Allometric Relationships of Maize Organ Development under Different Water Regimes and Plant Densities

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Abstract: Allometric relationships of plant organs reflect internal coordination of different aspects of organ development, allowing the linking of plant structural development and underlying physiological processes for the development of functional-structural plant models (FSPMs). This paper aims to (i) explore the allometric relationships between organ morphology and fresh biomass in maize; (ii) develop equations to describe these relationships; and (iii) examine the response of allometric relationships to crop water availability and plant density. Datasets were obtained from field experiments in which three commercial maize cultivars (Pioneer 34N43, Pioneer 31H50 and NongDa 108) were grown under different water regimes and plant densities. Relationships are described between (i) lamina length and biomass for all phytomers by a power function, (ii) lamina maximum width and biomass by a power and a logarithmic function separated at ear position, (iii) sheath length and biomass by power and logarithmic functions separated at eighth sheath position where the sheath length peaked, and (iv) internode length and biomass by two power functions separated at the ear position across water regimes and plant densities. The allometric relationships of organ development were not affected by the mild water stress, but were modified by the increased plant densities. Consequently, the allometric relationships found in this study and their expressions using mathematical equations enable plant morphology to be predicted from physiological output (biomass accumulation), which provides a biologically robust mechanism of realizing functional-structural communication used in FSPMs.

Key words: Canopy development, Drought stress, FSPMs, Growth relationships, Interplant competition, Plant growth modelling, Zea mays.
straightforward way to develop FSPMs is to integrate architectural models and existing physiological models with possibly improved resolution of plant architectural description for physiological models (Hanan, 1997; Fournier and Andrieu, 1999; Hanan and Hearn, 2003; Renton et al., 2005; de Reffye et al., 2009). Another way to develop FSPMs is to directly couple plant architectural development and plant physiological functions mechanistically during each simulation (Yang et al., 2004; Luquet et al., 2006; Evers et al., 2010; Cieslak et al., 2011), which may require reconstructing the model framework de novo. Nonetheless, both approaches require robust linkages between plant structure and physiological functions at the organ level that effectively realize the communication during simulation.

Developing allometric relationships in plants requires the study of size-correlated variations in organic form and process (Huxley, 1932), which reflect internal growth coordination and can be used in modelling plant growth (Reddy et al., 1998; Vega et al., 2000; Niklas, 2004). In FSPMs, the organ biomass can be defined as the accumulated photoassimilate allocated from the source i.e., leaves. The allocation of biomass into individual organs has been simulated for a general plant (Yang et al., 2004) and subsequently for maize (Guo et al., 2006) and wheat (Evers et al., 2010). Organ dimension is a morphological trait which is important in constructing the canopy. Allometric relationships between organ biomass and morphological traits are useful in linking plant architecture and physiological functions. For example, specific leaf area (a leaf allometric relationship, g cm⁻²) is currently used as a key parameter to convert leaf function (biomass accumulation) to leaf morphology (leaf area), the latter being then used to integrate into functional computation (Fournier and Andrieu, 1999; Wang et al., 2002; Yang et al., 2004; Guo et al., 2006). Thus allometric relationships at the organ level are required to develop FSPMs, and consequently to enhance modelling capability.

Dry matter rather than fresh matter is commonly used to simulate biomass accumulation and allocation in crop models (e.g. Wang et al., 2002). Recently, fresh matter of individual organs was used to establish the model framework in FSPMs (Yang et al., 2004) and later by application in maize (Guo et al., 2006), showing that the use of fresh weight can simplify the process of seeking relationships between plant morphology and biomass accumulation. Yet the relationships between organ dimension and fresh biomass are generally not available. Therefore, our study investigated the allometric relationships between the morphology and fresh biomass of maize laminae, sheaths and internodes and expressed the allometric relationships as mathematical models. Organ development is sensitive to water supply (Song et al., 2010) and plant population density (Fournier and Andrieu, 1999), thus the organ allometry may or may not be adjusted in response to water stress and increased plant density. Hence we also assessed the sensitivity of allometric relationships to water stress and increased plant densities.

Materials and Methods
1. Field experiments

Datasets were available from two maize field experiments carried out in Australia and China. The same methods of sampling and data collection were used in both experiments.

2. 2006 experiment – Gatton, Australia

The experiment in Australia was conducted at The University of Queensland, Gatton Campus (Latitude 27°34′ S, longitude 152°20′ E) commencing on September 6, 2006. The experiment details are given in Song et al. (2008, 2010), and are briefly outlined here. The field site has a moderately fertile typic chromustert soil (Vertosol, Lawes). Urea was incorporated into the soil at 150 kg N ha⁻¹ before sowing to prevent nitrogen stress. Other nutrients were supplied adequately according to soil analysis results and local standards. Irrigation was realized with trickle application using T-tape at 2.0 mm h⁻¹. Two commercial maize cultivars, Pioneer 34N43 and Pioneer 31H50 (referred to as 34N43 and 31H50) were grown in differing water regimes and produced 18 and 21 leaves respectively. The sowing density was 6 plants m⁻² for both cultivars. The rows were 0.75 m apart. Two water regimes were used: (i) fully irrigated (FI) throughout growth with total 225 mm of irrigation as the control treatment, (ii) rainfed (RF) in which crops were completely dependent on rainfall. In RF, the fraction of extractable soil water (FESW) was used to indicate water conditions during canopy development (Song et al., 2008). From tassel initiation, FESW in rainfed treatment was lower compared to fully irrigated, decreasing from 0.88 at 38 days after emergence (DAE) to 0.51 at 60 DAE, and then increasing to 0.80 at 67 DAE due to significant rainfall, followed by a quick decline again to 0.46 at anthesis (75 DAE) when canopy development was complete, and therefore canopy development was exposed to transient mild water stress (Song et al., 2010). A randomized split-plot design with water regimes as main plot and cultivar as subplot was used in two replicates.

3. 2009 experiment – Shangzhuang, PR China

The experiment was carried out at Shangzhuang experimental station of China Agricultural University, Beijing, China (Latitude 40°02′ N, Longitude 116°20′ E) in 2009. A commercial maize cultivar NongDa 108 (referred to ND108) was grown at four plant densities (2, 6, 12, and 20 plants m⁻²) [referred to as PD2, PD6, PD12 and PD20 respectively with PD2 (the control treatment), PD6
(close to local farming practice), PD12 and PD20 (both higher than local practice) representing no or low, mild, moderate and severe interplant competition (plants competing for light resource)]. This experiment was commenced with sowing on July 7, 2009 and terminated when the canopy was fully expanded at the end of August, 2009. ND108 had, on average 20 leaves, with no difference among plant populations. The soil type at the field site was calcareous with low to medium fertility. Irrigation was applied to ensure seed germination. Fertilizer was applied at sowing to supply 60 kg N ha$^{-1}$ (Urea), 56 kg P ha$^{-1}$ (Ca(H$_2$PO$_4$)$_2$), 100 kg K ha$^{-1}$ (K$_2$SO$_4$), and 3.5 kg Zn ha$^{-1}$ (ZnSO$_4$.7H$_2$O). A randomized block design of four plant densities in three replicates was used. Rows were 75 cm apart in PD2, PD6 and PD12 and 50 cm apart in the PD20, and thus plants within a row were 1.5, 4.5, 9 and 10 plants m$^{-1}$ respectively. Each subplot was 7 m long and 6 m wide. Plots were separated by a 1 m wide unplanted guard area within replicates, and replicates were separated by a 2 m wide unplanted guard area. The boundary of the whole experimental area was planted with two extra guard rows. Seeds were evenly spaced in individual rows of the experimental area, and seedlings were thinned to the desired plant densities at the 3 leaf stage. Subsequently, irrigation was applied to ensure optimal plant water supply. Weeds were controlled manually.

4. Data collection

Ten representative plants in each plot were chosen and marked according to the methods described in Birch et al. (2007) and Song et al. (2008). These were used as reference plants, and were non-destructively sampled to guide destructive samplings for measurement of canopy production that commenced when plants had 4 fully expanded leaves and continued at 1 – 2 day intervals until canopy production was complete. Prior to each destructive sampling, plant height, total leaf number, number of expanding leaves and lengths of expanding leaves on reference plants were recorded. These data provided an objective quantitative basis for choosing a similar single representative plant for destructive sampling in each subplot. The sampled plants were kept in a container with water, and taken to the laboratory for dissection into individual organs for minimum delay measurement. The lengths of laminae, sheaths and internodes (cm), and the maximum width of laminae (cm) were measured. At each phytomer, the fresh weights of laminae, sheaths and internodes (g) were determined in all destructive samplings. The position of each phytomer was counted acropetally and the position of the ear was recorded according to its subtending phytomer. Modern maize hybrids rarely produce tillers even at a low plant population density, and very few tillers occurred in any treatment in this study, so only plants without tillers were sampled.

5. Data processing and statistical analysis

The relationships between lamina length (LL) and lamina fresh biomass (LB), lamina maximum width (LW) and lamina fresh biomass (LB), sheath length (SL) and sheath fresh biomass (SB) and internode length (IL) and internode fresh biomass (IB) for individual phytomers were first fitted using Microsoft Excel 2007 (Microsoft Inc., Seattle, WA, USA) and the suitable functions with the greatest $r^2$ were chosen for subsequent use. To facilitate the statistical analyses between treatments, the relationship was re-fitted using non-linear modelling (characterised with the above chosen function from Excel) in JMP 9.0 (SAS Institute, Cary, NC). The average parameter values, standard errors and confidence intervals (95% CI) were derived. The difference between two treatments was calculated and then represented with average±2*standard errors with 95% confidence interval (CI). If the difference fell between minus and plus, it indicates there is no significant difference, otherwise significant difference.

The first six internodes were excluded from statistical analyses as they were very short, and last internode bearing flag leaf was also excluded because of atypical behavior (Birch et al., 2002; Song et al., 2010).

Results

1. Relationship between lamina length and lamina biomass

The relationship of LL and LB across both experiments is shown in Fig. 1. LL and LB were closely related in both experiments (Fig. 1). The data points from rainfed treatments followed a similar trend to that of the irrigated (Fig. 1A, B). The data points under differing plant densities formed a number of relationships related to plant population density (Fig. 1C). The relationship between LL and LB was described by a power function $LL = b0*LB^{k0}$ ($LB > 0$, $r^2 > 95\%$) for cultivars 34N43 and 31H50 under fully irrigated and rainfed conditions in 2006 and for cultivar ND108 under different plant densities. The extracted parameter values and $r^2$ for different treatments in both experiments are listed in Table 1. There were no significant differences in $b0$ and $k0$ between water regimes (Table 1), suggesting that the relationship between LL and LB was conserved under water stress. The $b0$ increased significantly as plant density increased from PD2 to PD12, but did not increase further in PD20. The $b0$ was similar across plant densities. This suggested that the relationship between LL and LB could be to some extent adjusted in adaptation to the increased interplant competition induced by higher plant densities.
2. Relationship between lamina maximum width and lamina biomass

The relationship between LW and LB in both experiments and treatments is shown in Fig. 2. The data for the two density treatments PD2 and PD20 are shown in Fig. 2C, inclusion of all points in Fig. 2 would have made trends visually unclear. The data under fully irrigated and rainfed conditions followed similar trends (Fig. 2A, B), except for the upper phytomers, data which deviated slightly (Fig. 2C). There was not a single model available for describing the relationships between LW and LB in both experiments, but the data were shown with two subgroups separated at ear position (Fig. 2). The relationship between LW and LB was quantified by a power function \( LW = b_1 \times LB^{k_1} \) (LB > 0, \( r^2 > 85\% \)) for phytomers at and below the ear and a logarithmic function as \( LW = b_2 \times \ln(LB) + k_2 \) (LB > 0, \( r^2 > 75\% \)) for phytomers above the ear for all experimental conditions. Average values of parameters \( b_1, k_1, b_2 \) and \( k_2 \) and \( r^2 \) are presented in Table 2. None of the parameters differed across water regimes for either cultivar, indicating that the relationship between LW and LB was conserved under water stress. The parameters \( b_1 \) and \( k_1 \) were similar for each plant density. The parameter \( b_2 \) declined significantly between PD6 and PD12 and again between PD12 and PD20. The parameter \( k_2 \) was not affected by plant population.

3. Relationship between sheath length and sheath biomass

The relationship between SL and SB across both experiments is shown in Fig. 3. Only data for PD2 and PD20 are shown. Data are presented for the lower 8 sheaths (Fig. 3A, C and E) and above the 8\textsuperscript{th} sheath (Fig. 3B, D and F). The 8\textsuperscript{th} sheath was the longest. The data for fully irrigated and rainfed conditions followed similar trends (Fig. 3A, B, C and D). Both SL and SB were reduced due to water stress. There were two different relationships describing the responses of SL and SB to plant density (Fig. 3E and F). The relationship between SL and SB (Fig. 3) was quantified by a power function \( SL = b_3 \times SB^{k_3} \) (SB > 0, \( r^2 > 95\% \)) for the first 8 sheaths and a logarithmic function \( SL = b_4 \times \ln(SB) + k_4 \) (SB > 0, \( r^2 > 95\% \)).

| Year  | Cultivar | Treatments | Ear and ear below | Ear above | Ear above |
|-------|----------|------------|-------------------|-----------|-----------|
|       |          |            | \( b_1 \) | \( k_1 \) | \( r^2 \) | \( b_2 \) | \( k_2 \) | \( r^2 \) |
| 2006  | 34N43    | fully irrigated | 2.04 ± 0.095 | 0.53 ± 0.017 | 0.89 | 1.71 ± 0.080 | 4.94 ± 0.177 | 0.86 |
|       |          | rainfed    | 2.19 ± 0.101 | 0.50 ± 0.019 | 0.87 | 1.56 ± 0.094 | 4.39 ± 0.178 | 0.79 |
|       | 31H50    | fully irrigated | 2.20 ± 0.096 | 0.47 ± 0.015 | 0.85 | 1.64 ± 0.054 | 5.19 ± 0.123 | 0.91 |
|       |          | rainfed    | 2.22 ± 0.100 | 0.48 ± 0.017 | 0.83 | 1.60 ± 0.057 | 4.63 ± 0.116 | 0.87 |
| 2009  | ND108    | 2 plants m\(^{-2}\) | 3.23 ± 0.117 | 0.41 ± 0.013 | 0.93 | 2.29 ± 0.068b | 5.82 ± 0.148 | 0.92 |
|       |          | 6 plants m\(^{-2}\) | 3.07 ± 0.118 | 0.43 ± 0.015 | 0.94 | 2.16 ± 0.069b | 5.63 ± 0.135 | 0.91 |
|       |          | 12 plants m\(^{-2}\) | 3.15 ± 0.128 | 0.41 ± 0.017 | 0.93 | 1.89 ± 0.068b | 5.36 ± 0.117 | 0.90 |
|       |          | 20 plants m\(^{-2}\) | 3.27 ± 0.134 | 0.40 ± 0.018 | 0.92 | 1.66 ± 0.065c | 5.44 ± 0.106c | 0.91 |

Different letters i.e. a, b and c indicate significant difference among treatments at \( P < 0.05 \).
85%) for higher sheaths. None of the constants and coefficients was significantly affected by water supply in either cultivar, indicating that water stress did not change the allometric relationship of sheath length and biomass. However, \( b_3, b_4 \) and \( k_3 \) all increased with increasing plant density, but \( k_4 \) was unaffected (Table 3). This suggested that the relationship between \( SL \) and \( SB \) was adjusted in adaptation to the increased interplant competition induced by higher plant population.

4. Relationship between internode length and internode biomass

The relationship between \( IL \) and \( IB \) in both experiments is shown in Fig. 4. As for other organs, the data for only PD2 and PD20 are shown in Fig. 4. The data under fully irrigated and rainfed conditions followed similar trends (Fig. 4A, B), while the data for higher plant density separated into identifiable groups (Fig. 4C, D). \( IL \) appeared to be closely related to \( IB \), but the data separated into two major groups at and below the ear position – phytomer 12 (34N43), 14 (31H50) and 12 (ND108) and above the ear. The relationship took the form of a broken power function \( IL = b_5*IB^{k_5} \) for phytomers at and below the ear and \( IL = b_6*IB^{k_6} \) for upper phytomers describing the relationship between internode length (IL) and biomass (IB) in maize grown under fully irrigated and rainfed conditions in 2006 and various plant populations in 2009.

Table 3. Average values and coefficient of determination \((r^2)\) for the parameter \( b_3, b_4, k_3 \) and \( k_4 \) in the relationships \( SL = b_3*SB^{k_3} \) (for sheaths 1 to 8) and \( SL = b_4*Ln(SB)+k_4 \) (for sheaths above the 8th) between sheath length (SL) and biomass (SB) in maize across water supply conditions in 2006 and plant populations in 2009.

| Year | Cultivar | Treatment | 8th sheath and below | 8th sheath above |
|------|----------|-----------|---------------------|-----------------|
|      |          |           | \( b_3 \) \( k_3 \) | \( r^2 \) | \( b_4 \) \( k_4 \) | \( r^2 \) |
| 2006 | 34N43    | fully irrigated | 3.22 ± 0.112 | 9.28 ± 0.232 | 0.93 | 5.46 ± 0.248 | 0.44 ± 0.018 | 0.95 |
|      |          | rainfed    | 3.12 ± 0.114 | 9.12 ± 0.229 | 0.91 | 5.18 ± 0.254 | 0.49 ± 0.023 | 0.94 |
| 31H50 |          | fully irrigated | 3.69 ± 0.131 | 9.74 ± 0.272 | 0.93 | 4.88 ± 0.272 | 0.50 ± 0.021 | 0.89 |
|      |          | rainfed    | 3.71 ± 0.134 | 9.78 ± 0.271 | 0.92 | 4.88 ± 0.287 | 0.52 ± 0.024 | 0.96 |
| 2009 | ND108    | 2 plants m\(^{-2}\) | 3.57 ± 0.117\(^a\) | 10.24 ± 0.210\(^b\) | 0.96 | 4.35 ± 0.181\(^c\) | 0.53 ± 0.017 | 0.97 |
|      |          | 6 plants m\(^{-2}\) | 3.86 ± 0.117\(^a\) | 10.54 ± 0.207\(^b\) | 0.95 | 4.81 ± 0.183\(^c\) | 0.54 ± 0.017 | 0.97 |
|      |          | 12 plants m\(^{-2}\) | 4.19 ± 0.133\(^a\) | 10.99 ± 0.215\(^b\) | 0.95 | 5.91 ± 0.176\(^c\) | 0.52 ± 0.015 | 0.97 |
|      |          | 20 plants m\(^{-2}\) | 4.46 ± 0.141\(^a\) | 11.50 ± 0.220\(^b\) | 0.95 | 6.38 ± 0.178\(^c\) | 0.53 ± 0.016 | 0.97 |

Different letters i.e. a, b and c indicate significant difference among treatments at \( P<0.05 \).

Table 4. Average values and coefficient of determination \((r^2)\) for the parameters \( b_5, b_6, k_5 \) and \( k_6 \) in a broken power function \( IL = b_5*IB^{k_5} \) for phytomers at and below the ear and \( IL = b_6*IB^{k_6} \) for upper phytomers describing the relationship between internode length (IL) and biomass (IB) in maize grown under fully irrigated and rainfed conditions in 2006 and various plant populations in 2009.

| Year | Cultivar | Treatment | Ear and ear below | Above the ear |
|------|----------|-----------|------------------|--------------|
|      |          |           | \( b_5 \) \( k_5 \) | \( r^2 \) | \( b_6 \) \( k_6 \) | \( r^2 \) |
| 2006 | 34N43    | fully irrigated | 1.65 ± 0.378 | 0.57 ± 0.062 | 0.74 | 3.30 ± 0.494 | 0.56 ± 0.057 | 0.82 |
|      |          | rainfed    | 1.39 ± 0.436 | 0.60 ± 0.106 | 0.81 | 3.61 ± 0.627 | 0.53 ± 0.081 | 0.81 |
| 31H50 |          | fully irrigated | 1.84 ± 0.366 | 0.52 ± 0.049 | 0.76 | 2.61 ± 0.270 | 0.56 ± 0.035 | 0.88 |
|      |          | rainfed    | 1.20 ± 0.347 | 0.62 ± 0.083 | 0.80 | 2.38 ± 0.295 | 0.60 ± 0.046 | 0.94 |
| 2009 | ND108    | 2 plants m\(^{-2}\) | 0.42 ± 0.192\(^a\) | 0.91 ± 0.134 | 0.86 | 2.27 ± 0.351\(^c\) | 0.55 ± 0.055 | 0.88 |
|      |          | 6 plants m\(^{-2}\) | 0.83 ± 0.284\(^a\) | 0.83 ± 0.108 | 0.79 | 2.86 ± 0.350\(^bc\) | 0.57 ± 0.050 | 0.88 |
|      |          | 12 plants m\(^{-2}\) | 1.34 ± 0.349\(^a\) | 0.81 ± 0.092 | 0.75 | 3.76 ± 0.389\(^bc\) | 0.59 ± 0.046 | 0.88 |
|      |          | 20 plants m\(^{-2}\) | 2.65 ± 0.476\(^a\) | 0.62 ± 0.069 | 0.73 | 4.27 ± 0.384\(^c\) | 0.61 ± 0.047 | 0.87 |

Different letters i.e. a, b and c indicate significant difference among treatments at \( P<0.05 \).

Discussion

Organ production and expansion depends on cell division, cell expansion and differentiation. While the cell is expanding, the biomass from photosynthesis is allocated to the cell, resulting in greater cell volume (size).
Fig. 1. The relationships between maize lamina length and biomass for 34N43 (A) and 31H50 (B) under fully irrigated (FI) and rainfed (RF) conditions in 2006, and for ND108 at 2, 6, 12 and 20 plants m$^{-2}$ in 2009 (C).

Fig. 2. The relationship between maize lamina maximum width and its biomass for 34N43 (A) and 31H50 (B) under fully irrigated (FI) and rainfed (RF) conditions in 2006, and for ND108 (C) at 2 (PD2) and 20 plants m$^{-2}$ (PD20) in 2009.

Fig. 4. The relationship between internode length and its biomass for phytomers at the ear position and below (excluding first 6 internodes) and phytomers above the ear (excluding topmost internode) under fully irrigated (FI) and rainfed (RF) conditions for 34N43 (A) and 31H50 (B) in 2006, and 2 (PD2) and 20 plant s$^{-2}$ (PD20) for ND108 (C and D) in 2009.
Morphology and biomass are closely related aspects of organ development. Growth analysis based on individual organs enables quantification of relationships that cannot be deduced from studies at the whole plant level. Allometric relationships between morphology and biomass of lamina, sheath and internode developed and quantified by simple equations in this study will now be discussed in a physiological, whole plant development and modelling context.

1. Allometric relationships between organ morphology and its biomass

The relationship between lamina length and biomass was continuous across phytomers while the relationship between lamina width and biomass was separated by the ear appearance, suggesting that the specific leaf area is also not continuous among phytomers though this parameter is commonly used in crop modelling as a constant (Fournier and Andrieu, 1998; Wang et al., 2002). To improve the modelling accuracy, leaf specific area dependent on ear appearance should be taken into account in maize modelling. The relationships between lamina width and biomass and internode length and biomass were discontinuous with the change occurring at the ear position; the critical role of the ear seems to be independent of factors such as water stress and interplant competition. In previous studies, leaf appearance and extension rates (Song et al., 2010) and internode extension rates (Birch et al., 2002) have been grouped below and above the ear. Taken together with the findings in this study, ear initiation, appearance and growth seem to play important roles in readjusting organ and thus canopy...
production, probably due to competition for photosynthate (Birch et al., 2002). The relationship SL and SB (Fig. 3, Table 3) was more complex, and had thresholds (phytomer 8) where sheath length was longest and the form of equations changed from power to logarithmic.

The 2006 rainfed water regime in 34N43 and 31H50 produced only mild water stress (Song et al., 2008). The general lack of impact of mild water stress on coefficients in equations indicated that the level of water stress experienced by the plants did not alter the relationship between leaf dimensions and biomass, probably attributable to proportionate changes in cell volume and biomass though reduced individual leaf area and biomass had occurred. However, the significant differences in coefficients and changes in equation form in plant density experiment provide quantitative relationships over a wide range (2 – 20 plants m\(^{-2}\)) for competitive effects due to increased plant population. As this paper aims to establish a robust linkage between organ morphology and biomass and test the allometry suitability from optimal to stressed conditions, we used a range of plant densities for ND108 in 2009 from “no interplant competition” (PD2) to “severe interplant competition” (PD20). The relationships developed here applying to practical plant populations, which fall in this range. However, they will need to be checked for other genotypes with differing parental backgrounds and/or modified morphology e.g. more erect leaves.

It is well documented that water stress reduces individual leaf area and total plant leaf area (Muchow and Carberry, 1989; Yang et al., 2009; Song et al., 2010), this has often been accommodated by using stress factors (range 0, no stress, to 1, severe stress) to reduce leaf area in response to water deficit, as in, for example, the APSIM group of models (Wang et al., 2002) and later models derived from them. Our findings confirmed a proportional reduction in leaf length and leaf width, consistent with the response of individual cells to water deficit to reduce expansion (Tardieu et al., 2000), at least under mild water stress. However, it can be expected to remain the case for more severe water stress, as in Tardieu et al. (2000). Despite the proportionate reduction in leaf length and leaf width, severe water stress induces other responses, including leaf rolling which will modify the canopy structure and is a water conservation measure taken by plants to reduce evaporative demand (Sanchez-Diaz and Kramer, 1971; Earl and Davis, 2005). However, interplant competition modified leaf shape and/or specific leaf area (cm\(^2\) g\(^{-1}\)) (and its reciprocal, specific leaf weight – g cm\(^{-2}\)) and resulted in differing values of most coefficients in the equations developed here. Conservation of the relationships under mild water stress is consistent with proportionate reductions in cell length and width reported in Tardieu et al. (2000). By contrast, the differences in coefficients of equations where interplant competition occurred, are consistent with changes of carbohydrate storage pattern (Turgut et al., 2005; Pagano et al., 2007) and competitive effects causing etiolation (lengthening) of cells and organs at the expense of width (Bos et al., 2000; Andreiu et al., 2006).

The fitted allometric relationships mostly had high coefficients of determination (\(r^2\)), but were lower for 34N43 rainfed in Table 2 and 34N43 fully irrigated and rainfed in Table 4 where the points were more scattered. These might be improved by more intensive sampling. It should also be noted that here fresh biomass has been used in developing the equations at this stage. Dry biomass may be considered in applying to FSPMs. The allometric relationship of organ dimensions and biomass is likely to remain but the coefficients will be altered to accommodate the removal of mass due to water if organ dry matter is used. The findings here are for maize, which has separate male (terminal tassel) and female (lateral ear) structures on the same plant. Similar analyses can be undertaken for cereal crops such as sorghum, rice and wheat, which have a terminal floral structure, with both male and female functions. It is possible that discontinuities of the relationships between organ dimensions and organ biomass may not occur. Nevertheless, they all initiate floral structures that grow especially during the latter part of canopy production and thus compete for assimilate. This competition may induce discontinuities as in maize, and for similar reasons (competition for carbohydrate among sinks of differing strengths) despite differences in positioning of reproductive structures.

2. Implications for reconstructing canopy morphology from biomass accumulation

The mathematical equations quantifying relationships between organ dimensions and biomass indicated that the organ morphology could be predicted if biomass of individual organs is provided. The prediction of ear position will be critical for use of the relationships in maize modelling, and can be achieved from empirical relationships of ear appearance and thermal time (Wang et al., 2002; Song et al., 2008). Biomass allocation and accumulation at the level of individual organs has been simulated for maize (Guo et al., 2006). The organ morphology predicted from its biomass, sometimes along with other architectural characteristics e.g. leaf angle (not considered in this study) can be used to calculate light environments and thus photosynthesis (biomass calculation) in modelling physiological functions (Espana et al., 1999; Pommel et al., 2001; Yan et al., 2004; Luquet et al., 2006; Chelle et al., 2007). Consequently, the findings of allometric relationships of organ development enable us to realize the feedback between plant functional processes and plant morphology at the organ level for FSPMs. It has
to be admitted that dry mass is commonly used in most of physiological models (Wang et al., 2002). If organ biomass is predicted from physiological modelling, the conversion from dry mass to fresh mass of organs via water content will be necessary, enabling the allometric relationships to be properly used.

Findings here showed that for fully irrigated and rainfed (having produced mild water stress) conditions, the relationships between organ dimensions and biomass were conserved and hence can be used to calculate morphology from growth (photosynthetic accumulation), with the impact of water stress being expressed through reduced photosynthetic accumulation, as in canopy-based models e.g. Ausim-Maize (Keating et al., 2003). However, the relationship may change under more severe water stress conditions, and thus the coefficients and constants need to be further assessed to explore the effects of more severe water stress and to better define the relationship between the constants and coefficients, and determine if there are any thresholds of severity of water stress that alter the relationships. By contrast, the change in coefficients under interplant competition will need to be accommodated in modelling. The experiment here had 4 populations, and it is clear that some coefficients changed with plant population, with mostly linear increases up to 12 plants m\(^{-2}\), and then a change in slope of the response, perhaps indicating the onset of severe competition. The exception was LW, in which there was a linear decline in the b value (coefficient) for leaves above the ear as plant population increased and may be due to assimilate supply limitations (Pommel et al., 2001). In contrast, the organ length response to plant density could be due to light signal i.e. ratio red: far red, but independent of assimilate availability (Maddonni et al., 2002). It should be noted that 2 plants m\(^{-2}\) is generally not a practical plant population density in which maize is commonly used. Consequently, in modelling use, any adjustment of model coefficients and parameters for high (or low) plant densities would be appropriately referenced to the values 6 plants m\(^{-2}\).

Conclusions

The allometric relationships between lamina length, lamina maximum width, sheath length, internode length and biomass of the respective organs remained insensitive to the mild water stress despite reductions in individual leaf area (and thus changes to canopy area and morphology) and biomass accumulation under rainfed conditions. However, they were affected by increasing plant density, suggesting that lamina, sheath and internode adjusted allometry to accommodate organ elongation in adapting greater plant population. These allometric relationships suggest that organ morphology can be predicted from biomass accumulation of individual organs (can be predicted from functional or physiological processes). These findings contribute to establishing the biologically valid linkages between physiological functions and plant morphological development for FSPMs.

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