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CANOPY STRUCTURE OF MAIZE (*ZEA MAYS* L.) AT DIFFERENT POPULATIONS: SIMULATION AND EXPERIMENTAL VERIFICATION

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GRANT R. F. and HESKETH J. D. *Canopy structure of maize* (Zea mayz *L.*) *at different populations: simulation and experimental verification.* BIOTRONICS **21**, 11-24, 1992. Understanding the dynamics of canopy growth is necessary to the understanding and simulation of plant growth in homogeneous populations and of population growth in heterogeneous communities. These dynamics should be studied and reproduced at the organ level of biological organization if they are to be represented at the population level in simulation models. In order to investigate organ growth under a range of conditions, maize (*Zea mays* L.) was planted at five populations (1.5, 4.3, 5.7, 8.6 and 10.3 plants m^{-2}). Masses and areas of individual leaves, and masses and lengths of individual sheaths and internodes were recorded periodically during canopy growth from the population of 5.7 plants m^{-2}. These data were used to parameterize simple algorithms for the expansion of these organs based on their growth in dry mass. These algorithms were then tested on plants hervested at silking from the other populations through the use of a simulation model. Leaf, sheath and internode mass were observed to decrease with higher population, with greater decreases at higher nodes. Specific leaf area (*SLA*), specific sheath length (*SSL*) and specific internode length (*SNL*) were observed to decrease with organ mass, such that reductions at higher populations in organ dimensions were less than those in organ mass. Changes in *SLA*, *SSL* and *SNL* with growth stage and population were reproduced in the model, enabling it to simulate nodal distributions of organ dimensions over time and population. Some uncertainty remains in the estimation of early sheath and internode elongation. A model that can function at this level of temporal and biological organization will be useful in studies of interspecific plant competition, and of insect infestation.

Key words: *Zea mays* L.; leaf area; sheath length; internode length; specific leaf area; canopy structure; simulation modelling.

INTRODUCTION

If the dynamics of plant growth at the population and community levels of biological organization are to be understood and reproduced in simulation models, then the dynamics of plant growth at the organ level of biological organization must be studied. Such phenomena as crop-weed competition for

irradiance at the community level, or tiller competition for irradiance at the population level, are based on dynamic changes in the vertical profiles of leaf area which arise from such phenomena as leaf, sheath and internode elongation at the organ level. Some insect infestations within the crop canopy are site-specific, such that only the function of targeted organs are impaired and crop damage arises from the secondary effects of this impairment.

Many studies of growth at the organ level under different growing conditions have focussed on the ratio of leaf area to mass, called the specific leaf area (*SLA*). *SLA* has been observed to decrease with increased irradiance (*16, 18*), CO_2 (*1*), growth stage (*6*) and with decreased population density (*27*). Straley and Cooper (*22*) observed that new leaves of alfalfa had a higher *SLA* if older leaves were shaded, suggesting that *SLA* is determined by the effect of environment on the growth of the plant. Similar effects of environment on stalk structure are commonly observed, as when thinner stalks arise from low irradiance or high population, although we are not aware of data in which this effect has been quantified.

In most crop models, dry matter (*DM*) growth is partitioned at the whole plant level into different organ classes (e.g. leaves, petioles, stalks, pods and seeds), using phenology-dependent algorithms (*7, 15*). Because the mechanisms determining *SLA* are not clearly understood, leaf expansion in some models is estimated from the time integral of temperature, independently of *DM* growth (*15, 21*). In others, *SLA* is assumed to remain constant during *DM* growth (*28*), or to change with growth stage (*19*). In the soybean model SOYGRO (*26*), leaf expansion is estimated from a growth stage-dependent potential rate modified by factors for population and water stress. This rate is constrained by growth stage-dependent minimum and maximum values for *SLA* at the whole plant level. At the individual leaf level, Mutsaers (*17*) used time-dependent logistics functions during phases of differentiation and expansion, for which node-specific parameters were required. Cao *et al.* (*3*) used a similar approach for estimating the areas of individual leaves of maize and soybean. In these approaches, leaf *DM* growth is not considered in the estimation of leaf area.

The estimation of petiole and internode lengths is often ignored in crop growth models (*24*), although these lengths are required in the estimation of vertical leaf area profiles. Without estimation of these lengths, some models of interspecific competition rely upon empirical calculations of plant height and vertical leaf area profiles (*20*).

During growth, organs expand in three dimensions : length, width and thickness. The simplest hypothesis of growth is one in which expansion in each dimension is proportional to that in the others. This hypothesis allows the use of simple equations to describe organ expansion as a function of organ *DM* growth. In order to test this hypothesis, a data set for the dimensions and *DM* of maize leaves, sheaths and internodes was acquired for a range of populations. Data from one population were used to establish relationships between changes in the dimensions and masses of each organ type. These relationships were then used in a simulation model of crop growth (*7, 8, 12, 13*) to determine the extent

to which they allowed the reproduction of organ dimensions recorded at the same and other populations. These relationships are incorporated into the crop growth component of a larger agroecosystem simulation model with the objective of enabling this component to reproduce dynamic changes in the nodal distributions of organ size under diverse growing conditions.

MATERIALS AND METHODS

Field experiment

Maize (*Zea mays* L. cv 'P3377') was planted on 28 April 1988 (day 119) on a Flanagan silt loam (fine montmorillonitic mesic Aquic Argiudoll) at the agronomy farm of the University of Illinois (40°N). Five populations (1.5, 4.3, 5.7, 8.6 and 10.3 plants m^{-2}) were planted in plots 9 m by 3 m with a row spacing of 0.76 m. Additional plots of 5.7 plants m^{-2} were included to allow more extensive data to be recorded at this population. Each plot was fertilized with 20 g m^{-2} of N as NH_4NO_3, and received an irrigation of 50 mm every 14 days. Weeds were controlled manually during the entire experiment.

During the pre-silking period two plants were harvested every 2 to 3 days from the additional plots of 5.7 plants m^{-2}. The area and *DM* of each leaf, and length and the *DM* of each sheath and internode were recorded from each plant at each harvest. On 18 July, 1988 (day 200), four days after silking, three plants from each population were harvested, and the size and *DM* of each organ recorded as for the pre-silking harvests. Leaf areas were recorded with a LI-3000 leaf area meter*.

Total irradiance (W m^{-2}), air temperature (℃), dewpoint (℃), and windspeed (m s^{-1}) were measured every 3 minutes during the experiment, and recorded as hourly averaged values on a Campbell CR-7 micrologger*. Rainfall and irrigation, if present, were recorded daily.

Model hypotheses

If the ratio among the three dimensions of an organ (length, width and thickness) is assumed to be maintained during growth, then the ratio between changes in dimension and those in *DM* may be calculated as functions of organ *DM*:

$$\delta A_i / \delta M_i = f(M_i) \quad (1)$$

and:

$$\delta L_i / \delta M_i = f(M_i) \quad (2)$$

where:

A_i = area
L_i = length

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M_i = dry mass of organ i
i = leaf, sheath or internde.

In general, if organ extension occurs proportionately in three dimensions, then areal expansion in two dimensions will vary with $M_i^{-0.33}$, and longitudinal extension in one dimension will vary with $M_i^{-0.67}$. Thus leaf (i = L) area expansion may be calculated as:

$$\delta A_L / \delta M_L = \alpha M_L^{-0.33} \quad (3)$$

where:

A_L = leaf (m^2)
M_L = leaf *DM* (g).

Leaf area expansion is also influenced by canopy turgor potential (Ψ_t) (*9, 13*) independently of organ *DM* (*2*). Leaf expansion rates may thus be calculated as:

$$\delta A_L / \delta t = \{f(\Psi_t) \alpha M_L^{-0.33}\} \delta M_L / \delta t \quad (4)$$

Because sheaths (i = S) are designed to support leaves, an association between leaf and sheath dimensions would be expected. If sheath growth occurs proportionately in three dimensions, with width being set by that of the leaf, itself a function of $M_L^{-0.67}$, then $\delta L_S / \delta M_S$ would be a function of the product of $M_S^{-0.50}$ and $M_L^{-0.67}$:

$$\delta L_S / \delta M_S = \beta M_L^{-0.67} M_S^{-0.50} \quad (5)$$

where:

L_S = sheath length (m)
M_S = sheath *DM* (g).

Sheath extension rates may therefore be calculated as:

$$\delta L_S / \delta t = \beta M_L^{-0.67} M_S^{-0.50} \delta M_S / \delta t \quad (6)$$

If internodes (i = N) grow uniformly in three dimensions, then $\delta L_N / \delta M_N$ would be a function of $M_N^{-0.67}$:

$$\delta L_N / \delta M_N = \chi M_N^{-0.67} \quad (7)$$

where:

L_N = internode length (m)
M_N = internode *DM* (g).

To maintain stalk stability, lower internodes must be thicker than upper ones, so that the value of χ will increase with internode number. If the relative increase in χ is constant at each internode I (where $I=1$ at the base of the stem), then:

$$\chi_I = \gamma e^{\lambda I} \quad (8)$$

where:

$\chi_I = \chi$ at internode I.

Internode extension rates may therefore be calculated as:

$$\delta L_N / \delta t = \gamma e^{\lambda I} M_N^{-0.67} \delta M_N / \delta t \quad (9)$$

Equations 4, 6 and 9 were used in the agroecosystem simulation model that runs on an hourly time step using recorded meteorological data. The simulation of irradiance interception and carbon fixation is based on distributions of leaf area among azimuth and inclination classes within horizontal canopy layers of 0.05 m (*10, 12*). The simulation of phenologic and ontogenetic development follows the phytomer concept of Hesketh *et al.* (*14*). The simulation of maize phenology is based upon temperature-dependent rates of leaf initiation and appearance during juvenile, inductive and reproductive stages. Validation of these rates for this experiment is reported in Grant (*8*). Fixed carbon is partitioned (*7*) among the five most recent phytomers (*14*) determined from simulated phenology. At each phytomer leaf growth occurs first, followed after an interval of one phyllochron by sheath growth, followed after a further interval of three phyllochrons by internode growth once tassel initiation has occurred. Thus internode growth at each phytomer begins after most of the leaf and sheath growth has been completed (*4*). The internodes do not grow of phytomers at which sheath growth is completed before tassel initiation. The highest phytomer to which carbohydrate is partitioned is the one above that at which the leaf tip has most recently appeared (*8*). The values of $\delta M_i / \delta t$ required for the model hypotheses described above arise directly from model algorithms for partitioning of fixed carbon to each phytomer.

Parameterization and validation of model hypotheses

Testing of model hypotheses first required the parameterization of α in Eq. 3, β in Eq. 5 and γ and λ in Eq. 8. This was done by regressing ratios of changes in dimensions to those in *DM* on *DM* for leaves, sheaths and internodes recorded on different sampling dates from a population of 5.7 plants m^{-2}. Parameterization was tested by observing the accuracy with which the parameterized model could reproduce the nodal distributions of leaf area and of sheath and internode length recorded from the same population during vegetative growth. The model was thus run from before planting to after silking under simulated soil, climate and management conditions that reproduced those recorded at the experimental site. The parameterized model was then validated against corresponding nodal distributions recorded from the other populations at silking in order to test the range of plant growth conditions over which the model hypotheses remained valid. The model was thus run under the same conditions as those for the first testing of the parameterization, but substituting different populations. The functions were also tested against nodal distributions of leaf area reported by Dwyer and Stewart (*5*) for shorter season

cultivars ('P3977', 'COOP S259', and 'P. A.G. SX111') planted at 5.0 m^{-2} on a Dalhousie clay (Typic Haplaquoll) near Ottawa, Ont. (45°N) from 1979 to 1981.

RESULTS

Parameterization of model hypotheses

Changes in the areas and *DM* of each leaf, and in the lengths and *DM* of each sheath and internode were calculated for the periods between each sampling date from the population of 5.7 plants m^{-2}. From these data, values of 0.016 were determined for α in Eq. 3 (R^2=0.88), 0.10 for β in Eq. 5 (R^2=0.78), 0.015 for γ in Eq. 8 (R^2=0.82) and 0.067 for λ in Eq. 8 (R^2=0.98).

The areas, lengths and masses of individual leaves, sheaths and internodes recorded for the population of 5.7 plants m^{-2} are shown in Fig. 1 for 8 June (day 160), 15 June (day 167), 23 June (day 175), 30 June (day 182) and 18 July, 1988 (day 200). Dates of primordia and leaf tip appearance for this date set are given elsewhere (8). Data for leaf area and *DM* (Fig. la and b), sheath length and *DM* (Fig. lc and d), and internode length and *DM* (Fig. le and f) indicate concurrent growth of the top four to five nodes proceeding up the main stem. Those for the sheaths were about one node lower than those for the leaves, and those for the internodes were about three nodes lower than those for the sheaths on any date. The model was able to reproduce nodal distributions of organ size *DM* during canopy growth at this population, although the lengths of the upper and lower sheaths and internodes tended to be overestimated during June.

Nodal distributions of *SLA* (m^2 g^{-1}), *SSL* (m g^{-1}), and *SNL* (m g^{-1}) for the same dates are shown in Fig. 2. The negative relationships between leaf *DM* (Fig. 1b) and *SLA* (Fig. 2a), and between sheath *DM* (Fig. 1d) and *SSL* (Fig. 2b) indicate that as organ *DM* increases, its length, width, and thickness increase in a manner consistent with that expressed in Eqs 3 and 5. Nodal distributions of *SNL* (Fig. 3c) indicate the exponential increases with node number (λ) used in Eq. 8.

Examples of leaf and sheath extension rates simulated for the fourth and fifth phytomers on 3 and 4 June, 1988 are shown in Fig. 3 to demonstrate the hourly behavior of the model. Leaf extension rates,calculated as $(13.3\ \delta A_L/\delta t)^{0.5}$, reached values of 2.5 mm h^{-1} at noon, and declined to less than 0.5 mm h^{-1} during the nights as carbohydrate reserves in the simulated crop were depleted. Sheath extension rates followed similar diurnal trends. The sum of simulated leaf and sheath extension rates are similar to those measured by Watts (*23*) on same phytomers of maize at the same growth stage under similar environmental conditions.

Validation of model hypotheses

Areas, lengths and masses of individual organs estimated by the model were validated against data recorded for all phytomers on 18 July, 1988 (day 200) for populations of 1.5, 4.3, 8.6 and 10.3 plants m^{-2}, in addition to that of 5.7 plants m^{-2} (Fig. 4). Data from populations other than 5.7 plants m^{-2} were not used in

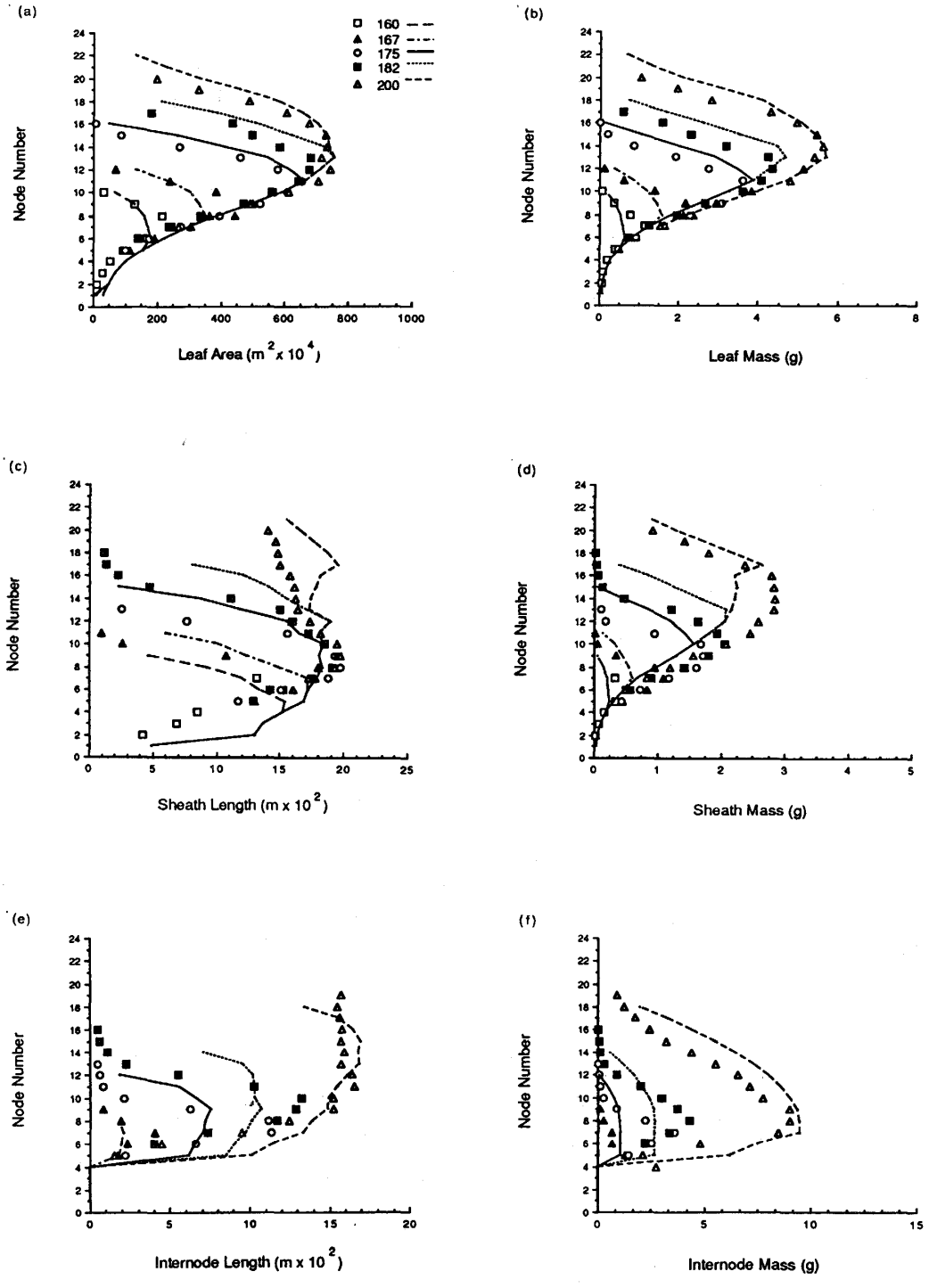

Fig. 1. (a) Leaf area, (b) leaf mass, (c) sheath length, (d) sheath mass, (e) internode length, and (f) internode mass measured (symbols) and simulated (lines) for each phytomer on days 160, 167, 175, 182 and 200 at a population of 5.7 plants m^{-2}. *S.E.* for measured data: leaf area: 35.1×10^{-4} m^2, leaf mass: 0.15 g, sheath length: 0.75×10^{-2} m, sheath mass: 0.14 g, internode length: 0.53×10^{-2} m, internode mass: 2.15 g.

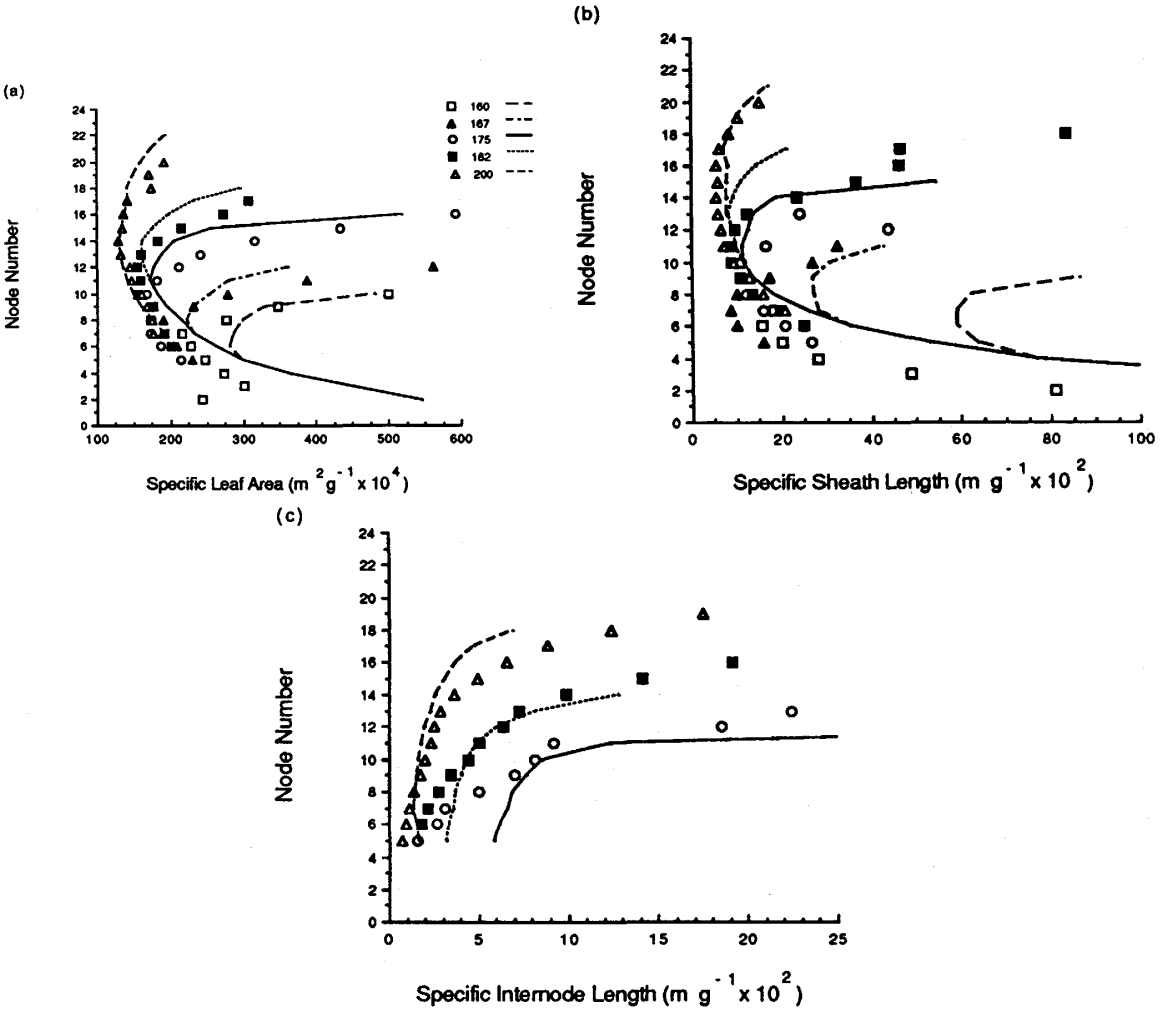

Fig. 2. (a) Specific leaf area, (b) specific sheath length, and (c) specific internode length measured (symbols) and simulated (lines) for each phytomer on days 160, 167, 175, 182 and 200 at a population of 5.7 plants m^{-2}.

model parameterization. The effect of population on measured leaf areas increased with node number (Fig. 4a), likely because interplant competition would increase more during canopy growth at higher populations than at lower. This effect was reproduced by the model as differences in simulated leaf area increased above node 10. From nodes 10 to 14 some overestimation of leaf area was apparent at 1.5 plants m^{-2}, and underestimation at 10.3 plants m^{-2}. The differences at these nodes reached 50 to 75×10^{-4} m^2, or about 10% of measured leaf area, for the extreme populations. The effect of population on leaf mass was greater than that on leaf area, and also increased with node number (Fig. 4b). These effects were also reproduced in the model, although the simulated effect of population on individual leaf mass was greater than that recorded.

Population had only a limited effect upon recorded and simulated sheath length (Fig. 4c). As for leaf area, this effect was more apparent at higher nodes. This limited effect of population was reproduced in the model because $\delta L_S/\delta M_S$

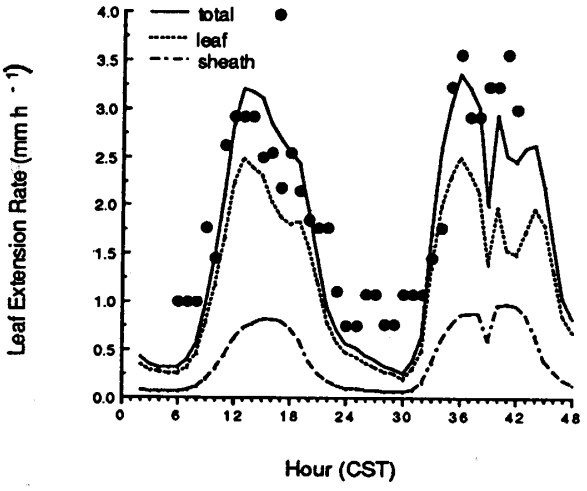

Fig. 3. Simulated (lines) diurnal profiles of leaf and sheath extension rates during 3 and 4 June, 1988 at Urbana, IL. Leaf extension was calculated from leaf area expansion assuming a constant leaf length; width ratio of 13.3. Data for 3 June (h 1 to 24) are from phytomer 4, while those for 4 June (h 25 to 48) are from phytomer 5. Also shown are measured (symbols) diurnal profiles of total phytomer extension rates over a two day period (23) for phytomers 4 (h 1 to 24) and 5 (h 25 to 48) from Watts (23).

increased as M_L decreased (Eq. 5) with higher population. However, overestimation of sheath length up to 0.03 m occurred at higher nodes. The effect of population on the nodal distribution of sheath mass (Fig. 4d) increased with node number, similarly to that of leaf mass (Fig. 4b). Sheath masses were generally underestimated at lower populations.

There was a marked effect of population on internode length (Fig. 4e) that increased with node number. While nodal distributions of internode length were reproduced by the model, the population effect was underestimated, such that lengths simulated at higher populations were greater than those measured by up to 0.03 m. Internode lengths measured at 1.5 plants m^{-2} were lower than those at 4.3 and 5.7 plants m^{-2}, although those simulated were not. Some evidence of reduced organ length at 1.5 plants m^{-2} was also apparent in the sheaths (Fig. 4c). The underestimation of the population effect on internode length was caused by that on internode mass (Fig. 4f). Reserve carbohydrate may be stored to an unknown extent in the sheaths (*4*) although in the model it is allocated entirely to the internodes (*7*). Allocation of reserves may partially account for the overestimation of internode masses, and the underestimation of sheath masses. However, these reserves would not affect organ extension.

Nodal distributions of leaf area measured and simulated on shorter season cultivars at Ottawa, Ontario during three growing seasons are shown in Fig. 5. Leaf areas were lower than from corresponding populations at Urbana, especially at higher nodes.

Data for commonly reported canopy-level indices of crop size are given in Table 1. Canopy height is an important index used, among other things, in estimating aerodynamic resistance to energy exchange and sites of insect

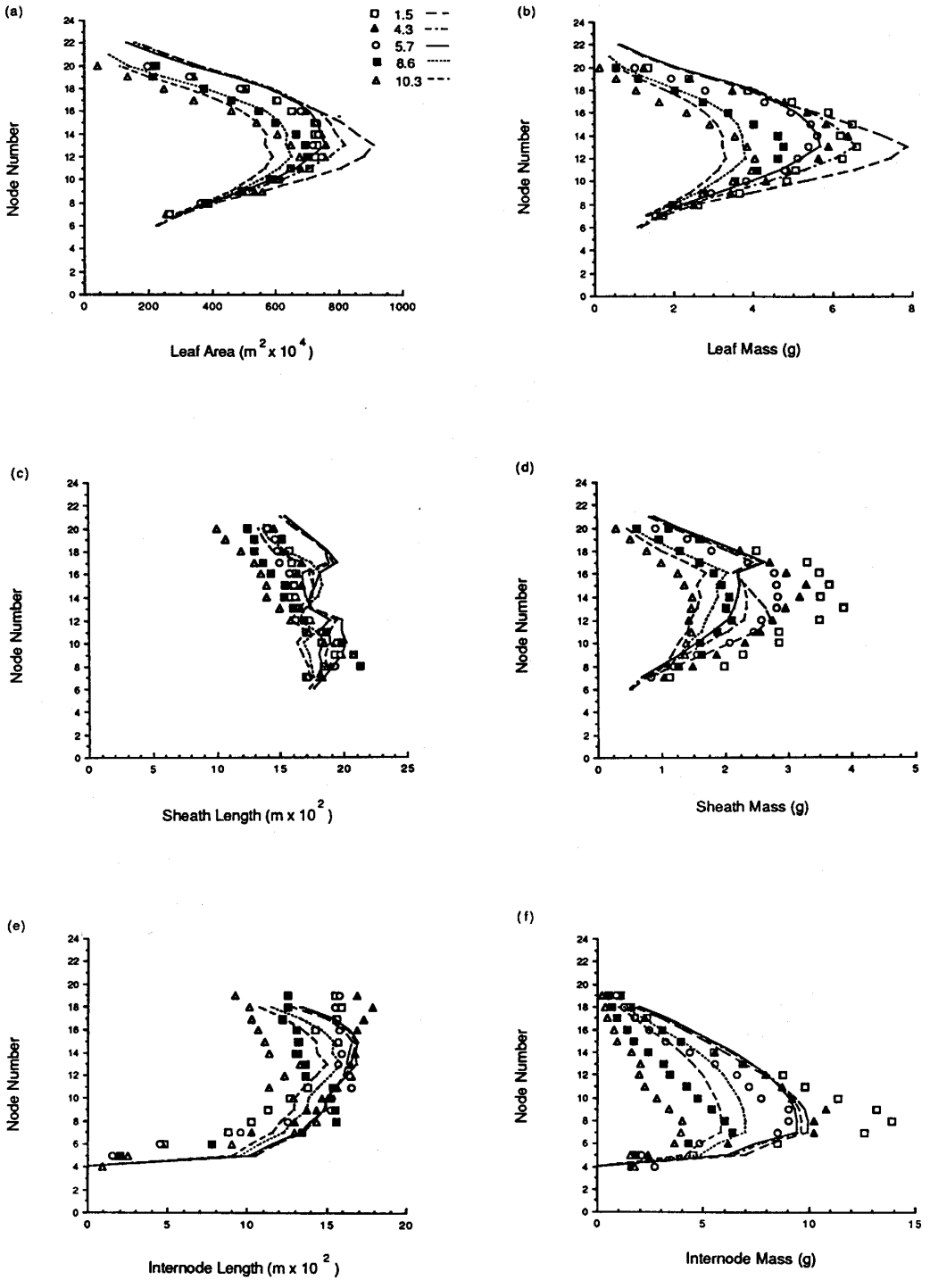

Fig. 4. (a) Leaf area, (b) leaf mass, (c) sheath length, (d) sheath mass, (e) internode length, and (f) internode mass measured (symbols) and simulated (lines) for each phytomer on day 200 at populations of 1.5, 4.3, 5.7, 8.6 and 10.3 plants m^{-2}. *S.E.* for measured data: leaf area: 68.5×10^{-4} m^2, leaf mass: 0.47 g, sheath lengeth 2.35×10^{-2} m, sheath mass: 0.43 g, internode length: 2.51×10^{-2} m, internode mass: 0.71 g.

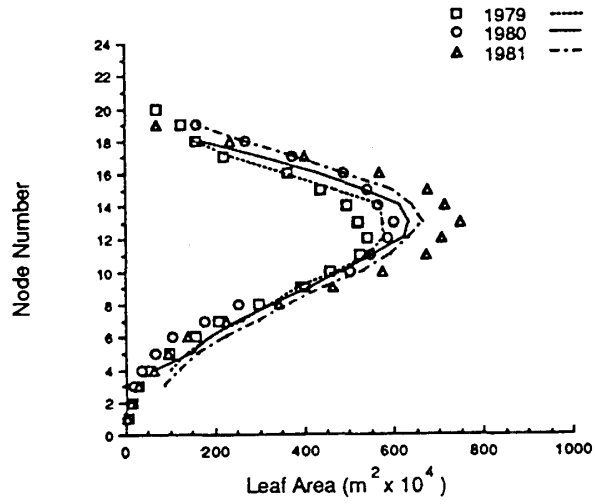

Fig. 5. Nodal distributions of leaf area measured (symbols) and simulated (lines) during three growing seasons at Ottawa, Ontario. Measured data are from Dwyer and Stewart (*5*).

infestation. The height simulated on 15 June was underestimated by 0.08 m, due to an underestimation of early internode elongation (Fig. 1e) arising from an underestimation of early internode *DM* growth. Because internode elongation begins after tassel initiation (*4*), the correct estimation of the date of tassel initiation, and of early partitioning of *DM* to the stalk, is important in the accurate estimation of canopy height during this period. Canopy height on 30 June was overestimated by 0.29 m, due to overestimation of elongation at the uppermost nodes. Heights of the top collars on 18 July were accurately estimated at all populations except the lowest, where reduced sheath (Fig. 4c) and internode (Fig. 4e) lengths caused the measured value to be 0.39 m lower than that estimated.

Leaf area index (*LAI*) is another important index of canopy size which is used in the calculation of irradiance interception. This index was generally overestimated by about 10%, but reproduced trends recorded over time and populations. Performance of the model at the population level is comparable to that of other models of maize growth (*15*) .

DISCUSSION

Equations 4, 6 and 9, as parameterized from the experimental data, are intended for use in the crop component of an agroecosystem simulation model. In this component, organ growth is estimated from the partitioning of *DM* to different organs at each node based on phenology-dependent algorithms. Equations 4, 6 and 9 may be used in such a model to estimate organ expansion and extension from organ *DM* growth, thereby generating dynamic estimates of the vertical leaf area profile at each hourly time step. This approach avoids the use of node-and population-specific scaling factors for leaf expansion currently used in some crop growth models (*15, 21*) to adjust simulated leaf area to

ambient growing conditions. The values of these factors reflect the conditions under which they were derived (e.g. atmospheric CO_2 concentration) and may not be used under different conditions.

An organ-level model of this detail will perform comparably with simpler population-level models in the study of population-level crop behavior (Table 1). However, the extension of biological organization to the organ level in this model allows a greater range of model application in the study of crop behavior. Vertical profiles of leaf area generated from organ growth are used in the finite difference approximation to the hourly interception of solar and sky irradiance in three dimensions (*10, 12*) to compute CO_2 fixation. These profiles may be generated for each of a number of independent tillers sharing a common root system, enabling the simulation of tiller competition for irradiance. These profiles may also be generated for each of a number of crop models running in parallel with other such models (*11*) in order to simulate intercropping or weed-crop competition. The representation of tiller or weed-crop competition at the organ level is an advance from some current techniques (*20*) in which competition is represented at the population level from assumed vertical distributions of leaf area and empirical estimates of crop height. These distributions and heights clearly change with population (Fig. 4). An organ-level model avoids the use of dimensionless 'competition factors' for irradiance interception used in some population-level models to account for changing

Table 1. Measured and simulated canopy leaf area index (*LAI*) and heights to the top collar (a) during canopy growth for a population of 5.7 plants m^{-2}, and (b) at anthesis for populations of 1.5, 4.3, 5.7, 8.6 and 10.3 plants m^{-2}.

(a) date	height (m)		*LAI* (m^2 m^{-2})	
	meas.	sim.	meas.	sim.
8 June	nd	0.15	0.63±0.01	0.63
15 June	0.31±0.04	0.23	1.25±0.11	1.25
23 June	0.57±0.01	0.64	2.34±0.09	2.79
30 June	0.83±0.01	1.11	3.31±0.17	3.93
18 July	2.19±0.13	2.25	4.45±0.38	4.85

(b) pop'n (m^{-2})	height (m)		*LAI* (m^2 m^{-2})	
	meas.	sim.	meas.	sim.
1.5	1.85±0.05	2.23	1.13±0.02	1.45
4.3	2.25±0.24	2.25	3.43±0.24	3.91
5.7	2.19±0.13	2.25	4.45±0.38	4.85
8.6	1.90±0.13	2.05	5.49±0.30	5.85
10.3	1.97±0.13	1.94	5.64±0.04	6.28

interception patterns over time (*25*). The values of these factors are likely specific to the conditions under which they were derived, and have no scientific meaning outside of the model in which they are used.

There are, however, some areas in the dynamics of crop growth at the organ level that require further clarification. The hypotheses in Eqs. 4, 6 and 9 could not be tested in the model independently of $\delta M_i/\delta t$ so that uncertainties in the partitioning of *DM* growth (e.g. Fig. 4d vs 4f) may have caused some uncertainty in the estimation of organ size. There was some evidence of overestimated $\delta L_S/\delta M_S$ at low M_S during early sheath elongation (Fig. 1c), and of overestimated $\delta L_N/\delta M_N$ at low M_N during early internode elongation (Fig. 1e), indicating that the performance of Eq. 5 at low M_S, and of Eq. 7 at low M_N may require further study.

To clarify some of these problems, in future research the dynamics of canopy growth at the organ level might be studied at different populations in a manner similar to those studied at 5.7 plants m^{-2} in this experiment. Stratified cuts during canopy growth would allow closer validation of estimated vertical profiles of leaf area. When our understanding of the dynamics of organ growth has been improved and more thoroughly tested in simulation models, then differing spatial arrangements of crops and weeds might be studied in a similar way in order to gain a better understanding of how crops and weeds compete for irradiance.

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