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Growth and Productivity of Irrigated Rice (Oryza sativa L.) for a Tropical High Altitude Environment in Rwanda

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Growth and Productivity of Irrigated Rice (*Oryza sativa* L.) for a Tropical High Altitude
Environment in Rwanda

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in Crop, Soil, and Environmental Sciences

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Abstract

Yield components, grain yield, biomass and plant N accumulation, and N fertilizer responses of irrigated rice (*Oryza sativa, L.)* were evaluated for a tropical inland valley environment in the high altitudes in Rwanda. Effects were measured for nitrogen (N) fertilizer rate (0, 60, 90,120,150,180 kg N ha^{-1}), season, growth stage and cultivar of different subspecies and plant types during 2012 dry season (DS) and 2013 wet season (WS) at Cyili Rice Research Farm (1380 m above sea level). Variations in irradiance (17.2± 0.32 MJ m^{-2} day^{-1} in DS and 9.4 ± 0.66 MJ m^{-2} day^{-1} in WS) were linked to seasonal differences in biomass and closely related to N responses, yield components and the grain yields which were greater in the DS (9.0 t ha^{-1}) than in the WS (5.3 t ha^{-1}). Total plant N uptake was in the same range (200 to 250 kg N ha^{-1}) for both seasons at maturity. Grain yields were highly correlated (r^2 = 0.89) to yield components and mostly with the number of spikelets per panicle (r^2 = 0.70) and spikelets per m^2 (r^2 = 0.80). In most cases, yield components were equivalent or greater to the potential under irrigated lowlands in the tropics of Asia and the highest farm yields (8 to 10 t ha^{-1}) in the temperate. Rice genotypes of Indica x Japonica subspecies combinations were overall greater in yield, harvest index and in important yield components. Crop growth rate (CGR) over seasons and cultivars was 11g m^{-2} day^{-1} at maturity. The average total crop duration of 145 days may be considered as the current optimal for achieving the yield potential obtained in the irrigated lowlands of the tropics in Asia. Responses to N fertilizer addition were generally minimal with most measured attributes maximized when the lowest N rate of only 60 kg N ha^{-1} was applied. This suggested a large contribution from the native soil N reserves linked to ample amounts of total soil N (2.80 ± 0.34 g kg soil^{-1}). The Indica x Japonica combinations may represent a cultivar improvement strategy for greater adaptation and grain yield and quality in Rwanda.

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Dedication

To

Jesus Christ my Lord and Savior for your grace and mercy brought me this far from the misery, sickness and constant fear of death from lions in the refugee camp in Burundi.

Freedom fighters including my brothers Retired Sergeant Eric and Private William, I owe liberty.

Wife Gloriose and daughters Ketia, Lisa, Stacey and Lauren for your patience and love.

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Chapter one:Introduction

The key role of rice (*Oryza sativa*, L.) in global food security is remarkably spreading since the 2000's beyond the traditional production areas in Asia to several African nations and Rwanda (Diagne et al., 2013a).Grown in the tropics to the temperate regions (35°S to 50°N) under a wide range of conditions in climate, soil fertility, water supply and topography, the greater yield potential for rice is obtained in irrigated systems with the cultivation of modern, photoperiod-insensitive, high-yielding cultivars under improved crop management (Peng et al., 2003; De Datta, 1981).Favorable rice crop growth conditions in the irrigated systems are associated with the presence of relatively good water control and anaerobic soil conditions during most of the cropping period (Haefele et al., 2013). Irrigated systems are globally the most widespread among all the other rice systems in lowland environments within deltas and plains in the tropics and subtropics of Asia and the temperate regions (Yoshida, 1981).

Air temperature and most notably irradiance determine differences in growth and yield potential for irrigated lowland rice across and within large geographic regions and countries. The yield potential is defined as the yield of a cultivar when grown in environments to which it is adapted, with nutrients and water non-limiting, and with insect pests, diseases, weeds, lodging, and other stresses effectively controlled (Peng et al., 2008). The increase in the yield potential is a strategy used in rice cultivar development toward enhancing farm yields mostly under irrigated systems(Zou et al., 2013; Zhang et al., 2009).Relatively cooler conditions combined with equivalent or greater irradiance in some cases (15-29 MJ m^{-2} day^{-1}) were associated with longer growth duration and greater growth rates in biomass and nitrogen (N) accumulation resulting in greater grain yield potential ($>$ 10-15 t ha^{-1}) for rice in the subtropics and the temperate regions compared to the tropical irrigated lowlands (8-10 t ha^{-1}) (Katsura et al., 2008; Horie et al., 1997).The yield potential of

8 to 10 t ha^{-1} for irrigated lowlands in the tropics is attained with greater irradiance (18-22 MJ m^{-2} day^{-1}) in the dry season (DS); however, 30 to 40% lower yields often occur in the wet season (WS) mostly due to the effects of cloudy conditions resulting in reduced irradiance ($\leq$ 15 MJ m^{-2} day^{-1}) and relatively high night-time temperatures (Horie et al., 2006). Greater rice biomass growth in the subtropics and the temperate regions seems to occur at all the crop growth stages with ranges in crop growth rate (CGR) of about 16-18 g m^{-2} day^{-1}; whereas the tropical irrigated lowlands have a lower CGR range of 14-15 g m^{-2} day^{-1} (Lafarge et al., 2009; Peng et al., 2003; Ying et al., 1998b). Additionally, greater than critical levels in the plant N uptake (> 150 kg N ha^{-1}) are generally achieved by the end of the vegetative phase or at heading stage in the subtropics and the temperate regions but not in the tropical irrigated lowlands (Katsura et al., 2008; Norman et al., 2003; Shimono et al., 2003).

The number of spikelets per unit area, grain weight and filled grain fraction of total spikelets are the primary yield components used to assess grain yield performance for different rice cultivars and environments (Yoshida, 1981). Variations in the number of differentiated spikelets during the reproductive phase and filled fraction at maturity account for the greatest proportion of yield differences among cultivars and environments (Sheehy et al., 2001). The number of spikelets per unit arearepresents60 to 80% of the variation in the rice grain yield in irrigated lowland systems (Ying et al., 1998a). Growth rates in biomass and plant N uptake during the vegetative and in particular the reproductive phases are closely related to the potential number of mature spikelets in the rice crop (Sheehy et al., 2000; Horie et al., 1997; Khush et al., 1993). Hence, the potential number of mature spikelets or the sink size in rice is generally greater in the subtropics and temperate regions than in the tropical irrigated lowlands. However, the number of spikelets in rice may potentially decline under extreme temperature conditions such as the cold stress in some high latitude areas and in high elevation (> 1000 m above sea level) regions in the tropics, particularly when irradiance is

lower in the WS (Farrell et al., 2006; Sheehy et al., 2006).Variations in the filled grain fraction and in particular the grain weight are generally small within cultivars for the tropical lowlands in Asia (Yang et al., 2008).

There exists a large variation for increasing rice grain yield potential and quality attributes across cultivated subspecies and in their crossbreds (Peng et al., 2008). The use of variation from some wild species was linked to large yield gains in hybrids and super hybrids in China (Zou et al., 2013). However, the variation in the cultivated subspecies of Indica and Japonica is mostly used for rice cultivar improvement. In particular, variations in Japonica and Indica x Japonica subspecies combinations were linked to greater (15 to 30%) and stable grain yields in cold-prone areas of Japan, Korea, Australia and California (Peng et al., 2003; Farrell et al, 2001).

Irrigated rice is also cultivated on a large scale in the tropical high altitude zones (> 1000 m above sea level) of Asia on over 7 million ha and in some high latitude regions of Japan, Korea and Australia where cold stress is the major factor reducing the yield performance especially in the tropics due to limited resources for the deployment of coping cultural strategies (Wang et al., 2013; Farrell et al., 2001). Studies conducted in Asia have reported complex patterns of cold stress within and across countries, and the tolerance level to this stress is cultivar and growth stage-dependent (Farrell et al., 2006; Farrell et al., 2001; Hee Lee, 2001).Similarly, cold stress was identified as a potential constraint to the recent development of irrigated rice systems in the valleys of the tropical high altitude regions in East Africa and Rwanda (NRDS, 2011; Zenna et al., 2010).However, published studies are scarce for irrigated systems in the high altitude areas, and plant and environmental determinants for rice growth and yield performance are unknown particularly in Africa and Rwanda. The average farm grain yield for irrigated rice is 4.5 t ha^{-1} in Rwanda; however, yield records equivalent to the best performances in the temperate regions and the current

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potential of 8-10 t ha^{-1} in irrigated lowlands of the tropics in Asia are often reported by local media, ministries or growers' cooperatives (NRDS, 2011; RSSP, 2011).This study examines patterns and magnitudes of responses in growth for biomass, plant N uptake, primary yield components and grain yield and relationships for irrigated rice as influenced by crop genotype, N fertilization, and the cropping season in an inland valley environment in the medium altitude zone (>1000-1500 m above sea level)in Rwanda. This zone is comprised of the majority of current and potential rice production areas (NRDS, 2011).

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Chapter two: Yield components and grain yield of irrigated rice in a tropical high altitude environment in Rwanda

Highlights

- Irradiance is the greater determinant of rice performance rather than temperature

- Yield components, in particular spikelets numbers are closely linked to grain yield

- Grain yield potential is equivalent to that of typical lowlands of tropical Asia

- Cultivars with Indica x Japonica subspecies combinations have greater performances

- Grain quality of rice can be improved for the high altitude environments in Rwanda

Keywords

Rwanda, cultivated rice subspecies, tropical high altitude, yield components, grain yield, irradiance, air temperature, season, inland valley

Abstract

The performance in yield components and grain yield and their relationships in the rice crop were evaluated for irrigated rice (*Oryza sativa*, L.) in a tropical inland environment in the high altitudes of Rwanda. Four inbred rice genotypes, belonging to different cultivated subspecies and combinations, were compared during the 2012 dry season (DS) and the 2013 wet season (WS) at Cyili rice research farm (1380 m above sea level) in Rwanda with sufficient inputs and pest management to ensure optimal growing conditions. Seasonal differences in air temperatures were small (mean of 18.6°C in DS and 19.6°C in WS) and diurnal variations averaged to 4°C. Total solar radiation intensity was 17.2 ± 0.32 MJ m^{-2} day^{-1} in the DS and decreased by 47% in the WS. This variation in irradiance was closely linked to seasonal differences in yield components and in particular grain yields (41%) which were greater in the DS than in the WS. Grain yields were highly correlated ($r^2 = 0.89$) to yield components and differences in grain yields were mostly associated with the numbers of spikelets per panicle ($r^2 = 0.70$) and spikelets per m^2 ($r^2 = 0.80$).In most cases, performances for yield components and grain yields were equivalent greater to the potential of modern high-yielding rice cultivars under irrigated lowlands in the tropics of Asia and the highest farm yields in the temperate regions. Grain yields ranged from 9.0in the DS to 5.3 t ha^{-1}in the WS and from 6.4 to 7.9 t ha^{-1} among cultivars when averaged over the two seasons. Rice genotypes of Indica x Japonica subspecies combinations, besides potentially having superior grain quality characteristics, overall had an advantage in grain yield and in important yield components in comparison to single subspecies-based genotype (Tropical Japonica cultivar) and to the Glaberrima x Japonica cultivar.

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Introduction

Rice plays a major role in global food security and its cultivation is remarkably expanding beyond traditional producing-areas of Asia to several African nations and Rwanda (Diagne et al., 2013a; Pingali, 2012). Grown in diverse environment sin the tropics to temperate regions (35°S to50°N), the highest potential and farm yields for rice are obtained with modern, semi-dwarf, photoperiod-insensitive, high-yielding cultivars in the lowland environments with irrigation and improved crop management (De Datta, 1981). Irrigated lowlands are generally considered as favorable, and climatic factors, most notably irradiance and temperature determine, the potential of the rice crop growth and grain yield (Yoshida, 1981). The potential is higher in the temperate and subtropics (>10-15 t ha^{-1}) than in the tropics (8-10 t ha^{-1}). These differences have been linked for the temperate and subtropics to relatively longer crop duration and greater growth rates resulting from relatively cooler conditions (mean daily air temperature of 20°C as opposed to 26°C for typical lowlands in the tropics of Asia) and to equivalent and in some cases greater irradiance (15-29 MJ m^{-2} day$^{-1)}$) (Katsura et al., 2008; Horie et al., 1997). In the tropics, at least two major rice crops are produced, one in the dry season (January to May) and one in the wet season (June to December). The two seasons are characterized by contrasted climatic conditions mainly in the intensity of irradiance (Yang et al., 2008). The yield potential of 8 to 10 t ha^{-1} for irrigated lowlands in the tropics is attained in the dry season (DS) with high irradiance (18-22 MJ m^{-2} day^{-1}), and 30 to 40% lower yields often occur in the wet season (WS) mostly due to the effects of intense cloudy conditions resulting in reduced irradiance (≤ 15 MJ m^{-2} day^{-1}) (Horie et al., 2006).

Subnormal climatic conditions; however, affect significant rice production areas and can cause substantial yield losses in certain regions of the world. Extreme cold has been reported as the most damaging climatic stress in over 20 countries where rice production

occurs in some high latitude zones and in the high elevation regions (> 1000 m above sea level).In the tropics of Asia, rice is grown on over 7 million ha in high elevation zones (Wang et al., 2013; Farrell et al., 2001) and lower yields are obtained in the WS than the DS when extreme low temperatures combine with the presence of limited irradiance .In Africa, high elevation areas are predominantly located in the East African region comprising Rwanda and they occupy over 80% of territories (Himeidan et al., 2012). In this region, rolling mountains constitute the dominant landscapes of variable sizes and in between them lay several encased valleys or inland environments (Hughes et al., 1992). These environments have sustained farming-based livelihoods for a majority of human populations over centuries. However, cold stress was identified as the potential constraint to recent development of rice cultivation in the region and in Rwanda since the 2000's (NRDS, 2011; Zenna et al., 2010).

Studies conducted in Asia have reported complex patterns of cold stress within and across countries, and the tolerance level to this stress is cultivar and growth stage-dependent (Farrell et al., 2006; Farrell et al., 2001; Hee Lee, 2001). Moreover, the critical low temperature for rice is generally below 17-20°C and natural variation for cold tolerance exists in major cultivated subspecies of Indica and mostly in Japonica and crossbreds of these subspecies (Farrell et al, 2001). In rice, the reproductive growth is the most sensitive to cold and associated major damages to grain yield result from reduced spikelets number and filled fraction as well as panicle degeneration. In the Philippines, Sheehy et al (2006) and Peng et al (2004) estimated0.5-0.7 t ha^{-1} of rice yield losses when average air temperatures vary by +/- 1°Cfrom a base of 22-26°C. Lyman et al (2012) found similar amounts of yield loss in a temperate environment in Arkansas, USA while investigating the effects of extreme heat. Irradiance and air temperature effects are confounded in nature. For example, Peng et al (2004) reported over 0.7-1 t ha^{-1} of grain losses during the WS in the Philippines following both reduced insolation and relatively high night temperatures. Similarly, Sheehy et al (2006)

measured equivalent yield losses for every 1 MJ m^{-2} day^{-1} decrease in the tropics of Asia. Agro-climatic studies in Rwanda are scarce and existing records pertain to the general climate for the upland conditions and the density of data are limited in time and space (McSweeney et al., 2011). The annual average air temperature in most hilly regions of Rwanda was estimated at 21°C, ranging from 13 to 25°C (McSweeney et al., 2011; Hughes et al., 1992).Extreme low temperatures (<15°C) during night time in particular have been reported in some rice producing valleys (USAID, 2008). On the other hand, Safari et al (2009) calculated as much as 15-18 MJ m^{-2} day^{-1} total solar radiation intensity prevailing in the uplands of hilly regions of Rwanda.

There exists a large variation for increasing rice yield potential and grain quality attributes across cultivated subspecies and in their crossbreds (Peng et al., 2008). The use of variation from wild species was linked to even larger yield gains with rice hybrids and super hybrids in Asia (Zou et al., 2013). Several cultivar improvement programs around the world have primarily relied on the existing variation in Japonica and Indica x Japonica subspecies combinations to achieve greater environmental adaptation and grain yield (Peng et al., 2003). In particular, these subspecies were central to achieving stable yields in cold-prone areas in Japan, Korea, Australia and California (Farrell et al, 2001). The cultivation of modern, high-yielding rice cultivars is widespread mostly in Asia and in the temperate regions. This was enabled by global networks for exchange and testing of germplasm and information sharing for over four decades (Peng et al., 2008). In addition, the advent of national rice research and development programs, especially in Asia, constituted an important value addition in developing and fine-tuning cultivars to fit into local biophysical and socio-economic conditions (Pingali, 2012; Mathews et al., 2006).

The number of spikelets per unit area, grain weight and filled grain fraction of total spikelets number are generally considered the primary yield components and are used to

examine grain yield performance for different cultivars and environments (Yoshida, 1981). Variations in the number of differentiated spikelets during the reproductive phase and filled fraction at maturity by and large account for the largest proportion of yield differences among cultivars and environments (Sheehy et al., 2001).The number of spikelets per unit area, also expressed as the product of the number of panicles per unit area and the number of spikelets per panicle, can represent up to 60 to 80% of the variation in rice grain yield (Ying et al., 1998a). Mature spikelets number per m^2, panicle number per m^2, and spikelet number per panicle can range from 20000 to 80000, 250 to1000 and from 100 to 200, respectively (Katsura et al., 2007; Horie et al., 1997).The filled spikelet fraction can vary from 60 to 97% and a value of at least 85% is considered optimal (Yoshida and Parao, 1976). Variation in the grain weight is rather small (Yoshida, 1983) and less than 5% differences are generally found within cultivars. The 1000-grain weight ranges from 24.7 to 27.7g (Fageria, 2007), but values as high as 29-30g have been reported in some elite inbreds, hybrids and in *Oryza glaberrima*-based interspecific cultivars (Zou et al., 2013; Somado et al., 2008).

Rice production output in Rwanda has doubled over the last decade following an increase in irrigated areas within inland environments while farm yields remained stagnant at 4.5 t ha^{-1} (Diagne et al., 2013b; NRDS, 2011). Cold and numerous other factors (sheath rot disease, blast disease, rice yellow mottle virus, stalk eyed fly, iron toxicity, soil acidity, mineral deficiencies and irrigation water deficit) were identified as potential yield limiting and reducing factors (Diagne et al., 2013a; RSSP, 2011). However, relatively high farm yield records are often reported by local media, ministries or growers' cooperatives (unpublished reports), including cases of over 8-10 tha^{-1} of grain which is equivalent to the best growers' performances in the temperate regions and the current potential in irrigated lowlands of the tropics in Asia (Ying et al., 1998a). The Government of Rwanda has set the goal of increasing farm yield to 7 t ha^{-1} (NRDS, 2011). The direct introduction, testing and

dissemination in Rwanda of various appropriate rice technologies from Asia including elite germplasm showed limited success (Gasore et al., 2010). Studies are therefore needed to identify and quantify important components of rice genotypes, the environment and their interactions as they relate to yield gaps, and potential under high altitude production systems in Rwanda (NRDS, 2011; RSSP, 2011). The aim of this study was to evaluate the variation and performance in primary yield components and grain yield and their relationships for the rice crop as influenced by the cropping season (DS and WS) and the cultivar diversity in an irrigated inland valley environment in the medium altitude zone of Rwanda (> 1000 to 1500 m above sea level). Four commonly grown rice genotypes (cultivars) in Rwanda and belonging to different cultivated subspecies or combinations-Facagro 56 (Indica x Japonica$_1$), Gakire (Indica x Japonica$_2$), UP12 (Glaberrima x Japonica) and Yunyine (Tropical Japonica) were considered in this study (Table 2.1). These cultivars were grown during the 2012 DS and 2013 WS at Cyili rice research farm (1380 m above sea level) in Rwanda under full flood irrigation and sufficient inputs and pests control to ensure optimum growing conditions. The medium altitude zone is comprised of the majority of current and potential rice production areas in Rwanda (NRDS, 2011).

Material and methods

Site description

Field experiments were conducted in the 2012 DS and 2013 WS at Cyili rice research farm of Rwanda Agriculture Board (RAB), Rubona Station, Huye District, Southern Province, Republic of Rwanda. The Cyili area is a 242 ha inland valley situated at an altitude of 1380 m above sea level, longitude 29°53'26'' East and latitude 2°28'18'' South. (Kayiranga, 2006). Over 1500 small households have grown rice in the Cyili area for more than four decades. The soil order in Cyili has been mapped as an Inceptisol (RSSP, 2011) with no further details on soil series or taxonomic description. The soil characteristics in the

plow layer (0-20 cm depth) were as follows: the texture (hydrometer method: Gee &Bauder, 1986) was a sandy clay loam (57% sand, 33% clay, 9% silt) with an average soil pH (1:2 soil/water suspension) of 5.3, total N (Kjeldahl acidic digestion, Bremner, 1965) of 2.80 g N kg^{-1}, organic C (Nelson-Sommers, 1982) of 29 g C kg^{-1}, CEC ($1N$ NH$_4$OAc, adjusted to the actual soil pH) of 26 cmole$_{(+)}$ kg^{-1}, and Mehlich-3-extractable nutrients of 4 mg P kg^{-1}, 119 mg K kg^{-1}, 2008 mg Ca kg^{-1}, 414 mg Mgkg^{-1}, 3.3 mg Zn kg^{-1}, 341 mg Mn kg^{-1}and 1026 mg Fe kg^{-1}. The climate data on air temperature and total solar radiation were collected with a weather station (Delta-T, DL6 automatic weather station) located at the Cyili rice research farm (Fig 2.1 and 2.2).

<u>Plant material, crop establishment and management</u>

Four inbred rice (*Oryza sativa*, L.) genotypes (cultivars) were used in both the DS and the WS. The cultivars were of similar maturity (145 days on average) and represented different genetic backgrounds, origins, production ecologies and grain characteristics in order to have a wide range in yield components and grain yield. These cultivars were: Facagro 56 (Indica x Japonica$_1$), Gakire (Indica x Japonica$_2$), UP12 (Glaberrima x Japonica) and Yunyine (Tropical Japonica). Detailed descriptions of cultivars are given in Table 2.1.

Land preparation in both seasons consisted of an initial deep plow (0-30 cm depth), then soil was puddled and levelled under saturated moisture conditions. In the DS, seedlings were raised on a wet bed nursery on July 15 by sowing pre-germinated seeds that had been incubated for 24 to 48 hours at 30°C. Twenty four day old seedlings (3-to 4-leaf stage) were manually transplanted on August 8, under saturated soil conditions, with one seedling per hill at a spacing of 0.2m x 0.2m (equivalent to a planting density of 25 seedlings m^{-2}). Saturated soil conditions were maintained for a week to allow seedling recovery from transplanting shock before permanent flood establishment. In the WS, a three-week flood in Cyili destroyed the seedling nursery. Therefore, direct seeding was adopted to avoid the potential

negative effect of late planting. Planting was conducted manually on February 17 by drill-seeding under dry soil conditions using pre-germinated seeds at the rate of 20 kg ha^{-1}. Seeds were immediately covered with a thin layer of soil and non-flood, saturated soil conditions were enabled in the field with frequent flush irrigations for three weeks to ensure maximal seedling emergence and establishment. Seedling emergence occurred within 7 to 10 days after seeding. Crop thinning and gap filling were completed leaving approximately 25 hills m^{-2}prior to flood establishment on March 12.In both seasons, each plot was 4 m long and 14 rows wide (spaced 20 cm apart). Throughout each cropping season, permanent flood (5-10 cm water depth) was ensured with water from the Cyili rice area dam and when required by pumping fresh water from a nearby river. The flood was maintained till physiological maturity. Pests were controlled to avoid significant loss in biomass and yield. The control of weed growth was achieved with frequent hand removal passes; rice stalk eyed fly (*Diopsis thoracica*) was mitigated with weekly sprays of 1.5 kg a.i. ha^{-1} Cypermethrin 40% WP for 8 weeks starting at seedling stage. All field operations were manually implemented and sufficient labourers were mobilized to achieve timely execution of the various field operations and data collection.

During both the DS and the WS, experiments were arranged in split plot design with four blocks; N rates assigned to whole plots and rice genotypes to subplots. Urea fertilizer (46% N) was used as the N source, and total rate splits of 0, 60 (20+20+20+0), 90 (20+20+30+20), 120 (20+30+40+30), 150 (20+40+50+40) and 180 (30+50+60+40) kg N ha^{-1}were applied, respectively, as preflood (PF) which was at 30 days from sowing on average, 30 days after PF (30DPF), at the beginning panicle initiation (PI) and at 50% heading stage (Hd). On average, PI and Hd occurred about 45 and 75 days from PF, respectively (equivalent to 75 and 105 days from sowing). Urea was applied on moist soil at PF and the flood was established within four hours from application. Subsequent N splits were made

directly into the flood. Rates of 180 kg K_2O ha^{-1} as muriate of potash (60% K_2O), 90 kg P_2O_5 ha^{-1} as single super phosphate (21% P_2O_5) and 30 kg Zn ha^{-1} as zinc sulfate (20% Zn) fertilizers were topdressed by hand in a single PF application across all treatments to ensure these nutrients were not limiting.

Yield components and grain yield measurements

Panicles were hand-harvested at maturity stage from an averaged 10-hill sample in each subplot for the quantification of yield components (Zhang et al., 2009). Panicles were counted in each sample to determine the number of panicles per m^2. Panicles were oven-dried at 60^oC until constant weight, hand-threshed and filled spikelets separated from unfilled spikelets by submerging them in tap water. Total weight of filled and unfilled spikelets was determined (Sartorius weighting scale, ED62025, precision= 0.01 g) for each subplot sample. Three subsamples of 5 g of filled spikelets and 1 g of unfilled spikelets were taken to count (Elmor seed counter, precision= 1/1000) the number of spikelets. The number of filled spikelets per panicle was computed as the product of total filled spikelets weight and the average number of filled spikelets in 5g divided by total panicles number in a10-hill sample. The number of unfilled spikelets per panicle was computed as the product of total unfilled spikelets weight and the average number of unfilled spikelets in 1g divided by total panicles number in a10-hill sample. The number of spikelets per panicle was calculated as the sum of filled and unfilled spikelets per panicle; the number of spikelets per m^2 was calculated as the product of the number of panicles per m^2 and the number of spikelets per panicle; the grain filling ratio as filled spikelets number divided by total spikelets number; 1000 filled grain weight in grams as 1000 divided by the number of filled grains divided by 5g. Rough rice grain yields were measured on a 9 m^2 area in each subplot. Both 1000 filled grain weight and grain yield values were adjusted to standard moisture content of 140 g H_2O kg^{-1}.

Experiments were arranged in a-four block split plot design in both seasons and the analysis of variance (ANOVA) was conducted following the linear mixed model (Gbur et al., 2012) in SAS 9.4 software (SAS Institute, Inc., Cary, NC) with cultivar and season as fixed effects and block as a random effect, to determine the overall statistical significance of the effects of explanatory variables (cultivar and season and their interaction). Means of rice cultivars, seasons and interaction effects on yield components and grain yields were compared based on the least significant difference procedure (LSD) at the 0.05 probability level. Partial regression analysis was conducted to determine the amount of association (coefficient of determination: R^2 and standardized regression coefficient) between grain yields and yield components using JMP Pro11 software (SAS Institute, Inc., Cary, NC). The coefficient of variation (CV %) served to quantify variations among rice cultivars within each season. The reporting of results was based on data pooled over N rates since most of the interaction effects involving cultivar and N rate were not significant for the grain yield and yield components (Table 2.2).

Results

Number of spikelets per panicle

The cultivar x season interaction effect was significant (*P<0.0001*) for the number of spikelets per panicle (Table 2.2). The average number of spikelets per panicle across the four cultivars was 58% greater in the DS (173) than in the WS (73) (Fig 2.3). The number of spikelets per panicle was greater and similar in the Indica x $Japonica_2$ (187) and Glaberrima x Japonica (183) than in the Indica x $Japonica_1$ (158) and Tropical Japonica (164) cultivars which were identical to each other in the DS. In the WS, the number of spikelets per panicle for the Indica x $Japonica_1$ (94) was greater compared to all other cultivars, except the Indica x $Japonica_2$ (80) which was not different from the Glaberrima x Japonica (67), and this latter

cultivar was not greater than the Tropical Japonica (50) cultivar. The variation in the number

of spikelets per panicle, across cultivars, ranged from 8 to 26% in the DS and the WS,

respectively. Averaged over seasons, the number of spikelets per panicle was identical in the

Indica x Japonica$_1$ (126), Indica x Japonica$_2$ (133) and Glaberrima x Japonica (125) cultivars

and greater than the tropical Japonica (107) cultivar.

Number of panicles per m^2

The cultivar x season interaction effect was significant ($P<0.0001$) for the number of

panicles per m^2 (Table 2.2).The average number of panicles per m^{2}across the four cultivars in

the DS (332) was not different from the WS (309) (Fig 2.4). Greater number of panicles per

m^2 was recorded in the DS for the Indica x Japonica$_1$ (425) followed by the Indica x Japonica$_2$

(378), Tropical Japonica (318) and Glaberrima x Japonica (208) cultivars. In the WS, the

number of panicles per m^2 was greater and not different between the Indica x Japonica$_1$ (339)

and Indica x Japonica$_2$ (351) which were followed by the Tropical Japonica (306) and

Glaberrima x Japonica (239) cultivars. The number of panicles per m^2 was not different

between the DS and the WS in the Tropical Japonica and in the Indica x Japonica$_2$ which was

not greater than Indica x Japonica$_1$ cultivar in the WS. The variation in the number of

panicles per m^2, across cultivars, ranged from 16% in the DS to28% in the WS. Averaged

over seasons, the number of panicles per m^2 was greater and similar in the Indica x Japonica$_1$

(382) and Indica x Japonica$_2$ (365) than in the tropical Japonica (312) which was greater than

the Glaberrima x Japonica (224) cultivar.

Number of spikelets per m^2

The cultivar x season interaction effect was significant ($P = 0.0004$) for the number of

spikelets per m^2 (Table 2.2). The average number of spikelets per m^2 across the four cultivars

was 60% greater in the DS (56954) than in the WS (22842) (Fig 2.5). The number of

spikelets per m^2 was consistently greater and similar in the Indica x Japonica$_1$ and Indica x

Japonica$_2$ cultivars during each season, followed by the Tropical Japonica which was greater than Glaberrima x Japonica in the DS. These two latter cultivars had identical the number of spikelets per m^2 in the WS. The variation in the number of spikelets per m^2, across cultivars, ranged from 26 to 37% in the DS and the WS, respectively. Averaged over seasons, the number of spikelets per m^2 was greater and identical in the Indica x Japonica$_1$ (49426) and Indica x Japonica$_2$ (49378) than in the tropical Japonica (33771) which was greater than the Glaberrima x Japonica (27017) cultivar.

Grain filling ratio

The cultivar x season interaction effect was significant ($P = 0.0042$) for the grain filling ratio (GFR) (Table 2.2). The average GFR across the four cultivars was 12% greater in the WS (0.90) than in the DS (0.79) (Fig 2.6). In the WS, the GFR was greater and similar in the Glaberrima x Japonica (0.95) and Tropical Japonica (0.96) followed by the Indica x Japonica$_1$ (0.88) which was greater than the Indica x Japonica$_2$ (0.81) cultivar. In the DS, the GFR for the cultivars from the highest to the lowest were as follows: Tropical Japonica (0.85)> Glaberrima x Japonica (0.81)> Indica x Japonica$_1$ (0.79)> Indica x Japonica$_2$ (0.71) cultivars. In the DS, the Glaberrima x Japonica was similar to Indica x Japonica$_2$ cultivar in the WS. The average variation in the GFR, across cultivars, was 8% within each season. Averaged over seasons, the GFR for the cultivars from the highest to the lowest were as follows: Tropical Japonica (0.91)> Glaberrima x Japonica (0.88)> Indica x Japonica$_1$ (0.84)> Indica x Japonica$_2$ (0.76) cultivars.

Thousand grain weight

The cultivar x season interaction effect was significant ($P<0.0001$) for the 1000 grain weight (1000GW) (Table 2.2). The average 1000 GW across the four cultivars was 15% greater in the WS (26g) than in the DS (22g) (Fig 2.7). The 1000 GW was greater in the Glaberrima x Japonica (33g) compared to all other cultivars in the WS, except for the

Tropical Japonica (28g) which was not greater than the Glaberrima x Japonica (25g) cultivar in the DS. The latter cultivar had the greatest 1000 GW in the DS which was not different from the Tropical Japonica (23g) as well as the Indica x Japonica$_1$ and Indica x Japonica$_2$ cultivars which did not differ from each other or vary between seasons. The variation in the 1000GW, across cultivars, ranged from 9 to 22% in the DS and the WS, respectively. Averaged over seasons, the 1000 GW was greater in the Glaberrima x Japonica (29g) but not different from the Tropical Japonica (25g) which was equivalent to the Indica x Japonica$_1$ (20g) and Indica x Japonica$_2$ (22g) cultivars.

Grain yield

The cultivar x season interaction effect was significant (*P<0.0001*) for the grain yield (Table 2.2). The average grain yield across the four cultivars was 41% greater in the DS (9.0 t ha^{-1}) than in the WS (5.3 t ha^{-1}) (Fig 2.8). In the DS, the Indica x Japonica$_2$ had greater grain yield (9.7 t ha^{-1}) compared to all other cultivars, except for the Indica x Japonica$_1$ (9.5 t ha^{-1}) which was not greater than the Tropical Japonica (8.9 t ha^{-1}) cultivar. The Glaberrima x Japonica had the lowest grain yield (7.7 t ha^{-1}) among the cultivars in the DS. In the WS, the Indica x Japonica$_1$ (6.2 t ha^{-1}) and Indica x Japonica$_2$ (5.8 t ha^{-1}) had greater and similar grain yields followed by the Glaberrima x Japonica (5.1 t ha^{-1}) and Tropical Japonica (4.0 t ha^{-1}) cultivars. The variation in the grain yield, across cultivars, ranged from 10 to 18% in the DS and WS, respectively. Averaged over seasons, greater and similar grain yields were recorded in the Indica x Japonica$_1$ (7.9 t ha^{-1}) and Indica x Japonica$_2$ (7.8 t ha^{-1}) than in the Glaberrima x Japonica (6.4 t ha^{-1}) and Tropical Japonica (6.5 t ha^{-1}) cultivars which had identical grain yields.

Discussion

The performances of cultivars in the number of spikelets per panicle, number of panicles per m², number of spikelets per m², and the grain yield were in most cases greater in the DS than in the WS; the opposite was observed for the GFR and 1000 GW in comparison to tropical irrigated lowlands and temperate regions in Asia (Yang et al., 2008; Akita, 1989; Yoshida, 1983). Greater yield components and grain yield in a majority of cases have been linked to greater irradiance. As much as 17 MJ m⁻² day⁻¹ intensity in total solar radiation, which prevailed in Cyili-Rwanda rice area in the DS, can support the greatest growth and rice grain yield potential so far reported of 13-16 t ha⁻¹ for a-150 day crop duration from sowing to maturity (Katsura et al., 2007; Sheehy et al., 2006; Yoshida, 1981).

In the DS, the numbers of spikelets per panicle and spikelets per m² and the grain yields were generally equivalent to or greater than attainable potential of modern high-yielding rice cultivars under irrigated lowland environments in the tropics of Asia and the highest farm yields in the temperate regions (Yang et al., 2008; Horie et al., 1997).The average numbers of spikelets per m² (56954) and spikelets per panicle (173) were characteristic of the greatest crop performances in the temperate and subtropical rice producing regions of Asia. They were also greater by about 20 and 40% compared to respective potential of 45000 spikelets per m² and 80-130 spikelets per panicle in the tropics of Asia. Conditions in Cyili-Rwanda, which combined cooler air temperatures (daily mean of 18.6°C in the DS and 19.6°C in the WS) during both seasons (Fig 2.1) and greater intensity in irradiance (17.2 ± 0.32 MJ m⁻² day⁻¹) in the DS (Fig 2.2) than in the WS, have been linked to greater number of spikelets (sink size) as Yoshida and Parao (1976) observed in the high latitude regions in the north of Japan. Moreover, the average grain yield of 9.0 t ha⁻¹ was realized in the DS and it was within the 8-10 t ha⁻¹ potential range for the irrigated lowland

rice in the tropics of Asia. Also, this yield level was equivalent to the highest farm yields of the temperate regions.

In the WS, a decrease relative to the DS occurred for the numbers of spikelets per panicle, and spikelets per m^2 and for the grain yield (Yang et al., 2008). The greatest reductions were measured for the numbers of spikelets per panicle (58%) and spikelets per m^2 (60%). These magnitudes of decline were about twofold greater than the levels reported with modern rice cultivars in the irrigated lowlands of the tropics in Asia (Ying et al., 1998a; Akita, 1989). The potential number of spikelets in rice is negatively correlated with low irradiance and extreme temperature conditions (Farrell et al., 2006; Sheehy et al., 2006). The decrease in irradiance (9.4 ± 0.66 MJ m^{-2} day^{-1}) in the WS in Cyili-Rwanda was below levels of the tropical lowlands in Asia (11-15 MJ m^{-2} day^{-1}), and may be responsible for the larger drop in the numbers of spikelets.

The overall grain yield decrease of 41% from the DS to the WS in Cyili-Rwanda was similar to irrigated lowlands in the tropics of Asia, and the grain yield of 5.3 t ha^{-1} in the WS fell within the potential range of 5-6 t ha^{-1} (Yang et al., 2008, Horie et al., 1997; Yoshida, 1981). This decline in grain yield was essentially close to a 47% decrease in the intensity of irradiance recorded in the WS in Cyili-Rwanda. This magnitude of variation between the grain yield and irradiance was consistent with the estimates of 0.7-1 t ha^{-1} decline in grain yield for every 1 MJ m^{-2} day^{-1} drop in the irrigated lowlands of the tropics in Asia (Sheehy et al., 2006; Peng et al., 2004). Also, this relationship seemed to indicate, by contrast to cold-prone areas in the high altitude and latitude zones of Asia, that the intensities in low air temperature recorded in Cyili-Rwanda (18.6°C in DS and 19.6°C in WS) in both seasons were probably not below critical levels (17-20°C range is considered critical during the reproductive crop growth phase) to adversely impact the tested cultivars, as suggested by the grain yield performances equivalent to those in the irrigated lowland environments in the

tropics of Asia typically known to be not limited by cold stress. Conditions for areas prone to cold stress, such as Nepal, Australia, Japan and Korea, are often marked by extreme low air temperatures ($\leq$ 10-15°C) in the beginning and at the end of the cropping season, resulting insignificant decreases in the number of spikelets and filled grain fractions (Katsura et al., 2007; Farrell et al., 2001; Hee Lee, 2001). Further, on a cultivar basis averaged over the DS and the WS, grain yields of the two top yielding cultivars (Indica x Japonica$_1$ and Indica x Japonica$_2$), which ranged from 7.8 to 7.9 t ha^{-1}, were apparently similar to the yield potential (8-10 t ha^{-1}) in the irrigated lowlands of the tropics in Asia despite significant decline in irradiance in the WS for Cyili-Rwanda. This may suggest the existence of even more tolerance to low irradiance in the rice crop as pointed out by Evans and De Datta (1979). On the other hand, longer crop growth in Cyili-Rwanda (145 days on average) (Table 2.1) may compensate for low irradiance in the WS, and synergize with favorable conditions in irradiance and air temperature to enable greater crop performance especially in the DS (Akita, 1989). The lack of publications on yield components and grain yields for areas prone to cold stress in the high altitudes of Africa or Asia precluded any comparison.

As for the other yield components in comparison to irrigated lowlands in the tropics of Asia, the number of panicles per m^2, averaged over cultivars, was within the potential range of 250-400 in the DS (332) and the WS (309), (Yang et al., 2008). The numbers of panicles per m^2 for the two top cultivars (Indica x Japonica$_1$ and Indica x Japonica$_2$) were in the higher end or greater than the potential range particularly in the DS. The number of panicles per m^2 was the lowest in the Glaberrima x Japonica cultivar in both seasons (Somado et al., 2008). The GFR values of 0.79 in the DS and 0.90 in the WS were in the higher end of the normal range of 0.60-0.97 (Yoshida and Parao, 1976). The GFR in the WS was even greater than the optimal value of 0.85 (Yoshida, 1981). The average 1000 GW was greater than the critical value of 25g only in the WS (Yoshida, 1981). Greater values of GFR

and 1000 GW, particularly in the WS for the Glaberrima x Japonica and Tropical Japonica cultivars, were in accord with studies in Asia and West Africa (Peng et al., 2008; Somado et al., 2008). However, the increases in the GFR and 1000 GW in the WS in Cyili-Rwanda were opposite to the common behaviour with these yield components generally remaining constant or marginally declining in the tropical lowlands in Asia (Yang et al., 2008). Location-specific conditions may strongly alter anticipated trends in rice yield components (Yoshida, 1983). On the other hand, compensation effects among yield components, common in rice, may have resulted in the increase in these yield components to balance for the great decline in the numbers of spikelets per panicle and spikelets per m^2 (Ying et al., 1998a).

The grain yields, averaged over cultivars and seasons, were strongly linked to yield components ($r^2 = 0.89$) as reported by other studies (Fageria, 2007; Ying et al., 1998a; Yoshida, 1981). However, the greatest variations in grain yields were accounted for by the differences in the numbers of spikelets per panicle ($r^2 = 0.70$) and spikelets per m^2 ($r^2 = 0.80$). These values fell within the reported range of 60 to 80% for most rice producing areas in Asia (Ying et al., 1998a; Akita, 1989). The GFR and the 1000 GW represented 10 and 14%, respectively, of the variation in grain yield.

Overall, the Indica x Japonica$_1$ and Indica x Japonica$_2$ performed the best (statistically or in absolute values) among the cultivars as concerns the numbers of spikelets per panicle (126 and 133), spikelets per m^2 (49426 and 49375) and panicles per m^2 (382 and 365) and in grain yields (7.9 and 7.8 t ha^{-1}). Improved Indica or Indica x Japonica cultivars potentially produce a greater number of spikelets and up to 30% grain yield advantage (Peng et al., 2008; Yoshida et al., 2006; Rutger et al., 1985). Grain yields in the Glaberrima x Japonica (6.4 t ha^{-1}) and Tropical japonica (6.5 t ha^{-1}) cultivars were lower by about 20% while their decline in the number of spikelets per m^2 was much greater (55 and 68%) in comparison to the Indica x Japonica cultivar$_1$ and Indica x Japonica$_2$cultivars. This may suggest a likely greater

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compensation effect from respective greater GFR (0.88 and 0.91) and 1000 GW (29g and 25g) to elevating their grain yields (Ying et al., 1998a).Overall, cultivars possessing the genetic backgrounds that combine Indica x Japonica subspecies, appeared to have an advantage in grain yield and important yield components than any other subspecies combination (Glaberrima x Japonica) or single subspecies-based (Tropical Japonica) cultivars. The benefit in the combinations of distantly related cultivated subspecies and wild species, for rice cultivar improvement, is widely recognized and linked to heterosis (Peng et al., 2004; Khush et al., 1993). Since the mid 1970's, this has led to important leaps in grain yields and quality as well as greater adaptation to major biotic and abiotic stresses. In particular, the Indica x Japonica combinations have been the most extensively used and the basis for grain yield stability in areas prone to cold in Japan, Korea, Australia and California (Farrell et al., 2006; Hee Lee, 2001).

Conclusion

Equivalent or greater performances to the best modern rice cultivars and favorable production environments in the world were observed for yield components and grain yield of rice in a tropical inland environment in the high altitudes in Cyili-Rwanda. This was shown in nearly all the cultivars tested in the favorable growth conditions of the DS and even in the WS when irradiance was drastically reduced in comparison to the tropics of Asia. Similar to irrigated lowland environments in Asia, measured grain yields in Cyili-Rwanda were closely related to the performances in yield components, the numbers of spikelets per panicle and spikelets per m^2 accounting for the greatest variation. Seasonal differences and variations in air temperatures were much smaller on average in comparison to rice production environments in Asia. The intensity of irradiance in the DS was sufficient to support the highest rice crop productivity ever reported in the literature; however, in the WS the intensity in irradiance was way below typical levels of the tropical lowlands in Asia. This variation in

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irradiance was closely linked to seasonal differences in yield components and in particular grain yields which were greater in the DS than in the WS. Of the four tested cultivars, those that were combinations of Indica and Japonica cultivated subspecies of rice generally exhibited the greatest performances in yield components in particular the number of spikelets per m^2, and the grain yields. These trends have been reported in diverse environments. Lastly, the grain yield achieved with the two top yielding cultivars nearly doubled the current farm yields of 4.5 t ha^{-1}in Rwanda while using recommended cultural practices.

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Table 2.1. Key characteristics of rice cultivars evaluated in 2012 dry season and 2013 wet season

Cultivar	Subspecies	Plant type	Original ecology	Origin	Release year	Growth duration (days)[a]	Grain type
Facagro 56	Indica x Japonica$_1$	Semidwarf	Irrigated	Burundi	1996	145	Medium/translucent
Gakire	Indica x Japonica$_2$	Semidwarf	Irrigated	West Africa	2003	144	Medium/translucent
UP12	Glaberrima x Japonica	Standard stature	Upland	West Africa	2010	145	Long/bold/chalky
Yunyine	Tropical Japonica	Standard stature	Irrigated	Taiwan	1980's	147	Short/chalky

[a] From sowing to physiological maturity

Table 2.2. Analysis of variance (ANOVA) for the number of spikelets per panicle, number of panicles per m^2, number of spikelets per m^2, grain filling ratio,1000 grain weight and grain yield

Source of variation[a]	Number of spikelets per panicle	Number of panicles per m^2	Number of spikelets per m^2	Grain filling ratio	1000 grain weight	Grain yield
	p value	*p value*	*p value*	*p value*	*p value*	*p value*
N	0.2937	0.0018	0.0002	0.0167	0.2051	0.0200
C	0.0014	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
N x C	0.9060	0.0722	0.8086	0.0002	0.7379	0.0950
S	< 0.0001	0.0018	< 0.0001	< 0.0001	< 0.0001	< 0.0001
N x S	0.0275	0.0250	0.0023	0.8384	0.5632	0.0083
C x S	< 0.0001	< 0.0001	0.0004	0.0042	< 0.0001	< 0.0001
N x C x S	0.6045	0.4213	0.5034	0.264	0.6946	0.8056

[a] N: N rate, C: cultivar, S: season
[b] significant at *p value ≤ 0.05*
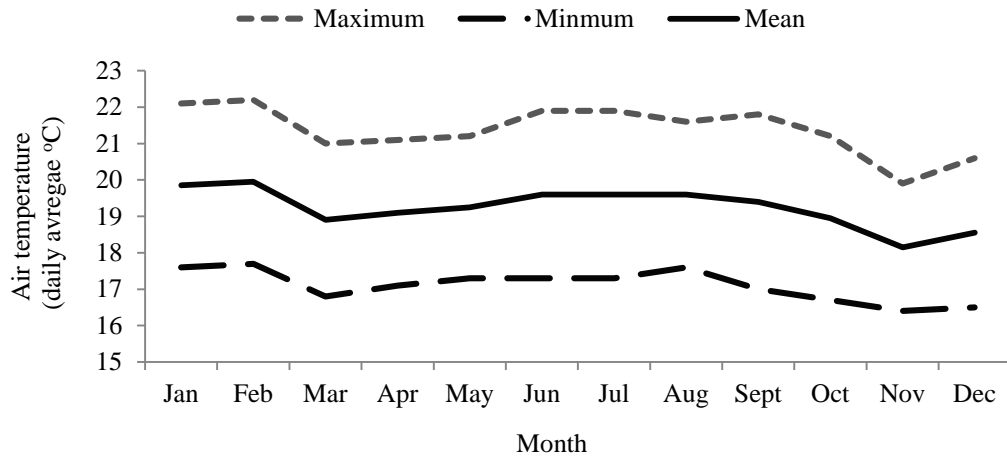
Fig 2.1. Air temperature records during the dry season 2012 and the wet season 2013
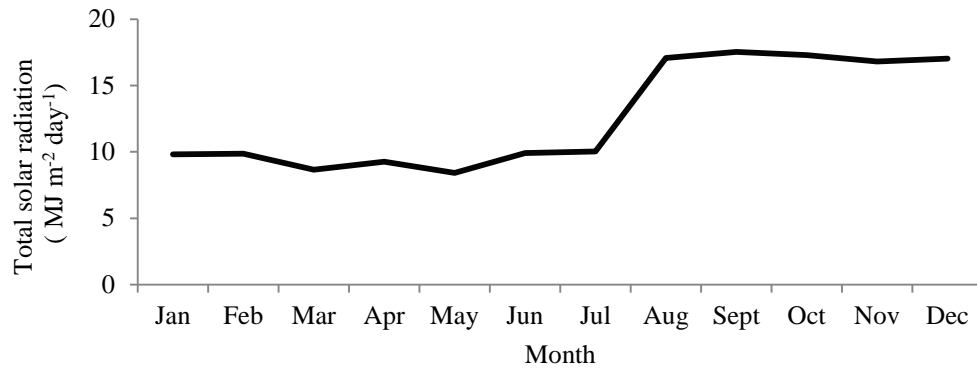
Fig 2.2. Total solar radiation records during the dry season 2012 and the wet season 2013
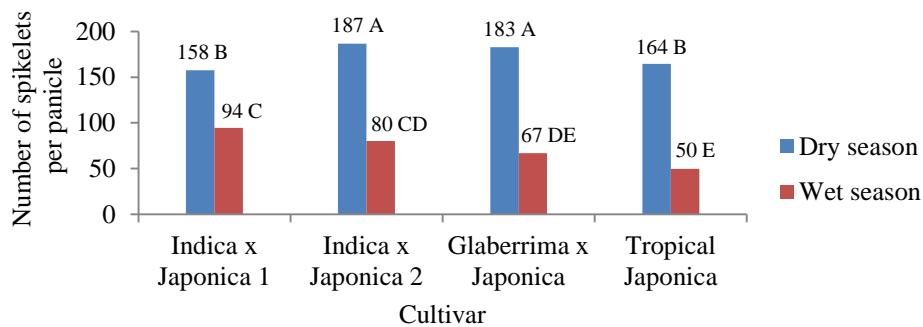
Fig2.3. Influence of season and cultivar interaction, averaged across N rates, on the number of spikelets per panicle. LSD (0.05) to compare the number of spikelets per panicle means among cultivars: same cultivar across seasons = 16.74; different cultivars within and across seasons = 17.58. Means followed by the same letter(s) are not significantly different.
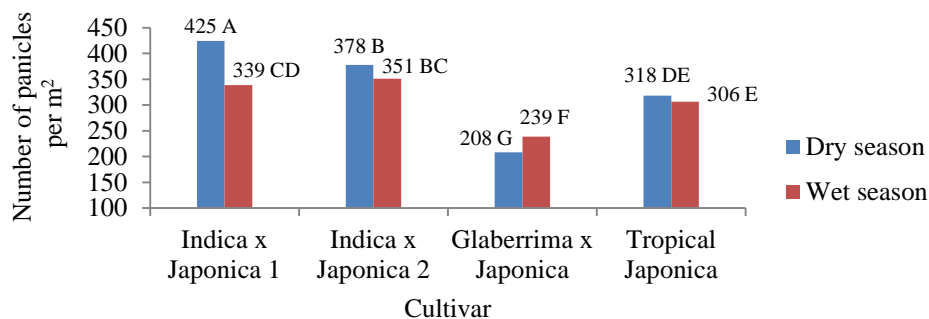
Fig2.4. Influence of season and cultivar interaction, averaged across N rates, on the number of panicles per m^2. LSD (0.05) to compare the number of panicles per m^2 means among cultivars: same cultivar across seasons = 28.85; different cultivars within and across seasons = 30.02. Means followed by the same letter(s) are not significantly different.
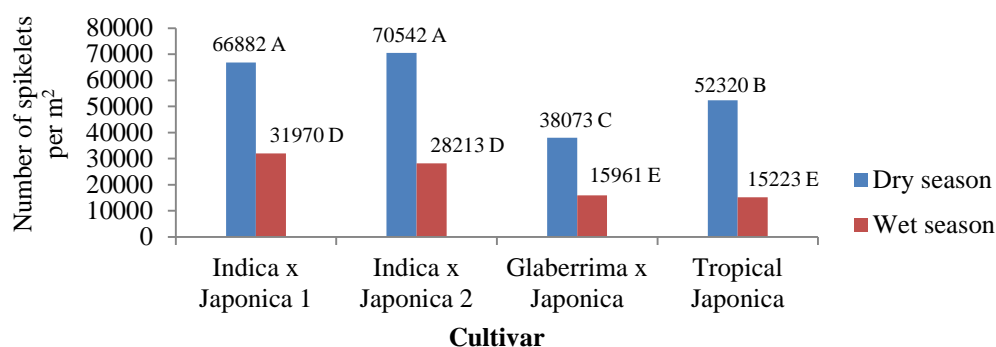
Fig2.5. Influence of season and cultivar interaction, averaged across N rates, on the number of spikelets per m^2. LSD (0.05) to compare the number of spikelets per m^2 means among cultivars: same cultivar across seasons = 5925; different cultivars within and across seasons = 5955. Means followed by the same letter(s) are not significantly different.
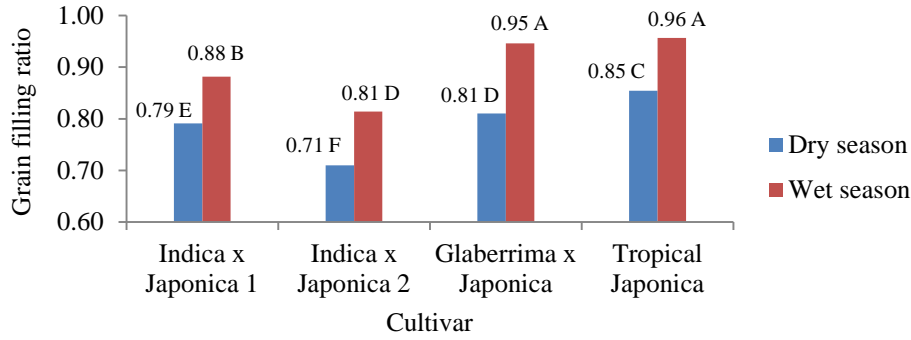
Fig2.6. Influence of season and cultivar interaction, averaged across N rates, on the grain filling ratio. LSD (0.05) to compare the grain filling ratio means among cultivars: same cultivar across seasons = 0.01600; different cultivars within and across seasons = 0.01611. Means followed by the same letter(s) are not significantly different.
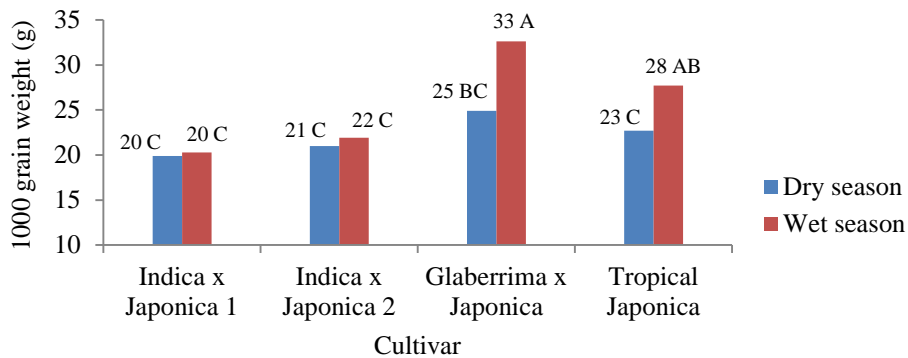
Fig2.7. Influence of season and cultivar interaction, averaged across N rates, on the 1000 grain weight (g). LSD (0.05) to compare the 1000 grain weight (g) means among cultivars: same cultivar across seasons =3.43; different cultivars within and across seasons = 5.28. Means followed by the same letter (s) are not significantly different.
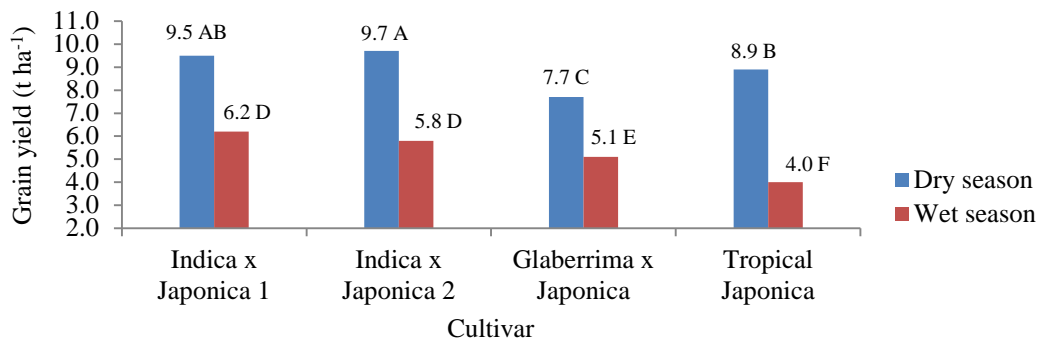
Fig 2.8. Influence of season and cultivar interaction, averaged across N rates, on the grain yield (t ha^{-1}). LSD (0.05) to compare the grain yield (t ha^{-1}) means among cultivars: same cultivar across seasons = 0.691; different cultivars within and across seasons = 0.693. Means followed by the same letter(s) are not significantly different.

Chapter three: Biomass and nitrogen accumulation and relationships with yield attributes for irrigated rice in a tropical high altitude environment in Rwanda

Highlights

- Irradiance is linked to differences in biomass accumulation

- Greater potential for biomass partitioning to panicle

- Total plant N uptake comparable to the greatest levels for rice

- Yield attributes best predicted by growth performance at heading stage

- Biomass more closely correlated with yield than with plant N uptake

- Panicle growth more closely correlated with yield than with total biomass

- Plant N uptake more closely correlated with biomass than with yield

- The yield potential of irrigated tropical lowlands attained in 145 days

Keywords

Rwanda, tropical high altitude, inland valley, irradiance, air temperature, plant type, cultivated rice subspecies, growth phase, season, biomass, plant N, yield components, grain yield

Abstract

Biomass accumulation and total plant nitrogen (N) uptake and relationships with the number of spikelets per m^2 and grain yield were evaluated for irrigated rice (*Oryza sativa, L.*) in a tropical inland valley environment in the high altitudes of Rwanda. Responses were measured at key crop growth stages in three cultivars of different subspecies and plant types: Indica x Japonica (semidwarf), Glaberrima x Japonica (standard stature) and Tropical Japonica (standard stature) grown with sufficient inputs and pest management to ensure favorable growth during the 2012 dry season (DS) and 2013 the wet season (WS) at Cyili rice research farm (1380 m above sea level). Variations in the total and panicle dry weight were linked to seasonal differences in irradiance which were greater in the DS than in the WS. The total plant N uptake at maturity was on average in the same range (200 to 250 kg N ha^{-1}) in both seasons. Average crop growth rate (CGR) over seasons and cultivars was 11g m^{-2} day^{-1} at maturity. The semidwarf Indica x Japonica cultivar had the greatest harvest index (HI) values (0.53 in DS and 0.48 in WS) compared to the standard statured cultivars of Glaberrima x Japonica (0.45 in DS and 0.40 in WS) and Tropical Japonica (0.45 in DS and 0.27 in WS). Average total crop duration of 145 days may be considered as the current optimal for achieving the yield potential (8-10 t ha^{-1}) obtained in tropical Asia. Higher correlations of biomass and total plant N uptake with the number of spikelets per m^2 and grain yield occurred during the reproductive growth period than at any other stage prior to maturity. Correlations of yield were the greatest with biomass and panicle dry weight than with total plant N uptake. The apparent potential for large panicle growth and in particular plant N uptake with the semidwarf Indica x Japonica subspecies combination may be an important plant characteristic for improved rice crop performance in an environment in the Cyili-Rwanda.

Introduction

Crop growth and final yield are the result of the formation and increase in size and weight of different organs which are enabled by the accumulation of organic C-rich compounds during photosynthesis. The key inputs in photosynthesis are light, CO_2 and nitrogen (N). The organic C-rich compounds are the main building blocks of dry matter (DM). The efficiency with which DM is accumulated and allocated to harvestable organs, grains in rice, determines the size of yield components and final yield (Fageria et al., 2006). Growth in annual plants consists of distinct phases of development marked by changes in morphology and physiology (cell division, enlargement, differentiation). In the rice crop, development is divided into the vegetative, reproductive and grain filling phases (De Datta, 1981; Yoshida, 1981). The vegetative phase refers to the period from seed germination to the initiation of panicle primordia. The numbers of internodes and effective tillers which will bear panicles are determined during this phase. The reproductive phase begins with the differentiation of panicles as microscopic white feathery cones inside the tip of growing shoots. This phase is featured by the emergence of fully developed panicles and anthesis. The potential number and size of spikelets, also termed sink size, is determined during this phase. The grain filling phase starts with the spikelet pollination and fertilization. This phase is characterized by grain growth through the increase in size and weight and colour change to yellow or straw-like at maturity. The grain filling ratio is determined during this phase.

The duration for a rice crop varies from 3 to 6 months between seed germination and maturity depending on the cultivar and the growing environment. In a given environment, differences are primarily caused by variations in the length of the vegetative phase, whereas the reproductive and ripening phases remain largely constant. Generally, high temperatures and near normal day length in the tropics result in relatively faster crop growth and shorter duration than in the subtropics and temperate regions (Ying et al., 1998a; De Datta, 1981;

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Yoshida, 1981). Medium crop duration of about 125-130 days in rice was suggested to be the optimum for sufficient growth and maximum yield under favorable production conditions of the tropics in Asia (De Datta, 1981; Yoshida, 1981). Under these conditions, rice cultivars spend about 60 days in the vegetative phase, and 25 and 35 days in the reproductive and grain filling phases, respectively. Similarly, most cultivars grown in low elevations of the subtropics and temperate regions (Stivers, 2009; Horie et al., 2006) can mature relatively early as a result of successful crop selection. Conversely, rice crop duration is generally longer in high elevation areas: 80-90, 25-30 and 45-60 days to complete the vegetative, reproductive and grain filling phases, respectively.

Irrigated rice production systems represent about one-half of rice areas and three fourths of the rice grain production in the world (Peng et al., 2003). Conditions in these systems are generally considered favorable and irradiance determines the rice canopy photosynthetic efficiency, growth rate, dry matter accumulation and final yield (Fageria et al., 2006; Yoshida, 1981). Leaves being the main component in the capture of solar radiation for a rice crop canopy, maximum leaf area index (LAI) values of 10 or greater can be attained at heading stage; however, a critical LAI of 7-8 is necessary to ensure maximum (95%) interception of irradiance and canopy photosynthesis for modern semi-dwarf, high yielding cultivars. These cultivars have in common an upper canopy architecture composed of thin, short, thick and erect leaves (Peng et al, 2000). This plant ideotype is believed to enhance an unsaturated light environment and greater light penetration, capture and conversion during photosynthesis. The radiation use efficiency (RUE) and crop growth rate (CGR) in rice have been estimated at 1.4 g of DM MJ^{-1} and 17 to 24 $g m^{-2} day^{-1}$, respectively (Fageria et al., 2006; Yoshida, 1981). A value as high as 2.2 g of DM MJ^{-1} for the RUE has been reported for recent high yielding rice varieties (Sheehy et al., 2000).

Over the last 60 years, improved yield potential with modern rice cultivars has resulted primarily from an increase in the accumulation of DM and most notably increased partitioning to a larger sink size (Khush et al., 1993). This combination of traits has led to a high grain harvest index (HI) widely reported as the major trait supporting the improvement of current yield potential for modern rice cultivars (Lafarge et al., 2009). These cultivars can produce up to 8-10 t ha^{-1} of grain yield, a level considered as the plateau in the tropics since the 1990's (Sheehy et al., 1998). Recent studies have indicated that realizing further increases in DM, rather than HI, is the avenue for breaking the current grain yield barrier. New cultivars such as IR 72, new plant types (NPTs) and hybrids in Asia have shown yield increases as high as 13 t ha^{-1}, and these increases were associated with at least 15 % more DM accumulation (Lafarge et al., 2009; Ying et al 1998a). Sustaining these gains; however, requires simultaneous improvement in plant tolerance to lodging, insects and diseases (Sheehy et al., 2008).

Growth analysis studies in crops are useful for examining patterns and magnitudes of growth attributes and relationships as they relate to yield components and grain yield potential (Gardner et al., 1985). However, such studies are lacking for irrigated rice production in the high altitude environments of the tropics, including Rwanda. Owing to the predominant mountainous landscapes in Rwanda, significant development for irrigated rice areas are underway exclusively in inland valleys located in high altitude regions (1000 to 1800 m above sea level) since the early 2000's (NRDS, 2011). This study aims to quantify biomass and plant N accumulation and patterns during rice development, and relationships with yield components and grain yield as influenced by plant types of different cultivated subspecies and the growing season (DS and WS) in an irrigated inland valley environment in the medium altitude zone of Rwanda (> 1000 to 1500 m above sea level). The medium

altitude zone is comprised of the majority of current and potential rice production areas in Rwanda (NRDS, 2011).

Material and methods

Site description

Field experiments were conducted in the2012 DS (DS) and 2013 WS (WS) at Cyili rice research farm of Rwanda Agriculture Board (RAB), Rubona Station, Huye District, Southern Province, Republic of Rwanda. The Cyili area is a 242 ha inland valley situated in the medium plateau region at an altitude of 1380 m above sea level, longitude $29^o53'26''$ East and latitude $2^o28'18''$ South. Over 1500 smallholder families have grown rice in the Cyili area for more than four decades. The soil order at this location has been mapped as an Inceptisol (RSSP, 2011) with no further details on soil series or taxonomic description. Characteristics of the soil in the plow layer (0-30 cm depth) were as follows: the texture (hydrometer method: Gee &Bauder, 1986) was a sandy clay loam (57% sand, 33% clay, 9% silt) with an average soil pH (1:2 soil/water suspension) of 5.3, total N (Kjeldahl acidic digestion, Bremner, 1965) of 2.80 g N kg^{-1}, organic C (Nelson-Sommers, 1982) of 29 g C kg^{-1}, CEC (*IN* NH_4OAc, adjusted to the actual soil pH) of 26 cmole $_{(+)}$ kg^{-1}, and Mehlich-3-extractable nutrients of 4 mg P kg^{-1}, 119 mg K kg^{-1}, 2008 mg Ca kg^{-1}, 414 mg Mgkg^{-1}, 3.3 mg Zn kg^{-1}, 341 mg Mn $kg^{-1}$and 1026 mg Fe kg^{-1}. Climate data (air temperature and total solar radiation) were collected with a weather station (Delta-T, DL6 automatic weather station) located at the Cyili rice research farm (Fig 2.1 and 2.2).

Plant material, crop establishment and management

Three inbred rice (Oryza *sativa*, L.) genotypes (cultivars) commonly grown in Rwanda were used in both the DS and WS. The cultivars were of similar maturity (145 days on average) and represented different genetic backgrounds, plant types, origins, production ecologies, and grain characteristics in order to have a wide range in growth attributes (

biomass and plant N), yield components and grain yield. The cultivars were: Facagro 56 (Indica x Japonica), UP12 (Glaberrima x Japonica) and Yunyine (Tropical Japonica). Detailed descriptions of cultivars are given in Table 3.1.

Land preparation in both seasons consisted of an initial deep plow (0-30 cm depth), of the soil, then puddling and levelling under saturated moisture conditions. In the DS, seedlings were raised on a wet bed nursery on July 15 by sowing pre-germinated seeds that had been incubated for 24 to 48 hours at 30°C. Twenty four day old seedlings (3-to 4-leaf stage) were manually transplanted on August 8, under saturated soil conditions, with one seedling per hill at spacing of 0.2m x 0.2m (equivalent to a planting density of 25 seedlings m^{-2}). Saturated soil conditions were maintained for a week to allow seedling recovery from transplanting shock before permanent flood establishment. In the WS, a 3 week flood in Cyili destroyed the seedling nursery. Therefore, direct seeding was adopted to avoid the potential negative effect of late planting. Planting was conducted manually on February 17 by drill-seeding under dry soil conditions using pre-germinated seeds at the rate of 20 kg ha^{-1}. Seeds were immediately covered with a thin layer of soil and non-flood, saturated soil conditions were enabled in the field with frequent flush irrigations for 3 weeks to ensure maximal seedling emergence and establishment. Seedling emergence occurred within 7 to 10 days after seeding. Crop thinning and gap filling were completed leaving approximately 25 hills m^{-2} prior to flood establishment on March 12. In both seasons, each plot was 4 m long and 14 rows wide (spaced 20 cm apart). Throughout each cropping season, permanent flood (5-10 cm water depth) was ensured with water from the Cyili rice area dam and when required by pumping fresh water from a nearby river. The flood was maintained till physiological maturity. Pests were controlled to avoid significant loss in biomass and yield. Control of weed growth was achieved with frequent hand removal passes; rice stalk eyed fly (*Diopsis thoracica*) was mitigated with weekly sprays of 1.5 g ha^{-1} Cypermethrin 40% WP for eight weeks starting at

seedling stage. All field operations were manually implemented and sufficient labourers were mobilized to achieve timely execution of the various field operations and data collection.

During both the DS and the WS, experiments were arranged in split plot design with four blocks; N rates assigned to whole plots and rice genotypes to subplots. Urea fertilizer (46% N) was used as the N source, and total rate splits of 0, 60 (20+20+20+0), 90 (20+20+30+20), 120 (20+30+40+30),150 (20+40+50+40) and 180 (30+50+60+40) kg N ha^{-1} were applied, respectively, as preflood (PF) (which was at 30 days from sowing on average), 30 days after PF (30DPF), at the beginning panicle initiation (PI) and at 50% heading stage (Hd).On average, PI and Hd occurred around 45 and 75 days from PF, respectively (equivalent to 75 and 105 days from sowing).Urea was applied on moist soil at PF and the flood was established within 4 hours from application. Subsequent N splits were made directly into the flood. Fertilizer rates of 180 kg K_2O ha^{-1}as muriate of potash (60% K_2O), 90 kg P_2O_5 ha^{-1} as single super phosphate (21% P_2O_5) and 30 kg Zn ha^{-1} as zinc sulfate (20% Zn) were topdressed by hand in a single PF application across all treatments to ensure these nutrients were not limiting.

Characterization of crop phenological stages

The timing and duration of key rice crop growth stages were recorded in days starting at sowing. Beginning of PI was determined by scouting for the appearance of the plant top neck node as a marker. From this time, two to three average hills in a subplot were uprooted every 3 days; a main tiller was vertically sectioned and its base examined under a dissection microscope (Lieca MZ 95, Lieca Microsystems Ltd., and Heerburgg, Switzerland). The beginning of PI was scored when a microscopic white cone-like structure (panicle primordia) was visible above the top node (Lafarge et al., 2009). Heading (Hd) was scored at the time when half of the panicles in a subplot had at least partially exserted from the flag leaf (Moldenhauer et al., 2011). Maturity (Mat) was determined when 90% of the spikelets in a

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subplot had turned from green to yellow or to straw-like color (Moldenhauer et al., 2011; Yoshida, 1981). Overall crop duration of each of the three rice genotypes was recorded as number of days from sowing to physiological maturity.

<u>Plant sampling and growth measurements</u>

The total aboveground biomass was collected by hand cutting a-10hill plant sample (green and all dead tissues) in each subplot to determine biomass (DM) and N accumulation (Ying et al., 1998a) at the following sampling time and crop growth stages: i) Mid tillering (MT) stage was scored at 30 days from transplanting in 2012 DS and at 55 days from sowing in 2013 WS, ii) panicle initiation (PI), iii) heading (Hd), iv) heading + 23days (Hd23)(equivalent to approximately half way to physiological maturity), and (v) at crop maturity (Mat). Biomass sampling occurred immediately before any N fertilizer split application. Biomass samples were processed within 24 hours of collection at the Rubona research station. Total dry weight and panicle dry weight (kg dry weight ha^{-1}) were measured (Sartorius weighting scale, ED62025, precision= 0.01 g) after oven-drying at 60°C to a constant weight. Average crop growth rate (CGR) (g dry weight m^{-2} d^{-1}) was derived from total dry weight at maturity (Lafarge et al., 2009). Harvest index (HI) was derived as the ratio of grain yield to total dry weight at maturity (Lafarge et al., 2009). Individual plant parts (top leaf, bottom leaf, leaf sheath + culm, and panicle) were ground (Foss mill, Cyclotec^{TM} 1039) and sieved to pass a 425 µm sieve (Guindo et al., 1994) for plant N analysis on a-0.1 g subsample using the Halais modified colorimetric method (Kilyobo et al., 2001). The following plant N characteristics were computed: i) Total plant N uptake (which represents fertilizer plus soil N) expressed as the product of plant concentration (N g kg^{-1}) and total dry weight per unit ground area (kg ha^{-1}), ii) total N uptake rate expressed in weight per ground area (g m^{-2}) over a time interval (in days), and iii) N harvest index as the ratio of grain yield to total plant N uptake at maturity (Lafarge et al., 2009; Guindo et al., 1994).

Experiments were arranged in a- four block split plot design in both seasons and the analysis of variance (ANOVA) was conducted following the linear mixed model (Gbur et al., 2012) in SAS 9.4 software (SAS Institute, Inc., Cary, NC) with N rate, cultivar, growth stage and season as fixed effects and block as random effect, to determine the overall statistical significance of the effects of explanatory variables (N rate, cultivar, growth stage and season, and their interactions). Means were compared based on the least significant difference procedure (LSD) at the 0.05 probability level. Pairwise correlation analysis was conducted to determine the amount of associations (coefficient of correlation: R) among biomass and plant N attributes with yield attributes (number of spikelets per m^2 and grain yield) using JMP Pro11 software (SAS Institute, Inc., Cary, NC). The reporting of results was based on data pooled over N rates since all interaction effects involving N rate with cultivar and growth stage were not significant (Table 3.2).

Results

Biomass accumulation

The three-way interaction effect (Table 3.2) of growth stage x cultivar x season was significant for the total dry weight ($P = 0.0005$) and panicle dry weight ($P = 0.0025$). None of the two-way and three-way interactions involving N rate were significant. The four-way interaction involving growth stage, season, N rate and cultivar was not significant. The total dry weight (Fig 3.1) and panicle dry weight (Fig 3.2), when averaged over cultivar and season, were different among growth stages. At maturity, the total and panicle dry weight averaged over cultivar were greater in the DS than in the WS. The total dry weight was also greater in the DS than in the WS at Hd stage. However, the total dry weight was greater in the WS than in the DS during the vegetative growth phase (sowing to PI) and Hd23 stage.

Similarly, the panicle dry weight was greater in the WS than in the DS at both Hd and Hd23 stages.

At maturity, both the total (Fig 3.1) and panicle dry weight (Fig 3.2) were greater in the DS than in the WS in the Tropical Japonica cultivar followed by Glaberrima x Japonica and the Indica x Japonica cultivars. The total dry weight was similar and greater in the Glaberrima x Japonica and Tropical Japonica than the Indica x Japonica cultivar in the WS at PI stage (Fig 3.1). At this growth stage, the total dry weight was greater during the DS in the Glaberrima x Japonica followed by Indica x Japonica and the Tropical Japonica cultivars. At MT stage, the total dry weight was greater during both seasons in the Glaberrima x Japonica followed by Tropical Japonica which was greater and similar to Indica x Japonica in the WS and the DS, respectively. The panicle dry weight was greater in the Indica x Japonica than the Glaberrima x Japonica cultivar in the DS at Hd23 stage (Fig 3.2). These cultivars dry weights were similar in the WS and greater than the Tropical Japonica cultivar in both seasons at Hd23. At Hd stage, the panicle dry weight was greater in the Indica x Japonica cultivar followed by Tropical Japonica and the Glaberrima cultivar in the WS. In the DS, the panicle dry weight at Hd stage was greater in the Tropical Japonica than in the Glaberrima x Japonica and Indica Japonica cultivars which were similar.

Plant nitrogen accumulation

The three-way interaction effect (Table 3.2) of growth stage x cultivar x season was significant for the total plant N uptake ($P < 0.0001$) and total plant N concentration ($P = 0.0042$). None of the two-way and three-way interactions involving N rate were significant. The four-way interaction involving growth stage, season, N rate and cultivar was not significant. The total plant N uptake, when averaged over cultivar and season, was different among growth stages (Fig 3.3). At maturity, the total plant N uptake, averaged over cultivar, was greater in the WS than in the DS. Similarly, the total plant N uptake was greater during

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the vegetative growth period. However, the total plant N uptake was greater at Hd23 than at maturity in the DS. The total plant N uptake was also greater at Hd and Hd23 stages in the DS than in the WS.

At maturity, the total plant N uptake in each season was greater in the Tropical Japonica cultivar followed by Glaberrima x Japonica and the Indica x Japonica cultivar (Fig 3.3). At Hd23, the total plant N uptake in the DS was the greatest in the Indica x Japonica cultivar followed by Tropical Japonica and the Glaberrima Japonica cultivar. The Glaberrima x Japonica and Indica x Japonica cultivars had similar and greater total plant N uptake than the Tropical Japonica cultivar in the WS. At Hd stage, the total plant N uptake was similar in the Glaberrima x Japonica and Indica x Japonica cultivars which were lower than the Tropical Japonica cultivar in the DS. In the WS, the total plant N uptake was greater in the Indica x Japonica cultivar followed by the Glaberrima x Japonica and tropical japonica cultivar. During the vegetative growth period, the total plant N uptake was greater in the DS at PI stage in the Glaberrima x Japonica cultivar than in all other cultivars. In the WS, the Glaberrima x Japonica and Tropical Japonica cultivars were similar and greater than the Indica x Japonica cultivar which had identical performance in both seasons. The total plant N uptake was the greatest in the Glaberrima x Japonica cultivar at MT stage in both seasons followed by the Tropical Japonica and Indica x Japonica cultivar in the WS. These two latter cultivars were identical in the DS.

The total plant N concentration (Fig 3.4), averaged over cultivar and season, was different among growth stages. The total plant N concentration was greater in the DS than in the WS at MT and Hd23 stages. However, the total plant N concentration was lower at PI, Hd and the maturity stages in the DS. Overall, the total plant N concentration decreased from MT to maturity stage. At MT stage, the Indica x Japonica and Tropical Japonica cultivars were similar and greater than the Glaberrima x Japonica cultivar in each season. At maturity, the

Indica x Japonica and Tropical Japonica cultivars were similar and had greater total plant N concentration than the Glaberrima x Japonica cultivar in the DS. This cultivar and the Indica x Japonica had identical and lower total plant N concentration than the Tropical Japonica cultivar in the WS.

Discussion

<u>Biomass accumulation</u>

At maturity, the biomass accumulation averaged over cultivar was greater in the DS than in the WS by 18% for the total dry weight and 29% for the panicle dry weight. Moreover, the total dry weight in the WS (14530 kg ha^{-1}) and in the DS (17723 kg ha^{-1}) was lower by 20% and 5%, respectively, in comparison to irrigated lowlands of the tropics in Asia (Lafarge et al., 2009; Ying et al., 1998a). Similarly, the panicle dry weight was lower by 14% in the WS (7737 kg ha^{-1}); in the DS (10953 kg ha^{-1}) it was comparable to irrigated lowlands of the tropics in Asia (Yang et al., 2008; Ying et al., 1998a). At Hd stage, the total dry weight was greater by 18% in the DS (7713 kg ha^{-1}) than in the WS (6333 kg ha^{-1}). The intensity in irradiance, which was the main difference between the DS and the WS (Fig. 2 2) in Cyili-Rwanda, may be the reason for the seasonal differences in biomass accumulation (Yoshida, 1983). Similarly, the intensity in irradiance, typically 25 to 30% greater in the irrigated lowlands of the tropics in Asia, may explain the greater performance in Asia than in Cyili-Rwanda (Fageria et al., 2007; Ying et al., 1998a). However, the potential for biomass partitioning to the panicle may be greater in Cyili-Rwanda given the lower proportion of decline in the panicle dry weight (14% in WS and none in DS) relative to the total dry weight (20% in WS and 5% in DS). Cooler temperatures such as those that prevailed in Cyili-Rwanda (18.6^{o}C in DS and 19.6^{o}C in WS) (Fig 2.1) along with the longer crop duration have been associated with greater photosynthate translocation and less biomass loss from maintenance respiration (Evans, 1993; Yoshida and Parao, 1976).

The total dry weight was; however, greater (57% at PI stage) in the WS (2737 kg ha^{-1}) than in the DS (1183 kg ha^{-1}) during the vegetative growth phase (sowing to PI). This may have resulted from the vigorous growth recorded in the early stage presumably due to the effect of direct seeding (Yoshida, 1981). While this greater performance in the WS occurred despite the presence of lower irradiance, Evans and De Datta (1979) suggested that the negative effect of reduced irradiance was small during the vegetative growth phase of the rice crop. Nonetheless, the reason for the lower (12%) total dry weight at Hd23 in the DS (9787 kg ha^{-1}) than in the WS (11083 kg ha^{-1}) could not be determined because the edge in growth during the early stage in the WS had been lost by the Hd stage. Also, we could not explain similar trends for the panicle dry weight which was greater at Hd and Hd23 in the DS compared to the WS.

The pattern of the total dry weight accumulation, averaged over cultivar and season, was typical of modern rice cultivars and similar to irrigated lowlands in the tropics of Asia. The greatest proportion accumulated during post-heading (55%) than during pre-heading growth (45%) period (Lafarge et al., 2009). The total dry weight was equivalent to 15% and 45% by the end of the vegetative (at PI) and the reproductive phases (at Hd), respectively. The remaining 55% of growth occurred during the grain filling phase (Hd to Mat) of which 20% by Hd23 and 35% between Hd23 and maturity. Similarly, the panicle dry weight in the DS, when averaged over cultivar, represented 6% at Hd, 12% at Hd23 and 82% between Hd23 and maturity. In the WS, values were 19% at Hd, 57% at Hd23 and 43% between Hd23 and maturity. These patterns revealed substantial growth in the panicle dry weight ongoing after Hd23 stage, and apparently this is a feature of the subtropics and temperate environments where the grain filling phase is longer (~ 35-45 days) than for the irrigated lowlands in the tropics (~21-30 days) of Asia (Lafarge et al., 2009; Peng et al., 2000; Ying et al., 1998a).

When cultivars were compared at maturity, greater biomass accumulation in both the total and panicle dry weight was found in the standard statured Tropical Japonica and Glaberrima x Japonica cultivars than in the semidwarf Indica x Japonica cultivar. The standard stature plant type was more strongly linked to greater biomass accumulation than in the semidwarf plant type (Guindo et al., 1994). However, the total dry weight which was greater in the Indica x Japonica cultivar during the reproductive (at Hd) and grain filling (at Hd23) phases was reported as crucial in determining the sink size and filling efficiency (Sheehy et al., 2000; Horie et al., 1997; Khush et al., 1993).

The biomass accumulation in Cyili-Rwanda was slower and lower in growth rate in comparison to irrigated lowland environments of Asia (Yoshida, 1981). Across cultivars and seasons, the pre-heading phase was around 75 days at PI and 105 days at Hd, and 45 days for the grain filling phase. These durations, compared to irrigated lowlands in the tropics of Asia, were longer by around 15 days at PI or Hd, 7 days during the reproductive phase (PI to Hd) and 10 to 15 days during the grain filling phase (Lafarge et al., 2009; Ying et al., 1998a; Horie et al., 1997). The total crop duration (sowing to maturity) which averaged 145 days in Cyili-Rwanda fell within the long maturity group and may be considered as the current optimal for achieving the grain yield potential (8-10 t ha^{-1}) (Fig 2.8) of tropical Asia (Akita, 1989). The average CGR for the whole crop growth duration was 11 g m^{-2} day^{-1} across cultivars and seasons. This CGR was lower than for typical inbred cultivars (14-15 g m^{-2} day^{-1}) in the irrigated lowlands of the tropics in Asia (Peng et al., 2003). The CGR was much lower compared to subtropical and temperate environments in Asia (CGR range of 16-18 g m^{-2} day^{-1}) despite the commonality of the longer crop duration (145 to 160 days) (Yoshida, 1981). This edge for the Asian environments may be attributed to greater irradiance and cultivar yield potential (Zou et al., 2013; Katsura et al., 2008; Shimono et al., 2002).

<u>Plant N accumulation</u>

The total plant N uptake averaged over cultivar at the Hd stage was 30% greater in the DS than the WS, and in the WS the N uptake was comparable to the critical value of about 150 kg N ha^{-1} for achieving the current rice grain yield potential (8-10 t ha^{-1}) in the irrigated lowlands of the tropics in Asia and farm yields in the USA (Norman et al., 2003; Dobermann et al., 1998). This tendency to accumulate greater plant N was also reflected in the total plant N concentration with values of about twice the standard level of 1% during the reproductive growth (PI to Hd) to Hd23 and 0.6 to 0.8% at maturity stage (Norman et al., 2003; Sheehy et al., 1998). Greater plant N uptake was also reported for the subtropics in China, and the temperate regions in Yanco-Australia as well as the north of Japan which experience longer crop duration and/or cooler temperatures compared to Cyili-Rwanda environment (Katsura et al., 2008; Shimono et al., 2002).

When cultivars were compared across seasons, the total plant N uptake was greater at maturity with the standard statured cultivars of the Glaberrima x Japonica and Tropical Japonica cultivars than with the semidwarf the Indica x Japonica cultivar (Guindo et al., 1994). However, the total plant N uptake which was greater in the Indica x Japonica cultivar during the reproductive (Hd) and grain filling growth (Hd23) phases was reported as crucial in determining the sink size and grain filling efficiency (Sheehy et al., 2000; Horie et al., 1997; Khush et al., 1993).

The pattern in total plant N uptake averaged over cultivar was typical of improved rice cultivars with the greatest portion accumulated by the Hd stage in each season (Norman et al., 2003). Plant N uptake was about 90% in the DS and 62% in the WS. Further, the proportion of uptake was typically greater (3 to 4 times) between PI and Hd than at any other crop stage (Ying et al., 1998b). In addition, plant N uptake followed the typical sigmoid pattern in the DS with the uptake starting to decline after Hd/flowering (precisely at Hd23) to

maturity (Norman et al., 2003). In the WS, the uptake showed a near linear pattern from the MT stage to maturity presumably due to lower plant N tissue dilution associated with lower biomass accumulation (Sheehy et al., 1998; Hasegawa et al., 1995). The NHI across cultivars at maturity was greater in the DS (0.82) and lower (0.54) in the WS in comparison to the reported range of 0.53-0.72 for different environments (Guindo et al., 1994). These trends in NHI may be reflective of greater sink capacity (Fig 2.5) and N demand associated with more panicle growth in the DS than in the WS (Sheehy et al., 1998). The Average plant N uptake rate across cultivars for the whole crop growth duration was 1.42 in the DS and 1.62 g m^{-2} day^{-1} in the WS.

Crop growth and relationships with yield attributes

Relationships were examined among the attributes of plant biomass and N accumulation with the number of spikelets per m^2 and the grain yield. At maturity, the edge in growth across seasons for the standard statured cultivars of Tropical Japonica and Glaberrima x Japonica was apparently small (8%) in both the total and panicle dry weight and the total plant N uptake (9-11%) compared to the semidwarf Indica x Japonica cultivar, and/or may have had little influence on the yield attributes which were greater (Fig 2.5 and Fig 2.8) in the latter cultivar. The Indica x Japonica cultivar had the greatest harvest index (0.53 in DS and 0.48 in WS) than the Tropical Japonica (0.45 in DS and 0.27 in WS) and Glaberrima x Japonica (0.45 in DS 0.40 in WS) cultivars. Greater HI in the Indica x Japonica may be linked to its greater sink size (number of spikelets per m^2) (Fig. 2.5) and presumably greater efficiency in resource conversion which resulted into greater grain yield (Fig .2.8) (Peng et al., 2003; Horie et al., 1997; Guindo et., 1994). Also, the importance of the greater total dry weight and total plant N uptake recorded in the Indica x Japonica cultivar during the reproductive (Hd) and grain filling (Hd23) phases in determining the sink size and filling efficiency has been reported in several studies (Sheehy et al., 2000; Horie et al., 1997).

When data were pooled over season, cultivar and N rate, the greatest correlations ($R = 0.62$ overall) of growth in biomass (total and panicle dry weight) and plant N attributes with the number of spikelets per m^2 and the grain yield (Table 3.3) occurred during the reproductive growth phase (PI to Hd) than at any other stage prior to maturity. Several studies found the reproductive growth to be closely linked to the sink size at Hd/flowering and crop performance at maturity (Sheehy et al., 2000; Hasegawa et al., 1994). Correlations were greater with the attributes of biomass ($R = 0.66$ overall) than with the total plant N uptake ($R = 0.60$) at the Hd stage. Values were the greatest ($R = 0.71$ overall) for the biomass attributes at maturity than at Hd. Correlations were negative, small or non-significant (the largest $R = -0.22$ overall) with plant N attributes at maturity. This may be reflecting the wide C/N ratio in rice as well as the plant N playing more of a metabolic than a storage role in biomass and grain yield build up. This observation is supported by the greatest correlations of plant N attributes ($R = 0.80$) with biomass growth at Hd (Yoshida, 1981). The panicle growth rather than the total dry weight attributes, particularly from Hd to maturity, showed the greatest correlations with grain yield ($R = 0.79$) and the number of spikelets per m^2 ($R = 0.67$) which suggested the importance of plant metabolism shift toward grain filling (Yang et al., 2008).

Conclusion

Seasonal differences in irradiance were apparently linked to the performances in total and panicle weight which were greater in the DS than in the WS at maturity. Differences in total and panicle dry weight were small between standard stature cultivars (Glaberrima x Japonica and Tropical Japonica) and the semidwarf Indica x Japonica cultivar. The Indica x Japonica cultivar had the greatest HI. The performances in total dry and panicle dry weight were lower in comparison to irrigated lowlands in the tropics of Asia. However, the potential for the translocation of photosynthate to panicle was apparently greater for Cyili-Rwanda. The biomass accumulation of the cultivars studied was much lower compared to subtropical

and temperate environments in Asia despite having in common the longer crop duration. Average total crop duration of 145 days from sowing to maturity may be considered as the current optimal for achieving the yield potential (8-10 t ha^{-1}) of tropical Asia in Cyili-Rwanda. The plant N uptake at maturity (> 200 kg N ha^{-1}) was comparable to the greatest rice performances reported in the literature. The correlations among biomass (total and panicle dry weight) and plant N attributes with the grain yield and the number of spikelets per m^2 were greater during the reproductive growth phase as opposed to any other stage prior to maturity. Panicle growth rather than total dry weight attributes, in particular from Hd to Mat stage, had the greatest correlations with grain yield and the number of spikelets per m^2. Plant N attributes were correlated more with biomass growth than with the grain yield and the number of spikelets per m^2. The apparent potential for large panicle growth and in particular plant N uptake with the semidwarf Indica x Japonica subspecies combination may represent important plant characteristics for improved rice crop performance in an environment as Cyili-Rwanda.

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Table 3. 1. Key characteristics of rice cultivars evaluated in 2012 dry season and 2013 wet season

Cultivar	Subspecies	Plant type	Original ecology	Origin	Release year	Growth duration (days)[a]	Grain type
Facagro 56	Indica x Japonica	Semidwarf	Irrigated	Burundi	1996	145	Medium/translucent
UP12	Glaberrima x Japonica	Standard stature	Upland	West Africa	2010	145	Long/bold/chalky
Yunyine	Tropical Japonica	Standard stature	Irrigated	Taiwan	1980's	147	Short/chalky

[a] From sowing to physiological maturity

Table 3.2. Analysis of variance (ANOVA) for the total dry weight, panicle dry weight, total plant N uptake and total plant N concentration

Source of variation[a]	Total dry weight	Panicle dry weight	Total plant N uptake	Total plant N concentration
	p value[b]	p value	p value	p value
GrSt	< 0.0001	< 0.0001	<0.0001	< 0.0001
GrSt x N	0.1166	0.2498	0.1377	0.1166
GrSt x S	< 0.0001	< 0.0001	<0.0001	0.0002
GrSt x C	< 0.0001	< 0.0001	< 0.0001	< 0.0001
GrSt x S x N	0.1966	0.0926	0.4751	0.8384
GrSt x C x N	0.3487	0.7369	0.0855	0.1675
GrSt x S x C	0.0005	0.0025	< 0.0001	0.0042
GrSt x S X N x C	0.7157	0.5992	0.1356	0.2641

[a] GrSt: Growth stage; N: N rate; S: season; C: cultivar

[b] significant at p value ≤ 0.05

Table 3.3. Pairwise correlation values among crop growth attributes with grain yield and the number of spikelets per m^2

Growth attributes	MT[d] Spikelet[a] m-2	YLD[b]	PI[e] Spikelet m-2	YLD	Hd[f] Spikelet m-2	YLD	Hd23[g] Spikelet m-2	YLD	Mat[h] Spikelet m-2	YLD
Total dry weight	-0.64	-0.68	0.41	0.36	0.72	0.72	0.4	0.39	0.67	0.76
Crop growth rate	-0.64	-0.68	0.6	0.57	0.57	0.6	-0.26 ns[c]	-0.28 ns	0.56	0.65
Panicle dry weight					0.73	0.68	-0.02 ns	-0.07 ns	0.75	0.85
Panicle growth rate					0.67	0.62	-0.34	-0.36	0.71	0.79
Reproductive Growth					0.64	0.66				
Panicle dry weight from Hd to Mat									0.67	0.79
Panicle dry weight from Hd23 to Mat									0.66	0.76
Whole crop duration growth rate									0.65	0.74
Total plant N uptake	-0.61	-0.64	0.25 ns	0.19 ns	0.57	0.62	0.46	0.45	-0.06 ns	-0.03 ns
Total plant N uptake rate	-0.61	-0.64	0.52	0.49	0.38	0.46	0.08 ns	0.04 ns	-0.41	-0.38

[a] number of spikelets per m^2, [b] YLD : grain yield, [c] ns: non significant correlation values, [d] MT: mid tillering, [e] PI: panicle initiation, [f] Hd: heading, [g] Hd23: heading + 23 days, [h] Mat: maturity

Fig 3.1. Influence of season, cultivar and growth stage interaction, averaged across N rates, on the total dry weight. LSD (0.05) to compare total dry weight means: same cultivar within seasons = 88.9; same cultivar across seasons = 90.4; different cultivars within and across seasons = 91.4. Means followed by the same letter(s) are not significantly different. † MT= mid tillering; PI= panicle initiation; Hd= heading; Hd23= heading + 23days; Mat= maturity
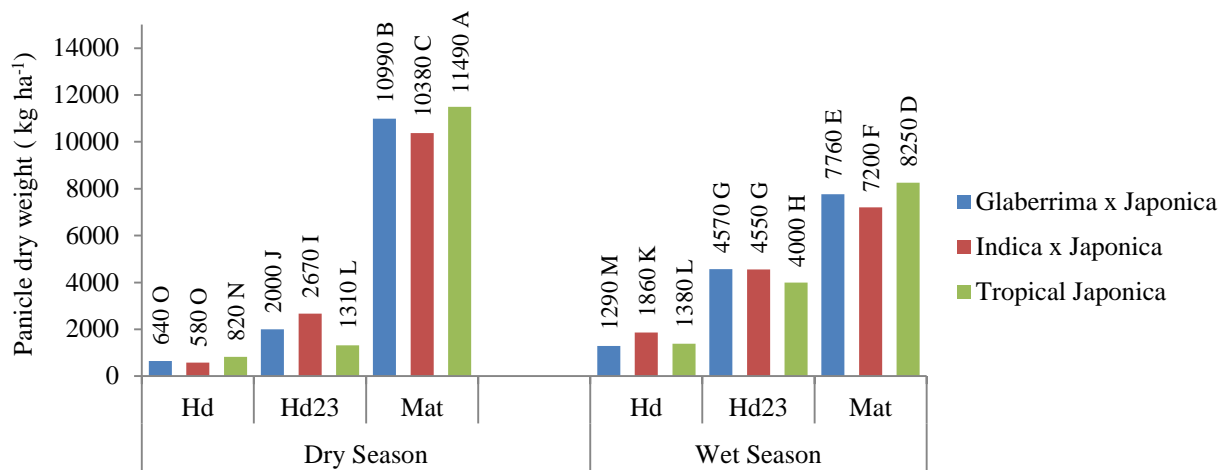
Fig 3.2. Influence of season, cultivar and growth stage interaction, averaged across N rates, on the panicle dry weight. LSD (0.05) to compare panicle dry weight means: same cultivar within seasons = 193.5; same cultivar across seasons = 161.6; different cultivars within and across seasons = 161.7. Means followed by the same letter(s) are not significantly different. †Hd= heading; Hd23= heading + 23days; Mat= maturity
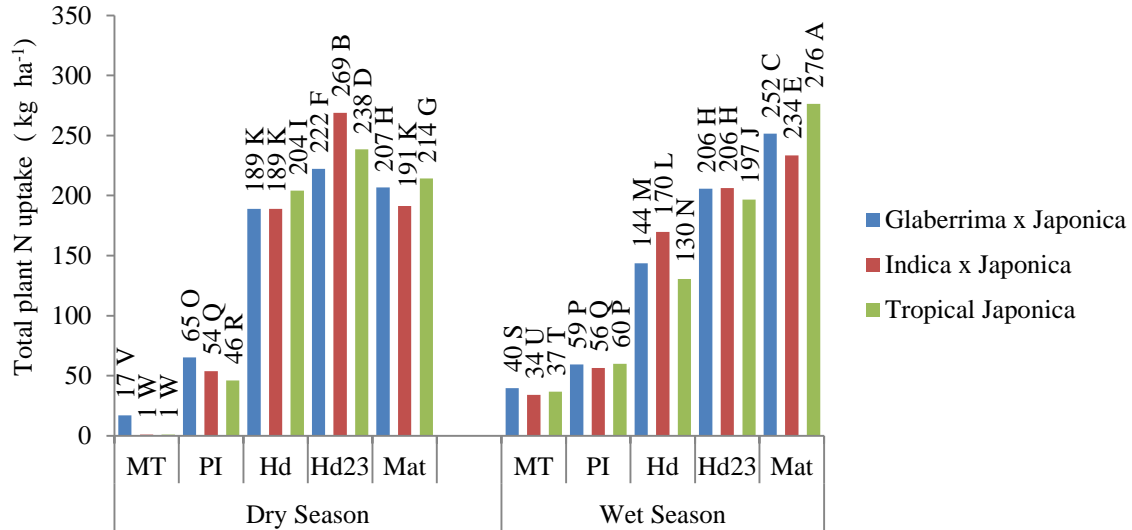
Fig 3.3. Influence of season, cultivar and growth stage interaction, averaged across N rates, on the total plant N uptake. LSD (0.05) to compare total plant N uptake means: same cultivar within seasons = 2.05; same cultivar across seasons = 2.08; different cultivars within and across seasons = 2.10.Means followed by the same letter(s) are not significantly different. †
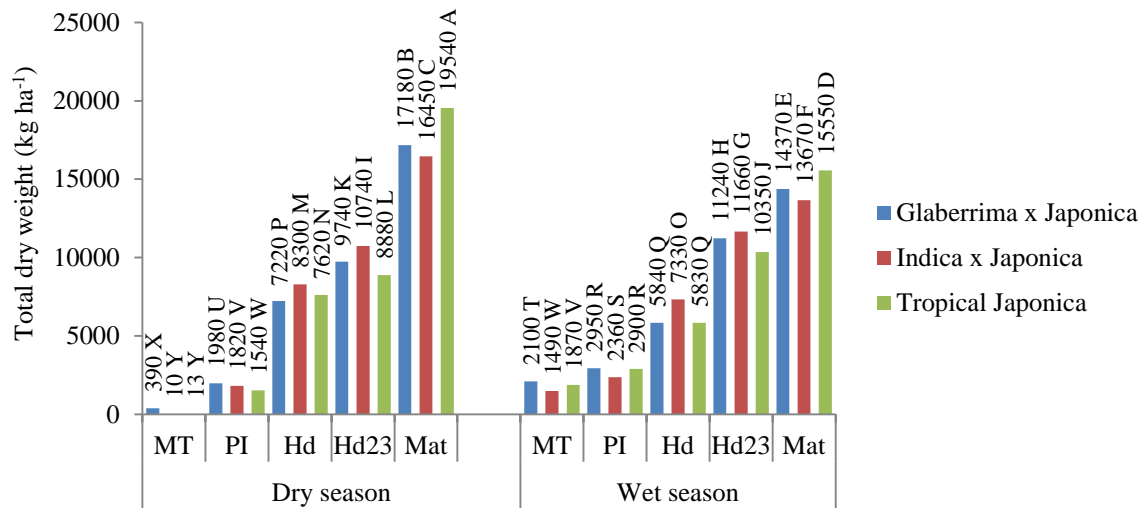Hd= heading; Hd23= heading + 23days; Mat= maturity
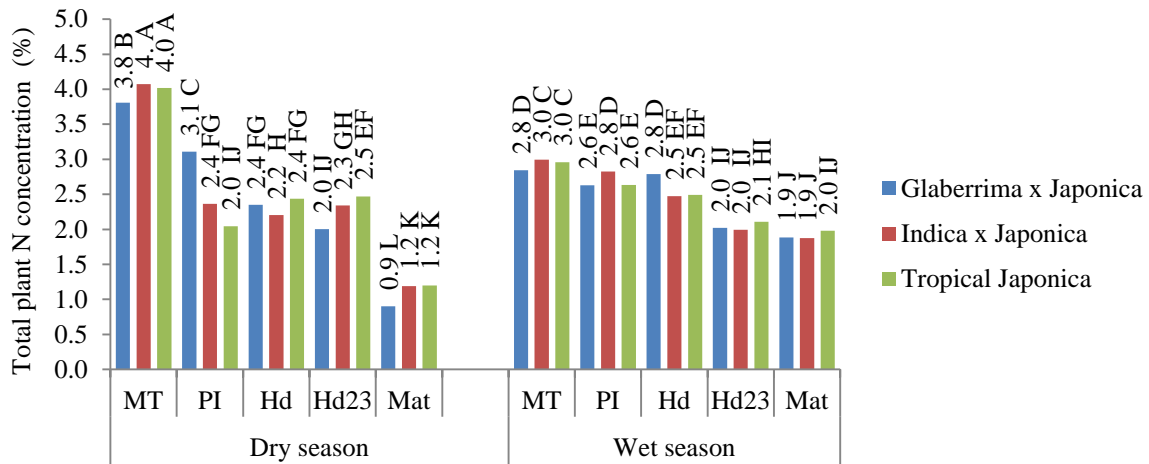
Fig 3.4. Influence of season, cultivar and growth stage interaction, averaged across N rates, On the total plant N concentration. LSD (0.05) to compare total plant N concentration means: same cultivar within seasons = 0.118; same cultivar across seasons = 0.120; different cultivars within and across seasons = 0.122. Means followed by the same letter(s) are not significantly different. † Hd= heading; Hd23= heading + 23days; Mat= maturity

Chapter four: Growth and yield responses to nitrogen fertilization for irrigated rice in a tropical high altitude environment in Rwanda

Highlights

- Nitrogen fertilizer responses closely linked to irradiance

- Yield responses closely related to responses in the number of spikelets m^{-2}

- Most responses maximized at a low N fertilizer rate of 60 kg N ha^{-1}

- Potential from large available and/or readily available native soil N reserves

Keywords

Rwanda, cultivated rice subspecies, N rate, tropical high altitude, inland valley, irradiance, yield components, grain yield, dry weight, plant N uptake, soil N reserves.

Abstract

Responses to nitrogen (N) fertilizer for irrigated rice (*Oryza sativa, L.*) were evaluated for a tropical inland environment in the high altitudes in Rwanda. Yield components and grain yield, and the total dry weight and the total plant N uptake at maturity were measured for six N fertilizer rates (0, 60, 90,120,150,180 kg N ha^{-1}) during the 2012 dry season (DS) and 2013 wet season (WS) at Cyili Rice Research Farm (1380 m above sea level). Responses were in most cases greater in the DS than in the WS. In particular, the number of panicles per m^2 and the total dry weight showed greater responses in both seasons. In the WS, responses were absent for the grain yield and the number of spikelets per m^2. Further, similar trends in both seasons between the grain yield and the number of spikelets per m^2 suggested this yield component may be determining the yield response to N fertilizer. The 1000 grain weight (25g) was constant, and the grain filling ratio varied in a narrow range (0.80-0.88). Responses to N fertilizer addition were generally minimal with most measured attributes maximized when the lowest N rate of only 60 kg N ha^{-1} was applied, which suggested a large contribution from the available and/or readily available native soil N reserves linked to ample amounts of total soil N (2.80 ± 0.34 g kg soil^{-1}).At this N rate, grain yield of 8.3 t ha^{-1} in the DS and plant N uptake > 200 kg N ha^{-1} were achieved. Grain yield of 6.5 t ha^{-1} in the DS and 4.6 t ha^{-1} in the WS were achieved without N application. Responses for the total dry weight were observed up to ≥ 150 kg N ha^{-1} applied. Large reserves (2.45 g kg soil^{-1}) of available and/or readily available native soil N may be widespread in the rice production environments of Rwanda and the current 80 kg N ha^{-1} recommendation or less may be required.

Introduction

Nitrogen is considered the most important plant nutrient because it is generally required in larger quantities than other nutrients, and remarkable crop yield improvements since the 1950's have been attributed to increased use and crop response to N fertilizers (Horie et al., 2010; Sinclair et al., 1989; Gardner et al., 1985). Higher grain yields for rice (5-10 t ha^{-1}) in the irrigated systems largely depend on the use of inorganic N fertilizers (Cassman et al., 1998). Plant N status determines rice yields through effects on leaf area development and canopy photosynthesis. Consequently, greater amounts of plant N accumulation are closely associated with higher DM production, grain number and final yields (Sheehy et al., 1998).

Low N fertilizer-use efficiency is; however, a characteristic of irrigated and lowland rainfed rice production attributable to rapid losses of applied N mainly via ammonia volatilization and denitrification (Norman et al., 2003; Cassman et al., 1998). Depending on crop management strategies, a wide range of fertilizer N recovery rates (10 to 70 %) have been reported in Asia (Cassman et al., 1998).Low efficiency was primarily linked to an imbalance between applied N inputs and crop demand. In response, several field studies have demonstrated the importance of split application of conventional urea fertilizer for a better match between crop growth needs and N supply (Cassman et al., 1998; Wilson et al., 1989). In particular, because plant N accumulation increases exponentially from the mid tillering to flowering stage, N split applied at around the panicle stage (PI) is critical to a sustained increase in growth during the reproductive and grain filling phases (Cassman et al., 1998; Ying et al., 1998b; Wells et al., 1994).

The agronomic efficiency of the N fertilizers is typically 18 to 20 kg grain per N kg^{-1} applied in the tropical irrigated systems of Asia. On the other hand, while these systems can supply 50 to 80 kg N ha^{-1} from indigenous soil resources, the current grain yield potential of

8-10 t ha^{-1} would require N uptake of 180 to 200 kg ha^{-1} and fertilizer-N input of 150 to 200 kg ha^{-1} (Cassman et al., 1998; Sheehy et al., 1998). In the subtropics and the temperate regions, 250 kg N ha^{-1} uptake would be necessary for 13-15 t ha^{-1} of rice grain yields. However, N supply that exceeds crop demand can increase lodging and disease incidence and severity. Hence, the knowledge of plant N uptake requirements at different rice development stages, to achieve a target grain yield, is vital for efficient N management (Cassman et al., 1998). On the other hand, because plant N nutrition drives the crop demand for other essential nutrients, limitations in these should be corrected, in particular P, K, Zn and S (Dobermann et al., 1998), as their limited supply is likely to reduce the expected N fertilizer response and grain yield.

Significant development for irrigated rice production in Rwanda has been taking place since the early 2000's exclusively in inland valleys located in the high altitude regions (1000 to 1800 m above sea level) (NRDS, 2011). Conditions in these valleys, particularly soil fertility characteristics, can vary quite substantially among and within rice areas as suggested by the recent nation-wide soil survey (RSSP, 2011). Along this line, the increasing cultivation of a wide range of rice cultivars with different characteristics suggest the need to review the current blanket inorganic fertilizer recommendation of 80 N - 37 P$_2$O$_5$ - 37 K$_2$O kg ha^{-1} still in use since the 1980's (NRDS, 2011; RSSP, 2011). The main objective of this study is to quantify responses to N fertilizer for key crop growth and yield attributes of irrigated rice during the DS and the WS in an inland valley environment located in the medium altitude zone (>1000-1500 m above sea level). The total dry weight and the total plant N uptake at maturity, and the yield components and grain yield were measured over six N fertilizer rates (0, 60, 90,120,150,180 kg N ha^{-1}) and four commonly grown rice genotypes (cultivars) differing in their origin, cultivated subspecies, plant type, original production ecology and grain characteristics (Table 4.1).The cultivars were grown during the 2012 DS and 2013 WS

at Cyili rice research farm (1380 m above sea level) in Rwanda under full flood irrigation and sufficient inputs and pests management to ensure favorable crop growth

Material and methods

Site description

Field experiments were conducted in the 2012 DS (DS) and 2013 WS (WS) at Cyili rice research farm of Rwanda Agriculture Board (RAB), Rubona Station, Huye District, Southern Province, Republic of Rwanda. The Cyili area is a 242 ha inland valley situated in the medium plateau region at an altitude of 1380 m above sea level, longitude $29^{o}53'26''$ East and latitude $2^{o}28'18''$ South. Over 1500 smallholder families have grown rice in the Cyili area for more than four decades. The soil order in Cyili has been mapped as an Inceptisol (RSSP, 2011) with no further details on soil series or taxonomic description. Characteristics of the soil in the plow layer (0-30 cm depth) were as follows: the texture (hydrometer method: Gee &Bauder, 1986) was a sandy clay loam (57% sand, 33% clay, 9% silt) with an average soil pH (1:2 soil/water suspension) of 5.3, total N (Kjeldahl acidic digestion, Bremner, 1965) of 2.80 g N kg^{-1}, organic C (Nelson-Sommers, 1982) of 29 g C kg^{-1}, CEC (*IN* NH_4OAc, adjusted to the actual soil pH) of 26 cmole $_{(+)}$ kg^{-1}, and Mehlich-3-extractable nutrients of 4 mg P kg^{-1}, 119 mg K kg^{-1}, 2008 mg Ca kg^{-1}, 414 mg Mgkg^{-1}, 3.3 mg Zn kg^{-1}, 341 mg Mn $kg^{-1}$and 1026 mg Fe kg^{-1}. Climate data (air temperature and total solar radiation) were collected with a weather station (Delta-T, DL6 automatic weather station) located at the Cyili rice research farm (Fig 2.1 and 2.2).

Plant material, crop establishment and management

Four inbred rice (*Oryza sativa*, L.) genotypes (cultivars) were used in both the DS and the WS. The cultivars were of similar maturity group (145 days on average) and represented different genetic backgrounds, origins, production ecologies and grain characteristics. These cultivars were: Facagro 56 (Indica x Japonica$_1$), Gakire (Indica x Japonica$_2$), UP12

(Glaberrima x Japonica) and Yunyine (Tropical Japonica).Detailed descriptions of cultivars are given in Table 4.1.

Land preparation in both seasons consisted of an initial deep plow (0-30 cm depth) of the soil, then puddling and levelling under saturated moisture conditions. In the DS, seedlings were raised on a wet bed nursery on July 15 by sowing pre-germinated seeds that had been incubated for 24 to 48 hours at 30°C. Twenty four day old seedlings (3-to 4-leaf stage) were manually transplanted on August 8, under saturated soil conditions, with one seedling per hill at spacing of 0.2m x 0.2m (equivalent to a planting density of 25 seedlings m^{-2}). Saturated soil conditions were maintained for a week to allow seedling recovery from transplanting shock before permanent flood establishment. In the WS, a three week flood in Cyili destroyed the seedling nursery. Therefore, direct seeding was adopted to avoid the potential negative effect of late planting. Planting was conducted manually on February 17 by drill-seeding under dry soil conditions using pre-germinated seeds at the rate of 20 kg ha^{-1}. Seeds were immediately covered with a thin layer of soil and non-flood, saturated soil conditions were enabled in the field with frequent flush irrigations for three weeks to ensure maximal seedling emergence and establishment. Seedling emergence occurred within 7 to 10 days after seeding. Crop thinning and gap filling were completed leaving approximately 25 hills m^{-2}prior to flood establishment on March 12. In both seasons, each plot was 4 m long and 14 rows wide (spaced 20 cm apart). Throughout each cropping season, a permanent flood (5-10 cm water depth) was ensured with water from the Cyili rice area dam and when required by pumping fresh water from a nearby river. The flood was maintained until physiological maturity. Pests were controlled to avoid significant loss in biomass and yield. Control of weed growth was achieved with frequent hand removal passes; rice stalk eyed fly (*Diopsis thoracica*) was mitigated with weekly sprays of 1.5 g ha^{-1}Cypermethrin 40% WP for eight weeks starting at the seedling stage. All field operations were manually implemented and sufficient labourers

were mobilized to achieve timely execution of the various field operations and data collection.

Nitrogen fertilizer rates and application

During both the DS and the WS, experiments were arranged in a split plot design with four blocks; N rates were assigned to whole plots and rice genotypes to subplots. Urea fertilizer (46% N) was used as the N source, and total rate splits of 0, 60 (20+20+20+0), 90 (20+20+30+20), 120 (20+30+40+30),150 (20+40+50+40) and 180 (30+50+60+40) kg N ha^{-1} were applied, respectively, as preflood (PF) which was at 30 days from sowing on average, 30 days after PF (30DPF), at the beginning panicle initiation (PI) and at the 50% heading stage (Hd).On average, PI and Hd occurred around 45 and 75 days from PF, respectively (equivalent to 75 and 105 days from sowing).Urea was applied on moist soil at PF and the flood was established within 4 hours from application. Subsequent N splits were made directly into the flood. Fertilizer rates of 180 kg K_2O ha^{-1}as muriate of potash (60% K_2O), 90 kg P_2O_5 ha^{-1}as single super phosphate (21% P_2O_5) and 30 kg Zn ha^{-1} as zinc sulfate (20% Zn) were topdressed by hand in a single PF application across all treatments to ensure these nutrients were not limiting.

Plant sampling and measurements

The total aboveground biomass was collected by hand cutting a-10 hill plant sample (green and all dead tissues) in each subplot to determine total dry weight and total plant N uptake (Ying et al., 1998a,b) at crop physiological maturity. Biomass samples were processed within 24 hours of collection at Rubona research station. Total dry weight (kg dry weight ha^{-1}) was measured (Sartorius weighting scale, ED62025, precision= 0.01 g) after oven-drying at 60°C to a constant weight. Individual plant parts (top leaf, bottom leaf, leaf sheath + culm, and panicle) were ground (Foss mill, Cyclotec^{TM} 1039) to pass a 425 µm sieve (Guindo et al., 1994) for use to analyze plant N accumulation on a 0.1-g subsample by the Halais modified

colorimetric method (Kilyobo et al., 2001). The total plant N uptake (which represents fertilizer plus soil N, kg N ha^{-1}) was expressed as the product of plant concentration (g N kg^{-1}) and total dry weight per unit ground area (kg ha^{-1})(Lafarge et al., 2009; Guindo et al., 1994).

Yield components and grain yield measurements

Panicles were hand-harvested at maturity from an averaged 10-hill sample in each subplot for the quantification of yield components (Zhang et al., 2009). Panicles were counted in each sample to determine the number of panicles per m^2. Panicles were oven-dried at 60°C to a constant weight, hand-threshed and filled spikelets separated from unfilled spikelets by submerging them in tap water. Total weight of filled and unfilled spikelets was determined (Sartorius weighting scale, ED62025, precision= 0.01 g) for each subplot sample. Three subsamples of 5 g of filled spikelets and 1 g of unfilled spikelets were taken to count (Elmor seed counter, precision= 1/1000) the number of spikelets. The number of filled spikelets per panicle was computed as the product of total filled spikelets weight and the average number of filled spikelets in 5g divided by total panicle number in a10-hill sample. The number of unfilled spikelets per panicle was computed as the product of total unfilled spikelets weight and the average number of unfilled spikelets in 1g divided by total panicle number in a10-hill sample. The number of spikelets per panicle was calculated as the sum of filled and unfilled spikelets per panicle; the number of spikelets per m^2 was calculated as the product of the number of panicles per m^2 and the number of spikelets per panicle; the grain filling ratio (GFR) was calculated as filled spikelets number divided by total spikelet number; 1000 filled grain weight (1000 GW) in grams as 1000 divided by the number of filled grains divided by 5g. Rough rice grain yields were measured on a-9 m^{2}area in each subplot. Both the 1000 GW and grain yields were adjusted to standard moisture content of 140 g H$_2$O kg^{-1}.

Experiments were arranged in a- four block split plot design in both seasons and the analysis of variance (ANOVA) was conducted following the linear mixed model (Gbur et al., 2012) in SAS 9.4 software (SAS Institute, Inc., Cary, NC) with N rate, cultivar and season as fixed effects and block as random effect, to determine the overall statistical significance of the effects of explanatory variables (N rate, cultivar and season, and their interactions). Means were compared based on the least significant difference procedure (LSD) at 0.05 probability level. The reporting of results was based on data pooled over cultivar since most of the interaction effects involving N rate with cultivar were not significant (Table.4.2).

Results

Effects of N fertilizer rate with season (S) and cultivar (C) were determined on the yield components, grain yield, total dry weight, and the total plant N uptake at maturity as shown in Table 4.2. The two-way interaction of N x S was significant for the number of spikelets per panicle ($p = 0.0275$), number of panicles per m^2 ($p = 0.0250$), number of spikelets per m^2 ($p = 0.0023$), grain yield ($p = 0.0083$) and the total dry weight ($p = 0.0153$), but not for the1000 GW ($p = 0.5632$), the GFR ($p = 0.8384$) or the total plant N uptake at maturity ($p = 0.3227$).The two-way interaction of N x C was significant only for the GFR ($p = 0.0002$). The three-way interaction of N x C x S was not significant for any of the response variables. The main effect of N was significant for total plant N uptake at maturity ($p = 0.0019$) but was not significant ($p = 0.2051$) for the 1000 GW.

The number of spikelets per panicle (Fig 4.1) was greater in the DS than in the WS at all the N fertilizer rates applied. The number of spikelets per panicle receiving no N fertilizer (0 N kg ha^{-1}) ranged from 82 in the WS to 150 in the DS. In the DS, the number of spikelets per panicle did not increase with N fertilizer addition and ranged from 150 to 168 spikelets per panicle over the six N rates. In the WS, the number of spikelets per panicle was the

greatest at 82 with no N applied and appeared to steadily decrease to 54 as N rate increased to 180 kg N ha^{-1}. However, the number of spikelets per panicle was not different among the 0 N kg ha^{-1} and the other applied N rates, except for the 120 kg N ha^{-1} and 180 kg N ha^{-1} which were lower and not different from all the other applied N rates.

The number of panicles per m[2] (Fig 4.2) was greater in the DS than in the WS at all the N fertilizer rates, except at 0 N kg ha^{-1} whose numbers were similar in both seasons. The number of panicles per m[2] was similar within each season over the N fertilizer rates of 60 to 180 kg N ha^{-1}. The number of panicles per m[2] increased from 221 with no N fertilizer to a range of 309-320 with N fertilizer in the WS and from 251 with no N fertilizer to a range of 347-360with N fertilizer in the DS.

The number of spikelets per m[2] (Fig 4.3) was greater in the DS than in the WS at all the N fertilizer rates applied. The number of spikelets per m[2] receiving no N fertilizer (0 N kg ha^{-1}) was 17393 in the WS and 38121 in the DS. In the DS, the number of spikelets per m[2] increased from 38121 to 57985 when N rate was increased from 0 kg N ha^{-1} to 60 kg N ha^{-1}and then displayed no significant increase as the N rate increased to 180 kg N ha^{-1}. In the WS, the number of spikelets per m[2] did not increase as the N rate was increased from 0 to 180 kg N ha^{-1}and ranged from 17393 to 19132spikelets per m[2].

The grain yield (Fig 4.4) was greater in the DS than in the WS at all the N fertilizer rates. The grain yield of the rice receiving no N fertilizer (0 N kg ha^{-1}) was 4.6 t ha^{-1} in the WS and 6.5 t ha^{-1} in the DS. In the DS, the grain yield increased from 6.5 t ha^{-1} with no N fertilizer to 8.3 t ha^{-1}when 60 kg N ha^{-1} was applied and then stayed relatively constant as the N rate was increased up to 180 kg N ha^{-1} and ranged from 8.1 to 8.6 t ha^{-1}. In the WS, the grain yield did not increase with the addition of N fertilizer and ranged from 4.6 to 4.9 t ha^{-1}. The average 1000 GW across seasons, cultivars and N rates was 25g. The GFR across N x C interaction varied in a narrow range of 0.80-0.88.

The total dry weight at maturity (Fig 4.5) was greater in the DS than in the WS for each specific N fertilizer rate. The total dry weight at maturity for the no N fertilizer (0 N kg ha^{-1}) treatment ranged from 11090 in the WS to 13750 kg ha^{-1} in the DS. The total dry weight steadily increased as N fertilizer rate increased in each season with the maximum total dry weight of 20070 kg ha^{-1} in the DS and 14570 kg ha^{-1} in the WS being achieved with N rates $\geq$ 150 kg N ha^{-1}.

The total plant N uptake of the rice at maturity (Fig 4.6) was 175 kg N ha^{-1} when no N fertilizer was applied. When the N rate of 60 kg N ha^{-1} was applied the total plant N uptake increased to 220 kg N ha^{-1} and then did not significantly increase as the N rate increased up to 180 kg N ha^{-1}. The maximum plant N uptake of 254 kg N ha^{-1} achieved at the total N rate of 180 kg N ha^{-1} was not different from all other lower applied N rates even though there appeared to be to be tendency for plant N uptake to increase as N rate increased.

Discussion

Crop responses to N fertilizer or the parameters measured were in most cases greater in the DS than in the WS. The irradiance which was greater in the DS (17.2± 0.32 MJ m^{-2} day^{-1}) than in the WS (9.4± 0.66 MJ m^{-2} day^{-1}) (Fig 2.2) drives N demand and crop response (Sinclair et al., 1989; Evans and De Datta, 1979). Moreover, greater response to N fertilizer addition in particular for the number of panicles per m^2 (25%) (Fig 4.2) and the total dry weight (28%) (Fig 4.5) under suboptimal irradiance in the WS was suggested as characteristic of long maturity rice cultivars (Table 4.1) (Fageria et al., 2006; Singh et al., 1998). On the other hand, Evans and De datta (1979) reported a small negative effect resulting from reduced irradiance on the vegetative growth phase during which the potential number of panicles is determined and substantial biomass formed including most of the photosynthetic organs. In contrast, responses to N fertilizer addition were absent for the grain yield (Fig 4.4) and the number of spikelets per m^2 (Fig 4.3) in the WS likely because of the greater reduction in the

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latter yield component resulting in less crop N demand, and the large available and/or readily available native soil N supply at Cyili-Rwanda rice research farm (Fig 4.6) (Farrell et al., 2001; Sheehy et al., 2006; Singh et al., 1998). Moreover, close similar trends in both seasons for the grain yield and the number of spikelets per m^2 suggested this yield component may be determining yield response to N fertilizer. Grain yield in rice is closely related to the number of spikelets per m^2 which is closely associated with plant N uptake and both are closely linked to irradiance (Sheehy et al., 2001; Sheehy et al., 2000; Hasegawa et al., 1994). The 1000 GW (25g) was constant and the GFR varied in a narrow range (0.80- 0.88) across N rate x Cultivar as reported in most studies (Singh et al., 1998; Yoshida, 1981; Evans and De datta, 1979).Unlike other measured parameters, total dry weight was quite responsive to N fertilizer and continued to increase until ≥150 kg N ha^{-1}in both the WS and the DS (Singh et al., 1998).

In contrast, responses to N fertilizer addition were generally minimal with most measured crop growth and yield attributes maximized when the lowest N rate of only 60 kg N ha^{-1} was applied, particularly in the DS. This low N rate is about two to three times lower than the N fertilizer amounts usually required to realize the rice crop potential in the tropics of Asia comparable to the grain yield of 8.3 t ha^{-1} in the DS (Fig 4.4) and plant N uptake > 200 kg N ha^{-1} (Fig 4.6) that were obtained in this study (Yang et al., 2008; Peng et al., 2000; Cassman et al., 1998). Further, substantial grain yields ranging from 4.6 t ha^{-1} in the WS to 6.5 t ha^{-1} in the DS were achieved without N fertilizer application. These responses were linked to the large contribution from the available and/or readily available native soil N reserves associated with ample amounts of total soil N (2.80 ± 0.34 g kg $soil^{-1}$) (Buresh et al., 2008; Sahrawat, 2006; Norman et al., 2003). Values of total soil N (TSN) and organic carbon (OC) at Cyili-Rwanda rice research farm were about twice or more compared to most of the tropical irrigated lowlands in Asia (Cassman et al., 1998; Sahrawat, 1983) and the rice culture systems of the mid-south in the United States(Fulford, 2014; Roberts, 2010; Ross, 2007).

Apparently, large stocks in the soil organic matter (SOM) and TSN were widespread (2.45 g kg soil[-1] for TSN and 35.38 g kg soil[-1]for OC) in the rice production environments of Rwanda as indicated by a recent nationwide soil survey (RSSP 2011).On the other hand, the lower N fertilizer recommendation of 80 kg N ha^{-1}in use in Rwanda since the 1980's (RSSP, 2011) may support the hypothesis of the large available and/or readily available native soil N reserves reported by this study.

These preliminary findings on the N fertilizer responses in Rwanda may have some technical and social implications in case validated with on-farm testing. First, the SOM could be not only in large stocks but also have greater N mineralization potential than the average levels of 50-80 kg N ha^{-1} reported in several studies (Buresh et al., 2008; Sahrawat, 2006). Responses in the DS, which were maximized when the lowest N rate of only 60 kg N ha^{-1} was applied, could indicate that it is not necessary to increase the N fertilizer requirement or efficiency in the short or medium term (RSSP, 2011). But instead soil and fertility research my need to be focussed on other potential growth and yield limiting constraints such as other macro and micronutrients (e.g., P, K, Zn) that might be deficient and/or elements (e.g., Fe, Mn)that might be in toxic amounts in the soil(RSSP 2011; Dobermann et al., 1998). Similarly, the absence of response to N fertilizer in the WS in Cyili-Rwanda for the grain yields which were comparable to the national farm average of 4.5 t ha^{-1} when irrigation water is not limited in most Rwandan rice schemes, could suggest that the application of the blanket recommendation of 80 kg N ha^{-1} is not entirely required, and in both cases of the DS and the WS, cost savings from lower fertilizer N inputs could ensue for the majority of small scale, resource-limited Rwandan rice growers (RSSP, 2011). Finally, water for irrigation remains a major challenge across rice schemes particularly in the DS. Hence, it should be considered as one of the priority entry points for long term rice productivity improvement and sustainability due to ramifications with N use efficiency and the majority of important limiting and

reducing factors (e.g. weeds, insects and diseases) in rice production(Diagne et al., 2013; Haefele et al., 2013; Buresh et al., 2008).

Conclusion

Seasonal differences for most of the measured crop responses to N fertilizer addition were closely related to the variation in irradiance between the DS and the WS. Responses to N fertilizer addition were generally minimal with most of measured growth and yield attributes maximized when the lowest N rate of only 60 kg N ha^{-1}was applied. At this N rate, responses particularly in the DS were at least equivalent to the potential performances under irrigated lowland environments in the tropics of Asia. In the WS, grain yields of 4.8 t ha^{-1}, comparable to the national farm grain yield (4.5 t ha^{-1}), were obtained with this low N rate and were not significantly greater than when no N fertilizer was applied. These trends in grain yield responses to N fertilizer addition suggest a large contribution from the available and/or readily available native soil N supplies linked to ample amounts of total soil N (2.80 ± 0.34 g kg soil^{-1}) which apparently could be widespread in the rice production environments of Rwanda.

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Table 4.1. Key characteristics of rice cultivars evaluated in the 2012 dry season and 2013 wet season

Cultivar	Subspecies	Plant type	Original ecology	Origin	Release year	Growth duration (days)[a]	Grain type
Facagro 56	Indica x Japonica$_1$	Semidwarf	Irrigated	Burundi	1996	145	Medium/translucent
Gakire	Indica x Japonica$_2$	Semidwarf	Irrigated	West Africa	2003	144	Medium/translucent
UP12	Glaberrima x Japonica	Standard stature	Upland	West Africa	2010	145	Long/bold/chalky
Yunyine	Tropical Japonica	Standard stature	Irrigated	Taiwan	1980's	147	Short/chalky

[a] From sowing to physiological maturity

Table 4.2. Analysis of variance (ANOVA) for the number of spikelets per panicle, number of panicles per m^2, number of spikelets per m^2, grain filling ratio, 1000 grain weight, grain yield, total dry weight and total plant N uptake

Source of variation[a]	Number of spikelets per panicle [b] p value	Number of panicles per m^2 p value	Number of spikelets per m^2 p value	[c]GFR p value	[d]1000 GW p value	Grain yield p value	Total dry weight p value	Total plant N uptake p value
N	0.2937	0.0018	0.0002	0.0167	0.2051	0.0200	0.0062	0.0019
C	0.0014	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.0017	0.0005
N x C	0.9060	0.0722	0.8086	0.0002	0.7379	0.0950	0.5641	0.3317
S	< 0.0001	0.0018	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	<.0001
N x S	0.0275	0.0250	0.0023	0.8384	0.5632	0.0083	0.0153	0.3227
C x S	< 0.0001	< 0.0001	0.0004	0.0042	< 0.0001	< 0.0001	0.4011	0.2259
N x C x S	0.6045	0.4213	0.5034	0.264	0.6946	0.8056	0.3736	0.2437

[a] N: N rate, C: cultivar, S: season

[b] significant at p value $\leq$ 0.05

[c] GFR: Grain filling ratio
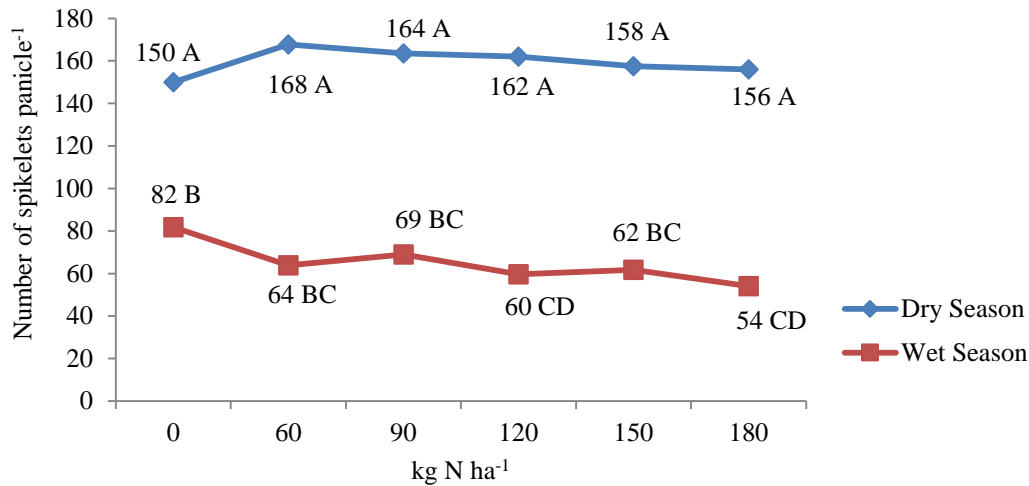
[d] 1000 GW: 1000 grain weight

Fig 4.1. Influence of season and N rate interaction, averaged across cultivars, on the number of spikelets per panicle. LSD (0.05) to compare the number of spikelets per panicle means among N rates: same N rate across seasons =20.50; different N rates within and across seasons =20.54. Means followed by the same letter are not significantly different.
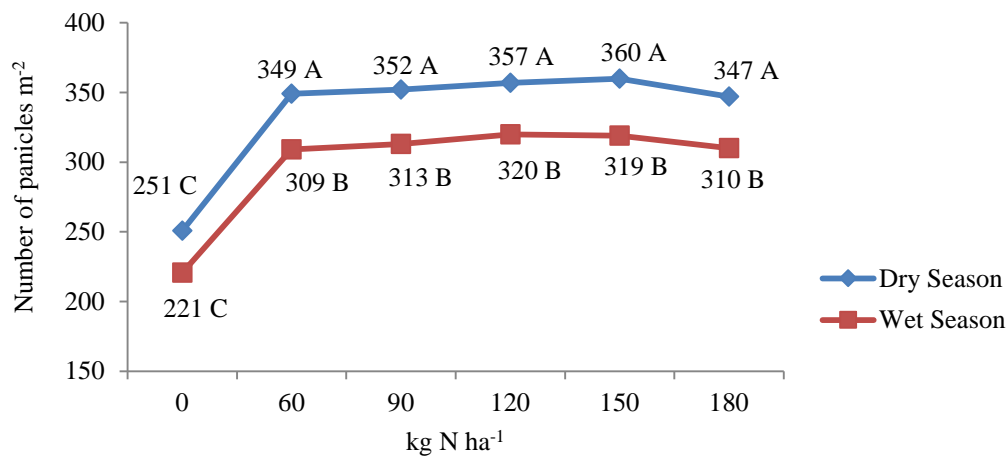

Fig 4.2. Influence of season and N rate interaction, averaged across cultivars, on the number of panicles per m^2. LSD (0.05) to compare the number of panicles per m^2 means among N rates: same N rate across seasons = 35.3; different N rates within and across seasons = 58.6. Means followed by the same letter are not significantly different.
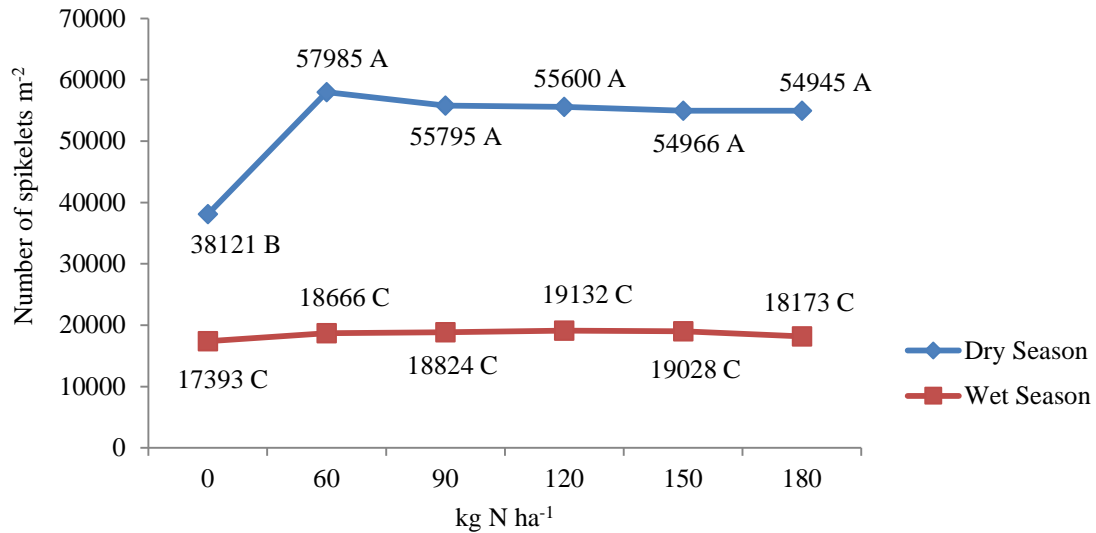
Fig 4.3. Influence of season and N rate interaction, averaged across cultivars, on the number of spikelets per m^2. LSD(0.05) to compare the number of spikelets per m^2 means among N rates: same N rate across seasons = 7954; different N rates within and across seasons = 7994. Means followed by the same letter are not significantly different.
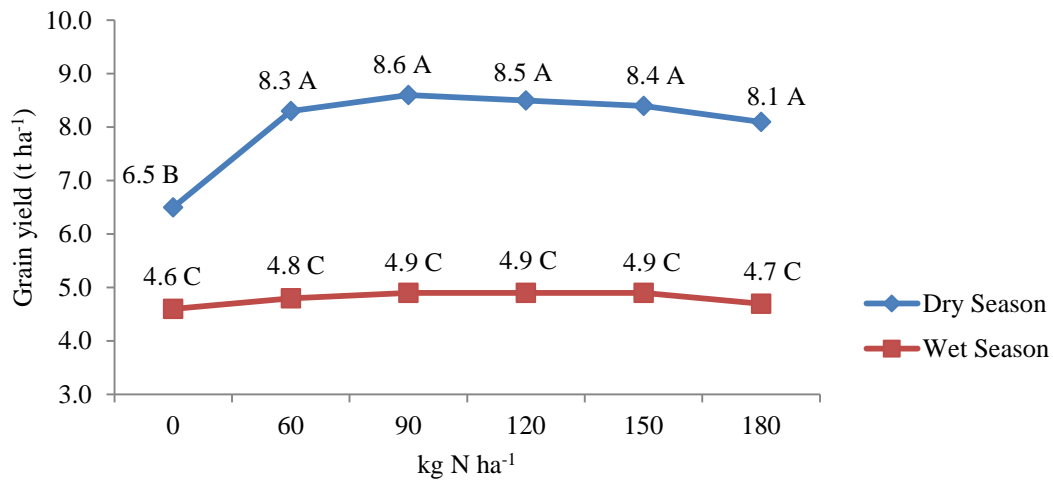

Fig 4.4. Influence of season and N rate interaction, averaged across cultivars, on the grain yield (t ha^{-1}). LSD (0.05) to compare the grain yield (t ha^{-1}) means among N rates: same N rate across seasons = 0.85; different N rates within and across seasons = 1.13. Means followed by the same letter are not significantly different.
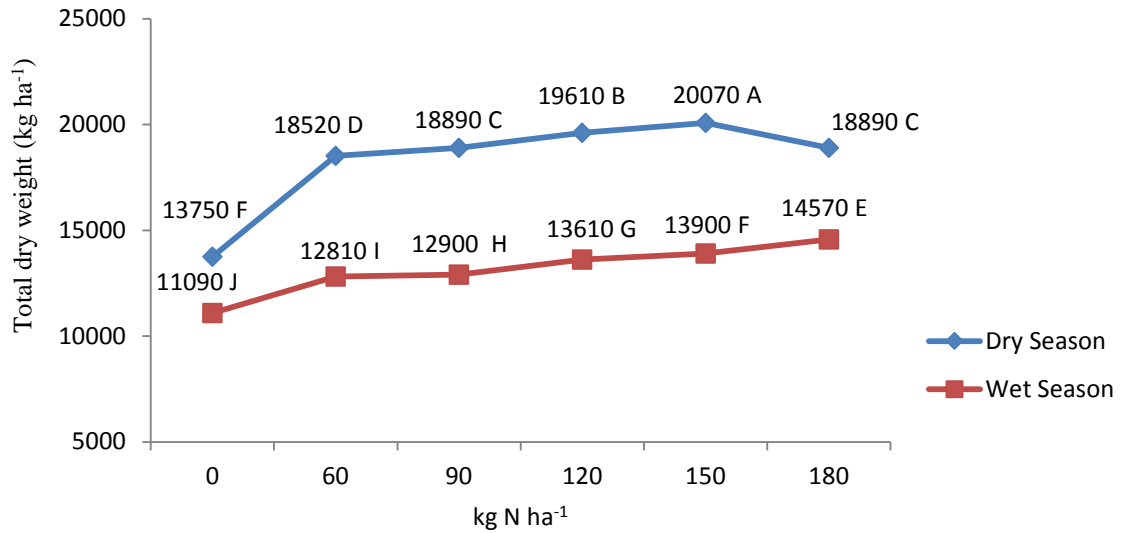
Fig 4.5. Influence of season and N rate interaction, averaged across cultivars, on the total dry weight at maturity (kg ha^{-1}). LSD (0.05) to compare the total dry weight (kg ha^{-1}) means at maturity among N rates: same N rate across seasons = 243; different N rates within and across seasons = 260. Means followed by the same letter are not significantly different.
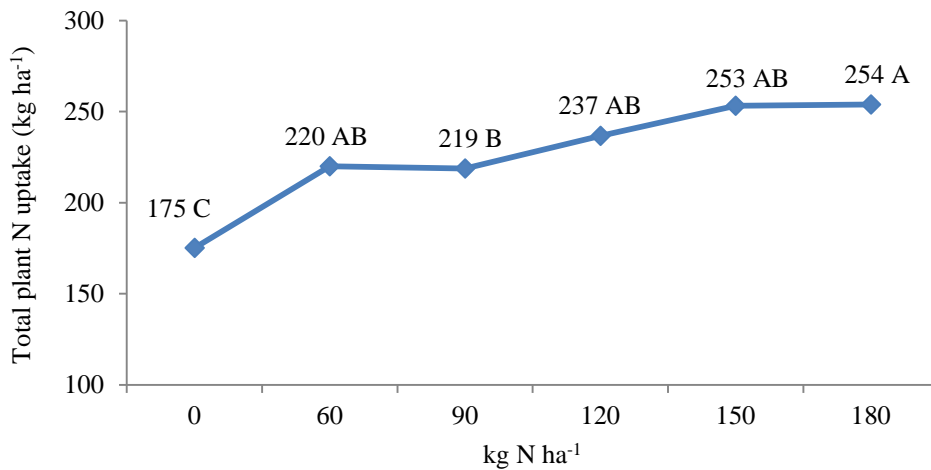

Fig 4.6. Influence of season and N rate interaction, averaged across cultivars and seasons, on the total plant N uptake at maturity (kg ha^{-1}). LSD (0.05) to compare the total dry weight (kg ha^{-1}) means at maturity among N rates = 34.94. Means followed by the same letter are not significantly different.

General conclusion

Seasonal differences in irradiance were linked to the rice biomass and plant N uptake and were closely related to the yield components and grain yield, and the N fertilizer responses. Grain yields were closely related to yield components with the number of spikelets per panicle and spikelets per m^2 accounting for the greatest variation. The cultivars studied had equivalent or greater performances for yield components and grain yield compared to the best modern rice cultivars in irrigated lowlands in the world. The performances in biomass were lower in comparison to irrigated lowlands of Asia. However, the potential for the translocation of photosynthate to the panicle was apparently greater in Cyili-Rwanda than in the irrigated lowlands in the tropics of Asia. The plant N uptake at maturity (> 200 kg N ha^{-1}) was comparable to the greatest performances for rice reported in the literature. Rice cultivars with the combinations of the Indica and Japonica subspecies generally exhibited greater performances in HI and yield components, in particular the number of spikelets per m^2, and in the grain yields. Average total crop duration of 145 days from sowing to maturity may be considered as the current optimal in Cyili-Rwanda for achieving the yield potential (8-10 t ha^{-1}) of irrigated lowlands in the tropics of Asia. Growth in biomass and plant N attributes were more closely related to the grain yield and the number of spikelets per m^2 during the reproductive phase than any other stage prior to maturity. Panicle growth rather than total dry weight attributes were closely related to the grain yield and the number of spikelets per m^2 during the post-heading growth phase. Plant N attributes were correlated more with biomass growth than with the grain yield and the number of spikelets per m^2. Responses to N fertilizer addition were generally minimal with most of measured growth and yield attributes maximized when the lowest N rate of only 60 kg N ha^{-1} was applied. Apparently, this was caused by a large contribution from the available and/or readily available native soil N supplies linked to ample amounts of total soil N (2.80 ± 0.34 g kg soil^{-1}).