GUMCAS: a model describing the growth of cassava (*Manihot esculenta* L. Crantz)

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Abstract

A process-oriented model, GUMCAS, describing the growth of cassava (*Manihot esculenta* L. Crantz) was developed for inclusion in the IBSNAT decision support system. Potential dry matter production is calculated from existing leaf area, and is modified by effects of light, temperature, water stress, and vapour pressure deficit. Leaf and stem growth are assumed to be the dominant sinks for assimilate, with fibrous roots receiving a fraction of that allocated to the shoot, decreasing as the crop ages. The storage roots receive any remaining assimilate. The Ritchie water balance model is used to estimate water status.

Leaf size is calculated empirically as a function of time. However, there was a strong correlation between leaf size and the assimilate supply/demand ratio represented by $\delta W/W$ (daily change in weight/total plant weight). This approach is included in the model as an option for simulating environmental influences on leaf size. This relationship functioned well, particularly on release of drought stress.

Phenology is described by assuming two independent "clocks" controlling vegetative and reproductive development respectively. Both clocks are influenced by temperature and water status, while reproductive development is also influenced by photoperiod (ϕ). Fitting the standard model for photoperiod response to observed reproductive branching data gave a minimum optimum photoperiod (ϕ_0) of 15.5 h and a sensitivity (S_ϕ) of 0.25 h^{-1}, assuming the crop was sensitive to photoperiod from emergence. However, an improved fit was obtained by also assuming branching is inhibited when the rate of change of photoperiod ($d\phi/dt$) was above 0.01 h day^{-1}.

Sensitivity analysis confirmed previous reports that leaf longevity is an important character determining storage root yield; other characters are the age at which first branching occurs, and specific leaf area. However, the importance of some characters changes under drought, such as the date at which the maximum leaf size occurs.

The model was validated with the limited number of datasets available; good agreement between simulated and measured values was obtained for a range of cultivars in a range of environments. Further validation is necessary, however, before widespread application. The factors controlling leaf size and times of branching were identified as areas in which there is a scarcity of knowledge, and to which future cassava physiology research should be directed.

Key words: Cassava; IBSNAT; *Manihot*; Model; Simulation

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1. Introduction

Cassava is one of the most important energy sources in the diet of people in the tropics; recent estimates suggest that its storage roots provide 8% or more of the minimum calorie requirement for more than 750 million people (Connor et al., 1981). It has also been under consideration as a starch or energy crop in developed countries such as Australia (Keating et al., 1982). National average yields vary widely, from 1.5 t ha^{-1} in Sudan to more than 32 t ha^{-1} in Fiji (FAO, 1991). Although the crop can be grown between the latitudes of 30°N and 30°S and at elevations that range from sea level up to 2000 m near the equator, most cassava is grown in areas where annual mean temperature is above 20°C and rainfall exceeds 700 mm year^{-1} (El-Sharkawy and Cock, 1987). Much cassava is grown without irrigation in tropical areas with a pronounced dry period (Connor et al., 1981), and often in soils of low fertility.

Cassava was one of the crops included in a priority list by IBSNAT (International Benchmark Sites Network for Agrotechnology Transfer), an organisation established to stimulate and coordinate research into cropping systems, with the aim of assisting the transfer of technology to less developed countries. A major thrust was the development of crop models that could be used to evaluate breeding and management experiments and to examine and identify promising cropping systems, allowing users to concentrate further field experimentation where the benefits are likely to be greatest. Computer software to allow easy use of models and analysis of output has also been developed. Progress has been made with many of the models (Harrison et al., 1990), but the cassava model has remained the least developed, partly due to a scarcity of reliable growth and climate data sets. This paper presents a first description of a process-based cassava growth model, GUMCAS, fitting within the IBSNAT framework.

2. Previous cassava models

Several detailed reviews of cassava physiology have been made in recent years (e.g., Hunt et al., 1977; Veltkamp, 1986), and a number of attempts have been made to incorporate this information into models of cassava growth. These models differ mainly in the description of the partitioning of dry matter to the various plant components, and the way in which leaf longevity and senescence are calculated. With respect to dry matter partitioning, the models fall into two groups: (1) those in which dry matter is partitioned according to a fixed pattern, and (2) "spill-over" models in which leaf or stem growth is calculated independently and are assumed to have "first-call' on newly produced assimilate, the storage roots receiving any that is remaining.

The first of the "fixed-pattern" models was that of Boerboom (1978), a simple two-parameter model based on the linear relationship between storage root dry weight and total dry weight for a number of cultivars under different conditions. This approach provided a robust method of analysis in several studies (e.g., Connor et al., 1981). Gutierrez et al. (1988) approached the problem using population theory concepts; most of the model components, however, were similar to other models. Again, dry matter was allocated according to fixed proportions, which altered slightly after a certain crop development stage. Gijzen et al. (1990) modified the Wageningen SUCROS model for cassava, in which dry matter partitioning was described by a "look-up" table defined at the start of the model. None of the papers on these three models describe the way in which leaf senescence is handled. Although requiring few input parameters, the disadvantage of the fixed-pattern approach is that it takes no account of the dynamic physiological processes in the plant that contribute to the final yield, and hence the response to variable environmental conditions is limited. The models described above give good results for a given cultivar in a given environment, but need to be recalibrated when either of these are changed.

The first of the "spill-over" models was that of Cock et al. (1979), in which leaf growth was simulated as a function of apex number, leaf appearance rate per apex (LAR), leaf size, and leaf longevity; crop growth rate (CGR) was assumed to be a function of leaf area index (LAI). Leaf and stem growth took whatever newly produced assimilate they required; any remaining was received by the storage roots. Leaf senescence was calculated by assuming that each leaf had a set lifespan, which could be reduced by shading. The model took no account of temperature, solar radiation or water stress effects, and although branching was an integral

part of the model, control of this characteristic was not included. Fukai and Hammer (1987) extended the Cock et al. (1979) concept of CGR as a function of LAI to take into account the effect of light, temperature, and water stress. Dry matter allocation was based on empirical relationships derived from data of Keating et al. (1982) for the cultivar MAus10, including effects of temperature, photoperiod, and leaf and shoot sink size. Leaf senescence was calculated by multiplying a potential senescence rate by temperature, water status, or shading modifiers. The model gave good results for the Australian data sets, but extrapolation into different environments with different cultivars required derivation of new multi-variate regression equations.

None of the five models takes into account the effect of high vapour pressure deficit (VPD) on stomatal closure and hence growth (El-Sharkawy et al., 1984). Most of the models are also cultivar and site specific; the model itself must be changed to accomodate different cultivar characteristics. Only the Gutierrez et al. (1988) model accounts for the growth of fibrous roots and their effect on water and nutrient uptake. All, therefore, have deficiencies for widespread application. The aim of the present work is to build on the progress made in the existing models by developing a process-based cassava model which includes extra components such as VPD, and which is able to deal with different cultivar characteristics. The work also aims at identifying the most widely varying parameters between cultivars and defining these as the "genotype coefficients" used in other applications within the IBSNAT software.

3. Structure of the model

3.1. Water balance

A version of the water balance sub-model described by Ritchie (1985) is used in GUMCAS. After calculation of runoff, drainage and soil evaporation, a soil water deficit 'factor', Φ, is calculated as the ratio of actual water uptake to potential water uptake, and is used to modify plant processes in other parts of the model. Drought stress acts by reducing both growth per unit leaf area and total canopy leaf area. The sub-model used by Ritchie (1985) assumes a root radius of 0.02 cm; several studies, however, have noted that cassava roots are thicker (e.g., Connor et al., 1981; El-Sharkawy and Cock, 1987). Using a value for root radius

of 0.038 cm (var. MCol1684, El-Sharkawy and Cock, 1987) to recalculate the $\ln(1/\pi r^2)$ term in the Ritchie model gave no appreciable difference in the value of Φ over a range of drought intensities, and the original equation was thus retained. The maximum uptake per unit length of root is also kept at the 0.03 cm^3 cm^{-1} value used in the original equation.

3.2. Crop phenology

General: Three growth phases are arbitrarily defined for present purposes:
1. Planting to emergence.
2. Emergence to first branching (the switch to the reproductive phase).
3. First branching to maturity or final harvest. Subsequent branchings may occur during this stage.

Phenological development of the crop is described by assuming that there are two independent "clocks" – one accounting for vegetative advancement, and the other for reproductive development. Rate of vegetative development (i.e., progression towards the stage at which leaf appearance is effectively zero) is influenced by temperature and drought stress, while rate of reproductive development (progression towards branching) is influenced by both of these factors as well as photoperiod (ϕ). Vegetative aspects may also be influenced by ϕ (Veltkamp, 1986; Fukai and Hammer, 1987), but this is not incorporated at present.

The concept of the "developmental day" (Dd) is used as the units of each time scale; this is equivalent to chronological days at the optimum temperature and photoperiod, with no drought or nutrient stresses operative. Sub-optimal conditions may reduce the daily rate of progression. As soon as a characteristic number of developmental days is reached, the succeeding phase is entered. The rate of progression (R) for each clock is described as

$$R_v = f(T_{min}, T_{max}),\tag{1}$$

$$R_r = f(T_{min}, T_{max}) \cdot g(\phi),\tag{2}$$

where R_v and R_r are the vegetative and reproductive rates of progression (Dd/day), T_{min} and T_{max} are the daily minimum and maximum temperatures (°C), ϕ is the photoperiod (h), and f and g are functions of temperature and photoperiod respectively. The effect of water status is accounted for by assuming that it acts

on the Dd requirement for each stage, rather than on the rate of progression towards that stage.

For the temperature function (f), the two-line method (e.g., Kiniry et al., 1991) requiring three cardinal temperatures (T_{base}, T_{opt}, and T_{high}) was used. To take into account fluctuating daily temperatures below T_{base} or above T_{opt}, hourly temperature (T_d) is calculated from T_{min} and T_{max} according to the relation:

$$T_d = (T_{min} + T_{max})/2$$
$$+ (T_{max} - T_{min})\cos(0.2618(h-14))/2, \quad (3)$$

where h is the time of day. Hourly increments in developmental time (HD, Dd/day) are calculated according to:

$T_d \leqslant T_{base}, T_d \geqslant T_{high}$:

HD = 0,

$T_{base} < T_d \leqslant T_{opt}$: $\qquad\qquad$ (4)

$$HD = (T_d - T_{base})/(T_{opt} - T_{base}),$$

$T_{opt} < T_d < T_{high}$:

$$HD = (T_{high} - T_d)/(T_{high} - T_{opt})$$

The daily increment in developmental time ($f(T_{min}, T_{max})$, Dd/day) is then calculated as:

$$f(T_{min}, T_{max}) = \sum_{h=1}^{24} (HD/24). \quad (5)$$

The effect of photoperiod is simulated using a modification of the function for a long-day plant described by Major and Kiniry (1991), expressing the response as a rate rather than a duration. The function (g) can be characterised by two parameters, the minimum optimum photoperiod (ϕ_o) and photoperiod sensitivity (S_ϕ):

for $\phi \geqslant \phi_o$: $\quad g(\phi) = 1$, $\qquad\qquad\qquad$ (6)

for $\phi < \phi_o$: $\quad g(\phi) = 1 - S_\phi (\phi_o - \phi)$, $\quad g(\phi) \geqslant 0$.

Crop emergence: The effects of soil temperature on developmental rates to emergence have been quantified for the cassava cultivars MAus7 and MAus10 by Keating and Evenson (1979) (Fig. 1). The cardinal temperatures were similar for the two cultivars (13, 30 and 42.5°C, respectively), and are the values used in GUM-
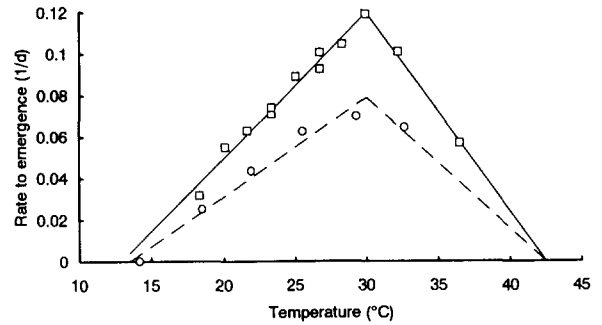

Fig. 1. The effect of temperature on developmental rate from planting to emergence for the cassava cultivars MAus7 (—) and MAus10 (----). Data from Keating and Evenson (1979).

CAS. The developmental time until emergence (A_e) in MAus7 (8.8 Dd) was considerably less than that for MAus10 (12.4 Dd); this character is therefore assumed to be cultivar specific.

Branching: Branches in cassava are of two kinds; lateral branches arising from auxillary buds below the main apex, and sympodial branches formed when an apex develops into an inflorescence marking the switch to the reproductive state. The former are important in determining the initial number of stems per unit area (SN_0), while the second influence the canopy leaf area dynamics of the crop. Despite the acknowledged importance of branching in determining canopy structure, leaf area, and hence growth and yield (e.g., Cock et al., 1979; Tan and Cock, 1979; also Keating et al., 1982), few studies have investigated branching in detail. It is known that the date of the first mainstem branching is dependent on temperature (Irikura et al., 1979) and photoperiod (Keating et al., 1982), but drought stress can also alter the branching pattern (Connor and Cock, 1981).

The study of Keating et al. (1982) involving a series of planting dates spanning the winter season in Queensland, Australia, demonstrates the effect of both temperature and photoperiod on the time to first branching (A_{b1}, Dd). Most treatments branched at very similar times despite widely differing planting dates; only those planted very late branched later. Accumulated thermal time using a range of base temperatures could not resolve the differences. Fitting the reproductive phenology model described above (Eq. 6) by least-squares analysis gave 'best-fit' values for the photo-
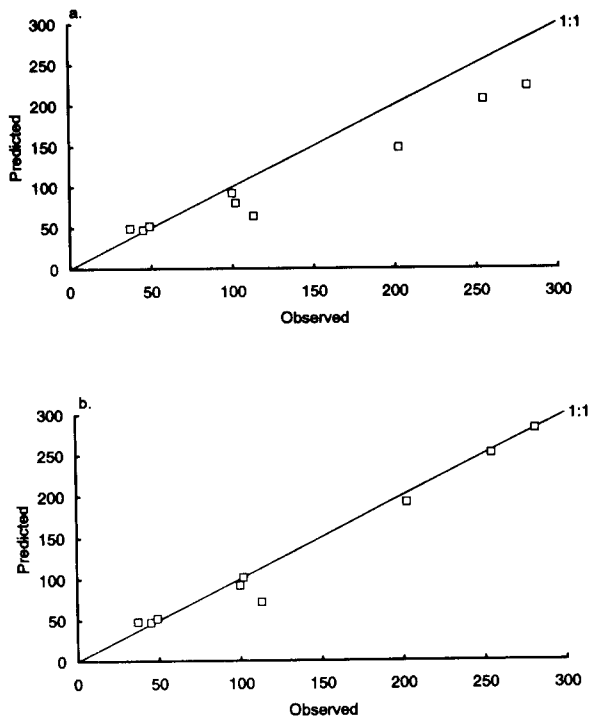
Fig. 2. Prediction of days to first branching in cultivar MAus10, using (a) best fit for the model described by Major and Kiniry (1991), and (b) inclusion of the effect of rate of change of photoperiod (dϕ/dt) (see text for details). Data from Keating et al. (1982).

period response parameters ϕ_o and S_ϕ of 15.5 h and 0.25 h^{-1} respectively, assuming the photoperiod-sensitive phase was from emergence. This predicted branching dates reasonably well, although there was some deviation for those plantings that had experienced

the cold period (Fig. 2a). However, if it was assumed in addition that branching was inhibited when the *rate of change* of photoperiod (dϕ/dt) exceeded the critical value of 0.01 h day^{-1}, then branching date could be predicted accurately (Fig. 2b). This approach is used in GUMCAS.

Once branching is initiated, it seems to proceed at a linear rate in a relatively constant environment (e.g., Veltkamp, 1986). It is assumed in the model that the slope of this rate (A_b) is cultivar specific, but that temperature and photoperiod have the same effect on subsequent branchings as on the rate towards first branching. Each time a branching event occurs, the resulting total number of apices ($N_b(t)$, m^{-2}) is calculated as:

$$N_b(t) = N_b(t-1) \cdot N_f, \tag{7}$$

where $N_b(t-1)$ is the total number of apices (m^{-2}) before the branching, and N_f is the number of forks at each branch event. An upper limit (B_{max}, m^{-2}) is set on the number of apices formed. Both N_f and B_{max} are assumed to be cultivar specific. Values of the branching parameters A_{b1}, A_b, N_f and B_{max} are shown for a number of cultivars in Table 1. Quantitative data on the effect of drought stress on branching are scarce. Although the developmental time between branchings (A_b) is reduced by drought before first branching, severe drought stress after this time will prevent branching (Connor and Cock, 1981). In the model, it is assumed, therefore, that branching is inhibited when Φ is less than 0.5. The maximum number of branches attained (B_{max}) is also reduced by drought stress early in the season.

Table 1

Parameters used in the model to describe branching in a number of cassava cultivars. See Appendix for a description of parameters

Cultivar	Parameter				Reference
	A_{b1}	A_b	N_f	B_{max}	
MCol22	44.4	58.8	3.40	28	Veltkamp (1986)
MMex59	41.3	29.4	2.8	35	Veltkamp (1986)
MCol1684	14.7	24.8	2.61	27	Veltkamp (1986)
MVen77	49.4	42.9	2.95	25	Veltkamp (1986)
MPtr26	64.7	50.0	3.00	20	Veltkamp (1986)
MCol638	44.4	28.2	2.95	52	Veltkamp (1986)
Ceiba	32.4	–	–	–	Manrique (1990a)
MAus10	14.7	41.2	3.09	50	Keating et al. (1982)
TMS 30572	44.1	–	–	–	Gutierrez et al. (1988)

3.3. Biomass production

The conservative relationship between potential crop growth rate (CGR) and leaf area index (LAI) used in previous models (Cock et al., 1979; Fukai and Hammer, 1987) was found to describe data well from a number of experiments at different sites with very little genotypic variation. A modified version of the exponential equation of Fukai and Hammer (1987) was therefore used in GUMCAS:

$$CGR = CGR_{max}(1 - exp(0.27 \, LAI)), \quad (8)$$

where CGR_{max} is the maximum crop growth rate, which can be derived from curve fitting to field data. Fukai and Hammer (1987) use a value for CGR_{max} of 21.7 g m^{-2} day^{-1}, while values for the Cock et al. (1979) and Manrique (1990b) data were slightly higher. Values of 25–27 g m^{-2} day^{-1} are used in GUMCAS to include fibrous roots. The potential CGR for a given LAI is calculated and then multiplied by factors representing the effects of temperature, light, and drought stress similar to those used in the Fukai and Hammer (1987) model.

An extension to previous models is the inclusion of a multiplier to take account of the effect of vapour pressure deficit (VPD) on crop growth described by El-Sharkawy et al. (1984). Vapour pressure deficit is calculated in a manner similar to that described by Stockle et al. (1992), except that the daily mean VPD is calculated using daylight values only. If no humidity data are available, the mean daily vapour pressure is assumed to be equal to the saturated vapour pressure at the minimum daily temperature, and VPD calculated accordingly. This latter method has been found to give good estimates of vapour pressure in humid environments, but may be in error in arid environments (Bristow, 1992).

3.4. Partitioning of biomass

The "spill-over" approach taken by Cock et al. (1979) is used to determine partitioning of new assimilate to various plant components. It is assumed that the growth of cassava leaves and stems is at a rate below that of the assimilate supply, and that remaining assimilate accumulates in the storage roots. A decreasing fraction of assimilate is allocated to fibrous roots as the crop ages, adjusted if supply is limiting. In reality, reproductive structures may have first call on assimilate, but these are so small in cassava they can be

ignored for modelling purposes (Gutierrez et al., 1988). Leaf growth rate (LGR) is calculated as:

$$LGR = N_b \cdot LAR \cdot LS / SLA, \quad (9)$$

where LGR (g m^{-2} day^{-1}) is the daily leaf weight increment, N_b is the number of active growing apices per unit area (Eq. 7), LAR is the leaf appearance rate per apex (leaves day^{-1}), LS is the individual leaf area of newly produced leaves (cm^2 $leaf^{-1}$), and SLA is the specific leaf area (cm^2 g^{-1}).

Rate of leaf appearance (LAR): Most cultivars detailed in the literature produce around 0.7 leaves day^{-1} per apex at the start of the season, decreasing as the plant ages (e.g., Cock et al., 1979; Irikura et al., 1979). In most cases, a quadratic equation can be used to describe cumulative leaf number per apex, hence the first derivative, or rate of leaf appearance (LAR), is linear. Within a cultivar, leaf appearance rates are influenced by temperature (Irikura et al., 1979) which can be accounted for by expressing LAR as a function of developmental age (Fig. 3). Using a base temperature of 13°C gives a leaf appearance rate of 0.83 leaves Dd^{-1} at emergence decreasing linearly to around 0.14 leaves Dd^{-1}, for the four cultivars MCol22, MCol113, MMex59 and Popayán. There appears to be some genotypic variation in leaf appearance rate; Gutierrez et al. (1988) use a value of 0.969 leaves Dd^{-1} for the cultivar TMS30572, MPtr26 has a value of 1.48 leaves Dd^{-1} (Veltkamp, 1986), and Ceiba has a rate as low as 0.41 leaves Dd^{-1} (Manrique, 1990a). Most other
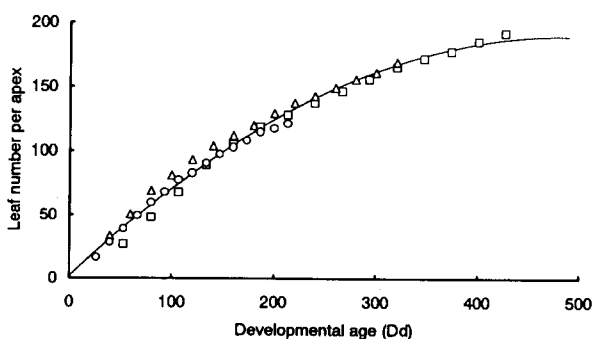

Fig. 3. Relationship between leaf number per apex and developmental age (Dd) for cassava cultivars MCol22, MCol113, MMex59 and Popayán grown at 20°C (O), 24°C (△) and 28°C (□). Developmental age calculated using $T_{base} = 13°C$ and $T_{opt} = 30°C$. Data from Irikura et al. (1979).

Table 2
Parameters describing leaf appearance rate, leaf size, specific leaf area, and leaf age for a number of cassava cultivars. See Appendix for a description of parameters

Cultivar	Parameter						
	LAR_0	A_{L0}	LS_{max}	t_{LS}	LS_{300}	SLA_0	P_{leaf}
MCol22	1.00	330	350	60	60	220	65
MMex59	1.21	212	450	60	50	250	65
MCol1684	0.94	370	220	55	40	270	45
MVen77	1.13	353	450	70	35	240	75
MPtr26	1.45	294	450	70	50	220	75
MCol638	1.1	235	350	60	35	220	80
MAus10	1.21	235	240	45	70	350	161

cultivars have initial values of around 1 leaf Dd^{-1}.

Daily leaf appearance rate (LAR, leaves day^{-1}) in the model is calculated as:

$$LAR = R_V \cdot LAR_0 (1 - t_{ve}/A_{L0}), \qquad (10)$$

where R_v is the daily rate of progression of vegetative development (Eq. 1), LAR_0 is the leaf appearance rate (leaves Dd^{-1}) at emergence, t_{ve} is the crop developmental age (Dd) since emergence, and A_{L0} is the developmental time (Dd) from emergence to the stage at which leaf production effectively ceases. The parameters LAR_0 and A_{L0} are cultivar specific, and are shown for a number of cultivars in Table 2. As in the Cock et al. (1979) model, it is assumed that leaves are fully open as soon as they emerge.

Drought stress reduces the rate of leaf appearance, but several studies have shown that on release of drought stress, there is some compensatory increase in leaf appearance rate (and leaf size) to values above what would have occurred if there had been no stress (e.g., Connor and Cock, 1981; Palta, 1984; Baker et al., 1989). These effects are described in the model by adjusting the LAR calculations as follows:

for $\Phi < 1$ $LAR' = LAR \cdot \Phi,$

for $\Phi = 1$ $LAR' = LAR \cdot (1 + 0.6\omega),$ (11)

where LAR' is the adjusted leaf appearance rate, and ω is the "stress release compensation factor" calculated as the mean value of $(1-\Phi)$ for the last 50 days weighted for proximity to the present:

$$\omega = \sum_{n=1}^{50} (1 - \Phi_n)(50 - n + 1) \Big/ \sum_{n=1}^{50} (50 - n + 1), \quad (12)$$

where n is the number of days before present. Use of a weighted mean of 50 days smooths out daily fluctuations in Φ.

Leaf size (LS): Final size reached by emerging leaves follows a characteristic curve described by Cock et al. (1979) in a wide range of environments and management conditions. A maximum size is reached 70–80 days after emergence, thereafter declining. The maximum size and the rate of decline are to some extent cultivar specific, but may also be influenced by environment. Temperature may alter the maximum size and the data at which this occurs (Irikura et al., 1979), but expressing leaf size as a function of thermal time with a range of base temperatures cannot resolve the differences. There is some evidence that assimilate availability may affect leaf size; this is discussed in more detail later.

For the moment, leaf size (LS) at t days after emergence is calculated from an adaptation of the empirical equation given in Cock et al. (1979):

$$LS = \frac{t \cdot LS_{300} \cdot LS_{max} \cdot (t_{LS} - 300)^2}{t_m \cdot (LS_{max} - LS_{300}) \cdot (t_{LS} - t)^2 + t \cdot LS_{300} \cdot (t_{LS} - 300)^2},$$
(13)

where LS_{max} is the maximum leaf size reached at t_{LS} days after emergence, and LS_{300} the leaf size at an arbitrary 300 days after emergence towards the end of the period of growth. Values for each of these three parameters are shown for a number of cultivars in Table 2.

The compensatory increase in leaf size on release of drought stress (Connor and Cock, 1981) is taken

account of by adjusting the expected leaf size from Eq. 13 when $\Phi = 1$ as follows:

$$LS' = LS \cdot (1 + 1.3\ \omega),\qquad(14)$$

where ω is the stress release compensation factor calculated in Eq. 12 for leaf appearance.

Specific leaf area (SLA): Typical specific leaf area (SLA) values in cassava vary from 200–300 cm^2 g^{-1}, depending on cultivar, temperature, light regime, water status, and crop age. Based on the equation used by Fukai and Hammer (1987), and observations of El-Sharkawy et al. (1992) on the effect of drought stress, the following equation was used to estimate SLA:

$$SLA = SLA_0(0.396 + 0.025\ T_{mean})$$
$$\cdot (0.85 + 0.15\ \Phi),\qquad(15)$$

where SLA_0 is the specific leaf area for a particular cultivar at a standard temperature of 24°C with no drought stress. Values of SLA_0 are shown for a number of cultivars in Table 2.

Stem growth: It is assumed that the stem/shoot fraction (*sf*) increases linearly from 0.2 at emergence (Fukai and Hammer, 1987) to a cultivar-specific value (sf_{max}) of around 0.6–0.7 at the development age of 120 Dd, and remains constant subsequently. The daily stem weight increment (SGR, g m^{-2} day^{-1}) is calculated as:

$$SGR = sf \cdot LGR / (1 - sf),\qquad(16)$$

where LGR is the daily leaf weight increment (Eq. 9).

Fibrous root growth: The model of Gutierrez et al. (1988) is the only model to explicitly consider fibrous roots; this assumes a root/shoot ratio (RSR) of 0.12 decreasing abruptly to 0.07 after a developmental time of 900°C day. In GUMCAS, in order to smooth this change, a RSR of 0.15 is assumed at the start of the season, declining exponentially to 0.05 at the end. The daily root weight increment (RGR, g m^{-2} day^{-1}) is calculated as:

$$RGR = (LGR + SGR)$$
$$\cdot (0.05 + 0.10 \exp(-0.0005\ t_{vc})),\qquad(17)$$

and the increment in total root length (δL_v, cm cm^{-3}) as

$$\delta L_v = RGR \cdot SRL \cdot \rho / 10000,\qquad(18)$$

where SRL is the mean specific root length (cm g^{-1}) and ρ is the population density (m^{-2}). The CERES maize model uses a value of SRL of 8000 cm g^{-1}; in view of the observation of Connor et al. (1981) that fibrous roots of cassava are somewhat thicker than those of other crops, a value of 5000 cm g^{-1} is used in GUMCAS. This was found to give root length density values in the upper layers of 1–1.5 cm cm^{-3}, slightly higher than the values given by Connor et al. (1981) and El-Sharkawy and Cock (1987).

A similar procedure to that in the Ritchie water balance model (Ritchie, 1985) is used for determining the distribution of the new root length in the soil profile, with minor modifications to balance root weight and length losses. A constant fraction of 0.5% root death per day is assumed for each soil layer. Rooting depth is assumed to extend at a rate (RDGR) of 2.2 cm Dd^{-1} to a maximum determined by soil depth.

3.5. Senescence

Potential leaf longevity (P_{leaf}, days) appears to be cultivar specific, ranging from as short as 50 days (MMex59, Connor and Cock, 1981) to as much as 160 days (MAus10, Fukai and Hammer, 1987). Environmental factors, however, have a distinct influence on the actual longevity (A_{leaf}) of leaves. Extreme shading markedly reduces longevity, although mild shading has little effect (Cock et al., 1979). Low temperatures (<19°C) are known to increase shedding (Fukai and Hammer, 1987), but temperatures above 20°C have also been found to decrease longevity (Irikura et al., 1979). Drought stress has little effect on leaf longevity and in some cases may actually increase it (MMex59, Connor and Cock, 1981). On release of drought stress, however, there is often a large loss of leaves as new ones are produced (Connor and Cock, 1981).

In the model, a "box-car" method is used to keep track of the age, dry weight, area and longevity of each "cohort" of leaf area produced per day. When a cohort is produced on a given day, its actual longevity (A_{leaf}) is set initially to the potential longevity (i.e., $A_{leaf} = P_{leaf}$), and entered in the first row of an array; cohorts produced earlier are 'aged' by shifting their values to the row immediately below it. The actual age (in days) of each cohort is therefore represented by its row number in the array.

The effect of temperature and shading on leaf longevity is taken into account by reducing A_{leaf}. For temperature, a curvilinear empirical relationship with a maximum at 20°C is assumed:

$$A_{leaf} = A_{leaf}$$

$$- (15 - 14.5 \cdot T_{mean} + 0.035 \cdot (T_{mean})^2), \quad (19)$$

while for shading, a critical value of LAI is assumed (L_{sen}), above which a reduction in longevity occurs each day with greater intensity the higher the LAI:

$$\text{for LAI} \leq L_{sen}, \quad A_{leaf} = A_{leaf}, \quad (20)$$

$$\text{for LAI} > L_{sen}, \quad A_{leaf} = A_{leaf} - \gamma_s (\text{LAI} - L_{sen}),$$

where γ_s is a parameter (day m^2 m^{-2}) representing the sensitivity of senescence to shading. In this way, both the duration and intensity of exposure of the crop to temperature and shading stress are taken into account. Each day, A_{leaf} for each cohort is adjusted, after which its age is checked; if the cohort is older than its A_{leaf} value, it is removed, returning 30% of its dry weight to the assimilate pool for that day (Fukai and Hammer, 1987). The parameters P_{leaf}, γ_s and L_{sen} are assumed to be cultivar specific. Values of P_{leaf} for a number of cultivars are shown in Table 2. This approach can account for the observation of Fukai and Hammer (1987) of leaf shedding in older plants but not in younger plants under moderately low temperatures, without assuming a change in critical temperature with age. An older plant merely has more leaves approaching their longevity, A_{leaf}, than a younger plant.

3.6. The program

GUMCAS is written in Turbo Pascal (Borland), and derives its name from *gumaya*, the word for 'simulate' in Tagalog, the national language of the Philippines. A detailed User's Manual containing technical details is available (Matthews and Hunt, 1993). The model and documentation is available as part of the IBSNAT DSSAT system (address: IBSNAT, Department of Agronomy and Soil Science, University of Hawaii, 2500 Dole Street, Krauss Hall 22, Honolulu, HI 96822, USA), or as a stand alone package. A Fortran version is also available.

4. Testing the model

For calibration of the model, crop parameters were generally estimated by trial and error. Where more detailed information was available, parameters were estimated as follows: The date of emergence was estimated by extrapolation of the cumulative leaf number curve to the point on the time axis where there were zero leaves. The parameters controlling branching were then adjusted until the predicted number of apices matched the observed numbers, the leaf appearance parameters until leaf numbers per apex were in agreement, and leaf size parameters until leaf size was correct. Senescence parameters were then adjusted until
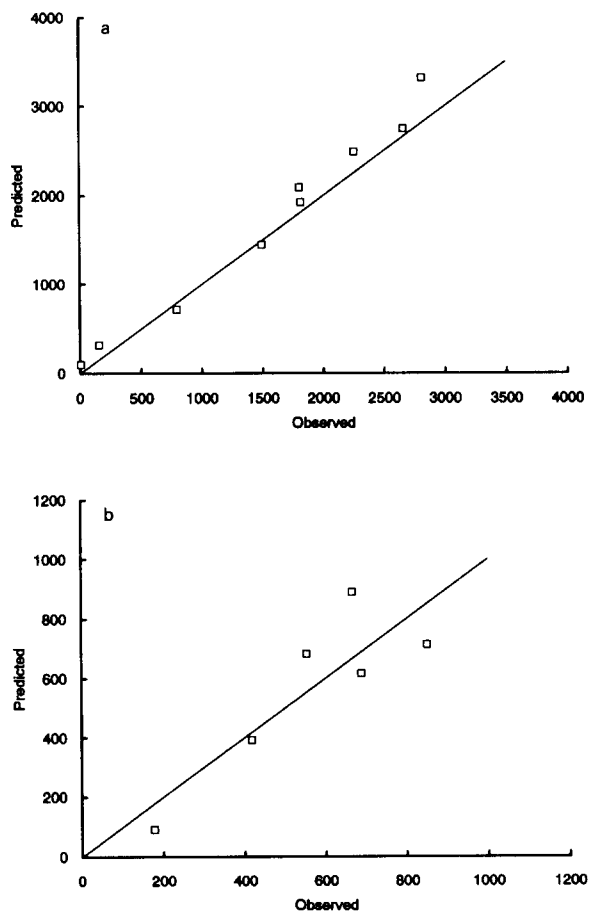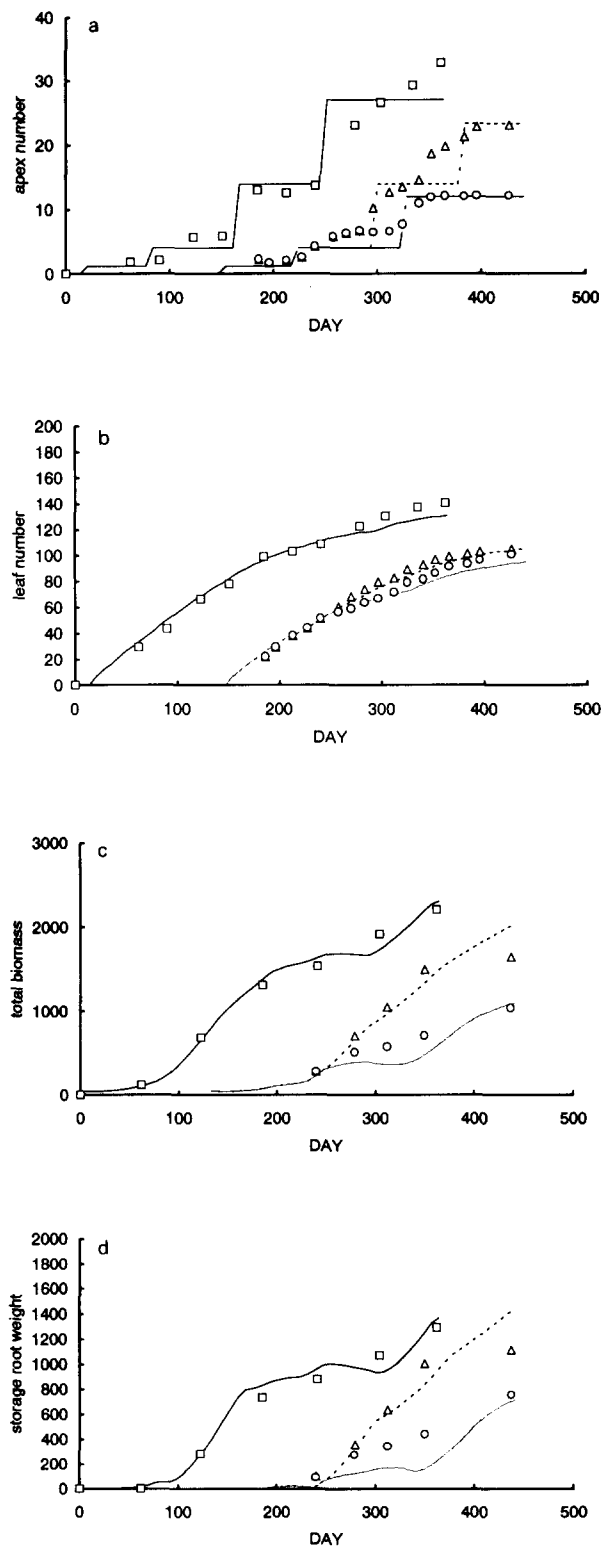

Fig. 4. Comparison of predicted and measured values of (a) total crop dry weight and (b) storage root dry weight for cassava cultivar MAus7 planted at a range of planting dates in Australia. Data from Keating et al. (1982).

predicted leaf area index values matched the observed. Photoperiod parameters were obtained with a reiterative convergence program using least-squares as the determining statistic.

4.1. Effect of temperature and photoperiod

Fig. 4 shows measured and simulated values of total biomass (excluding fibrous root weight) and storage root weight for a number of different planting dates in Queensland, Australia (Keating et al., 1982). Values are for 30 June before colder temperatures were encountered. Agreement for total biomass is excellent ($r = 0.99$, $P < 0.01$), although there is a tendency for the model to predict slightly higher values in the upper range. Agreement for storage root weight is more variable ($r = 0.87$, $P < 0.05$), but still satisfactory. There was less agreement between measured and simulated values after the cold period. It seems likely that this was due to failure of the model to predict an increase in leaf size as growth started again as temperatures rose.

4.2. Effect of drought stress

The data of Connor et al. (1981) and Veltkamp (1986) were used to determine the ability of the model to predict the effect of drought. Both datasets refer to the cultivar MCol22 and were grown in a similar environment in the same year at CIAT, Colombia. In Experiment 1 of Veltkamp (1986) there was a dry period between 200–280 days after planting (DAP), while in the experiment of Connor et al. (1981) it occurred from 60–80 DAP in both treatments, which was artificially extended in treatment 2 to around 180 DAP.

Figs. 5a and b show measured and simulated values of apex number and leaf number per apex for the three treatments. Agreement for both variables is good, although there is a tendency for leaf appearance rates to be underestimated later in the season. The model also successfully predicted the compensatory increase in leaf size after the release of drought stress. Although branching is represented in the model as a step-wise process while the measured data show that branching

Fig. 5. Comparison of predicted (lines) and measured values (symbols) for cassava cultivar MCol22 growing at CIAT Colombia. (a) number of apices, (b) number of leaves per apex, (c) total crop dry weight, and (d) storage root dry weight. Key: □ Veltkamp (1986), Experiment 1; △ Connor et al. (1981), control treatment; ○ Connor et al. (1981), drought treatment.

Table 3

Sensitivity analysis for 15 of the 28 model parameters for an "average" cassava cultivar growing at CIAT under well-watered and drought stress conditions. See text for definition of β and $\beta°$ values. Parameters ranked on absolute $\beta°$ values of storage root. VPD, photoperiod, temperature senescence parameters not included, as they have no effect on model output in CIAT conditions. See Appendix for a description of parameters

Parameter	Parameter values			β		$\beta°$	
	Default	Min	Max	Total biomass	Storage root	Total biomass	Storage root
No drought stress[a]							
P_{leaf}	70	45	161	0.54	0.83	0.64	0.99
sf_{max}	0.65	0.56	0.76	−0.03	−1.56	−0.01	−0.61
SLA_0	240	220	350	0.13	0.96	0.06	0.45
A_{bl}	44.1	14.7	64.7	−0.52	−0.37	−0.59	−0.42
CGR_{max}	27.5	23.5	27.5	1.13	1.99	0.18	0.33
A_{L0}	235	212	370	0.42	−0.24	0.18	−0.19
SN_0	1	1	3	0.49	0.39	0.39	0.19
LS_{max}	300	220	450	0.21	0.22	0.16	0.19
B_{max}	30	20	52	0.07	−0.13	0.09	−0.15
A_b	35.3	24.8	58.8	−0.45	−0.09	−0.41	−0.14
A_e	11.8	8.8	19.7	−0.04	−0.07	−0.08	−0.13
N_f	3	2.61	3.6	0.82	0.22	0.21	0.11
LAR_0	1.21	0.94	1.45	0.52	0.2	0.24	0.11
LS_{300}	50	35	75	0.31	−0.03	0.25	−0.05
t_{LS}	60	45	70	0.09	−0.01	0.04	0.00
Drought stress conditions[b]							
A_{bl}	44.1	14.7	64.7	−6.13	−6.02	−2.92	−1.96
P_{leaf}	70	45	161	0.86	1.11	1.30	1.61
A_{L0}	235	212	370	3.87	3.77	1.85	1.33
A_e	11.8	8.8	19.7	0.21	0.22	1.15	0.99
t_{LS}	60	45	70	2.12	2.07	0.82	0.80
A_b	35.3	24.8	58.8	−0.12	−0.13	−0.57	−0.55
SLA_0	240	220	350	−0.87	−0.60	−0.38	−0.33
N_f	3	2.61	3.6	0.75	0.75	0.25	0.25
CGR_{max}	27.5	23.5	27.5	1.08	1.38	0.16	0.20
LAR_0	1.21	0.94	1.45	−0.26	−0.26	−0.11	−0.11
SN_0	1	1	3	−0.51	−0.48	0.11	0.10
LS_{300}	50	35	75	−0.11	−0.11	−0.11	−0.10
B_{max}	30	20	52	0.05	0.04	0.03	0.03
LS_{max}	300	220	450	0.01	−0.02	0.03	0.02
sf_{max}	0.65	0.56	0.76	0.26	−0.02	0.08	−0.02

[a] Default parameter values give a total dry matter of 28.5 t ha^{-1} and storage root weight of 16.4 t ha^{-1} at 300 days after planting.
[b] Default parameter values give a total dry matter of 7.9 t ha^{-1} and storage root weight of 6.2 t ha^{-1} at 300 days after planting.

occurs in distinct but protracted phases (Fig. 5a), this approach seems to provide an adequate description of the number of apices per plant over the period of growth. Figs. 5c and 5d show the predicted and observed values of total biomass and storage root weight for the three treatments. Again agreement is satisfactory, although there was an underestimation of both total and storage root weight in the stress treatment of Connor et al. (1981).

4.3. Sensitivity analysis

An "average" cassava cultivar growing at CIAT was taken as the base to determine the effect of perturbations in each parameter. Parameters of the "aver-

age'' cultivar were determined as the mean of all values encountered, both from the literature and from fitted data estimates for that parameter. Both non-drought stress and drought stress conditions were considered; nutrient levels were assumed to be non-limiting in both cases. Sensitivity (β) was defined as the ratio of the fractional change in an output variable to the fractional change in a particular parameter. A range of 5% on either side of the parameter value was used.

Sensitivity relative to the range of values encountered for the parameter was also determined ($\beta°$). The minimum and maximum parameter values encountered in fitting the model to measured datasets were taken as the best estimates of the natural range; as these were limited in number, it is recognised that they may not be completely representative. Table 3 shows values for each parameter of β and $\beta°$ for both total dry weight and storage root weight as output variables. Use of $\beta°$ rather than β changes the sensitivity ranking of the parameters (Table 3a); for example, the maximum crop growth rate, CGR_{max}, was found to be a sensitive parameter in the model (high β value), but was not found to vary much between any of the cultivars examined (lower $\beta°$ value). The rankings of the parameter sensitivities also change markedly under drought stress (Table 3b). The fraction of shoot weight allocated to the stem, sf_{max}, an important parameter in determining yield in non-stress conditions, becomes relatively unimportant under drought. The reverse is true of t_{LS}, the date at which maximum leaf size occurs, and A_e, the developmental time until emergence.

5. Discussion

GUMCAS adequately describes cassava growth in at least two different environments, and is able to account well for the influence of water shortage on various processes in the plant. However, wider validation is necessary, as it has not been possible yet to validate the model on independent datasets that have not been used in its calibration.

The assumption, first made by Cock et al. (1979), that leaf and associated stem production is the preferred sink in the carbohydrate allocation, seems to explain most of the observed environmental effects on partitioning in cassava. The increase in the fraction of assimilate partitioned to the shoot (PTF) with a rise in temperature (e.g., Boerboom, 1978; Fukai and Ham-

mer, 1987) can be explained by an increase in leaf appearance rate. Similarly, the increase in PTF with shading (Fukai et al., 1984) is probably due to a reduction in total assimilate produced, with less available for storage root growth. The effect of drought stress on leaf production (Connor and Cock, 1981) reduces the canopy requirement for assimilate without proportionally reducing assimilation (at LAI > 3), resulting in greater storage root growth. Abundant nitrogen is also known to alter the distribution in favour of the shoot (Hunt et al., 1977), probably by stimulating leaf area development. The effect of long photoperiods on increasing PTF (Bolhuis, 1966; Fukai and Hammer, 1987) may be due to stimulation of branching and hence leaf-producing apices.

The factors controlling branching in cassava are not well understood and require further research. It is not clear whether the delay in branching by low temperatures (Irikura et al., 1979) is due to a thermal effect on development rate, or by an effect on assimilate supply. In the model of Gutierrez et al. (1988) it is assumed that branching occurs when the ratio of computed assimilate supply to demand exceeds an arbitrary value of 3; the reduced branching observed by increased competition (Tsay et al., 1987) and delayed branching in drought-stressed plants (Connor and Cock, 1981) would seem to support this hypothesis. On the other hand, altering source/sink relationships by pruning has had little effect on branching dates (Cock, pers. commun.), and assimilate supply/demand ratios alone cannot explain the variation in branching dates in the data of Keating et al. (1982). In future versions of the cassava model the method of calculating the maximum number of branches formed (B_{max}) should be improved; at present this is assumed to be a cultivar-specific parameter, which can be reduced by drought stress, but a more mechanistic approach, perhaps based on assimilate availability, is preferable.

The influence of photoperiod on cassava growth and development also requires further investigation. Several studies have reported that assimilate partitioning is altered in favour of the shoot by long days (e.g., Bolhuis, 1966; Da Cunha and Da Coneiçao, 1975; Lowe et al., 1976; De Bruijn, 1977; Veltkamp, 1986). Long days have been shown to increase leaf number and leaf size (Keating et al., 1985), and also the maximum number of apices reached and the leaf appearance rate per apex (Veltkamp, 1986). This would result in

increasing shoot requirements for assimilate, thus reducing that available for storage root growth, but can not explain all of the shift in partitioning.

GUMCAS gave accurate predictions of branching date using a minimum optimum photoperiod of 15.5 h, with the rate of progression towards branching declining at shorter photoperiods. This is consistent with the data of Veltkamp (1986), showing earlier branching in most cultivars at a photoperiod of 16 h than at 12 h, and with the observation of De Bruijn (1977) that branching is promoted by longer photoperiods. The decline in the response of 0.25 h^{-1} at photoperiods less than 15.5 h suggests that branching in MAus10 would not occur at photoperiods below 11.5 h, a prediction that could be tested in field or growth chamber experiments. Although a significant improvement in the fit to the data was obtained by taking into account the rate of change in photoperiod $d\phi/dt$, further testing with a wider range of datasets is necessary to confirm that this is a controlling factor in the switch to the reproductive state. It has been observed that $d\phi/dt$ is correlated with leaf appearance rate in some cereals (e.g., wheat, Baker et al., 1980). The evolutionary significance of sensitivity to $d\phi/dt$ is unclear, particularly in a tropical crop, although Baker et al. (1980) have argued that it is the only unambiguous key to the time of year.

The prediction of leaf size is at the moment the most empirical part of the canopy dynamics sub-model, particularly the way in which compensatory growth after release of drought stress is dealt with. Its description as a function of time is also unsatisfactory in that environmental influences can not be accounted for. The coincidence of the onset of storage root bulking with the decline in leaf size, thereby acting as an increasingly competitive sink for assimilate, suggests that assimilate availability may in part determine leaf size. The lack of effect of decreasing temperature until 20°C in some cultivars (Irikura et al., 1979) and increase in leaf size on restriction of branching (Tan and Cock, 1979) support this hypothesis.

If it is assumed that the final size reached by each newly emerged leaf is proportional to the ratio of supply to demand of assimilate, and that supply is represented by the assimilate produced each day (δW, g plant^{-1}), and demand is proportional to total plant weight (W, g plant^{-1}), then leaf size (LS, cm^2) can be expressed as

$$LS = k \cdot \delta W/W, \tag{21}$$

where k is a constant of proportionality with units cm^2. It was found that the time course of LS and $\delta W/W$ followed remarkably similar patterns (Fig. 6a), even to the extent of the sudden rise after an intense period of drought. Regression of LS upon $\delta W/W$ (Fig. 6b) gives a value for k of 11 000 cm^2 for the cultivar MCol22. The use of this relation to predict leaf size was found to work well for well-watered and constant drought conditions, but, while giving the correct response on release of drought, tended to significantly overestimate leaf size and hence crop growth rate at the end of the season. This may have been due to the positive feedback involved; a higher $\delta W/W$ results in a larger leaf area and hence more assimilate being partitioned to the leaves, which in turn results in a higher δW, etc. This effect has to some extent been observed in reality, with a larger LAI attracting a larger fraction of assimilate (Fukai and Hammer, 1987), but there may be a need to build in a negative feedback mechanism to control this. The overall model is relatively
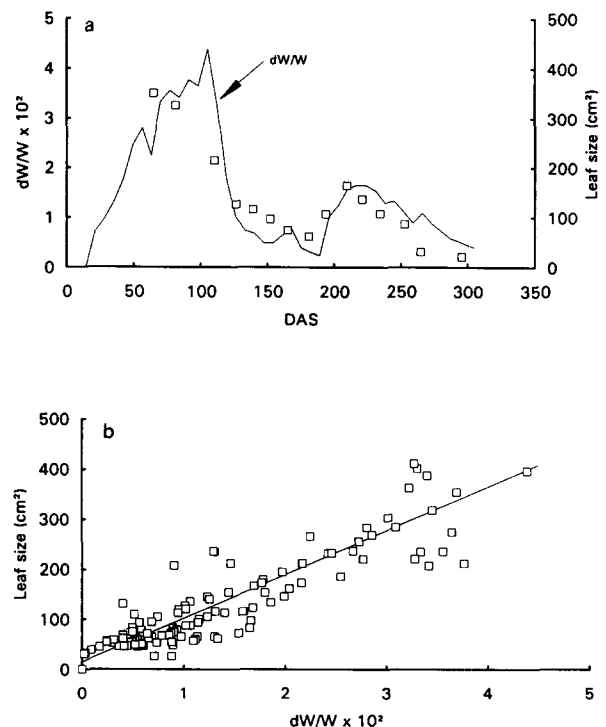

Fig. 6. Comparison of $\delta W/W$ and size of newly emerged leaves for (a) cultivar MCol22 subjected to drought (Connor et al., 1981) and (b) for a range of cultivars in a range of conditions (data from Connor et al. (1981), Keating et al. (1982), and Veltkamp (1986)).

sensitive to leaf size towards the end of the season, where any errors in its estimation, though maybe small in absolute terms, are multiplied by the large number of apices present.

Despite these problems, this approach provides marked advantages over the empirical function used by Cock et al. (1979) in that leaf size is calculated as a function of processes within the plant, rather than as a function of chronological time. This enables responses to environmental influences to be included; the success in predicting the increase in leaf size on release of drought stress (Fig. 6a) is an example. At present, both approaches are included in the model as options; future development, however, should focus on defining more accurately the processes controlling leaf size; factors other than assimilate availability are probably also important. For example, while leaf weight may be determined by the assimilate supply/demand ratio, leaf area may be more influenced by water and nutrient status, resulting in variation in specific leaf area. There is also a need to investigate whether W is the best estimate of assimilate demand; a method of estimating the fraction of actively respiring tissue may give a more accurate assessment. Similarly, further work is necessary to see if k, the proportionality constant (Eq. 21), varies significantly between cultivars.

Results of the sensitivity analysis confirmed the finding of Cock et al. (1979) that leaf longevity is an important factor in determining yield, both in well-watered and drought conditions. Not only is the model output sensitive to changes in its value, but there seems to exist considerable natural variation in leaf longevity, suggesting that significant improvements in cassava yields could be achieved by selecting for this character. However, this assumes the values of the other parameters do not change; the lower storage root yields despite the higher shoot weight of MAus10 compared to the Colombian cultivars would suggest a negative correlation between leaf longevity and some of the other parameters. Further work is also required to clarify the effect of drought stress on leaf longevity; while Connor and Cock (1981) found that lower leaf area under drought was mainly due to restricted leaf area development rather than leaf loss, Baker et al. (1989) found increased leaf senescence with onset of drought.

Other IBSNAT models define a limited subset of the total number of parameters in the model as *genotype coefficients*, i.e., parameters which have a significant

effect on model output over their range of possible values. If a genotype coefficient is defined as a parameter that alters the model output by more than 10% over its range of values, and assuming storage root weight is the desired output of a cassava model, then the following 12 parameters could be classified as genotype coefficients for well-watered conditions (in decreasing order of importance): P_{leaf}, sf_{max}, SLA_0, A_{b1}, CGR_{max}, A_{L0}, SN_0, LS_{max}, B_{max}, A_b, A_e and LAR_0 (see Appendix for parameter details). The importance of some parameters changes markedly under drought; for example, the date at which maximum leaf size occurs (t_{LS}) is not very important in well-watered conditions, but becomes relatively so under drought stress. The array of genotypic coefficients necessary to describe differences between cultivars in all conditions should thus encompass all characteristics that influence performance in each environment even though they may have little or no impact in other environments. To accomplish this with the current model, 25 parameters are included in the cultivar file.

Acknowledgements

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Appendix
Input crop parameters used in the cassava model, their description, and units

Parameter	Description	Units
A_e	developmental time from sprouting to emergence	Dd
CGR_{max}	maximum crop growth rate	$g\ m^{-2}\ day^{-1}$
VPD_c	critical VPD for reduction in growth	kPa
γ_v	sensitivity to increasing VPD	kPa^{-1}
SN_0	number of stems set before first branching (lateral branches)	dimensionless
A_{b1}	developmental time to first branching	Dd
A_b	developmental time between subsequent branching levels	Dd
ϕ_o	minimum optimum photoperiod	h
S_ϕ	sensitivity to photoperiod	h^{-1}
N_f	no of branches at each branch point	dimensionless
B_{max}	maximum number of branches that can be produced	dimensionless
LAR_0	leaf appearance rate at time of emergence	leaves Dd^{-1}
A_{L0}	developmental age at which leaf production ceases	Dd
LS_{max}	maximum leaf size	cm^2
t_{LS}	date at which max leaf size occurs	days after emergence
LS_{300}	leaf size at 300 DAE	cm^2
SLA_0	standardised specific leaf area	$cm^2\ g^{-1}$
P_{leaf}	maximum leaf age	days
L_{sen}	critical LAI for leaf aging relationship	$m^2\ m^{-2}$
γ_s	slope of LAI and leaf aging relationship	$day\ m^2\ m^{-2}$
sf_{max}	maximum fraction of new nodal weight going to stem tissue	dimensionless
RDGR	root depth growth rate	$cm\ Dd^{-1}$
SRL	specific root length	$cm\ g^{-1}$