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Effect of leaf thinning on shoot growth and tuber yield of white Guinea yam

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ABSTRACT

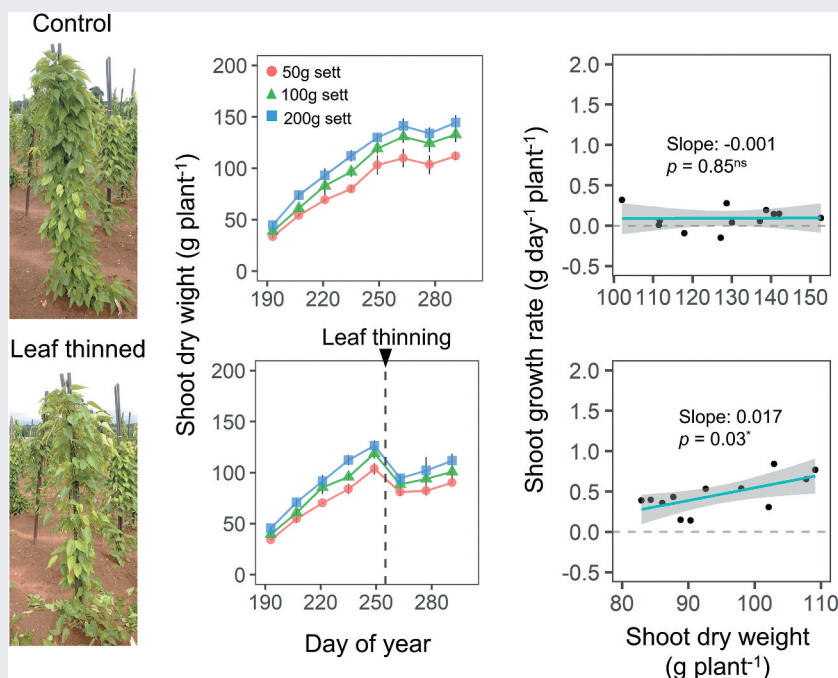
Mutual leaf shading can inhibit the growth of yam, reducing tuber yield. To improve light utilization, approximately 25% of leaves in a plant were thinned during the period of maximum shoot growth. Shoot dry weight was estimated every two weeks using a non-destructive method. Leaf thinning caused higher shoot growth rates (SGRs) after thinning, while control plants had SGRs close to zero. The higher SGRs in the thinned plants was attributed to an increase in new leaf development. This indicates that the plateau in shoot growth commonly observed during the late growth period is reversible and could be improved artificially. In thinned plants, there was a positive relationship between shoot dry weight and SGR, although no such relationship was observed in control plants after the middle growth period. This positive correlation indicates a higher shoot growth per unit leaf area in the thinned plants than in the control plants, presumably due to improved light utilization and a higher photosynthetic rate of new leaves. However, leaf thinning reduced tuber yields, presumably because of a lower total carbon assimilation per plant and greater growth competition between shoots and tubers. High correlations between shoot dry weight and tuber yield indicated that a high shoot biomass is more important than improving light utilization for increased tuber yields.

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growth; tuber yield



Introduction

Yams are a staple tuber crop widely cultivated in the Guinea savanna climate zone, West Africa, where yams contribute 10%–20% of the average dietary energy

requirement (FAOSTAT, 2020). White Guinea yam (*Dioscorea rotundata*) is indigenous to West Africa and is the most important yam species in terms of

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Supplemental data for this article can be accessed [here](#).

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production in this region (Darkwa et al., 2020). Yam production in West Africa has doubled in the last 30 years to meet the demand of a growing population, but the average yield per unit area has not changed for decades (FAOSTAT, 2020). This is partly due to poor land-use efficiency due to the long cultivation time (from planting to harvest) and a low planting density under the traditional mount cultivation. In addition, there is competition between the use of tubers as either food or planting material, with seed yams representing up to 30% of the harvest, further reducing edible yam yield (Agbarevo, 2014).

In our previous study, the use of small cuttings of tubers (setts) for cultivation of edible yam was tested to reduce the amount of seed tuber required (Iseki & Matsumoto, 2020). The results indicated that even a small sett size of 50 g could yield marketable tubers that were larger than 1 kg when the plant had enough shoot biomass at the early growth stage under staking and ridge cultivation. The adoption of staking and ridge cultivation instead of the generally employed non-staking and mount cultivation enabled higher plant density and improved land-use efficiency. However, the results also showed that tuber yield did not significantly differ among the sett sizes, although the plants from larger setts had larger plant biomass in early growth periods (Iseki & Matsumoto, 2020). This was because of the lower shoot growth rate of plants from larger setts during middle and late growth periods, which diminished the advantages of larger shoot biomass in early growth periods. These results indicate that tuber yield could be further increased by improving the shoot growth in the middle and late growth periods.

Mutual leaf shading can inhibit yam growth, especially during the later growth period when the plant biomass is established and when plants have elongated and tangled vines with long heart-shaped horizontal leaves. Law-Ogbomo and Osaigbovo (2014) reported that higher plant density decreased light interception and tuber yield due to leaf shading. Moreover, overgrowth can result in a lower distribution of sunlight into the canopy, thus reducing radiation use efficiency (Hgaza et al., 2010). In addition to the shading effect on light interception, carbon loss due to maintenance respiration of over-grown plants might also lower carbon partitioning to tubers (Timlin et al., 2006). In other cases, plants under staking cultivation had a larger tuber yield compared to those under non-staking cultivation, even though plants had similar leaf areas (Igwilu, 1989). This could be due to the better leaf arrangement for light interception under staking. Conversely, Suja et al. (2005) reported that, even when plants were staked, the net assimilation rate tended to decrease in the later

growth periods, which might be attributed to the shading effect of outer leaves. Removal of the lower 1/4 to 1/3 of leaves in Jerusalem artichoke increased tuber yield (Gao et al., 2019), and it is possible that a similar approach may improve yield of yam.

In addition to shading, day length affects yam shoot growth and yield. In yam plants, it is known that shoot growth is depressed and tuber growth is stimulated under photoperiods less than 12 hours (Vaillant et al., 2005). However, there is little information if this response is irreversibly controlled by physiological phase changes (Poething, 2003). If the shoot growth depression is reversible by reducing mutual shading, shoot growth is expected to continue even under the threshold day length, and this could subsequently effect tuber yield. This warrants further investigation.

Our hypothesis was that leaf thinning of yam at the maximum growth period would improve the light utilization of the whole plant and increase shoot growth and tuber yield. A field study in which yams, grown under staking and ridge cultivation, were either thinned or not was established, and shoot growth was determined throughout different growth periods. The effect of leaf thinning on shoot growth and tuber yield was analysed.

Materials and methods

Plant materials and growth conditions

Four accessions, TDr_1533, TDr_1649, TDr_3325, and TDr_3357, were selected from the mini core collection developed for white Guinea yam (*D. rotundata*) genetic resources stored at the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria (Pachakkil et al., 2021). All accessions were male and had similar plant architecture, maturity, and tuber yield. *Dioscorea rotundata* does not produce aerial tubers. The field study was conducted in 2017 and 2018 in the experimental field (7° 29' N, 3° 54' E) of the IITA. The soil was a sandy loam with moderate acidity (pH 5.7–6.2). Soil organic carbon, total nitrogen, and available (Bray-1) phosphate contents were 4.3 g kg⁻¹, 0.39 g kg⁻¹, and 3.1 mg kg⁻¹, respectively.

To avoid any effect of uneven tuber sprouting on shoot growth (Ayankanmi et al., 2006), plant materials were planted in plastic pots to screen well-sprouted plants. The planting materials were made from normal-sized tubers weighing approximately 1–2 kg, which were cut horizontally to remove the head and tail parts. Next, the center part was cut into small pieces (seed setts), each with a skin surface where a shoot bud could emerge. Three seed sett sizes were used following Iseki and Matsumoto (2020): 50 g, 100 g, and 200 g. The setts were treated with a fungicide before planting. The setts

were planted on 3 May 2018, and 10 May 2019, in plastic pots (12-cm diameter and 10-cm height) filled with topsoil (sandy loam, pH 7.6). After one month, plants that had adequate sprouts were selected and transplanted into the field with stakes on ridges that were approximately 40 cm high and 60 cm wide. The ridge interval and plant interval on ridges were both 1 m. For each combination of the four accessions and three sett sizes, a 7-m line plot was constructed containing eight plants. The plots were laid in a randomized block design with five replications, and the total number of plots was 60: 4 accessions \times 3 sett sizes \times 5 replications. Weeding was performed manually, as required. After the start of tuber enlargement, soil was added as necessary to avoid the exposure of tuber heads due to soil erosion, but additional hilling was not done.

Fertilizers and irrigation were not applied. Meteorological conditions were obtained from a field-installed weather station.

The total precipitation, average temperature, and average solar radiation during the field experimental periods (from June to October) were 995 mm, 25.8°C, and 12.9 MJ d⁻¹ in 2018 and 1153 mm, 25.8°C, and 12.6 MJ d⁻¹ in 2019. The rainfall pattern was bimodal with a dry spell in early to mid-August corresponding to the day of year (DOY) 210–230 (Figure 1). Average temperature and solar radiation tended to be higher in 2019 than in 2018 before mid-September (DOY260). However, the opposite was observed in later growth periods after mid-September due to the higher precipitation in 2019 during this period. The day length

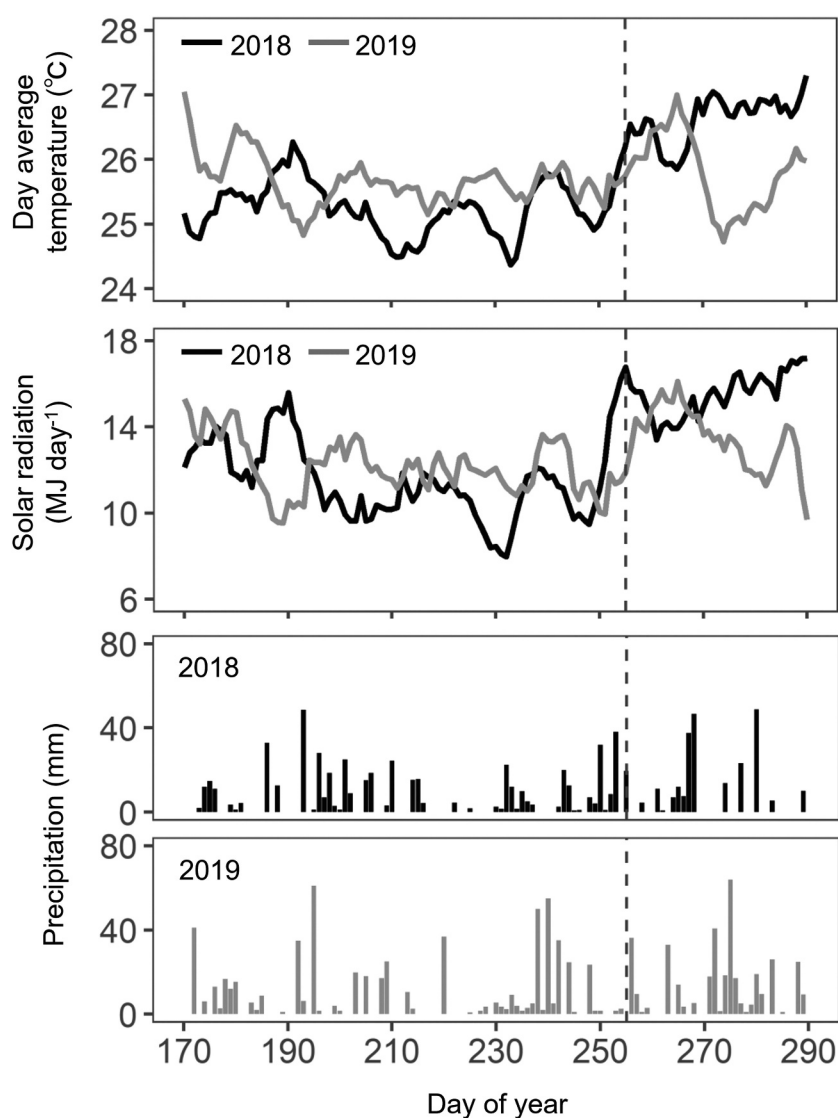


Figure 1. Meteorological conditions during the field experiment in 2018 and 2019. Moving averages of seven-day intervals from the 170th to the 290th day of the year are shown for daytime (6:00–18:00) average temperature and solar radiation. Daily cumulative values are shown for precipitation.

reached a maximum around late June (DOY170–175) and then shortened toward the late growth period (Supplemental Figure S1).

Leaf thinning treatment

For each plot, four of the eight plants were subjected to leaf thinning during the maximum growth period in mid-September (DOY255). In each line plot, every second plant was selected for leaf thinning. The outer leaves of plants were removed uniformly from the bottom to the top until the total plant leaf area had been reduced by approximately 25%. The removal intensity of 25% was visually determined.

Measurements

The time-course changes in shoot dry weight were evaluated using a non-destructive method. The normalized difference vegetation index (NDVI) was measured using a handheld sensor (GreenSeeker, Nikon Trimble, Tokyo, Japan) with simultaneous measurements of plant height also being recorded. Shoot dry weight (g plant^{-1}) was estimated using an equation including NDVI and plant height as explanatory variables according to Iseki and Matsumoto (2019). The evaluation was conducted every two weeks from approximately one month after transplanting (DOY192) to the onset of shoot senescence (DOY290).

The experimental period was separated into three periods: early, middle, and late growth periods corresponding to DOY192–220, DOY220–248, and DOY262–290, respectively. The shoot growth rate (SGR) was calculated for each stage according to the following equation: $\text{SGR (g day}^{-1} \text{ plant}^{-1}) = (\text{SDW}_{t_2} - \text{SDW}_{t_1}) / (t_2 - t_1)$, where SDW_{t_1} and SDW_{t_2} are shoot dry weight at time points t_1 and t_2 , respectively.

At full shoot senescence, the tubers of each plant were harvested, and the fresh weight was measured.

A subset of tubers from each plot was used to measure fresh and dry weights for the calculation of tuber moisture content. Tuber yield was expressed as fresh tuber weight at 65% moisture content to eliminate the effect of moisture content, which varied among plants and tubers.

Statistical analysis

For each plot, the average of the four plants in the thinning treatment and the four plants in the control treatment were determined for each variable measured. Correlations between SGR and shoot dry weight were determined using R version 3.4.1 (R Core Team, 2018). Analysis of variance and multiple comparison analysis using Tukey's HSD test were also performed to detect any statistically significant differences in shoot dry weight and tuber yield using R.

Results

The effects of accession and the interaction between accession and other factors on shoot dry weight were small throughout the growth period (Table 1). Therefore, time-course changes in shoot dry weight are shown as the averages of all accessions in Figure 2. In control plants (without leaf thinning), shoot dry weight continued to increase until DOY260 and then plateaued (Figure 2(a)). A similar trend was observed regardless of sett size or year. Plants from larger setts had larger shoot dry weights than plants from smaller setts in 2018 (Figure 2(b)). Conversely, in the middle and late growth periods in 2019, the shoot dry weight of plants from 100-g setts were the same as those of plants from 50-g setts. Shoot dry weight during the early growth stage was higher in 2019 than in 2018, which was consistent with the ANOVA results showing a larger effect of year during DOY192–235 (Table 1). Leaf thinning decreased shoot dry weight by 20–30% at DOY255. In 2018, shoot growth

Table 1. *F*-values obtained in analysis of variance for the variations in shoot dry weight and tuber yield.

	Shoot dry weight								Tuber yield
	DOY193	DOY207	DOY221	DOY235	DOY249	DOY263	DOY277	DOY291	
Year	1026.8 **	372.8 **	233.8 **	86.8 **	0.0 ^{ns}	0.2 ^{ns}	1.5 ^{ns}	30.9 **	18.0 **
Accession	10.0 **	23.3 **	18.3 **	4.3 **	4.6 **	5.5 **	22.8 **	17.3 **	5.9 **
Sett size	237.1 **	436.5 **	317.2 **	386.1 **	135.5 **	60.8 **	124.9 **	114.8 **	40.0 **
Thinning						672.7 **	575.8 **	490.1 **	126.3 **
Year × Accession	2.6 ^{ns}	3.9 *	2.1 ^{ns}	3.4 *	5.5 **	0.9 ^{ns}	1.4 ^{ns}	0.9 ^{ns}	2.2 ^{ns}
Year × Sett size	3.6 ^{ns}	0.0 ^{ns}	2.0 ^{ns}	7.7 *	3.7 ^{ns}	18.1 **	11.9 **	15.0 **	0.5 ^{ns}
Accession × Sett size	2.6 ^{ns}	4.7 **	4.9 **	2.8 *	1.8 ^{ns}	6.1 **	3.0 *	3.3 *	0.4 ^{ns}
Year × Thinning						0.0 ^{ns}	11 **	4.3 *	0.3 ^{ns}
Accession × Thinning						0.4 ^{ns}	1.9 ^{ns}	1.3 ^{ns}	0.9 ^{ns}
Sett size × Thinning						14 **	6.5 *	3.4 ^{ns}	3.8 *

DOY: day of year.

* and ** represent significant difference at $p < 0.05$ and $p < 0.01$ level, respectively, and 'ns' represents no significance.

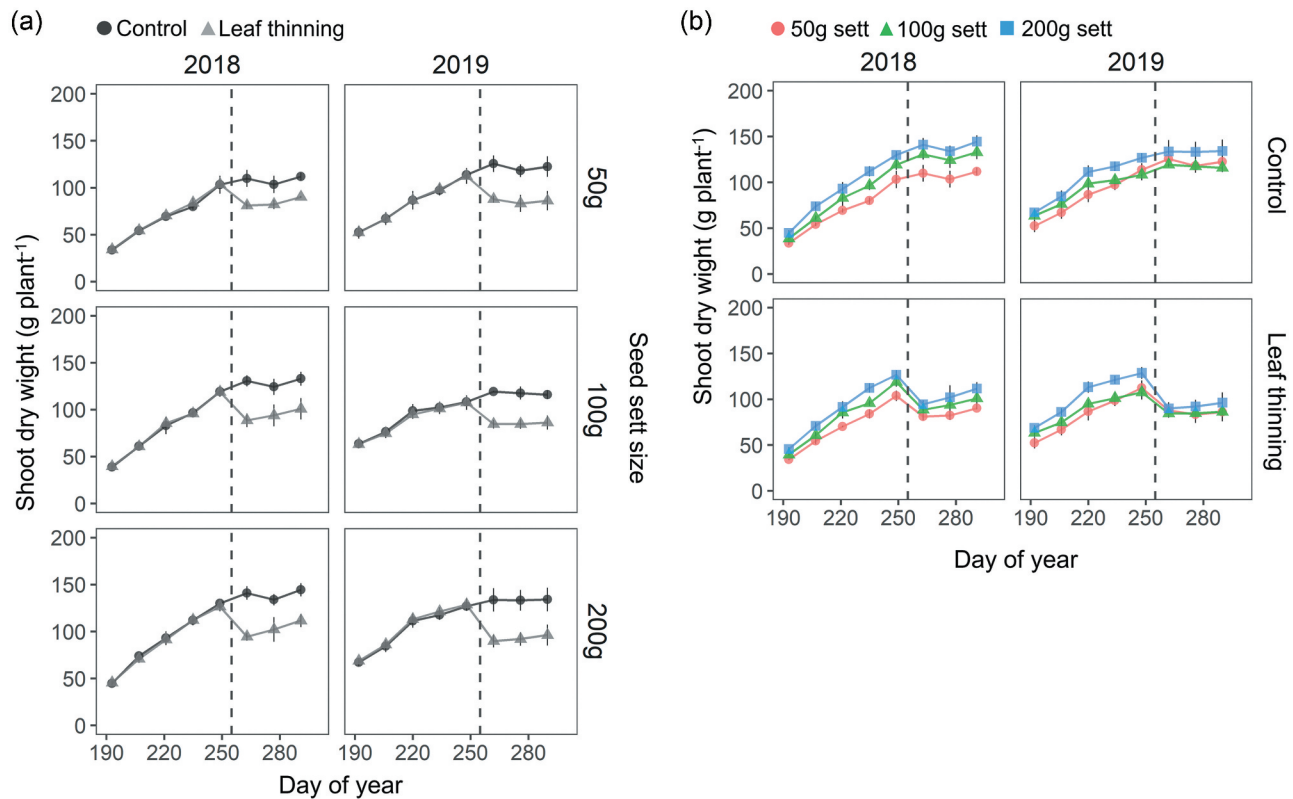


Figure 2. Time-course changes in shoot dry weight. (a) The effect of thinning and (b) the effect of sett size on shoot dry weight. Values are mean and standard deviations for 20 data samples consisting of 5 replications \times 4 accessions. The vertical dashed line represents the date of leaf thinning.

tended to recover after leaf thinning for all sett sizes. In 2019, this trend was observed in plants from 200-g setts but not in plants from smaller sett sizes.

This growth recovery after leaf thinning was analyzed using the SGR. The slope of the correlation between SGR and shoot dry weight represents the efficiency of shoot growth per unit leaf area generally recognized as the relative growth rate (Suja et al., 2005). This is dependent on the notion that shoot dry weight has a linear relationship with the total leaf area per plant (Supplemental Figure S1). During the early growth period (DOY192–220), a positive correlation was observed (Figure 3(a)); SGR linearly increased with increasing shoot dry weight. However, during the middle growth period (DOY220–248), there was no positive correlation. At this time, SGR was similar among plants with different shoot dry weights, although SGRs were positive. These trends were similar for both control and thinned plants. During the late growth period, SGR decreased to almost zero in control plants regardless of shoot dry weight. However, during this time period, in thinned plants there were significant and positive correlations between SGR and shoot dry weight (Figure 3(b)). The slopes of the correlations were 0.017 in 2018 and 0.031 in 2019, which were comparable with those in the early growth period.

In 2018, the SGR was positive for all plants. In 2019, negative SGRs were observed in plants with smaller shoot dry weights (<90 g plant $^{-1}$).

Plants from larger setts produced larger yields in both years (Figure 4). Tuber yields of thinned plants were significantly lower than those of control plants, with a 37% reduction in yield on average. This yield reduction was consistent across all sett sizes. Significant effects of year and accession on tuber yield were detected by ANOVA. The yield was higher in 2018 than in 2019 and was higher in TDr_3357 than in other accessions, but the *F*-values for year and accession, representing the effect size, were smaller than those for sett size and thinning (Table 1). Positive correlations between shoot dry weight and tuber yield were observed throughout the growth periods (Figure 5). The correlation coefficients after leaf thinning were much higher than those before leaf thinning in both years. The coefficients for the last two sampling times (after DOY270) were higher than those just after leaf thinning (DOY262).

Discussion

Yam shoot growth is generally depressed after tuber growth is induced by shorter day lengths (Vaillant

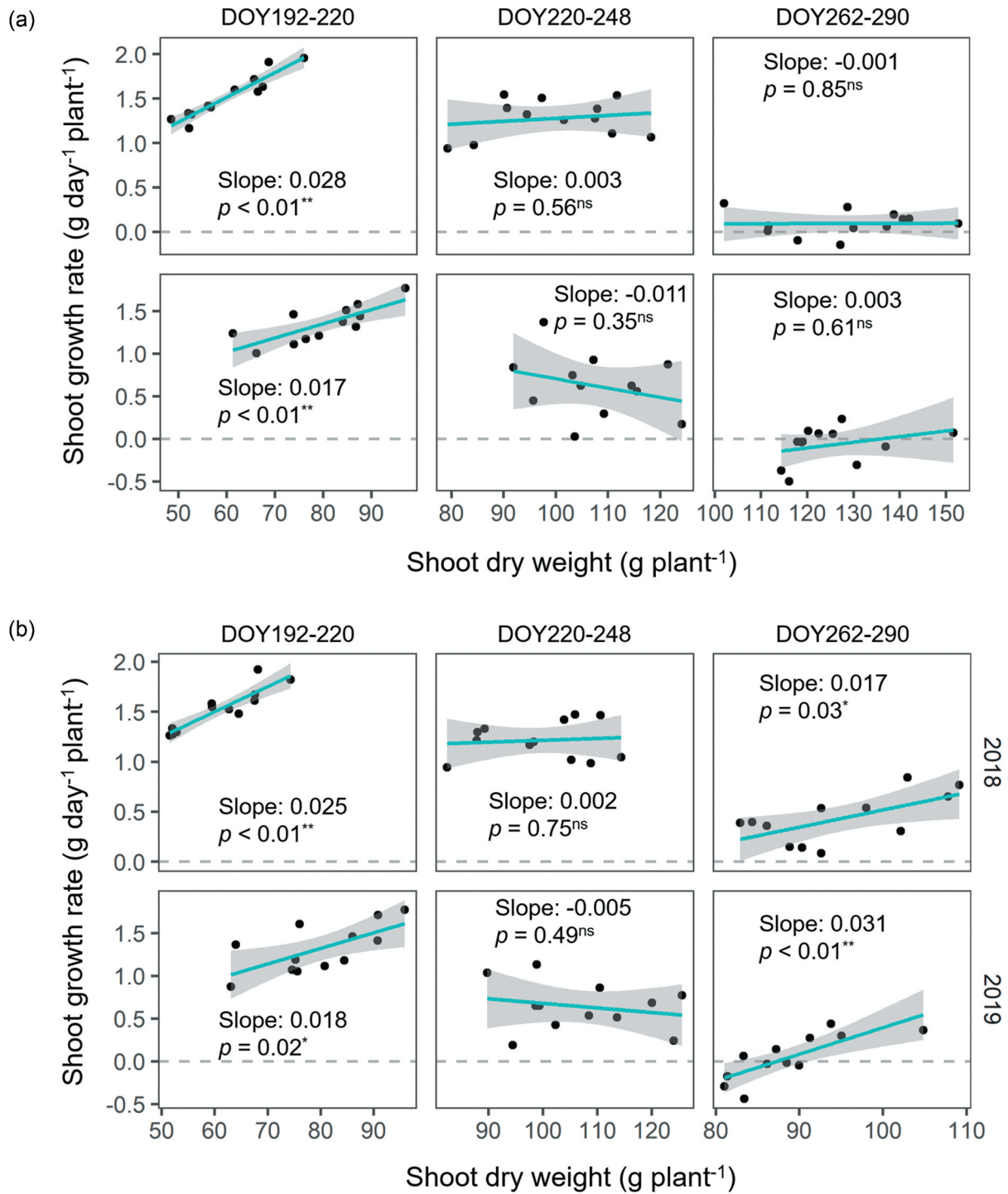


Figure 3. Relationships between shoot growth rate and shoot dry weight among the sett sizes and accessions. The relationships for (a) control plants and (b) thinned plants are shown separately for early, middle, and late growth periods, corresponding to DOY192–220, DOY220–248, and DOY262–290, respectively. DOY: day of year. Each point is the mean of 5 replications. The blue line and gray area represent the linear regression line and 95% confidence interval, respectively. Values of the slope and statistical significance of the regression line are shown in each box. A shoot growth rate of zero is indicated by a horizontal dashed line.

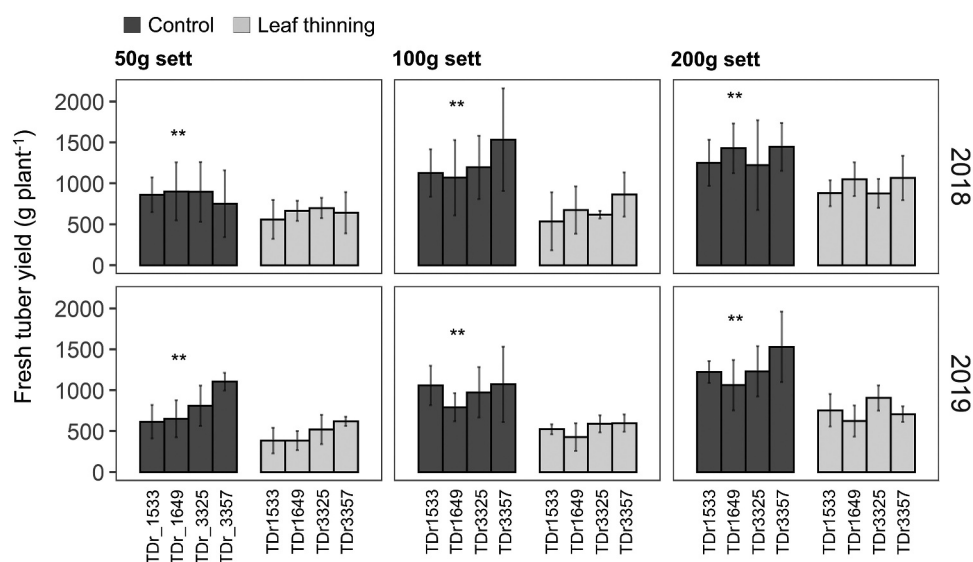


Figure 4. The effect of leaf thinning on tuber yield. Values are means and standard deviations of 5 replications. ** represents a significant difference between the thinning plants and control plants at $p < 0.01$.

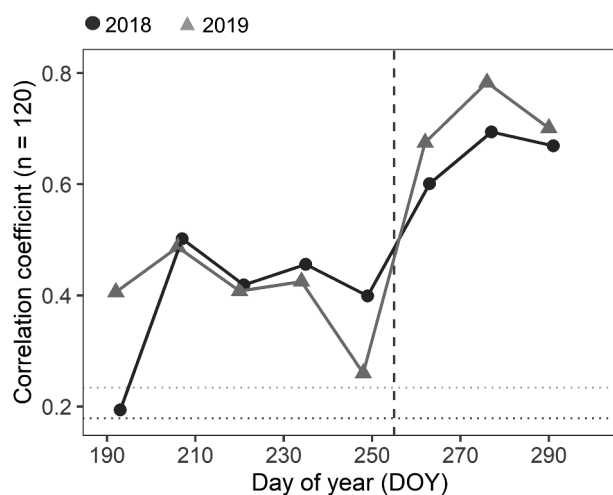


Figure 5. Changes in correlation coefficients between tuber yield and shoot dry weight during the experimental periods. Values are the correlation coefficients for 120 data samples consisting of 3 sett sizes \times 5 replications \times 4 accessions \times 2 treatments. The vertical dashed line represents the date of leaf thinning. The horizontal dotted lines in black and gray represent the statistical threshold of the coefficient at $p < 0.05$ and $p < 0.01$, respectively.

et al., 2005). In this study, day length peaked at around DOY172 and then shortened toward the late growth period. Tuber enlargement is known to start in late August (approximately DOY230–240) at the experimental site. Therefore, in the current study, the day length after thinning was shorter than the threshold day length for tuber growth. In the late growth period, control plants had SGRs close to zero, but thinned plants had higher SGRs (Figures 2 and Figures 3). This indicates that

a reduced SGR in response to shorter day lengths is not an irreversible physiological change. Therefore, shoot growth can be improved even during the late growth period.

The absence of a relationship between shoot dry weight and SGR in control plants after the middle growth period indicated that the larger leaf area did not contribute to the SGR (Figure 3). In contrast, positive relationships between SGR and shoot dry weight were observed in the thinned plants during the late growth period (Figure 3(b)). This might be due to the increase in newly developed leaves, which have a higher assimilation rate than old leaves (Aighewi & Ekanayake, 2004). Additionally, it could be due to greater light utilization by the leaves inside the plant mass (Liu et al., 2015) and lower respiratory carbon loss due to a lower total leaf area (Di Matteo et al., 2018).

However, the thinning treatment did not always induce a growth recovery. Thinned plants with smaller shoot dry weights ($<90 \text{ g plant}^{-1}$) showed negative SGRs during the late growth period in 2019, indicating a decrease in shoot dry weight. This might be due to the lower solar radiation and air temperature during this period in 2019 causing lower dry matter production (Figure 1). It could also be due to growth competition between the shoot and tuber. The correlation coefficient between shoot dry weight and tuber yield increased even after the thinning treatment (Figure 5), indicating that tuber growth and shoot growth occurred simultaneously in the thinned plants. The partitioning of

photosynthate is affected more by growth rate than by biomass (Marcelis, 1996). The rate of tuber growth during the late growth period is much higher than that of shoot growth (Marcos et al., 2011); therefore, newly assimilated carbon will be primarily allocated to tubers, which could explain the negative SGRs in small plants.

During the late growth period, control plants with small shoot dry weights (<110 g plant⁻¹) had lower SGRs than thinned plants, although their shoot dry weights were comparable (Figure 3(a)). This could be explained by leaf age. A plateau in leaf area can correspond to a high proportion of old but not senescent leaves (Marcos et al., 2011). In potato, shoot growth interacts with tuber growth through signal transduction with phytohormones (Roumeliotis et al., 2013), resulting in dynamic changes depending on leaf age (Woo et al., 2019). The control plants had a higher proportion of old leaves than the thinned plants; therefore, the decrease in shoot growth in control plants might be physiologically determined even in those that had small shoot dry weights with better light utilization.

The thinning treatment improved SGR during the late growth period, but it largely decreased tuber yield regardless of the shoot dry weight. The strong correlation between shoot dry weight and tuber yield indicates that a decrease in total carbon assimilation per plant and growth competition between shoots and tubers were the major reasons for the yield reduction. Therefore, greater shoot biomass is more important than greater light utilization efficiency for yield. Another possible reason for the yield reduction could be that leaf thinning disrupted hormonal signals regulating tuber growth (Vreugdenhil & Struik, 1989). In addition, leaf thinning might also depress root growth (Hodgkinson & Becking, 1978). Although the relationship between root growth and tuber yield was not clear in white Guinea yam (Hgaza et al., 2012), Villordon et al. (2014) indicated that lateral root development is related to yield formation in tuber crops. These results suggest that leaf thinning after the onset of tuber growth should be avoided and thinning at an earlier growth stage is preferable.

In this study, leaf thinning was performed after tuber growth had begun, and thus both the tuber growth and shoot growth were interrupted. It also caused the failure of full shoot recovery and reduction in tuber yield. It is possible that if thinning was done at the early growth stage and it was combined with early season planting, a sufficient growth period for full biomass recovery with new leaves would be ensured before the starting of tuber growth. This would bring continuous shoot growth with sufficient biomass at a later growth period and then

subsequently increase tuber yield. Other measures to improve light utilization should also be considered, such as the use of a trellis. However, because the growth recovery would also be affected by climate conditions and soil fertility, further studies are needed to clarify these environmental effects.

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Disclosure statement

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