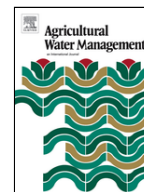




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Research paper

Water productivity and its allometric mechanism in mulching cultivated maize (*Zea mays* L.) in semiarid KenyaXiao-Feng Zhang^{a,1}, Chong-Liang Luo^{a,1}, Hong-Xu Ren^b, David Mburu^c, Bao-Zhong Wang^a, Levis Kavagi^d, Kiprotich Wesly^a, Aggrey Bernard Nyende^c, You-Cai Xiong^{a,*}^a State Key Laboratory of Grassland Agro-ecosystems, School of Life Sciences, Lanzhou University, Lanzhou 730000, China^b The Institute of Botany, Chinese Academy of Sciences, Xiangshan, Beijing 100093, China^c Jomo Kenyatta University of Agriculture and Technology, P.O. Box 31382-00600, Nairobi, Kenya^d United Nations Environment Programme, P.O. Box 47074-00100, Nairobi, Kenya

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ABSTRACT

Allometry is extensively used to describe the scaling relationship between individual size and metabolite allocation. Micro-field rain-harvesting system can improve soil water availability and thus alter the allocation of individual biomass among organs. Yet the eco-physiological mechanism based on allometric scaling theory has been little investigated under various mulching conditions. A field experiment was conducted using maize variety Yuyuan7879 in Juja, Kenya for two growing seasons (cross-year) from 2015 to 2016, and from 2016 to 2017 respectively. Four treatments were designed as ridge-furrow mulching (RFM) with black plastic mulching (RFMB), transparent plastic mulching (RFMT), grass straw mulching (RFMG) and conventional flat planting (CK). We found that RFMB, RFMT and RFMG significantly increased grain yield by 106%, 109% and 32% in 2015, and 101%, 96% and 30% in 2016 respectively, in comparison with CK. Mulching treatments improved soil temperature and moisture and significantly increased crop water productivity (CWP). Mulching treatments drastically changed the allometric relationship between metabolic rate (leaf biomass) and individual size ($\lg y = \alpha \lg x + \lg \beta$), and optimized the size-dependent reproductive allocation. In the relationship between leaf biomass (y-axis) vs aboveground biomass (x-axis), mulching treatments significantly declined the value of α ($\alpha < 1$; $P < 0.01$), suggesting that less photosynthetic product was allocated in leaves in mulching treatments than in CK. As for the allometric relationship between grain yield and aboveground biomass, the α was generally significantly more than 1 in RFMB and RFMT, and significantly less than 1 in RFMG and CK, demonstrating that more photosynthates were allocated to reproductive growth under plastic mulching. Also, the variation of allometric relationship between reproductive and vegetative biomass provided further evidence that plastic mulching facilitated substance transportation from vegetative to reproductive organs. In conclusion, plastic mulching significantly improved soil hydrothermal condition, increased individual reproductive allocation and ultimately improved grain yield and CWP at population level.

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1. Introduction

Allometry is extensively used to describe the scaling relationship between trait size and body size (Gayon, 2000). Using a dynamic and developmental perspective, the standard dictionary definition of allometry is the growth of one part of an organism relative to the growth of the entire organism, or some other part of it (Klinkhamer, 1995). This relationship is generally expressed using a power function $y = ax^b$, where y and x refer to the trait size and body size, respectively; a is the allometric constant, and b is the allometric coefficient (Huxley, 1932; Huxley and Teissier, 1936). At a logarithmic scale, this relationship becomes linear as $\log(y) = \log(a) + b \cdot \log(x)$, where $\log(a)$ is the intercept and b is the slope (Egset et al., 2012).

Energy allocation is one of the central concepts in ecology, providing the theoretical basis explaining different growth and reproduction strategies (Jackson et al., 1997). From allometric perspective, energy allocation is generally viewed as a size-dependent process in higher plant. In this case, allometry can elucidate the quantitative relationship between growth and allocation (Qin et al., 2013). Higher plants can produce biomass and then distribute it to different structures with the respective function for individual survival, growth and development. This can reflect internal coordination of different aspects of organ development, and underlie physiological processes for the development of functional-structural plant models (Guo et al., 2012). To most extent, the plasticity in allocation can be understood as a change in a plant's allometric trajectory in response to growth environment (Weiner, 2004). For dryland crops such as maize, the biomass allocation plasticity may imply the mechanisms underlying yield formation and crop water productivity, particularly under the improved soil moisture or temperature conditions.

Recent progress indicated that ridge-furrow mulching (RFM) system displayed great potential to improve crop production and reduce surface runoff in rainfed agricultural areas (Chai et al., 2014; Eldoma et al., 2016; Zhou et al., 2009). Currently, RFM system has become a principal form of crop production in northwest China (Chai et al., 2014; Kiers et al., 2008). This farming system generally comprises three major components with alternative ridge-furrow configuration units, soil surface mulching with various materials and furrow culture management. The ridges and furrows are used to collect and retain rainwater, and the wide-low ridges can be used for operation by farmer (Eldoma et al., 2016). The mulching material including plastic film, plant straw and others, serve as a medium to modify soil water-thermal balance and suppress weeds (Chai et al., 2014). Technically, rainwater collected by ridges is first channelled to furrow surface and then infil-

trated into deep soil, prolonging water availability for plant sown in furrows (Zhou et al., 2009). The planting in furrows can offer advantageous condition such as light, thermal, moisture, air, nutrient, then crop can maximize water uptake from furrows for growth and development (Mo et al., 2016). Under different mulching with polyethylene film (transparent or black film) or grass straw, the hydro-thermal condition will be significantly changed in rainfed maize field. The individual size and energy allocation are frequently affected by soil hydro-thermal status. It is a fundamental issue to improve the hydro-thermal environment, plant size and yield under RFM system in rainfed maize field. Therefore, how to alter the individual size and allocation of energy among organs from the perspective of metabolic theory is critical. Till now, there is little information available to address the above issue. Metabolic scaling theory provides an efficient tool to analyze energy distribution and metabolic rate in rainfed crop production.

Kenya is located at the east Africa Plateau (EAP), where arid and semiarid areas cover more than half of total area. It is characterized as low and erratic rainfall, and extensive evaporation (Nicholson, 2001; Li et al., 2013b). In semiarid Kenya, water availability is the primary limiting factor for crop growth (Brashares et al., 2011). Insufficient harvest and utilization of rainwater frequently lead to soil degradation and nutrient loss, which cause the productivity gap between current and potential yield (Barron and Okwach, 2005). Maize (*Zea mays* L.) production plays a critical role in regional food security, as it is by far the primary staple food for most people living there (Grace et al., 2014). The RFM system has been proved to significantly improve maize yield and WUE in northwest China (Liu et al., 2010), since it can increase soil temperature (Li et al., 2013a), prevent soil moisture loss and improve water availability (Jia et al., 2006). It also can reduce soil surface evaporation (Zhang et al., 2013), and change ground light and temperature conditions, thus improving water use efficiency (Zhou et al., 2009), yields and economic benefits (Zhao et al., 2012). It is unclear whether the RFM system exerts a similar effect in semiarid EAP. Moreover, the mechanism underlying plant ecology perspective is also not clear. In the semiarid environment, water availability is a major constraint to influence the growth and individual size, particularly in dryland crop. Reproductive allocation should be analyzed and interpreted allometrically because ratios or fractions such as reproductive effort (RE) or harvest index (HI) are size dependent. Cereal breeders should focus on reproductive allometry when interpreting HI, and select for allometric patterns that are most advantageous in a given agronomic context, especially when there is large variation in productivity among individuals, locations or years (Qin et al., 2013).

Existing studies indicated that the allometric slope (exponent) of the R–V relationship decreased with increasing elevation in plant populations (Guo et al., 2012, Qin et al., 2013). The slope of log R–log V relationship under the fertilized conditions was significantly greater than that of non-fertilization (Wang et al., 2014). In most cases, metabolic scaling theory provided an efficient approach to analyze energy distribution and metabolic efficiency in rainfed crop production. Therefore, we proposed a hypothesis that allometric scaling may account for water productivity and yield formation in crop farming system of RFM. The main objectives of this study are as follows: (1) to determine yield formation and water use in dryland maize under RFM system in semiarid Kenya, (2) to elucidate the size-dependent metabolic rule and (3) to clarify how allometric theory as a key eco-physiological approach account for water productivity. In light of allometry theory, we conducted the interdisciplinary research incorporating crop cultivation science, plant physiology and population ecology. It is expected that the high-yielding and water-saving mechanism would be elucidated and analyzed using the allometry theory in the RFM farming system in semiarid east African Plateau.

2. Materials and methods

2.1. Description of experimental site

The field experiment was conducted at the Experimental Farm, Jomo Kenyatta University of Agriculture and Technology (JKUAT), Juja, Kiambu County, Kenya. It is 35 km from Nairobi, with the altitude of 1520 m (1°06'S, 37°01'E) and a warm and temperate climate (Muthuri et al., 2005). Multi-year average temperature is 19.7 °C, and average annual rainfall is 856 mm with the bimodal characteristics, i.e. primary and secondary peaks in April and November respectively (Muthuri et al., 2005). The least amount of rainfall occurs in July with the average of only 12 mm, and the highest precipitation was in April with an average of 175 mm. March is the hottest month with average temperature of 21.3 °C, while July is the coldest one with average temperature of 18.4 °C. Mean annual maximum and minimum temperatures are 22.7 °C and 10.4 °C respectively. Mean annual potential evaporation is 5.05 mm d⁻¹. Local soil is poorly drained, dark grey and extremely firm cracking clay (Wanjogu and Kamoni, 1986). Soil pH ranges from 5.2 to 5.8 in topsoil and from 4.8 to 7.0 in subsoil. The soil type is identified as chromic vertisols with low fertility. The soil bulk density is 1.49 g/cm³, and the field water-holding capacity is 34.65% (determined gravimetrically).

2.2. Experimental design and field management

The micro-field rain-harvesting farming system was used in this study, including alternative ridge-furrow configuration units, soil surface mulching with various materials and furrow culture man-

agement (MFRHs) (Fig. 1). One of core configuration of MFRHs was alternating ridges and furrows, and each ridge-furrow unit comprised a wide-low ridge (0.6 m in width and 0.10 m in height) and a narrow-high ridge (0.4 m in width and 0.15 m in height), the naturally occurring furrows at the junction between wide-low ridge and narrow-high ridge can be used for collecting water and sowing crops. The crops were planted in the furrows in order to use water more effectively. Before sowing, plastic film was laid out over the plot where two pieces of plastic films were jointed in the midline between wide and narrow ridges, and the joint was fixed stably by placing soil on the top of film. Weeds can be manually cleared through lifting film at junction of two pieces of films during the growing season, usually, the weeds can be oppressed by film and can not grow.

There were two growing seasons in this study, i.e. two cross-year growing seasons. The first growing season ranged from November 2015 to March 2016, and the second one covered from October 2016 to January 2017. To get a more convenient expression, we called them as 2015 growing season and 2016 growing season. In 2015 growing season, maize was sown on November 22nd, 2015 and harvested on February 16th, 2016, with the precipitation of 157.7 mm and the growing period of 86 days. In 2016 growing season, sowing period was October 10, 2016, and harvesting period was January 8th, 2017 respectively, over 90 days with 192.34 mm. Four treatments were designed as: (1) ridge and furrow with mulching black plastic film (RFMB), (2) ridge and furrow with mulching transparent plastic film (RFMT), (3) ridge and furrow with mulching grass straw (RFMG) and (4) flat plant (local conventional farming pattern) (CK). The plastic film material was polyethylene with the width of 120 cm (made by Lanzhou Gold Field Corporation of China, Lanzhou, China), and the thickness of transparent film was 0.012 mm while the black film was 0.014 mm. The experiment was arranged in a randomized, complete block design with three replicates in both growing seasons. Each plot was 5 m long and 4.8 m wide. 75 kg rotten sheep manure was applied in each plot. The planting density was 165 plants per plot (equal to 6.9

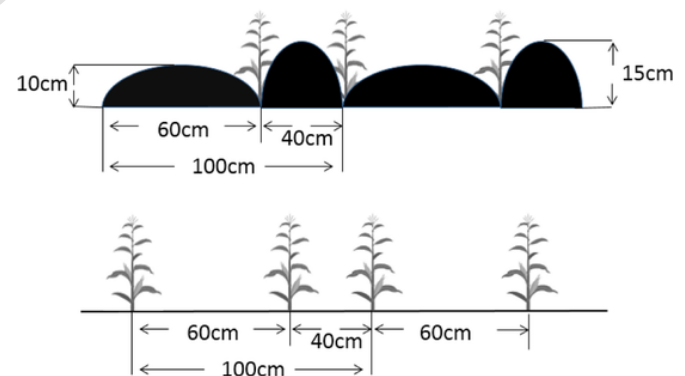


Fig. 1. The schematic diagram of ridge-furrow mulching (RFM) system and flat plant in both experimental seasons.

$\times 10^4$ plants per hectare) with 30 cm between plants. For both growing seasons, China's middle-late mature maize variety Yuyuan7879 was sown in the furrows using a hole-sowing machine.

2.3. Measurements and methods

Soil water content (SWC, %) was determined gravimetrically each 20 days at each 20-cm increment within the depth of 120 cm across each whole growing season. In each plot, soil samples were taken in the center of furrows with three replicates using a soil auger (5 cm diameter, 20 cm height). The SWC was also measured before sowing and after harvesting. In the meantime, soil bulk density was determined at each 20 cm layer throughout the soil profile of 120 cm. The average soil bulk density across soil layers was 1.49 g/cm^3 . Soil water storage (SWS, mm) was calculated as follows:

$$\text{SWS} = \text{SWC} \times \Delta b \times H$$

where SWC is soil water content (%), Δb is soil bulk density (g/cm^3) and H refers to as the thickness of the soil layer (mm).

Crop water productivity (CWP) was calculated as the ratio of grain yield or aboveground biomass per unit area to total water consumption (evapotranspiration, ET) over the whole growing season. In study site, crop growth was completely dependent on precipitation and the precipitation was too low to bring about drainage at the underground below 1 m. There was no runoff due to the ridges around each ridge-furrow plot, and no irrigation was applied throughout the whole growing season. Seasonal evapotranspiration (ET) in each plot was determined using the equation:

$$\text{ET} = \text{P} + \Delta W$$

where P is total precipitation in one growing season (mm) and ΔW is the difference in SWS between before sowing and after harvesting. Crop water productivity of grain yield (CWP_G) and of aboveground biomass (CWP_A) was calculated as follows:

$$\text{CWP}_G = Y/\text{ET}; \quad \text{CWP}_A = A/\text{ET}$$

where Y is grain yield (kg/ha), A is above-ground biomass (kg/ha) and ET is evapotranspiration amount in each growing season. In addition, soil temperature was measured at the topsoil of 20 cm in the middle point between two individual plant in the furrow using the U disk temperature recorder. Meteorological data were supplied from local weather station.

The relationship between leaf biomass (L) and grain yield (G) versus aboveground biomass (A) of individuals respectively in each treatment was analyzed. The data was log-transformed to homogenize variances. Visual inspection of residual versus predicted y-value confirmed that the residuals were consistent with the assumptions of the analysis. Linear regression was used to determine scaling exponents (slope) and allometric constants (intercept), according to the allometric equa-

tion (Weiner et al., 2009):

$$Y = \beta X^\alpha \quad (1)$$

which is usually analyzed as:

$$\log Y = \log \beta + \alpha \log X \quad (2)$$

The β is often referred to as allometric coefficient, $\log \beta$ as the intercept and α as the "allometric exponent" in Eq. (1) or the "slope" in Eq. (2). Y is leaf biomass or grain yield, and X is aboveground biomass. Allometric coefficient and intercept were calculated by SMATR 2.0 software.

Growth traits were recorded each 20 days after sowing (DAS) till maturity stage. Three individual plants were randomly chosen in each plot and marked to be measured for plant height and leaf area. The leaf area was calculated as follows (Mckee, 1964):

$$\begin{aligned} \text{Leaf area (cm}^2 \text{ per plant)} &= \text{leaf length (cm)} \\ &\quad \times \text{leaf width (cm)} \times 0.75 \end{aligned}$$

At harvesting stage, three rows of plants in middle of each plot were sampled for determination of yield and yield components. Grain yield, aboveground biomass weight, corncob length, corncob diameter, corncob weight, bare tip length, bract weight, kernel number were recorded for each plot. All the biomass samples were put into the forced-air oven at 105°C for 1 h and at 80°C for a minimum of 72 h.

2.4. Statistical analysis

Analysis of variance (ANOVA) was performed using the SPSS 20.0 program in Windows. Figures were drawn using the Origin 9.1 software (OriginLab, USA, <http://www.originlab.com/>). Allometric coefficient and intercept were calculated by SMATR 2.0 software (<http://www.bio.mq.edu.au/ecology/SMATR/>). Comparisons were conducted using the least significant difference (LSD) at 0.05 probability level. Mean values were reported in the tables and figures.

3. Results

3.1. Climatic characteristics at study site and soil temperatures under RFM treatments

Due to the El Niño event, the pre-sowing rainfall amount was much higher (244.2 mm in 2015 and 163.6 mm in 2016) than average value of multiple years (81.7 mm) (data was provided by Juja Meteorological Station, Kenya) (Fig. 2). Actually, the rainfall amount in first growing season was 157.7 mm. In order to eliminate influence of rainfall factor on experiment, the sowing date was postponed, but the initial soil moisture was higher in 2015 than in 2016. According to the multi-year records (582.4 mm and 20.12°C), a general trend was that year 2015 was relatively hot and wet (875.6 mm and 21.03°C), and year 2016 was relatively cool and dry (727.9 mm and 21.01°C) respectively. In November and December 2015, and January and February 2016 (first growing sea-

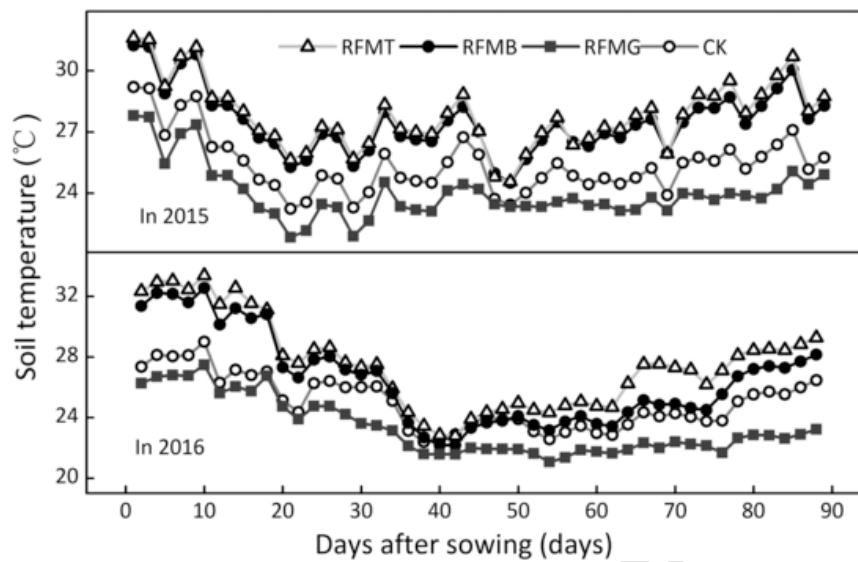


Fig. 2. Dynamics of daily soil temperature in 10 cm depth among various treatments in experimental site of Kenya over two years.

son), the mean air temperature was 21.0 °C, 20.5 °C, 21.2 °C and 21.8 °C respectively, which was higher than that of respective month over last 9 years by 1.32 °C, 1.64 °C, 1.7 °C and 1.14 °C, respectively. Also, the monthly rainfall amount was 244.22, 56.81, 5.23 and 55.65 mm, being 127.05, 27.54, 0.99, 42.38 mm higher than that of respective month over last 9 years. In second growing season, similar temperature trend was observed while rainfall was less. The mean air temperature in October, November and December 2016 and January 2017 was 22.1 °C, 21 °C, 19.7 °C and 20.3 °C respectively, being 1.23 °C, 1.32 °C, 0.84 °C and 0.8 °C higher than that of respective month in multiple years. The monthly rainfall of four months was 38.5, 163.55, 11.75 and 0 mm, which was lower by 47.63, -46.38, 17.52 and 4.24 mm than the same month in last 9 years.

In this study, initial soil moisture at sowing was obviously greater in 2015 than in 2016, and the difference in soil water storage between sowing and harvesting stages (Δ SWS) was also greater in 2015 (i.e. 170.9 mm) than in 2016 (i.e. 148.2

mm) (Table 1). The Δ SWS was higher by 19.43% in RFMB, 15.1% in RFMT and 10.53% in RFMG in 2015, and 15.99% in RFMB, 17.41% in RFMT and 8.16% in RFMG in 2016 respectively, in comparison with CK. The evapotranspiration in control group was 328.6 mm and 340.5 mm in 2015 and 2016 respectively. RFMB, RFMT and RFMG decreased the evapotranspiration by 10.1%, 7.85%, 5.48% and 6.96%, 7.58%, 3.55% in two years, respectively. Plastic mulching significantly increased topsoil temperature. Across two growing seasons, topsoil temperature was increased by 2.07 °C (2015) and 1.48 °C (2016) in RFMB, and 2.44 °C (2015) and 2.56 °C (2016) in RFMT respectively, compared with CK (Fig. 2). Transparent film mulching led to higher soil temperature than black film mulching in both growing seasons. Yet, grass straw mulching turned to reduce soil temperature by 1.4 °C in 2015 and 1.67 °C in 2016 respectively, compared with CK (Fig. 2). Better thermal condition facilitated the accumulation of aboveground biomass,

Table 1

Comparisons of grain yield, water use efficiency and above-ground biomass among various treatments at experimental site of Kenya over two growing seasons.

Year	Treatment	Rainfall (mm)	Δ SWS (mm)	ET (mm)	Grain yield (kg ha ⁻¹)	Above-ground biomass (kg ha ⁻¹)	CWP _G (kg ha ⁻¹ mm ⁻¹)	CWP _A (kg ha ⁻¹ mm ⁻¹)
2015	RFMB	157.7	137.7c	295.4c	4751.6a	14,508a	16.1a	49.1a
	RFMT		145.1c	302.8c	4813.4a	14,628a	15.9a	48.3a
	RFMG		152.9b	310.6b	3052.2b	11,273b	9.8b	36.3b
	CK		170.9a	328.6a	2300.4c	8811.8c	7.0c	26.8c
2016	RFMB	192.3	124.5c	316.8c	4288.6a	13,531a	13.5a	42.7a
	RFMT		122.4c	314.7c	4174.3a	12,818a	13.3a	40.7a
	RFMG		136.1b	328.4b	2776.3b	10,472b	8.5b	31.9b
	CK		148.2a	340.5a	2128.2c	8241.8c	6.3c	24.2c

Abbreviations: Rainfall: total rainfall from planting to harvesting; Δ SWS: difference in soil water storage in the 0–120 cm layer within growing season; ET: evapotranspiration. Values are given as means. Values followed by different letters within a column are significantly different ($P < 0.05$).

while larger plant individual tended to allocate more dry matter into grain (Fig. 4).

3.2. Grain yield, water use and yield formation in response to RFM treatments

RFM treatments significantly improved grain yield and crop water productivity (CWP), and lowered the evaporation amount across two growing seasons (Table 1). Compared with CK, RFMB and RFMT increased grain yield by 106.56% and 109.24% in 2015, and 101.51%, and 96.14% in 2016, respectively (Table 1). Grass straw mulching (RFMG) increased the yield by 32.68% and 30.45% in 2015 and 2016 respectively. Straw and plastic mulching significantly reduced the evaporation and improved CWP accordingly. The CWP_G was increased by 130%, 127.14% and 40.29% in 2015, and 114.29%, 111.11% and 34.92% in 2016 in RFMB, RFMT and RFMG. In addition, the CWP_A was enhanced by 83.07%, 80.09% and 35.35% in 2015, and 76.45%, 68.18% and 31.82% in 2016 in RFMB, RFMT and RFMG, respectively (Table 1).

There were no significant differences in bract weight, row number per ear, kernel weight per ear, and 100-grain weight per ear between two plastic mulching treatments (Table 2). However, the bract weight per ear in CK was the lowest, i.e. 11.58 g and 8.5 g in 2015 and 2016, respectively. The bract weight per ear was increased by 66.58%, 23.4% and 52.59% in 2015, and 58.2%, 58.59% and 16.71% in 2016 in RFMB, RFMT and RFMG, respectively. Moreover, row number per ear under CK was 13.02 and 12.96 in 2015 and 2016, respectively. It was increased on average by 36.94%, 42.63% and 23.96% in 2015, and 36.19%, 39.74% and 21.68% in 2016 in RFMB, RFMT and RFMG, respectively. The kernel weight per ear was 39.44 g and 35.47 g under CK. It was increased by 97.9%, 102%, 28.98% in 2015, and 99.77%, 94.78% and 29.49% in 2016 in RFMB, RFMT and RFMG, respectively (Table 2).

On the other hand, the 100-grain weight per ear was significantly increased by 21.4%, 27.41% and 15.06% in 2015, 16.9%, 19.76% and 8.49% in 2016 in RFMB, RFMT and RFMG compared with CK, respectively (Table 2). The kernel abortion was lowered by 40.75%, 39.69% and 5.25% in 2015, and 32.04%, 44.38% and 7.4% in 2016 in RFMB, RFMT and RFMG, respectively. The cob weight was also improved by 87.66%, 98.73% and 8.98% in 2015, and 101.44%, 100.19% and 24.06% in 2016 in RFMB, RFMT and RFMG respectively. The kernel number per ear was massively improved by 63.03%, 58.52% and 20.72% in 2015, and 70.84%, 62.62% and 19.32% in 2016 in RFMB, RFMT and RFMG, respectively. The bare tip length was decreased by 27.98%, 24.13% and 1.46% in 2015, and 15.4%, 31.84% and 2.59% in 2016 in RFMB, RFMT and RFMG respectively. As a result, the greatest yield

and above-ground biomass were achieved in RFMT in 2015, and in RFMB in 2016, respectively. The greatest CWP_G and CWP_A were recorded in RFMB across two growing seasons (Table 2). The minimum water consumption within growing season was observed in RFMB in 2015 and RFMT in 2016, respectively.

3.3. The relationship between metabolic rate (leaf biomass) and individual size under RFM

Leaf growth and its proportion with other typical organs were recorded in this study (Table 3). Two plastic mulching treatments significantly enhanced leaf area, compared with straw mulching and CK. No significant difference was observed between straw mulching and CK (Table 3). In addition, specific leaf area (flag) followed a similar situation as leaf area did among four treatments. The ratio of leaf to above-ground biomass varied from the treatments. The ratio ranked as CK > RFMG > RFMT > RFMB across two growing seasons (Table 3).

Mulching treatments changed the size-dependent allometric pattern ($\lg y = \alpha \lg x + \lg \beta$) in comparison with CK. The relationship between leaf biomass (y-axis) vs aboveground biomass (x-axis) followed a similar trend ($\alpha < 1$) among various treatments across two growing seasons, and the mulching treatments significantly declined the value of α ($P < 0.01$) (Table 4(a); Fig. 3). The lowest value of α was observed in the black plastic mulching treatment (RFMB) (i.e. 0.738 in 2015 and 0.804 in 2016, respectively), and the highest value of α was in CK (0.938 in 2015 and 0.912 in 2016, respectively). The α of RFMT was similar as that of RFMB in two growing seasons, and that of RFMG was in the middle. On the other hand, the intercepts among three mulching treatments were of no obvious change. It was noted that most data fell into the right side of crossing point between regression lines.

3.4. Size-dependent reproductive allocation under RFM

The allometric relationships of log (grain yield) vs log (aboveground biomass) and log (reproductive biomass) vs log (vegetative biomass) were compared (Table 4(b)–(c); Figs. 4 and 5). The allometric relationship between grain yield and aboveground biomass was typically size-dependent. There were generally two parameters to determine the changes in allometric scaling, i.e. the exponent α and the intercept. In the relationship between log (grain yield) and log (aboveground biomass), the intercept was -81.4 in 2015 and -72.8 in 2016 respectively, and it dropped down to below -130 in 2015 and -119 in 2016 in mulching treatments. The lowest values were found in RFMB and RFMT in two growing seasons. In the meantime, the α was generally signifi-

Table 2

Comparisons of yield components among the treatments in experimental site of Kenya over two growing seasons.

Year	Treatments	Bract weight (g)	Ear length (mm)	Bare tip length (cm)	Kernel abortion (%)	Ear diameter (mm)	Row number per ear	Cob weight (g)	Kernel number per ear	Kernel weight per ear (g)	100-grain weight (g)
2015	RFMB	19.29a	145.13 a	30.11b	20.75% b	28.52a	17.83a	20.68a	529.14a	78.05a	14.75a
	RFMT	18.32a	150.20 a	31.72b	21.12% b	29.25a	18.57a	21.90a	514.50a	79.67a	15.48a
	RFMG	14.29b	124.16 b	41.20a	33.18% b	16.86b	16.14b	12.01b	391.82b	50.87b	13.98b
	CK	11.58c	119.38c	41.81a	35.02% a	15.06b	13.02c	11.02b	324.57b	39.44c	12.15c
2016	RFMB	13.48a	145.12 a	35.60b	24.61% b	26.43a	17.65a	20.93a	525.27a	70.86a	13.49a
	RFMT	12.97a	142.40 a	28.68b	20.14% b	27.46a	18.11a	20.80a	500.00a	69.09a	13.82a
	RFMG	9.92b	122.26 b	40.99a	33.53% a	19.53b	15.77b	12.89b	366.85b	45.93b	12.52b
	CK	8.50c	116.20c	42.08a	36.21% a	11.04b	12.96c	10.39b	307.46b	35.47c	11.54c

Notes: Values are given as means. Values followed by different letters within a column are significantly different ($P < 0.05$).

Table 3

The comparison on biomass allocation pattern and yield-related components of field-grown maize in response to planting densities in two growing seasons.

Year	Treatments	Reproductive effort	Ratio of leaf to above-ground biomass	Leaf area (cm ²)	Specific leaf area of flag leaf (cm ² g ⁻¹)
2015	RFMB	0.323b	0.311d	5685.7a	184.9aa
	RFMT	0.327a	0.320c	5546.4a	189.4a
	RFMG	0.270c	0.344b	5328.1b	175.8b
	CK	0.268d	0.356a	5228.5b	170.7b
2016	RFMB	0.314b	0.292d	5595.2a	226.8a
	RFMT	0.323a	0.295c	5362.9a	221.6a
	RFMG	0.263c	0.318b	5025.8b	213.2b
	CK	0.258d	0.336a	4827.6b	184.9c

Notes: The values are given as means of three replications. The values followed by different letters within a column are significantly different ($P < 0.05$).**Table 4**

Allometric relationships between leaf mass (L), grain yield (G) and aboveground biomass (A), and between reproductive biomass (R) and vegetative biomass (V) in field-grown maize under contrasting planting pattern in two growing seasons.

Y	X	Year	Treatments	n	R2	P	Slope (95% CI)	Intercept (95% CI)
<i>(a) log (leaf mass) = a log (aboveground mass) + log β</i>								
L	A	2015	RFMB	60	0.967	0.001	0.738 ** c (0.704, 0.774)	-103.3 (-111.8, -94.7)
			RFMT	60	0.978	0.740 ** c (0.710, 0.770)	-102.5 (-109.5, -95.5)	
			RFMG	60	0.970	0.839 ** b (0.802, 0.878)	-93.0 (-100.1, -85.8)	
			CK	60	0.979	0.938 ** a (0.903, 0.974)	-85.4 (-90.7, -80.2)	
		2016	RFMB	60	0.957	0.002	0.804 ** c (0.762, 0.849)	-115.4 (-125.2, -105.6)
			RFMT	60	0.986	0.862 ** b (0.835, 0.888)	-121.1 (-126.7, -115.4)	
			RFMG	60	0.984	0.898 ** ab (0.869, 0.928)	-101.2 (-106.4, -96.0)	
			CK	60	0.977	0.912 ** a (0.877, 0.949)	-79.2 (-84.2, -74.2)	
<i>(b) log (grain yield) = a log (above-ground mass) + log β</i>								
G	A	2015	RFMB	60	0.971	0.001	1.056 * a (1.010, 1.105)	-177.4 (-188.9, -165.9)
			RFMT	60	0.974	1.071 ** a (1.027, 1.118)	-181.4 (-192.5, -170.3)	
			RFMG	60	0.967	0.973ns b (0.928, 1.021)	-132.0 (-140.8, -123.3)	
			CK	60	0.973	0.823 ** c (0.788, 0.859)	-81.4 (-86.6, -76.2)	
		2016	RFMB	60	0.966	0.001	1.100 ** a (1.049, 1.155)	-177.3 (-189.2, -165.3)
			RFMT	60	0.990	0.989ns b (0.963, 1.015)	-142.2 (-147.8, -136.6)	
			RFMG	60	0.983	0.945 ** c (0.914, 0.977)	-119.0 (-124.5, -113.4)	
			CK	60	0.971	0.788 ** d (0.754, 0.824)	-72.8 (-77.6, -68.0)	
<i>(c) log (reproductive biomass) = a log (vegetative biomass) + log β</i>								
R	V	2015	RFMB	60	0.886	0.001	11.9 ** b (10.9, 13.0)	-24.4 (-26.8, -22.1)
			RFMT	60	0.931	12.1 ** b (11.3, 13.0)	-25.0 (-26.8, -23.1)	
			RFMG	60	0.898	14.4 ** a (13.2, 15.7)	-29.1 (-31.7, -26.5)	
			CK	60	0.933	9.7 ** c (9.1, 10.4)	-18.1 (-19.4, -16.8)	
		2016	RFMB	60	0.878	0.001	11.0 ** b (10.1, 12.1)	-22.3 (-24.6, -20.1)
			RFMT	60	0.842	20.6 ** a (18.6, 22.9)	-42.6 (-47.3, -38.0)	
			RFMG	60	0.896	19.4 ** a (17.8, 21.1)	-39.2 (-42.6, -35.7)	
			CK	60	0.921	8.7 ** c (8.1, 9.4)	-16.0 (-17.3, -14.7)	

Notes: The values followed by different letters within a column are significantly different ($P < 0.05$). Slope is the allometric parameter, different from 1.0 at * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$ (ns, not significant).

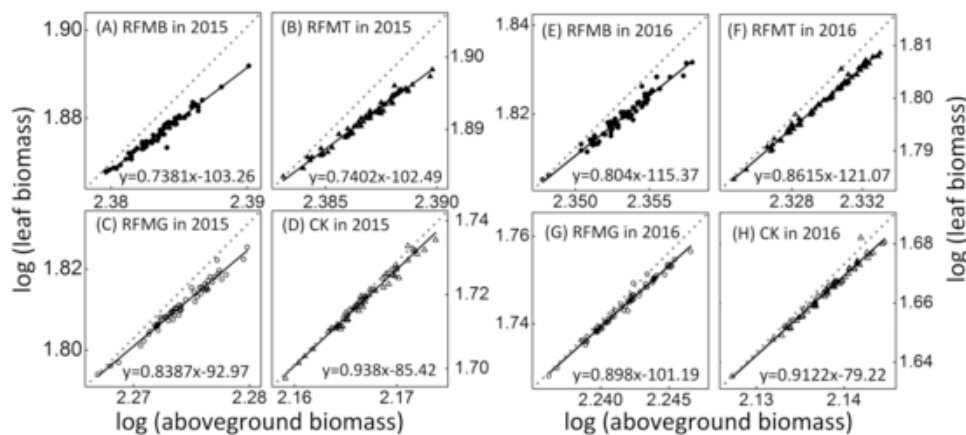


Fig. 3. Allometric relationship between the aboveground biomass and leaf biomass among various treatments in experimental site of Kenya over two years. Note: The dotted diagonal line indicates the aboveground biomass and leaf biomass allometric relationship of 1:1.

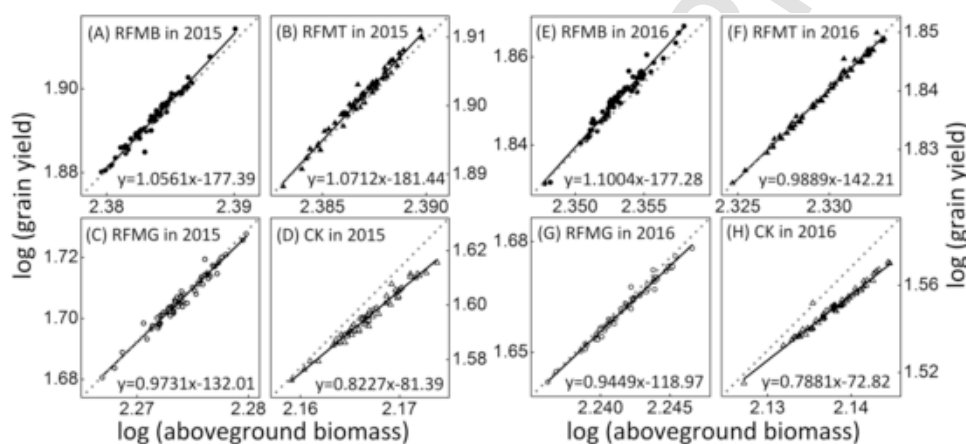


Fig. 4. Allometric relationship between the aboveground biomass and grain yield among various treatments in experimental site of Kenya over two years. Note: The dotted diagonal line indicates the aboveground biomass and grain yield allometric relationship of 1:1.

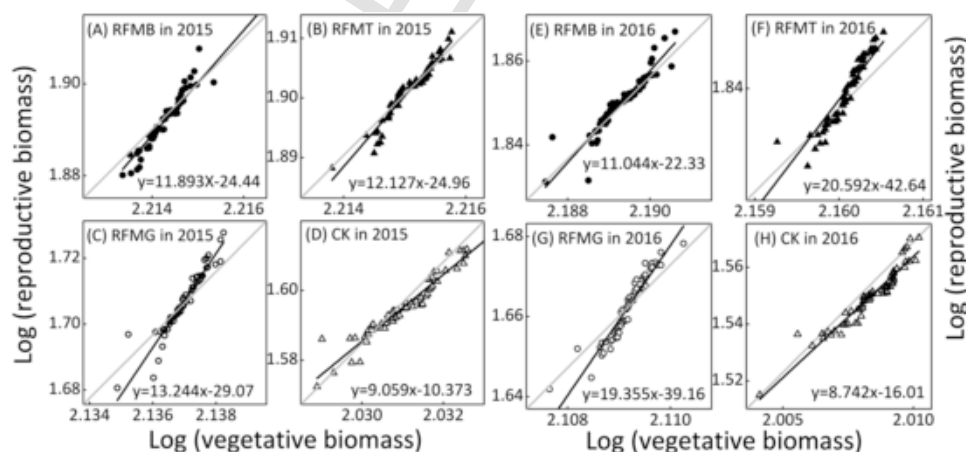


Fig. 5. Allometric relationship between the aboveground biomass and grain yield among various treatments in experimental site of Kenya over two years. Note: The dotted diagonal line indicates the vegetative biomass and reproductive biomass allometric relationship.

cantly more than the constant 1 in RFMB and RFMT in two growing seasons (Table 4(b); Fig. 4). In contrast, it was generally significantly less than 1 in RFMG and CK in two seasons, and the values of CK were the lowest. As aforementioned,

there was a crossing point between two regression lines which were drawn from CK and each treatment. It was noted that most data was allocated in the right side of crossing point, since the intercepts among the treatments were of pro-

nounced differences with each other. This trend suggested that plastic mulching treatments can distribute more photosynthetic products into reproductive growth in terms of a given individual size. Relatively, grass straw mulching and CK followed an opposite trend (Table 4(b); Fig. 4).

Finally, the allometric relationships between reproductive and vegetative (R-V) growth and the reproductive efforts in four treatments were compared (Table 4(c); Fig. 5). A general trend of reproductive effort (RE) was to increase orderly from CK to RFMB. The RE was 0.268 in 2015 and 0.258 in 2016 respectively, and increased to 0.27 in 2015 and 0.263 in 2016 in grass straw mulching respectively. The greatest values of RE were found in RFMB and RFMT, ranging from 0.314 to 0.327 across two growing seasons (Table 3). This outcome was similar as the trend of size-dependent reproductive allocation (see the above). It was also supported by the R-V relationship (Fig. 5). The slope of R-V regression equation was the lowest in CK, only 9.7 in 2015 and 8.7 in 2016 respectively. It ranged from 11 to 20 in three mulching treatments across two growing seasons (Table 4(c); Fig. 5). In relatively hot and wet 2015, the slope was 11.9 in RFMB, 12.1 in RFMT and 14.4 in RFMG respectively. In relatively cool and dry 2016, it reached up to 11.0 in RFMB, 20.6 in RFMT and 19.4 in RFMG respectively (Table 4(c)).

4. Discussion

In semiarid rainfed environment, the RFMs substantially improved soil water availability. Rainfall can be harvested and transformed into the runoff on the ridge surface. Thereafter, the runoff would be collected in the furrow and then stored in the root-zone soils. In this case, crop water consumption mode was changed accordingly. The evaporation would be reduced in the early growth period, while the transpiration was increased in the late growth period, since deep soil water can be transferred to the upper soil layer for better absorption by crops. The improvement on soil water availability provided a solid basis for the increased accumulation of dry matter and crop water productivity under RFMs. Despite overall increase in aboveground production, the dry matter allocation into different functional organs (i.e., leaves, stem, and grain, etc.) is of significant importance. Metabolic scaling theory provided a powerful tool to analyze energy distribution and metabolic efficiency in rainfed crop production.

Allometric relationship is considered as an adaptive strategy in the life history of higher plant (Stearns, 1992; Weiss, 1999). Crop would modify to adapt to changes of environment. Due to RFM system's improvement on micro-ecological environment, especially the growth environment of roots, the soil microorganism diversity and activity can be improved massively (Li et al., 2004), which help provide suitable soil temperature and nutrition for crop growth. In present study, the application of RFM significantly improved the hydrological (Table 1) and thermal conditions (

Fig. 2), and accordingly modified the allometric relationship. Under RFM farming pattern, crop grew more robust with enough moisture, nutrient and suitable temperature around roots in soil (Li et al., 2004; Chai et al., 2014). At the same time, leaves as assimilation organs whose photosynthetic function would become stronger. Leaf is a critical organ to perform the photosynthetic carbon assimilation, and leaf biomass can be used as a physiological indicator to reflect metabolic rate in higher plant. Those physiological and biochemical response enabled the RFMB, RFMT treatments to reduce slope value (Table 3), increase intercept value in the allometry equation between leaf biomass and aboveground biomass (Fig. 3). It suggested that under the same size of aboveground biomass condition, RFMB and RFMT allocated less energy and biomass to leaves. To say, fewer leaves can provide the energy or biomass to meet the demand required by whole plant growth. In the same way, RFMB and RFMT allocated more energy or biomass to grain yield in allometric relationship between grain and aboveground biomass (Table 4). According to Fig. 3 and Table 3, the results indicated that more photosynthetic products would be allocated in leaves under a given biomass increase in aboveground part in CK. To say, less energy would be fixed in leaves under the same condition in mulching treatments, particularly in RFMB and RFMT. In control group (CK), more photosynthetic assimilation products were stored in leaves, the other organs, particularly reproductive organs acquired fewer products. The opposite outcome was observed in mulching treatments. This would benefit the improvements on grain yield and CWP.

Another explanation is that crops with the same aboveground biomass can produce more grain yield in RFM treatments (Fig. 4). As is well recognized, allometric growth is closely associated with body size, which is bound to change the allometry of leaf vs aboveground biomass, as well as grain yield vs aboveground biomass (Weiner and Thomas, 1992). Allometric protocol is a standardized tool to quantify size-dependent eco-physiological process, particularly including biomass partitioning and ontogenesis (Qin et al., 2013). Due to the improvement of moisture and temperature conditions, individuals would grow larger in the RFM treatments, thus optimizing life history strategy and allocating more biomass or energy to reproductive organs. This would ultimately obtain better fitness (Weiner et al., 2009). This mechanism can be illuminated from the modification in the slope of R-V relationship which was caused by the variation of altitude and nutrient status in the living environment of plants (Guo et al., 2012; Wang et al., 2016).

We first employed the principles of classic ecology to elucidate water productivity and yield formation in the RFM system. The yield formation and water use can be mechanically explained by allometric relationship between leaf biomass and body size, since its allometric exponent (<1) was decreased under the RFM condition. In this

case, relatively less energy was allocated in leaves. Also, allometric relationship between grain yield and body size provided supporting evidence for the above phenomenon, since its allometric exponent was increased in the RFM system, and relatively more energy was transferred to reproductive organs. In conclusion, the RFM application significantly improved soil water availability and thereby boosted yield and CWP_G in semiarid Kenya.

5. Conclusions

Crops produce biomass and then allocate some of it to reproductive organs. Allometric protocols have become a standardized tool to quantify the characteristics of reproductive allocation and water use. In the present study, micro-field rainwater-harvesting system (MFRHs) substantially improved soil water storage and soil temperature in rain-fed maize fields. With the improvement on soil hydro-thermal status, grain yield and CWP can be increased massively. Under MFRHs, the allometric relationships between leaf mass vs body size and seed mass vs body size were modified, so as to allocate more mass or energy to grain filling. For the first time, we explained why the RFM system can improve grain yield at the population level using the allometric scaling theory (i.e. metabolic theory) in ecology. In the allometry relationship between leaf biomass (i.e. metabolic rate) and body size, the slope was significantly less than 1 regardless of treatments, while the slopes in RFM treatments were increased. In the allometric relationship between grain biomass and body size, the slope was significantly less than 1 across all treatments, while it was reduced in RFM treatments. This phenomenon demonstrated that in RFM farming system, more energy or mass would be shifted into grain yield, and accordingly less energy or mass into leaves. It also suggested that as a result of RFM application, the functional trait of leaves would become more powerful, and accordingly the same-size leaves can support or supply larger individual body. According to principle of size-dependence metabolic theory, individual maize body should grow larger under the conditions of RFM application. Therefore, it can be argued that RFM farming system can modify the allometric exponent, and then optimize energy allocation strategy for improving production and water use efficiency. The findings would help further enhance the insight into the adaptability and feasibility of RFM farming system.

Uncited reference

CRediT authorship contribution statement

Xiao-Feng Zhang: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing - original draft, Writing - review & editing. **Chong-Liang Luo:** Data curation, Investigation, Software, Formal analysis, Methodology, Visualization. **Hong-Xu Ren:** Resources. **David Mburu:** Re-

sources, Writing - review & editing. **Bao-Zhong Wang:** Investigation. **Levis Kavagi:** Writing - review & editing. **Kiprotich Wesley:** Investigation. **Aggrey Bernard Nyende:** Resources, Writing - review & editing. **You-Cai Xiong:** Writing - review & editing, Conceptualization, Formal analysis, Funding acquisition, Project administration, Resources, Supervision, Validation, Writing-original draft, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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