Patterns of Biomass Allocation in Upland Rice Cultivars Grown on Soils along a Toposequence

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ABSTRACT

Biomass allocation to root, culm, leaf, and grain of 20 upland rice cultivars was assessed in pots set up in an open field experiment. The cultivars consisted of 18 upland NERICA rice (N 1 to N 18) and Funaabor 1 and 2. The rice cultivars were grown under rainfed condition on 5 kg soils collected along a toposequence designated as Upper Crest (UC), Middle Slope (MS), and Valley Bottom (VB) soils. Plants were harvested at maturity for biomass allocation pattern into various organs. Toposequence soils and cultivar significantly (p<0.01) influenced all the fractions of biomass and standing biomass to different organs except root dry weight (RDW) and root mass fraction (RMF) for the latter. The lowest standing and fraction of biomass to root (3.64g and 0.08 respectively), culm (17.92g and 0.42 respectively), and leaf (3.59g and 0.08 respectively) of the rice cultivars were observed on VB soils. Principal Component (PC) biplot accounted for 95.67% and 97.38% of the total variation in standing biomass and fractions of biomass to organs respectively. Higher grain weight per plant was observed in NERICA 2 and 15 and was closely associated with standing biomass to root than to culm and leaf. Upland rice grown on UC soil accumulated more biomass to vegetative parts with concomitant decrease in fraction of biomass allocated to reproductive structures unlike rice cultivars grown on VB soils. Hence, growing upland rice on VB of a toposequence promotes increase of biomass allocation to grains.

Keywords: Biomass fractions, PC biplot, standing biomass, toposequence, upland rice

INTRODUCTION

The proportion of biomass partitioned to various organs of a plant is a key feature in its survival strategy (Sultan, 2001; Poot & Lambers, 2003; Grigg et al., 2010; Pichancourt & van Klinken, 2012). The roots, stems, leaves, and grains are the main organs within which biomass accumulated by plants are being partitioned and this is done at the expense of other organs involved in the partitioning process. The proportion of total biomass that is partitioned to these organs is influenced by plant size, its growth environment and species (Niklas, 1994; Reich, 2002).

A widely observed feature of tropical upland rice ecology is the unpredictability of rainfall as well as hot and dry conditions which create variable drought conditions at different stages of crop growth. Reduced biomass allocation to leaves as compared to stems or roots is one of the features of plants adapted to these conditions (Callaway et al., 1994; Bazzaz & Grace, 1997; Roa-Fuentes et al., 2012). The NERICA rice cultivars are released for cultivation in similar environments where continuous access to water during growth cycle is almost impossible. Ability to cope with periodic drought through the deep root system is the major characteristics of these rice cultivars. Increasing allocation of biomass to the root is one of the ways by which plants achieve extensive root system development. Based on the Optimal Partitioning Theory (OPT), plants partitioned biomass to various organs depending on the need and demand for growth by the latter and at a proportion that ensures balance in growth of all organs (McCarthy & Enquist, 2007; Zhang et al., 2015). The difference in potential of upland rice cultivars for biomass yield and allocation to different organs, especially root when grown in different soils, therefore, needs to be explored.

Soils play a major role in influencing biomass allocation to roots. Soil condition can influence biomass allocation to different component of plants (Chaudhary et al., 2015). The fraction of biomass allocated to reproductive structure, otherwise termed harvest index, is also highly influenced by environmental factors like soil conditions (Yoshida, 1981; Dalling, 1985). Physical, chemical, and biological properties of soil can influence root growth (Bengough et al., 2011) and this can influence biomass accumulation and distribution in plants. Variation in edaphic properties of different soil types related to topography can influence productivity of annual crops (Cambardella et al., 2004; Ontl et al., 2013). Soil texture is one of the important soil physical properties that influences root growth (Alameda et al., 2012; Kobaissi et al., 2013) and is characterised by relative proportion of sand, silt, and clay. The proportion of these soil components determines the amount of available pores within which root grows (Giménez et al., 2002; Dexter, 2002; Keith & Buchan, 2002). Soil physical and chemical properties change with changing slopes due to deposition of sediments carried from upper slopes to lower slopes along a toposequence (Cambardella et al., 2004). Due to reduced penetration resistance, plants

grown on light soils with larger number of pores have the tendency to grow more roots unlike heavy soils with reduced soil pores and high penetration resistance (Bengough et al., 2011). The survival of rice plant, especially under moisture limitation, is expected to be influenced by type of soil on which it is grown.

Biomass allocation and partitioning are used interchangeably in literature referring to the standing biomass in roots, stems, and leaves at a particular point in time and dividing accumulated biomass to root, stem, and leaves (Reich, 2002; McCarthy & Enquist, 2007). Many studies have also been conducted on biomass allocation in plants but only a few of such studies were reported on upland rice cultivars at harvest. In this study, we focused on standing biomass and fractions of biomass to these various organs of upland rice cultivars.

The use of biomass fractions in the analyses of allocation patterns has been criticised; nevertheless, it provides an easy-to-understand scaling relations between biomass allocated to organs (Poorter et al., 2012). Analysing fractions of biomass allocated to different organs could provide a means of linking plant biomass investment to different plant functions under contrasting environmental condition (Poorter & Nagel, 2000; Poorter et al., 2012; Kumordzi et al., 2016). Modification of biomass allocation to different organs is one opportunity to improve yield in wheat (Xie et al., 2016). Differences in allocation of biomass to different organs of rice could also be the major contributor to differences in yield.

Therefore, understanding the proportion of biomass allocated to different organs of rice is a prerequisite to identifying upland rice with potential for higher yield. The objectives of this study are to address the following hypotheses, namely (1) Biomass allocation to different organs are the same in upland rice cultivars, (2) Soils collected along a toposequence influence biomass allocation to different organs similarly among upland rice cultivars and, (3) Grain weight in upland rice is influenced by standing biomass or fractions of biomass to other organs

MATERIALS AND METHODS

NERICA rice

NERICA rice are selections from crosses of *Oryza sativa* and *Oryza glaberrima*, which are known for their high yields and disease resistance respectively. NERICA 1 to 7 were released in 2000 (Kaneda, 2007; Manneh & Ndjiondjop, 2008) while 11 NERICA cultivars i.e. NERICA 8 to 18 were released in March 2005 (Semagn et al., 2006). The 18 NERICA rice cultivars were bred for upland condition and are released to cope with the present erratic rainfall that characterised most part of the tropics (Wainaina et al., 2015). NERICA 1 to 18 and the two other upland rice cultivars, Funaabor 1 and Funaabor 2, also called "Ofada white" and "Ofada Gold" respectively, are mostly cultivated in rainfed areas. The NERICA cultivars were sourced from African Rice (WARDA) Ibadan station while the two Funaabor cultivars were sourced from

Federal University of Agriculture, Abeokuta (FUNAAB).

Experimental sites

The study was conducted in an open field in the premises of College of Agricultural Sciences, Olabisi Onabanjo University Ayetoro Campus. The Campus is located in derived savannah ecology of South Western Nigeria (6.5°N, 10°E). The area is characterised with rainfall pattern different from its neighbouring town. The topography of the area (where the soils were collected) slopes towards a river which is found in the western part of the area.

Experimental method

Soil sample collection and analyses. Soils were collected along the toposequence which stretched from the upper to the lower of the slope near the river side. Soil samples were taken from the upper, middle, and valley bottom of the slope designated as upper crest (UC), middle slope (MS), and valley bottom (VB) respectively. The different toposequence soils were scooped with shovel up to 15 cm depth, homogenised, bagged, and taken to nursery station within the field where 5 kg each of the soil samples were later potted. Sub-sample of each toposequence soil was collected, air dried, and sieved with 2 mm sieve for routine analyses in soil laboratory. Particles size distribution was determined by the hydrometer method (Bouyoucos, 1951). The pH of the soils in soil water ratio of 1:2 was determined using electrode pH meter. Using 1N ammonium acetate (NH_4OAc pH 7.0), exchangeable bases –Calcium (Ca), Magnesium (Mg), Potassium (K), and Sodium (Na), were extracted after which Ca and Mg were subjected to reading on Atomic Absorption Spectrophotometer (AAS) while K and Na were determined with flame photometer. The effective cation exchange capacity (ECEC) was estimated using summation method. The ratio of sum of exchangeable cations to ECEC expressed in percentage was used in calculating base saturation. Total N were determined by micro-Kjeldahl method. Organic carbon content was determined using dichromate ($K_2Cr_2O_7$) as an oxidising agent (Walkley & Black, 1934). Available P was determined colourimetrically using Bray-1 method.

Seedling establishment and plant sample collection. The 20 upland rice cultivars were sown in pots containing 5 kg soils. The twenty upland rice cultivars were each sown in pots prepared for the nursery. The rice cultivars were nursed for 21 days in pots using the same soil collected from the upper slope in order to ensure uniformity in growth conditions of seedlings at initial stage of growth. The seedlings were later transplanted into pots already prepared using the different soils collected along the toposequence. Two weeks after transplanting (WAT), NPK 15:15:15 (15% N: 15% P_2O_5: 15% K_2O) fertiliser was applied at a recommended rate of 40 kg: 40 kg: 40 kg ha^{-1}. At reproductive stage (4 WAT); the

second dose of nitrogen fertiliser at 60 kg ha^{-1} of nitrogen was applied using urea. The experiment was rainfed and supplemental irrigation was applied at 40mm of water/pot/day for 21 days- a long dry spells that characterised the area during the cropping period. At harvest maturity, whole plant parts were carefully recovered from the pots by dipping the root with soils in water to loosen the soils. Roots and other plant parts were carefully removed and were separated into root, culm, leaf, and grain. Plant parts were oven dried at 65°C to constant weight after which they were weighed again and recorded. Fractions of total biomass for each organ were estimated as follows:

$$\text{Organ biomass fraction (g/g)} = \frac{\text{Dry weight of organ (g/plant)}}{\text{Total biomass including grains (g/plant)}}$$

Statistical analyses

Data collected on weight of different organs were subjected to Analyses of Variance (ANOVA) using Genstat software package, 12th Edition (Payne et al., 2009). The design used was the Complete Randomized Design (CRD). Significant treatment means for toposequence soils and cultivars were later separated using Duncan Multiple Range Test (Gomez & Gomez, 1982). Data on fractions of biomass that violates the assumption of ANOVA were transformed by using square root transformation. Principal Component Analysis (PCA) was conducted to assess the new variables that formed among RDW, CDW, LDW, and yield in contributing to the variation (explanation rates) in standing biomass, and among RMF, CMF, LMF, and HI for fraction of biomass variation. The PCA was also descriptively used to assess the relationships among the recorded variables.

RESULTS

Table 1 shows the physico-chemical properties of different soils used in growing the rice cultivars. The textural class of UC and MS soil is loamy-sand while that of VB was sandy-loam and sand proportions among them were 83.20%, 85.20% and 74.20% respectively. The upper crest and middle slope soils had similar proportion of silt (12.60 and 10.40) and clay (4.20 and 4.40) respectively while valley bottom soil had highest silt (13.60) and highest clay (12.20) content than the other two toposequence soils. The pH of the soils was moderately acidic to neutral (6.35 to 7.00). Effective cation exchange capacity (ECEC) was higher in upper crest soil (26.24 cmol kg^{-1}) than the other two toposequence soils (20.27 in MS and 16.81 cmol kg^{-1} in VB). Total organic carbon (Total Org.C) and total nitrogen (Total N) was high in UC soil (3.59 and 0.24%) compared with MS (1.67 and 0.14%) and VB (1.69 and 0.15%) soils respectively. Available phosphorus was high in UC soil (9.31 mg kg^{-1}) when compared with VB soils (3.25 mg kg^{-1}).

Table 1
The physico-chemical properties of soils collected along a toposequence

Soil Property	Upper Crest soil	Middle slope soil	Valley bottom soil
Sand (%)	83.20	85.20	74.20
Silt (%)	12.60	10.40	13.60
Clay (%)	4.20	4.40	12.20
Textural class	Loamy sand	Loamy sand	Sandy loam
pH (H_2O)	7.00	6.35	6.55
Ca (cmol kg^{-1})	19.36	15.26	11.83
Mg (cmol kg^{-1})	4.38	3.54	3.34
Na (cmol kg^{-1})	1.60	0.94	1.04
K (cmol kg^{-1})	0.85	0.46	0.54
Al+H (cmol kg^{-1})	0.05	0.07	0.06
ECEC (cmol kg^{-1})	26.24	20.27	16.81
Base saturation %	99.81	99.65	99.64
Total N (%)	0.24	0.14	0.15
Total Org. C. (%)	3.59	1.67	1.69
Available P. (mg kg^{-1})	9.31	5.83	3.25

The mean square values of all the standing biomass as well as fractions of biomass to different organs for toposequence soils and cultivars are shown in Table 2. Toposequence soils and cultivars exhibited significant effect ($p<0.01$) on all the standing biomass and fractions of biomass with the exception of RDW and RMF for cultivar effect. Interaction between toposequence soils and cultivars were significant only for total biomass (TB) and yield per plant among the variables.

Differences in toposequence soils and cultivars were observed in all the variables with the exception of RMF and RDW for cultivar effect (Table 3). The lowest biomass and fractions of biomass were recorded in valley bottom with the exception of harvest index (0.41) and yield $plant^{-1}$ (17.75 g). Funaabor 2 had the highest CDW (29.32 g) and leaf dry weight LDW (7.18 g) as well as highest LMF (0.15) and CMF (0.59). The cultivar however, recorded the lowest harvest index HI (0.15) and grain (7.70 g).

Figure 1 shows the interactions of cultivars by toposequence soils on total biomass (TB) of upland rice cultivars grown on soils collected along a toposequence. The TB accumulated by the rice cultivars across the toposequence soils was similar with the exception of few cultivars. NERICA 9 accumulated the highest TB when grown in UC and MS than in VB while NERICA 16 accumulated higher biomass when grown in UC than in MS.
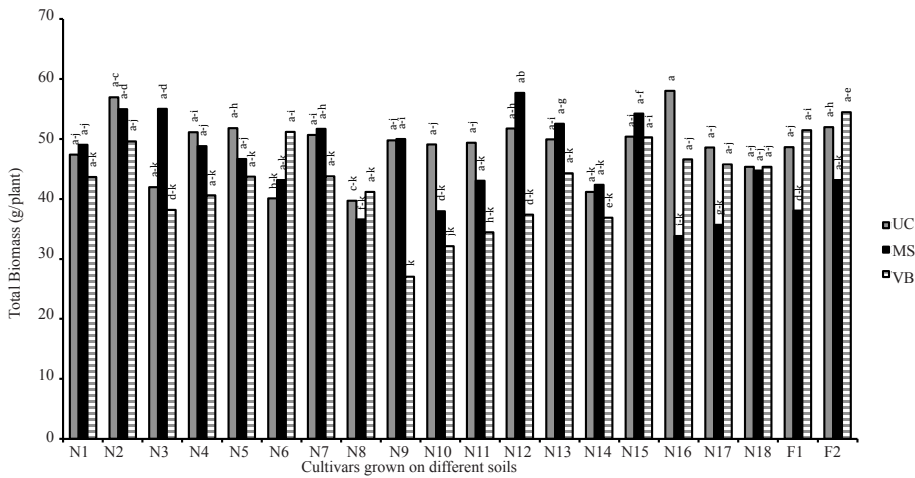
Figure 1. Interactions of Cultivars x Toposequence soils on Total Biomass of upland rice cultivars grown on soils collected along a toposequence
Note: UC= Upper Crest; MS= middle slope; VB= valley bottom; N1 to N18= NERICA 1 to 18; F1 & 2 = Funaabor 1 and 2. Bars with the same letter(s) are not significantly different from one another using Duncan Multiple Range Test (DMRT) at p=5% among all treatment combinations of soils x cultivars

Interaction of toposequence soils by cultivar on yield plant-1 of the rice cultivars when grown on soils collected along a toposequence is shown in Figure 2. The grain weight per plant of the rice cultivars were similar across the toposequence soils with the exception of NERICA 4, 16, 17 and 18 where grain produced when grown in UC soil were higher than those grown in MS soil. NERICA 6, and Funaabor 1 and 2 however, produced higher grain weight per plant when grown in VB than in UC and MS. Table 4 shows the Eigen vector loadings

Table 2
Mean square values of standing biomass and fractions of biomass to organs of upland rice cultivars grown on soils collected along a toposequence

Source of variation	RDW	CDW	LDW	RMF	CMF	LMF	TB	HI	Yld plt⁻¹
Topo_soil	90.41**	1056.67**	52.21**	0.021**	0.330**	0.020**	712.73**	0.720**	1129.47**
Cultivar	7.81ns	100.18**	9.15**	0.002ns	0.020**	0.004**	185.41*	0.050**	95.32**
Topo_ soil*Cultivar	12.56ns	38.74ns	2.62ns	0.003ns	0.010ns	0.001ns	158.75*	0.010ns	44.24*
Residual	9.06	37.29	2.27	0.002	0.01	0.001	98.50	0.01	29.05

Note: **,* significant at 1% and 5% level of probability respectively. The mean square values for RMF, CMF, LMF, and HI were based on non- transformed data but the associated significances are based on square root transformed data
Topo_soil= Toposequence soil; RMF= root mass fraction; CMF= culm mass fraction; LMF= leaf mass fraction; HI= harvest index; RDW= root dry weight; CDW= culm dry weight; LDW= leaf dry weight; Yld plt⁻¹= yield plant⁻¹; and TB=Total biomass.
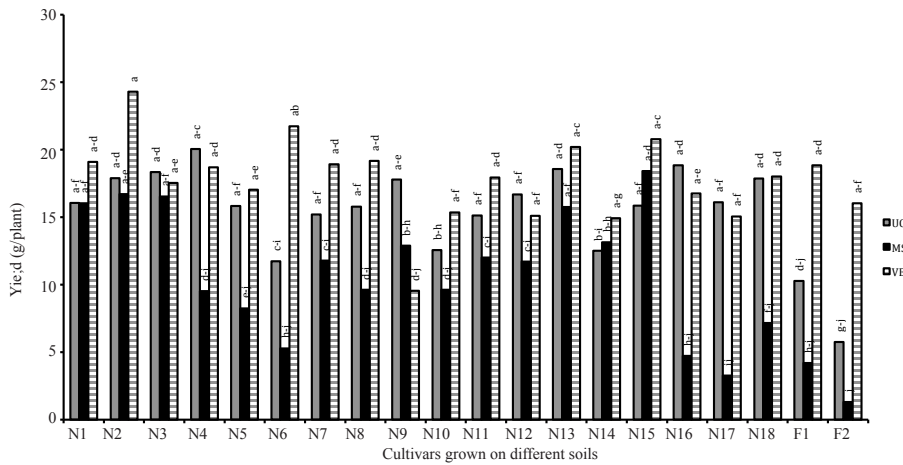
Figure 2. Interactions of Cultivars x Toposequence soils on Yield Plant-1 of upland rice cultivars grown on soils collected along a toposequence

Note: UC= Upper Crest; MS= middle slope; VB= valley bottom; N1-N18= NERICA 1to 18; F1 & 2 = Funaabor 1 and 2. Bars with the same letter(s) are not significantly different from one another using Duncan Multiple Range Test (DMRT) at p=5% among all treatment combinations of soils x cultivars

and explanation rates from PCA for the rice cultivars across and on each toposequence soil. Principal component 1 (PC 1) contributed about 64% explanation rate (ER) of the biomass standing. Based on the eigen vector loadings, PC 1 was basically determined by CDW, yield, and LDW in that order. On the other hand, principal component 2 (PC 2) that was majorly determined by yield and CDW contributed 32% variation of biomass standing. Summing up the PC 1 and PC 2, both had contributed 96% variation in the biomass standing. Culm dry weight, yield and to certain extent of LDW had caused variation in biomass standing. Practically speaking, the RDW had little contributory role for the above variation. As for fraction of biomass variation, PC 1 had almost played total role in the variation, i.e. with ER of 92%. Principal component 1 was

determined by HI and CMF. This may indicate partitioning was to culm and grain (trade-off). Other principal components (PC 2 - PC 4) had very little or insignificant role in the variation of fraction of biomass across all types of soil.

In the case of UC soils, PC 1 contributed 60% ER of the biomass standing. Based on the eigen vector loadings, PC 1 was basically determined by CDW, yield, and LDW in the same order as it was observed in PCA across soil types. On the other hand, PC 2 was majorly determined by yield, CDW, and RDW and contributed 24% variation of biomass standing. The first two principal components had contributed 84% variation in the standing biomass. Basically, RDW and LDW contributed little to the variation in the first and second principal components respectively. As for fractions of biomass variation, PC 1 contributed 74%

and was majorly determined by HI and CMF which also cuts across other toposequence soils. Principal component 2, however, contributed an additional 20% variation in fraction of biomass with RMF, CMF, and HI causing the variation in that order. Summing up these two components, PC 1 and PC 2 contributed 94% of the variation in fraction of biomass for UC soils.

The first and second principal component of MS soil contributed 59 and 34% variations in the biomass standing respectively. Based on the eigen vector loadings, PC 1 was basically determined by yield and CDW in that order and vice-versa for PC 2 while LDW and RDW played little role in the two above variations. Summing up the PC 1 and PC 2, both had contributed 94% variation in biomass standing. As for fractions of biomass, PC 1 alone contributed 88% while PC 2 contributed additional 9% of the variation with RMF and CMF being the main determinants. Summing these two components, both had contributed

97% variation in the fraction of biomass to organs.

In the case of VB soil, PC 1 contributed 64% ER of the biomass standing and based on eigen vector loading, CDW, yield per plant, and RDW are the main determinants of this component. In PC 2, yield per plant and CDW were the main determinants and it contributed 33% of the variation. Summing up the two components, both had contributed 96% of the variation in standing biomass. The PC 1 and 2 for fraction of biomass in VB soils were respectively similar to that of MS soil with PC 1 and 2 also contributing 88 and 9% variation, respectively. Summing up the two components, both contributed 97% variation in fraction of biomass.

Figures 3a and b show the PC biplot for standing biomass and fractions of biomass to various organs of rice respectively. NERICA 2 and 15 had the highest yield which was closely related to RDW than CDW and LDW (Figure 3a). The lowest yield was recorded by Funaabor 2 but with
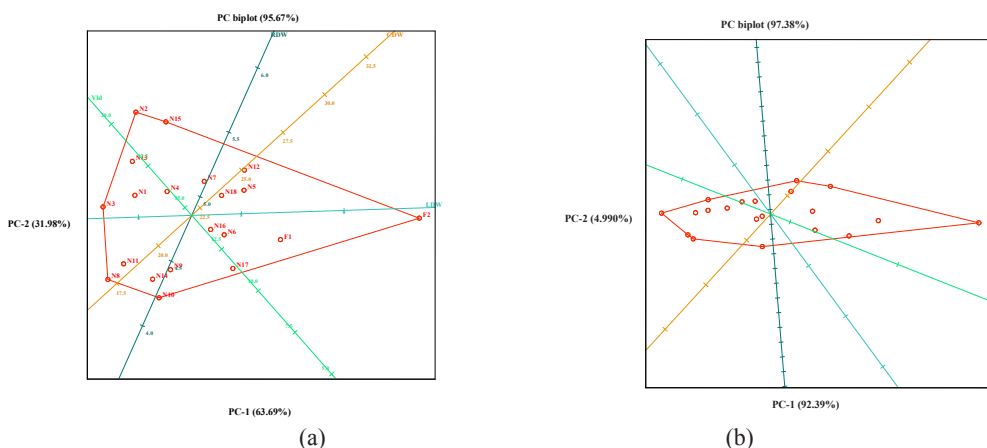

(a)   (b)

Figure 3. PC biplot of (a) standing biomass and (b) fractions of biomass to organs of upland rice cultivars grown on soils collected along a toposequence over all soils

higher LDW. Wider angle of separation was observed between HI axis and CMF axis than that between CMF and LMF axes with Funaabor 2 recording the highest value for CMF and LMF (Figure 3b and Table 3.)

Table 3

Means of standing biomass and fractions of biomass to organs of upland rice cultivars grown on soils collected along a toposequence

Sources of Variation		RDW	CDW	LDW	RMF	CMF	LMF	TB	HI	Yld plt[-1]
		g/plant			g/g			g/plant	g/g	g/plant
Toposequence Soils	Upper Crest	5.29a	23.23a	4.91a	0.11b	0.47b	0.10b	48.87a	0.32b	15.44b
	Middle Slope	5.63a	24.88a	5.05b	0.12a	0.55a	0.11a	45.96ab	0.22bc	10.40c
	Valley Bottom	3.64b	17.92b	3.59c	0.08c	0.42c	0.08c	42.90b	0.41a	17.75a
Cultivars	Nerica 1	4.15a	20.69b-e	4.78b-e	0.09a	0.44c-e	0.10b-e	46.68a-d	0.37a-d	17.06a-d
	Nerica 2	6.86a	22.98b-e	4.37b-e	0.12a	0.42de	0.09ef	53.84a	0.37a-d	19.64a
	Nerica 3	4.52a	19.35b-e	3.71c-e	0.10a	0.42e	0.08ef	45.05a-d	0.41a	17.48a-d
	Nerica 4	4.54a	21.98b-e	4.23b-e	0.09a	0.47b-e	0.09d-f	46.84a-d	0.35a-e	16.04a-e
	Nerica 5	4.96a	24.68a-c	4.07c-e	0.10a	0.53ab	0.09d-f	47.40a-d	0.28d-g	13.70b-e
	Nerica 6	5.57a	22.54b-e	4.77b-e	0.10a	0.50b-d	0.11b-e	44.81a-d	0.29b-g	12.91c-e
	Nerica 7	5.28a	23.40b-e	4.72b-e	0.10a	0.47b-e	0.10b-f	48.71a-d	0.32a-f	15.30a-e
	Nerica 8	3.47a	17.49 e	3.33d-e	0.09a	0.45b-e	0.09d-f	39.16d	0.37a-d	14.87a-e
	Nerica 9	4.42a	19.59b-e	4.86bc	0.09a	0.46b-e	0.11b-d	42.28b-d	0.33a-f	13.41b-e
	Nerica 10	5.51a	18.43de	3.26e	0.14a	0.46b-e	0.09d-f	39.71d	0.32a-g	12.51d-e
	Nerica 11	4.47a	18.17de	4.62b-e	0.10a	0.42e	0.11b-e	42.28b-d	0.38a-c	15.03a-e
	Nerica 12	4.45a	25.27ab	4.74b-e	0.09a	0.51b-d	0.10b-f	48.96a-d	0.31a-g	14.50a-e
	Nerica 13	4.88a	21.64b-e	4.23b-e	0.10a	0.44c-e	0.08ef	48.92a-d	0.38ab	18.17a-c
	Nerica 14	3.87a	18.93c-e	3.82c-e	0.10a	0.48b-e	0.09c-f	40.15a-d	0.34a-f	13.53b-e
	Nerica 15	5.60a	24.02a-d	4.07c-e	0.11a	0.47b-e	0.07f	51.64ab	0.36a-e	18.35ab
	Nerica 16	5.84a	22.04b-e	4.81b-d	0.12a	0.50b-e	0.11b-e	46.13a-d	0.28e-g	13.44b-e
	Nerica 17	5.22a	21.68b-e	4.97bc	0.12a	0.51bc	0.12a-c	43.35b-d	0.25fg	11.48ef
	Nerica 18	3.76a	23.83a-d	4.47b-e	0.08a	0.51bc	0.10b-f	46.41a-d	0.31b-g	14.35b-e
	Funabor 1	5.10a	24.12a-d	5.73b	0.11a	0.53ab	0.13ab	46.06a-d	0.23g	11.11ef
	Funabor 2	5.65a	29.32a	7.18a	0.12a	0.59a	0.15a	49.86a-c	0.15h	7.70f

Means followed with same letter within a column for each factor are not different at p=5% by DMRT. The mean comparisons (rankings) associated with RMF, CMF, LMF, and HI are based on the square-root transformed data. RMF= root mass fraction; CMF= culm mass fraction; LMF= leaf mass fraction; HI= harvest index; RDW= root dry weight; CDW= culm dry weight; LDW= leaf dry weight; Yld plt[-1]= yield plant[-1]; and TB=Total biomass

Table 4

Eigen vector loadings and explanation rates from Principal Component Analyses (PCA) of standing biomass and fractions of biomass based on culm, leaf, root, and grains of upland rice cultivars grown on soils collected along a toposequence

Toposequence soils	Rice organs	Standing Biomass				Organs biomass fraction	Fractions of Biomass			
		PC 1	PC2	PC3	PC4		PC 1	PC2	PC3	PC4
Over all soils	CDW	0.72	0.66	0.16	0.14	CMF	0.56	0.61	0.25	0.50
	LDW	0.21	0.01	-0.09	-0.97	LMF	0.19	-0.25	-0.81	0.50
	RDW	0.06	0.14	-0.98	0.10	RMF	0.06	-0.68	0.54	0.50
	Yld plt^{-1}	-0.65	0.74	0.05	-0.14	HI	-0.81	0.32	0.02	0.50
	%ER	63.69	31.98	2.86	1.47	%ER	92.39	4.99	2.62	0.00
Upper Crest	CDW	0.76	0.60	0.23	-0.12	CMF	0.57	0.44	0.49	0.50
	LDW	0.20	-0.07	0.05	0.98	LMF	0.18	0.13	-0.84	0.50
	RDW	0.06	0.30	-0.95	0.06	RMF	0.06	-0.84	0.18	0.50
	Yld plt^{-1}	-0.61	0.74	0.21	0.17	HI	-0.80	0.27	0.17	0.50
	%ER	60.04	23.79	12.90	3.28	%ER	74.29	19.46	6.25	0.00
Middle Slope	CDW	0.20	0.97	-0.14	0.08	CMF	0.56	0.60	0.27	0.50
	LDW	-0.04	0.11	0.18	-0.98	LMF	0.16	-0.19	-0.83	0.50
	RDW	0.03	0.12	0.97	0.19	RMF	0.08	-0.72	0.48	0.50
	Yld plt^{-1}	0.98	-0.19	0.00	-0.07	HI	-0.81	0.31	0.07	0.50
	%ER	59.26	34.45	4.97	1.32	%ER	88.38	9.11	2.52	0.00
Valley Bottom	CDW	0.91	0.32	0.25	0.03	CMF	0.64	0.58	0.09	0.50
	LDW	0.16	0.10	-0.68	0.72	LMF	0.06	-0.39	-0.77	0.50
	RDW	0.23	-0.08	-0.68	-0.69	RMF	0.06	-0.60	0.62	0.50
	Yld plt^{-1}	0.29	-0.94	0.13	0.08	HI	-0.76	0.40	0.06	0.50
	%ER	63.71	32.71	2.66	0.92	%ER	88.22	9.08	2.70	0.00

Note: RMF= root mass fraction; CMF= culm mass fraction; LMF= leaf mass fraction; HI= harvest index; RDW= root dry weight; CDW= culm dry weight; LDW= leaf dry weight; Yld plt-1= yield plant-1; %ER = Percentage explanation rates

DISCUSSION

Earlier findings (Cambardella et al., 2004; Alameda et al., 2012; Kobaissi et al., 2013; Ontl et al., 2013) had established the important role of soils on plant growth and development. This important role of soils is also established in this study. Significant amount of variations in standing biomass and fractions of biomass to organs were captured by toposequence soils as indicated by high mean square values with high significant effect (p<0.01) recorded by the soil (Table 2). The toposequence soils belong to different textural classes (loamy sand and sandy loam, due mainly to reduced proportion of sand coupled with increased proportion of clay) observed in valley bottom soil. The higher clay content observed in valley bottom soils could have caused restriction in root growth, especially

with limited moisture and concomitant high bulkiness, resulting in reduced fraction of biomass allocated to the root and other vegetative organs of the rice cultivars as well as standing biomass accumulated to these organs. The increased biomass generated by the rice cultivars grown on upper crest and middle slope soil could be linked to reduced restriction to root growth in these soils compared with valley bottom soils which resulted in overall increase in biomass accumulated to other vegetative parts of rice grown on the soils. Soil exploration by roots is limited by strong mechanical resistance in the soil which is the most common physical limitation to plant roots (Hodge et al., 2009) and it can result in reduced biomass accumulated by upland rice.

Toposequence soils varied more in chemical properties than physical properties and this could have also contributed to variation in standing biomass and fractions of biomass to various organs of rice observed in this study. The higher total organic C, N, ECEC, and available P of UC soils and corresponding low values observed in VB soils appears to be some of the major soil chemical properties influencing biomass fractions and standing biomass to organs of rice (Table 1). Strong relationship between topography and total organic C and N had earlier been reported (Wood et al., 1990; Senthilkumar et al., 2009) and may likely be due to soil redistribution (Pennock et al., 1994). Increased biomass accumulated by the rice cultivars and fractions of biomass to various organs of rice grown in UC soils as compared with reduced biomass

and fractions of biomass observed in VB soils are based on the trend of soil nutrient availability. It has been shown that root productivity responds positively to nutrient concentration within soils as predicted by optimal partitioning theory and could vary among plant species (McCarthy & Enquist, 2007). The increased root productivity in UC and MS soils could have contributed to higher biomass observed in the rice cultivars. This is in contrast with the findings of Ontl et al. (2013) who noted non-significant influence of topography or soil properties on root productivity of annual plants.

The variations in standing biomass as well as fractions of biomass to different organs of the rice cultivars indicate differences in potential of the rice cultivars to allocate biomass to different organs. Going by the non-significant effect observed for toposequence soil by cultivar interaction (Table 2), the differences in standing biomass and fractions of biomass to organs among the rice cultivars can be concluded to be relatively similar across toposequence soils meaning that each soil along the toposequence is distinct in its influence on standing biomass and fractions of biomass among various organs of upland rice cultivars. This could as well imply that standing biomass and fractions of biomass to organs could be a reliable means of assessing biomass yield potential of upland rice under fairly contrasting soil environments.

The trend of biomass distribution among various organs of the rice cultivars grown on soil collected along the toposequence revealed the possibility of increased fractions

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of biomass to reproductive structure for rice grown on VB soil (Table 3). With higher proportion of clay and lower total N, C, ECEC and available phosphorus in soils collected down the gradient, the amount of biomass accumulated by the rice cultivars decreased coupled with increase in fractions of biomass allocated to reproductive structures (Table 1). This was revealed by higher harvest index in rice cultivars grown on valley bottom soils. It can be deduced that conditions that reduce the amount of biomass allocated to vegetative parts such as higher clay content and lower total N, C, ECEC, and available P of the soil could amount to increased fractions of biomass to the grains (less vegetative growth in VB).

There was a trade-off in grain weight per plant and standing biomass to other organs in rice grown on upper crest soil and between LDW and other standing biomass in middle slope soil under PC1 while no trade-offs in standing biomass between the organs were observed in valley bottom soil (Table 4). However, trade-offs between harvest index (HI) and fractions of biomass to other organs were consistent across the toposequence soils under PC1 while under PC2, trade-offs were between LMF, RMF and CMF, HI. Among the various fractions of biomass assessed, HI contributed most to yield increase of upland rice cultivars. This was also confirmed by the trade-offs between HI and other fractions of biomass i.e. root, culm, and leaf mass fractions as explained by the PC1. Harvest index has been considered as a measure of biological success in biomass allocation to harvestable products (Donald & Hamblin, 1976; Hay, 1995; Sinclair, 1998) and was given high priority in the identification of best genotypes (Tardieu, 2013). The fraction of biomass allocated to the reproductive part was therefore, an important trait to be explored in the identification of high yielding upland rice. The second principal component (PC2) loadings further revealed the trade-offs between CMF and HI, and other fractions of biomass implying that CMF was next to HI among organ's fractions of biomass that could be considered in the identification of high yielding cultivars. This observation confirms previous findings that amount of biomass allocated to culm contributed significantly (about 10-40%) to grain weight of rice at harvest (Gebbing & Schnyder, 1999; Takai et al., 2005) and an inverse relationship exists between these two fractions (Figure 3b).

The trade-offs between standing biomass to grain and other organs of the rice cultivars was comparable to trade-off observed between HI and fractions of biomass to other organs (Table 4). However, this was not consistent across the toposequence soils for standing biomass. This could imply that fraction of biomass allocated to reproductive parts was key in the determination of higher grain weight in upland rice cultivars at harvest and can be more important than actual biomass allocated to this organ. Atlin et al. (2008) reported that grain weight was associated with biomass production and fractions of biomass to grain (harvest index) at vegetative and reproductive stages respectively.

The highest yield observed in NERICA 2 and 15 provided information on the ability of the cultivars to produce reasonably well when grown on contrasting soil environment (Figure 3a). The potential of these two cultivars can be attributed to higher total biomass accumulated across toposequence soils coupled with increased fraction of biomass allocated to the grains. The ability of a cultivar to combine increased biomass with increased fraction of biomass to reproductive parts is therefore, a useful trait to be considered in the breeding of high yielding cultivars.

CONCLUSION

Biomass accumulated by rice and its differential distribution to other organs of the rice plant was a reliable way of estimating plant performance on different soils. Toposequence soils influenced biomass allocation into various organs similarly among upland rice cultivars with most biomass allocated to the culm. However, total biomass and yield were influenced differently by toposequence soils among the rice cultivars. Grain weight per plant is greatly influenced by fractions of biomass compared with standing biomass to organs. Fractions of biomass to other organs, especially the reproductive part, could be a more reliable estimate for identifying rice cultivars with higher yield potential at harvest. Soil environment that promotes greater allocation of biomass to reproductive structure through restriction in expansion of vegetative organs is well suited for upland rice cultivation.

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REFERENCES

Alameda, D., Anten, N. P. R., & Villar, R. (2012). Soil compaction effects on growth and root traits of tobacco depend on light, water regime and mechanical stress. *Soil and Tillage Research, 120*(April), 121–129. https://doi.org/10.1016/j.still.2011.11.013.

Atlin, G. N., Venuprasad, R., Bernier, J., Zhao, D., Virk, P., & Kumar, A. (2008). Rice germplasm development for drought-prone environments: Progress made in breeding and genetic analysis at the International Rice Research Institute (IRRI). In R. Serraj, J. Bennett & B. Hardy (Eds.), *Drought frontiers in rice: Crop improvement for increased rainfed production* (pp. 35−59). IRRI/World Scientific, Los Banos, Philippines/Singapore.

Bazzaz, F. A., & Grace, J. (1997). *Plant Resource Allocation*. USA: Academic Press.

Bengough, A. G., McKenzie, B. M., Hallett, P. D., & Valentine, T. A. (2011). Root elongation, water stress, and mechanical impedance: a review of limiting stresses and beneficial root tip traits. *Journal of Experimental Botany, 62*(1), 59–68. doi: 10.1093/jxb/erq350.

Bouyoucos, G. H. (1951). A recalibration of the hydrometer for testing mechanical analysis of soil. *Agronomy Journal, 43*(9), 434 – 438.

Callaway, R. M., DeLucia, E. H., & Schlesinger, W. H. (1994). Biomass allocation of montane and desert ponderosa pine: An analog for response to climate change. *Ecology, 75*(5), 1474–1481. https://doi.org/10.2307/1937470.

Cambardella, C. A., Moorman, T. B., Andrews, S. S., & Karlen, D. L. (2004). Watershed scale assessment of soil quality in the loess hills of southwest Iowa. *Soil and Tillage Research, 78*(2), 237–247. http://dx.doi.org/10.1016/j.still.2004.02.015.

Chaudhary, N., Narayan, R., & Sharma, D. K. (2015). Differential biomass allocation to plant organs and their allelopathic impact on the growth of crop plants: A case study on the invasibility of *Ageratum conyzoides* in Indian dry tropics. *Indian Journal of Agricultural Sciences, 85*(11), 1405–11.

Dalling, M. J. (1985). The physiological basis of nitrogen redistribution during filling in cereals. In J. E. Harper, L. E. Schrader & H. W. Howell (Eds.), *Exploitation of physiological and genetic variability to enhance crop productivity* (pp 55–71). Rockville M.D: American Society of Plant Physiology.

Dexter, A. R. (2002). Soil structure: the key to soil function. In M. Pagliai & R. Jones (Eds.), *Sustainable Land Management-Environmental Protection, A Soil Physical Approach* (pp 57-70). IUSS.

Donald, C. M., & Hamblin, J. (1976). The biological yield and harvest index of cereals as agronomic and plant breeding criteria. *Advances in Agronomy 28*, 361–405. doi: 10.1016/s0065-2113(08)60559-3

Gebbing, T., & Schnyder, H. (1999). Pre-anthesis reserve utilization for protein and carbohydrate synthesis in grains of wheat. *Plant Physiology, 121*(3), 871–878. http://dx.doi.org/10.1104/pp.121.3.871

Giménez, D. J., Karmon, A. P., & Shaw, R. (2002). Fractal dimensions of mass estimated from intact and eroded soil aggregates. *Soil and Tillage. Research, 64*(1), 165-172. http://dx.doi.org/10.1016/S0167-1987(01)00253-7.

Gomez, K. A., & Gomez, A. A. (1982). Statistical *Procedures for Agricultural Research* (pp. 306-308). Los Banos, Philippines.

Grigg, A. M., Lambers, H., & Veneklaas, E. J. (2010). Changes in water relations for *Acacia ancistrocarpa* on natural and mine-rehabilitation sites in response to an experimental wetting pulse in the Great Sandy Desert. *Plant and Soil, 326*(1-2), 75–96. http://doi: 10.1007/s11104-009-9957-5.

Hay, R. K. M. (1995). Harvest index: a review of its use in plant breeding and crop physiology. *Annals of Applied Biology 126*(1), 197–216. doi: 10.1111/j.1744-7348. 1995.tb05015. x.

Hodge, A., Berta, G., Doussan, C., Merchan, F., & Crespi, M. (2009). Plant root growth, architecture and function. *Plant and Soil, 321*(1-2), 153–187. doi:10.1007/s11104-009-9929-9

Kaneda, C. (2007). Breeding and dissemination efforts of 'NERICA', 1: Breeding of upland rice. *Japanese Journal of Tropical Agriculture, 51*(4), 1–4.

Keith, C. C., & Buchan, G. D. (2002). Porosity and pore size distribution. In Lal, R. (Ed.), *Encyclopedia of Soil Science* (pp. 1350-1353). USA: Marcel Dekker, Inc.

Kobaissi, A. N., Kanso, A. A., Kanbar, H. J., & Kazpard, V. A. (2013). Morpho-physiological changes caused by soil compaction and irrigation on *Zea* mays. *Eurasian Journal of Soil Science, 2*(2), 114 – 121. doi:10.18393/EJSS.36878

Kumordzi, B. B., Gundale, M. J., Nilsson, M. C., & Wardle, D. A. (2016). Shifts in Aboveground Biomass Allocation Patterns of Dominant Shrub Species across a Strong Environmental Gradient. *PLOS ONE, 11*(6), e0157136. doi: 10.1371/journal.pone.0157136.

Manneh, B., & Ndjiondjop, M. N. (2008). Drought screening of upland NERICA varieties. In E. A. Somado, R. G. Guei & S. O. Keya (Eds.), NERICA: *The new rice for Africa – A compendium* (pp. 62–64). Cotonou, Rome, Tokyo: Africa Rice Center, FAO, Sasakawa Africa Association.

Mccarthy, M. C., & Enquist, B. J. (2007). Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation. *Functional Ecology, 21*(4), 713–720. doi: 10.1111/j.1365-2435.2007. 01276.x

Niklas, K. J. (1994). *Plant allometry: The scaling of forms and process.* University of Chicago Press, Chicago.

Ontl, T. A., Hofmockel, K. S., Cambardella, C. A., Schulte, L. A., & Kolka, K. A. (2013). Topographic and soil influences on root productivity of three bioenergy cropping systems. *New Phytologist, 199*(3), 727–737. doi: 10.1111/nph.12302.

Payne, R. W., Murray, D. A., Harding, S. A., Baird, D. B., & Soutar, D. M. (2009). *GenStat for Windows* (12th Ed.) *Introduction*. VSN International, Hemel Hempstead.

Pennock, D. J., Anderson, D. W., & de Jong, E. (1994). Landscape scale changes in indicators of soil quality due to cultivation in Saskatchewan, Canada. *Geoderma 64*(1-2), 1–19. doi: 10.1016/0016-7061(94)90086-8.

Pichancourt, J. B., & van Klinken, R. D. (2012). Phenotypic plasticity influences the size, shape and dynamics of the geographic distribution of an invasive plant. *PLOS ONE, 7*(2), e32323. http://dx.doi.org/10.1371/journal.pone.0032323

Poorter, H., & Nagel, O. (2000). The role of biomass allocation in the growth response of plants to different levels of light, CO_2, nutrients and water: a quantitative review. *Australian Journal of Plant Physiology, 27*(12), 595–607. doi: 10.1071/pp99173

Poorter, H., Niklas, K. J., Reich, P. B., Oleksyn, J., Poot, P., & Mommer, L. (2012). Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytologist, 193*(1), 30-50. doi:10.1111/j.1469-8137.2011. 03952.x

Poot, P., & Lambers, H. (2003). Are trade-offs in allocation pattern and root morphology related to species abundance? A congeneric comparison between rare and common species in the south-western Australian flora. *Journal of Ecology, 91*(1), 58–67. doi/10.1046/j.1365-2745.2003. 00738.x

Reich, P. B. (2002). Root–shoot relations: optimality in acclimation and adaptation or the. 'Emperor's New Clothes'? In Y. Waisel, E. Amram & U. Kafkafi (Eds.), *Plant Roots: The Hidden Half* (pp. 205–220). USA: Marcel Dekker Inc.

Roa-Fuentes, L. L., Campo, J., & Parra-Tabla, V. (2012). Plant biomass allocation across a precipitation gradient: an approach to seasonally dry tropical forest at Yucatán, Mexico. *Ecosystems, 1*5(8), 1234–44. doi:10.1007/s10021-012-9578-3.

Semagn, K., Ndjiondjopd, M. N., & Cissoko, M. (2006). Microsatellites and agronomic traits for assessing genetic relationships among 18 New Rice for Africa (NERICA*) varieties. African* Journal of Biotechnology, 5(10), 800–810.

Senthilkumar, S., Kravchenko, A. N., & Robertson, G. P. (2009). Topography influences management system effects on total soil carbon and nitrogen. *Soil Science Society of America Journal, 7*3(6), 2059–2067. doi:10.2136/sssaj2008.0392

Sinclair, T. R. (1998). Historical changes in harvest index and crop nitrogen accumulation. *Crop Science, 38*(3), 638–643. doi: 10.2135/cropsci1998.0011183X003800030002x.

Sultan, S. E. (2001). Phenotypic plasticity for fitness components in Polygonum species of contrasting ecological breadth. *Ecology, 82*(2), 328–343. doi: 10.1890/0012-9658(2001)082[0328:ppffci]2.0.co;2

Takai, T., Fukuta, Y., Shirawa, T., & Horie, T. (2005). Time-related mapping of quantitative trait loci controlling grain-filling in rice (*Oryza sativa* L). *Journal of Experimental Botany, 5*6(418), 2107–2118. doi: 10.1093/jxb/eri209.

Tardieu, F. (2013). Plant response to environmental conditions: assessing potential production, water demand, and negative effects of water deficit. *Frontiers in Physiology, 4*(1), 1-11. doi: 10.3389/fphys.2013.00017

Wainaina, C. M., Inukai, Y., Masinde, P. W., Ateka, E. M., Murage, H., Kano-Nakata, M., & Makihara, D. (2015). Evaluation of cold tolerance in NERICAs compared with Japanese standard rice varieties at the reproductive stage. *Journal of Agronomy and Crop Science 201*(6), 461–472. doi/10.1111/jac.12125.

Walkley, A., & Black, C. A. (1934). An examination of the Degtjareff method for determining soil organic matter and a proposed modification of the chromic acid titration method. *Soil Science, 37*(1), 29-38.

Wood, C. W., Westfall, D. G., Peterson, G. A., & Burke, I. C. (1990). Impacts of cropping intensity on carbon and nitrogen mineralization under no-till dryland agroecosystems. *Agronomy Journal, 82*(6), 1115–1120. doi: 10.2134/agronj1990.00021962008200060018x.

Xie, Q., Mayes, S., & Sparkes, D. L. (2016). Pre-anthesis biomass accumulation of plant and plant organs defines yield components in wheat. *European Journal of Agronomy, 81*, 15–26. http://dx.doi.org/10.1016/j.eja.2016.08.007.

Yoshida, S. (1981). *Fundamentals of rice crop science.* Los Banos Philippines: International Rice Research Institute (IRRI).

Zhang, H., Wang, K., Xu, X., Song, T., Xu, Y., & Zeng, F. (2015). Biogeographical patterns of biomass allocation in leaves, stems, and roots in China's forests. *Scientific reports, 5*, 15997-16008. doi: 10.1038/srep15997.