Industrial Crops & Products 109 (2017) 570–578

Contents lists available at ScienceDirect

Industrial Crops & Products

journal homepage: www.elsevier.com/locate/indcrop

Dry-season deficit irrigation increases agricultural water use efficiency at the expense of yield and agronomic nutrient use efficiency of Sacha Inchi plants in a tropical humid monsoon area

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ARTICLE INFO

Keywords:
Carbohydrate
Deficit irrigation
Fertilization
Growth
Yield
Resource use efficiency

ABSTRACT

Application of deficit irrigation (DI) will be problematic in tropical humid monsoon areas, since high relative air humidity during growth there leads to stomata malfunctioning. A field split-plot experiment was used to evaluate the physiological features, growth and seed and oil yield of Sacha Inchi (*Plukenetia volubilis* Linneo) plants, a tropical promising woody oilseed crop, responded to DI and fertilization in southwest China. The field experiment consisted of a factorial combination of five irrigation levels applied in the dry season [rainfed; DI20, DI50, DI100 (i.e., with irrigation amount of 20, 50 and 100% crop evapotranspiration, respectively); and full irrigation (irrigation of water saturated soil)] combined with two levels of compound fertilizer (0 and 200 kg ha^{-1}) over two growing seasons, in a randomized complete block design with three replicates.

Results showed the growth and root to stem mass ratio had lower sensitivity responded to DI, probably owing to their extremely low root mass fraction and seasonal short-term effect of DI on leaf photosynthetic traits. Irrigation affected the seasonal variations in seed size, seed oil concentration and seed yield, depending on the harvest date; whereas, with constant mean seed size and mean seed oil concentration across irrigation and fertilization treatments, the total seed and seed oil yield over the growing seasons were largely determined by the seed numbers per unit area. The soluble sugar and nitrogen storages as the active process, are related to effective flower formation, fruit (seed) development and enhance productivity of Sacha Inchi plants, which was indicated by the positive relationships between total seed yield and total nitrogen pool in the vegetative tissues or sugar pool in stems across all treatments. Fertilization increased total seed and seed oil yield, but no interaction between irrigation and fertilization was found. Compared with DI100, DI50 and DI20 had significant lower total seed yield, especially under the fertilized condition, although having higher agronomic water use efficiency (WUEagr, yield divided by irrigated water applied) but lower agronomic nutrient use efficiency (NUEagr, increased yield divided by fertilization rate). As a water-demanding crop species, Sacha Inchi plants under DI100 with the similar values to full irrigation had the highest total seed yield and NUEagr, but at the expense of water use efficiency. The maximum seed yield and maximum WUEagr, or maximum WUEagr and maximum NUEagr of Sacha Inchi plants are not compatible because the negative relationships existed between each of them. The polynomial regression relationships between total seed or seed oil yield and relative evapotranspiration could help to develop appropriate water-saving techniques for Sacha Inchi plantation in the tropical humid monsoon region.

1. Introduction

Sacha Inchi (*Plukenetia volubilis* Linneo), a tropical woody vine, is a promising new oilseed crop species belonging to the family Euphorbiaceae. It is well known that Sacha Inchi seed contains a high concentration of polyunsaturated fatty acid, which is beneficial to human health (Noratto et al., 2012). As an evergreen, recurrent species, *P. volubilis* plants flower continuously throughout the growing season;

Abbreviations: DI, deficit irrigation; HI, harvest index; Gs, stomatal conductance; Pn, light-saturated photosynthetic rate; PNUE, photosynthetic nitrogen use efficiency; Tr, transpiration rate; SLA, specific leaf area; WUEi, instantaneous water use efficiency; WUEagr, agricultural water use efficiency; NUEagr, agricultural nutrient use efficiency

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http://dx.doi.org/10.1016/j.indcrop.2017.09.022
Received 13 May 2017; Received in revised form 8 August 2017; Accepted 13 September 2017
0926-6690/

the capsule fruits consist four-to-seven pods, with one seed per pod. The seed and oil yield of Sacha Inchi plants are highly variable and depend on environmental conditions and suitable agricultural management practices (Cai, 2011; Cai et al., 2012, 2013; Jiao et al., 2012; Yang et al., 2014). In the previous research, we found that natural drought conditions decreased plant growth rate, numbers of female flowers and fruit per plant, and fruit set of Sacha Inchi plants compared with the well-watered plants in the dry season (Jiao et al., 2012). Thus, irrigation in the dry season is helpful to optimize yield of the field-grown Sacha Inchi plants.

Defined as the application of irrigated water below full crop water requirement for evapotranspiration, deficit irrigation (DI) is a water-saving irrigation technique that theoretically allows the production of root-to-shoot signals that modify the physiology of the above-ground parts of the plant; specifically reducing stomatal conductance and improving water use efficiency (WUE) (Dodd et al., 2008). However, the physiological and biochemical responses are difficult to quantify; given that DI is usually applied to plants in accordance with both temporal and spatial droughts, depending on the quantification of crop's response to water limitations and total soil water availability (Dodd et al., 2008; Romero et al., 2012). Moreover, little is known about how long stomata remain partially closed with prolonged soil drying and what role re-watering may play in stimulating root growth under drying soils (Chai et al., 2016).

It has been identified that DI can save irrigated water and increase WUE greatly with a subtle or even positive impact on crop yield and quality simultaneously of some annual and woody crops, especially in arid and semiarid regions (Chai et al., 2016). But field trials have also reported reductions in crop yield under DI associated with lacks of the physiological responses (Tognetti et al., 2007; Trigo-Córdoba et al., 2015; Dbara et al., 2016; Gasque et al., 2016). The varied and inconsistent effects of DI have been found due to the multiple reasons: different soil types (Chai et al., 2016), environmental and experimental conditions (Marsal et al., 2008), different intensities and modulation of the chemical signal (Tardieu et al., 2015), different distribution of the soil water content (Dodd et al., 2008), different species/varieties adaptations to soil moisture heterogeneity (Martin-Vertedor and Dodd, 2011), root hydraulic redistribution (Bauerle et al., 2008) and methodological problems in applying DI (Shahrokhnia and Sepaskhah, 2017). Especially, the effect of application of DI is uncertain in tropical humid monsoon areas (Renault et al., 2001; Trigo-Córdoba et al., 2015), since such climates have relatively high annual rainfall with distinct wet and dry seasons and heterogeneous soils, and long-term high relative air humidity during leaf expansion hampers stomatal responsiveness to closing stimuli (Arve et al., 2013; Carvalho et al., 2016), resulting in uncontrolled water stress when species/varieties with higher stomatal sensitivity to high relative air humidity are transferred to of high evaporative demand conditions (Fanourakis et al., 2016).

Likewise, crop nutrient status often depends on soil nutrient and water availabilities (Jiao et al., 2012; Afshar et al., 2016); fertilization is a critical component of Sacha Inchi yield production (Yang et al., 2014). If both soil moisture and fertilizer are managed properly, a synergistic interaction between them could probably increase crop yield, WUE and nutrient use efficiency (NUE) (Quemada and Gabriel, 2016). In this paper, we conducted field experiments to investigate the effects of different levels of DI and fertilization on the physiological traits, plant growth, yield, and resource use efficiency (i.e., WUE and NUE) of *P. volubilis* plants in Xishuangbanna, a tropical humid monsoon area in southwest China. The overall goal was to provide a better understanding of irrigation and fertilizer managements for this species at both the local and regional levels, and thus to increase seed and oil yields for commercial-scale oil production.

2. Materials and methods

2.1. Study site and experimental design

The study was carried out in Xishuangbanna Tropical Botanical Garden (21°56′N, 101°15′E, altitude 560 m), Chinese Academy of Sciences, Yunnan, southwest China. The climate at Xishuangbanna is dominated by the southwest monsoon with two distinct seasons (a wet season from May to October, and a dry season from November to April). The average annual temperature is 22.9 °C and the mean annual precipitation is 1500 mm, of which approx. 85% occurs in the wet season. The minimum and maximum temperatures are about 8.7 and 34.2 °C in January and April, respectively; the relative air humidity is very high over the years (> 74%). According to the mean monthly air temperature, the dry season can be divided into the cool and dry season (November to January) and the hot and dry season (February to April) (Zhang, 1963; Cai et al., 2007), with heavy fog partially compensating for the shortage of rainfall during the cool and dry season (Liu et al., 2005).

The field experiments were arranged in a split-plot design with randomized complete blocks and 3 replications in a 2 m × 40 m sized plot, using 2-year-old *P. volubilis* plants cultivated in open site at intra- and inter-row spacing of 2.0 m and 2.0 m, over two consecutive growth seasons (2015 and 2016). Since *P. volubilis* is a liana species, all plants were supported to a height of 1.6 m using steel wires. The soil was a red-brown type and the characteristics of the top (0–20 cm) layer of soil were: field capacity 26% on gravimetric base; pH 5.42; organic carbon 5.65% (w/v); total nitrogen 0.34 g kg^{-1}; available N 46.0 mg kg^{-1}; available P 14.1 mg kg^{-1}; and available K 22.0 mg kg^{-1}. Rainfall can meet water requirement of *P. volubilis* plants during the wet season (Cai et al., 2007); thus, irrigation treatment was only investigated in the dry season. Weeding was done monthly, pest and insect was controlled in early May.

Fertilization rates were assigned to the main plots and consisted of 0 and 200 kg ha^{-1} of a 1:1:1 (w/w/w) mix of $N:P_2O_5:K_2O$ spread in an approx. 1.0 m-wide zone in June in 2014 and 2015, respectively, according to previous research (Yang et al., 2014). Irrigation was assigned to the sub-plots included rainfed (control) and four levels of irrigation regimes [DI20, DI50, DI100, and full irrigation (i.e., irrigation of water saturated soil); with irrigation amount of 20%, 50%, 100% and approx. averaged 147% crop evapotranspiration (ETc), respectively] from early December to late April in the dry season; irrigated once every second week. Irrigation was built between blocks, and the amount of irrigation water was monitored with flow meters (LXSG-50 Flow meter, Shanghai Water Meter Manufacturing Factory, Shanghai, China) installed in the irrigation pipelines. Each sub-plot was irrigated independently. Two pipelines with emitters were joined at both sides to the trunk and placed underneath each row; irrigation water was supplied simultaneously to both sides of the root system. Deep leakage did not occur because of shallow depth of wetted-soil of irrigation in this experiment. Crop evapotranspiration ($ETc = ET_0 \times K_c$) was estimated using crop coefficients (K_c) based on those proposed by the FAO and reference evapotranspiration (ET_0) values, calculated by the Penman-Monteith-FAO method (Allen et al., 1998) and using the daily climatic data collected in the Xishuangbanna Station for Tropical Rain Forest Ecosystem Studies (XSTRES) nearby belonging to Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences. Crop coefficient (K_c) of the field-grown *P. volubilis* plants in this study was estimated as 1.0 with the reference to tropical fruit trees and grapevine.

2.2. Measurements

Leaf gas exchange parameters (net photosynthetic rate, Pn; transpiration rate, Tr; and stomatal conductance, Gs) were measured under light-saturating irradiance (photosynthetic photon flux density = 1800 μmol m^{-2} s^{-1}) and ambient CO_2 concentration on recently matured, sun canopy leaves, using a portable infrared gas analyzer in open system mode (Li-6400XT, Li-Cor, Lincoin, NE, USA) during 8:30–11:00 in January, April and July, respectively, in 2015; subsample of leaves was also collected for the measurement of nitrogen (N) concentration. Photosynthetic N utilization efficiency (PNUE = Pn/N) and instantaneous water use efficiency (WUEi = Pn/Tr) were then calculated.

Mature fruit from all *P. volubilis* plants were harvested by hand in each sub-plot throughout the period of fruit ripening. The total dry mass of fruit per plot was measured at each harvest, and sub-samples of harvested fruit were peeled and the dry weight (size) of seeds was recorded. Seed oil concentrations were determined by the minispec mq-one Seed Analyzer (Bruker Optik GmbH, Germany). A calibration curve was obtained using known reference samples of the oil extracted from *P. volubilis* seeds. The total seed and seed oil yield (kg ha^{-1}) throughout the growing season was then calculated by the sum of the values from each harvest.

Four to five plants were harvested from each treatment at the end of April 2015. The plants were separated into leaves, stems, roots, and fruit [both green (less than 2%) and mature]; and were dried to a constant mass and weighed. Then, the biomass fraction of each component was calculated. For the calculation of total plant biomass and fruit mass fraction (i.e., harvest index), the value of total fruit yield throughout the year was used. Sub-samples of leaves were scanned with CanoScan 4400F scanner, and leaf areas were calculated using ImagJ software; specific leaf area (SLA; i.e. area of the leaf in cm^2 g^{-1} DW) was calculated. Nitrogen (N) concentration of vegetative organs (i.e. leaf, stem and root) was determined by micro Kjeldahl digestion. Dry subsamples of total soluble sugar concentration in stems were determined by UV spectrophotometry methods modified from DuBois et al. (1956). Total N pool of the vegetative tissues was calculated with the sum of the N concentration multiplied by the dry weight of each organ; and soluble sugar pool in stem was calculated by the soluble sugar concentration multiplied by the dry weight of stem. Agronomic water use efficiency (WUEagr) was calculated as kg seed yield per water applied as irrigation; and agronomic nutrient use efficiency (NUEagr) was calculated as: NUEagr = (total seed yield in fertilized plot − total seed yield in non-fertilized plot)/fertilizer used in fertilized plot.

2.3. Statistical analysis

For each morphological and physiological and yield variable, data were analyzed with a two-way ANOVA, with irrigation (I) and fertilization (F) as main fixed factors plus an I × F interaction term; followed by a Tukey HSD post hoc test within irrigation treatment. Data were checked for normality and homogeneity of variances, and a $\log_{10}$ or square-root transformation was applied when necessary to satisfy the assumptions of ANOVA. Correlations amongst traits were analyzed with a Pearson's correlation; all reported correlations were significant at an alpha level of $P < 0.05$. All statistical analyses were conducted using SPSS version 21.0 (SPSS, Chicago, IL, USA).

3. Result

3.1. Leaf and whole-plant traits

Seasonal climates had strong effects on the gas exchange parameters in leaves of Sacha Inchi plants: Pn, Gs, Tr and PNUE were highest in the wet season (July) and lowest in the cool and dry season (January), whereas the highest WUEi was found in the hot and dry season (April) across all irrigation regimes (Fig. 1). Effect of irrigations on the gas exchange parameters was only found in the hot and dry season. Pn, Gs, Tr, and PNUE generally increased, whereas WUEi decreased with increasing amount of irrigation in the hot and dry season; PNUE was negatively correlated with WUEi across all irrigation regimes ($r = 0.86$, $P < 0.01$). Fertilization increased total nitrogen pool in vegetative

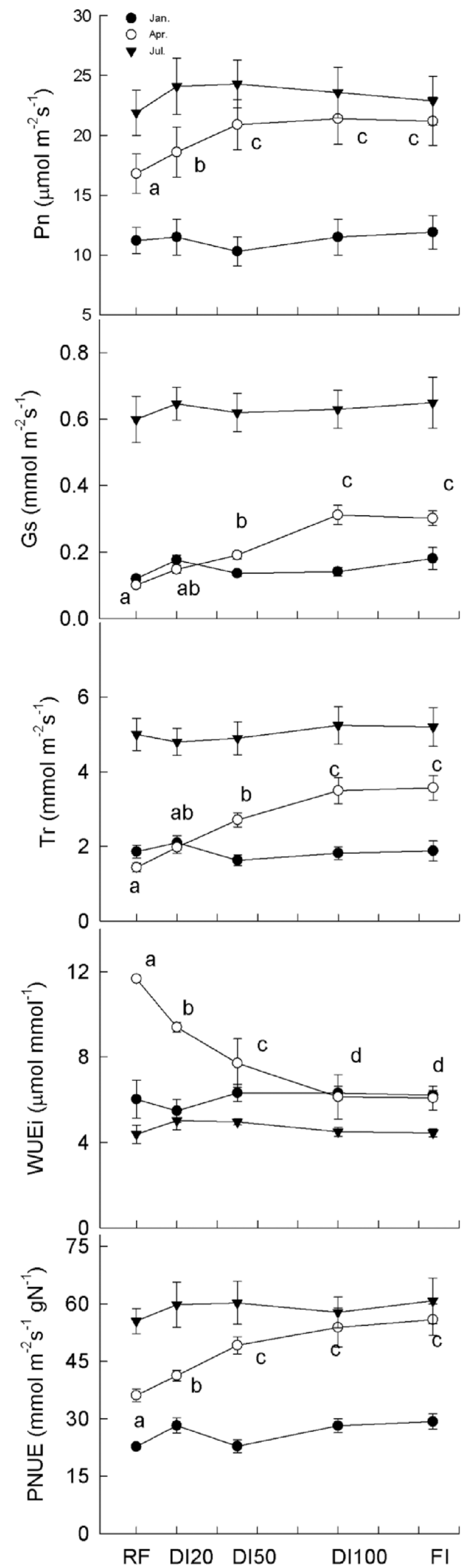

Fig. 1. Seasonal variations of leaf gas exchange parameters of *P. volubilis* plants in response to different irrigations under non-fertilized conditions. The values with different letters within the hot and dry season denote significantly at $P < 0.05$ level. Pn, light-saturated net photosynthetic rate; Gs, stomatal conductance; Tr, transpiration rate; WUEi, instantaneous water use efficiency; PNUE, photosynthetic nitrogen-use efficiency. RF, rainfed; DI20, DI50, DI100 = irrigation amount of 20, 50 and 100% crop evapotranspiration, respectively; FI, full irrigation = irrigation of water saturated soil.

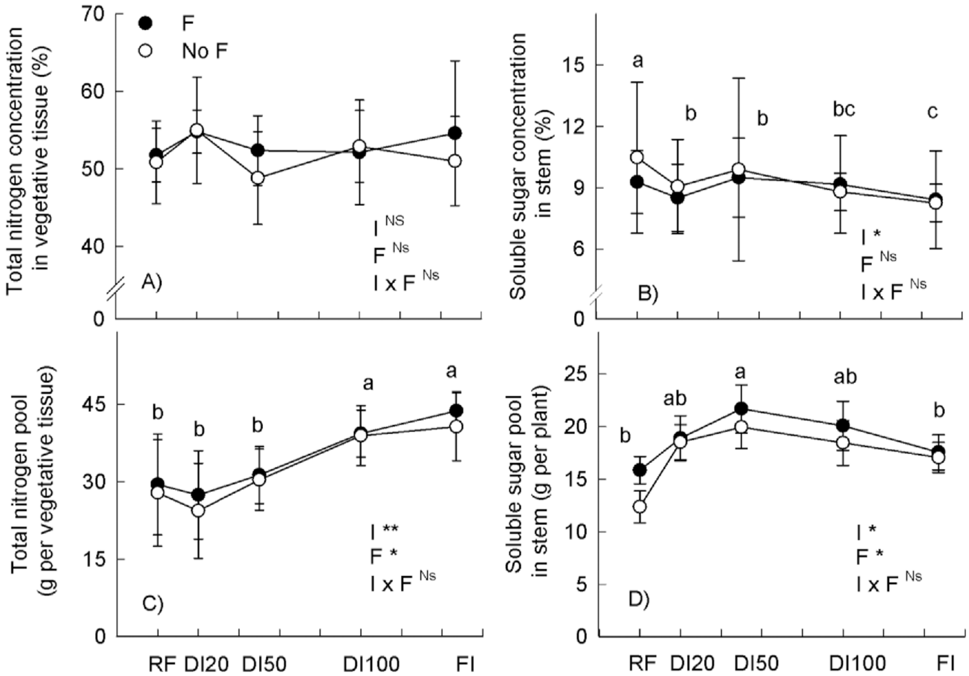

Fig. 2. Effects of different irrigation (I) and fertilization (F) treatments on the total nitrogen concentration (NC) and pool (NP) in the vegetative tissues, and soluble sugar concentration (SSC) and pool (SSP) in stem of *P. volubilis* plants. The values with different letters between irrigation treatments denote significantly at $P < 0.05$ level. Ns, no significance; * $P < 0.05$; ** $P < 0.01$. Abbreviations of irrigation treatments are as defined in Fig. 1.

tissues and soluble sugar pool in stem, rather than the sum of vegetative tissue nitrogen concentrations and soluble sugar concentrations in stem (Fig. 2). Total nitrogen pools in vegetative tissues of Sacha Inchi plants in rainfed, DI20 and DI50 were similar, but were much lower than those in DI100 and full irrigation (FI) conditions. With increasing amount of irrigation applied in the dry season, soluble sugar concentrations in stem generally decreased, but total nitrogen pools in vegetative tissues increased. Soluble sugar pool in stem had a quadratic response to the irrigation amount of the relative evapotranspiration; the highest value was found in the middle amount of irrigation. Moreover, the rate of fertilization and DI were assumed to have independent effects because no irrigation × fertilizer interactions on total nitrogen pool of the vegetative tissues per plant or soluble sugar pool in stem were found.

An extremely low biomass proportion was allocated into underground (i.e., root mass fraction < 6%), whereas more biomass was allocated to stem (46% on average) and fruits (38% on average) (data not shown). Fertilization increased total biomass and HI, but decreased SLA and root to stem mass ratio (Fig. 3). The total biomass and root to stem mass ratio were not greatly affected by irrigation. Specific leaf area and HI generally decreased with the decreasing amount of irrigation, whereas over irrigation (i.e., FI) decreased SLA. Across the irrigation and fertilization treatments, total biomass was positively correlated to total nitrogen pools in the vegetative tissues, but was negatively related to soluble sugar concentration and pool in stem, although not significantly (Table 1).

3.2. Yield components and yield

The phenological development of Sacha Inchi plants over the growing seasons, including the initial time of maturity and the dynamic pattern of fruit ripening (from early December to the end of April; dry season), was not affected by irrigation or fertilization. Seed size, seed oil concentration, and seed and seed oil yield differed among the harvest dates (all $P < 0.05$); the lowest values of seed and seed oil yield were found in the middle of the dry season (February), and were not affected by irrigation or fertilization. Seed size and seed oil concentration at a certain harvest date was not affected by fertilization (all $P > 0.05$). However, the drought responses in the seasonal yield and its component are complex: seed size, seed oil concentration and seed yield were affected by irrigation, depending on the date of harvest (Fig. 4).

Neither fertilization nor irrigation significantly affected the mean seed size and mean seed oil concentration over the growing seasons (Table 2). Total seed and seed oil yield generally increased with increasing amount of irrigation and fertilization; the highest values occurred in DI100 combined with fertilized conditions in both 2015 and 2016 (Table 2). Full irrigation had a slightly lower total seed and seed oil yield than DI100, but there was no significant difference. Compared with DI100, DI50 and DI20 resulted in significant loss of the total seed oil yield by 10.2% and 11.1% under non-fertilized condition in 2015, and 23.5% and 24.6% under fertilized condition across 2015 and 2016, respectively. The mean seed size and mean seed oil concentrations were similar, but the total seed yield and total seed oil yield were higher across irrigations under fertilized conditions in 2016 compared with 2015. Regression analysis indicated that the relationships between irrigation amount of the relative ETc and total seed or oil yields at any fertilization level were best expressed by polynomial equations ($R^2 = 0.89$–0.96; $P < 0.01$), namely:

$$Y = a + b(\mathrm{ETc}) + c(\mathrm{ETc})^2$$

where Y was the total seed yield or total oil yield (kg ha^{-1}), and a (intercept), b (linear coefficient), and c (quadratic coefficient) were parameters.

The regressions exhibited that full evapotranspiration crop demand was attained at or near the respective maximums of cumulative irrigation water.

3.3. Water and nutrient use efficiency

Fertilization increased WUEagr, whereas with increasing irrigation amount, WUEagr greatly decreased but agronomic nutrient use efficiency (NUEagr) generally increased (Fig. 5A and B). Agronomic nutrient use efficiency was negatively related with WUEagr (Fig. 5C). Total seed yield in 2015 was positively related with SLA, HI, total nitrogen pool of the vegetative tissues per plant, soluble sugar pool in stem, and was marginally related with NUEagr, rather than plant biomass and nitrogen concentrations in the vegetative tissues or soluble sugar concentration in stem, across all irrigation and fertilization regimes. Agronomic water use efficiency was negatively related with total seed yield and total biomass (Table 1).

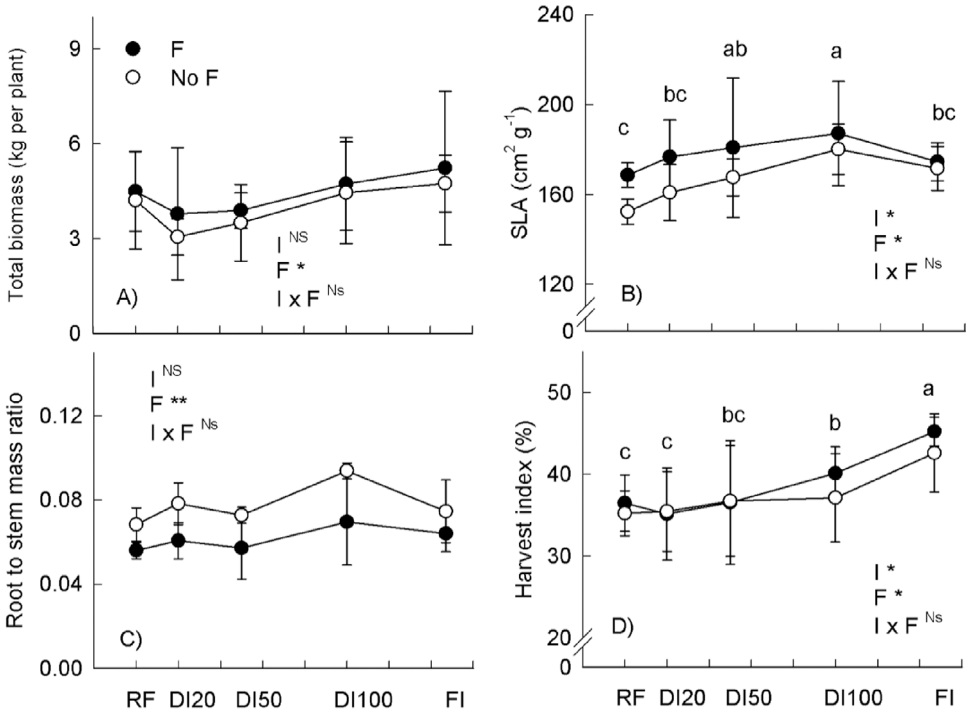

Fig. 3. The whole-plant traits of *P. volubilis* plants under different irrigation (I) and fertilization (F) treatments. The values with different letters each variable denote significantly at $P < 0.05$ level between irrigation treatments. Ns, no significance; * $P < 0.05$. SLA, specific leaf area. Abbreviations of irrigation treatments are as defined in Fig. 1.

Table 1
The correlation coefficients (r) between plant biomass or total seed yield and morphological or physiological variables across different irrigation and fertilization treatments. The significant coefficients were reported by the values in parentheses.

	Total biomass (kg)	Total seed yield (kg ha^{-1})
[a]SLA (cm^{2}g^{-1})	0.10(0.375)	0.74(0.015)
HI (%)	0.60(0.066)	0.81(0.0046)
SSC (%)	−0.15(0.673)	0.49(0.152)
NC (%)	0.14(0.691)	0.25(0.826)
SSP (g)	−0.02(0.559)	0.82(0.0034)
NP (g)	0.52(0.019)	0.80 (0.0059)
WUEagr (kg m^{-3}H$_2$O)	−0.78(0.042)	−0.77(0.045)
NUEagr (kg kg^{-1})	0.26(0.177)	0.75(0.058)
Total biomass (kg)	–	0.23(0.165)

[a] SLA, specific leaf area; HI, harvest index; SSC, soluble sugar concentration in stems; NC, nitrogen concentration in the vegetative tissues; SSP, soluble sugar pool in stems; NP, nitrogen pool in the vegetative tissues; WUEagr, agronomic water use efficiency; NUEagr, agronomic nutrient use efficiency.

4. Discussion

4.1. Leaf and growth traits

In response to DI, the decreased SLA values of Sacha Inchi plants are important to maintain leaf function and allow a conserve water use under drought conditions (Jiao et al., 2012). Although water-stress induced abscisic acid accumulation is generally regarded as an inhibitor of shoot growth (Dodd et al., 2008), the constant root to stem mass ratio of Sacha Inchi plants in DI conditions was probably owing to their very large stem proportion and extremely small root proportion distributed in shallow soil layers (< 50 cm) as a liana species (Fig. 3; Ichihashi and Tateno, 2015). It's well expected that leaf photosynthetic and transpiration rate in Sacha Inchi plants in the cool or hot dry season was much lower compared with the wet season when environmental conditions were close to optimal (cf. Cai et al., 2007). Although irrigations significantly affected the leaf gas exchange parameters in the hot and dry season, the short-term influences disappeared in the wet season and the cool and dry season (Fig. 1). That means that Sacha Inchi plants under DI regimes may rapidly resume to the normal plant physiological performance, once rainfall in the wet season occurred. The decrease in photosynthetic capacity during the cool and dry season is likely to be caused by low temperatures, as most plants growing year round in the wet tropics are particularly vulnerable to low temperatures (Cai et al., 2007). In addition, in the cool and dry season in Xishuangbanna, the leaves are covered with water droplets from fog each day from midnight to midmorning of the following day, and the soil is continuously wet (Liu et al., 2005). Thus, DI did not significantly affect the leaf physiological traits in the cool and dry season, because fog may help ameliorate plant water stress by reducing transpiration or evaporation and may also be the important source of water for the local plants (Liu et al., 2005). Although DI significantly decreased stomatal conductance and transpiration rate of Sacha Inchi plants in the hot and dry season, scaling up the stomatal responses to the environment from individual leaf to canopies is essential to assess the impact of stomatal closure on canopy transpiration. The high relative humidity in the atmosphere during the study period (never lesser than 74%) may lead to slow responsive stomata to closing stimuli on leaflets as a consequence of low leaf abscisic acid concentration (Arve et al., 2013; Tardieu et al., 2015). Even if with an active transpiration behavior, the growth characteristics of evergreens Sachi Inchi plants might have relatively low responsiveness to irrigation treatments (Fig. 3), which differentiated from other annual oilseed crops (Hergert et al., 2016; Pavlista et al., 2016) and some deciduous fruit trees (Marsal et al., 2008; Trigo-Cordoba et al., 2015) during the reproductive stage. Moreover, the regulation of vegetative growth by DI depends on multiple factors, such as soil type and total soil water availability, species differences in stomatal sensing of water deficit (Romero et al., 2012; Tardieu et al., 2015), and differences of the long-transport hydraulic and chemical signals among woody species (Dodd et al., 2008). Across irrigation and fertilization regimes, the negative trend between soluble sugar concentration and pool relative to plant growth (Table 1) indicated that, prior to plant growth, carbohydrates may be an active carbon sink of Sacha Inchi plants, crucial to maintaining hydraulic function under drought conditions (Palacio et al., 2014; Yang et al., 2016).

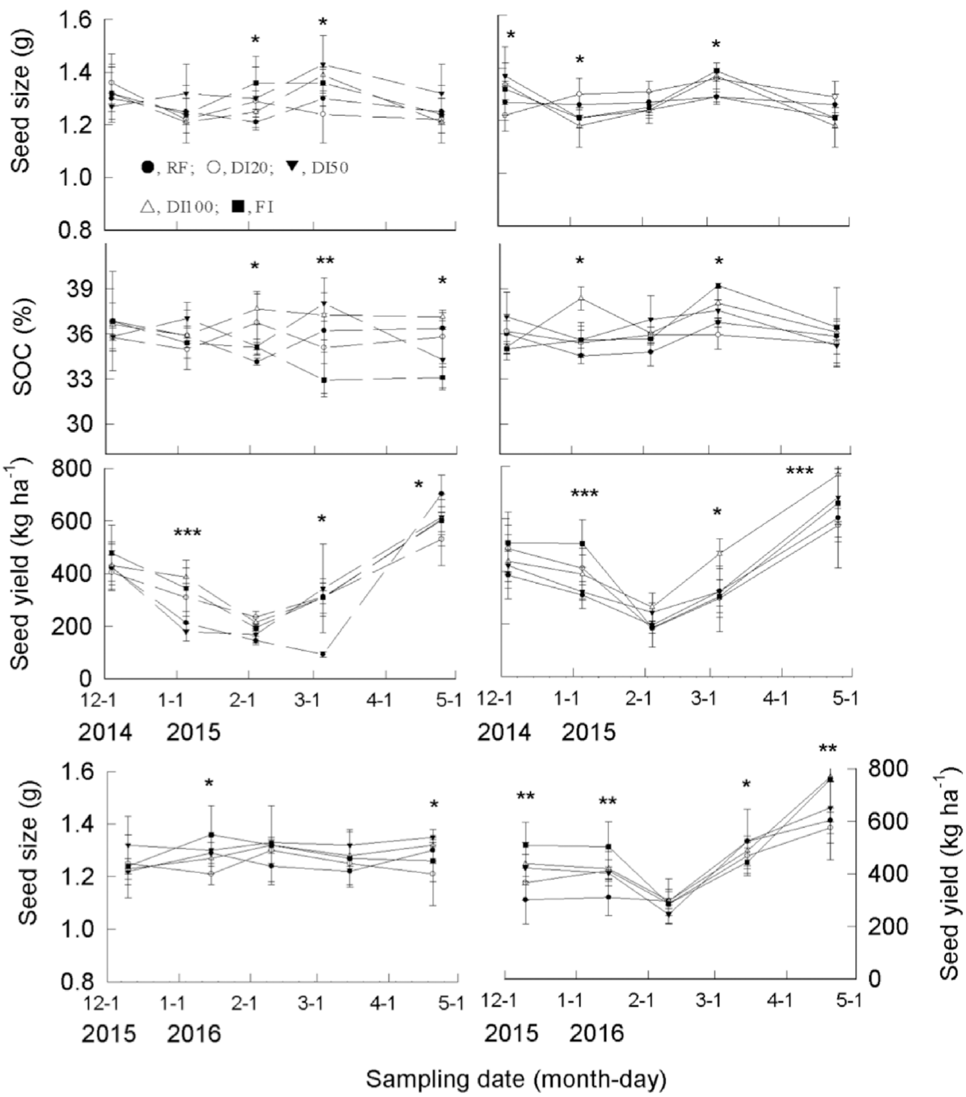

Fig. 4. Seasonal dynamic of the seed size, seed oil concentration (SOC) and seed yield of *P. volubilis* plants under different irrigation (I) and fertilization treatments. Dashed lines, unfertilized group; solid lines, fertilized group. The asterisk denotes significantly between different irrigation regimes for a given harvested date. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Abbreviations of irrigation treatments are as defined in Fig. 1.

4.2. Yield and resource use efficiency

Consistent with our previous researches (Cai et al., 2013; Yang et al., 2014, 2016), irrigation and fertilizer did not affect the initial time of maturity and the dynamic fruit-ripening pattern of Sacha Inchi plants (Fig. 4). This was due to the fact that the time of flowering (or fruit maturity) within one season in tropical plants with no requirement for vernalisation is largely determined by their inherited responses to temperature and photoperiod. The drought responses in the seasonal yield and its component are complex: seed size, seed oil concentration and seed yield were affected by irrigation, depending on the date of harvest (Fig. 4). As a recurrent flowering plant, seasonal variations in seed size, seed oil concentration, and seed and seed oil yield of Sacha Inchi plants, were probably owing to the fluctuations in average temperature and the source-sink relation through the growing season (Sintim et al., 2015; Wassner et al., 2016; Króla and Paszko, 2017). There is usually an interaction between irrigation and fertilizer on cropyield. For example, under semi-arid conditions, yield of sunflower supplied by N fertilization increased in the medium irrigation level, but decreased in the severe deficit irrigation (García-López et al., 2016); the seed cotton yield reduction in response to soil water shortage was much more severe at high N rates (Singh et al., 2010). In our study, no irrigation × fertilizer interaction on total seed or seed oil yield was found, indicating the magnitude of increase in total seed and seed oil yield by fertilization was similar among different irrigation regimes. Both total seed and seed oil yield were increased by fertilization, corresponding to other annual and perennial oilseed crops (Sintim et al., 2015; García-López et al., 2016; Sampaio et al., 2016). Moderate and sever DI (DI50 and DI20) greatly decreased yield of Sacha Inchi plants in both 2015 and 2016, especially under the fertilized condition (Table 2). That means that originated from a humid tropical lowland forest in Amazonia, South America, Sacha Inchi is a water-demanding crop species for its seed production. Irrigation to 100% of ETc is preferable for higher yield are also reported for olive trees (Dbara et al., 2016) and seed cotton (Singh et al., 2010) in the semi-arid regions, and also for olive (Tognetti et al., 2007) and tomato (Kusçu et al., 2014) in the sub-humid environments. Sacha Inchi plants under DI100 with the similar values to full irrigation had the highest total seed yield, thus over irrigation did not continuously increase the yield of Sacha Inchi plants. The polynomial correlation between seed yield and relative irrigation could be expressed. Similarly, several other studies have noted polynomial relations between irrigation and yield for irrigated olive (Chetoui) (Dbara et al., 2016) and spring canola (Hergert et al., 2016) in semi-arid areas, and soybean in sub-humid climatic conditions (Candogan et al., 2013). Based on the regression curves, optimal solutions could be reached by finding a compromise between the levels of crop production and water productivity.

It is likely that due to the reduced photo-assimilates available for fruit (seed) growth, abiotic stress during the seed-filling period resulted in a reduced seed size and seed oil concentration (Cai, 2011). For spring

Table 2
Effects of different irrigation (I) and fertilization (F) treatments on the mean seed size, mean seed oil concentration (SOC), and total seed and seed oil yield over the growing seasons of *P. volubilis* plants. The value (means ± SD) with different letters denote significantly at $P < 0.05$ level within each fertilized group.

Treatments	Mean seed size (g)	Mean SOC (%)	Total seed yield (kg ha^{-1})	Total oil yield (kg ha^{-1})
2015				
RF	1.26(0.040)	35.9(1.04)	1581.4(64.2)c	567.6(23.0)c
DI20	1.27(0.061)	35.7(0.72)	1752.0(358.5)b	625.00(127.9) bc
DI50	1.33(0.060)	36.1(1.49)	1733.1(10.5)b	575.7(3.8)b
DI100	1.28(0.078)	36.9(0.68)	1949.8(134.9)a	720.0(49.8)a
FI	1.30(0.060)	36.0(1.64)	1931.9(278.9)a	669.9(96.7)a
RF + F	1.27(0.015)	35.6(0.92)	1701.0(155.1)c	647.9(40.7)c
DI20 + F	1.29(0.052)	35.8(0.35)	1854.2(269.3)b	699.7(52.4)b
DI50 + F	1.26(0.066)	36.5(1.02)	1804.8(239.8)b	713.7(66.1)b
DI100 + F	1.26(0.088)	36.7(1.40)	2319.8(295.3)a	856.0(111.1)a
FI + F	1.28(0.054)	36.4(1.07)	2165.5(238.5)a	788.0(55.8)a
ANOVA				
I	Ns	Ns	**	**
F	Ns	Ns	**	**
I × F	Ns	Ns	Ns	Ns
2016				
RF + F	1.28(0.034)	35.6(0.22)	1781.0(125.4)c	643.8(65.3)c
DI20 + F	1.31(0.054)	35.9(0.15)	1844.2(219.3) bc	711.7(34.6)c
DI50 + F	1.29(0.065)	36.1(1.12)	1945.8(209.5)b	850.1(23.6)b
DI100 + F	1.30(0.078)	36.2(1.20)	2598.7(214.2)a	920.1(45.3)a
FI + F	1.29(0.012)	36.6(0.34)	2499.7(198.7)a	916.4(71.2)a
Year (Y)				
	Ns	Ns	*	*

Ns, no significance; * $P < 0.05$; ** $P < 0.01$. RF, rainfed; DI20, DI50, DI100 = irrigation amount of 20, 50 and 100% crop evapotranspiration, respectively; FI, full irrigation = irrigation of water saturated soil.

canola, it was reported that seed oil concentration depended on yearly variation and irrigation level: oil content was increased by irrigation during drier years with no effect shown in the wet years (Hergert et al., 2016). As there were no great differences in the values of climatic variables (e.g., temperature, annual rainfall) between our studied two consecutive growing seasons (data not shown), the differences in plant size may mainly result in the yearly variation in the total seed yield; the large plants in 2016 had higher seed yields than the relative small plants in 2015. Although effects of irrigation on the seed size, seed oil concentration and seed yield depend on the date of harvest, neither irrigation nor fertilization significantly affected mean seed size and mean seed oil concentration of Sacha Inchi plants under different irrigation and fertilization treatments over the growing seasons (Table 2). This result was consistent with our previous researches concerning with fertilization and planting density (Jiao et al., 2012; Cai et al., 2013; Yang et al., 2014). Therefore, seed quality was not affected by different levels of irrigation or fertilization. The increased seed (fruit) numbers per unit area was mainly responsible for the influences of irrigation and fertilization on the total seed oil yield of Sacha Inchi plants. The positive relationships between total seed yield and C or N pools, rather than plant biomass, across different irrigation regimes (Table 1), indicating C and N shortages were an essential factor for yield formation of Sacha Inchi plant (Yang et al., 2016). Irrigation in the dry season increased the number of flower and decreased abortion of fruitlet of Sacha Inchi plants (Jiao et al., 2012). This, when coupled with the irrigation-induced mobilization of metabolites to the flower formation and fruit (seed) development when current available photo-assimilates were limited during the seasonal drought (Lebon et al., 2008), may have stimulated the switch from vegetative to reproductive growth and hence, caused an increase in harvest index and seed yield (Table 2; Fig. 3). Moreover, the mature stage of Sacha Inchi plants coincided with the dry season in our studied region (Fig. 4; Cai et al., 2013; Yang et al., 2014, 2016). Thus proper combination of irrigation and fertilizer can achieve higher yield, which might be associated with higher fertilization rate promoting reproductive growth (i.e., HI) and increasing yield under DI100 conditions.

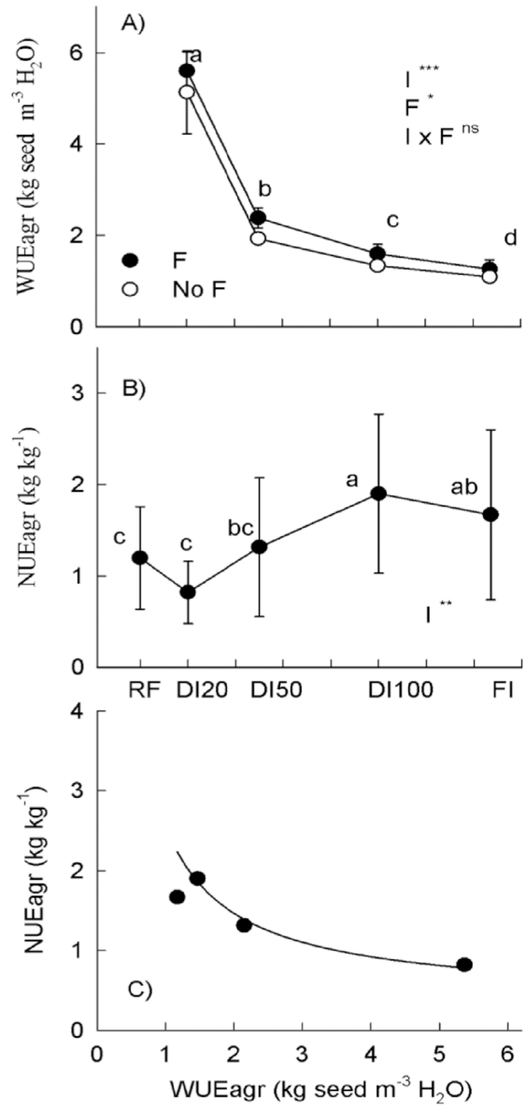

Fig. 5. Agronomic water use efficiency (WUEagr) and agronomic nutrient use efficiency (NUEagr) of *P. volubilis* plants in response to different irrigation (I) and fertilization (F) treatments and their relationships. The values with different letters denote significantly at $P < 0.05$ level. Ns, no significance; * $P < 0.05$; ** $P < 0.01$. Abbreviations of irrigation treatments are as defined in Fig. 1.

Expressed as seed yield per unit irrigation water applied, WUEagr is often considered an important determinant of yield under water deficit conditions. Effective use of water implies maximal soil moisture capture for transpiration, which also involves reduced non-stomatal transpiration and minimal water loss by soil evaporation. In agreement with the results of other studies (Singh et al., 2010; Afshar et al., 2016), WUEagr increased by fertilization regardless of irrigation treatments. Compared with DI100 and FI, WUEagr was much higher in DI50 and DI20 (Fig. 5A). Such a water saving phenomenon of using DI to increase WUE was also widely reported in herbal (Singh et al., 2010; Hergert et al., 2016) and woody crops (Romero et al., 2012; Gasque et al., 2016), with little or no yield penalty in some cases (but not in Sacha Inchi plant). But it still remains debatable if DI could achieve the dual goal of increasing the yield and saving water for woody crops (Fereres et al., 2014), as stomatal control over transpiration may differ between densely populated annual crops and trees that are more sparsely planted

(Marsal et al., 2008). Theoretically, crop yield is the product of transpiration, the ratio of aboveground biomass accumulation to plant transpiration, and harvest index. The three parameters, however, are not strictly independent of each other and there are tradeoffs among them, particularly between the first two. The negative relationship between total seed yield and WUEagr of Sacha Inchi plants supported the contention that maximum yield and maximum water productivity of woody crops are not always compatible goals (Fereres et al., 2014). However, in the case of agricultural management, there is probably no tradeoff between yield and water productivity (the ratio between yield and crop evapotranspiration); rather, improved managements are most likely to enhance both entities. Along other management practices (e.g., optimum planting density, high stand uniformity, and concentrating irrigation on the developmental stages that are most sensitive to water deficits), optimum irrigation scheduling could possibly lead to both higher yield and ceiling water productivity values (Quemada and Gabriel, 2016; Zhang et al., 2016). Agricultural nutrition use efficiency was marginally positively related to total seed yield and the highest value was found in FI across different irrigation regimes (Table 1). As the oil production in Sacha Inchi plants required high levels of fertilizer (Yang et al., 2014), the maximum NUEagr is expected when water inputs are close to crop water demand. However, the economics of nutrient and water use during photosynthesis is primarily interlinked through their mutual dependence on stomatal conductance, especially during drought. Stomatal closure contributes to increasing WUE but decreasing NUE, resulting in a trade-off between both traits. The negative relationships between WUEi and PNUE in the hot and dry season at the leaf level and between WUEagr and NUEagr at the field scale of Sacha Inchi plants are in line with this concept. In other words, although at the expense of WUEagr, maintaining NUEagr need to be paid the utmost attention in the water-rich areas (e.g., our studied site) where water supply is not the major limiting factor for Sacha Inchi plantation. But in arid areas where saving water will be given priority, more fertilizer should be applied to maintain high yield and to compensate the decreased NUEagr.

5. Conclusions

Irrigation should be applied to meet full evapotranspiration of Sacha Inchi plants at the cost of water use efficiency, but did not greatly influence their growth. Irrigation and fertilization treatments did not significantly affect seed quality (i.e., mean seed size and mean seed oil concentration); the seed (fruit) numbers per unit area was largely responsible for the total seed oil yield of Sacha Inchi plants. Carbon storage may be an active process, occurring at the expense of growth, whereas carbon and N shortages during the reproductive growth periods affected the final seed yield under drought conditions. The magnitude of their increases in total seed yield or total seed oil yield by fertilization was similar among different irrigation treatments (no irrigation × fertilization interaction). Compared with DI100, DI can save water but reduce the yield and need more fertilizers used (i.e. lower NUEagr), whereas DI100 and FI had higher total seed oil yield and NUEagr but reduced water use greatly. Moderate and severe DI (DI50 and DI20) applied in the dry season are not successful in increasing total seed yield or total seed oil yield over growing seasons of Sacha Inchi plants in tropical humid monsoon areas. Instead, relative to irrigation of water saturated soil, irrigation to 100% crop evapotranspiration in the dry season might be advisable to achieve high yield and NUEagr, while saving consistent amounts of water.

Acknowledgments

We thank the XSTRES for the meteorological data and the Public Technology Service Center of Xishuangbanna Tropical Botanical Garden for help with sample measurement. This work was financially supported by grants (31370684 and 31670686) from the National Natural Science Foundation of China. The first two authors contributed equally to this work.

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