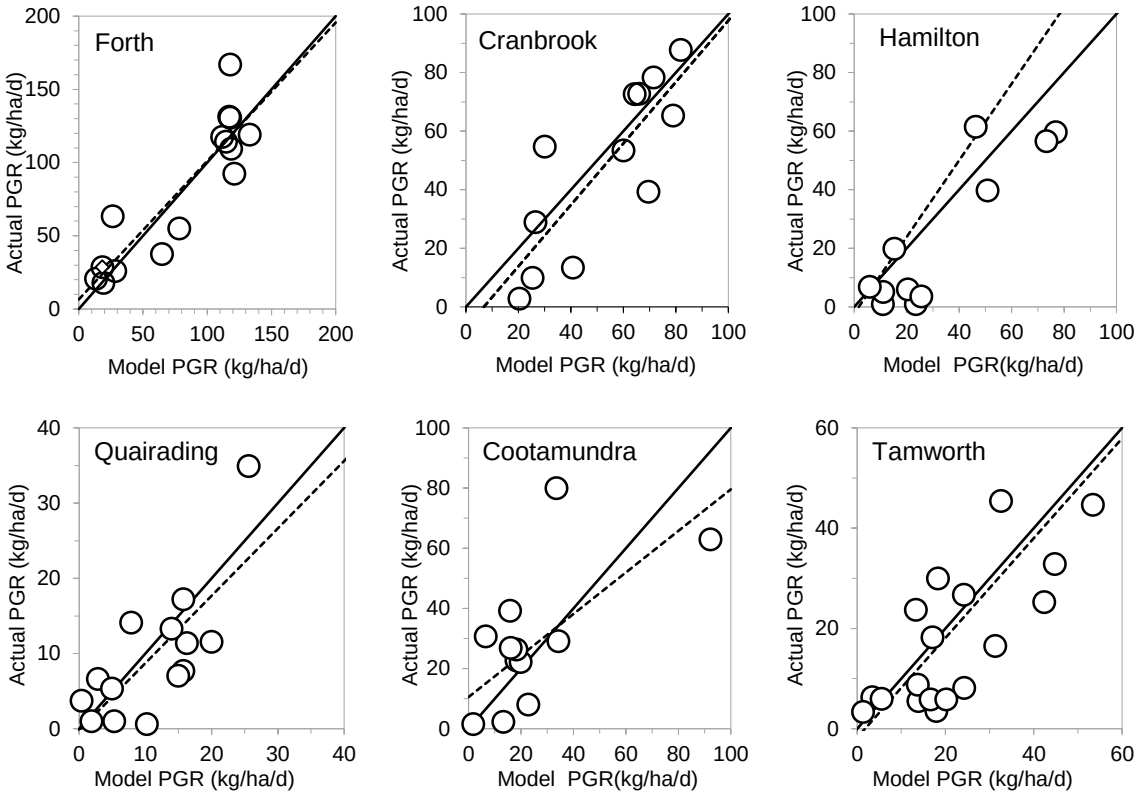


Figure 3. Average daily growth rate (kg/ha/d) of lucerne modelled with GRAZPLAN (open) and experimental data (grey) over four seasons for various locations throughout Australia. Seasons are: winter (Win), spring (Spr), summer (Sum) and autumn (Aut); genotypes are WD (winter dormant), SWA (semi-winter active), WA (winter active), HWA (highly winter active). Note: Tamworth is the Boschma data set; Lodge dataset is not shown.



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896

897 Figure 4. Actual and predicted (modelled) harvested daily pasture growth rates (PGR, kg/ha/d) for winter-active lucerne
898 growing at various locations. In the actual-vs-model chart, a 1:1 relationship is shown as a solid line and the regression of
899 actual on modelled PGR is shown as a segmented line. Note: the Tamworth dataset shown is from Boschma, the Lodge dataset
900 is not shown.

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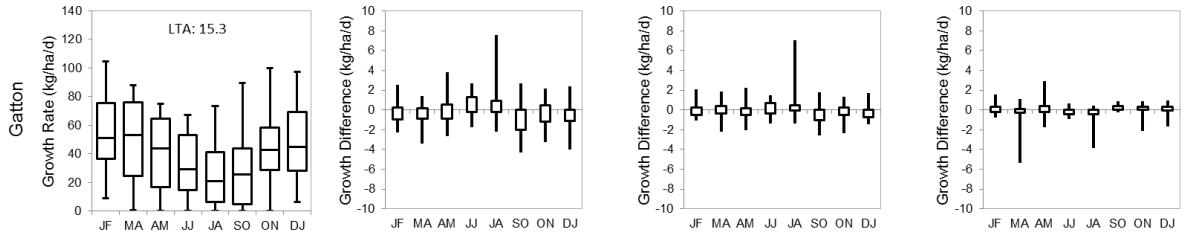

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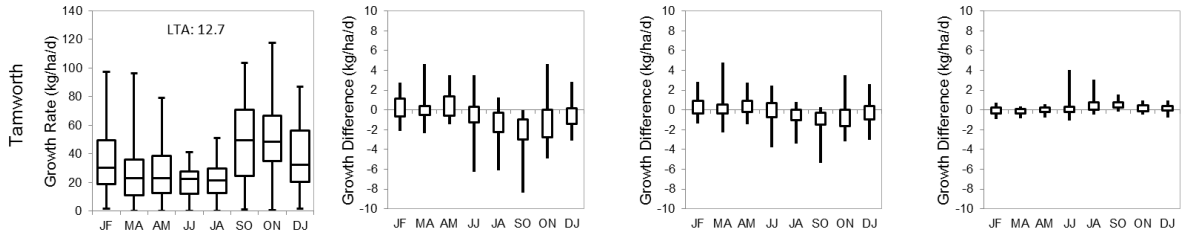

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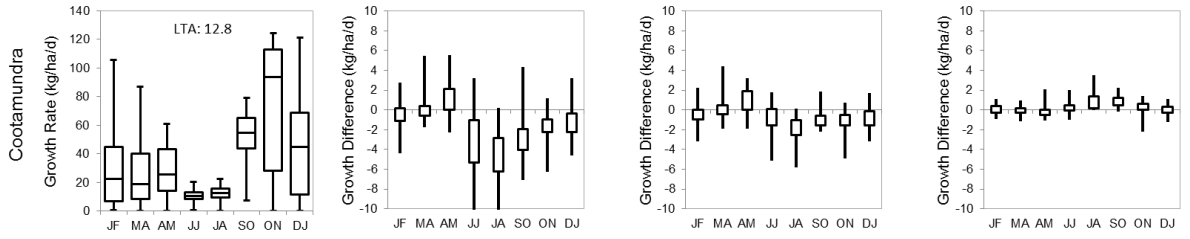

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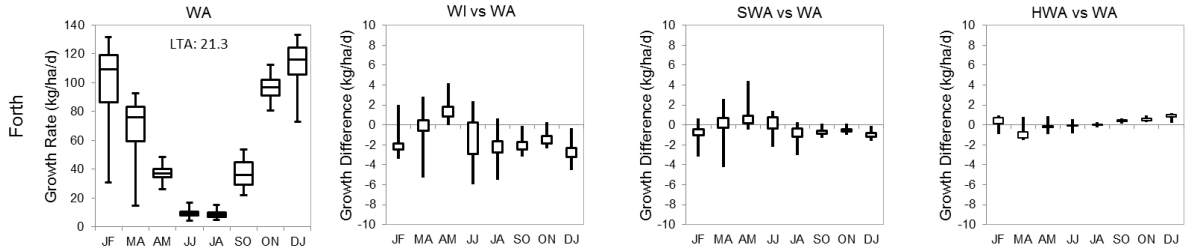

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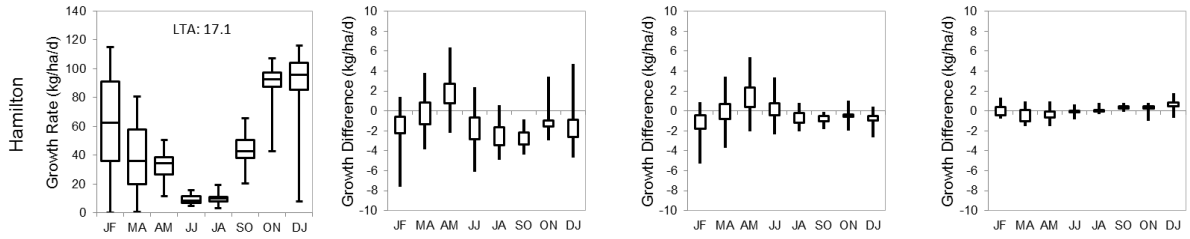

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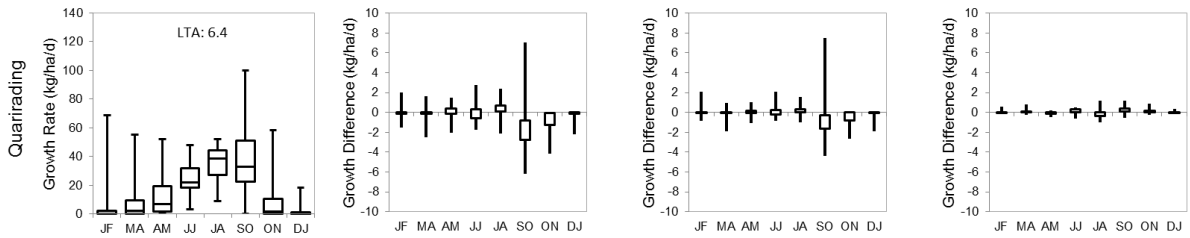

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908 Figure 5. Modelled, long term (over 40 year period) daily pasture growth rates (kg/ha/d) of four winter activity types of lucerne
909 in contrasting rainfed environments (boxes show the 25th and 75th percentile; whiskers show the maximum and minimum).
910 The furthest left-hand charts show modelled daily pasture growth rate for winter-active lucerne. Inset is the long-term average
911 (LTA) annual pasture growth (t/ha/y) and their variability (standard deviation). The remaining columns show the difference
912 between pasture growth rates of other winter activity types of lucerne relative to the winter-active genotype.

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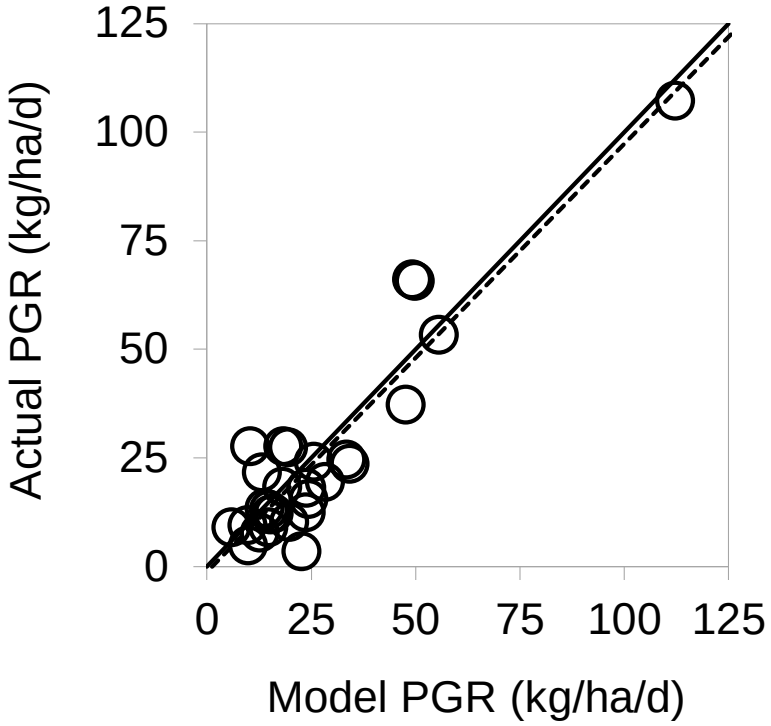

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915 Figure 6. Actual vs modelled average seasonal growth rates in each of the 7 experiments. A 1:1 relationship is shown as a
916 solid line and the regression of actual on modelled PGR is shown as a segmented line.

917

Table 2. Details of experimental datasets used in the evaluation of the new GRAZPLAN parameters for lucerne (Climate summaries are for 1950-2013.) The Cootamundra experiment was the only one with forage nutritive value; both Cootamundra and Quairading also had soil water information. Soil descriptions are based on the Australian soil classification system (Isbell 2002).

Location (descriptor)	Latitude	Average temperature (°C)	Average Rainfall (mm)	Soil	Genotype Classes* WD	SWA	WA	HWA	Key references
Forth	41°20'S	12.1	975	Red Ferrosol	X	X	X	X	Pembleton *et al.* 2010
Cranbrook	42°01'S	12.9	632	Red Ferrosol	X	X	X	X	Pembleton *et al.* 2010
Tamworth (Boschma)	31°15'S	16.7	678	Brown Chromosol	X			X	Li *et al.* 2010
Tamworth (Lodge)				Brown Chromosol	X	X	X	X	Lodge 1985
Hamilton	37°84'S	13.1	681	Brown Chromosol		X	X	X	Li *et al.* 2010
Cootamundra	34°40'S	15.3	572	Yellow Dermosol			X		Hayes *et al.* 2010
Quairading	32°02'S	17.6	366	Gravelly pale deep sand			X		Dolling *et al.* 2005b Latta and Lyons 2006

*Genotype classes were winter dormant (WD), semi-winter active (SWA), winter active (WA) and highly winter active (HWA).