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**Growth response of lowland rice to diurnal temperature
patterns under varying vapor pressure deficit**

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ABSTRACT

In arid and semi-arid areas, large diurnal temperature amplitudes and high evaporative demands are challenging rice cultivation. Since paddy rice is grown under flooded conditions, its growth is affected by both water and air temperature. However, water temperature may have a larger impact on the growth of rice due to its control of the plant's meristem temperature, particularly before booting stage when the meristem is below the water surface. Also, vapor pressure deficit (VPD) is an important climatic factor that determines the growth of rice due to changing canopy temperature and evaporative demand. Our greenhouse experiment aimed to determine growth responses of two rice varieties (IR64 and Sahel108) to three day/night water temperature regimes (constant temperature; warm day/cold night; cold day/warm night) under two VPD conditions (2.18 and 0.92 kPa). Individual plants were grown in pots containing one liter of the temperature-controlled nutrient solution. Leaf elongation rate (LER) was measured for the 9–10th leaf of the main tiller for 48 hours. Leaf appearance was determined by the water thermal time interval between appearances of leaves. At 4, 7 and 10 weeks after transplanting, three random plants from each treatment were selected to measure gas exchange, leaf area, morphological parameters and dry matter. Our results indicated a positive effect of low VPD and high meristem/root temperature during the night on leaf growth. Hence, low VPD induced a higher LER and earlier leaf appearance compared to high VPD for both varieties. Remarkably, under high VPD, highest LER were found during the night and in the early morning (12 a.m–8 a.m), whereas, under low VPD, the rate was highest between 8 a.m and 4 p.m. Under low VPD conditions, constant temperature led to a higher LER but only for IR64, whereas under high VPD, highest leaf growth was observed under cold day/warm night treatments for both varieties. Under low VPD, cold day/warm night conditions led to a greater root growth, a higher root/shoot ratio and more total dry matter in both varieties, while under high VPD this effect was only found for IR64, but not for Sahel108. Low VPD induced higher stomatal conductance for both varieties, but no significant impact on the photosynthetic rate was recorded. Remarkably, there was no significant influence of water temperature treatments on stomatal conductance and photosynthetic rate. Our results suggested that VPD has a larger impact on diurnal leaf growth patterns than temperature alone. Since under high evaporative demand, rice leaves mainly grow during the night and in the early morning, night temperature can have a larger effect on plant growth than day temperature. Furthermore, cold day/warm night conditions largely increased leaf and root growth, which might enable rice plants to

tolerate a high VPD during the day and therefore promoted plant growth. Also, our results confirmed the differences in growth responses of the two varieties which have already been described; accordingly IR64 is more sensitive to VPD and root and meristem temperature than Sahel108.

Key words: leaf elongation rate, water temperature, rice leaf, rice root, VPD

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Abbreviation

CD: cold day/warm night

CN: warm day/cold night

CT: constant temperature

FAO/STAT: Food and Agriculture Organization of the United Nations

Gs: stomatal conductance

LER: leaf elongation rate

LA: leaf area

RL: total root length

RSA: root surface area

RD: root diameter

R/S: root/shoot

T_{ns}: nutrient solution temperature

VPD: vapor pressure deficit

WAT: weeks after transplanting

1. Introduction

1.1. Background

Rice serves as the staple cereal in many countries; particularly in the Asia-Pacific region where more than 90% of global rice are produced and consumed. With the third largest harvested area (after wheat and maize, respectively) and the second highest production worldwide, rice plays a crucial role in food security and nutrient balance (Papademetriou, 2000; FAOSAT, 2015). It provides the primary food and calorie source for more than a half of the world's population, especially in developing countries. According to Gnanamanickam (2009), about 21% of energy and 15% of the protein in human consumption are derived from rice. Remarkably, it contributes up to 35-60% of caloric intake annually for three billion people in Asia (Guyer et al., 1998). In the future, even though per capita rice consumption is expected to decline, the total rice consumption will increase due to the increasing population. The rice demand is predicted to reach over 700 million tons by the year 2025, and thus enhancing rice production is necessary to meet the increasing rice consumption (Papademetriou, 2000).

Generally, lowland rice cultivated under adequate irrigated conditions has a higher yield than upland rice. Worldwide, irrigated rice accounts for about 57% of the total rice area, but contributes 76% to the total rice production. Also, it is believed that improving rice productivity under irrigation is easier than under rain-fed or other rice ecosystems. Moreover, approximately 70% of the additional rice production in the future is expected to come from irrigated rice, while almost 21% may be produced in rain-fed lowlands (Papademetriou, 2000).

However, rice production is facing many challenges such as climate change, environmental degradation and even the difference in cultivated condition between regions. In arid and semi-arid environments, large diurnal temperature amplitudes and a high evaporative demand by the atmosphere are considered among the most limiting factors for rice growth. The difference in air temperature between day and night might leads to direct change in meristem temperature under non-flooded condition or indirect change under flooded condition due to the influence on water temperature. According to Stuerz et al. (2014b), meristem temperature was lower without a ponded water layer compared to flooded conditions. Since lowland rice is grown under flooded conditions, the temperature of the standing water may have a larger impact on the plant's meristem and therefore on rice growth than air temperature (Shimono et al., 2002; Stuerz et al., 2014a,b,c). Also, studies have been investigated the influence of water

and meristem temperature on gas-exchange (Stuerz et al., 2014b), metabolism (Jia et al., 2015), nutrient uptake (Shimazaki et al., 1963), growth of tillers and leaves (Matsushima et al., 1964, Stuerz et al., 2014 a,c), biomass production and the yield of rice (Shimazaki et al., 1963; Matsushima et al., 1964; Shimono et al., 2002). However, most previous experiments were done with short-time temperature treatments at a particular time of the day or with a constant extreme-temperature between day and night.

As mentioned above, high evaporative demand (low humidity) is another constraint for rice production, particularly in arid and semiarid areas. The relative humidity is expressed as the percentage between the actual vapour pressure and the vapour pressure at saturation of the atmosphere at the same temperature, whereas the vapour pressure deficit (VPD) presents difference between the saturated and the actual vapour pressure at the same temperature. The VPD has a strong impact on gas exchange and water use efficiency of plants due to changing canopy temperature and stomatal activity (Thomas et al., 1996). Some studies have reported the sensitivity of rice to evaporative demand, indicating that high VPD significantly reduces plant growth rate (Estela et al., 2009) or delays the flowering open time (Kobayasi et al., 2010; Julia and Dingkuhn, 2012). However, the effect of VPD should be taken into account in relation to air temperature due to the heat capacity of water vapor. Low VPD under high air temperature conditions caused higher spikelet sterility and lower grain yield, resulting from increasing organ temperature (Ayinde et al., 2013; Weerakoon et al., 2008). In contrast, a larger difference between air temperature and organ temperature was observed under high VPD resulting from a transpirational cooling; hence, high VPD could diminish the adverse effect of high air temperature (Weerakoon et al., 2008; Yan et al., 2008; Wassmann et al., 2009).

Moreover, high evaporative demand in low humidity regions may lead to higher plant's water consumption due to increase of transpiration. The water loss via the transpiration can be compensated by water take up via root; however, the process was affected by several factors involved root temperature (Ku wagata et al., 2012). Some previous studies indicated that a decrease of water uptake under low root temperature caused by a reduction in root hydraulic conductivity (Nagasuga et al., 2011; Ku wagata et al., 2012).

Until now, the impact of changing day/night water temperature as well as root and meristem temperature in combination with different VPD levels on rice growth has barely been studied so far. Therefore, an adequate study on the growth responses of rice to diurnal temperature patterns at the level of root and meristem under varying

VPDs could be crucial for a deeper understanding of morphological growth responses and physiological processes as well as it could help improving growth model of rice. The research was expected to answer the following questions:

1. How does rice respond to diurnal root and meristem temperature patterns under different VPD levels?
2. Are there any variations between genotypes in the responses to diurnal root and meristem temperature patterns and different VPD levels?

1.2. Hypothesis

In traditionally flooded lowland systems, the plant's meristem is below the water surface during the vegetative stage and therefore affected by water temperature. It has been proposed that night temperature at meristem level can have a larger impact on gas exchange parameters and leaf growth than day temperature (Stuerz et al., 2014a,b). To estimate morphological and physiological responses of rice to diurnal root and meristem temperature patterns under varying VPD, a hydroponic rice cultivation system was designed. In this hydroponic system, root and meristem temperature was regulated via the temperature of the nutrient solution T_{ns} . Since it has been shown that the evaporative demand from the atmosphere has an effect on diurnal leaf growth patterns (Laferge et al., 1998; Parent et al., 2010), the experiment was conducted under low and high vapor pressure deficit. Therefore we hypothesize:

1. Day/night temperature patterns and VPD influence the rate of leaf elongation and leaf expansion and thus leaf area;
2. Root growth dynamics are affected by day/night root and meristem temperature patterns and VPD;
3. Gas exchange is influenced by diurnal root and meristem temperature and VPD leading to changes in dry matter;
4. Varieties will show differences in their response to diurnal temperature patterns under varying VPD.

2. Literature review

2.1. Global rice production

Rice in the World

Worldwide, there are two main cultivated rice species which are *Oryza glaberrima* (African rice) and *Oryza sativa* (Asian rice); however, the Asian rice is the most widely produced (Linares, 2002). Rice production worldwide and in each rice-growing region are determined by harvest area and grain yield per ha. In recent years, rice is cultivated in 113 countries with varying growth conditions, but the highest prevalence is in Asia, which has the biggest annual rice production. In 2011, the global rice production was approximately 722 million tons; of those, Asia contributed 655 million tons. From 1992 to 2002, global rice area strongly fluctuated in the range from 146 to 157 million ha; remarkably, the area dropped from approximately 157 million ha in 1999 to around 147 million ha in 2002 (Fig. 1). Even though there was a slight fluctuation, the rice area increased strongly in recent years and reached 162 million ha in 2011 (FAOSAT, 2015).

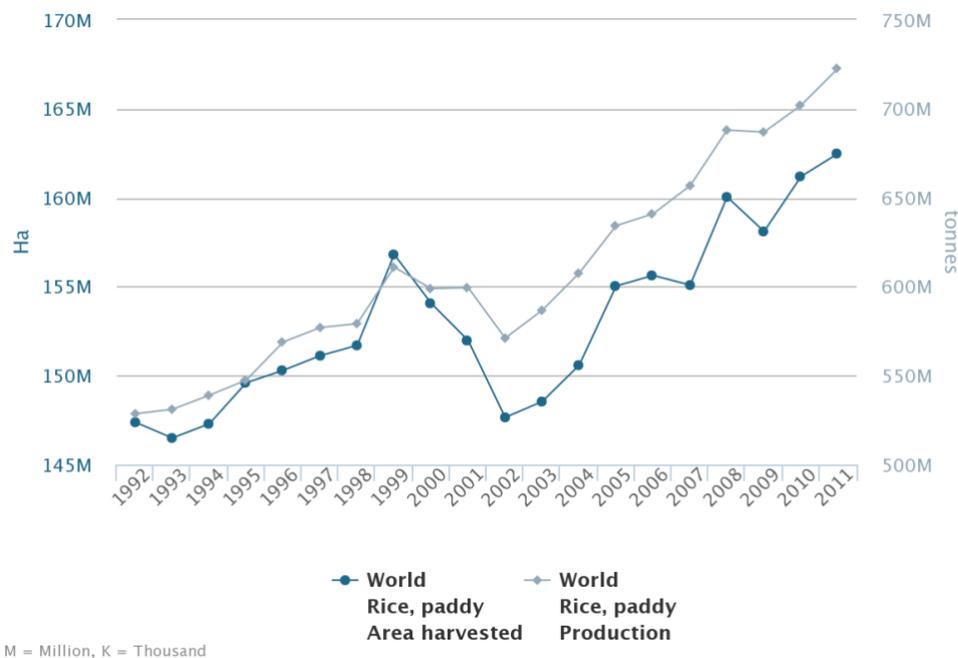


Figure 1. Productivity and harvested area of paddy rice over the world
(Source: FAOSAT-access date: 3/2015)

The global average yield in 2013 was 4.48 tons per ha, which was an increase of 13.5% and 23.5% compared to the yields in 2003 and 1993, respectively. Although the rice yield consistently increased during the last decade, there existed a big gap among regions due to the difference in climatic condition and cultivation techniques. In general, the highest yield of rice was found in Oceania, whereas the lowest yield was

recorded in Africa. In recent years, China, India, Vietnam and Bangladesh were the four top rice producers, respectively (FAOSAT, 2015).

Trends in rice production

With over 90% of rice production and consumption in Asia, the world's rice trend mostly depends on the trend in this region (Kubo and Purevdorj, 2004). In accordance to Zhang et al. (2004), there was a linear increase in the rice area from 1961 to 2011 in most of the rice-growing regions, with an exception in South America. According to this, growth rates of rough rice areas were 748,240 and 589,630 ha per year for the World and Asia respectively. Kubo and Purevdorj (2004) also reported an increase of 34 million ha in total harvested area between 1960 and 2000 worldwide. In Asia, the yield per ha in this region doubled from 2.0 tons/ha in 1960 to 4.0 tons/ha in 2000. The highest increase of yield was found in Oceania with 275% over the past 40 years, resulting from the favorable climatic conditions and advanced technology application. In contrast, the lowest increase in rice yield was observed in Africa, where upland rice is grown in combination with poor cultivation techniques.

Remarkably, in the international market, the share of traded rice is very low with less than 5 percent of the total rice production (Papademetriou, 2000). Of 722 million tons of rice produced in 2011, only 36.2 million tons reached to global market and a half of those came from Southeast Asia (FAOSAT, 2015). This implies that almost the entire rice production does not leave the local market. According to Kubo and Purevdorj (2004), rice consumption increases faster than the increase of population. For example, the rice consumption worldwide increased from 242 million tons in 1961 up to 599 million tons in 2000 with an annual rate of 2.4%, while the global population increased by 1.8% annually. Until 2030, the world population is predicted to increase by a factor of 1.4 compared to 2000 and will reach 8.27 billion. Following the trend of the past, rice production is expected to rise by a factor of 1.5 and reaches 904 million tons by 2030. Also, Zhang et al. (2004) predicted an increase trend in yield and harvested area of rice for the future. By 2025, the rice area would increase by 17.47% in total compared to 2002 and reach around 172 million ha; of those, 152 million ha will be in Asia, which is predicted to have the highest growth rate. Moreover, the yield of rice is forecasted to increase to 5.32 and 5.41 tons per ha in 2025 in the world and in Asia, respectively. However, Papademetriou (2000) indicated the challenges for rice production of the future such as less land and less water. Irrigated rice is expected to largely contribute to increasing rice production, but increasing water scarcity, competition for water, salinisation or emission of greenhouse gases are challenges that

irrigated rice production has to face. Moreover, climate change will be an important factor that could cause a reduction of rice yields in the future.

2.2. Meristem temperature and root temperature

Water temperature and plant meristem temperature

The water temperature in the field is dependent on several climatic factors such as solar radiation, relative humidity and air temperature or non-climatic factors including crop cover, depth of the water and soil color (Dingkuhn, 1992). However, the difference between water temperature and air temperature is mostly driven by plant cover. Dingkuhn et al., (1995) indicated a close relation between water temperature and LAI (leaf area index) of rice in the Sahel region. Accordingly, the maximum water temperature decreased with an increase in LAI and remained constant starting at an LAI value of 4-5. Without crop cover, the minimum water temperature was 1°C lower than the minimum air temperature, whereas under fully-established crops, the minimum temperature was 2.5°C higher than the minimum air temperature. However, mean water temperature was lower than mean air temperature, especially with higher leaf cover and on dry day. In a rice experiment, Stuerz et al. (2014c) found the dependence of water temperature on season; thereby, the difference between minimum water temperature and air temperature was higher in cold dry season than in hot wet season.

Since lowland rice is sown and grown under flooded conditions, growth and development of rice are affected by both air and water temperature. However, the water layer in the field plays a larger role for plant's meristem temperature, particularly during the vegetative stage, when the meristem is below a flooded water layer. Therefore, water temperature may have a greater impact on plant growth than air temperature. Stuerz et al., (2014a,b) reported a higher meristem temperature of rice during the night under a ponded water layer compared to that under wet soil conditions. However, the effects of water temperature on rice growth depend on the position of the meristem or on the growth stage of the plant, respectively (Tsunoda and Matsushima, 1962). Sié et al., (1998a) indicated a linear correlation between the development rate of rice before the first leaf appearance and water temperature in the large range from 14-30°C. Also, cold water delayed germination of seeds and the emergence of the second to the fifth leaf. At a later development stage, the length of the panicle induction phase was mainly determined by photoperiod and water temperature (Sié et al., 1998b). During the vegetative phase, cold water stress caused reductions in tillering rate, leaf emergence, and leaf elongation rate (LER), the number

of panicles, spikelet number per panicle, fertility and thus reduced the yield of rice (Shimazaki et al., 1963; Matsushima et al., 1964; Yoshida, 1981; Shimono et al., 2002). Also, Shimono et al. (2002) reported a higher sterility and lower grain yield caused by low water temperature during the reproductive stage.

Since the rice meristem is below the water surface during the first half of growth duration, changes of water temperature significantly affects the meristem temperature and thus leaf growth. Some studies have indicated the high relation between leaf growth and water temperature or meristem temperature. Shimono et al. (2002) reported a close correlation between relative leaf growth rate and irrigation water temperature, where the growth rate decreased by 50% on average with a reduction of water temperature of 5°C. Lower irrigation water temperature induced lower LER and lower leaf appearance rate (LAR) (Matsushima et al., 1964; Shimono et al., 2002; Shimono et al., 2004). Stuerz et al., (2014a) demonstrated a positive correlation between LER and meristem temperature of rice during the night; consequently the rate increased with increasing meristem temperature. Ishii et al. (2011) reported an increase in leaf expansion of rice caused by higher water temperature. Also, leaf area (LA) was significantly correlated with meristem temperature; therefore, low meristem temperature led to a reduction in LA. Under non-flooded conditions, leaf area per plant decreased by 17% with an average decrease in meristem temperature of 1.8°C (Stuerz et al., 2014b). Shimono et al., (2002) also indicated a significant reduction in LA caused by cold irrigation water in almost all growth stages, induced by the inhibition of growth rate. Moreover, Parent et al. (2010) reported a difference in leaf growth rate between day and night; therefore higher LER was observed during the day than during the night due to a higher day temperature.

The influence of meristem temperature on leaf growth was also reported for other crops. Ben-Haj-Salah and Tardieu (1995) found a high correlation between meristem temperature and LER of maize. In growth chambers, the rate was constant during the study period, resulting from the consistent meristem temperature. However, under field conditions, LER increased with rising meristem temperature in the range from 13°C to 30°C during the day and decreased during the night due to a drop in temperature. Also, Rymen et al. (2007) reported a negative impact of low night temperature on leaf growth of maize. Hence, cold night conditions (25/4°C day/night temperature) reduced the final leaf size and leaf elongation over a 24 hours period by 20% and 35%, respectively compared to control conditions (25/18°C). On sorghum, Lafarge et al. (1998) indicated a linear relationship between meristem temperature and LAR. For leaf elongation, under low evaporative demand, LER positively correlated to the meristem temperature in a broad range from 13°C to 32°C.

The effects of environmental temperature on leaf growth can be explained by the alteration in cell cycle duration in meristem. In monocotyledonous, leaf elongation involves cell division in the meristem followed by cell expansion; both processes overlap partly in time and space and correlate with cell temperature (Silk, 1992). Many studies have reported that higher meristem temperature stimulates these processes. Ben-Haj-Salah and Tardieu (1995) indicated that the cell division rate of maize leaves was five times higher at 30°C than at 13°C. Cell division and expansion were coordinated; therefore, rapid cell elongation under high temperature also led to rapid cell division. Moreover, in the elongation zone, cells responded rapidly and simultaneously to changing temperature; thus the length of the elongation zone increased with rising temperature. Rymer et al. (2007) also found that cold nights led to a reduction in cell production rate in the basal meristem of leaves by 22% due to a prolonged cell cycle progression and an alteration in the cell expansion dynamics. The longer cell cycle duration under low temperature was attributed to an increase of cell cycle inhibitors or the down-regulation of positive regulators of cell division.

Moreover, previous experiments showed the influence of water temperature on gas-exchange and biomass production. Ishii et al. (2011) conducted field experiments in two years (2008 and 2009) to examine the effects of irrigation water temperature and nitrogen application on rice productivity under a cool climate. Rice plants were exposed to a control water temperature ($21.3 \pm 3.0^\circ\text{C}$ and $21.2 \pm 2.6^\circ\text{C}$ in 2008 and 2009, respectively) and higher water temperatures treatments ($24.1 \pm 2.9^\circ\text{C}$ and $23.9 \pm 2.9^\circ\text{C}$, respectively) during the vegetative stage. The result showed that high water temperature during vegetative stage led to a strong reduction in photosynthesis and SPAD value at the grain filling period. This could be attributed to a lower N supply at the reproductive stage caused by a higher N mineralization rate in the soil under warmer water condition. However, plant growth rate was promoted under higher water temperature, resulting from a larger leaf expansion and a higher canopy radiation capture. They also observed no significant effect of water temperature on the number of tillers, total biomass, and grain yield of rice in the experiment. In another experiment, Stuerz et al. (2014c) estimated the gas-exchange response of rice to meristem temperature. The research was carried out with three rice varieties and five different sowing dates under flooded and non-flooded condition. The results showed that G_s (stomatal conductance) strongly correlated with minimum meristem temperature. The study also hypothesized a regulatory influence of meristem temperature on G_s and assimilation rate. However, Shimono et al. (2004) indicated that the relation depends on growing stage; hence, lower meristem temperature

significantly reduced G_s and assimilation rate of rice, but only in the reproductive phase. Remarkably, radiation use efficiency was not affected by water temperature. Shimono et al. (2002) estimated the effects of cool irrigation water on growth responses of rice at three different growth stages (vegetative, reproductive and early grain filling) during 20 to 34 days of each stage. However, no significant effect of water temperature on radiation use efficiency was recorded during the vegetative and reproductive stage, which was explained by an acclimation of the plants to low water temperature. Moreover, under low water temperature, the leaves became thicker and showed a higher N content due to smaller leaf area and thus probably compensated the adverse effect of low water temperature. However, the experiment demonstrated that cold water at all periods sharply reduced crop growth rate which is mainly attributed to a lower leaf area, lower canopy radiation interception and lower radiation use efficiency. Moreover, high water temperature induced a lower tiller number resulting from a shortened duration.

Furthermore, some studies have reported the influence of water temperature on the duration of rice and development rate. In general, lower temperature leads to longer duration. Evidence from Shimono et al. (2002) indicated an increase in duration of rice with a decrease in water temperature. In the experiment of Ishii et al. (2011), higher water temperature resulted in shorter growth duration of plants and thus heading stage occurred earlier.

In addition, changes in the metabolism of rice under different water temperatures have found in some studies. Jia et al. (2015) showed the adverse effect of low water temperature on the metabolism of rice, but also its variation with the duration of exposure. Correspondingly, glutamate aminobutyric acid (GABA) content was increased under a short time treatment (3-6 days), but decreased under a longer time treatment (9-15 days). Glutamate content and glutamate dehydrogenase (GDH) activity have a greater impact on grain yield and spikelet sterility. The decrease in photosynthesis under stress causes a high demand for energy which is compensated by deamination of amino acids via GDH. However, most of the cold water treatments led to a reduction in GDH (Ueki, 1960).

Also, water temperature has a significant effect on rice yield. Low water temperature (below 20°C) during all growth stages induced a significant reduction in grain yield of rice, resulting from a higher sterility and lower panicle number (Shimono et al., 2002). The same research group also found a strong increase in sterility caused by low water temperature during the vegetative stage (Shimono et al., 2004). However, the

reduction in rice yield caused by low water temperature depended on the duration of exposure and on the genotype (Jia et al., 2015). Shimono et al. (2004) reported that warmer irrigation water during a later growth stage could diminish sterility caused by low air temperature or by low water temperature during an earlier growth stage. Increased water depth extended the duration of the panicle being below the water surface, which reduced sterility under low air temperature when water temperature was higher than air temperature (Nishiyama et al., 1969; Jia et al., 2015). It is known that high temperature may promote rice growth, but the relation between water temperature and yield is not linear. Ueki (1960) studied the influence of high water temperature during early panicle development of rice. The result indicated that plants grown under high water temperature (32°C and 37°C) had more spikelets compared to the control treatment (26°C).

Water temperature and root temperatures

Water temperature does not only influence meristem temperature, but also soil and therefore root temperature. The effects of water and root temperature on root growth have been determined in previous studies. Ueki (1960) found a negative influence of high water temperature during early panicle development on root growth of rice. Hence, the total amount of roots decreased, while the number of rotten roots increased at water temperatures of 32°C and 37°C compared to 26°C. Rice grown under root temperature at 18°C led to lower cation uptake but an increase in root dry matter in comparison to that at 30°C (Ehrler and Bernstein, 1958). In contrast, in a rice experiment, Kuwagata et al. (2012) reported a decrease of water up take caused by low root temperature. Moreover, low root temperature significantly reduced transpiration, leaf area, total dry matter and root dry matter. Also in the experiment, they found a lower stomatal conductance caused by low root temperature at high humidity but not at low humidity. Engels (1994) indicated a reduction in root growth of maize and wheat under low root zone temperature. For wheat, the reduction of shoot growth was stronger than that of root growth, while the opposite was true for maize, which led to a lower ratio of shoot:root dry matter for wheat, but not for maize. Moreover, Shimazaki et al. (1963) indicated a decrease in nutrient uptake of rice including nitrogen (N), phosphorus (P) and potassium (K) in plants treated with cold water of 17°C during 30 days.

In maize, Pritchard et al. (1990) found a decline in cell expansion rate caused by low root temperature. In a long-term experiment, the elongation rate of a root at cold condition (5°C) was 0.02 mm h⁻¹, while it was 1.2 mm h⁻¹ under warm conditions. The

low growth rate in the root tip under low temperature could be explained by a decrease in root cell pressure, which affected the cell elongation. With the transfer of the roots from the cold to the warm, root elongation rate was fully restored after 100 hours in the long-term experiment and within 25 minutes in the short-term experiment. Ymakawa and Kishikawa (1957) also estimated the effect of temperature on cell division and elongation of rice root; therefore, the cell division was highest stimulated at 25°C while the largest cell elongation was found at 30°C.

So, the effect of root or water temperature on root growth varied between experiments, which depended on the temperature and time of treatments. However, many studies showed the stimulation of root growth by high root temperature, whereas, low temperature inhibits root growth. The process was driven by the inhibition of positive regulators or by the stimulation of negative regulator of the cell cycle under low temperature (Rymen et al., 2007; Cruz-Ramírez et al., 2012; Kuwagata et al., 2012; Zhu et al., 2015). Zhu et al. (2015) found the reduction of root growth under low temperature with a decrease in auxin content due to changes in auxin transport and biosynthesis, which affected cell division.

2.3. Rice and vapor pressure deficit

Relative humidity represents the amount of water vapor in the atmosphere at a particular temperature. According to Thomas et al. (1996), "Relative humidity can be defined as the ratio of the amount of moisture in a volume of air to the total amount of moisture that can be held at saturation at a given temperature and atmospheric pressure, and is expressed as a percentage". Atmospheric humidity can also be described as vapor pressure deficit (VPD) which presents difference between the saturated and the actual vapour pressure at the same temperature. With regard to plants, VPD determines the transpiration rate, resulting from the difference in the vapor pressure in the air and inside the leaf. Relative humidity or VPD mostly depends on air temperature and the amount of vapor in the air; hence there is a close relation between absolute humidity and air temperature (Ayinde et al., 2013). Kobayasi et al. (2010) found that radiation and air temperature had a high correlation with VPD, while wind speed showed a weak correlation. In the tropics and subtropics, we might divide rice cultivation regions into hot/dry and hot/humid regions based on the temperature and relative humidity (Wassmann et al., 2009).

Some previous studies have reported the impact of VPD on LER and LAR of rice. Estela et al. (2009) assessed the responses of different rice genotypes to the interactive effect of temperature and VPD. Two growth chambers were used with the

same day/night temperature regime (32°C/22°C), but different relative humidity levels (0.74 kPa and 1.84 kPa). Seedlings of four rice genotypes (Akihikari, IR64, N22, and Takanari) at the age of 21 days were grown in the growth chambers for 30 days. The results showed a strong effect of VPD on leaf temperature; therefore the leaf temperature was significantly higher under low VPD in comparison to that under high VPD. There was a significant interaction between VPD and genotype for leaf elongation, resulting from the variation in leaf temperature among varieties. Moreover, high VPD sharply reduced leaf area and plant height with an interactive effect of VPD and genotypes. Interestingly, the number of tillers was significantly increased under high VPD without significant variation among genotypes. Parent et al. (2010) reported a negative effect of high VPD on LER of rice. Therefore, greater LER was found during the night than during the day if the rate was presented per equivalent hour at 20°C due to lower evaporative demand at night. In a greenhouse experiment, the LER decreased at the beginning of the day resulting from increasing evaporative demand and dropped to the lowest point at the afternoon with highest evaporative demand. However, a variation in the responses to VPD among genotypes was reported. Under the same growth conditions, the highest LER was found in *O. japonica* followed by *O. indica* and *O. glaberrima*, respectively. Lafarge et al. (1998) also indicated that under the same air temperature, VPD has a stronger effect on LER of sorghum than meristem temperature. LER responded linearly, but inversely proportional to evaporative demand; thus, low VPD led to a higher rate than high VPD. Moreover, Kuwagata et al. (2012) also indicated a significant reduction of total leaf area and total dry matter of rice under low humidity in comparison to that under high humidity.

The vapor pressure deficit also has an impact on the time of flowering and on sterility. Low VPD resulted in earlier anthesis, while high VPD delayed this process. Early flowering in the morning reduces sterility caused by later rising temperature. The late flowering under high VPD can be associated with the decrease in tissue temperature, resulting from transpirational cooling (Julia and Dingkuhn, 2012; Kobayasi et al., 2010). Many studies have indicated the effect of VPD on grain yield of rice via changing spikelet and pollen temperature (Abeyasiriwardena et al., 2002; Matsui et al., 2007; Weerakoon et al., 2008). Interestingly, a larger difference in organ temperature under high VPD could diminish grain sterility caused by high air temperature. Under high air temperature, high VPD enhanced spikelet fertility and thus significantly reduced sterility due to lower spikelet temperature (Abeyasiriwardena et al., 2002; Weerakoon et al., 2008; Yan et al., 2008). Also, Ayinde et al. (2013) reported an

adverse effect of high humidity in combination with high air temperature on rice production in Niger state, Nigeria; accordingly, rice production decreased on average by 17% for every 1% increase in humidity. The impact of relative humidity was closely related to air temperature, since it caused a difference in organ temperature and air temperature (TD_s). The increase in relative humidity could lead to a rise in organ temperature. Increasing the relative humidity from 55-60% to 85-90% at a constant temperature regime (day/night temperature: 35/30°C) induced an increase of 1.5°C in spikelet temperature (Abey Siriwardena et al., 2002). Yan et al. (2008) also reported a significant effect of relative humidity on TD_s , therefore, under the same air temperature, the TD_s was larger under low humidity compared to that under higher humidity. Wassmann et al. (2009) reported that VPD had a larger impact on transpirational cooling than temperature. In regions with temperatures exceeding 40°C, transpirational cooling becomes an advantage for rice growth due to a lower organ temperature. Weerakoon et al. (2008) determined spikelet sterility under high temperature (32-36°C) for different relative humidity levels (60 and 85%). The results showed that spikelet sterility increased with simultaneously increasing temperature and humidity. However, at temperatures below 30°C, high humidity did not cause a reduction in spikelet fertility. Using a simple heat budget model, Matsui et al. (2007) indicated a lower canopy temperature under hot and dry conditions compared to humid conditions. Canopy temperature was 0.6°C below ambient temperature at 30°C and 60% relative humidity while the difference was 4.6°C at 30°C and 20% relative humidity. Canopy temperature was 6.8°C lower than ambient air at 34.5°C and 20% relative humidity (VPD=4.32 kPa) with the support of substantial wind speed. The lower canopy temperature under higher temperature and higher VPD was mainly attributed to the intense transpirational cooling.

Earlier studies have shown the species-dependent effect of VPD on stomatal activity. In rice, low humidity led to significant higher transpiration per unit leaf area in comparison to high humidity (Ku wagata et al., 2012). Increasing VPD in the range from 0.5 to 1.5 kPa did not affect stomatal conductance and apparent CO_2 uptake rate of coffee, tea, cacao, whereas these parameters linearly decreased at VPDs above 1.5 kPa. The results also indicated that high VPD rapidly decreased leaf conductance, without an effect on leaf water potential (Hernandez et al. 1989). However, the response in stomatal conductance to VPD varied among species. Transpiration rate of sunflower decreased with increasing VPD in the range from 1-4 kPa, whereas the rate of coffee, cacao, and tea slightly increased for VPDs from 1-1.5 kPa and then strongly decreased at higher VPD levels above 1.5 kPa. The differences in leaf conductance and

transpiration were partially attributed to stomatal sensitivity to VPD (Hernandez et al. 1989). Also, Pallardy and Kozlowski (1979) showed the effect of VPD on stomatal conductance of *Populus*. Thereby, higher VPD led to stomata closure especially under low light, which reduced transpiration and thus increased water use efficiency under unfavorable conditions. However, the sensitivity of stomata to VPD varied between varieties.

To conclude, rice is an important food crop in many regions, particularly in Asia. In general, rice productivity is expected to increase in the future; however, rice production is also challenged by environmental changes and increasing water scarcity. Also, there is large gap in yield between rice growing regions due to variation in climatic conditions and cultivation techniques. In arid and semi-arid regions, one of the most limiting factors for rice yield is the high difference in diurnal temperatures and the high evaporative demand, which influences organ temperature, especially meristem and canopy temperature and thus plant growth. Many previous studies have been shown the greater impact of water temperature on rice growth in comparison to air temperature. Since lowland rice is mostly grown under flooded conditions, water temperature has a larger effect on root and meristem temperature, particularly during vegetative growth stage when the plant's meristem is under the surface water layer. On the whole, high root and meristem temperature and low VPD stimulates leaf and root growth, gas-exchange and thus enhances plant growth. However, some studies indicated a larger effect of VPD on leaf growth compared to meristem or water temperature; therefore, lower VPD leads to stronger leaf elongation rate and leaf expansion. Low VPD leads to higher canopy temperature at the same ambient temperature than that under high VPD. Furthermore, under high temperature, high VPD led to a greater difference between organ and air temperature caused by transpirational cooling, which can diminish the adverse effect of high air temperature.

3. Materials and Methods

3.1. Research site and materials

Research site: The research was carried out from September to December 2014 in a greenhouse of the Institute of Plant Production and Agroecology in the Tropics and Subtropics, University of Hohenheim, Germany.

Plant materials: In our experiment, we used two *indica* rice varieties (IR64 and Sahel108). Sahel108 comes from West Africa and is targeted for the dry season, whereas IR64 comes from the Philippines and is adapted to the humid tropics. Both are short duration, improved rice varieties.

3.2. Experimental set up

The experiment was arranged in a randomized block design with three replications to estimate the impact of three diurnal root and meristem temperature regimes under two VPD conditions on the growth of two rice varieties during the vegetative stage.

Seed germination: Seeds of two varieties were germinated on wet filter paper in separate plastic boxes for 72h. After that, germinated seeds were transferred to two seeding trays containing clean sand. The trays were placed in tight trays containing 25% YOSHIDA nutrient solution and were exposed to light (Fig. 2).

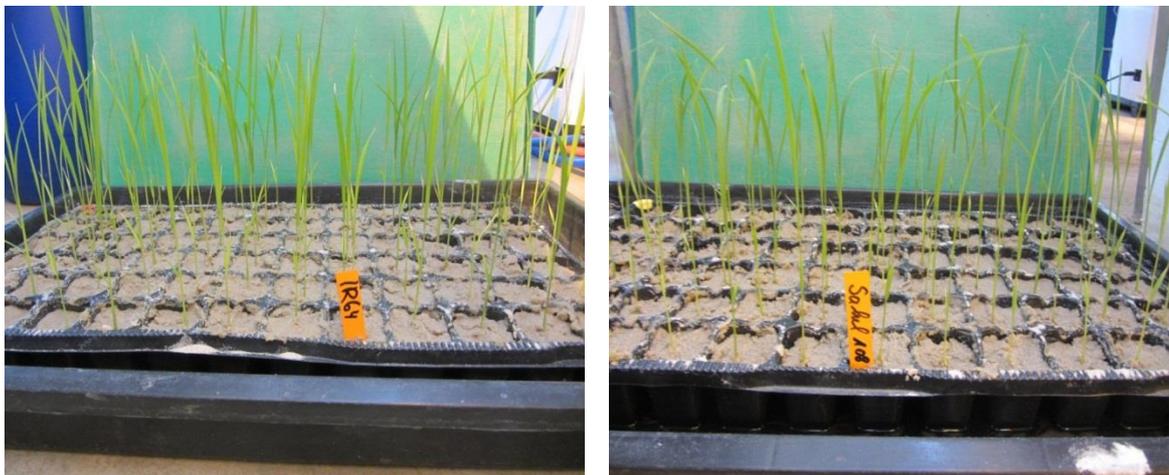


Figure 2. Seedlings of two rice varieties

Plant growth: After ten days, the seedlings were transplanted to culture pots; each was filled up with one liter of YOSHIDA nutrient solution. Only in the first week, plants were grown in 50% YOSHIDA nutrient solution to avoid salt stress, and then the nutrient solution was renewed every week using 100% YOSHIDA nutrient solution. The

ingredients of the nutrient solution in the experiment are listed in Table 1. Sodium hydroxide (NaOH) was used to adjust the pH of the solution to the value of 5.5.

Table 1. The ingredients of YOSHIDA culture solution

Element	Chemical	Concentration (mg/L)
N	NH ₄ NO ₃	2089
P	NaH ₂ PO ₄ *2H ₂ O	850
K	K ₂ SO ₄	111
Ca	CaCl ₂ *2H ₂ O	986
Mg	MgSO ₄ *7H ₂ O	710
Citric acid	C ₆ H ₈ O ₇	750
Fe	FeCl ₃ *6H ₂ O	685
Mn	MnCl ₂ *4H ₂ O	700
Zn	ZnSO ₄ *7H ₂ O	965
Cu	CuSO ₄ *5H ₂ O	203
Mo	(NH ₄) ₆ Mo ₇ O ₂₄ *4H ₂ O	430
B	H ₃ BO ₃	50

(Source: Institute of Plant Production and Agroecology in tropics and subtropics)

VPD treatments: Growth chambers were designed to create two different VPD conditions; one was low VPD (0.92 kPa) and other was high VPD (2.18 kPa). Fans were fitted to ensure movement of air and a uniform microclimate in each growth chamber. Relative humidity and air temperature were automatically recorded every 10 minutes with Tinytag data loggers, which were placed 20 cm above the canopy. The data was used to calculate VPD for each growth chamber (Table 2).

Root and meristem temperature treatments: In order to estimate the effect of root and meristem temperature on plant growth, three diurnal nutrient solution temperature (T_{ns}) regimes were established: constant temperature (CT) and warm day/cold night (CN), cold day/warm night (CD). Temperature of the nutrient solution was indirectly controlled via a tube system inside the culture pots. Water, which was temperature controlled by a heating-cooling unit, was used as cooling agent and pumped through the tubes inside culture pots. The systems are illustrated in figure 3 and figure 4.

HOBO[®] sensors were placed inside the pots to record the solution temperature every 10 minutes. The mean day and night nutrient solution temperature of each treatment is presented in Table 2. Root and meristem temperatures were not measured, but they were expected to be equal to nutrient solution temperature, because roots and meristems were exposed to the nutrient solution during the time of the experiment.

Water temperature between day and night time was adjusted automatically with 12/12h day/night cycle based on photoperiod regime.

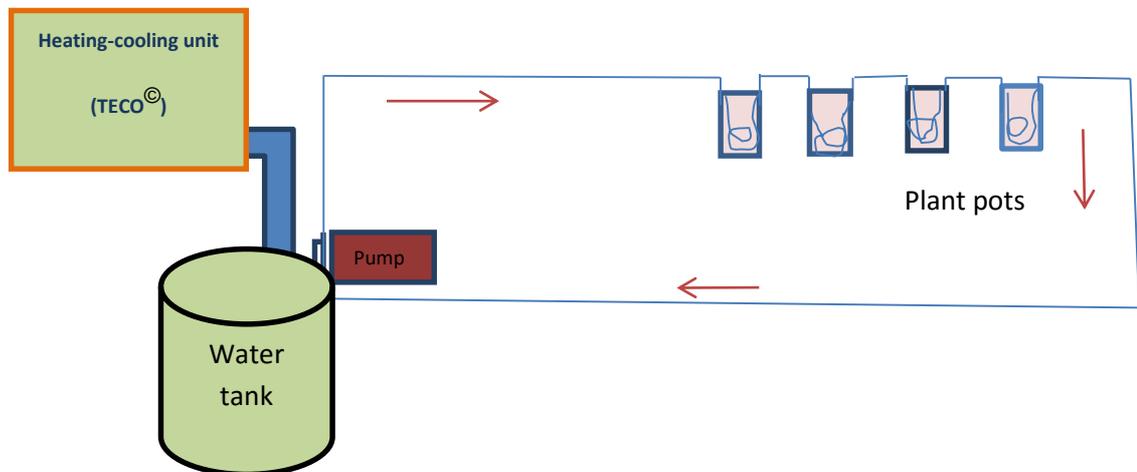


Figure 3. Diagram of root and meristem temperature control system



Controlled water temperature machines



Water tanks and pump tube connection



Plant pots



Tube and HOBO sensor inside a pot

Figure 4. Pictures of the root and meristem temperature control system

The light was set to 12/12 h day/night with lamps being switched on from 8 a.m to 8 p.m. Due to transpirational losses, deionized water was added to the pots every day to maintain the same volume in each pot. All tubes and culture pots were covered with aluminum foil to avoid algal growth and the impact of light on water temperature during daytime.

Table 2. Average water temperature, air temperature and VPD during day and night in the experiment

Treatment		Experiment condition					
		Water temperature (°C)		Air temperature (°C)		VPD (kPa)	
VPD	Water	Day/Night	Average	Day/Night	Average	Day/Night	Average
High	CT	23.4/23.0	23.2	31.3/27.5	29.4	2.51/1.84	2.18
High	CN	27.0/19.3	23.2	31.3/27.5	29.4	2.51/1.84	2.18
High	CD	19.1/27.3	23.2	31.3/27.5	29.4	2.51/1.84	2.18
Low	CT	24.0/23.1	23.6	31.5/26.9	29.2	1.16/0.67	0.92
Low	CN	27.7/19.5	23.6	31.5/26.9	29.2	1.16/0.67	0.92
Low	CD	20.0/27.1	23.6	31.5/26.9	29.2	1.16/0.67	0.92

Note: CT-constant temperature, CN-warm day/cold night, CD-cold day/warm night

3.3. Data collection and sampling methods

Leaf appearance: The number of leaves on the main culm was counted every day at a fixed time. The appearance of a visible leaf tip was recorded and marked with a color marker. The calculation of the leaf appearance was based on the appearance time of a new leaf, the base temperature and the mean temperature of the nutrient solution to elude the possible influence of the slightly lower water temperature but slightly higher air temperature under high VPD. Hence, the leaf appearance was determined by phyllochron that was thermal time interval between leaves appearance and was calculated using Equation from Ritchie and Nesmith (1991):

$$T_d = (T_a - T_b) * n$$

T_d : accumulated thermal time

T_a : is daily mean nutrient solution temperature

T_b : is the base temperature.

n : is the number of days of leaf appearance

In the experiment, we did not indicate the T_b values for both varieties but they were already mentioned in previous experiment (Dingkuhn et al., 1995). Correspondingly, the T_b values are 9.55 and 9.70°C for IR64 and Sahel108, respectively.

Leaf elongation rate (LER): Leaf elongation rate was measured for the 9-10th leaf in all treatments. Three plants with the respective leaves at a length of 3-5 cm were randomly selected to measure LER for each treatment. The leaf tip was connected with a fishing thread using a clamp and then attached to a small metal piece (3g) as counterweight and a mark. The thread was led over a pulley system and the counterweight together with the mark moved along a ruler in response to the elongation of the leaf. The increase of the leaf length could be therefore read on the ruler, which was recorded every 30 minutes during 48h using cameras. The method is illustrated in figure 5.



Figure 5. Leaf elongation measurement

Gas-exchange: during the experiment, leaf gas exchange was determined at three times: 4, 7 and 10 weeks after transplanting. Three random plants in each treatment were selected to measure stomatal conductance and photosynthetic rate. These parameters were determined at the youngest fully developed leaf using a ADC- LCi portable photosynthesis system between 10 a.m and 3 p.m.

On the following day, on the same plants, plant height, tiller number, leaf number, leaf area, root parameters and dry matter were measured. Leaf area was determined for green leaves using a LI3050C leaf area meter. Roots were scanned with an EPSON scanner (Fig. 6) and analyzed with WinRhizo version 2013 to determine total root length, average root diameter and root surface area. Roots, stems and leaves were separately dried in a dry oven for 48h at 70°C and weighed to determine dry matter and root/shoot ratio.

Canopy temperature: at 9 week after transplanting, canopy temperature was measured between 11 a.m to 12 p.m by image investigation using thermal camera (FLIR camera).

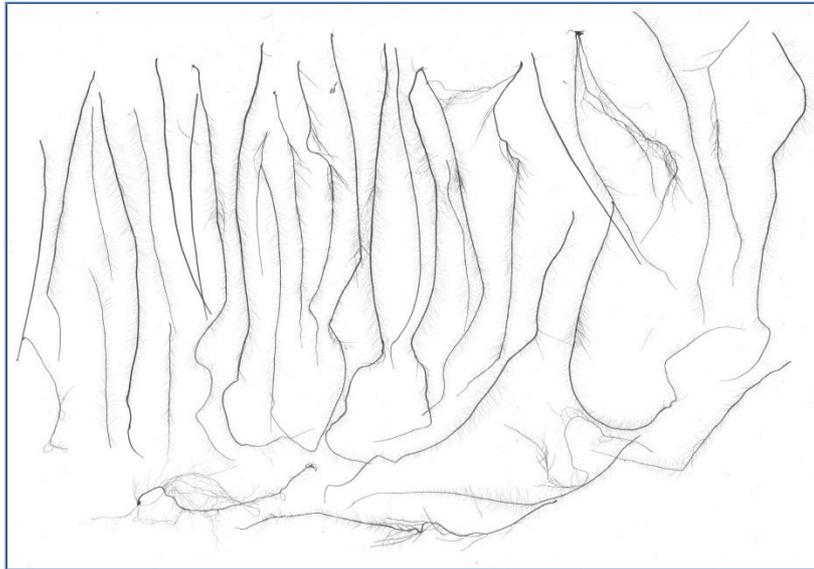


Figure 6. Example of root scan

Data analysis: Statistical data analysis was performed with STATISTICA version 6 using a factorial analysis of variance (ANOVA). Differences between treatments were determined using Tukey Test at the 0.05 probability level. Figures were done using SigmaPlot version 12.5.

4. Results

4.1. Effects of diurnal root and meristem temperature and VPD on leaf growth

Leaf elongation rate (LER): the leaf elongation rate (mm h^{-1}) was determined for the 9-10th leaf of the main tiller during 48 hours. Four-hour average values are presented in figure 7. Significant effects ($p < 0.05$) of VPD, nutrient solution temperature (T_{ns}) and time on LER were found.

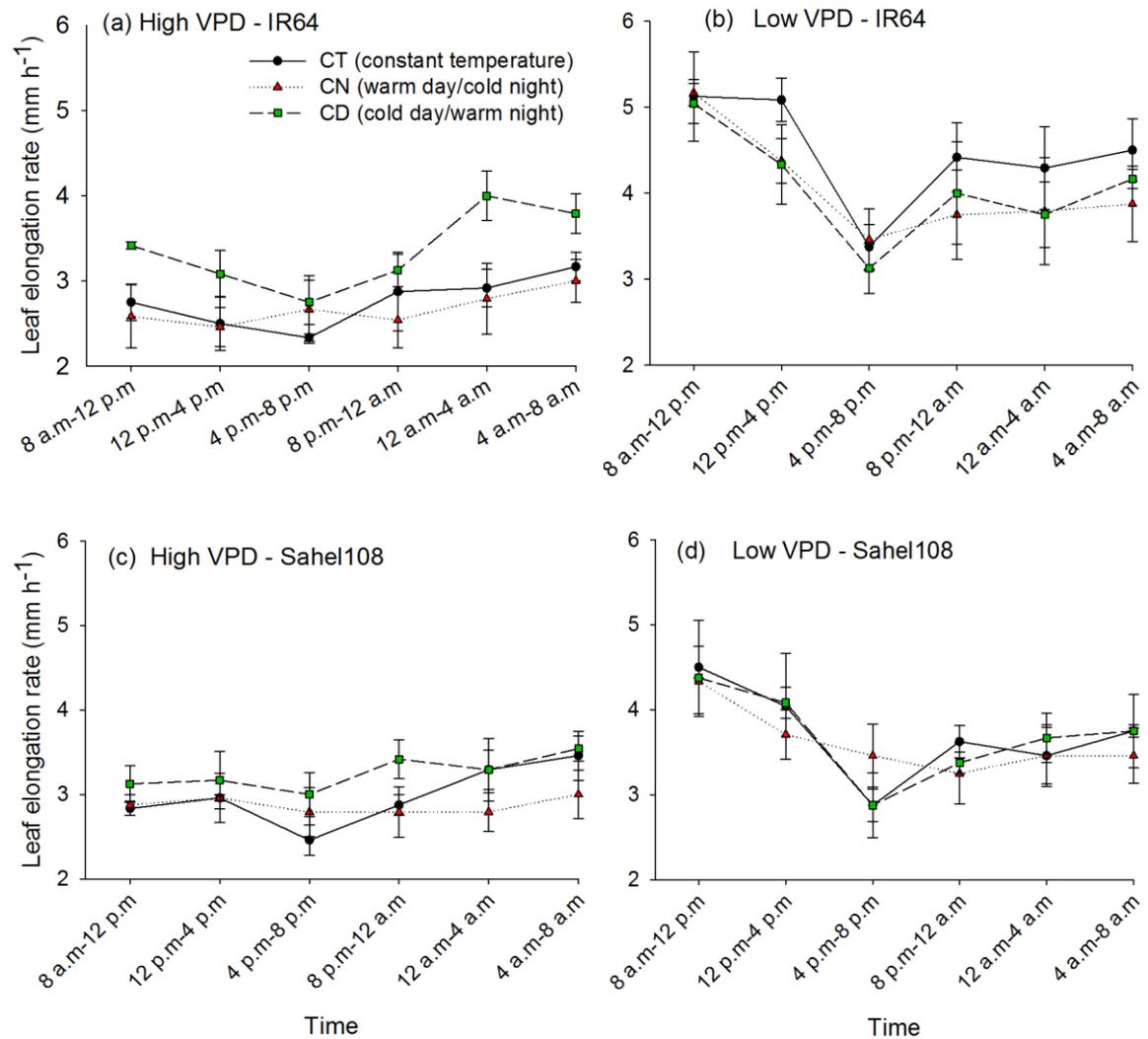


Figure 7. The interactive effect of three diurnal root and meristem temperature regimes (CT, CN, and CD) and two different VPD levels (high and low) on leaf elongation rate of two rice varieties (IR64 and Sahel108)

LER of IR64 fluctuated from 2.5 to 3.7 mm h^{-1} and 3.1 to 5.2 mm h^{-1} under high and low VPD respectively, while the LERs of Sahel108 were 2.7 to 3.5 mm h^{-1} and 2.9 to 4.5 mm h^{-1} . Both varieties showed a lower LER at high VPD than at low VPD. The combinative effect of VPD and time on LER was significant. Hence, under high VPD,

the LER was highest during the night and in the early morning (12 a.m to 8 a.m), whereas under low VPD, the highest rate was found between 8 a.m to 4 p.m.

Furthermore, a sharp reduction in LER was observed between 4 p.m and 8 p.m in most cases, except for IR64 grown under CN treatment, where the rate slightly increased. Remarkably, the reduction in LER of plants grown in CT and CD treatments was stronger than that in the CN treatments during this period. However, a rapid recovery in LER from 8 p.m to 12 a.m in the CT and CD treatments was recorded, whereas a slight decrease was observed in the CN treatment in most cases.

Under high VPD, the CD treatments induced a stronger leaf elongation in comparison to the CT and CN treatments for both varieties. In contrast, under low VPD, the effect of temperature treatment on LER was different between varieties. Hence, a slightly higher LER was found in plants grown under the CT treatment for IR64, while no clear difference in LER between three temperature treatments was observed in Sahel108.

Leaf appearance: The responses of two rice varieties in leaf appearance to day/night temperature treatments and VPDs are presented in figure 8. In order to elude the possible effect of the small difference in mean T_{ns} between the two VPD levels, leaf appearance was expressed in phyllochron value, which was calculated as the sum of daily mean water temperature minus the base temperature. Generally, summing temperature for appearance of early leaves was lower than that of late leaves.

A high difference in phyllochron values between leaf positions was observed for both varieties. Therefore, no effect of VPD on phyllochron value was found for the 5-7th leaves, whereas from 8th leaf onwards, low VPD induced a lower phyllochron value than high VPD. Even though there was a considerable variation in the value among leaf positions, the phyllochron values of both varieties tended to be lower in the CD treatment in IR64 and in the CT and CD treatments in Sahel108 under low VPD.

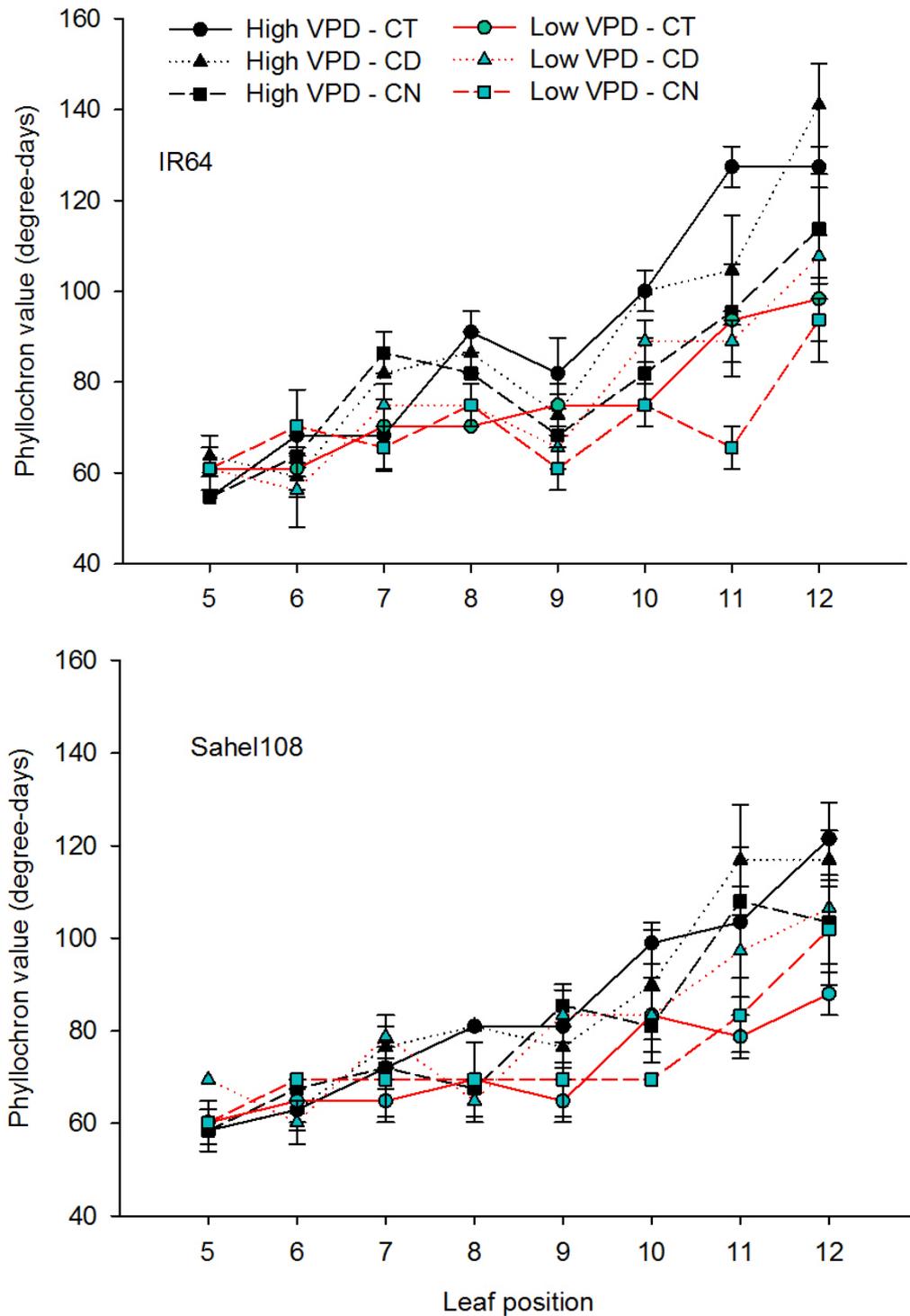


Figure 8. Phyllochron values expressed in unit of degree-days of two rice varieties as a function of diurnal root and meristem temperature, VPD, and leaf position
 CT: constant temperature; CN: warm day/cold night; CD: cold day/warm night

Leaf area (LA): Leaf area per plant is shown in figure 9 for the two rice varieties under different VPDs and diurnal root and meristem temperatures. For both varieties, there was no significant effect of either VPD or temperature on LA at 4 weeks after transplanting (WAT), whereas significant differences between treatments were found at 7 and 10 WAT.

For IR64, low VPD led to a significantly higher LA in all temperature treatments at 7 WAT in comparison to high VPD, while at 10 WAT, low VPD strongly increased LA of plants grown in CT treatment but not for CD and CN treatments. At 10 WAT, a sharp increase in LA of plants grown under the CD and high VPD was observed, leading to the fact that there was no significant difference between VPD levels for the CD treatment.

In IR64, there was no considerable effect of nutrient solution temperature on LA at 7 WAT, whereas a significant difference between temperature treatments was observed at 10 WAT. Therefore, under low VPD, at 10 WAT, the CD treatment led to a much higher LA than the CN treatment, but no significant difference between the CD and CT treatments was observed. Under high VPD, at 10 WAT, the CD treatment led to a significantly higher LA compared to the CT and CN treatments. Interestingly, plants grown in CT and CN treatment at high VPD showed the smallest LA through three sampling times.

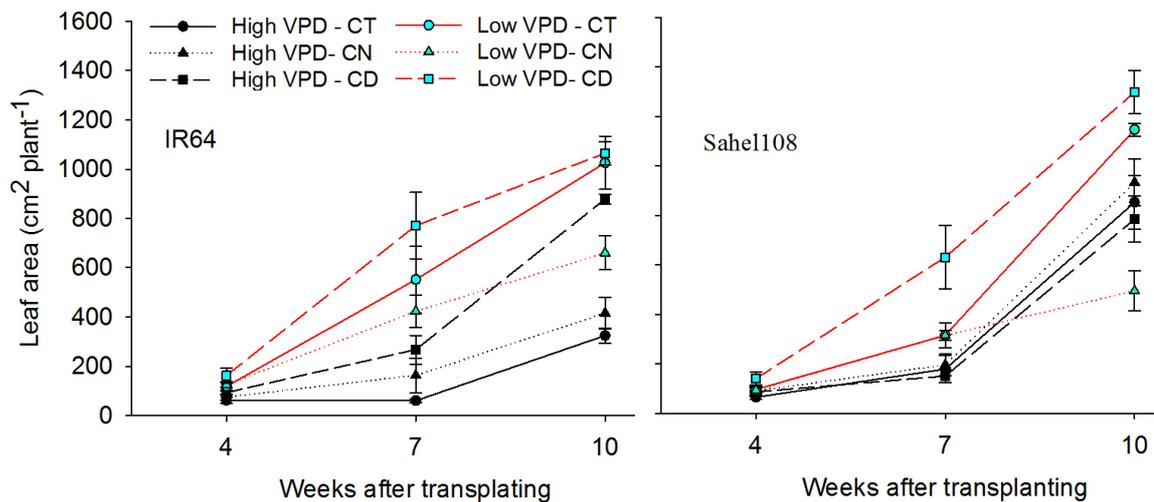


Figure 9. Leaf area of two rice varieties (IR64 and Sahel 108) under three different diurnal root-rhizosphere temperatures and two VPD levels at three samplings
CT: constant temperature; CN: warm day/cold night; CD: cold day/warm night

In Sahel108, low VPD led to significant higher LA in plants grown under CD at 7 and 10 WAT compared to high VPD. Under high VPD, no significant effect of nutrient solution temperature on LA was found through the three samplings. In contrast, under low VPD, there was a remarkable difference in LA between temperature treatments. Therefore, at 7 WAT, the CD treatment induced a significant higher LA compared to that in the CT and CN treatments. At 10 WAT, a strong increase of LA in the CT treatment was observed, leading to a significantly greater LA in plants grown in the CT and CD than those in the CN treatment.

In general, there was no difference in LA between the two varieties grown under low VPD, whereas a significant difference was observed under high VPD at 10 WAT. Here, Sahel108 had a significantly higher LA than IR64 in the CT and CN treatments, but not in the CD treatment. Remarkably, under low VPD, the smallest LA was found in the CN conditions for both varieties.

4.2. Effect of diurnal root and meristem temperature and VPD on root growth

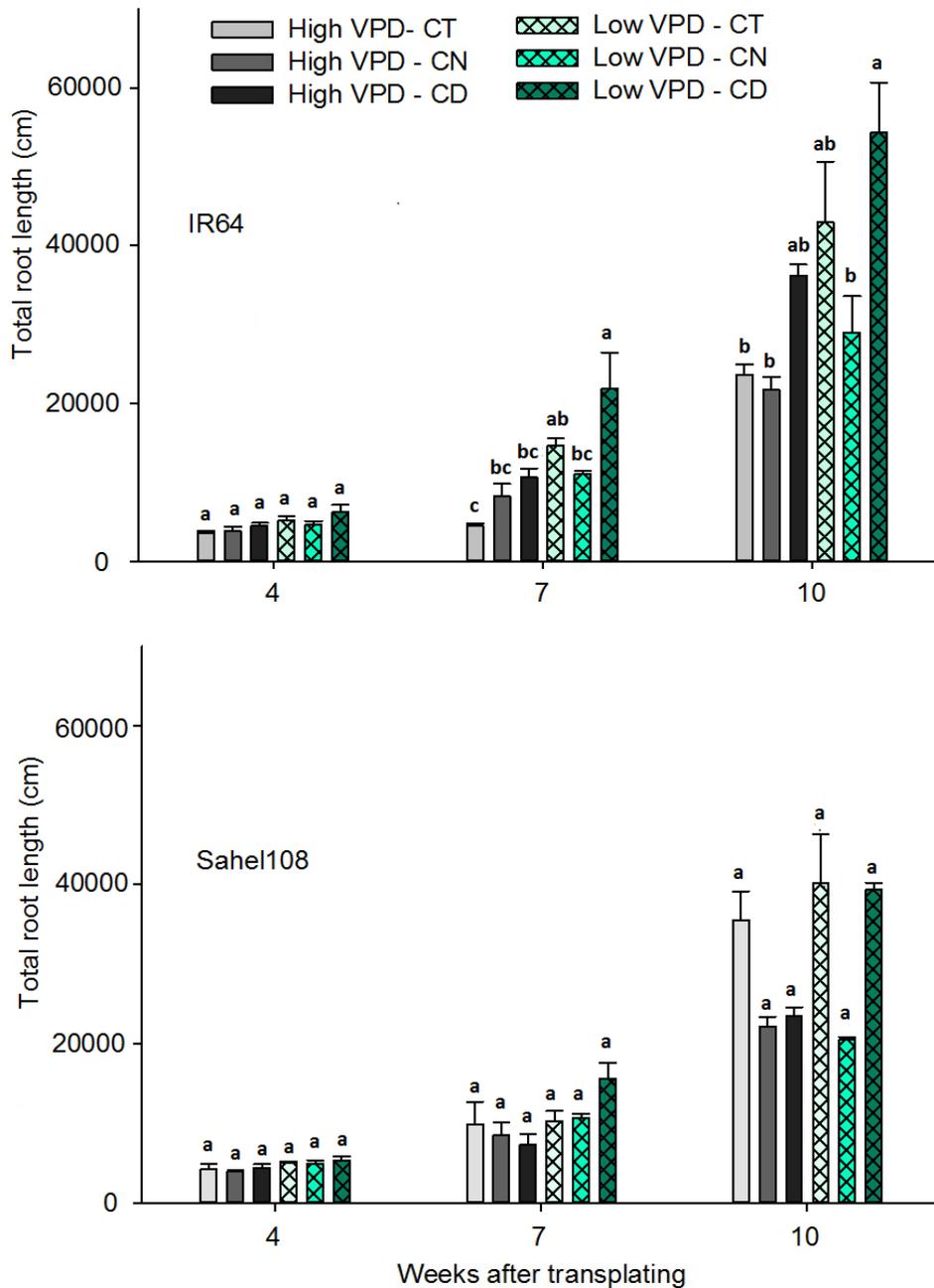


Figure 10. Total root length of two varieties under three day/night root and meristem temperature regimes and two different VPD levels. Different letters above bars indicate significant differences (at $p \leq 0.05$) between treatments at the particular sampling time. CT: constant temperature; CN: warm day/cold night; CD: cold day/warm night

Total root length (RL): Figure 10 shows the variation in total root length of the two varieties grown under two VPD levels and three diurnal temperature patterns. RL increased slowly between 4 and 7 WAT, whereas a stronger growth was observed between 7 and 10 WAT. For both varieties, no significant effect of VPD and diurnal temperature patterns on RL was observed at 4 WAT.

For IR64, even though the difference was not significant, the greatest RL was found in plants grown in CD treatment under low VPD at 7 and 10 WAT. Under high VPD, no significant difference between plants grown under different temperatures was observed, but RL tended to be greater in the CD treatment. Under low VPD, the CD led to significantly greater RL compared to CN, while there was no statistical difference between the CT and CD treatments.

On the contrary, there was no significant effect of VPD or temperature on the RL of Sahel108 through the three samplings. However, the CT treatments under both VPDs and the CD treatment under low VPD strongly enhanced root growth of Sahel108 between 7 and 10 WAT, whereas the increase of RL in the other treatments was rather small.

Root surface area (RSA): As seen in Fig.11, the different VPDs and nutrient solution temperatures did not lead to differences in RSA of both varieties at 4 WAT. In IR64, low VPD led to a significantly higher RSA of plant grown under the CD treatments at 7 WAT compared to that under high VPD, whereas no considerable effect of low VPD on RSA was observed at 10 WAT. Under high VPD, at 10 WAT, RSA of plants grown in the CD treatment was 2332 ± 130 cm² on average while it was 1305 ± 259 cm² and 1205 ± 109 cm² in the CT and CD treatments, respectively. Under low VPD, average RSA values were 4014 ± 580 cm², 3122 ± 767 cm², 1994 ± 400 cm² in the CD, CT and CN treatments, respectively. Only in low VPD, significant effect of T_{ns} on RSA was found; accordingly, the CD treatment led to significant higher RSA compared to the CN treatment at 7 and 10 WAT while there was no significant difference between the CD and CT treatments.

For Sahel108, hardly any effect of VPD on RSA was found at 7 and 10 WAT. At 10 WAT, under high VPD, average RSA values of plants were 2557 ± 334 cm², 1915 ± 75 cm², 1724 ± 201 cm² in the CT, CD and CN treatments, respectively. Under low VPD, the values were 3501 ± 89 cm², 3268 ± 501 cm², 1558 ± 201 cm² for plants grown in the CD, CT and CN treatments, respectively. There was a significant effect of T_{ns} on RSA but only under low VPD at 10 WAT. Here, RSA measured for the CD treated plants was statistically higher than that in the CN treatment.

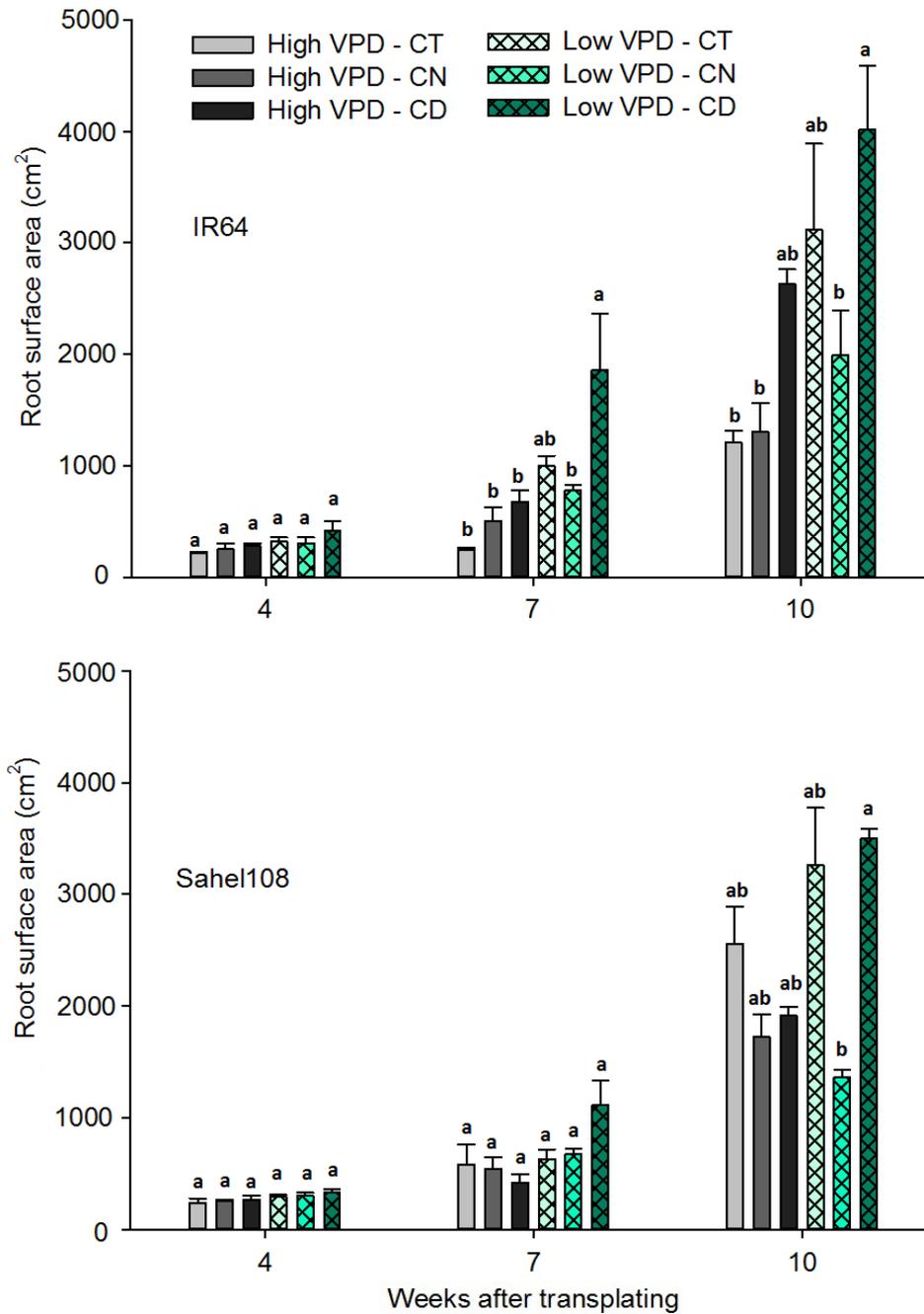


Figure 11. Root surface area of two rice varieties under three diurnal root and meristem temperatures and two VPDs at three samplings. Different letters above bars indicate significant differences (at $p \leq 0.05$) between treatments at the particular sampling time. CT: constant temperature; CN: warm day/cold night; CD: cold day/warm night

Root diameter (RD): Root diameter did not differ between treatments in both varieties at 4 WAT (Fig. 12). In IR64, low VPD induced a statistical higher RD in CD treatment at 7 WAT and in CT treatment at 10 WAT compared to those under high VPD. At 10 WAT, no statistical difference between temperature treatments was observed under low VPD, whereas under high VPD, the CD treatment strongly stimulated RD of the plants in comparison to the CT treatment.

In Sahel108, there was no significant effect of VPD on RD at three sampling times. Under low VPD, significant effect of T_{ns} on RD was found at 10 WAT, where plants grown under the CD had a significant higher RD in comparison to the CN treatment. Under high VPD, no considerable effect of diurnal nutrient solution temperature on RD was observed during the experiment.

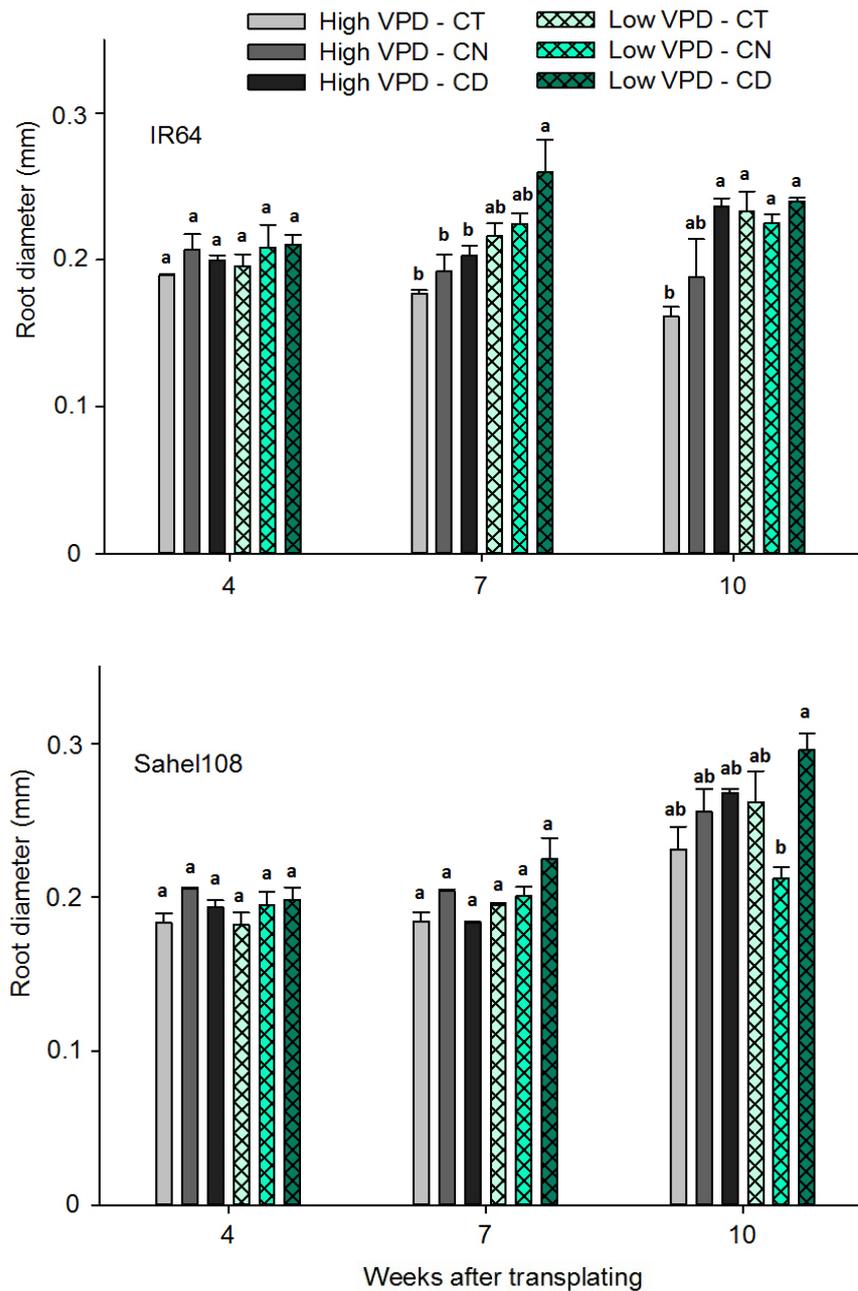


Figure 12. Root diameter of two rice varieties under three diurnal root and meristem temperatures and two VPD levels at three samplings. Different letters above bars indicate significant differences (at $p \leq 0.05$) between treatments at the particular sampling time. CT: constant temperature; CN: warm day/cold night; CD: cold day/warm night

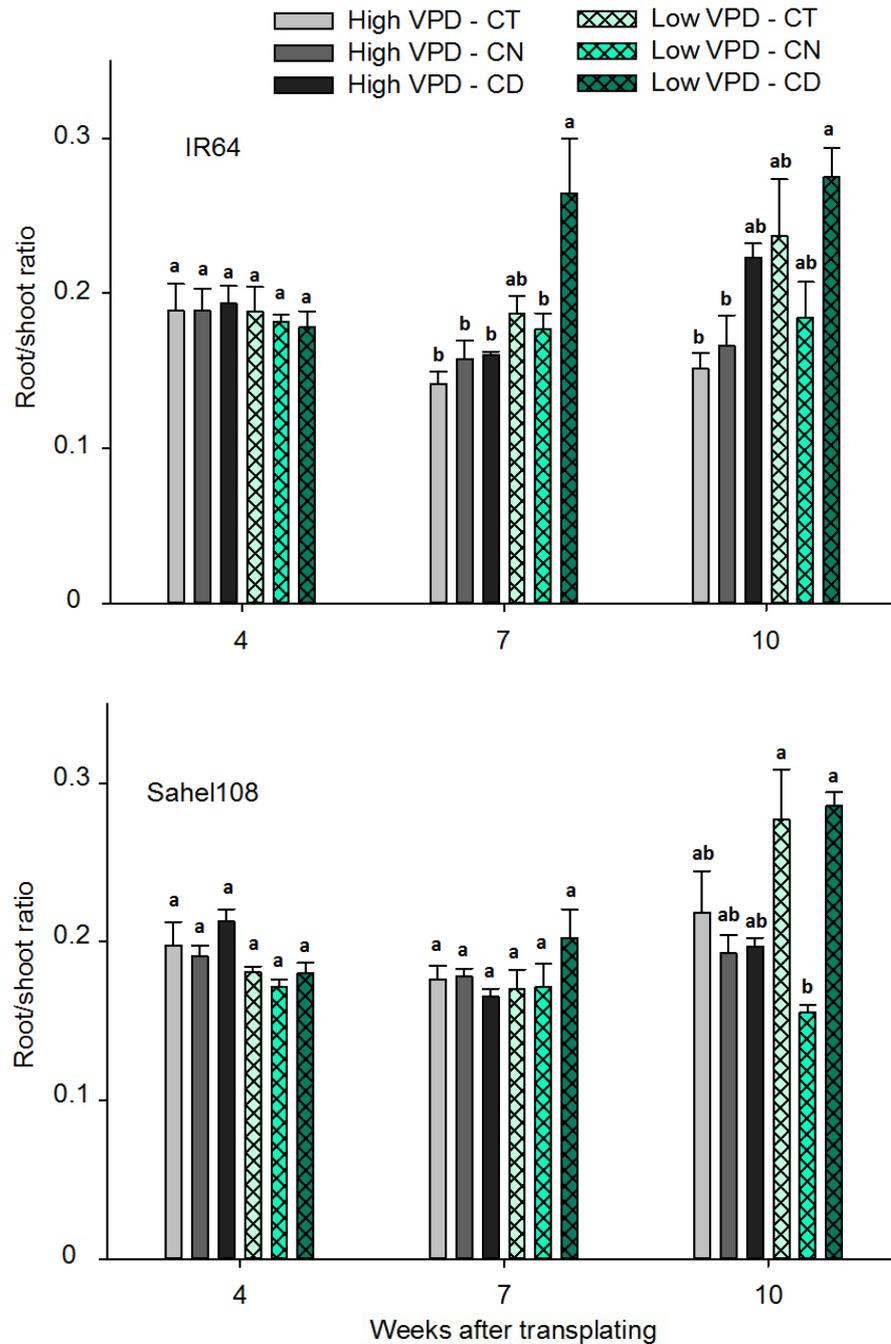


Figure 13. Root/shoot ratio of two rice varieties under three diurnal root and meristem temperatures and two VPD levels at three samplings. Different letters above bars indicate significant differences (at $p \leq 0.05$) between treatments at the particular sampling time. CT: constant temperature; CN: warm day/cold night; CD: cold day/warm night

Root/shoot (R/S) ratio: The effect of VPD and T_{ns} on R/S ratio of IR64 and Sahel108 was shown in Fig. 13. There was no significant effect of VPD and temperature treatments on R/S ratio at 4 WAT in both varieties.

For IR64, low VPD induced significantly higher R/S ratio in the CD treatment at 7 WAT in comparison to high VPD, but no considerable difference between two VPDs

was found at 10 WAT. At 7 WAT, there was no significant difference between temperature treatments at high VPD, whereas at low VPD, plants grown in the CD treatment had a higher R/S ratio than in the CN treatment. There was no significant effect of diurnal root and meristem temperature on R/S ratio of IR64 was found at 10 WAT; however, it tend to be higher in plants grown in the CD treatments. At 10 WAT, average R/S ratio of plant grown at high VPD ranged from 0.15 ± 0.01 in the CT treatment to 0.22 ± 0.01 in the CD treatment, while at low VPD, the R/S ratio ranged from 0.18 ± 0.02 in the CN treatment to 0.28 ± 0.02 in the CD treatment.

For Sahel108, no significant effect of VPD on R/S ratio was observed through the three sampling times. Temperature treatments did not have any significant effect at 7 WAT but at 10 WAT. Here, at low VPD, R/S ratio was significantly reduced by CN treatment in comparison to the CT and CD treatments. At 10 WAT, R/S ratio of Sahel108 at high VPD ranged from 0.19 ± 0.01 in the CN to 0.22 ± 0.01 in the CD treatment, while the R/S ratio of plants grown at low VPD ranged from 0.16 ± 0.01 in the CN to 0.29 ± 0.01 in the CD treatment.

4.3. Effect of diurnal root and meristem temperature and VPD on number of tillers, plant height, and dry matter accumulation

Number of tillers: There was a difference between two rice varieties on tillering response to VPD and diurnal nutrient solution temperature. No clear trend was observed in the number of tillers of IR64 between sampling times while in Sahel108, the number of tillers increased stronger in the second half of the experiment (Fig. 14). At 10 WAT, the number of tillers of IR64 ranged from 4.7 ± 0.3 in the CT treatment at high VPD to 13.7 ± 1.7 in the CD treatment at high VPD, whereas in Sahel 108, the tiller number ranged from 7.7 ± 0.3 in the CN treatment at low VPD to 13.3 ± 1.8 in the CD treatment at high VPD.

In IR64, at 4 and 7 WAT, no significant effect of T_{ns} on the number of tillers was observed, but there was a significant interaction between VPD and T_{ns} . Hence, at 4 WAT, the CN treatment at low VPD led to a significantly higher tiller number than the CT treatment at high VPD, while at 7WAT, plants grown in the CD at low VPD had a higher tiller number than that in the CT at high VPD. However, from 4 WAT until 7 WAT, the number of tillers in the CT treatments under high VPD and in the CN treatment under low VPD did not increase, whereas a slight increase was observed in the other treatments. Until 10 WAT, the number of tillers of plants in the CD treatment at high VPD increased remarkably and was then significantly higher than in the CT and CN treatments. Under low VPD, there was no significant difference between

temperature treatments during the experiment. Remarkably, no considerable difference in the number of tillers between two VPDs was found in IR64 at 10 WAT. In contrast, no significant effect of VPD and temperature treatments on the number of tillers of Sahel108 was observed during the experiment.

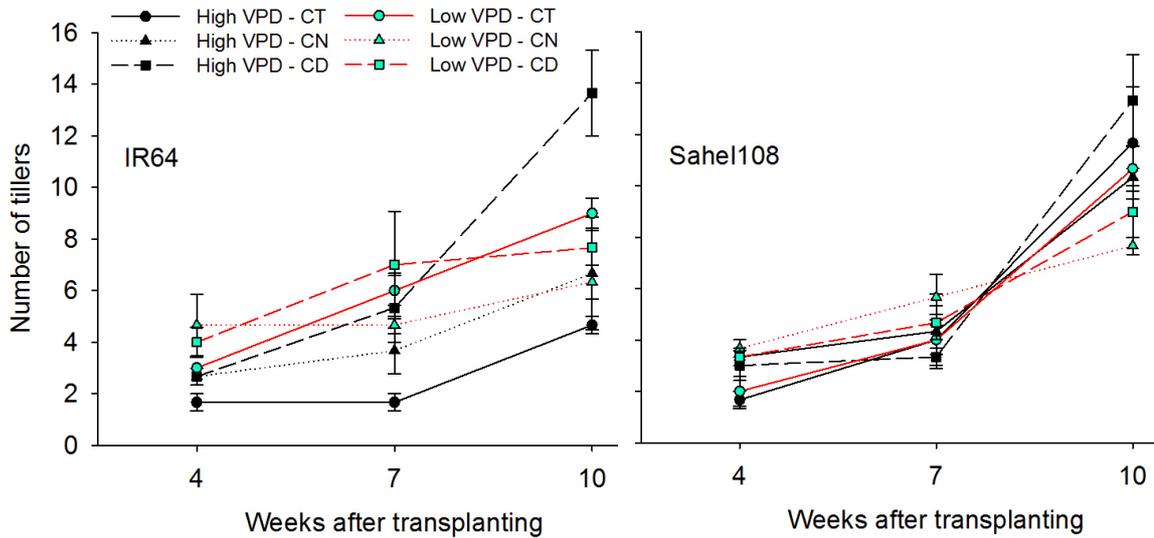


Figure 14. Number of tillers of two rice varieties under three diurnal root and meristem temperatures and two VPD levels at three samplings
CT: constant temperature; CN: warm day/cold night; CD: cold day/warm night

Plant height: In most cases, a stronger increase in plant height was found at the first half of the experiment and low VPD stimulated plant height in both varieties (Fig. 15). For IR64, high VPD resulted in a significantly lower plant height than low VPD, but not in the CD treatment at 7 and 10 WAT. There was no significant effect of diurnal temperature treatments on plant height of IR64, with an exception at 7 WAT under high VPD, where the CT treatment led to a significantly lower plant height in comparison to the CD treatment.

In contrast, no significant difference in plant height was found between temperature treatments for Sahel108 through the three samplings. However, a significant effect of VPD on plant height was observed at 7 and 10 WAT. Therefore, low VPD led to a significant higher plant height in the CD treatment at 7 WAT and in the CD and CT treatments at 10 WAT in comparison to the high VPD treatment.

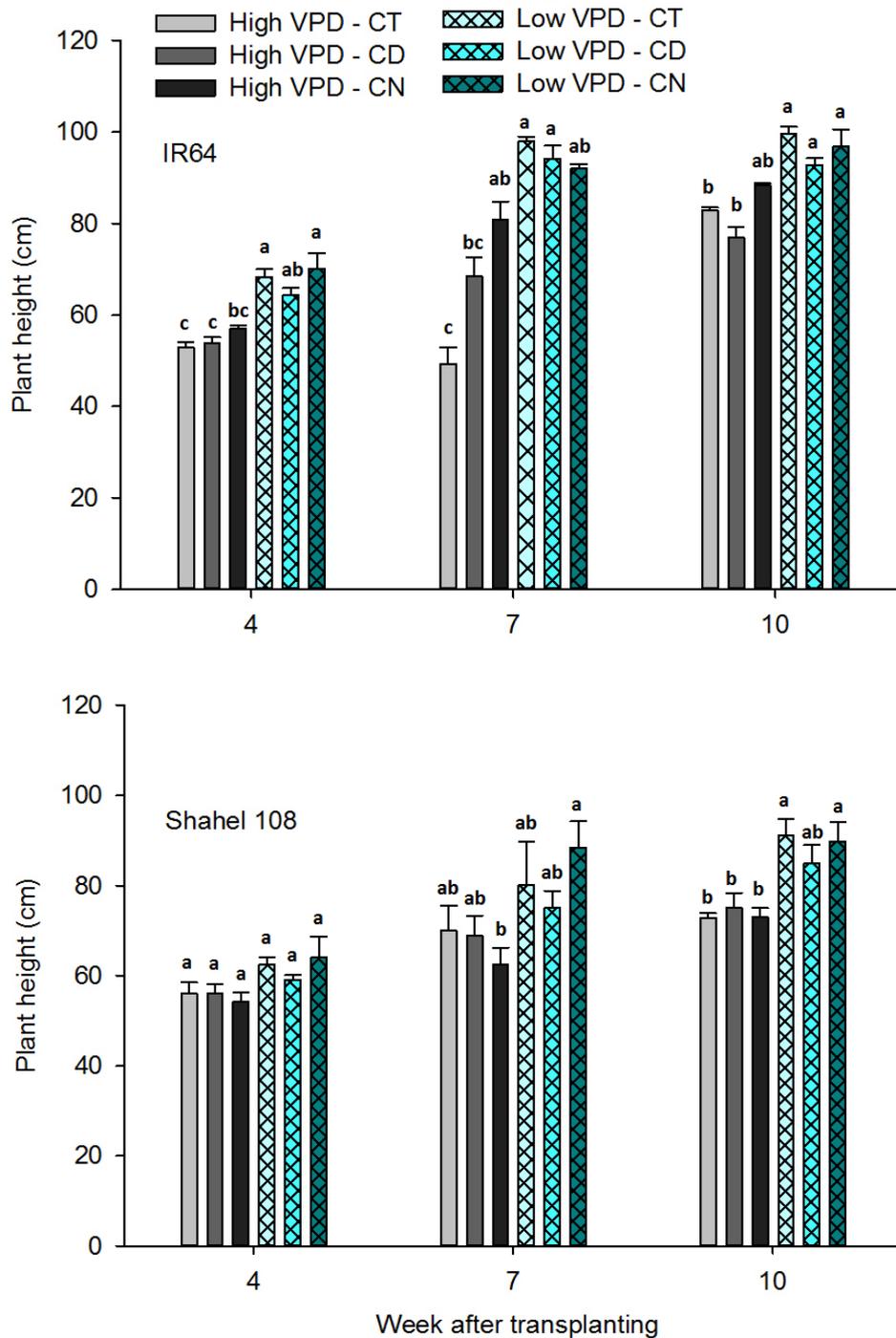


Figure 15. Plant height of two rice varieties under three diurnal root and meristem temperatures and two VPD levels at three samplings. Different letters above bars indicate significant differences (at $p \leq 0.05$) between treatments at the particular sampling time. CT: constant temperature; CN: warm day/cold night; CD: cold day/warm night

Total dry matter (DM): At 4 WAT, no considerable differences in DM were found between plants grown under different treatment for both varieties (Fig. 16). At 7 WAT, there was no significant effect of VPD and T_{ns} on DM of Sahel108, whereas in IR64, low VPD significantly increased DM of plants grown in the CD treatment than that at high VPD.

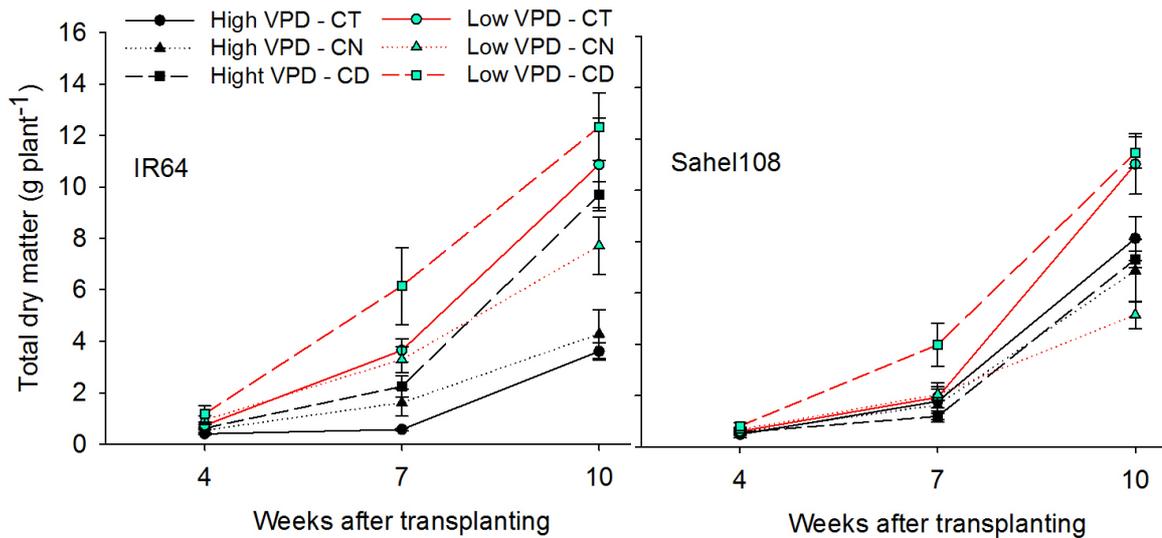


Figure 16. Total dry matter of two rice varieties under three diurnal root and meristem temperatures and two VPD levels at three samplings

CT: constant temperature; CN: warm day/cold night; CD: cold day/warm night

At 10 WAT, a significant effect of VPD on DM was found in IR64; accordingly high VPD significantly reduced DM of plants grown in the CT treatment in comparison to low VPD. For IR64, there was no significant effect of T_{ns} on DM at low VPD, whereas at high VPD, the CD led to significantly higher DM than in the CT and CN treatments.

In contrast, VPDs did not lead to any statistical difference in DM of Sahel108 at 10 WAT. In Sahel108, no significant effect of T_{ns} treatments was found at high VPD, whereas at low VPD, the CN treatment significantly reduced DM in comparison to the CT and CD treatments at 10 WAT.

4.4. Effect of diurnal root and meristem temperature and VPD on leaf gas exchange parameters

Stomatal conductance (Gs): In general, Gs of two varieties were relatively stable during the experimental period (Fig. 17). Gs of Sahel108 was slightly higher than that of IR64 and a higher Gs was found under low VPD compared to high VPD. Through the three times of measurement, Gs under high VPD was below $0.2 \text{ mol m}^{-2}\text{s}^{-1}$, while under low VPD, Gs value was always above $0.3 \text{ mol m}^{-2}\text{s}^{-1}$ in both varieties.

During the experiment, no significant effect of the T_{ns} treatments on the Gs was observed for both varieties. There was a variation in responses of two varieties to VPDs. For example, in Sahel108, low VPD led to a significantly higher Gs value during the experiment, whereas the effect of VPD on Gs of IR64 was not consistent. Therefore, in IR64, low VPD increased remarkably Gs compared to high VPD but not in the CT treatment at 7 WAT and in the CD and CN treatments at 10 WAT.

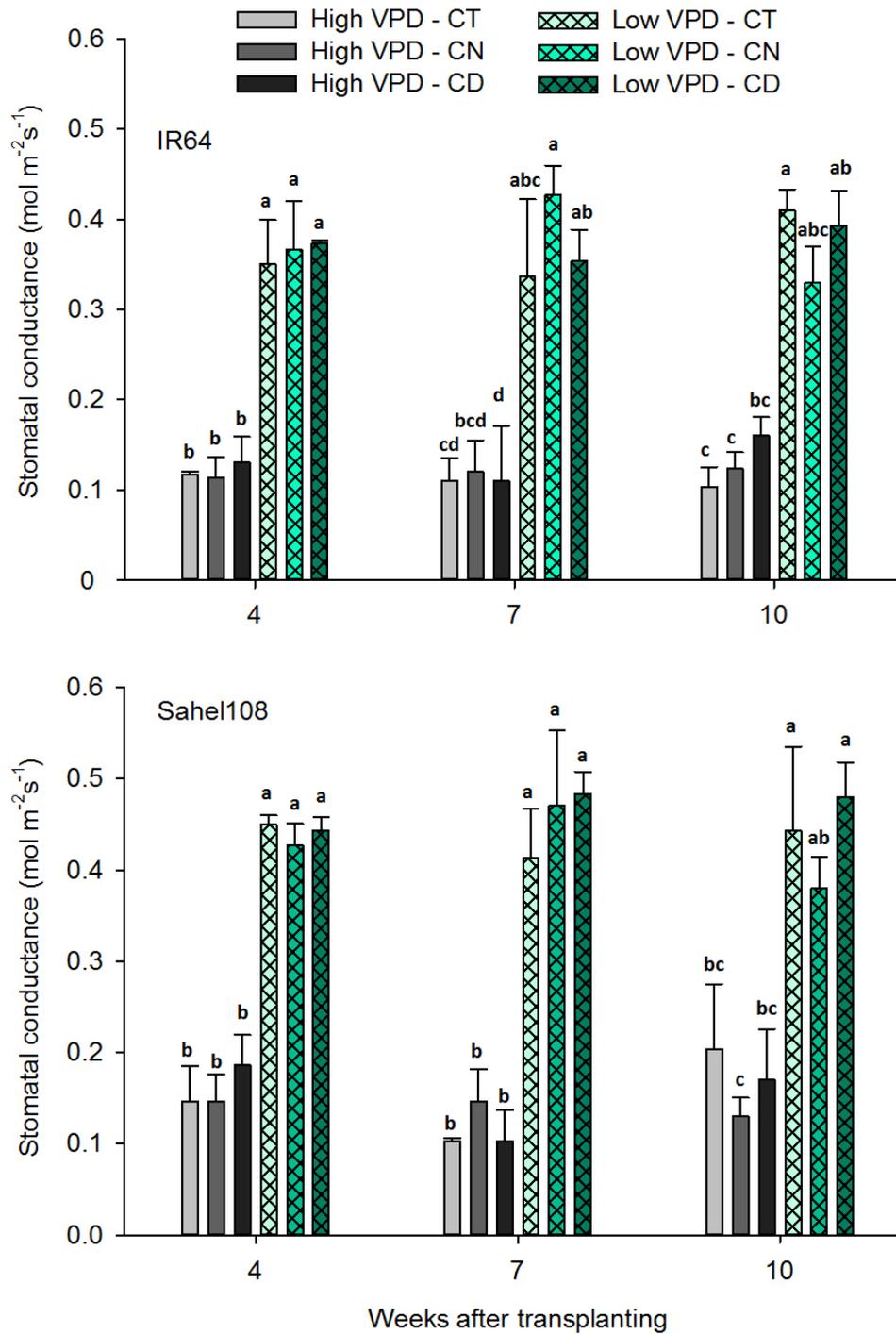


Figure 17. Stomatal conductance of two rice varieties under three diurnal root and meristem temperatures and two VPD levels at three measured times. Different letters above bars indicate significant differences (at $p \leq 0.05$) between treatments at the particular sampling time. CT: constant temperature; CN: warm day/cold night; CD: cold day/warm night

Photosynthetic rate: Hardly any significant effects of VPD and T_{ns} on photosynthetic rate were found for both varieties, with an exception for Sahel108 at 7 WAT, where low VPD led to a higher photosynthetic rate in the CD treatment than that at high VPD (Fig. 18). At 10 WAT, photosynthetic rate of IR64 ranged from $4.8 \pm 0.1 \mu\text{mol m}^{-2}\text{s}^{-1}$ at high VPD in the CN treatment to $9.4 \pm 1.7 \mu\text{mol m}^{-2}\text{s}^{-1}$ at high VPD in the CD treatment. In

Sahel108, the photosynthetic rate ranged from $5.3 \pm 0.1 \mu\text{mol m}^{-2}\text{s}^{-1}$ at low VPD in the CT treatment to $8.8 \pm 2.1 \mu\text{mol m}^{-2}\text{s}^{-1}$ at high VPD in the CD treatment.

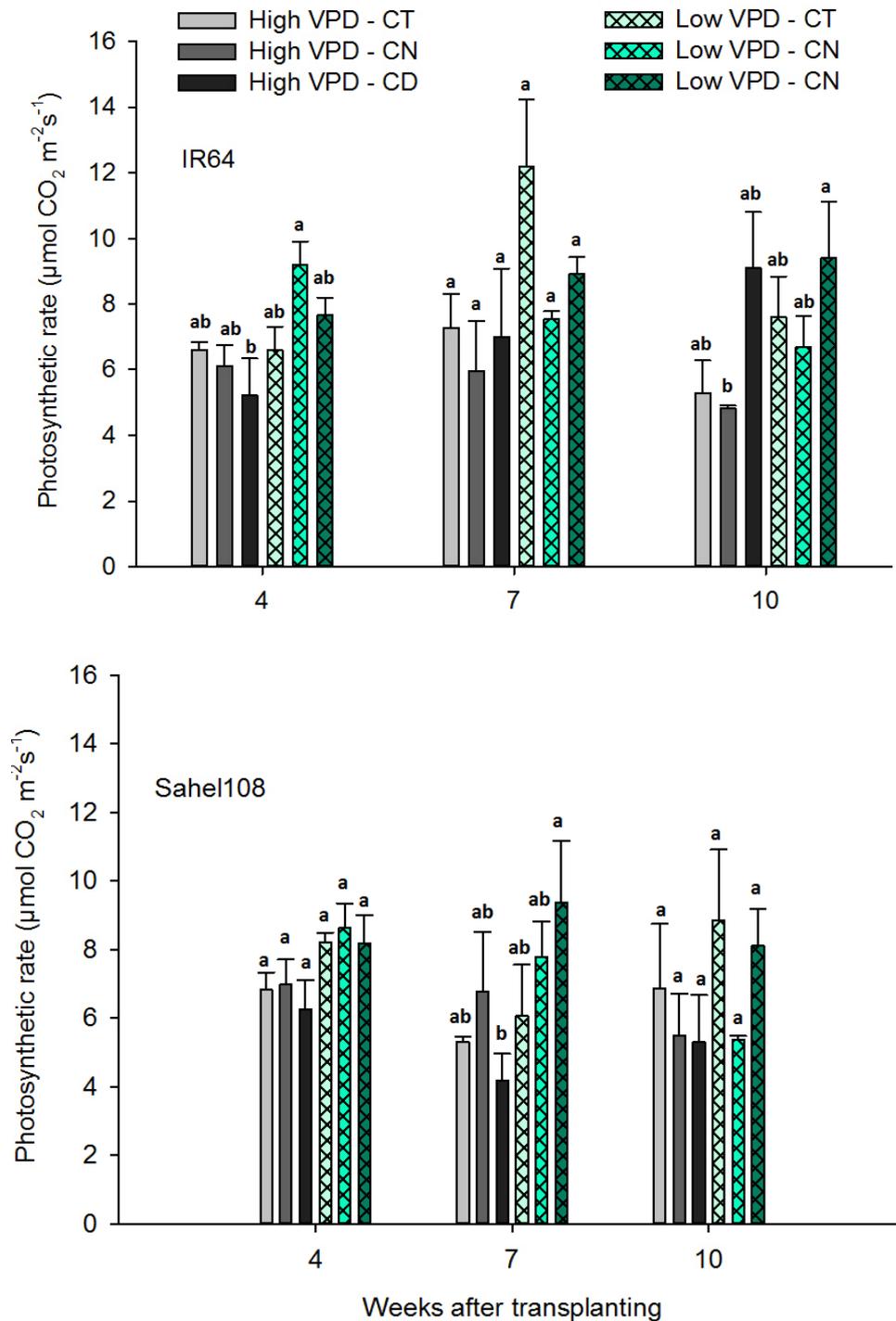


Figure 18. The photosynthetic rate of two rice varieties under three diurnal root and meristem temperature regimes and two VPD levels at three measured times. Different letters above bars indicate significant differences (at $p \leq 0.05$) between treatments at the particular sampling time. CT: constant temperature; CN: warm day/cold night; CD: cold day/warm night

5. Discussion

Hypothesis 1: Day/night temperature patterns and VPD influence the rate of leaf elongation and leaf expansion and thus leaf area

A clear difference in LER and leaf appearance between the two VPD levels was found, with a low VPD leading to a higher LER and a faster leaf appearance. Low VPD also significantly increased LA in CT treatment in IR64 and in CD treatment in Sahel108 at 10 WAT. Previous studies have indicated a linear response of LER to evaporative demand (Lafarge et al., 1998; Estela et al., 2009). Estela et al. (2009) also found a greater leaf growth under low VPD, with a large variation between genotypes. Since low VPD can induce a higher canopy temperature, the different responses in leaf growth to VPD could be attributed to a difference in canopy temperature. Yan et al. (2008) indicated a lower organ temperature under high VPD than under low VPD at the same air temperature. In our experiment, under low VPD, canopy temperature was 1.6-3.6°C higher than that under high VPD (Table 3). This may be partially attributed to a low transpiration of plant under high vapour pressure (low VPD) and thus increased the leaf temperature (Yan et al., 2008). Moreover, transpirational cooling inducing from high VPD can lead to decrease in tissue temperature, which is probably a reason for lower leaf temperature (Kobayasi et al., 2010). Lower canopy temperature may induce to lower tissues temperature, especially in meristem and elongation zone and therefore reduced cell division and expansion (Ben-Haj-Salah and Tardieu, 1995; Rymen et al., 2007). Also, as previously reported by Bouchabké et al. (2006), high VPD led to a significant reduction in tissue turgor, which could also inhibit leaf elongation. In our experiment, we did not determine tissue turgor, but a reduction of stomatal conductance at high VPD (Fig. 17) could be seen as a response to a decrease in tissue turgor.

Moreover, a sharp reduction in LER between 4 p.m to 8 p.m was found in most cases, especially in CT and CD treatments and at low VPD. The reasons are unknown, but the result could be partly explained with a decline in air temperature at this time (Fig. 19). The decrease in air temperature during the afternoon may lead to a reduction in leaf and stem temperature, which then affected the tissue temperature at the elongation zone. Ben-Haj-Salah and Tardieu (1995) also indicated the effect of a reduction in air temperature and meristem temperature on leaf growth; thereby, a change in temperature could lead rapid and simultaneous responses of all cells in growing zone. In our finding, the smallest reduction of LER in the late afternoon was observed on plants in the CN treatment, which were exposed to the highest T_{ns} during this period, which might support this hypothesis. Moreover, with the decrease in air

temperature, VPD also reduced, which could be a reason for a smaller reduction in LER of plant grown under high VPD.

Table 3. Canopy temperature of two rice varieties and microclimate in the growth chambers of two rice varieties under three diurnal root and meristem temperatures and two VPD levels

Treatments			Leaf temperature			Condition in the growth chambers	
VPD	T _{ns}	Variety	Max	Min	Average	Air temperature	VPD
High	CT	IR64	31.1	25.9	28.7	29.8	2.14
	CN	IR64	31.7	25.7	28.4		
	CD	IR64	30.9	25.2	28.0		
	CT	Sahel 108	30.4	23.8	26.3		
	CN	Sahel 108	30.5	24.8	27.4		
	CD	Sahel 108	30.1	24.3	27.0		
Low	CT	IR64	32.1	29.9	30.7	30.0	1.07
	CN	IR64	31.8	29.9	30.7		
	CD	IR64	32.3	30.3	31.0		
	CT	Sahel 108	31.1	29.2	29.9		
	CN	Sahel 108	31.5	28.6	29.6		
	CD	Sahel 108	31.3	29.4	30.4		

T_{ns}: nutrient solution temperature CT: constant temperature, CN: warm day/cold night, CD: cold day/warm night

There was a large variation in time of leaf elongation between the two VPD levels. Under low VPD, the rate was highest between 8 a.m and 4 p.m, whereas under high VPD, the highest LER was found between 12 a.m and 8 a.m. In an experiment on rice, Parent et al. (2010) reported a higher LER during the day than during the night, resulting from a higher air temperature at daytime. However, if LER was calculated by equivalent hours at 20°C, it was reported to be higher during the night due to the adverse effect of high evaporative demand. This implies that higher temperature and lower VPD stimulates LER. In our experiment, the difference in air temperature between day and night was not taken into account for LER, but lower VPD and lower air temperature at night were recorded (Fig. 19). As seen in Fig. 19, both VPD and

temperature rapidly increased from 8 a.m to 12 p.m, followed by a reduction of both parameters. However, both VPD and air temperature were virtually constant during the night. In the high VPD chambers, VPD dropped from 2.6 kPa at daytime to 1.8 kPa during the night, which promoted leaf growth, especially in the CD treatment, where meristem temperature was higher during the night. From 8 a.m, a rapid increase in VPD caused a decrease in LER of plants grown at high VPD. The inhibition of leaf growth under higher VPD was reported in previous studies (Lafarge et al., 1998; Estela et al., 2009). Moreover, Lafarge et al. (1998) found that a lower VPD during the night stimulated LER of sorghum, which related to leaf water potential. In contrast, the increase in air temperature at day time increased leaf growth under low evaporative demand. Moreover, at low VPD, the highest LER was observed between 8 a.m and 4 p.m in all temperature treatments, which may be attributed to the combined effect of light, air temperature and VPD.

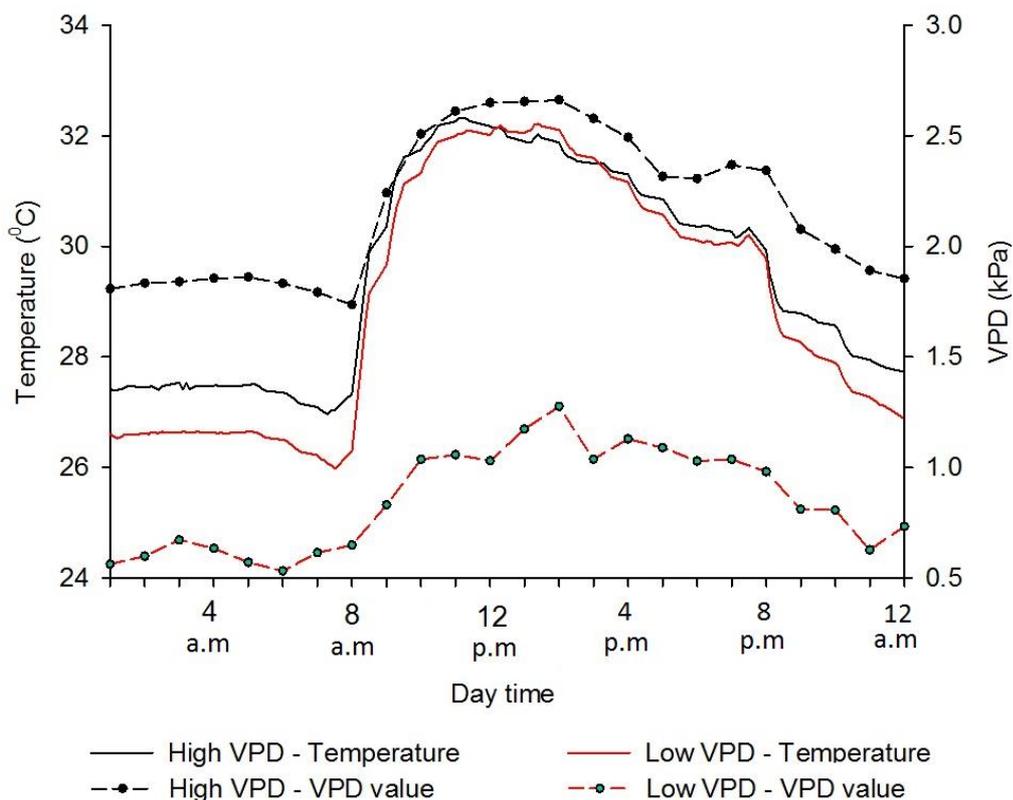


Figure 19. Mean air temperature and VPD values in growth chambers (high and low VPD) during the days, when leaf elongation rate was measured

Under high VPD, the highest LER was observed on plants in the CD treatment, followed by CT and CN respectively, especially at the night time and in early morning. However, under low VPD, there was no apparent difference in LER between T_{ns}

treatments was observed. Previous studies indicated a greater leaf growth under high meristem temperature, but our finding did not find any positive effect of a high meristem temperature during the daytime (in CN treatment) on leaf growth. Moreover, even though the results were not consistent over leaf positions, leaf appearance tended to be faster in cold day/warm night treatment (CD). In IR64 at high VPD, the CD treatment led to a significant higher leaf area in comparison to the CT and CN treatments. Moreover, the number of tillers was higher at the CD and high VPD, this implies that a higher number of leaves. A higher leaf area in the CD can result from a higher LER, a faster leaf appearance and a strong tillering. The positive effect of high meristem temperature, especially during the night, on leaf growth has previously reported (Ben-Haj-Salah and Tardieu, 1995; Matsushima et al., 1964; Lafarge et al., 1998, Shiono et al., 2002). In sorghum, Lafarge et al. (1998) reported that the LER during the night linearly responded to meristem temperature at night. Stuerz et al. (2014a) indicated an increase in LER of rice with increasing meristem temperature during the night. Also, some previous studies reported that higher water temperature at night promoted leaf growth and leaf emergence of rice (Tsunoda, 1964; Tanaka et al., 1968). This can be explained by a faster cell division and a faster cell expansion under high nighttime meristem temperature and then promote leaf growth (Ben-Haj-Salah and Tardieu, 1995). Shiono et al. (2002) found a reduction of relative leaf growth rate and leaf emergence rate caused by low water temperature and thus decreased leaf area. Rymen et al. (2007) also reported that cold nights strongly reduced cell production rate in the basal meristem of leaves due to a prolonged cell cycle progression. Since in our experiment, the mean temperature of the nutrient solution was kept constant, the results suggest that meristem temperature during the night is of higher importance for leaf growth than day temperature.

The difference in leaf growth among treatments allows the conclusion that both VPD and meristem temperature have substantial impacts on leaf elongation rate, leaf appearance, and leaf area of rice. In general, leaf growth is stimulated by low VPD and higher meristem temperature at night. Since low evaporative demand stimulates leaf growth; therefore under high VPD, leaf growth is stronger during the night and early morning when VPD is generally lower.

Hypothesis 2: Root growth dynamics are affected by day/night root and meristem temperature patterns and VPD

Hardly any significant effect of VPD on root morphology was observed, whereas there was a significant effect of T_{ns} on root growth. For IR64, there was a trend for larger roots in the CD treatment for both VPD levels. At low VPD, CN led to a significantly

lower root length and root surface area of IR64. For Sahel108, there was no significant difference in root morphology between temperature treatments at high VPD; however, roots tended to be larger in the CT treatment. In contrast, at low VPD, roots of Sahel108 were smallest in the CN treatment. Therefore, the results indicated a larger effect of nutrient solution temperature on root growth than of VPD.

Previous studies reported a variation in effects of root temperature on root growth, but most results indicated adverse effect of low root temperature than high temperature. Ehrler and Bernstein (1958) found a higher root dry matter of rice grown under constant temperature at 18°C than that at 30°C. In contrast, a reduction in the total amount of roots under high temperature was found in rice by Ueki (1960). A lower RSA, root number and root dry matter caused by low root temperature was reported by Nagasuga et al. (2011). Also, low root temperature led to a decrease of root length elongation (Pritchard et al., 1990) and root dry matter (Ku wagata et al., 2012). Cool root zone caused a decrease in root growth of maize and wheat was reported by Engels (1994). The decrease in root growth under low water temperature could be explained with the inhibition of cell division in the root meristem (Pritchard et al., 1990) or lower auxin accumulation in the root (Zhu et al., 2015). However, in most previous experiments, root was subjected to rather extreme temperatures above 30°C (Ueki, 1960) or below 16°C (Engels, 1994) or even around 5°C (Pritchard et al., 1990). Moreover, mean temperatures differed between treatments in these studies. In our finding, the cold day/warm night treatment generally stimulated root growth while the warm day/cold night treatment led to a significant reduction in root growth, especially in IR64 and at low VPD. Therefore, we hypothesized that low root temperature during the daytime and high root temperature during the night may have a positive impact on root growth. In our experiment, day/night nutrient solution temperatures (root temperature) were set to around 18/28°C for the cold day/warm night, 23/23°C for the constant temperature, and 28/18°C for warm day/cold night treatment. These temperatures were not in the extreme temperature ranges that were reported to damage roots. Furthermore, mean temperature was kept constant, which may be a main reason for our results.

Even though the difference was not significant, plants grown in the CD treatments showed a trend to increase root/shoot ratio, number of tillers, leaf area and total dry matter of IR64 compared to the CN and CT treatments. Therefore, the findings suggest that cold day/warm night stimulates not only root, but also shoot growth of IR 64. Smaller roots in the CN treatment under low VPD in both varieties indicated an adverse effect of warm days and/or cold night, on root growth.

Hypothesis 3: Leaf gas-exchange is influenced by diurnal root and meristem temperature and VPD leading to changes in dry matter

For both varieties, low VPD led to a significantly higher stomatal conductance than that at high VPD in most cases, while no significant effect of root and meristem temperature was found. The results indicated that stomatal conduction mostly depended on evaporative demand. In a rice experiment, Kuwagata et al. (2012) found a significant reduction of G_s caused by a high evaporative demand, but the highest reduction was found in the combination of high evaporative demand and low root temperature treatment. Also, the reduction of G_s at high VPD has previously reported for tea, cacao, coffee (Hernandez et al., 1989). Stomata are sensitive to evaporative demand; and high VPD causes more stomatal closure. Lower stomatal conductance at high evaporative demand is a response of the plant to increase water use efficiency (Pallardy and Kozlowski, 1979). Stuerz et al., (2014c) indicated the dependence of G_s on minimum meristem temperature and minimum relative humidity in the canopy; accordingly, high meristem temperature and high humidity led to a higher G_s . Shimono et al. (2004) also indicated that low meristem temperature induced a significantly reduction of G_s but only in the reproductive phase. In our experiment, we determined the effect of the diurnal pattern of nutrient solution temperature on gas exchange in the vegetative stage and did not find a significant impact of changing day/night root and meristem temperature on G_s .

Interestingly, there was no significant difference in photosynthetic rate between two VPD levels for both varieties. Some previous studies reported a high correlation between stomatal conductance and photosynthetic rate (Hirasawa et al., 1988; Ishihara and Saitoh, 1987; Kusumi et al., 2012). Stuerz et al. (2014c) also confirmed a close dependence of assimilation rate on G_s . Higher stomatal conductance might stimulate photosynthetic rate due to increased CO_2 uptake. In the contrary, Kuwagata et al., (2012) reported no considerable effect of relative humidity on assimilation rate of rice, although G_s was significantly increased at higher relative humidity.

In our experiment, there was a variation in photosynthetic rate values between temperature treatments, but no significant effect of root and meristem temperature on the photosynthetic rate was found in both varieties. Stuerz et al., (2014c) found a significant reduction in assimilation rate caused by low meristem temperature. However, Shimoni et al. (2002) found no significant effect of water temperature on radiation use efficiency at vegetative and reproductive stage; thereby they hypothesized a small influence of water temperature on photosynthetic rate. In a latter experiment, Shimono et al. (2004) indicated that low water temperature reduced

photosynthetic rate of rice at reproductive stage but not at the vegetative stage. Moreover, Kuwagata et al., (2012) also indicated no significant effect of low root temperature on assimilation rate of rice, even though a lower G_s was observed under low root temperature.

The result in our experiment could be explained by the acclimation of the plants in the long-term experiment and/or a higher N content caused by a lower leaf area at high VPD or in CT and CN treatments (Shimono et al., 2002, 2004). Another possible reason could be that photosynthetic activity was affected by other factors such as content of the enzyme Rubisco (1-5 ribulose biphosphate carboxylase) (Makino et al. 1987) or nitrogen content in the leaf (Makino et al. 1988); however, the impact of these factors was not determined in our experiment. Moreover, the outcome of our experiment may result from a similar mean nutrient solution temperature between the treatments.

Even though no significant difference in photosynthesis between treatments was observed, VPD and T_{ns} showed a significant effect on dry matter in some cases. Therefore, high VPD strongly reduced DM of IR64 in CT at 10 WAT, whereas, no significant effect was found in Sahel108. CN treatment led to lower dry matter compared to CD treatment at high VPD in IR64 and at low VPD in Sahel108. Kuwagata et al. (2012) reported a larger effect of root temperature on dry matter of rice than evaporative demand; thereby, low root temperature reduced dry matter and leaf area, and the reduction was greater at low humidity. Shimono et al. (2002) also found a lower crop growth rate, lower relative leaf growth rate and crop biomass under low water temperature. The effect of root temperature on plant growth could be partly explained by root water uptake capacity and thus affected on plant water status (Hurd et al., 1985; Nagasuga et al, 2011; Kuwagata et al., 2012). The lower dry matter in the CN treatments in our experiment was partially associated with a lower leaf area and a smaller root (Nagasuga et al., 2011).

Hypothesis 4: Varieties will show differences in their response to diurnal temperature patterns under varying VPD

In most cases, no significant differences in morphological and physiological parameters between the two rice varieties were observed; however, there was a difference in the growth responses of the two varieties to temperature and VPD treatments. Different VPD conditions did not lead to any significant difference in leaf area, total dry matter, RL, RSA and R/S ratio in Sahel108, whereas low VPD stimulated leaf and root growth of IR64 in comparison to high VPD. The difference between the varieties could be

interpreted on the basis of their origins. IR64 has been selected for the humid tropical climate, while Sahel 108 is adapted to the dry season of an semi-arid environment.

Under high VPD, cold day/warm night treatment increased leaf growth, leaf area, root growth, tiller number and total dry matter of IR64, but no significant difference between temperature treatments was found in Sahel108. Moreover, in IR64, there was no significant difference in all measured parameters of plants grown in the cold day/warm night treatment between two VPDs. Under high VPD, constant day/night temperature tended to enhance the growth of Sahel 108, whereas it led to the smallest plants of IR 64. Notably, no growth of IR 64 grown under constant temperature was observed from 4 to 7 weeks after transplanting. In contrast, under low VPD, warm day/cold night conditions led to the smallest plants for both varieties. The findings suggest that cold day/warm night stimulates the growth of rice at high VPD but not for Sahel108; whereas, warm day/cold night inhibits the growth of both varieties, especially at low VPD.

Our results suggest that growth responses of IR64 are more sensitive to VPD and nutrient solution temperature than that of Sahel108. Stuerz et al. (2004c) also indicated a variation in growth response of rice to meristem temperature; accordingly, Sahel108 is less influenced by cold temperature than IR64. In our experiment, the cold day/warm night treatment enhanced growth of IR 64 under high VPD, and it appears that the stimulation by warm nutrient temperature during the night can compensate the adverse effects caused by high VPD. That higher meristem temperature during the night stimulated plant growth, has been previously reported (Stuerz et al., 2014a).

6. Conclusion

A pot experiment in the greenhouse was carried out to estimate the growth responses of two rice varieties to different diurnal root and meristem temperatures and different VPD levels. Our findings indicated a positive effect of low VPD and higher root and warm day/cold night water on the leaf growth of rice. It was shown that low VPD and higher root and meristem temperature during the night enhanced leaf elongation rate, leaf appearance rate and leaf area. Under low VPD, leaf elongation rate was highest from 8 a.m to 4 p.m due to the positive effect of higher air temperature, whereas under high VPD, the rate was higher during the night due to its reduction by evaporative demand during the day. The effect of nutrient solution temperature on leaf growth was larger under high VPD than under low VPD. Even though cold day/warm night root and meristem temperature enhanced leaf growth, our result indicated a larger impact of VPD than temperature alone.

The experiment has shown an effect of root temperature and VPD on root growth, but also a variation among varieties. In general, cold day/warm night root temperature improved total root length, root surface area, root diameter and root/shoot ratio, but not for Sahel 108 under high VPD. Root growth was generally stimulated under low VPD. Under low VPD, the warm day/cold night treatment relatively reduced root growth in both varieties.

In the experiment, a positive effect of low VPD on the stomatal conductance of both varieties could be shown, but there was no impact of VPD on the photosynthetic rate. Interestingly, root and meristem temperature did not show any significant effect on stomatal conductance and photosynthetic rate. However, stomatal conductance and photosynthetic rate tended to be increased under cold day/warm night in IR64 and under constant temperature or cold day/warm night in Sahel108.

Moreover, the results confirmed that IR64 is more sensitive to VPD and root and meristem temperature than Sahel108. Low VPD strongly enhanced growth of IR64, whereas Sahel108 was less affected. In general, the cold day/warm night temperature pattern stimulated the growth of IR64 under both VPD conditions, whereas the growth of Sahel108 was enhanced either by constant temperature under both VPD levels or by the cold day/warm night pattern under low VPD. For both varieties, the warm day/cold night treatment inhibited plant growth under low and high VPD conditions.

From these results we conclude that cold day/warm night nutrient solution has a positive influence on growth of rice, especially in IR64 and under high VPD. For further

research, the effect of root and meristem temperature in a larger range of temperature and at difference growing stages could be determined.

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