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Simulation studies of nitrogen concentration in the diet of sheep grazing Mitchell and mulga grasslands in western Queensland

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Abstract. This study examined the potential to simulate the quality, as indicated by nitrogen concentration, of the diet of sheep grazing the Mitchell and mulga grasslands of western Queensland. Development of this simulation capability will allow pasture growth and animal production models to be more easily coupled. Modifications and optimisation of an existing beef cattle diet selection model, in conjunction with a single sward pasture model, accounted for 69.1% ($P < 0.001$) and 41.9% ($P < 0.001$) of variation in sheep dietary nitrogen concentrations observed from grazing trials on Mitchell and mulga grasslands, respectively. Failure to simulate some of the higher recorded dietary nitrogen concentrations was probably associated with high forb content in the diet. Examination of the results indicated that development of pasture growth models which simulate major pasture species, or groups of species (e.g. perennial grasses, annual grasses, browse, forbs, legumes), would appear to be necessary before diet selection models will be better able to explain the variation in dietary quality observed in grazing animals.

Additional keywords: modelling, *Acacia aneura*, mulga, *Astrebla* spp., Mitchell grass.

Introduction

The Queensland wool industry covers approximately 600 000 km², or 35% of the State, and includes many different soil and vegetation types (Weston *et al.* 1981; Carter *et al.* 1996). In 1996–97 approximately 10.43 million sheep and lambs were shorn in Queensland, producing 51.2 million kg of greasy wool valued at \$AU206 million (Anon. 1998). The mulga and Mitchell grass pasture communities are the most important in terms of western Queensland wool production. Mulga grasslands occur in the south-west of the State and are named after the shrub/tree *Acacia aneura* (mulga), which varies in density from sparse (1/ha) to very dense (8000/ha; Perry 1970). The Mitchell grasslands are located throughout western Queensland. Trees and shrubs are sparse in the northern Mitchell grasslands, whereas further south, grasslands merge with open wooded areas. Mitchell grass (*Astrebla* spp.) is the dominant pasture species but forbs and annual grasses grow in response to rainfall at specific times of the year (Orr and Holmes 1984).

In rangelands, rainfall is the primary determinant of pasture growth and hence potential animal productivity. The modelling of pasture production, which may include other

factors such as soil and pasture type, temperature, humidity, and the presence of trees, provides a further refinement of this indicator. In terms of simulation capability, the pasture growth model GRASP (McKeon *et al.* 1980, 1982, 1990, 1993; Rickert and McKeon 1982; Day *et al.* 1993; Scanlan and McKeon 1993; Littleboy and McKeon 1997) has been parameterised for most land systems/pasture communities of the Queensland rangelands (Day *et al.* 1997). Therefore, development of a model which simulated the quality of diet selected by grazing sheep was the next logical step to link pasture models to animal production models such as GrazFeed (Freer *et al.* 1997).

Modelling of diet selection and feed intake has been identified by numerous workers as a major challenge to the successful modelling of grazing animal production systems (White *et al.* 1979; Black *et al.* 1982; Kenney and Black 1984; Denham and Spreen 1986; Ketelaars 1986; Ungar and Noy-Meir 1986). Often in pen experiments examining diet selection, one factor is examined in isolation, whereas a wide range of factors influences grazing sheep. Dove (1996) suggested that there was a need for further experimental work to measure 'available herbage in botanical, physical, chemical,

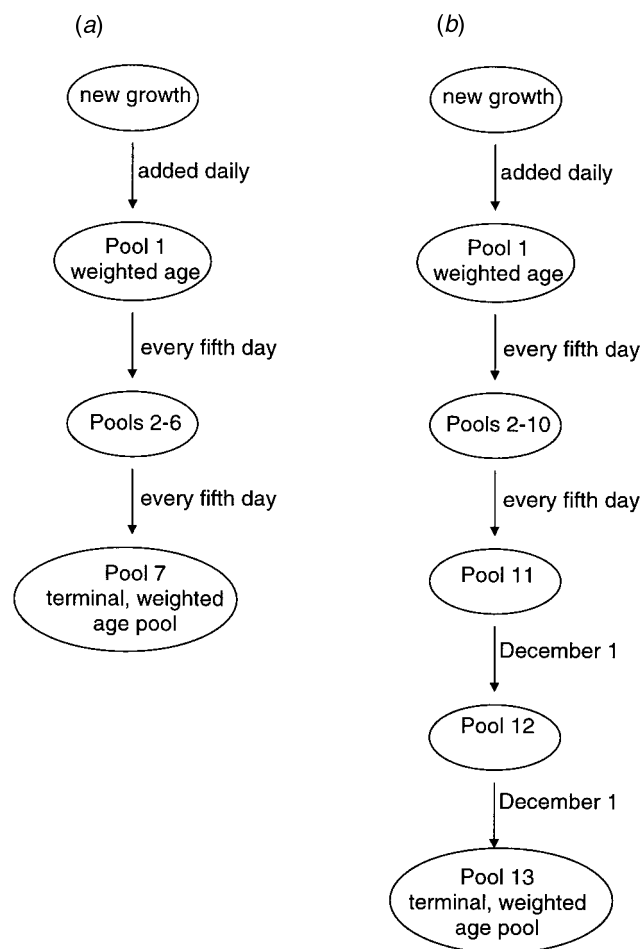


Fig. 1. Schematic representation of flow of pasture through the age pools of (a) the initial diet selection model; and (b) the final diet selection model.

and spatial terms, and to conduct experiments in which factors influencing diet selection are examined in an unconfounded way'.

Few models exist which link the grazing animal to the pasture community in rangelands. GrazFeed (Freer *et al.* 1997) requires the user to enter the mean digestibility and yield of the green and dead pasture pools. For example, mean digestibility of the green pool (range 0.5–0.8) is entered and the mass of green pool is partitioned into 4 digestibility classes: 0.5, 0.6, 0.7, 0.8. Similarly, the mean digestibility of the dead pool (range 0.3–0.7) is used to proportion the dead pool mass into 5 digestibility classes: 0.3, 0.4, 0.5, 0.6, 0.7. Dove (1996) noted that in the 'absence of appropriate data, the distributions are conceptual'. Sheep are assumed to select their diet from the highest digestibility class first, moving to less digestible classes as dictated by the availability of feed in each class and their predicted feed intake. GrazFeed calculates the potential feed intake of sheep based on their size and condition assuming *ad libitum* access to a forage of high digestibility (>0.8). This potential intake is then adjusted for physiological

state, presence of supplements, and pasture quality and availability. As GRASP does not estimate the mean digestibility of green and dead pools, and the distribution of the green and dead pools in GrazFeed is conceptual only, the approach adopted in this work was to use existing equations from a beef cattle diet selection model which estimated dietary nitrogen concentration and had been part of the early development of GRASP (Hendricksen *et al.* 1982; McKeon *et al.* 1982). This model of diet selection was based on the following concepts:

- nitrogen content and digestibility of plant components decline with age (Wilson and Marnette 1978)
- animals prefer and select for higher quality plant components, e.g. high green leaf content of diet (Ash *et al.* 1982)
- the age classes of a sward can be simulated, and the preferences of animals for younger ages can be described mathematically (Hendricksen *et al.* 1982; McKeon *et al.* 1982).

GRASP is a single sward model with parameters optimised for specific pasture communities being the average across a range of species in the sward. For example, the maximum nitrogen content of a sward (e.g. 1.7% N for mulga grasslands) will be less than the maximum nitrogen content of some species (e.g. forbs 2.6% N) which are a small fraction of the sward (Beale 1975). These differences in nitrogen content are also likely to be reflected in digestibility. However, whilst simulation models of botanical composition exist in early developmental stages for some rangeland communities, e.g. Ash *et al.* (1994), only conceptual models exist for Mitchell and mulga grasslands (Jones and Burrows 1994; McArthur *et al.* 1994). Hence, in this paper the amount of variation in diet quality from 6 separate grazing trials, which can be explained by age alone, is examined. The development of the diet selection model, as a subroutine within GRASP, is also described.

Model development

General approach

Model development was performed separately for the Mitchell and mulga grasslands in 2 stages:

- (1) optimisation of the existing GRASP relationship between the proportion of green in the diet of cattle relative to the pasture in line with available field data for sheep (Mitchell grass only);
- (2) construction and optimisation of a diet selection subroutine based on the preference and nitrogen content of age pools of pasture.

The first stage was necessary as the proportion of green in the diet influences the GRASP model via its effect on the green pool, and subsequent pasture growth response to available soil water. The GRASP model had, until this work was conducted, been used primarily in conjunction with either data from exclosures or cattle grazing trials. The potential for greater selection of green material by sheep

Table 1. Key features of the three versions of the diet selection model

Preference for each age pool calculated as a function of age (Fig. 2a). Calculations begun with youngest age pool		
Preference for each age pool modified by dry matter availability index		
<i>Diet Selection I</i>	<i>Diet Selection II</i>	<i>Diet Selection III</i>
Preference for each age pool recalculated as a ratio of each pool's preference to the sum of preferences for all age pools	Sum of preferences for all age pools had maximum value of 1.0. Thus final preference for each pool was the minimum of the pool preference from Eqn 1 adjusted for dry matter availability, or (1.0 – provisional sum of preferences). If sum of preferences at end of calculations <1.0, remaining preference was attributed in a stepwise method to the oldest pool first until sum of preferences equalled 1.0	As for Diet Selection II but if sum of preferences at end of calculations <1.0, remaining preference (1.0 – sum of preference) distributed to those pools having a preference >0 as a proportion of their contribution to the sum of preference
Annual dry matter intake of 40 kg DSE assumed to be 400 kg		
Nitrogen concentration of material selected from each age pool calculated as a function of age (Fig. 2b)		
Nitrogen intake from each pool summed to give daily nitrogen intake		

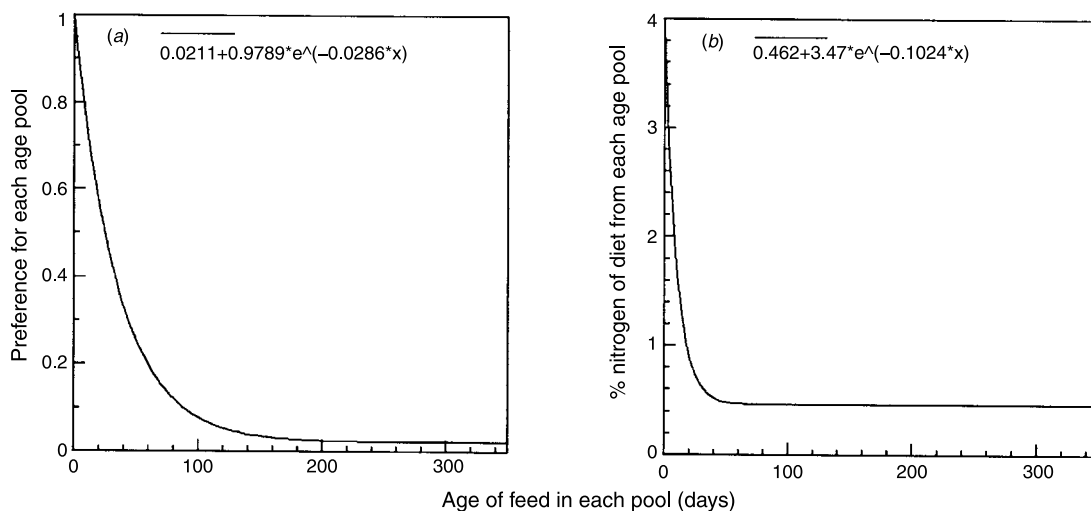


Fig. 2. Relationship between (a) preference index and age of pasture pool (Hendricksen *et al.* 1982); and (b) nitrogen content of the diet from each pasture pool and age of pasture pool (Hendricksen *et al.* 1982).

required that the cattle function be tested against available experimental data, and recalibrated if necessary prior to development of the diet selection subroutine based on pasture age pools. The proportion of green material in the diet was not utilised in this work as an indicator of diet quality, given the tendency of grazing sheep to have either 0% or 100% of green material in their diet, with few 'intermediate' values, as indicated in Fig. 4.

In the second stage, an initial diet selection model was developed using 7 pasture age pools derived from GRASP simulations. The first age pool was accumulated daily growth (kg DM/ha) for a 5-day period. The age of the pool was calculated by weighting for daily growth. After each 5-day

period the age and mass of pasture was passed to the next age pool; the 7th pool (pasture >30 days) was a terminal pool weighted for age (Fig. 1a).

Three versions of a diet selection model with a daily time step were developed and tested. Each model applied the following 3 functions in a different manner (Table 1):

- (1) A preference index from the beef production model of Hendricksen *et al.* (1982) was used as the starting point for the differential selection of material from each age class (Fig. 2a):

$$Pref = 0.0211 + 0.9789 \times \exp(-0.0286 \times age) \quad (1)$$

where *Pref* is the preference rating for a particular age pool, and *age* is age in days of material in each pool.

- (2) A dry matter availability index, represented by a simple ramp function, with no restriction when age pools exceeded 50 kg DM/ha. Below 50 kg DM/ha, the index declined linearly to a value of 0.0 at 0.0 kg DM/ha.
- (3) The nitrogen content of the diet selected from each age pool (*Nit%*) was calculated by the following equation from Hendricksen *et al.* (1982; Fig. 2*b*):

$$Nit\% = 0.462 + 3.47 \times \exp(-0.1024 \times age) \quad (2)$$

Initial work with the diet selection models found that long intervals occurred when there was no plant growth. All feed was in the 7th age pool and the weighted age of this pool did not allow for adequate diet selection in terms of preference and nitrogen content of diet. Thus, the number of age pools was increased to 13, the first 11 pools being updated every 5 days (Fig. 1*b*). This number of pools with a turnover of 5 days allowed for a greater range of possible dietary nitrogen concentrations to occur. The function describing dietary nitrogen as a function of age produced a relatively constant value just under 0.5% from approximately 50 days of age onwards (Fig. 2*b*). The final 2 age pools were included to mimic possible carryover of pasture material from previous growing seasons. On 1 December of each year, material in Pool 11 was transferred to Pool 12, and that in Pool 12 to Pool 13. Pool 13 became the terminal age pool.

The 3 versions of the diet selection models (I, II, and III) were then incorporated into the GRASP model as subroutines

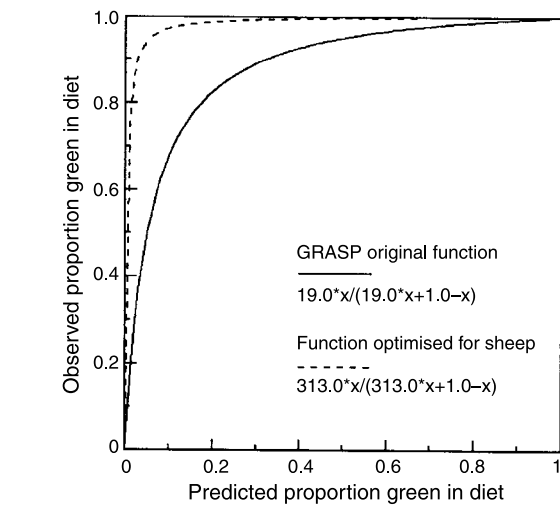
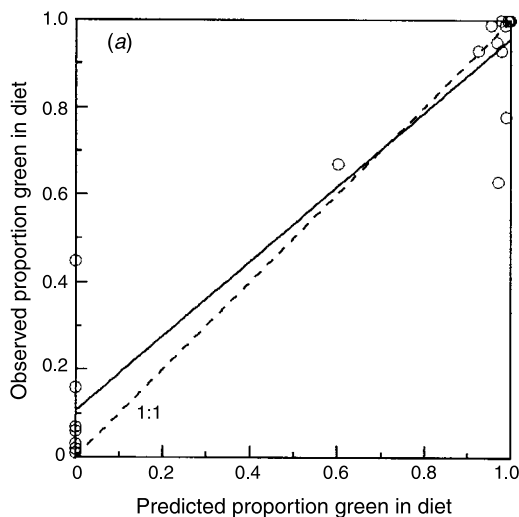


Fig. 3. Proportion of green in the diet as calculated using the original GRASP function for cattle and the optimised function from Lorimer's (1976) data for sheep.

for further testing. After preliminary work with observed data, modifications were made to the calculation of nitrogen concentration of the age pools replacing Eqn 2; new growth had a set nitrogen concentration, and as it aged, the decline in nitrogen content was calculated as a linear function of a growth index (*GIX**) with nitrogen decay occurring fastest under better growing conditions (Wilson 1982):

$$\text{Rate of nitrogen decay} = a - b \times GIX \quad (3)$$

$$Nit\%_t = (1.0 - \text{rate of nitrogen decay}) \times Nit\%_{t-1} \quad (4)$$

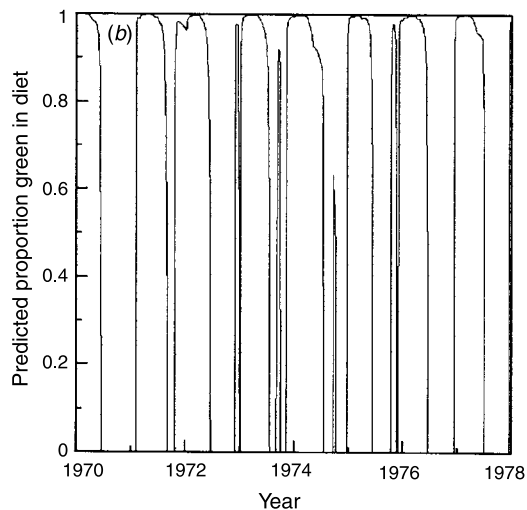
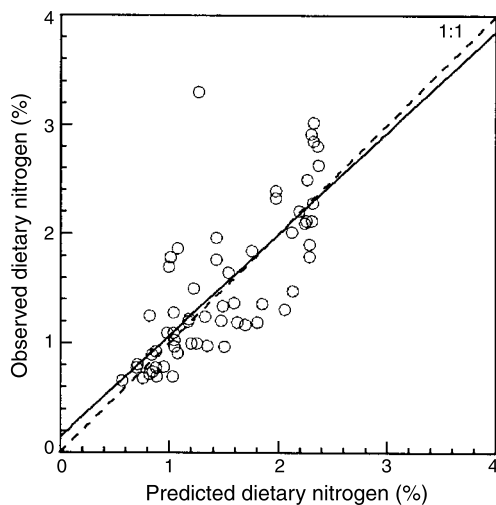


Fig. 4. (a) Predicted and observed values for green material present in the diet of Lorimer's (1976) sheep using the optimised GRASP parameter; and (b) predicted green proportion of the diet for sheep grazing at Toorak, north-western Queensland, for 1970–78, using the optimised GRASP parameter.

* Growth index based on soil water availability, radiation, and temperature represented the percentage of days in which the growth index was at a level ensuring that pasture growth would occur. This variable represents the length of the growing season for areas with a seasonal growth pattern.

Table 2. Parameter values for the Diet Selection II model for Mitchell (two stages of development) and mulga communities

Parameter/variable	Mitchell grasslands	Mulga
k value for decline in diet preference with age (Eqn 1)	$-1.0E-10$	$-1.0E-10$
Level of dry matter availability which no longer restricts preference or intake from individual age pools (kg DM/ha)	261	11.9
Nitrogen concentration (%) of new growth and maximum possible concentration in diet	2.39	2.18
y intercept for rate of nitrogen decay function (%/day; Eqn 3)	0.0041	0.0021
Slope for rate of nitrogen decay function (Eqn 3)	$-1.0E-10$	$-1.0E-10$

**Fig. 5.** Predicted and observed dietary nitrogen levels for Mitchell grass data using Diet Selection II following optimisation.

where $Nit\%_t$ is dietary nitrogen content of pool today, and $Nit\%_{t-1}$ is dietary nitrogen content of pool yesterday.

Using optimisation software (PEST, Watermark Computing 1994), each model was then tested against observed diet selection data. Parameters optimised in each model included:

- k value dictating the decline in diet preference of pools with increasing age, being -0.0286 in Eqn 1
- the value at which dry matter availability of each age pool had no restrictive effect on preference/intake of that pool
- maximum nitrogen content (%) of new growth, and therefore the maximum possible nitrogen content of the diet
- y intercept for rate of nitrogen decay (Eqn 3)
- slope for rate of nitrogen decay function (Eqn 3).

Mitchell grass: proportion of green in diet

The function in GRASP relating the percentage green material in diet to percentage green material in pasture was based on the work of Hendricksen *et al.* (1982) and Ash *et al.* (1982) with cattle (Fig. 3).

Lorimer (1976) recorded the percentage of green material in the diet of sheep at Toorak, north-western Queensland, with oesophageal fistulations (OF) but did not record the pro-

portion of green material in the pasture. GRASP was used to generate data on the proportion of green material in the pasture, and the data of Lorimer (1976) were then used to test the existing GRASP functions. Optimisation of the original equation resulted in a new line of best fit (Fig. 3) which displays the ability of sheep to select more green material relative to cattle. Lorimer (1976) made 24 observations of which 2 outliers, in terms of predicted *v.* observed values, were excluded from the analysis to ensure that the best overall function resulted from the optimisation process. Fig. 4a shows predicted and observed values using the optimised parameter and Fig. 4b shows the predicted proportion of green in the diet for sheep grazing at Toorak as a time series during 1970–78.

Mitchell grass: dietary nitrogen

Following optimisation of the function describing the proportion of green in the diet, the 3 diet selection models were optimised using Mitchell grassland dietary nitrogen data from Toorak in north-western Queensland, collected between 1970 and 1979 (39 observations; Lorimer 1976; Pritchard *et al.* 1986; Pritchard 1988), the Burenda grazing trial (10 observations; McMeniman *et al.* 1986a, 1986b), and the Biddenham experiment (11 observations; Orr *et al.* 1988). One observation in the Biddenham data set, where the observed nitrogen level was 3.3% (highest level of all data sets) and the predicted was only 1.27%, was excluded from the optimisation process as there was no supporting evidence for such a high quality diet (e.g. botanical composition of the diet was not available; yield, botanical composition, and frequency of occurrence of species in the pasture were not available; no rain was reported to fall in the 2 months prior to dietary sampling; the equivalent observed dietary nitrogen content for a paddock modified in an attempt to increase the forb yield was 1.71%). As such, this particular diet observation cannot currently be explained in terms of climate or pasture modelling.

The best results were obtained using the Diet Selection II model. The optimised parameters (Table 2) were able to explain 58.1% ($P < 0.001$) of the variation (all 60 data points, Fig. 5) and 69.1% ($P < 0.001$) of the variation (59 data points, Biddenham outlier excluded) in dietary nitrogen concentration of the Mitchell grassland data. The optimised k

Table 3. Worked example of the Diet Selection II model for Mitchell grasslands (Mitchell grass specific parameters are shown in italics)

Initial values for each age pool (dry matter and weighted age)	Pool 1: 50 kg DM/ha, 4.2 days Pool 2: 100 kg DM/ha, 8.1 days Pool 3: 100 kg DM/ha, 12.0 days	Pools 4–11: 0 kg DM/ha Pool 12: 1000 kg DM/ha, 420 days Pool 13: 0 kg DM/ha
Step 1, Pool 1	Calculate preference for Pool 1: $Pref = 0.0211 + 0.9789 \times \exp(-1.0E-10 \times 4.2) = 1.0$	
Step 2, Pool 1	Adjust preference for Pool 1 using dry matter availability index (<i>DMAI</i>): $DMAI = \min(1.0, 50/261) = 0.19$ $Pref = 1.0 \times 0.19 = 0.19$	
Step 3, Pool 1	Adjust preference for Pool 1 based on provisional sum of preferences (<i>Sum pref</i> , initial value = 0), and update provisional sum of preferences (max. value = 1.0): $Pref = \min(0.19, 1.0 - 0.0) = 0.19$ $Sum\ pref = \min(1.0, 0.0 + 0.19) = 0.19$	
Step 4, Pool 1	Calculate rate of nitrogen decay assuming <i>GIX</i> = 0.6: Rate of nitrogen decay = $0.0041 - 1.0E-10 \times 0.6 = 0.0041$	
Step 5, Pool 1	Calculate nitrogen content of Pool 1 assuming the nitrogen content of Pool 1 yesterday was 2.35%: $Nit\%_t = (1.0 - 0.0041) \times 2.35 = 2.34\%$	
Step 6, Pool 1	Calculate daily nitrogen intake from Pool 1 assuming daily dry matter intake of 1.1 kg/DSE: Nitrogen intake/DSE = $(0.19 \times 1.1) \times 2.34/100 = 0.0049$ kg N/day	
Step 1, Pool 2	Calculate preference for Pool 2: $Pref = 0.0211 + 0.9789 \times \exp(-1.0E-10 \times 8.1) = 1.0$	
Step 2, Pool 2	Adjust preference for Pool 2 using dry matter availability index (<i>DMAI</i>): $DMAI = \min(1.0, 100/261) = 0.38$ $Pref = 1.0 \times 0.38 = 0.38$	
Step 3, Pool 2	Adjust preference for Pool 2 based on provisional sum of preferences and update provisional sum of preferences: $Pref = \min(0.38, 1.0 - 0.19) = 0.38$ $Sum\ pref = \min(1.0, 0.19 + 0.38) = 0.57$	
Step 4, Pool 2	Rate of nitrogen decay for Pool 2 is the same as calculated for Pool 1, i.e. 0.0041	
Step 5, Pool 2	Calculate nitrogen content of Pool 2 assuming the nitrogen content of Pool 2 yesterday was 2.31%: $Nit\%_t = (1.0 - 0.0041) \times 2.31 = 2.30\%$	
Step 6, Pool 2	Calculate daily nitrogen intake from Pool 2 assuming daily dry matter intake of 1.1 kg/DSE: Nitrogen intake/DSE = $(0.38 \times 1.1) \times 2.30/100 = 0.0096$ kg N/day	
The above steps are repeated for each age pool and the nitrogen intake from each pool summed to give the total daily nitrogen intake		

value in Diet Selection II for the pool preference function (Eqn 1) was the lower boundary of the optimisation process ($-1.0E-10$) and represented a constant preference for all pools irrespective of the age of the pasture. However, in Diet Selection II, preference calculations begin with the youngest age pool with 'sum of preferences' having a maximum value of 1.0; hence, there is a forced preference for younger pools. The optimised value in Diet Selection II for the slope of the rate of decay function (Eqn 3) was also the lower boundary of the optimisation process ($-1.0E-10$) and represents a constant rate of decay irrespective of *GIX*. A worked example of the Diet Selection II model for Mitchell grasslands is shown in Table 3.

Mulga grasslands: dietary nitrogen

A much smaller data set existed for mulga grasslands in terms of diet selection; 16 observations of dietary nitrogen

were available from the Halton experiment (Beale 1975) and the Arabella grazing trial (McMeniman *et al.* 1986a, 1986b). Application of the Mitchell grass parameters and Diet Selection II to the mulga data resulted in a non-significant ($P > 0.05$) relationship between predicted and observed values with a consistent underprediction of dietary nitrogen content.

The observation of Beale (1975) of a dietary nitrogen concentration of 3.3% (predicted value 1.1% using Mitchell grass parameters) was excluded from optimisation as this level of dietary quality was not supported by the observed nitrogen content for pasture forbs (1.7%), the availability of forbs, and overall pasture nitrogen content relative to other dietary sampling periods.

Optimisation of the Diet Selection II model resulted in 41.9% of the variation in mulga dietary nitrogen concentration being explained (Fig. 6). The parameters for the mulga

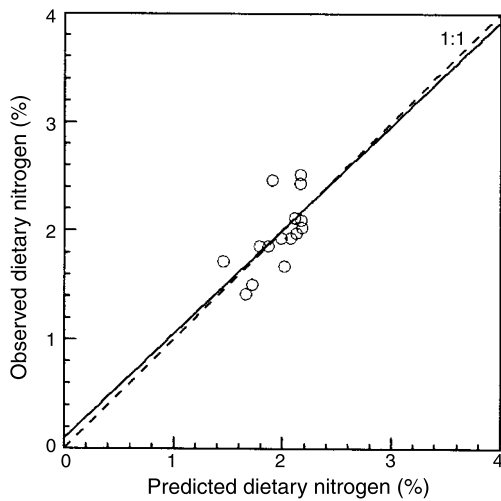


Fig. 6. Predicted and observed mulga dietary nitrogen concentrations using Diet Selection II mulga parameters.

model are listed in Table 2 and represent, relative to those of the Mitchell grass model:

- lower nitrogen concentration of new growth and therefore maximum concentration in diet
- reduced rate of nitrogen decay
- lower level of dry matter at which preference/intake of age pools is restricted.

Possible causes for the differences in parameters between the Mitchell and mulga models include:

- markedly reduced dry matter availability of mulga grassland (mean of experimental observations \approx 425 kg DM/ha) associations compared with Mitchell grasslands (mean of experimental observations \approx 1400 kg DM/ha)
- mulga leaf on trees and leaf litter were not considered in the predicted and observed dry matter yields.

Time series

The selected Mitchell and mulga diet selection models, developed from data pooled for their respective pasture types, were then used to examine how well individual trials were simulated (Fig. 7).

The Mitchell grass model was able to explain 73% ($P < 0.001$) of the variation in the Toorak data, although the higher observed dietary nitrogen levels were not well simulated. The Burenda data sets were obtained from different levels of utilisation with only 5 records per utilisation. The model simulated the general trend in observed values, although the results were not significant ($P > 0.05$). The Biddenham data were simulated well, 86.7% ($P < 0.001$) of the variation was explained when the observation (3.3% dietary nitrogen) not used in the optimisation was excluded from the regression. When this single outlier was included, the variation accounted for was not significant ($r^2 = 0.35$, $P = 0.547$), showing the potential difficulty of developing

diet selection models when data include variation that defies ecological explanation.

The mulga model was able to explain 51.3% ($P < 0.01$) of the variation in the Halton data when the outlier (3.3% dietary nitrogen) was excluded, and 32.9% ($P < 0.05$) when it was included. The time series plot shows that the model failed to adequately predict the 2 higher levels of dietary nitrogen (one of which was excluded from the optimisation process), but in general did a satisfactory job. The Arabella data set has only 3 data points and the model ranked the 3 points correctly but was unable to simulate the higher dietary nitrogen concentrations.

The diet selection models were able to account for a high proportion of variation in observed diets. The most likely source of outliers were very high nitrogen concentrations associated with forbs or new growth.

Discussion

This paper described work carried out to produce a diet selection model that would link with the GRASP model, producing dietary variables that would then be available for use in animal production models.

Modification, and optimisation of the GRASP function (from Hendricksen *et al.* 1982 and Ash *et al.* 1982) for calculating the proportion of green in diet, produced results consistent with generally accepted diet selection theories, i.e. the greater ability of sheep relative to cattle to graze selectively (Arnold 1981; Hodgson 1982; Forbes and Hodgson 1985).

The 3 theoretical diet selection models were initially based on Eqns 1 and 2 from the beef production model of Hendricksen *et al.* (1982), and a dry matter availability index. Eqns 1 and 2 related the preference (scale 0–1) and dietary nitrogen content of pasture to the age of that pasture, respectively. By using 11 age pools (Fig. 1b) in which transfer of material occurred every 5th day, pasture ages at which the nitrogen content dropped from its maximum to minimum value (Fig. 2b) were adequately simulated, allowing the selected dietary nitrogen to cover the range of observed concentrations. Pool 11 was a weighted age pool and represented 'older' material from the current growing season with the minimum nitrogen concentration, whereas Pools 12 and 13 represented carryover pasture from previous growing seasons. The nitrogen content of pasture (Eqn 2) was then replaced by Eqns 3 and 4. Eqn 3 calculated the rate of nitrogen decay as a linear function of a growth index, *GIX*, occurring fastest under better growing conditions.

Optimisation of Diet Selection II produced extremely small *k* values for Eqn 1, indicating that the best predicted and observed values were obtained with a constant preference for all age pools. However, there was an inherent selection for younger age pools in Diet Selection II because 'sum of preferences' had a maximum value of 1, with preference calculated first from youngest to oldest pools. Preference for subsequent age pools was the minimum of '1 – sum of pref-

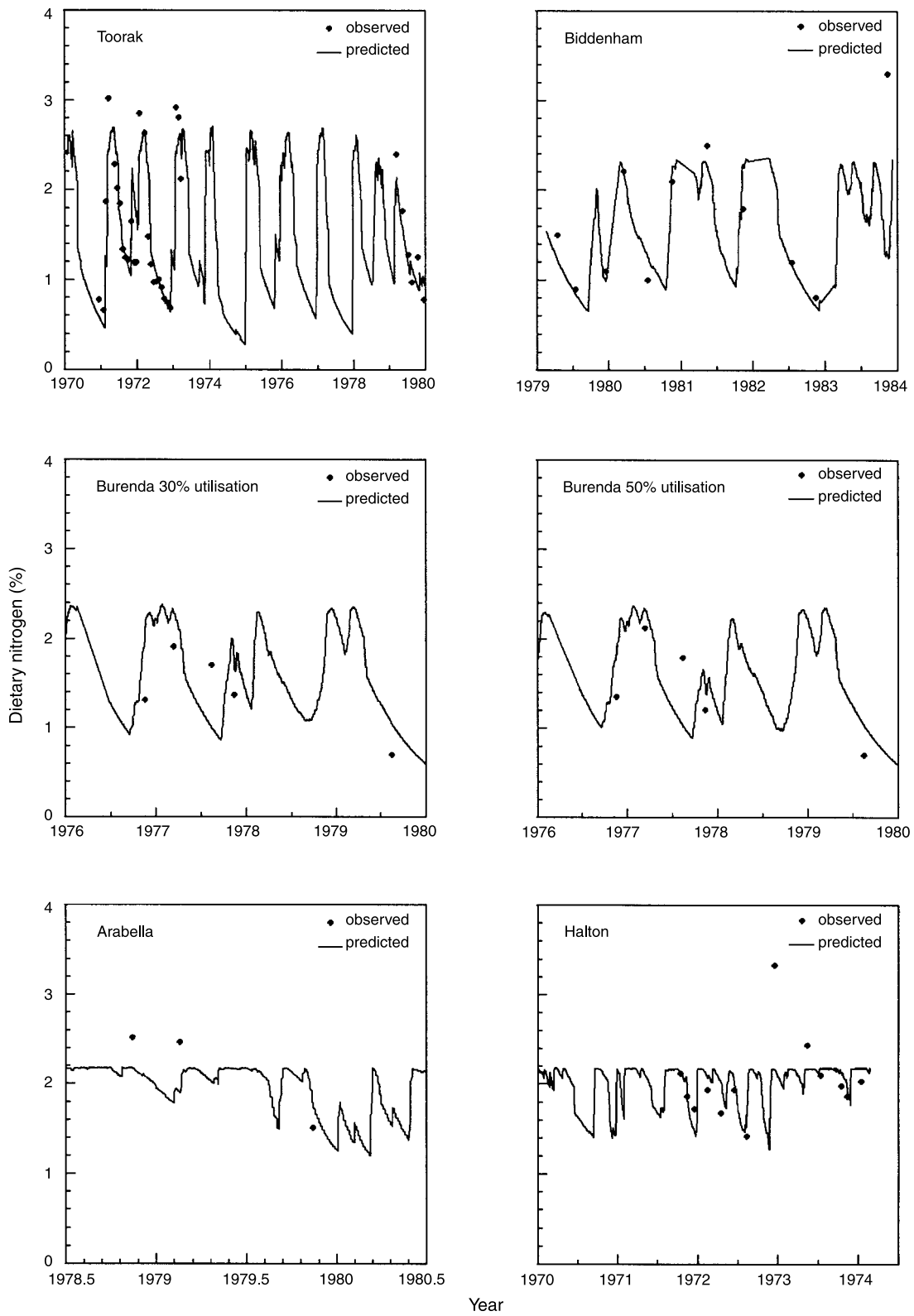


Fig. 7. Time series comparison of predicted and observed dietary nitrogen concentrations for Toorak, Biddenham, Burenda (30 and 50%), Arabella, and Halton using Diet Selection II and the appropriate parameters.

ferences' or the preference calculated using Eqn 1. Optimisation of Diet Selection II also produced parameters for Eqn 3 which represented a constant rate of decay irrespective of *GIX*. Thus, although rapid growth may dilute nitrogen content of overall pasture, it does not affect the nitrogen content of the selected diet.

Extreme outliers in terms of predicted and observed dietary nitrogen concentrations (Fig. 7) may represent diets composed of a large proportion of forbs with high nitrogen contents. For example, in Lorimer's (1976) data the dietary nitrogen contents greater than 2.5% all occurred when what was classified as 'other forbs', when measured (3 out of 5 observations), were the single largest component of the diet. Similarly, high dietary nitrogens (>2.5%) at Biddenham were associated with high forb content in the selected diet (Orr *et al.* 1988).

Differences between the parameters optimised for the Mitchell and mulga data sets represented lower nitrogen concentration from mulga new pasture growth, slower rate of mulga nitrogen decay, and a very low level of mulga pasture at which preference for each pool is affected by the dry matter availability index. The marked differences in Diet Selection II parameters for Mitchell and mulga data sets (Table 2) highlight the main difference in these 2 pasture communities. Mulga leaves, when available, may form a major dietary component, especially during periods of pasture shortage. The failure to measure/estimate the availability of mulga leaves would appear to be a major problem in grazing experiments conducted in mulga grasslands. The underlying assumption in this mulga dietary work is that the availability of mulga to grazing sheep is a constant resource, with no allowance for the dynamic nature and feedbacks operating within this ecosystem, such as the yield of mulga being inversely proportional to pasture yield. The height of available mulga forage is also important, with leaves above a certain level being unavailable to browsing sheep. Further, the mulga data set was limited in size.

Overall, Diet Selection II, optimised for the Mitchell and mulga data sets, accounted for a reasonable amount of the variation in dietary nitrogen, although there was a failure to simulate some of the higher recorded dietary nitrogen concentrations which are likely to be associated with high forb content diets. The studies also showed that a diet selection model developed for cattle grazing subtropical woodlands could be adapted for sheep grazing the 2 major vegetation communities of western Queensland. This suggests that the model may be adapted to other plant communities provided the necessary diet selection data are available. Further development of GRASP to simulate botanical composition, or major species groups (e.g. perennial grasses, annual grasses, browse, forbs, legume species), is also likely to lead to improvements in the modelling of diet selection. Similarly, a more comprehensive understanding of the nitrogen cycle in these pasture communities would allow this key process to be better incorporated in

the GRASP model. This would allow the equations presented here to be revised, particularly with regard to seasonal fluctuations in available soil nitrogen and the resulting nitrogen concentration in components of the pasture.

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References

- Anon. (1998) 'Australian commodity statistics: 1998.' (ABARE: Canberra)
- Arnold GW (1981) Grazing behaviour. In 'Grazing animals'. (Ed. FHW Morley) pp. 79–104. (Elsevier: Amsterdam)
- Ash AJ, Bellamy JA, Stockwell TGH (1994) State and transition models for rangelands, 4. Application of state and transition models to rangelands in northern Australia. *Tropical Grasslands* **28**(4), 223–228.
- Ash AJ, Prinsen JH, Myles DJ, Hendricksen RE (1982) Short-term effects of burning native pasture in spring on herbage and animal production in south-east Queensland. *Proceedings of the Australian Society of Animal Production* **14**, 377–380.
- Beale IF (1975) Forage intake and digestion by sheep in the Mulga Zone of Queensland, Australia. PhD Thesis, Colorado State University, Fort Collins.
- Black JL, Faichney GJ, Sinclair RE (1982) Role of computer simulation in overcoming limitations to animal production from pastures. In 'Nutritional limits to animal production from pastures'. (Ed. JB Hacker) pp. 473–493. (Commonwealth Agricultural Bureaux: Farnham Royal)
- Carter J, Flood N, Danaher T, Hugman P, Young R, Duncalfe F, Barber D, Flavel R, Beeston G, Mlodawski G, Hart D, Green D, Richards R, Dudgeon G, Dance R, Brock D, Petty D, *et al.* (1996) Development of a national drought alert strategic information system. Volume 3: Development of data rasters for model inputs. Final report on QPI 20 to Land and Water Resources Research and Development Corporation.
- Day KA, McKeon GM, Carter JO (1997) Evaluating the risks of pasture and land degradation in native pastures in Queensland. Final report for the Rural Industries Research and Development Corporation, Project No. DAQ 124A.
- Day KA, McKeon GM, Orr DM (1993) Comparison of methods for assessing productivity of native pastures in Queensland. In 'Proceedings of the XVII International Grassland Congress'. pp. 784–785. (NZ Grassland Association, Tropical Grassland Society of Australia, NZ Society of Animal Production, Australian Society of Animal Production–Qld Branch, NZ Institute of Agricultural Science)
- Denham SC, Spreen TH (1986) Introduction to simulation of beef cattle production. In 'Simulation of beef cattle production systems and its use in economic analysis'. (Eds TH Spreen, DH Laughlin) pp. 39–61. (Westview Press: Boulder, CO)
- Dove H (1996) Constraints to the modelling of diet selection and intake in the grazing ruminant. *Australian Journal of Agricultural Research* **47**, 257–275.

- Forbes TDA, Hodgson J (1985) Comparative studies of the influence of sward conditions on the ingestive behaviour of cows and sheep. *Grass and Forage Science* **40**, 69–77.
- Freer M, Moore AD, Donnelly JR (1997) GRAZPLAN: Decision support systems for Australian grazing enterprises—II. The animal biology model for feed intake, production, reproduction and the GrazFeed DSS. *Agricultural Systems* **54**, 77–126.
- Hendricksen RE, Rickert KG, Ash AJ, McKeon GM (1982) Beef production model. *Proceedings of the Australian Society of Animal Production* **14**, 208–210.
- Hodgson J (1982) Influence of sward characteristics on diet selection and herbage intake by the grazing animal. In 'Nutritional limits to animal production from pastures'. (Ed. JB Hacker) pp. 153–166. (Commonwealth Agricultural Bureaux: Farnham Royal, UK)
- Jones P, Burrows WH (1994) State and transition models for rangelands, 13. A state and transition model for the mulga zone of south-west Queensland. *Tropical Grasslands* **28**(4), 279–283.
- Kenney PA, Black JL (1984) Factors affecting diet selection by sheep. I. Potential intake rate and acceptability of feed. *Australian Journal of Agricultural Research* **35**, 551–563.
- Ketelaars JJMH (1986) Prediction of feed intake in ruminants. In 'Modelling of extensive livestock production systems'. (Eds N De Riddler, H Van Keulen, NG Seligman, PJH Neate) pp. 108–156. (International Livestock Centre for Africa: Addis Ababa)
- Littleboy M, McKeon GM (1997) Subroutine GRASP: Grass production model, Appendix 2 for evaluating the risks of pasture and land degradation in native pastures in Queensland. Final report for the Rural Industries Research and Development Corporation, Project No. DAQ 124A.
- Lorimer MS (1976) Forage selection by sheep grazing Mitchell grass in north-west Queensland. MAgSc Thesis, University of Queensland, Brisbane.
- McArthur SR, Chamberlain HJ, Phelps DG (1994) State and transition models for rangelands, 12. A state and transition model for the Mitchell grass, bluegrass-browntop and Queensland bluegrass pasture zones of northern Australia. *Tropical Grasslands* **28**(4), 274–278.
- McKeon GM, Day KA, Howden SM, Mott JJ, Orr DM, Scattini WJ, Weston EJ (1990) Northern Australian savannas: management for pastoral production. *Journal of Biogeography* **17**, 355–372.
- McKeon GM, Howden SM, Abel NOJ, King JM (1993) Climate change: adapting tropical and subtropical grasslands. In 'Proceedings of the XVII International Grassland Congress'. pp. 1181–1190. (NZ Grassland Association, Tropical Grassland Society of Australia, NZ Society of Animal Production, Australian Society of Animal Production—Qld Branch, NZ Institute of Agricultural Science)
- McKeon GM, Rickert KG, Ash AJ, Cooksley DG, Scattini WJ (1982) Pasture production model. *Proceedings of the Australian Society of Animal Production* **14**, 201–204.
- McKeon GM, Rickert KG, Robbins GB, Scattini WJ, Ivory DA (1980) Prediction of animal performance from simple environmental variables. In 'Fourth Biennial Conference, Simulation Society of Australia'. pp. 9–16. (Simulation Society of Australia)
- McMeniman NP, Beale IF, Murphy GM (1986a) Nutritional evaluation of south-west Queensland pastures. I The botanical and nutrient content of diets selected by sheep grazing on Mitchell grass and mulga grassland associations. *Australian Journal of Agricultural Research* **37**, 289–302.
- McMeniman NP, Beale IF, Murphy GM (1986b) Nutritional evaluation of south-west Queensland pastures. II The intake and digestion of organic matter and nitrogen by sheep grazing on Mitchell grass and mulga grassland associations. *Australian Journal of Agricultural Research* **37**, 303–314.
- Orr DM, Evenson CJ, Jordan DJ, Bowly PS, Lehane KJ, Cowan DC (1988) Sheep productivity in an *Astrelba* grassland of south-west Queensland. *Australian Rangeland Journal* **10**, 39–47.
- Orr DM, Holmes WE (1984) Mitchell grasslands. In 'Management of Australia's rangelands'. pp. 241–254. (CSIRO Australia: Melbourne)
- Perry RA (1970) Arid shrublands and grasslands. In 'Australian grasslands'. (Ed. RM Moore) pp. 246–259. (Australian National University Press: Canberra)
- Pritchard DA (1988) Some studies on the productivity of high and low wool producing sheep in western Queensland. MSc Thesis, James Cook University, Townsville.
- Pritchard DA, Connelly PT, Kelly JG, Hopkins PS (1986) Diet selection and wool growth of high and low producing sheep at pasture in north west Queensland. *Proceedings of the Australian Society of Animal Production* **16**, 307–310.
- Rickert KG, McKeon GM (1982) Soil water balance model: WATSUP. *Proceedings of the Australian Society of Animal Production* **14**, 198–200.
- Scanlan JC, McKeon GM (1993) Competitive effects of trees on pasture are a function of rainfall distribution and soil depth. In 'Proceedings of the XVII International Grassland Congress'. pp. 2231–2232. (NZ Grassland Association, Tropical Grassland Society of Australia, NZ Society of Animal Production, Australian Society of Animal Production—Qld Branch, NZ Institute of Agricultural Science)
- Ungar ED, Noy-Meir I (1986) Behavioural aspects of intake at pasture in ruminants. In 'Modelling of extensive livestock production systems'. (Eds N De Riddler, H Van Keulen, NG Seligman, PJH Neate) pp. 80–106. (International Livestock Centre for Africa: Addis Ababa)
- Watermark Computing (1994) 'PEST: Model-independent parameter estimation. User's manual.' (Watermark Computing)
- Weston EJ, Harbison J, Leslie JK, Rosenthal KM, Mayer RJ (1981) Assessment of the agricultural and pastoral potential of Queensland. Map No. 3; Native pasture communities. Queensland Department of Primary Industries, Agricultural Branch, Technical Report No. 27, Brisbane.
- White DH, Nagorcka BN, Birrell HA (1979) Predicting wool growth of sheep under field conditions. In 'Physiological and environmental limitations to wool growth'. (Eds JL Black, PJ Reis) pp. 139–161. (University of New England Publishing Unit: Armidale)
- Wilson JR (1982) Environmental and nutritional factors affecting herbage quality. In 'Nutritional limits to animal production from pastures'. (Ed. JB Hacker) pp. 111–131. (Commonwealth Agricultural Bureaux: Farnham Royal, UK)
- Wilson JR, 'tMannetje L (1978) Senescence, digestibility and carbohydrate content of buffel grass and green panic leaves in swards. *Australian Journal of Agricultural Research* **29**, 503–516.

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