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Simulation of growth and development of diverse legume species in APSIM

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Abstract. This paper describes the physiological basis and validation of a generic legume model as it applies to 4 species: chickpea (*Cicer arietinum* L.), mungbean (*Vigna radiata* (L.) Wilczek), peanut (*Arachis hypogaea* L.), and lucerne (*Medicago sativa* L.). For each species, the key physiological parameters were derived from the literature and our own experimentation. The model was tested on an independent set of experiments, predominantly from the tropics and subtropics of Australia, varying in cultivar, sowing date, water regime (irrigated or dryland), row spacing, and plant population density. The model is an attempt to simulate crop growth and development with satisfactory comprehensiveness, without the necessity of defining a large number of parameters. A generic approach was adopted in recognition of the common underlying physiology and simulation approaches for many legume species. Simulation of grain yield explained 77, 81, and 70% of the variance (RMSD = 31, 98, and 46 g/m²), respectively. Biomass at maturity was simulated less accurately, explaining 64, 76, and 71% of the variance (RMSD = 134, 236, and 125 g/m²) for mungbean, peanut, and chickpea, respectively. RMSD for biomass in lucerne (n = 24) was 85 g/m² with an R^2 of 0.55. Simulation accuracy is similar to that achieved by single-crop models and suggests that the generic approach offers promise for simulating diverse legume species without loss of accuracy or physiological rigour.

Additional keywords: peanut, lucerne, mungbean, chickpea, model.

Introduction

The development of the Agricultural Production Systems Simulator (APSIM) (McCown *et al.* 1996) has enabled the simulation of diverse cropping systems that can be targetted at issues such as crop rotation (e.g. Carberry *et al.* 1996; Probert *et al.* 1998), intercropping (Carberry *et al.* 1996), and resource degradation (Probert *et al.* 1995). In order to be relevant to a wide variety of agricultural systems, APSIM requires the capability to simulate legume crops and pastures grown in association with cereal, oilseed, and fibre crops. Accordingly, the purpose of this paper is to describe the physiological basis and performance of the APSIM-Legume model as it applies to 4 legume species. The approach taken was to develop a generic legume module that adopted well-established approaches to modelling physiological process but adding new insight where necessary.

The design criteria for APSIM-Legume included: (*i*) the capability of simulating the development, growth, and yield of a wide range of legume species using generic code; (*ii*) the desire to address legume physiology at a level commensurate with the simulation of other biological and physical processes within APSIM; (*iii*) compatibility of legume module requirements and outputs with other components of the APSIM library of modules (e.g. soil water balance, soil N balances, etc.); (*iv*) ability to simulate the consequence of

legume crops on the system beyond the life-span of the crop itself (e.g. residual carbon and nitrogen effects of legumes); and (v) maximal utility of the current knowledge on legume physiology and of the existing approaches to simulating crop development and growth.

There are currently a number of 'families' of crop simulation models that include a wide diversity of species; for example, the CERES group of cereals (maize, wheat, barley, sorghum). Within these model 'families', similar subroutines are used to simulate the same physiological processes, with often only the coefficients of functional relationships differing between species. Whenever model improvements are made, they must be incorporated into each crop model, thus making source code maintenance and version control complicated and costly. In addition, if a new crop is to be added to the 'family', source code must be replicated adding to future software maintenance costs.

In recognition of the common underlying physiology and simulation approaches for crops within a family, others have attempted to develop generic models that are able to be parameterised for a wide range of species. For example, the CROPGRO model (Boote *et al.* 1998) can simulate growth and development of 3 crop legumes [common bean (*Phaseolus vulgaris*), peanut (*Arachis hypogaea*) and soybean (*Glycine max*)]. Other generic models include STICS (Brisson *et al.* 1998) and EPIC (Williams *et al.* 1989). Such models consist of a single set of subroutines and are parameterised with coefficients that are external to the code. However, it has been acknowledged that such an approach, while improving the functionality of the model for a range of species, can result in a compromise in physiological rigour and predictive ability.

Current models of legume production differ in approaches taken to simulating growth and development. One relatively simple approach is the soybean model of Sinclair (1986), subsequently modified to also simulate cowpea (Vigna unguiculata) and black gram (Vigna mungo) (Sinclair et al. 1987) and chickpea (Cicer arietinum L.) (Soltani et al. 1999). On the other hand, the CROPGRO model is more detailed in its coverage of various physiological processes. Both models simulate biomass and nitrogen dynamics in response to climate, nitrogen, and water supply. Although the Sinclair model has been tested in northern Australia (Sinclair et al. 1987), Florida (Sinclair 1986), and Argentina (Sinclair et al. 1992), it does not simulate cultivar differences in phenology, the growth of roots, and is limited in ability to simulate crops at different plant populations and row spacings. On the other hand, CROPGRO requires the specification of over 40 crop-specific and cultivar-specific parameters, which can make it difficult to interpret how the model works and limits its portability across environments and cultivars. The APSIM-legume model attempts to chart a middle course between these two types of models, so that crop growth and development can be simulated with satisfactory

comprehensiveness, without the necessity of defining a large number of parameters.

This paper describes the development and testing of a generic model, APSIM-Legume, for a wide range of legume species, covering the temperate grain legume chickpea, the warm-season grain legumes mungbean (*Vigna radiata* (L.) Wilczek) and peanut, and the perennial forage legume lucerne (*Medicago sativa* L.).

Model overview

The legume module, like other crop modules of APSIM, simulates crop development, growth, yield, and nitrogen accumulation in response to temperature, radiation, photoperiod, soil water, and nitrogen supply. The concepts used in APSIM-Legume have been extended from the modelling approaches first developed by Ritchie (1986), Sinclair (1986), Monteith (1986), and others, and summarised by Ritchie (1991). The model uses a daily time-step, and is designed to simulate a uniform field and predict, on an area basis, grain yield, crop biomass, crop nitrogen uptake and fixation, and partitioning within the plant. Approaches used in modelling crop processes balance the need for comprehensive description of the observed variation in crop performance across diverse production environments and the need to avoid large numbers of parameters that are difficult to measure.

In parameterising a generic model for different legume species it is helpful to introduce the concept of essential, desirable, and optional parameters. Essential parameters are those to which the model has greatest sensitivity, often differ significantly across species, and hence must be derived from experimentation for individual species. Examples of essential parameters are phyllochron, radiation extinction coefficient, and radiation-use efficiency. Although it is often possible to define essential parameters from published sources, because of their importance it is often necessary to confirm the value of such parameters in local experimentation using commonly grown cultivars. Desirable parameters are those to which the model has less sensitivity, but are often difficult to derive, and hence can often be estimated or assumed to vary little across individual species. Examples of desirable parameters could be the fraction of above-ground biomass partitioned to roots, or the transpiration efficiency coefficient. Optional parameters are those that have least impact upon simulations in the majority of cases and would be expensive to derive exhaustively for each species. Examples of optional parameters could be those that control crop survival under severe water stress, maximum temperature for thermal time accumulation, or the fraction of stem dry weight used in translocation to grain. The present paper will apply the concept of essential, desirable, and optional parameters in describing the derivation of parameters for the different species covered by the generic model.

Many physiological parameters vary among cultivars within a species. In this paper we differentiate between crop species parameters that are considered to vary little within a species, and cultivar parameters where there is good evidence to support different parameter values for cultivars within a species. While, in theory at least, it is possible for all crop species parameters to vary across cultivars, it is our intention to minimise the number of cultivar parameters so that characterisation of a new cultivar is relatively easy.

Materials and methods

The parameters and relationships that were necessary to build the functions in the model were derived mostly from previously published studies, with the exception of those for leaf canopy expansion, which were derived from experimental studies conducted by the authors.

Experimental studies for parameter derivation

A number of field studies were undertaken to derive parameters not available from published studies, or where it was thought that derivation of a parameter was required to confirm its applicability to local conditions or cultivars.

Experiment 1

This experiment was designed to collect data on canopy development and biomass partitioning of mungbean (cv. Berken). The crop was sown on day of year (DOY) 32 of 1991 at Lawes, Qld, Australia ($27^{\circ}34'S$, $152^{\circ}20'E$) under irrigation on an alluvial clay soil. There were 2 plant population densities (10 and 36 plants/m²) at a row spacing of 32 cm, with 2 replications and a plot size of 21.5 m by 36 m. Net above-ground biomass and components, and leaf area index (LAI), were sampled from 1.9-m^2 quadrats on DOY 51, 58, 66, 75, 81, 87, 94, and 101, with final maturity sampling occurring on DOY 108. At samplings before flowering, 4 plants per plot were analysed for the distribution of individual leaf area as a function of nodal position on the mainstem. Mainstem node number, total plant leaf number, and senesced mainstem node number were recorded on 5 tagged plants in each plot every 3–5 days. The cotyledonary node was numbered 0. Pests, diseases, and weeds were controlled with appropriate measures.

Experiment 2

This experiment was designed to collect data on canopy development and biomass partitioning of chickpea (cv. Amethyst). The crop was sown on 2 sowing dates: DOY 150 and 221 in 1991 at Lawes, under irrigation on an alluvial clay soil. The plant population density was 28 plants/m² at a row spacing of 50 cm, with 2 replications and a plot size of 10 m by 5.5 m. Net above-ground biomass and components, and LAI, were sampled from 2.0-m² quadrats on DOY 190, 213, 235, 261, and 292 for the first sowing and 261, 303, 317, and 332 for the second sowing. Flowering was on DOY 261 and 286 and physiological maturity on DOY 291 and 332, respectively. Mainstem node number, total plant leaf number, and senesced mainstem node number were recorded on 5 tagged plants in each plot every 3–5 days. At samplings before flowering, 4 plants per plot were analysed for the distribution of individual leaf area as a function of nodal position on the mainstem. Pests, diseases, and weeds were controlled with appropriate measures.

Experiment 3

A field study was conducted under irrigated conditions at Lawes for the purpose of deriving model parameters for lucerne that were unavailable from the literature. Replicated plots of cv. Hunter River were sown on DOY 134 in 1994 at 10 kg/ha on an alluvial clay soil. The stand was managed according to commercial best practice (irrigation and weed control). Forage was cut and removed (harvest height 50 mm) at 10% flowering. Sequential samplings, between forage harvests, were made on 24 occasions over 19 months. Leaf and stem weight, leaf area, and stem number per unit area were determined, and leaf and stem components were analysed for nitrogen. Biomass in the stubble (below 50 mm) was also sampled. Tube solarimeters (Delta-T) were placed within and above the stands to log light interception continuously in order to calculate radiation use efficiency and the radiation extinction coefficient.

Experiment 4

In a separate study at Lawes, area of individual lucerne leaves with differing node position along the stem was determined on 3 occasions (DOY 306, 320, and 329 in 1996) in an irrigated established stand of cv. Hunter River. Five stems from a single plot were cut at ground level and the area of leaf lamina at each node measured with a planimeter.

Re-analysis of published studies

The size of individual leaves as a function of mainstem node position was derived for the same cultivar of mungbean (cv. Berken), using unpublished data from the fully irrigated studies of Muchow *et al.* (1993*a*, 1993*b*). The fully expanded area of individual leaves from mainstem node positions along the stem was determined at various samplings through the season. Data were from the 5 January 1988 and 28 February 1989 sowings at Katherine, NT, Australia (14°28'S, 132°18'E), taken from 5 plants in each of 4 replicate plots.

Experimental studies for model testing

Published and unpublished datasets were collated for testing of the model (Table 1). Data were from experiments mostly conducted in the subtropics and tropics of Australia under both dryland and irrigated conditions, with sowing date, plant density, row spacing, and cultivar being the primary agronomic factors that were manipulated.

Model description and parameterisation

Phenology

Phenology parameters were derived from already published studies. Thermal time is used in the model to drive phenological development and canopy expansion. In APSIM-Legume, thermal time is calculated using 3 cardinal temperatures: base, optimum, and maximum. For all species, cardinal temperatures were derived from the literature (Table 2). Each day, the phenology routines calculate daily thermal time (in degree-days) from 3-hourly air temperatures interpolated from the daily maximum and minimum temperatures (Jones et al. 1986). These daily thermal time values are accumulated into a thermal time sum, which is used to determine the duration of each phase. Crop phenology is divided into phases separated by stages, the duration of each based on daily temperature and photoperiod (Carberry et al. 1992). The duration from sowing to flowering is simulated as 4 phases: sowing to emergence; emergence to the end of the basic vegetative (or juvenile) period, which is a photoperiod-insensitive phase; a photoperiod-induced phase, which depends upon the cultivar's photoperiod sensitivity and which ends at floral initiation; and a floral development phase, which ends at flowering. The duration from flowering to physiological

N^{A}	Location	Sowing date	Agronomy	Cultivar	Reference
			Mungbean		
1	Katherine, NT	1 Dec. 1987	Irrigated	King	RC Muchow, unpubl.
2	Katherine, NT	28 Feb. 1989	Irrigated, dryland	King	Muchow et al. 1993a, 1993b
1	Katherine, NT	7 Feb. 1989	Dryland	King	Muchow et al. 1993a, 1993b
1	Lawes, Qld	9 Jan. 1990	Irrigated	King	Muchow et al. 1993a, 1993b
3	Kununurra, WA	1 Apr. 1980	Water regimes	Berken	Muchow and Sinclair 1986
6	Dalby, Qld	10 Dec. 1976, 10 Jan. 1978	Water regimes	Berken	Lawn 1982
2	Lawes, Qld	1 Feb. 1991	Irrigated, 10 & 35 plants/m ²	Berken	PS Carberry, unpubl.
9	SE Qld	Various	Dryland	Various	PS Carberry, unpubl.
8	Douglas Daly, NT	15 Jan., 2 Feb., 15 Feb. 1988	Irrigated	King, Putland, Satin	SJ Yeates, unpubl.
3	Katherine, NT	14 Jan., 17 Jan. 1990, 15 Jan. 1991	Irrigated	King, Putland	SJ Yeates, unpubl.
9	Kununurra, WA	1 Jan., 17 Jan. 1988	Irrigated	King, Putland	SJ Yeates, unpubl.
			Chickpea		
9	Lawes, Qld	24 May 1993	Irrigated, 17–79 plants/m ² , 17–70 cm row spacing	Amethyst	R Brinsmead, unpubl.
2	Lawes, Qld	20 May, 6 Aug. 1990	Irrigated	Amethyst	PS Carberry, unpubl.
2	Lawes, Qld	29 May, 8 Aug. 1991	Irrigated	Amethyst	PS Carberry, unpubl.
2	Lawes, Qld	14 June 1995	Dryland and irrigated	Amethyst	JE Turpin, unpubl.
4	Emerald, Qld	5 Mar., 13 Apr., 2 May, 18 July 1989	Irrigated	Amethyst	R Brinsmead, unpubl.
4	Biloela, Qld	12 Mar., 26 Apr., 18 June, 13 Sept. 1990	Irrigated	Amethyst	R Brinsmead, unpubl.
6	Windridge, NSW	7 May 1992	Dryland, various N rates	Amethyst	H Marcellos and W Felton, unpubl.
2	Warwick, Qld	14 June, 19 Aug. 1990	Dryland	Amethyst	R Brinsmead, unpubl.
			Peanut		
13	Kingaroy, Qld	1 Nov., 5 Dec. 1984, 15 Jan., 20 Nov. 1985, 8 Nov. 1987	Irrigated, densities 8.8–17.6 plants/m ²	Early bunch, McCubbin	Bell et al. 1991a
5	Kunnunura, WA	6 Dec., 29 Dec. 1982, 18 Jan., 7 Feb., 1 Mar. 1983	Irrigated	Early bunch	Bell 1986
2	Bundaberg, Qld	23 Nov., 11 Dec. 1989	Irrigated, densities 8.8–9.5 plants/m ²	Early bunch	Bell <i>et al.</i> 1992, Wright <i>et al.</i> 1993
1	Gainsville, FL, USA	14 May 1990	Irrigated	Early bunch	KJ Boote, unpubl.
2	Kingaroy, Qld	18 Dec. 1989	Dryland, irrigated	Early bunch	GC Wright, unpubl.
9	Redvale, Qld	Various 1986–94	Dryland	Virginia bunch	M Bell, unpubl.

Table 1. Details of the datasets used to test APSIM-Legume

^A Number of crops/treatments in each dataset.

maturity is simulated as 3 phases, the duration of each based on fixed thermal time targets: flowering to the start of grain filling growth, start of grain filling to end of grain filling, and end of grain filling to maturity.

Sowing to germination is dependent on soil water status. If soil water in the soil layer in which the seed is sown is sufficient, the minimum level being specified by the parameter *pesw_germ*, then germination takes place one day after sowing. The thermal time target for the germination to emergence phase includes an effect of sowing depth. The phase is comprised of an initial period of fixed thermal time during which shoot elongation is slow (the 'lag' phase), and a linear period, where the rate of shoot elongation towards

the soil surface is linearly related to air temperature (measured in degree-days/mm). Most studies on seedling emergence have simply recorded the accumulated thermal time between germination and 50% emergence from a given sowing depth (e.g. Angus *et al.* 1980). For the purposes of model parameterisation, the value of *shoot_lag* has been assumed to be around 15 degree-days, and *shoot_rate* has been derived from studies where thermal time to emergence was measured and where sowing depth was known (Table 2). The parameters controlling the duration of phases between emergence and maturity are cultivar-specific. The duration from emergence to the end of the basic vegetative (or juvenile) period is determined by temperature, modified by

Parameter none	Units	Parameter description	Chickpea	Mungbean	Peanut	Lucerne
Cardinal temperatures for thermal time calculation	°C	Base temp. Optimum temp. Maximum temp.	0^{A} 30^{A} 40^{A}	7.5 ^B 30 ^B 40 ^B	9 ^C 29 ^C 39 ^C	5 ^D 30 ^D 40 ^D
Shoot_rate	Degree-days/mm	Thermal time required per mm elongation by young shoot before emergence	2.0 ^E	0.6 ^E	2.5 ^F	1.0 ^G

Table 2. Model parameters for phenology, including sources

^ASingh and Virmani (1996). ^BEllis et al. (1994). ^C Leong and Ong (1983), Bell et al. (1991a). ^DFick et al. (1988), Denison and Loomis (1989). ^EAngus et al. (1980). ^FHammer et al. (1995). ^GAssumed.

vernalisation. The length of the phase is a function of the number of accumulated 'vernal days', as used in some models of plant development (e.g. Habekotte 1997). The rate at which vernal days accumulate varies with temperature. None of the 4 species examined in this paper exhibited a vernalisation response, so the length of the basic vegetative phase was not parameterised to vary with vernalisation. Following the end of the basic vegetative phase, the phase ending in floral initiation stage is sensitive to photoperiod. This photoperiod-induced phase increases as photoperiod increases above a base photoperiod for short day species (such as mungbean), or decreases for a long-day species (such as chickpea). In order to be truly generic, APSIM-Legume must be able to simulate the different photoperiod responses found across species, including quantitative (facultative) or qualitative (obligate) response types. This is achieved by defining the relationship between photoperiod and the thermal time from the end of the basic vegetative phase to floral initiation so that any photoperiod response can be flexibly configured. The values of base and critical photoperiod for each species were determined from the literature, and the photoperiod sensitivity was derived by using an optimisation program, as described by Carberry (1996).

The rate of phenological development may be increased or decreased under water or nitrogen deficit. The phenological development of some legumes species appears to be particularly plastic in response to environmental stresses. Effects of deficits on phenology can be simulated with the current model framework, but there is a lack of published information enabling the functional relationships to be parameterised.

Leaf area development

Experiments 1 and 2 were used to derive functions for the appearance, expansion and senescence of leaves (Table 3). Leaf appearance is determined from the rate of node appearance on the main stem (*node_app_rate*) and the potential number of leaves per mainstem node

(leaves per node). This latter parameter is designed to account for leaf appearance on branches in widely spaced plants. Nodes are assumed to produce more than one leaf (i.e. begin branching) when the plant has attained a set node number. Linear regression relationships between mainstem node number and cumulative thermal time from emergence to flowering produced values for node app rate of 46 and 100 degree-day per node for chickpea (Fig. 1a) and mungbean (Fig. 1b), respectively. The parameter leaves_per_node was derived from the low density treatments in Expts 1 and 2, where it was assumed that potential leaf number was realised. Parameter *leaves_per_node* is the regression slope of the relationship between total plant leaf number and mainstem node number, with values of 13.4 and 2.1 leaves per node for chickpea (Fig. 1c) and mungbean (Fig. 1d), respectively. The x-intercept represents the effective start of branching. Node and leaf appearance can potentially occur from emergence until maturity, depending upon the available supply of assimilate for leaf growth.

The studies of Sato (1971) and Pearson and Hunt (1972) were analysed for the rate of appearance of nodes in lucerne. These authors measured node appearance during primary growth from seed, and Pearson and Hunt (1972) also measured node appearance during regrowth after cutting. There is consistency between the two studies of primary growth, and evidence that node appearance is faster during regrowth, compared with growth from seed. In the absence of further information, we assumed values of 51 and 34 degree-days (base 5°C) per node for the seedling and regrowth phases, respectively. As the primary unit in the lucerne model is the stem, the model does not simulate branching *per se*. Hence, it is assumed that for each node produced in the model for lucerne, there is one leaf, i.e. *leaves_per_node* = 1.

Potential leaf area expansion is the product of leaf appearance and the maximum size of leaves, which varies as a function of nodal position. Maximum leaf size as a function of node number was derived for mungbean from Expt 1 and

Parameter name	Units	Parameter description	Chickpea	Mungbean	Peanut	Lucerne
		Leaf gro	owth			
node_app_rate	Degree-days	Thermal time required for node appearance on main stem	46 ^A	100 ^B	56 ^E	51 (seedling) ^F 34 (regrowth)
Leaves_per_node	lf/node	No. of leaves per plant per main stem node	13.4 ^A	2.0 ^B	17 ^D	1
		Node no. at start of branching	7.0 ^A	8.0^{B}	7^{D}	1 ^C
node_sen_rate	Degree-days	Rate of death of nodes on the main stem	47 ^A	60 ^B	130 ^C	107 ^C
Fr_lf_sen_rate		Fraction of total leaf number senescing for each node that senseces	0.02 ^A	0.07 ^B	0.03 ^C	0.10 ^C
		Radiation interception, b	iomass accum	ulation		
Extinction_coef		Extinction coefficient (at default row	0.55 ^{AG}	0.40 ^{BH}	0.45 ^D	0.43 (seedling) ^F 0.80 (regrowth)
Rue	g/MJ	Radiation-use efficiency	0.69 ^G	0.94 ^I	1.20 ^K	0.6 (seedling) ^F 1.0 (regrowth) 0.6 (regrowth winter)
Ave_Temp v stress_photo		Cardinal temperatures for relationship between average temperature and 0–1 stress factor on RUE	0, 15, 30, 40 ^L	10, 20, 30, 40 ^C	10, 21, 30, 40 ^M	0, 8, 25, 32 ^J
		Biomass par	titioning			
frac_leaf_pre_flower		Fraction allocated to leaves pre-flowering	0.48 ^{LN}	0.55 ^{BI}	0.58 ⁰	0.45 ^{JP}
frac_leaf_post_flower		Fraction allocated to leaves post-flowering	0.40	0.55	0.45	0.1
frac_leaf_grain_fill		Fraction allocated to leaves in grain fill	0.00	0.30	0.45	0.2
frac_stem2pod		Fraction allocated to pod before grain fill	0.10	0.46	0.10	0.1
frac_pod2 grain		Fraction allocated to pod relative to grain during grain fill	0.28	0.28	0.20	1.0
hi_incr	/day	Potential rate of increase in harvest index	0.010 ^{AQ}	0.017^{B}	0.0064 ^D	0.0001 ^C

Table 3. Model parameters for simulation of leaf growth, radiation interception, and biomass accumulation and partitioning

^A Expt 2. ^B Expt 1. ^CAssumed. ^DHammer et al. (1995). ^ELeong and Ong (1983). ^F Sato (1971), Pearson and Hunt (1972). ^GHughes et al. (1987), Thomas and Fukai (1995a). ^HMuchow and Charles-Edwards (1982). ^IMuchow et al. (1993a, 1993b). ^JExpt 3. ^KBell et al. (1992), Wright et al. (1993). ^LSingh and Virmani (1996). ^MBell et al. (1993b). ^NSingh (1991). ^OBell et al. (1993a). ^PBrown and Tanner (1983). ^QSoltani et al. (1999).

analysis of unpublished results from the studies of Muchow *et al.* (1993*a*), and for chickpea and lucerne from Expts 2 and 4 (Fig. 2). Such distributions are corroborated by data from Singh and Virmani (1996) for chickpea and Brown and Tanner (1983) for lucerne. Leaf size distribution used for peanut assumed that the maximum leaf size of 40 cm² used by Hammer *et al.* (1995) in their model was attained at a nodal position of 7 and higher.

Actual simulated leaf area production differs from potential leaf area expansion only if carbon supply is insufficient to meet a maximum specific leaf area for the daily increase in leaf area (*sla_max*). Carbon supply may become limiting, for example, at high plant population densities. The current model specifies *sla_max* as a function of LAI to constrain daily leaf area increase where carbon is limiting. However, as the value of the maximum specific leaf area operates to limit the daily increase in leaf area, it is not readily derived from experimental data and must be calibrated by trial and error. Fig. 3 shows such a calibration exercise for the low and high population densities of mungbean in Expt 1. As a first step, the model is run with *sla_max* unconstrained, with the result that high numbers of



Fig. 1. Derivation of parameters for node appearance (closed symbols) and senescence (open symbols) for (*a*) chickpea and (*b*) mungbean. Data were measured in Expts 1 (mungbean) and 2 (2 sowings of chickpea). Fitted equations are y = 2.54 + x/46.1, $R^2 = 0.98$ for chickpea node appearance; y = x/46.6 - 23.7, $R^2 = 0.99$ for chickpea node senescence; y = 4.2 + x/101.1, $R^2 = 0.99$ for mungbean node appearance; y = x/33.9 - 18.0, $R^2 = 0.91$ for mungbean node senescence. Derivation of parameters for branching (leaves produced per mainstem node) for (*c*) chickpea and (*d*) mungbean. Data were measured in Expts 1 (mungbean) and 2 (2 sowings of chickpea). Fitted equations are y = 13.4x - 92.4, $R^2 = 0.84$ for chickpea; y = 2.1x - 16.9, $R^2 = 0.82$ for mungbean.



Fig. 2. Leaf size *v*. node number for (*a*) chickpea (Expt 2) and lucerne (Expt 4), and (*b*) mungbean under high and low density (Expt 1).

leaves are produced, the specific leaf area of the canopy attains high levels (i.e. leaves become very thin) because carbon is not constraining leaf area expansion, and consequently, LAI is over-predicted, especially in the high population density treatment. The next step in calibration is to progressively reduce the value of *sla_max* so that carbon supply becomes progressively more limiting to expansion, until the simulated canopy specific leaf area and LAI matches the observed (Fig. 3). The functional relationship between *sla_max* and LAI that best fits LAI and SLA of the whole canopy at both densities is then used in the model. The calibration exercise described above was conducted for all species, using Expt 1 for mungbean, Expt 2 for chickpea, Expt 3 for lucerne, and the data from Bell and Wright (1998) for peanut.

Leaf senescence is a product of leaf senescence from mainstem nodes (*node_sen_rate*) and the fraction of total plant leaf number senescing for each mainstem node that



Fig. 3. Calibration of *SLA max* using mungbean at low and high plant population density in Expt 1. The upper curve in each graph is the simulated attribute with *SLA_max* set to a high value so as to be not constraining leaf area increase. The lower curves are the simulated attributes with the calibrated function for *SLA_max*, and the points are the observed data for the low and high plant population densities for mungbean in Expt 1.

senesces $(fr_lf_sen_rate)$ following the framework for pigeonpea described by Ranganathan *et al.* (2000). Senescence of mainstem nodes is assumed to occur as a linear function of thermal time after flowering. Fig. 1*a*, *b* shows the derivation of this relationship for mungbean in Expt 1 and chickpea in Expt 2, and Table 3 lists values for all species. The value of $fr_lf_sen_rate$ was obtained by calibration of the model against the observed post-flowering decline in leaf area in Expts 1–3 (data not shown).

The rate of leaf senescence may be enhanced in dense canopies (light competition), under drought conditions, and with the occurrence of frost, and may occur before flowering. These parameters were considered optional and hence values for each species were set bearing in mind known qualitative differences among species in the sensitivity of leaf senescence to low temperature and water deficit (data not shown).

Biomass accumulation and partitioning

Potential daily above-ground biomass production is predicted from LAI, a radiation extinction coefficient (*extinction_coef*), and the crop's radiation use efficiency (*rue*). Values for *extinction_coef* and *rue* and their sources are tabulated in Table 3. Radiation interception and photosynthesis by pods can also be parameterised for top-podding species, although this did not apply to any of the 4 species considered here.

In the model, *extinction_coef* declines with row spacing as found by Flenet *et al.* (1996*b*) for soybean and Bell *et al.*

(1993) for peanut. The approach is an approximation to deal with the hedgerow structure that generates incomplete canopy cover.

Values for rue have been determined for lucerne growing in temperate France (Khaiti and Lemaire 1992); however, we could find no published studies where rue has been determined for warmer climates, such as in the subtropics. Hence, rue was derived from the measurements made in Expt 3. Fig. 4 shows a scatter plot of biomass increase between samplings versus the amount of intercepted radiation, measured with tube solarimeters through a 19-month period. It is possible to distinguish an outer envelope of points, which lie in a line around a fitted RUE value of 1.0 g/MJ. From this observation it was assumed for the model that RUE was 1.0 g/MJ, similar to the value determined for the summer regrowth period for lucerne in the study of Khaiti and Lemaire (1992), and for many other legumes (Muchow et al. 1993a). Lucerne is unusual compared with annual legumes in that rue varies between seedling and regrowth crops and also shows a pronounced seasonal trend with lower values in the autumn and winter, associated with declining daylength (Khaiti and Lemaire 1992). Accordingly, rue, expressed on an above-ground basis, varies in the model between seedling crops (0.6 g/MJ)and regrowth crops (1.0 g/MJ) and is lower in the autumn and winter for regrowth crops (0.6 g/MJ), to account for higher partitioning of total biomass to roots (Khaiti and Lemaire 1992).

Fig. 4. Derivation of radiation use efficiency for lucerne. Data are biomass increase and intercepted solar radiation from individual growth intervals between harvest cuts. The slope of the line drawn is the upper limit of biomass produced per unit of intercepted radiation, i.e. the radiation use efficiency (1.0 g/MJ).

The value of *rue* can be limited by suboptimal or supra-optimal average daily temperature. The cardinal temperatures defining the effect of temperature stress on *rue* are listed in Table 3, and are largely derived from the literature where leaf photosynthetic rate was measured as a function of temperature. An additional effect on *rue* is the depression of photosynthetic activity by extremes of temperature the previous day. Although this function has been defined for peanut for the case of low night temperature reducing the following day's *rue* (Bell *et al.* 1992), it has not been well quantified for the other species and this effect has not been included in the model.

Actual daily biomass increase is calculated from the minimum of 2 potential crop growth rates, one determined by the intercepted radiation, limited by temperature and nitrogen stresses, and the other by soil water supply. Daily biomass production is partitioned to 6 different plant parts in different ratios, depending on crop phase (Table 4).

Between emergence and flowering, a proportion of biomass produced (*frac_leaf_pre_flower*, Table 3) is partitioned to leaf and the remainder to stem. However, if the amount of carbon partitioned to leaves is more than can be used for the calculated increase in leaf area (i.e. the leaves have a maximum thickness, *sla_min*), then the residual is partitioned to stems. The value of *sla_min* is assumed to be 10000 mm²/g for all species. Likewise, if the carbon partitioned to leaves is too little to grow the potential increase in leaf area, leaf area increase is reduced (see *Leaf area development* section).

Between flowering and start-of-grainfill the same procedure is used for determining leaf biomass

Table 4. Plant parts and their description in the legume module

Element in the plant part array	Plant part	Description
1	Root	Below-ground fibrous roots
2	Leaf	Leaf lamina
3	Stem	Stem
4	Pod	Hull (or pod wall)
5	Grain	Grain (or seed)
6	Energy	Energy required to synthesise lipids in grain, expressed in dry weight equivalents

(*frac_leaf_post_flower*). Of the carbon remaining after leaf demand has been satisfied, a proportion goes to stem and pod wall in the ratio specified by the parameter *frac_stem2pod*. A value of *frac_stem2pod* for mungbean derived from Expt 1 and re-analysed data from Muchow *et al.* (1993*a*) is 0.46 ± 0.06 . In the absence of any published information, a value of 0.10 was assumed for lucerne and a value of 0.10 for chickpea was derived through calibration of the model to data in Expt 2. A value of 0.10 was used for peanut, consistent with the observation that pod wall weight accumulation largely precedes grain-filling (Schenk 1961).

Between the start-of-grainfill and maturity, biomass is partitioned, in order of priority, between grain plus pod wall, and stem plus leaf. Partitioning to grain depends on calculated grain-demand (see below). The pod wall accounts for a fraction of the grain demand (*frac_pod2 grain*). If there is any biomass remaining after grain demand has been satisfied, it goes to leaf as specified by *frac_leaf_grain_fill*, with the remainder going to stem. In this way if there is low demand for assimilate by grain during grainfill, leaf area may be produced, as occurs in indeterminate species and cultivars. The parameter *frac_pod2 grain* was derived from measurements in Expts 1 and 2 for mungbean and chickpea.

Grain demand for carbohydrate (biomass) is driven using a cultivar-specific daily rate of harvest index (HI) increase (*hi_incr*) up to a genetic maximum defined by *hi_max_pot*. Spaeth and Sinclair (1985) were the first to note the constancy of the increase in HI during grain fill in soybean. Since then, the concept has been applied by Sinclair (1986) and Hammer et al. (1995) to simulate grain yield accumulation in soybean and peanut, respectively. In the current model, we modify the HI increase concept to calculate the *demand* for assimilate, to account for those situations where assimilate supply may not be adequate to meet demand, so that the realised daily increase in HI may not be equal to hi_incr. The parameter hi_incr is cultivar-specific to account for known variation in some species (e.g. soybean, Spaeth and Sinclair 1985; peanut, Hammer et al. 1995). Sinclair et al. (1987) use a value of 0.016/day in a model for cowpea. However, there is little published information on *hi_incr* for mungbean, chickpea, and lucerne. Calculating from Expts 1 and 2 and Muchow



Where a single value is given, the concentration does not change with stage of development. The critical concentration is that below which growth is reduced								
Parameter name	Unit	Plant part	Chickpea	Mungbean	Peanut	Lucerne		

Table 5. Critical nitrogen concentrations for growth of plant parts, given as a range from emergence to maturity

Parameter name Unit	Plant part	Chickpea	Mungbean	Peanut	Lucerne
n_conc_crit g/g	Root	0.015 ^A	0.015 ^B	0.020 ^C	0.025 ^D
	Leaf	0.06–0.017	0.06–0.02	0.046–0.020	0.06–0.02
	Stem	0.06–0.017	0.06–0.02	0.020–0.010	0.06–0.02
	Pod	0.06–0.017	0.06–0.02	0.045–0.015	0.06–0.02
	Grain	0.036	0.045	0.048	0.017

^AAssumed. ^BChapman and Muchow (1985), Muchow *et al.* (1993*b*). ^CTonn and Weaver (1981), De Vries *et al.* (1989). ^DSmith (1969).

et al. (1993*a*) gave average rates of increase of 0.010 (chickpea) and 0.017/day (mungbean). A small value of 0.0001/day was arbitrarily assigned to lucerne to account for the low amounts of seed mass accumulated by this forage species. Values of 0.005–0.009/day for peanut published by Hammer *et al.* (1995) include pod wall and so were adjusted down by *frac_pod2 grain* to account for the fact that *hi_incr* is for grain only.

In species in which there is an energy cost to grain dry weight synthesis above that which is standard for grain carbohydrate (e.g. oilseeds such as peanut), account must be taken of the extra assimilate required (Penning de Vries 1974). This is specified by the parameter *grain_energy*, which is a coefficient for conversion of assimilate to seed mass, and this is used to accumulate a conceptual *energy* plant part. This is not included in the summing of plant parts to give the weight of biomass. The value of *grain_energy* is 1.6 for peanut, following Hammer *et al.* (1995). In the other species it is set to 1.0, indicating no extra energy demand for grain dry matter synthesis.

The ability to meet the grain demand for assimilate is determined by the concurrent rate of biomass accumulation and the potential for retranslocation of dry matter that had accumulated in the leaves and stems before the start of pod-filling. Parameters that set the fraction of stem and leaf dry weight available for re-translocation to grain are *stem_trans_frac* and *leaf_trans_frac*, respectively.

Plant height is needed in the legume module to simulate competition for light with companion crops in an intercropping situation (Keating and Carberry 1993). Daily increase in plant height is simulated via a table that specifies the relationship between stem mass and height, and it is able to be specified for different cultivars to account for known differences in growth habit within a species (e.g. bunch-type ν runner-type peanuts).

Plant nitrogen relations

The demand, uptake, and retranslocation of N is simulated by the model, and is a modified version of that used in the CERES models. The model assumes that there are 3 processes that contribute to N uptake. 'Mass flow' is estimated as the product of transpiration and the nitrate concentration in soil solution. 'Active uptake' represents a diffusive process whereby concentration at the root-soil interface is less than the bulk solution; it is estimated in terms of the rate at which plants can use nitrate and ammonium from soil. The third process is fixation.

The crop has a defined minimum, critical, and maximum N concentration for each plant part (Table 5). Demand for N in each part attempts to maintain N at the critical (non-stressed) level. N demand on any day is the sum of the demands from the pre-existing biomass of each part required to reach critical N content, plus the N required to maintain critical N concentrations in that day's potentially assimilated biomass. If N demand cannot be satisfied by mass flow, then it is supplied by either active uptake or N fixation, depending upon the 'preference' of the particular species. This feature is designed to account for the observation that some species will fix N in the presence of a high mineral N supply (e.g. Lucerne; Blumenthal and Russelle 1996), whereas in other species, fixation will only occur when soil mineral N supply is inadequate to meet plant demand (e.g. soybean; Herridge et al. 1984). At present, there is little published information to define the N preference for other species. The model does not account for any direct effects of soil mineral N on *N_fix_rate* through impaired nodulation.

There is currently no method for making an *a priori* estimate of the value of the minimum, critical, and maximum N concentrations for each plant part as a function of crop development. In order to arrive at values for each species it was assumed that the minimum N concentration was equal to the N content of plant parts at senescence (Table 5). Critical N concentrations were taken from studies where plants were well nodulated and apparently well supplied with N.

The potential daily rate of nitrogen fixation (N_fix_rate) is a function of standing crop biomass, discounted for soil water stress, following the logic of Sinclair (1986) that N fixation rates are well correlated with the amount of nodule material in the roots, which is in turn well correlated with the size of the plants. N_fix_rate may vary with crop development stage in order to account for low N fixing capacity while nodules are being established early in growth

	439)

Parameter name	Units	Parameter description	Chickpea	Mungbean	Peanut	Lucerne
Ratio_root_shoot used to grow root						
Emergence Flowering			1.0 ^A 0.5	1.0 ^B 0.33	1.0 ^B 0.33	1.0 ^B 0.5
Maturity Specific_root_length Root_depth_rate (stage) Trans_eff_coef	mm/g mm/day Pa	Specific root length Extraction front velocity Transpiration efficiency coefficient	0.0 45 500 ^C 17 ^D 0.003 ^H	$0.0 \\ 65000^{B} \\ 35^{E} \\ 0.0055^{B}$	$\begin{array}{c} 0.0 \\ 65000^{\rm B} \\ 35^{\rm F} \\ 0.0035^{\rm I} \end{array}$	0.1 65000 ^B 12 ^G 0.005 ^J

Table 6. Parameters for simulation of root growth and development, and crop water use

^AGregory (1988). ^B Assumed. ^CSingh and Virmani (1996). ^DBrown *et al.* (1989), Thomas *et al.* (1995). ^EAngus *et al.* (1983). ^FSquire (1990), Dardanelli *et al.* (1997). ^GMeyers *et al.* (1996). ^HThomas and Fukai (1995*b*), G. C. Wright, unpubl. ^IHammer *et al.* (1995). ^JSmeal *et al.* (1991).

and also as a consequence of nodule senescence during pod-filling.

Water deficit effects

Root growth and development and soil water extraction

Root biomass is grown daily in proportion to the tops production. This proportion (*ratio_root_shoot*) is specified for each development stage (Table 6).

The depth of rooting is simulated via a daily potential elongation rate (*root_depth_rate*) that varies with stage of crop development. Species differ in the extent of root depth increase during grain-filling. Indeterminate legume crops continue to allocate assimilate to the root system during early pod filling so that the total size of the root system continues to increase but often at a slower rate than before flowering (e.g. Thomas *et al.* 1995 with chickpea). A root exploration factor that varies from 0 to 1 is used for each soil layer to constrain *root_depth_rate* if soil properties, such as compaction or pH, are known to limit root elongation.

Values of *root_depth_rate* were derived from published studies where either rooting depth or extraction depth was monitored through time (Table 6). In general the warm-season species have values of *root_depth_rate* of 30–40 mm/day, whereas chickpea uses a value of 17 mm/day to reflect its cool-season adaptation. The value of 12 mm/day for lucerne was taken from the study of Meyers *et al.* (1996), who measured root elongation rates of 11–14 mm/day for a range of 12 lucerne cultivars.

Root biomass is converted to root length via *specific root length*. Data on this parameter for the various species are rare. The value of 65000 mm/g was used by Boote *et al.* (1998) in their peanut model. As this parameter can be considered optional, a value of 60000 mm/g is assumed for species where information was not found in the literature. Use of a constant specific root length is necessarily a simplification of root growth in that it ignores that specific root length will decline with stage of crop development because root dry weight increase at later stages of development is used to thicken existing roots as well as grow new roots. Root length is used by some water and solute balance modules in APSIM such as SWIM (Verburg *et al.* 1996).

Soil water infiltration and redistribution, evaporation, and drainage are simulated by the water balance modules in the APSIM framework. Currently there is a choice of APSIM-SOILWAT (Probert *et al.* 1998) or APSIM-SWIM (Verburg *et al.* 1996).

Water stress in the model reduces the rate of leaf area expansion via a soil water deficit factor (swdef_expansion), which varies from 0 to 1.0, following the concepts embodied in the CERES models (Ritchie 1986). The variable swdef_expansion is calculated daily from the ratio of potential soil water supply from the root system and the transpiration demand. Following Sinclair (1986) and Monteith (1986), transpiration demand is modelled as a function of the current day's crop growth rate, divided by the transpiration efficiency. When soil water supply exceeds transpiration demand, photosynthesis is a function of radiation interception and *rue*. When soil water supply is less than transpiration demand, photosynthesis is a function of water supply and transpiration efficiency, which is related to the daylight averaged vapour pressure deficit (vpd). Values of the transpiration efficiency coefficient are tabulated for each species in Table 6. In the model, vpd is estimated using the method proposed by Tanner and Sinclair (1984), which uses daily maximum and minimum temperatures. In this method, it is assumed that the air is saturated at the minimum temperature.

When the model is coupled to APSIM-SOILWAT (Probert *et al.* 1998), potential soil water uptake is calculated using the approach advocated by Monteith (1986). The potential rate of extraction in layers occupied by roots is calculated using a rate constant (kl), which defines the fraction of available water able to be extracted per day. The actual rate of water extraction from the profile is the lesser of the sum of the potential extraction rates from all layers and the transpiration demand. Root water extraction constants (kl) must be defined for each combination of crop species and soil type. Representative values of kl are given by Dardanelli *et al.* (1997) for lucerne, peanut, and soybean.



Fig. 5. Time-course of crop growth for mungbean cv. King grown at Katherine, NT, under dryland conditions (\bullet) and at Lawes, Qld, under full irrigation (\bigcirc). Symbols are observed data and lines are simulated.

In the model, dry soil can reduce the value of N_fix_rate , via a stress factor, *swdef_fixation*, based on the fraction of available soil water in the root-zone (Sinclair *et al.* 1987). In the model, species have differing sensitivity of N fixation to soil dehydration, as shown by Sinclair *et al.* (1995) in peanut and Sall and Sinclair (1991) and Sinclair *et al.* (1987) in soybean, cowpea, and mungbean. In the absence of published information it was assumed that chickpea and lucerne have a similar sensitivity to soybean, cowpea, and mungbean.

Harvesting and perenniality

As APSIM-Legume is used to simulate the growth of both annual and perennial species it must be able to cope with the impact of harvesting and grazing on growth and development. The harvesting operation in the model can be specified to remove plant tops at variable heights above the soil surface. In annual species, complete defoliation, harvesting, or grazing initiates death of the crop, whereas in perennials, such as lucerne, regrowth can occur after complete defoliation or harvesting. In the event of a harvest or grazing operation, it is assumed that all grain and pod wall are removed, but the user may flexibly specify the fraction of leaf and stem that is removed as a function of the height of the crop being removed. On the day of harvest or grazing, a set fraction of root biomass is also assumed to senesce and detach. The model accounts for known physiological differences between crops growing from seed versus crops re-growing after harvest. In the lucerne configuration there are different parameters for seedling versus regrowth crops to reflect known differences in physiology between the different types of plant (see Table 3).

Model validation

Data used for testing of the model (Table 1) were from experiments mostly conducted in the subtropics and tropics of Australia under both dryland and irrigated conditions. Sowing date, plant density, row spacing, and cultivar were the primary agronomic factors manipulated.

Examples of the time course of simulated and observed growth attributes of crops of mungbean and peanut are given in Figs 5 and 6, respectively. In Fig. 5 the same cultivar is simulated under irrigation in the subtropics and under dryland conditions in the tropics. The model demonstrates an ability to simulate the time-course of LAI, total biomass, and its partitioning into components and N uptake. Fig. 6 shows simulated and observed growth and root water extraction by a peanut crop growing in a continuous drying cycle under a rainshelter. Good agreement is obtained between measured data and simulated model output.

High quality datasets for lucerne suitable for model testing were difficult to access. Fig. 7 shows model performance against Expt 3. Expt 3 was used to derive some



Fig. 6. Time course of growth for peanut cv. McCubbin under a rainshelter at Kingaroy, Qld. Symbols are observed data and lines are simulated. Plant available soil water to 1.5 m depth.



Fig. 7. Time course of observed and simulated biomass, leaf area index, and nitrogen uptake in lucerne in Expt 3 at Lawes, Qld.

	Ν	Observed mean (range) (g/m ²)	RMSD	Linear regression Slope	between simulated and Intercept	l observed R ²
		Mur	ıgbean			
Grain yield (g/m ²)	40	123 (33–250)	31	1.08 ± 0.096	-5.59 ± 12.7	0.77
Biomass at maturity (g/m ²)	17	255 (83 - 494)	134	1.19 ± 0.231	27.9 ± 65.3	0.64
		Pe	eanut			
Grain yield (g/m ²)	30	421 (71-723)	98	1.02 ± 0.093	26.8 ± 43.1	0.81
Biomass at maturity (g/m ²)	21	977 (302–1290)	236	1.33 ± 0.170	-168 ± 170	0.76
		Chi	ickpea			
Grain yield (g/m ²)	31	196 (97–388)	46	0.76 ± 0.096	56.4 ± 20.3	0.70
Biomass at maturity (g/m ²)	24	557 (196–1114)	125	0.56 ± 0.080	249 ± 48.0	0.71
		Lu	cerne			
Biomass (g/m ²)	24	254 (73-568)	84.5	n.a.		
Leaf area index	24	2.15 (0-3.96)	1.40	n.a.		
Nitrogen uptake (g N/m ²)	20	7.95 (3.0–13.7)	2.12	n.a.		

Table 7. Statistics for goodness-of-fit of the model in testing against datasets listed in Table 1

n.a., Not applicable.

of the model parameters, so this test is not independent. Nonetheless, Fig. 7 illustrates that the combined effect of the derived parameters is able to simulate LAI, biomass, and N uptake over a 19-month period and 11 growth cycles.

Overall the model was able to explain 70–80% of the observed variation in grain yield and 64–76% of the variation in maturity biomass for mungbean, peanut and chickpea (Table 7, Fig. 8). The RMSD for grain yield was 31, 98, and 46 g/m² for mungbean, peanut, and chickpea, respectively, corresponding to 25, 23, and 23% of the observed mean grain yield. For biomass at maturity, the RMSD was 134, 236, and 125 g/m² for mungbean, peanut, and chickpea, respectively, corresponding to 53, 24, and 22% of the observed mean biomass. Hence, biomass was simulated with similar accuracy to grain yield, except for the case of mungbean. The reasonable simulation of biomass is surprising given that the extent of leaf senescence and detachment in legumes near maturity can be variable, making accurate simulation difficult.

Discussion

This paper has shown that it is possible to simulate diverse legumes species using a generic approach. The 4 species chosen for this paper were intended to represent species with cool-season adaptation (chickpea), warm-season adaptation (mungbean and peanut), high energy content seeds (peanut), and with contrasts of degree of perenniality (lucerne v. others) and determinacy (peanut and chickpea v. mungbean). The degree of agreement between observed and predicted grain yield and biomass is comparable to that achieved for other single-species models used in APSIM (Carberry 1996).

The intention with the development of this generic model is that it would be comparatively easy to develop the capability to simulate new legumes species, as the need arises. This is achieved by the externalisation of parameters, constants, and coefficients from the code to be read from files at the time of initialisation. Users can thus alter the contents of this initialisation file, to simulate a new species, without alterations to the source code.

The current model incorporates some innovative approaches to the simulation of crop growth, particularly faced with legumes.

Firstly, the concepts of the supply of, and demand for, carbon for leaf growth are used to simulate canopy expansion. The daily demand for carbon by leaves is calculated based on the appearance and size of leaves on freely branching plants (grown at low plant population density). The daily supply of carbon is based upon the fraction of above-ground dry weight increase able to be partitioned to leaves multiplied by a maximum specific leaf area for the daily increase in leaf area. This approach is an advance on those of Sinclair (1984) and Hammer et al. (1995), who modelled leaf area expansion as a daily leaf appearance rate, governed by temperature, multiplied by a leaf size. The Sinclair and Hammer approach would be expected to under-predict leaf area at low plant population densities, and over-predict it at high plant population densities. This limitation was recognised by Hammer et al. (1995), who warned that their model for peanut does not account for density effects on branching and leaf area. The present model offers an approach to this situation, with little added complexity to the model. To parameterise the current model for this approach requires quantifying leaf appearance on branching plants (as in Expt 1) and then calibrating the maximum specific leaf area for daily increase in leaf area (Fig. 3).

Secondly, the continuation of leaf and stem growth during grain-filling is simulated based upon the supply and demand



Fig. 8. Observed and simulated grain yield for (*a*) mungbean, (*b*) peanut, and (*c*) chickpea.

for carbon by the grain. The variable occurrence of leaf growth during grain filling is recognised in the models of Sinclair (1986) and Hammer et al. (1995) through specifying the end of leaf growth as a phenological stage, which varies with cultivar. The current model will simulate the cessation of leaf growth during grain-filling dependent upon the 'excess' assimilate available, once the requirements for grain and pod wall growth have been satisfied. A fraction of the excess assimilate is converted to leaf area through the maximum specific leaf area for daily increase in leaf area, with the remainder going to stem. In this way, crops that have a low demand for carbon for reproductive growth (through a low rate of increase in harvest index) will tend to have continued leaf and stem growth during grain-fill. Such an approach is largely untested, although evidence comes from diverse cultivars of pigeonpea, where some types will tend to

have a low rate of harvest index increase over a longer pod-filling duration and continued leaf and stem growth (Robertson *et al.* 2000). This approach has promise in solving the problem of Hammer *et al.* (1995), who noted difficulty in simulating high LAI values in peanut due to unexplained variation in the timing of end of leaf growth.

Thirdly, the model attempts to deal with variation in the capacity for nitrogen fixation with stage of crop development. This is to accommodate the observation that both early and late in the crop's lifecycle, N fixation capacity may be reduced. During early crop growth, N fixation may be reduced because of the delay in establishing effective root nodules. Herdina and Silsbury (1990) discuss the phenomenon of N deficit in legumes during the period preceding nodulation. Trimble et al. (1987) recorded herbage yield responses to applied N during the establishment phase of a lucerne crop and concluded that fixation was unable to meet plant N demand. N fixation capacity may also be reduced during seed growth (Lawn and Brun 1974), thought to be due to carbohydrate deprivation of nodules as assimilates are partitioned preferentially to developing seeds. There is conflicting evidence on the maintenance of N fixation during grain-filling. For example, Herridge and Pate (1977) and Beverly and Jarrell (1984) observed that N accumulation occurred during seed filling in cowpea. This is in contrast to Muchow et al. (1993b), who showed N accumulation continuing during seed filling in soybean, cowpea, and mungbean, although the N accumulated by cowpea and mungbean was always less than that by soybean. Bell et al. (1994b) showed that N fixation continued during grain-filling in irrigated peanut crops. There is a need for further research to derive simple functional relationships to simulate N fixation in crop legumes, and elucidate a basis for simulating N fixation late in the crop lifecycle.

Fourthly, in contrast to the models of Sinclair (1986) and Hammer *et al.* (1995), the linear harvest index represents the *potential* rate of grain growth, rather than the *actual*, which may be less due to assimilate shortage during grain-fill. Previous approaches did not deal explicitly with retranslocation to meet grain demand. This approach may have the advantage of accounting for various effects on harvest index increase via assimilate shortage and degree of retranslocation of dry matter. For instance, Soltani *et al.* (1999) in their chickpea model found that they had to force HI increase to cease under conditions of severe water limitation.

There are a number of known characteristics of legume growth and development that are not accounted for in the present model, due to insufficient physiological understanding to parameterise the functional relationships. One is the occurrence of multiple flushes of flowers and pods in some species, especially in response to intermittent stress, which has the effect of prolonging the duration of grain growth. This phenomenon will not be accounted for by the linear harvest index approach adopted in the present model (Thomas *et al.* 1998). A second limitation is the effect of stresses upon root nodule survival and consequent limited N fixation capacity when favourable conditions return (e.g. Venkateswarlu *et al.* 1990). Currently, the model reduces N fixation capacity only on the basis of the daily soil water status. A third limitation is that the rate of leaf senescence during pod filling is not linked to the grain demand for, and retranslocation of, leaf N. In the model, although leaf N is

retranslocated to the stem when a leaf senesces, the rate at which this happens is not determined by the 'self-destruct' principles described by Sinclair and de Wit (1976). Finally, the model does not currently deal with the effect of waterlogging (root oxygen deficit) on growth and development, through impaired root function.

Documented model source code in hypertext format can be obtained by writing to the senior author.

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