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Growth trajectories and interspecific competitive dynamics in wheat/maize and barley/maize intercropping

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Abstract

Background and Aims Competition between intercropped species is important for yield advantage, but little attention has been given to interspecific competitive dynamics in intercropping.

Methods A field experiment with five cropping systems (wheat/maize, barley/maize intercropping, wheat, maize and barley sole cropping), two N levels (0 and 225 kg N ha⁻¹) and two maize mulching treatments (with and without) were performed. Sequential harvest of subplots was performed between 7 and 10 times, and the data were fitted to a logistic growth model.

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Results Intercropping significantly increased the maximum biomass and maximum growth rates of wheat and barley, but suppressed the early and maximum growth rate of intercropped maize. Maize growth recovered after the wheat or barley was harvested. In the presence of film mulch and/or fertilization, maximum biomass of intercropped maize was close to or significantly higher than that of maize alone. Fertilization and film mulching had much stronger effects on growth of maize than on wheat and barley.

Conclusions Interspecific competitive dynamics regulated by fertilization and film mulching can be quantified by the logistic model, which is helpful to understand the yield advantage of intercropping. This has important implications for managing interspecific competition through agronomic practices at field.

Keywords Competition · Growth dynamics · Maximum biomass · Maximum growth rate · Temporal niche · Yield advantage

Introduction

The role of interactions among plant species for the structure and dynamics of natural and agricultural plant communities has received wide attention (Tilman 1988; Callaway 2007; Li et al. 2007). The effects of one species on another can be negative (decreasing survival, growth or reproduction), positive or zero (Hauggaard-Nielsen and Jensen 2005; Callaway 2007). Earlier, competition was considered as the most important



interaction among plant species, but over the past two decades we have learned that facilitative and competitive interactions operate simultaneously in a wide range of plant communities (Bertness and Callaway 1994; Brooker et al. 2008; Zhang et al. 2013). Interspecific interactions sometimes result in a net positive effect on one species and a net negative effect on another (Callaway 2007). Interspecific interactions are inevitable in intercropping ecosystems as two crops are grown together (Vandermeer 1992; Zhang and Li 2003).

Intercropping has been widely practiced in many parts of the world for thousands of years (Francis 1986; Li et al. 2013). In China, approximately 28 million hectares are sown with more than one crop (Liu 1994). Both wheat/maize and barley/maize intercropping are long-established agricultural production systems in arid northwest China, especially in the irrigated areas with only one cropping season per year (Li et al. 2001a, b). Compared with monocropping, intercropping can significantly increase crop yields through more effective use of water, nutrients and solar energy as well as facilitative interactions (Willey 1979; Vandermeer 1992). Interspecific interactions between intercropped species play an important role in the yield advantage of intercropping (Vandermeer 1992; Zhang and Li 2003; Hauggaard-Nielsen and Jensen 2005). Yield advantages have been documented in cerealcereal intercropping, as well as legume-cereal intercropping (Hauggaard-Nielsen et al. 2001a; Li et al. 2001a, b). Recent research has worked towards integrating agronomy, plant physiology and ecology to improve intercropping systems (Brooker et al. 2014).

In plant communities, interaction among species is usually measured as the ratio of biomass of plants with and without competing species (Weigelt and Jolliffe 2003; Armas et al. 2004), and plant-plant interactions are usually measured only at the end of a single period of growth (Andersen et al. 2007). Plant biomass at one harvest is an outcome of plant growth up to that point, so a single harvest cannot reveal the processes involved (Trinder et al. 2012). Plants' competitive interactions are dynamic and change over the course of growth (Zhang et al. 2011, 2012; Trinder et al. 2012, 2013). Studying plant competition dynamically can provide a better picture of how interspecific interactions develop over the course of the growing season (Andersen et al. 2007) and improve our understanding of the mechanisms underlying plant-plant interactions. By explicitly modelling plant growth using parameters that are biologically

interpretable, we can understand dynamics of interspecific interactions between intercropped species and make predictions for improving intercropping systems.

Recent studies have begun to do this with sequential harvest data fitted to a logistic growth model (Andersen et al. 2007; Trinder et al. 2012), mostly in greenhouse pot experiments. Growth trajectories for the competing species are modelled with four parameters (Trinder et al. 2012): the initial growth rate, the asymptotic maximum biomass, the maximum instantaneous growth rate and the time to attain it. Here we use this approach to analyze the interspecific competitive dynamics in two similar widely practiced intercropping systems.

Application of N fertilizer to produce high agricultural yields has increased over recent years (Zhang and Li 2003). Plastic film mulching has long been used in the cultivation of many crops (Li et al. 2004). Mulches can increase yield by retaining soil moisture, increasing soil temperature, improving soil physical and chemical properties and enhancing soil biological activity (Pan et al. 2003). Plant-plant interactions change along productivity gradients (Brooker et al. 2008; Zhang et al. 2013), showing that environmental conditions influence competitive dynamics. Here we focus on the effects of nitrogen fertilization and mulching of maize on crop growth curves in intercropping.

The objectives of this study are to (1) analyze the crop growth trajectories and interspecific competitive dynamics in wheat/maize and barley/maize intercropping, and (2) investigate the effects of fertilizer and film mulching on these trajectories and on the interspecific competitive dynamics between intercropped species. It is important to understand how agricultural practices influence the dynamic trajectories of crop growth and competition between intercropped species if we are to maximize the advantages of intercropping.

Materials and methods

Site description

The field experiments were conducted in 2003 at the Baiyun experimental sites (38°37′N, 102°40′E) of the Institute of Soils, Fertilizers and Water-Saving Agriculture, Gansu Academy of Agricultural Sciences, Gansu Province, China. The site is located 15 km north of Wuwei City, Gansu Province at altitude of 1504 m.



Annual mean temperature is 7.7 °C. Annual mean precipitation is 150 mm, and potential evaporation is 2021 mm. The duration of sunlight is 3034 h and total solar radiation is 5988 MJ m $^{-2}$ year $^{-1}$. The average cumulative temperature above 10 °C per year is 3016 °C and that after wheat or barley harvest is 1350 °C. The frost-free period is 170–180 days. The soil is an alkaline (pH 8.8) Orthic Anthrosol (Institute of Soil Science, CAS, 2001) and contains 19.1 g organic matter, 1.18 g total N, 17.3 mg Olsen-P, and 233 mg exchangeable K per kilogram dry soil.

Experimental design

The experiment was conducted using a three factors randomized block design with three replicates (Table 1, Appendix 1 Fig. S1). The first factor was five cropping systems (sole wheat, barley and maize, wheat/maize intercropping and barley/maize intercropping), the second factor was two N levels (0 and 225 kg N ha⁻¹), and the third factor was two mulching treatments for maize (not mulched and mulched with plastic film). There were a total of 16 treatments (Table 1). The wheat (*Triticum aestivum* L.) cultivar was Long No. 17, the barley (*Hordeum vulgare* L.)

was Ganpi No. 3, and the maize (*Zea mays* L.) was Zhongdan No. 2, which was the same as in our previous studies (Li et al. 2001a, b, 2011).

Crop management and sample collection

There were a total of 48 plots, each with an area of $24.75 \text{ m}^2 \text{ (5.5} \times 4.5 \text{ m)}$. A 0.5 m wide ridge separated adjacent plots, and a 1.0 m wide ridge separated the blocks. Wheat/maize and barley/maize intercrops were planted in alternating 1.5 m wide strips, which included a 0.72 m wide wheat or barley strip (six wheat or barley rows with 0.12 m inter-row distance) and a 0.78 m wide maize strip (two maize rows with 0.39 m inter-row distance and 0.30 m plant distance), and the distance between adjacent border rows of two intercropped crops was 0.06+0.195=0.255 m. Each plot consisted of three strips for each crop; two strips were used to collect samples for biomass measurement during growth, and the last one for measuring yield at maturity. There were 38 rows of wheat and barley with 0.12 m inter-row distance, and 11 rows of maize with 0.39 m inter-row distance in their corresponding sole cropping plots, respectively. Maize occupied 52 % (i.e. 0.78/1.5) of intercropped area and wheat or barley 48 % (i.e. 0.72/

Table 1 Experimental treatments in intercrops and monocrops of wheat, barley and maize

| Treatment no. | Cropping | N rate (kg ha ⁻¹) | | | | | Film mulching | P rate (kg ha ⁻¹) |
|---------------|--------------|-------------------------------|-------|-------|-------|-------|----------------|-------------------------------|
| | | 24/3 | 5/5 | 25/5 | 23/7 | Total | | |
| 1 | Sole wheat | 0 | 0 | 0 | 0 | 0 | None | 90 |
| 2 | Sole barley | 0 | 0 | 0 | 0 | 0 | None | 90 |
| 3 | Wheat/maize | 0 | 0 | 0 | 0 | 0 | None | 90 |
| 4 | Barley/maize | 0 | 0 | 0 | 0 | 0 | None | 90 |
| 5 | Sole maize | 0 | 0 | 0 | 0 | 0 | None | 90 |
| 6 | Wheat/maize | 0 | 0 | 0 | 0 | 0 | Mulching maize | 90 |
| 7 | Barley/maize | 0 | 0 | 0 | 0 | 0 | Mulching maize | 90 |
| 8 | Sole maize | 0 | 0 | 0 | 0 | 0 | Mulching maize | 90 |
| 9 | Sole wheat | 112.5 | 112.5 | 0 | 0 | 225 | None | 90 |
| 10 | Sole barley | 112.5 | 112.5 | 0 | 0 | 225 | None | 90 |
| 11 | Wheat/maize | 112.5 | 0 | 56.25 | 56.25 | 225 | None | 90 |
| 12 | Barley/maize | 112.5 | 0 | 56.25 | 56.25 | 225 | None | 90 |
| 13 | Sole maize | 112.5 | 0 | 56.25 | 56.25 | 225 | None | 90 |
| 14 | Wheat/maize | 112.5 | 0 | 56.25 | 56.25 | 225 | Mulching maize | 90 |
| 15 | Barley/maize | 112.5 | 0 | 56.25 | 56.25 | 225 | Mulching maize | 90 |
| 16 | Sole maize | 112.5 | 0 | 56.25 | 56.25 | 225 | Mulching maize | 90 |



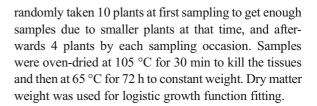
1.5). The densities of intercropped crops within the strips were the same as those of sole crops on equivalent land area, giving 600 plants m⁻² for wheat and barley and 8.55 plants m⁻² for maize.

On 24 March, before sowing, all the P fertilizer (90 kg P₂O₅ ha⁻¹) for each plot and first half of the designated N fertilizer (112.5 N kg ha⁻¹) for N application plots were evenly broadcast and incorporated into the top 20 cm soil layer for all cropping systems including sole barley, wheat, maize, and wheat/maize and barley/maize intercropping (Table 1). For sole wheat and barley, the second half of the designed N fertilizer (112.5 kg N ha⁻¹) was top dressed at the first irrigation (5 May). For sole maize and intercropped maize with barley or wheat, the second half of designated N fertilizer was divided into two equal rounds (56.25 kg each), and applied into holes close the maize plants by small fertilization tool, at the V6 (elongation) stage (25 May) and the V12 (pre-tasseling) growth stage (23 July). The 80 cm wide and 0.008 mm thickness plastic film was covered to two maize rows after maize sowing for mulching plots. When maize emerged, the plastic film was cut at the position of maize plant.

Sole and intercropped wheat and barley were sown on 26 March, and seedlings emerged on 8 April. Maize was sown on 21 April and seedlings emerged 1–3 May. All plots were irrigated according to local farmers' practice; seven irrigations of 70 mm each were carried out on 5 May, 25 May, 10 June, 30 June, 23 July, 5 August and 27 August.

Sole and intercropped wheat, barley and maize were sampled at approximately 2-week intervals after wheat (barley) emergence. Sole and intercropped wheat and barley were sampled seven times: 22 April, 8 May, 24 May, 7 June, 21 June, 5 July and 21 July. Non-mulched maize was sampled ten times: 24 May, 7 June, 21 June, 5 July, 21 July, 5 August, 19 August, 2 September, 14 September, and the last time was between 24 September and 8 October for different treatments, since the maize matured at different times. Mulched maize was sampled eight to ten times: 24 May, 7 June, 21 June, 5 July, 21 July, 5 August, 19 August, 2 September, while the last one or two times were between 5 September and 20 September for different treatments. In the wheat/maize or barley/maize intercropping ecosystems, two crops had 70 to 80 day co-growth period.

The sampling areas were $0.3 \text{ m} \times 6$ rows for intercropped wheat and barley, and $0.3 \text{ m} \times 4$ rows for sole wheat and barley. Samples for maize were



Growth model

Unlike simpler functions, logistic growth curves can characterize plant growth from emergence until death or harvest, and have therefore been increasingly used to fit plant growth (Andersen et al. 2007; Trinder et al. 2012). Biomass data for each crop component of soleand intercrops from all harvests were fitted to the logistic growth function using least squares (Andersen et al. 2007).

$$M_t = \frac{K}{1 + \exp(r \times (t_{50} - t))} \tag{1}$$

where M_t (kg ha⁻¹) is the aboveground dry matter weight per unit ground area of a given crop species grown in a given treatment at t days after wheat emergence over the course of the growth season. An intercrop strip has a width of 1.5 m (i.e. 0.72 m wheat or barley+0.78 m maize). The measured wheat or barley biomass is based on the sown width of wheat or barley (0.72 m). In the case of maize, the biomass is based on the sown width of maize (0.78 m). K (kg ha⁻¹) is a parameter representing the maximum biomass, r (d⁻¹) is the initial per capita growth rate (d M_t /dt×1/ M_t), and t₅₀ (d) is the time of maximum instantaneous growth rate (see below). These parameters were estimated using the Slogistic1 procedure of the OriginPro8 software (OriginLab Corporation, Northampton, MA, USA).

The instantaneous growth rate can be estimated as:

$$\frac{\mathrm{d}M_t}{\mathrm{d}t} = rM_t \left(1 - \frac{M_t}{K} \right) \tag{2}$$

The instantaneous growth rate reaches a maximum at M_t =K/2, therefore the maximum instantaneous growth rate, I_{max} =rK/4, occurs at the time t_{50} .

Statistical analyses

The main and interaction effects of three factors (cropping treatments, nitrogen application and film mulching) for maize and two factors (cropping



treatments and nitrogen applications) for wheat or barley on the four parameters (r, K, t_{50} and I_{max}) were determined with ANOVA analysis. Two-way ANOVAs for wheat and barley were used because there was no mulching treatment for them. In order to compare the significance of difference between all treatments (specific combinations for each factor level), we used oneway ANOVA analysis and multiple comparisons by least significance difference (LSD). All analyses were carried out in PASW Statistics 18 (SPSS Inc., Chicago, IL, U.S.A.).

Results

Wheat

Wheat growth fit the logistic function well (0.947≤ adjusted $R^2 \le 0.999$, P < 0.001). The initial stage of growth was close to exponential, and then growth slowed and stopped at maturity (Fig. 1a, c). Cropping treatment (C) and N fertilizer (N) had no significant effect on wheat's initial growth rate (r) or the time to reach the maximum growth rate (t_{50}) except for wheat intercropped with maize without both mulching and N application (Table 2, Fig. 2a, c). The maximum biomass (K) and maximum growth rate (I_{max}) of intercropped wheat were significantly higher compared to sole wheat (Table 2, Figs. 1 and 2), while N fertilizer had no significant effect on the maximum biomass and maximum growth rate of both intercropped and sole wheat. Wheat attained the maximum growth rate at about 60 days after its emergence (Table 2).

Barley

Barley biomass under different treatments also fit the logistic model well $(0.953 \le \text{adjusted } R^2 \le 0.997, P < 0.001$. Fig. 1e, g). There was no significant difference in the initial growth rate between sole barley and barley intercropped with non-mulched maize. In contrast, when intercropped with mulched maize, the initial growth rate of barley was significantly higher than that of sole barley under both fertilizer treatments (Table 2, Fig. 2e, g). N fertilizer did not have a significant effect on the initial growth rate of barley. Intercropping with mulched or non-mulched maize significantly increased the maximum biomass and maximum growth rate of barley (Table 2, Figs. 1 and 2). Barley attained the

maximum growth rate at about 60 days after its emergence. Cropping treatment and N fertilizer had no significant effects on the time for barley to reach maximum growth rate (Table 2, Fig. 2e, g).

Maize

Growth in biomass of maize under the different treatments also fit the logistic model well (0.971 \leq adjusted $R^2 \leq$ 0.997, P < 0.001; Fig. 1). The initial growth rate of intercropped wheat or barley was higher than that of maize in wheat/ maize and barley/maize intercropping (Tables 2 and 3). The initial growth rate of maize was significantly affected by intercropping, N fertilizer and maize mulching treatments, as well as their interactions (Table 3, Fig. 2). There is no difference in initial growth rate between intercropped and sole maize when not mulched. In contrast, when maize was mulched, intercropping significantly decreased the initial growth rate of maize under both N fertilizer treatments. N fertilizer had no significant effect on the initial growth rate of non-mulched maize; however, when maize was mulched, N fertilizer significantly increased the initial growth rate of sole maize and maize intercropped with barley (Table 3, Fig. 2).

The growth of intercropped maize was significantly lower than that of sole maize during the early growth stage, under all N fertilization and mulching treatments, however, the maximum biomass of intercropped maize was close to or significantly higher than that of sole maize, when mulched and/or fertilized with N (Table 3, Fig. 1). The maximum biomass of intercropped maize was still significantly lower than that of sole maize under no-mulch and no N-fertilizer treatments. In addition, N fertilization and mulching resulted in a significant increase in the maximum biomass of maize (Table 3, Fig. 1).

Maize attained the maximum growth rate at about 110 days after wheat or barley emergence. Intercropping and film mulching treatments, as well as their interactions significantly affected the time to reach maximum growth rate (Table 3, Fig. 2). Intercropping postponed, while mulching advanced, the time for maize to reach its maximum growth rate, but N fertilizer did not significantly affect it (Table 3, Fig. 2).

The maximum growth rate of maize was significantly affected by all three factors, as well as their interactions (Table 3, Fig. 2). Intercropping significantly decreased the maximum growth rate, except for non-mulched maize with wheat and nitrogen application. Nitrogen



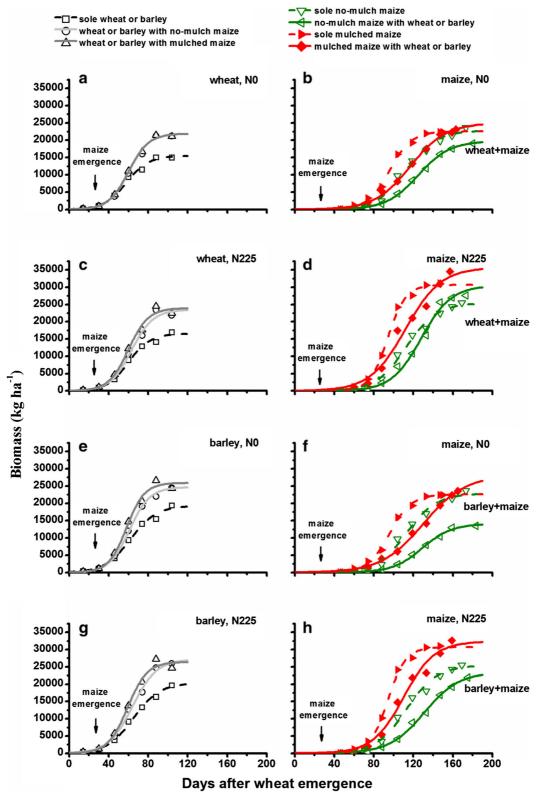


Fig. 1 Aboveground biomass growth of wheat, barley and maize in relation to cropping treatments, film mulching and nitrogen rates. Each *symbol* represents a single harvest and is the mean of three replicates



application significantly increased the maximum growth rate of both sole and intercropped maize, except for sole maize without mulch. Mulching significantly increased the maximum growth rate of maize in sole and intercropping, except for intercropped maize with wheat and nitrogen application (Table 3, Fig. 2).

Discussion

Maximum biomass

Intercropping with maize significantly increased the final biomass (Fig. 1) and maximum growth rate (Fig. 2) of wheat and barley (Table 2), indicating that intercropping can lead to a yield advantage for wheat and barley. A previous study also found that there is a significant yield increase of wheat when intercropped with maize, due to increased yield in the first row next to maize (Li et al. 2001b). This border row effect was attributed to increased light interception (Zhang et al. 2007; Zhu et al. 2015) and better nutrient acquisition of wheat than maize (Lesoing and Francis 1999; Li et al. 2001b).

The growth of intercropped maize was impaired during co-growth period in two intercropping systems for all N fertilization and mulching treatments, but thereafter it increased sharply after harvest of wheat or barley. As a result, the maximum biomass of intercropped maize was equal to or greater than sole maize, when mulched and/or fertilized (Table 3, Fig. 1). Our results can be explained in terms of "competition-recovery production principle" of intercropping (Madhavan and Shanmugasundaram 1990; Li et al. 2001a, b). In wheat/ maize intercropping, intense competition occurs between two intercropped species during the 70 to 80day co-growth period (from maize emergence to wheat harvesting; Li et al. 2001a, b). After wheat harvest, maize grows alone for about 60 days. The growth of the subordinate species (maize) is reduced due to interspecific competition during the period in which both crops are growing together. Maize recovers after the wheat is harvested, so that the final maize yields are the same or even increase compared with sole maize (Li et al. 2001a, b). Therefore, our results indicate that the better recovery here is due to extending the growing season.

Because of limited nutrient availability and lower competitive ability than wheat and barley, intercropped maize growth cannot recover at the later growth stage

Fable 2 Parameters estimated from fitting logistic growth curves to wheat and barley biomass growth in relation to cropping treatments and nitrogen application

| Treatments | Wheat biomass | | | | Barley biomass | | | |
|-----------------------|--|-----------------------|--------------------------|---|------------------------|-------------------------|----------------------------|------------------------------------|
| | / (×10 ³ d ⁻¹) | $K 		 (t ha^{-1})$ | t_{50} (d) | $I_{\rm max} $ (kg ha ⁻¹ d ⁻¹) | $r \times 10^3 d^{-1}$ | K (t ha ⁻¹) | <i>t</i> ₅₀ (d) | $I_{ m max}$ (kg ha $^{-1}$ d $^-$ |
| Sole, N0 | $90\pm11^{\mathrm{a}}$ | 15.5±0.3 ^b | 58±0.9 ^b | 347±39 ^b | 77±3 ^{bc} | 19.3±0.9 ^b | 62 ± 0.8^{ab} | 369±11 ^b |
| /No-mulch maize, N0 | 97 ± 8^{a} | 22.1 ± 1.5^{a} | $62\!\pm\!1.1^a$ | 537 ± 58^{a} | $98\pm14^{ m abc}$ | 24.7 ± 1.1^{a} | $61{\pm}1.9^{ab}$ | 595 ± 57^{a} |
| /Mulched maize, N0 | 99 ± 3^{a} | 21.9 ± 0.8^{a} | $60{\pm}1.0^{ab}$ | 544 ± 26^{a} | 109 ± 16^{a} | 25.9 ± 1.0^{a} | $58\pm2.0^{\mathrm{b}}$ | $709\!\pm\!105^{\mathrm{a}}$ |
| Sole, N225 | 91 ± 9^a | 16.5 ± 1.2^{b} | $60\pm1.9^{\mathrm{ab}}$ | 372 ± 13^{b} | 75±7° | 20.4 ± 0.9^{b} | 65 ± 2.9^{a} | 378 ± 19^{b} |
| /No-mulch maize, N225 | 92 ± 1^a | 23.5 ± 0.9^{a} | $63\!\pm\!0.4^{\rm a}$ | 541 ± 14^{a} | 82 ± 1^{abc} | 27.2 ± 1.3^{a} | 64 ± 1.2^{ab} | $556{\pm}32^{\mathrm{a}}$ |
| /Mulched maize, N225 | $100{\pm}3^{\rm a}$ | 24.0 ± 1.4^{a} | 60 ± 1.7^{ab} | 596 ± 31^{a} | $101\!\pm\!5^{ab}$ | $26.4\!\pm\!1.6^a$ | $59{\pm}0.9^{\rm b}$ | 669 ± 61^{a} |
| Significance | | | | | | | | |
| Cropping (C) | 0.259 | 0.000 | 0.046 | 0.000 | 0.022 | 0.000 | 0.088 | 0.000 |
| N fertilizer (N) | 0.934 | 0.133 | 0.303 | 0.370 | 0.410 | 0.202 | 0.200 | 0.777 |
| $C \times N$ | 0.737 | 0.710 | 0.518 | 696.0 | 0.551 | 0.841 | 0.733 | 0.653 |

 $\frac{\mathrm{d}^{-1}}{\mathrm{d}}$

r (d-1) is the initial growth rate, K (t ha-1) is the asymptotic maximum biomass, t₅₀ (d) is time of maximum instantaneous rate, I_{max} (kg ha⁻¹ d⁻¹) is the maximum instantaneous growth rate. Values (mean $\pm SE$, n=3) with the same letter within each column are not significantly different between all treatments (one-way ANOVA, P<0.05)



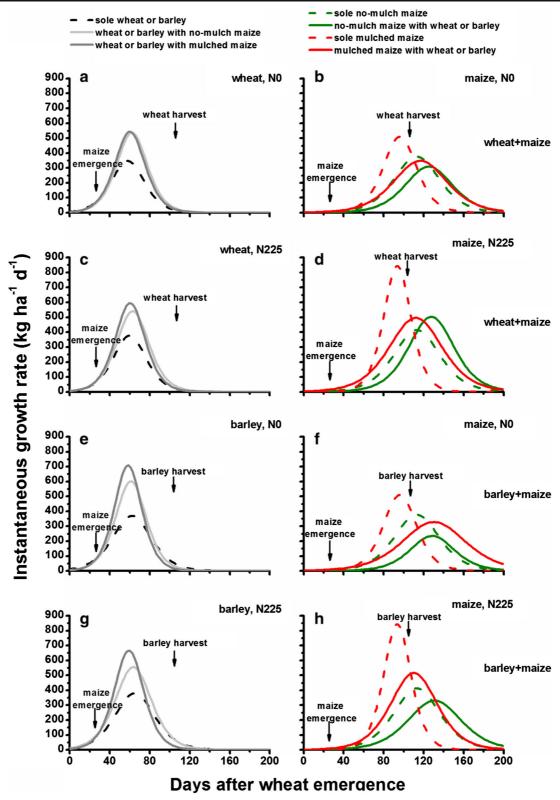


Fig. 2 Instantaneous growth rates of wheat, barley and maize in relation to cropping treatments, film mulching and nitrogen rates



compared with sole maize under treatments without mulch and fertilizer application (Fig. 1). Present results are consistent with the limited recovery of maize in wheat/maize intercropping in the absence of additional nitrogen and phosphorus (Li et al. 2001a).

In present study, N fertilizer did not have a significant influence on maximum biomass, maximum growth rate or initial growth rate of wheat and barley (Table 2, Figs. 1 and 2). Wheat and barley have a high ability to take up soil N (Li et al. 2001a, b, 2006, 2011; Andersen et al. 2007), and the existing soil fertility may be sufficient to meet the nutrient requirements due to previous long-term over-fertilization. The average nitrogen fertilizer application rate is 450 kg N ha⁻¹ year⁻¹ for wheat/maize intercropping in the irrigated areas of northwest China (Zhang and Li 2003).

Maximum growth rate and the time to reach it

Each species occupies a unique niche, determined by environmental factors that influence the growth, survival and reproduction of a species (Molles 1999). Temporal or spatial niche of species is important for interspecific competition and resource use in plant communities (Brokaw and Busing 2000; Hauggaard-Nielsen et al. 2001b). In our study, wheat and barley reached the maximum growth rate at about 60 days after their emergence; in contrast, maize reached the maximum growth rate at approximately 110 days after wheat or barley emergence. Our results indicated that the time for intercropped species to reach maximum growth rate was different in the intercropping, so the resource use of intercropped species was separated in temporal scale, as a consequence, temporal niche differentiation reduces

Table 3 Parameters estimated from fitting logistic growth curves to maize biomass growth in relation to cropping treatments, film mulching and nitrogen application

| Treatments | Maize biomass | | | | | | |
|--------------------------|--------------------------------|--------------------------------|----------------------------|--|--|--|--|
| | $r \times 10^3 \text{ d}^{-1}$ | <i>K</i> (t ha ⁻¹) | <i>t</i> ₅₀ (d) | $I_{\rm max}$ (kg ha ⁻¹ d ⁻¹) | | | |
| No mulch (sole, N0) | 66±3 ^{cd} | 22.8±0.4 ^e | 113±0.8 ^{cd} | 378±23 ^{cd} | | | |
| No mulch (/Wheat, N0) | 63 ± 5^{cd} | $19.8 \pm 0.7^{\rm f}$ | 125 ± 0.5^{b} | 311 ± 32^{e} | | | |
| No mulch (/Barley, N0) | 67±5° | 14.1 ± 0.5^{g} | 129 ± 2.2^{ab} | $235{\pm}8^{\rm f}$ | | | |
| Mulch (sole, N0) | 90 ± 2^{b} | 22.6 ± 0.2^{e} | 96 ± 0.3^{e} | 511 ± 14^{b} | | | |
| Mulch (/Wheat, N0) | 56 ± 3^{de} | 25.0 ± 0.4^{d} | 117±3.1° | $348\!\pm\!16^{de}$ | | | |
| Mulch (/Barley, N0) | 47 ± 2^{e} | 28.1 ± 0.3^{c} | 130 ± 0.8^{a} | $329\!\pm\!19^{de}$ | | | |
| No mulch (sole, N225) | 65 ± 4^{cd} | $25.5 {\pm} 0.5^d$ | 113 ± 1.6^{cd} | 413 ± 17^{c} | | | |
| No mulch (/Wheat, N225) | 66 ± 7^{cd} | 30.5 ± 1.8^{b} | 128 ± 3.3^{ab} | 498 ± 31^{b} | | | |
| No mulch (/Barley, N225) | 56 ± 1^{cde} | 23.6 ± 0.6^{de} | 131 ± 1.4^{a} | $332{\pm}8^{de}$ | | | |
| Mulch (sole, N225) | 110±2 ^a | 30.7 ± 0.3^{b} | 94 ± 0.3^{e} | 846 ± 11^{a} | | | |
| Mulch (/Wheat, N225) | 56 ± 2^{de} | 35.7 ± 0.1^a | 112 ± 1.0^{cd} | $496\!\pm\!18^b$ | | | |
| Mulch (/Barley, N225) | 64 ± 3^{cd} | 32.4 ± 0.7^{b} | 110 ± 1.5^{d} | $514\!\pm\!18^b$ | | | |
| Significance | | | | | | | |
| Cropping (C) | 0.000 | 0.406 | 0.000 | 0.000 | | | |
| N fertilizer (N) | 0.023 | 0.000 | 0.052 | 0.000 | | | |
| Mulch (M) | 0.000 | 0.000 | 0.000 | 0.000 | | | |
| $C \times N$ | 0.174 | 0.073 | 0.238 | 0.421 | | | |
| $C \times M$ | 0.000 | 0.004 | 0.023 | 0.000 | | | |
| $N \times M$ | 0.002 | 0.437 | 0.008 | 0.000 | | | |
| $C \times N \times M$ | 0.359 | 0.036 | 0.058 | 0.001 | | | |

r (d⁻¹) is the initial growth rate, K (t ha⁻¹) is the asymptotic maximum biomass, t_{50} (d) is time of maximum instantaneous rate, and I_{max} (kg ha⁻¹ d⁻¹) is maximum instantaneous rate. Values (mean $\pm SE$, n=3) with the same letter within each column are not significantly different between all treatments (one-way ANOVA, P < 0.05)



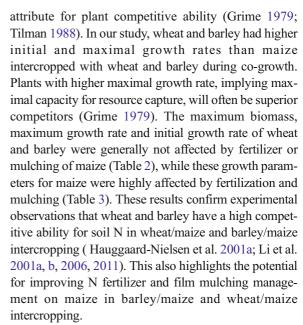
interspecific competition (Brokaw and Busing 2000) and increases total resource capture of intercropped species (Hauggaard-Nielsen et al. 2001b). In addition, compared to sole maize, intercropped maize postponed the time to reach its maximum growth rate for 10–30 days, dependent on different management practices (i.e. N fertilization and mulching) (Table 3), suggesting that intercropping strengthens the temporal niche differentiation. These may be the major factor contributing to yield advantage in wheat/maize and barley/maize intercropping (Hauggaard-Nielsen et al. 2001b; Li et al. 2001a).

Earlier emergence and greater root extension are the most likely explanations for the competitive advantage of wheat and barley over maize (Li et al. 2001a, b, 2006), so intercropping significantly reduced the maximum growth rate of maize (Table 3, Fig. 2). Accordingly, intercropping significantly increased the maximum growth rate of wheat and barley (Table 2, Figs. 1 and 2). Reduced competition was not only found in wheat/maize (Li et al. 2006) but also in barley/maize intercropping (Li et al. 2011). In present study, mulching increased the maximum growth rate of maize (Table 3, Fig. 2), presumably due to increased soil temperature and moisture conservation (Pan et al. 2003; Li et al. 2004). N fertilizer did not affect the maximum growth rate of wheat and barley, but increased the maximum growth rate of maize (Tables 2 and 3, Fig. 2), which indicates that maize can utilize additional N better than wheat and barley can.

Crops attained their maximum growth rate during the period of canopy closure and maximum leaf area (Zhang et al. 2007). Therefore, when the crop reaches its maximum growth rate is clearly linked to its growth stage. The length of a crop growth stage is related to the accumulated and minimum temperatures (Tian et al. 2012). Therefore N fertilizer did not significantly affect the time it took wheat, barley or maize to reach their maximum growth rates. Soil warming due to mulch can shorten the period of crop growth (Pan et al. 2003; Li et al. 2004; Tian et al. 2012), thus increasing the development rate of maize and significantly advancing the time at which maize reaches its maximum growth rate and maturity (Fig. 2).

Initial growth rate

The initial growth rate reflects the plant's growth potential and the availability of resources, and thus is a key



N fertilizer and mulching in sole and intercrops interacted to affect the initial growth rate of maize. The growth season in arid northwestern China is too short to grow two crops sequentially in one year because of temperature limitations (Li et al. 2001b). Plastic film mulching has a large effect on crop production in this area (Li et al. 2004), as it increases soil temperature and moisture on the upper soil layer (Pan et al. 2003). When maize was mulched, it grew rapidly and therefore could use more nitrogen than non-mulched maize. At the same time, competition from wheat or barley significantly decreased the initial growth of intercropped maize compared to sole maize, in part because they were sown earlier.

Our previous studies have investigated overyielding and interspecific interactions in these wheat/maize and barley/maize intercropping systems (Li et al. 2001a, b, 2006, 2007, 2011), and the final biomass of the component species in these previous studies were similar to the present results. Therefore, the present results are reliable even though this field experiment was performed in only one year. Our previous studies did not quantify the growth dynamics of intercropped components and corresponding sole cropped species, however, because there was limited sampling over the course of growth. By using dynamic data and an explicit growth model, we can quantify the dynamics of growth and interspecific competition, which helps us to understand the processes underlying the patterns.



Conclusions

The maximum biomass of both dominant and subordinate species in intercropping was generally higher than that in corresponding sole crops. In addition, the growth performance (including initial growth rate and maximum growth rate as well as maximum biomass) of the earlier sown wheat and barley was not affected by fertilization or mulching of maize. In contrast, fertilization and especially mulching increased the maximum biomass, initial growth rate and maximum growth rate of maize in most treatments. Wheat and barley were better competitors than maize in wheat/maize and barley/maize intercropping, as wheat and barley had higher initial and maximum growth rates than intercropped maize. Studying the dynamics of growth in intercropping ecosystems can help us develop optimal film mulching practices and fertilizer application rates. When designing species combinations for intercropping, the timing of maximum growth rate should be different for the intercropped species.

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