

Maize canopy development in response to increasing plant population density

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Abstract

Improving crop production via adjustment of plant population density (PPD) largely depends on canopy development and light interception. Accordingly, it is essential to investigate the details of how canopy development responds to PPD. A field experiment was undertaken in China in 2009 to examine maize organ development across plant densities i.e. 2, 6, 12 and 20 plants m⁻². Lengths of laminae and sheaths were both increased in lower phytomers due to greater extension duration and decreased in upper phytomers due to reduced extension rate in response to more interplant competition as PPD increased. However, sheath extension appeared less affected by competition stress than lamina extension. Internode length was increased due to higher extension rate at high PPD. This study indicated that leaves and internodes utilized different strategies to cope with interplant competition induced by increased plant density. In addition, the findings can be used in modelling canopy production under different plant densities.

Key Words

Zea mays, canopy production, interplant competition, organs

Introduction

High plant density may improve the potential in achievement of greater crop yield since there are more plants available per single harvesting unit (e.g. per hectare). Crop production improvement via adjustment of plant population density (PPD) is largely dependent on canopy production and light distribution in the canopy. The effects of PPD on maize canopy production have been examined extensively at whole plant level, including effects on plant height, leaf area per plant and leaf area index (e.g. Maddonni et al., 2001; Bavec and Bavec, 2002). For example, the effect of plant density on leaf area expansion is through two components i.e. lamina width and lamina length. But the processes underpinning the effects have not been quantified adequately for use in crop growth modelling. The effects of PPD on whole canopy production are integrated with responses of individual organs that may vary with positions and organ type (Bos et al., 2000; Maddonni et al.,

2001; Chelle, 2005). It is essential to precisely quantify canopy response to PPD at organ level for understanding of whole plant physiology and for use in functional-structural crop modelling. Therefore, this paper aims to investigate the effects of increasing PPD on extension and expansion of individual laminae, sheaths and internodes.

Methods

A field experiment with maize cultivar NongDa 108 (ND108) grown under four PPDs i.e. 2 plants m^{-2} , 6 plants m^{-2} , 12 plants m^{-2} , and 20 plants m^{-2} (PPD2, PPD6, PPD12 and PPD20 respectively) was undertaken at Shangzhuang experimental station of China Agricultural University, Beijing, China (Latitude 40°02'N, Longitude 116°20'E) in 2009. A randomized block design of four plant densities with three replicates was used. The lowest density (PPD2), was used as the control (the plot size being 40 m^2), and represented 'no' intraspecific competition; PPD6 (close to local farming practice (Song et al., 2003), the plot size being 40 m^2), PPD12 (the plot size being 30 m^2) and PPD20 (the plot size being 20 m^2) represented mild, moderate and severe intraspecific competition respectively. Destructive sampling commenced when the 4th leaf was fully expanded and continued at 1–2 day intervals until canopy expansion was complete. Data on lamina length and width, sheath and internode length in each phytomer (a phytomer typically comprise a node where a leaf is attached, a subtending internode, and an axillary bud, used to indicate plant structural unit in whole plant physiology) were measured for each destructive sampling. Data on daily minimum and maximum temperatures were collected at a weather station near the field site for use in thermal time calculation using 8°C as base temperature as in Song et al. (2010). All significant effects are reported at $P < 0.05$; we present data for representative low, mid ranking and upper phytomers in the figures.

Results

Final length of laminae, sheaths and internodes

Lamina length was significantly increased in phytomers 7 to 11 in response to increased PPD, but was reduced in phytomers 13 to 18, especially in PPD20 (Figure 1a); sheath length was increased in phytomers 6 to 9, but was reduced in phytomers 11 to 18 (Figure 1b); internode length increased in phytomers 7 to 14 but there was little effect in phytomers 15 to 18 (Figure 1c) (Data in Figure 1a-c are for PPD = 2 and 20, organ lengths PPD6 and PPD12 were intermediate (data not shown)). ND108 had a total 19 phytomers, but the last phytomer was not used since it often behaved atypically (Song et al. 2010).

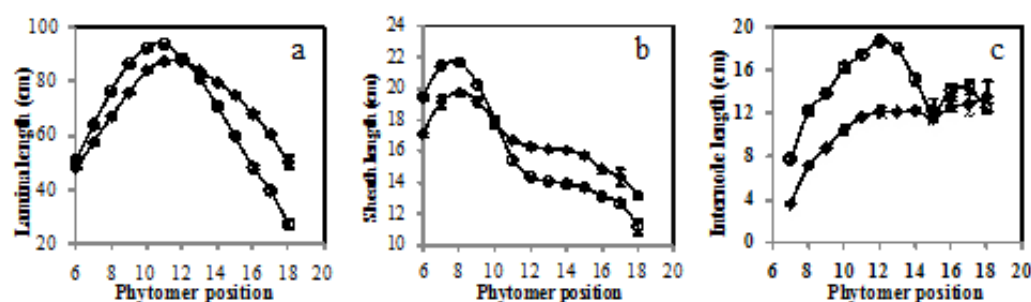


Figure 1. Final lengths of lamina (a), sheath (b) and internode (c) in different phytomer positions between PPD2 (filled symbol) and PPD20 (open symbol) (Vertical bars indicate standard errors, most of which fall within the symbols).

Lamina extension and expansion

Lamina length in low ranking phytomers (e.g. phytomer 8) was increased as PPD increased via greater extension duration, but decreased in upper phytomers (e.g. phytomer 18) via lower extension rate (Figure 2a), whereas lamina length in mid ranking phytomer 12 was unaffected. Lamina width was reduced for phytomers 8 and above due to lower expansion rate (Figure 2b). Same with final lamina length, lamina expansion rates in PPD6 and PPD12 were intermediate between PPD2 and PPD20.

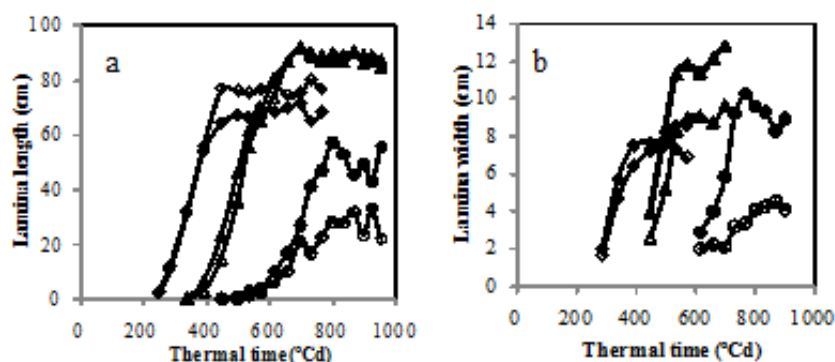


Figure 2. Extension of lamina length (a) and width (b) against thermal time for phytomers of 8 (diamond), 12 (triangle) and 18 (circle) in PPD2 (filled symbol) and PPD20 (open symbol).

Sheath extension

Sheath length was increased for lower phytomers (e.g. phytomer 7) via greater extension duration, while it was reduced for upper phytomers (e.g. phytomer 14) via slightly though significantly lower extension rate (Figure 3). There were insufficient data points on sheath extension for phytomers 16–18, hence only examples of extension of sheaths below phytomer 16 are shown. Sheath extension in PPD 6 and PPD12 were again intermediate.

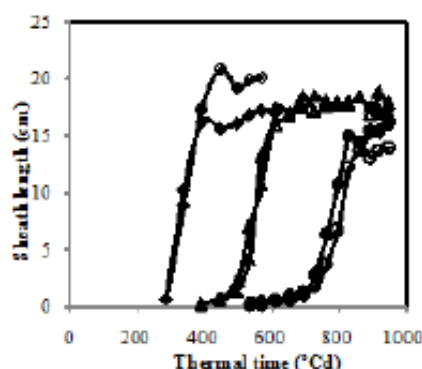


Figure 3. Sheath extension against thermal time for three phytomers of 7 (diamond), 10 (triangle), and 14 (circle) in PPD2 (filled symbol) and PPD20 (open symbol).

Internode extension

Internode length was consistently increased for phytomers 7–14 in response to increasing PPD via extension rate (Figure 4). For phytomers above 14, internode extension rate was not affected by increasing PPD, and as with the other organs internode extension in PPD6 and PPD12 was intermediate between PPD2 and PPD20.

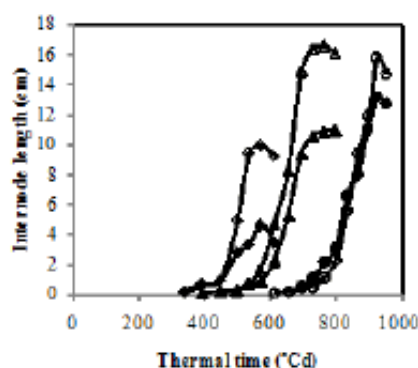


Figure 4. Internode extension against thermal time for three phytomers of 7 (diamond), 10 (triangle) and 14 (circle) in PPD2 (filled symbol) and PPD20 (open symbol).

Discussion

Maize canopy production in response to increased PPD and thus increasing interplant competition was analysed in detail at the level of individual organs. Lamina and sheath lengths in higher plant densities were increased in low-mid ranking phytomers of the plant, but decreased for upper phytomers, as in Andrieu et al. (2006). Either leaf cell expansion rate or duration or both would have been responsible for the adaptation, since these are the processes that influence leaf extension and expansion (Andrieu et al., 2006). Internode extension, thus length, was increased most likely by etiolation (longer individual cells) in response to light attenuation and low light intensity in the canopy due to increased PPD. This increase in organ length is triggered by changes in light quality (red: far red ratio) (Markham and Stoltenberg, 2009).

The organ level responses will also be useful for integration into crop modelling for different plant densities. However, these findings need to be confirmed in a range of maize cultivars from differing maturity groups and a means of generalizing the effects for programming efficiency in modeling sought. Final crop biomass and grain yield responses to PPD will then be able to be associated with canopy responses, and potentially provide guidance to traits useful for breeding cultivars more tolerating high interplant competition.

Conclusion

This study indicated that individual organ production changed to adapt to interplant competition caused by increased plant density. Either duration or rate of extension of organs was responsible for the effects. The study showed that the effects of PPD varied with the organ and phytomer position, and provides a useful framework for inclusion in functional and structural crop modeling.

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