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Nursery Water Supply and Biomass Accumulation Relationships in Super Sweet Maize (*sh2***)**

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Authors' contributions

This work was carried out in collaboration between all authors. All authors read and approved the final manuscript.

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ABSTRACT

An agricultural intensification with maize transplanted crops for increasing food production is needed. However, super sweet maize water management during nursery has been designed from old genotypes in the 90´s decade, which indicate that a water stress during nursery did not change plant growth. The aim of this work was to determine the effects of the watering regime during nursery on biomass accumulation for three different super sweet *sh2* maize hybrids to test the hypothesis that a different nursery water supply driven pre- and post-transplant super sweet maize biomass accumulation. Our results from seedlings watered with 100%, 75% or 50% daily evaporation are not in agreement with this previous report and showed that a water stress during nursery would be considered as a limiting source to decrease maize early biomass accumulation. A very early water stress during nursery decrease early post-transplant biomass accumulation, leaf area expansion and change photo assimilates partitioning. These results would force to a change in the commonly accepted water management when a transplant routine from plug trays was used for improving agricultural intensification.

Keywords: Growth; transplant; water management.

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1. INTRODUCTION

Sweet corn (*Zea mays saccharata*), considered a vegetable, is a special type of corn destined exclusively for human consumption, in fresh form or in processed foods. As the demands for food increase in coming decades, society will be pressed to increase agricultural production by increasing yields on already cultivated lands, by cultivating currently natural areas or to change current crop consumption patterns. For the future, a strong increase in food demand is expected, which may be fulfilled by further agricultural intensification rather than expansion of agricultural area [1,2,3], especially because climate change can affect both crop yield and the land area suitable for agriculture [4].

Because transplanting provides optimal environmental conditions for seed germination, sweet corn has been transplanted experimentally in an attempt to improve stands and hasten maturity [5,6]. The growing period was significantly shortened with transplantation of sweet corn plants compared to direct seeded [7], although growth and development at early growth stages could become of critical importance for final yield [8]. On the other hand, Orgaz et al. [9] indicate that canopy development and management of some greenhouse horticultural crops is quite different from that of outdoors.

Drought stress is a major cause of yield instability in crops across diverse eco-geographic regions worldwide. In the scenario of global warming, drought is indeed considered to be one of the most important abiotic stresses that adversely affect food security [10]. Limited water supply to roots and/or higher transpiration rate due to elevated atmospheric temperature induces drought stress [11], which severely impairs growth and yield [12].

Maize has been reported in the literature as having high irrigation requirements; a frequent and uniform supply of water is extremely important for maize yield to meet the water requirements of plants [13]. In this way, Oktem et al. [14,15] showed that water applied as 100, 90, 80 and 70% of evaporation, decreased yield. Their results indicate that a 2-day irrigation frequency, with 100% evapotranspiration water application by a drip system, would be optimal for sweet corn grown in semi-arid regions. Seasonal dependence of biomass production on transpiration and linear relationships between

relative yield and relative evapotranspiration has been previously found as well [16].

When plants do not receive sufficient water, plant growth is negatively affected [17]. Previous modeling studies indicated that changes in root architecture and water acquisition capacity directly affect biomass accumulation and yield increases [18]. The spatial configuration of root systems is an important factor determining belowground resource acquisition. Campos et al. [19] attributed the differences in water uptake between old and modern maize hybrids to differences in root depth and root density. Under water-limited situations, they observed that the old hybrid took up more water from shallow soil depth, whereas the new hybrid appeared to be more effective in acquiring water from the deeper soil layers. Plants growing in soil with less water, can survive the condition either by escape or by resistance. The resistance can be by two means, drought avoidance (maintenance of tissue water potential) and drought tolerance [20]. Recently, Rattin et al. [21] showed a close coordination between roots and shoot growth.

Moisture management, or watering, accounts for the greatest loss in plug vegetable production and adversely affects plug crops. Because water is essential in plants for many processes, plugs must never be allowed to dry completely. The smaller the cell size (or higher plant relative growth rate), the more vulnerable the plug is to fluctuations in moisture. According to Styer and Koransky's suggestions [22] for the best both root and shoot growth, in Stage 1 (sowing to radicle emergence), most crops require uniformly high moisture levels. Once radicle emergence occurs, the moisture levels would be reduced for many crops (Stage 2); by allowing the soil surface to dry out slightly, the roots will tend to go down into the media. Once crops enter Stage 3 (full leaves expansion), leaves and roots are actively growing. The alternating wet/dry pattern increases in depth with advancing growth stages. However, Water et al. [23] using old shrunken-*2* (*sh2*) and sugary (*su*) sweet corn hybrids mutants showed no impact on plant growth and development related to moisture during nursery.

The aim of this work was to determine the effects of the watering regime during nursery on biomass accumulation for three different super sweet *sh2* maize hybrids to test the hypothesis that a different nursery water supply driven preand post-transplant super sweet maize biomass accumulation.

2. MATERIALS AND METHODS

2.1 Plant Material and Experiments

Two experiments were performed:

2.1.1 Experiment 1: solute leakage

Three maize super sweet hybrids (*sh2*) ('Butter', '1441' and '3475') with yields ranging between 15 to 17 ton ha⁻¹ were provided by Semillería Basso (Argentina). For the experiment, four replications of 100 seeds from each maize hybrid were immersed in 1,000 cm³-distilled water for 96 hours and water volume was kept during all the time.

2.1.2 Experiment 2: plug and pot responses

A greenhouse experiment was carried out at the Faculty of Agronomy, University of Buenos Aires, Argentina (34° 35' 59''S, 58° 22' 23''W) between October and November 2017.

Three super sweet maize hybrids (*sh2*) ('Butter', '1441' and '3475') seeds were sown in plastic plug trays (128 cells tray⁻¹; 17.37 cm³ cell⁻¹) using a commercial growing media (Klasmann 411® medium, Klasmann-Deilmann, GmbH, Germany). Daily water irrigation makes up for 100%, 75% or 50% evapotranspiration. Seed emergence (%) was recorded five days from sowing.

At the transplant stage (15 days from sowing), seedlings were kept in 5-litre pots filled with a *Sphagnum maguellanicum*-river wasteperlite (40-40-20, v/v/v) medium [24]. The plants were arranged at a density of 4 plants $m⁻²$, which avoided mutual shading. A weekly fertiirrigation of 1.0: 0.5: 1.0: 0.5 (v/v/v/v) N: P: K: Ca (nitric acid, phosphorus acid, potassium nitrate, and calcium nitrate) (150 mg L^{-1} N) was included through to the overhead irrigation water.

Half hourly averages of the air temperature were measured using a HOBO H08-001-02 data logger (Onset Computer Corporation, MA, USA) protected from direct radiation by aluminum foil shades. Minimum temperature, maximum temperature and mean global solar radiation during the experiment were 25.11°C, 28.31°C and 25.60 MJ m^{-2} day⁻¹ respectively.

2.2 Growth Evaluations

For experiment 1, solute leakage was estimated as electrical conductivity (dS $m⁻¹$) changes during the first 96 hours.

Seedling emergence rates (SER) is calculating by dividing the number of normal seedlings per each 128 -plug cell tray⁻¹ obtained by each counting in the seedling emergence by the number of days until true leaf expansion. The values obtained at each count are then summed at the end of emergence period to obtain SER according to the method adapted from Maguire [25].

For experiment 2, plants for destructive measurements were harvested (five per treatment and block) at emergence and at 7-day intervals during the experiment. Roots were washed and root, stem, leaf and petioles fresh weights (FW) were recorded. Dry weights (DW) were recorded after drying roots, stems, leaves and petioles to constant weight at 80°C for 96 hours. The number of leaves was recorded and each leaf area was determined using a leaf area meter LI-COR FL16 (LI-COR Inc., Lincoln, NE, USA)

The rate of leaf area expansion (RLAE) was calculated as the slope of the regression of the natural logarithm of total leaf area versus time (in days). The rate of leaf appearance (RLA) was calculated as the slope of the number of fully expanded leaves versus time (in weeks). The relative growth rate (RGR) was calculated as the slope of the regression of the natural logarithm of the whole plant on a DW basis versus time (in days).

The mean net assimilation rate (NAR), and the leaf area ratio (LAR) were calculated as follows:

$$
NAR = \frac{k_w W_0 e^{k_w t}}{A_0 e^{k_a t}}
$$

$$
LAR = k_a / \frac{A_a e^{k_a t}}{k_w W_0 e^{k_w t}}
$$

where: k_w : RGR (days⁻¹); W_0 : extrapolated value of total dry weight at time zero (g); A_0 : extrapolated value of leaf area at time zero

(cm²); k_a : RLAE (days⁻¹); t: time (in days) at the midpoint of the experimental period and e: base of natural logarithms.

The specific leaf area on a FW basis (SLA) was calculated as the ratio between the area of the new individual leaf and leaf FW.

The allometric coefficients between root and shoot fraction were calculated as the slope (**β**) of the straight-line regression of the natural logarithm of the root DW versus the natural logarithm of the shoot DW. On the other hand, the **β** allometric coefficients between leaf blades + petioles and the stems were calculated as the natural logarithm of the leaf blade + petiole DW versus the natural logarithm of the stem DW.

2.3 Statistical Analysis

We used a complete aleatory design for both experiments. Data were subjected to one-way analysis of variance for experiment 1 and to twoway analysis of variance for experiment 2. Means were separated by Tukey's test (P < 0.05) and STATISTICA 8 (StatSoft) software was

used. Slopes from straight-line regressions of RLA, RLAE, RGR, NAR, LAR and allometric values were tested using the SMATR package [26].

3. RESULTS

Solute leakage (experiment 1), estimated through the changes in electrical conductivity increase during the first 96 hours of imbibition in distilled water with significant differences between the three sweet maize hybrids tested (Fig. 1).

Seedling emergence (%) was higher in plants fully watered with no significant differences between 75% and 50% evapotranspiration rate for the three maize hybrids tested (Fig. 2). For 'Batter' and '1441' hybrids, the seedling emergence rate (SER) (seeds day⁻¹) was significantly higher between 100% water supply and the rest of the watering treatments. However, '3475' maize hybrid showed no SER differences for the two higher water supply (Fig. 2). Both seedling emergence and SER differences between maize hybrids tested were found as well.

Fig. 1. Changes in solute leakage during the first 96 hours of the imbibition period in three maize F1 hybrids ('Batter', '1441' and '3475') seeds

Fig. 2. Seedling emergence (%) for three super sweet maize mutants under three water supply levels (100%, 75% and 50% evapotranspiration rate) (n = 4). Lower case letters indicate statistically significant differences (*P* **< .05) among water supply level for each sweet maize hybrid tested. SER (seeds day-1) is indicated as well**

At the transplant stage, the higher water supply the higher fresh weight for 'Batter' and '3475' maize mutant hybrids. The accumulated '1441' mutant fresh weight showed no significant differences between plants watered with 75% and 50% of daily evapotranspiration (Fig. 3).

A decrease in root: shoot ratio on a dry weight base from transplant and four weeks later with no significant differences between water supply regimes or sweet maize hybrid tested were found. Anyway, at the transplant stage, seedlings watered with 100% evapotranspiration gave the higher root:shoot ratios (Fig. 4).

 0100% 0.75% 0.50%

Fig. 4. Changes in root: shoot dry weight ratio during the experiment for three super sweet maize mutants (A: Butter; B: 1441 and C: 3475) grown under three water supply levels (100%, 75% and 50% evapotranspiration rate) (n = 4)

At the transplant stage, there are no significant differences in shoot dry weight in plants watered to compensate evapotranspiration in different degree but the higher water supply the higher root dry weight (Fig. 5).

A linear increase between LMA during the experiment was found for the three maize hybrid mutants tested with no significant differences neither between them nor straight-line regression slopes of the watering routines (Fig. 6).

There is no significant differences in total leaf area at the end of experiment 2; this is when plants 100% watered have expanded near five leaves ($V₅$ stage). However, a decrease in water supply to compensate 75% daily evapotranspiration give a decrease in '1441' total leaf area but no changes in both 'Batter' and '3475' maize hybrid mutants. A strong decrease in water supply of 50% daily evapotranspiration significantly decreased total leaf area in 'Batter' and '1441' but no in '3475' maize hybrids (Fig. 7).

A decrease in water supply during nursery decrease RLA and RLAE and increase SLA in 'Butter' and '1441' maize mutant hybrids. However, there is no significant changes in these growth parameters values for '3475' hybrid (Table 1).

Fig. 5. Changes in both shoots and roots dry weight ratio at the transplant stage for three super sweet maize mutants (A: Butter; B: 1441 and C: 3475) grown under three water supply levels (100%, 75% and 50% evapotranspiration rate) (n = 4)

Table 1. Changes in the rate of leaf appearance (RLA), the rate of leaf area expansion (RLAE) and the specific leaf area (SLA) for three super sweet maize grown under three water supply levels (100%, 75% and 50% evapotranspiration rate, ET) (n = 4). Lower case letters indicate statistically significant differences (*P* **< .05) among water supply level for each sweet maize hybrid tested**

Fig. 6. Changes in leaf dry mass per unit leaf area (LMA) during the experiment for three super sweet maize mutants (A: Butter; B: 1441 and C: 3475) grown under three water supply levels (100%, 75% and 50% evapotranspiration rate) (n = 4)

Both 'Butter' and '1441' maize hybrids decreased RGR and NAR when water supply decreased from 100% daily evapotranspiration, without changes in '3475'. These results would be explained by increases in NAR and minor changes in LAR (Table 2).

When plotting the data from all treatments, we found a close direct relationship ($r^2 = 0.672$) between RGR and NAR and a weak direct relationship between RGR and LAR (r^2 = 0.479) (Fig. 8). Nevertheless, plants watered to compensate 100% evapotranspiration showed higher both NAR and LAR values.

The lower water supply the higher root: shoot and stem: leaves allometries for all maize mutant hybrids tested (Table 3).

Positive relationships between RLAE $(r^2 = 0.672)$ P < .001) (Fig. 9A), RGR (r^2 = 0.611 P < .001) (Fig. 9B) and NAR $(r^2 = 0.608 \text{ P} < .001)$ (Fig. 9C) and root DW were found. The higher values were those from plants grown with the higher water supply during nursery.

Fig. 7. Changes in leaf area during the experiment for three super sweet maize mutants (A: Butter; B: 1441 and C: 3475) grown under three water supply levels (100%, 75% and 50% evapotranspiration rate) (n = 4). Vertical lines indicate least significant differences (LSD)

Fig. 8. The net assimilation rate (NAR) (empty symbols) and the leaf area ratio (LAR) (full symbols) related to the relative growth rate (RGR). The straight-line regressions were NAR = 63.20 RGR + 3.46 (r^2 = 0.672 P < .001) and LAR = 270.71 RGR + 74.28 (r^2 = 0.479 P < .01). (n = 4). **Water supply: 100%: , 75%:○ and 50%: □**

Table 3. Changes in allometric relationships between roots and shoots and between stem and leaves for three super sweet maize grown under three water supply levels (100%, 75% and 50% evapotranspiration rate, ET) (n = 4). Lower case letters indicate statistically significant differences (*P* **< .05) among water supply level for each sweet maize hybrid tested**

Water supply (% ET)	Root: shoot	Stems: leaves
	ß	ß
'Butter'		
100	0.529^{b}	0.875^{b}
75	0.587 ^a	0.889^{a}
$50\,$	0.591 ^a	0.885^{a}
'1441'		
100	0.566 ^c	0.841 ^c
75	0.594^{b}	0.867^{b}
50	0.648 ^a	0.957 ^a
'3475'		
100	0.521 ^c	0.918 ^c
75	0.582^{b}	0.971^{b}
50	0.653^{a}	1.004 ^a

4. DISCUSSION

Low field emergence and early field vigor are major problems in *sh2* maize. The reduced field emergence is due to lower levels of storage carbohydrate and pathogenic infection that thrive on electrolytes leaching out through fractures in the pericarp [27,28]. Sweet maize hybrids with the highest levels of emergence and marketable yield tended to have lower levels of soluble solids [29]. Seed vigor is defined as those properties that determine the potential for rapid, uniform emergence, and the development of normal seedlings under a wide range of field conditions [30]. The anion leakage of isolated embryos correlated closely to seed vigor, but sugar leakage was not closely related to total soluble sugar content of seeds. Electrical conductivity measurements of seed leachates are routinely used to determine seed vigor [31]. Results from Fig. 1 showed significant solute leakage differences between the three sweet

Fig. 9. Relationship between RLAE (A), RGR (B), NAR (C) and root dry weight for three super sweet maize grown under three water supply levels (100%, 75% and 50% evapotranspiration rate) (n = 4). The straight-line regressions were RLAE = 0.0084 root DW + 0.119 (r² = 0.672 P < .001), RGR = 0.011 root DW + 0.104 (r² = 0.611 P < .001), NAR = 0.92 root DW + 9.40 (r² = 0.608 P **< .001) (n = 4). Water supply: 100%: , 75%:○ and 50%: □**

maize hybrids tested, which are in agreement with results from Cardoso et al. [32] who showed that there is genetic variability in traits such as pericarp thickness. On the other hand, Fig. 2 did not show both low seedling emergence and a clear leachate losses and seedling emergence relationships.

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Although a major goal of *sh2* maize-breeding programs is an increase in field emergence [33], transplant routine has shown an alternative to reach better field emergence [34]. When a dry seed is water imbibed, the uptake of water occurs in three stages. Stage I give a rapid initial water uptake due to the seed´s low water potential. During this phase, proteins are synthesized using existing mRNA and DNA and mitochondria are repaired. In stage II, there is a slow increase in seed water content, but physiological activities associated with germination are initiated, including synthesis of proteins by translation of new mRNAs and synthesis of new mitochondria. There is a rapid uptake of water in stage III where the process of germination is completed culminating in radicle emergence [35]. In our experiments, the effect of a decrease in water supply on seed vigor status of three super sweet corn hybrids was examined by standard seedling emergence percentage and seedling emergence rate. The lower water supply during nursery, the lower both seedling emergence percentage and SER; differences

between sweet maize hybrids were found as well (Fig. 2).

Working with old *sh2* and *su* sweet corn hybrids, Waters et al. [23] showed that seed moisture had no impact on plant growth and development. Our results are not in agreement with this previous report. Data from Fig. 3 showed the higher water supply during nursery, the higher the fresh weight in super sweet *sh2* maize plants sowed and grown in plug cell tray under the best greenhouse environmental facilities. In field adult plants, generally, when water availability is limited, the root: shoot ratio of plants increases because roots are less sensitive than shoots to growth inhibition by low water potentials [36], however, an inverse response was found in seedlings grown in cell plug trays at the transplant stage. When dry weight data were plotted against time (Fig. 4), we found significant differences in the root: shoot ratio at the transplant stage, which decreased during the first four post-transplant weeks to pots. Significant differences between water supply treatments disappeared after transplant as well. A more detailed analysis of the dry weight differences at the transplant stage showed that they were the result of higher root dry weight accumulation in those seedlings 100% watered with no significant differences in shoot dry weight (Fig. 5). In agreement with Ahmed et al. [37], the growth of maize root system is regulated by its endogenous genetic program, but also by interactions with the soil and changing environmental conditions.

Leaf dry mass per unit leaf area (LMA) was introduced as a concept in the analysis of plant growth and defined at the plant level as the total leaf dry mass divided by the total leaf area. LMA is used in crop simulation models to predict leaf area from leaf dry mass. In this way, Drouet et al. [38] showed that LMA increased about two-fold during the first 37 days after sowing in maize plants; similar increments for the sweet *sh2* maize hybrids tested in our experiments were found (Fig. 6) and let to explain the decrease in the root: shoot ratios previously discussed (Fig. 4). Although LMA has been considered either as a constant for the whole growth cycle, as a function of the plant development stage and it has been correlated with variables as diverse as net photosynthesis, relative growth rate, leaf structure and yield [38], our results are not in agreement because LMA increased during our experiment (Fig. 6).

The susceptibility of plants to drought stress varies in dependence of stress degree, different accompanying stress factors, plant species, and their developmental stages [39]. Water deficit stress is more vulnerable at the germination and early seedling growth stages of plants [12]. Identifying corn hybrids with faster rates of seedling emergence and leaf appearance may allow development of a corn crop that achieves earlier canopy closure and better seasonal light interception. Water deficits reduce the number of leaves per plant and individual leaf size by decreasing the soil's water potential. Leaf area expansion depends on leaf turgor, temperature, and assimilating supply for growth. Our data showed that during nursery and four weeks posttransplant, the higher water supply the higher total leaf area (Fig. 7) but with significant differences in response to the three sweet maize hybrids tested. Results can be explained by higher as RLA as RLAE growth parameters (Table 1).

A common adverse effect of water stress on crop plants is the decrease in fresh and dry biomass production. Kamara et al. [40] revealed that water deficit imposed at various developmental stages of maize reduced total biomass accumulation at silking by 37%, at grain-filling period by 34% and at maturity by 21%. In the same way, Anjum et al. [10] indicated that drought stress in maize led to considerable decline in net photosynthesis (33.22%), transpiration rate (37.84%), stomatal conductance (25.54%), water use efficiency (50.87%), intrinsic water use efficiency (11.58%) and intercellular $CO₂$ (5.86%) as compared to well water control. In agreement, our results showed a fresh and dry weight decrease of 19- 36% and 13-28% respectively at the transplant stage when water supply decrease from 100% to 50% daily evaporation (from Figs. 3 and 5). During the last four weeks, post-transplant dry weight differences were maintained and a decrease in RGR was found (Table 2). In previous reports [41,42,43] changes in RGR were associated exclusively with NAR changes. However, Fig. 8 showed RGR as the result of additive positive effects of NAR and LAR.

Water deficit stress has a profound adverse effect on photosynthesis, photosynthetic apparatus, and pigment content in adult field maize crops [44]. As a result, a considerable decline in net photosynthesis has been reported in drought-stressed maize in contrast to wellwatered control plants [10,12]. The same

response during nursery and early posttransplant in our experiment because NAR (the "photosynthetic" component of RGR) was higher in full watered plants (Table 2). On the other hand, the decrease in SLA in plants fully watered is an advice of higher leaf thickness (a morphological trait related to higher photosynthetic rate).

A water stress alters biomass allocation to shoots and roots or by changing the metabolic activities in these organs. According to the theory of functional balance, plants increase the allocation of biomass to shoots if limited resources aboveground affect carbon gain, such as light and $CO₂$. Similarly, plants increase biomass allocation to roots in the presence of low levels of belowground resources, such as water and nutrients [45]. Allometries from Table 3 showed that a full water supply during nursery, redirect photo assimilate partitioning from shoots and particularly to stems during at least four post-transplant weeks.

Maize yield was positively correlated in field adult plants with total root number and the ratio of root mass below 20 cm to total root mass [18], while Rattin et al. [21] showed a close coordination between roots and shoot growth as well. Longdistance signaling between the root and shoot is intrinsic to the control of plant growth and development, and its response to environmental perturbations. With respect to plant water use and control of plant water relationships, Vandeleur et al. [46] currently know more about root-to-shoot signaling because of the important role of root-derived signals in informing the shoot of changes in soil water content. Although emerging evidence suggests that there may be a requirement for shoot water demand to be communicated to roots, to allow root water uptake to fulfil the shoots requirements [47], shoot-to-root signals have been investigated only rarely in respect to plant water relations [48,49]. Our results showed positive relationships between RLAE (Fig. 9A), RGR (Fig. 9B), NAR (Fig. 9C) and root dry weight during the early post-transplant growth with the higher values from plants grown with the higher water supply during nursery.

Cramer et al. [50] defined abiotic stress as an environmental condition that reduces growth and yield below optimal levels. Puig et al. [51] and Chen et al. [52] concluded that plants can sense the volume of the rooting space available, and a limited number of studies on individual roots

have shown that plant roots may sense the identity of neighboring roots and respond accordingly [53,54]. Our results showed that a water stress during nursery would be considered as a limiting source to decrease maize early biomass accumulation and, presumably, plant yield. However, the validation of this hypothesis goes beyond the present experimental design and is the matter of further experiments.

5. CONCLUSIONS

Contrary to previous reports, our results showed that a water stress during nursery decrease seedling emergence and may be avoided during nursery for plants sown in plug trays. On the other hand, a very early water stress during nursery decrease early post-transplant biomass accumulation, leaf area expansion and change photo assimilates partitioning. These results would force to a change in the commonly accepted water management when a transplant routine from plug trays was used for improving agricultural intensification.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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