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Composition of weed communities in seasonally flooded rice environments in East Africa is determined by altitude

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Abstract

Weeds are major biotic constraints to rice production worldwide. Compared to other sub-regions, weed communities of rice are not well described for East Africa and there is limited information on environmental factors affecting the distribution of species. This study aimed to address these knowledge gaps. Seasonally flooded rice production fields of 31 sites in Rwanda, Tanzania, Kenya and Uganda, across three altitude classes (Low: <200 m; Medium 200-1,000 m; High: >1,000 m), were surveyed for weed species using quadrats. Data analyses involved multivariate approaches, non-parametric Kruskal–Wallis tests and logistic regressions, followed by calculation of ranked species abundance and Shannon Weiner Index diversity analyses. A total of 286 weed species, belonging to 59 families, were recorded with 42 species not previously reported as lowland rice weed in the sub-region. Twenty-four species were identified as abundant across altitudes. Weed species diversity was higher at medium altitudes compared to high and low altitudes. Significant patterns of floristic distinction between altitudinal classes were observed, with 80% of dissimilarity. The high altitude was dominated by *Echinochloa colona*, *Leptochloa squarrosa* and *Sphaeranthus suaveolens,* the medium altitude was dominated by *Crassula granvikii*, *Pycreus lanceolatus* and *Ageratum conyzoides* while the low altitude was dominated by *E. colona, Cyperus difformis* and *Cyperus esculentus*. The weed species composition of seasonally flooded rice fields in East Africa is diverse. Identification of a limited group of (24) commonly abundant weed species as well as the articulation of altitude-specific weed species groups will facilitate the development of better tailored weed control programmes.

Keywords

Oryza sativa L., weed abundance, indicator species, Rwanda, Tanzania, Uganda, Kenya

Introduction

Rice is an increasingly important staple food in Africa (Seck et al., 2012). In 2013, the total area under rice in Africa was estimated at nearly 10 million ha, of which 61% in West and 26% in East Africa (Diagne et al., 2013). It is primarily grown in three types of environment, conventionally classified as irrigated lowland, rainfed lowland and rainfed upland. The classification in lowland and upland is not referring to the altitude of the production site, but rather to their soil and water characteristics. Upland rice fields have freely draining soils that are rarely flooded while lowland fields have waterlogged soils that are subject to controlled (irrigated lowlands) or uncontrolled (rainfed lowlands) seasonal flooding. In East Africa 55% of the area under rice is characterised as rainfed lowland, and 27% as irrigated lowland (Nhamo et al., 2014). Compared to West Africa a relatively large share of these production areas is located on higher altitudes, between 700 and 1,600 m a.s.l. (Balasubramanian et al., 2007).

Among the biological constraints to rice production, competition from weeds is the most important (Seck et al., 2012). Across rice systems in Africa weeds have been conservatively estimated to cause US $1.4 billion worth of produce losses annually (Rodenburg and Johnson, 2009), of which parasitic weeds may be responsible for US $200 million (Rodenburg et al., 2016a). At the field level, weed-inflicted yield losses despite control efforts have been estimated at 15% in irrigated and 23% in rainfed lowlands (Becker et al., 2003; Becker and Johnson, 2001a, 2001b) and weed-inflicted yield loss abatements by frequent weeding interventions were estimated at 1.5 t ha^{-1} in rainfed lowland and 2 t ha^{-1} in irrigated lowland rice (Rodenburg et al., 2019). African smallholder rice farmers are however often limited by poor access to the necessary resources, technologies, markets and information that would enable them to implement effective control to prevent such weed-inflicted yield losses (Rodenburg et al., 2019). One of the requirements for effective weed control strategies is knowledge about the species composition of the targeted weed vegetation. Compared to other important rice production areas worldwide, the available information about weed species in rice in East Africa is fragmentary at best and therefore a thorough inventory is required. A survey in this region, where rice is grown at a wide range of altitudes, also enables the analysis of an elevation effect on weed species distribution.

There are two, non-exclusive, overarching factors influencing the distribution of weed species in arable agriculture. Climatic and edaphic properties determine the occurrence and distribution of weed species (Pinke et al., 2012, 2010). Topographical variables such as slope, altitude, longitude and latitude further influence the plant diversity and community composition (Hanzlik and Gerowitt, 2011; Lososová et al., 2004; Nowak et al., 2016). Human interventions—through different agronomic practices, including the use of herbicides, tillage, crop rotations and organic or inorganic fertilisers— affect presence and abundance of species in the weed community (Fried et al., 2008; José-María et al., 2011; Lim et al., 2015; Pinke et al., 2014). For rice in Africa previous studies assessed effects of flooding depth and duration (Kent and Johnson, 2001) or water management and crop diversification (Kent and Johnson, 2001) on weed species composition. Information concerning the distribution of rice weed species along an altitudinal gradient is lacking. If weed species groups could be established according to relatively simple environmental criteria, tailored and more effective weed management strategies could be developed for smallholder farmers.

The objectives of the current study are therefore to (1) assess the current composition of weed species in lowland rice fields in East Africa, and (2) determine whether species composition and abundance in East Africa is influenced by altitude, allowing weed species grouping to facilitate the development of better tailored weed control programmes.

Material and Methods

Study sites

A survey was conducted between October 2010 and November 2013 in 31 lowland rice production sites in Rwanda, Tanzania, Kenya and Uganda (Table 1; Figure 1). Along an altitudinal gradient ranging from 4 to 1,596 m above sea level, from sites located between -10.92 and 2.20 latitude and 29.74 and 40.19 longitude, weed vegetation was sampled (Table 1). The schemes were grouped in three altitudinal classes: Low (<200 m a.s.l.), Medium (200 – 1,000 m a.s.l.) and High (>1,000 m a.s.l.). All surveyed fields in our study area were categorised as flooded rice as they were subject to season-long flooding, with water management ranging from fully controlled (irrigated) to uncontrolled (rainfed).

The seasonal flooded rice environments across East Africa includes schemes of Doho and Olweni (Uganda), Tana Delta (Kenya), Ifakara, Wami, Kilasilo, Namatuyi, Makondoni A, Mkula, Namtumbo, Mabogini, Igurusi, Chauru-Ruvu, Jica-Bagamoyo, Songea, Iringa, Kyela and Zanzibar (Tanzania), Rusuli, Rwasave, Cyili, Cyaruhogo, Rwabikwano and Rwabutazi (Rwanda). Information about seasonal flooded rice environments per country and altitude class in East Africa are presented in the Table 1 and Figure 1. The annual average temperature in the study sites at low and medium altitude ranged between 20° C and 34° C.

In the highlands (>1,000 m a.s.l.) the annual temperature ranged between 10° C and 30° C. Except for rice production sites located in coastal regions in Kenya (e.g. Garsen-Tana Delta Irrigation Project) and Tanzania (e.g. Pwani-Bagamoyo and Pwani-Chauru/Ruvu), flooded rice is commonly produced on foot slopes and flood plains on hydromorphic soils (Moormann and van Breemen, 1978; Nawaz, 2010). The cultivated rice species in the study sites was *Oryza sativa* L., commonly known as Asian rice.

Sampling methods and species identification

Rice production sites were visited between 60 and 120 days after planting. In each site, one field was randomly selected. Quadrats of 1 m^2 were thrown randomly in each rice field for weed sampling. The number of quadrats varied between three and ten per rice field, depending on the field size. A total of 201 quadrats were sampled. To enable a fair comparison across altitudes, we only used a random sub-sample of three quadrats from each rice scheme for statistical analyses, hence 93 quadrats in total. All 201 quadrats were however considered to construct the list of weed species presented in the Supplementary Information section (S1).

Identification and recording of weed species were done alongside an estimation of their soil cover inside each quadrat. Coverage is the percentage of the surface area of the sample plot covered by a given species, and not normally limited by the size or distribution of individuals (Floyd and Anderson, 1987)). It is scored based on a cover-abundance-dominance scale estimated as the vertical projection of vegetation on the ground (Daubenmire, 1968). Plant soil coverage of each species was visually scored using a scale from one to five: 1 = 0-10% coverage, 2 = 10-30%, 3 = 30-60%, 4 = 60-80%, 5 = 80-100% (Savary and Castilla, 2009). In the current study, the species abundance refers to the percentage of coverage of each species calculated from the cover-abundance-dominance scale of species to each altitude class. Species were grouped into one of the three taxonomic categories (i.e. monocotyledons, dicotyledons and ferns), into one of the five life-cycle groups (i.e. annuals, short-lived perennials/bi-annuals, perennials, parasitic and unknown and into three photosynthesis pathways (C_3, C_4 and CAM); Supplementary Information S1). Identification of species was done with the help of field guides (Agyakwa and Akobundu, 1987; Ivens, 1967; Johnson, 1997), regional flora (Beentje, 2000; Gillett, 2017; Gillett et al., 1971; Haines and Lye, 1983; Troupin, 1982-1988; Whitehouse and Gardens, 2001) and the AFROweeds identification tool (Rodenburg et al., 2016b). All weed species that could not be identified immediately in the field were collected for later determination at the National Herbarium of Rwanda (NHR), University of Dar es Salaam (UDSM) and Eastern African Herbarium (EA) of the National Museum of Kenya. Taxonomy and nomenclature of the plant names followed that of the Plant List Data Base (2010). Registration of altitude (m), longitude and latitude (expressed in the Universal Transverse Mercator coordinate system; UTM) were recorded using a GPS device (eTrex Legend ®; GARMIN International Inc., USA).

Grouping of species according to their photosynthesis pathway was done following information published by Tieszen et al. (1979) and Hesla et al. (1982), for grasses and sedges families of East Africa, and additional sources for weed species of other families (i.e. (Barnes et al., 1983; Bruhl and Wilson, 2007; Cabido et al., 1997; Cavagnaro, 1988; Ehleringer et al., 1987; Ellery et al., 1992; Elmore and Paul, 1983; Hnatiuk, 1980; Kalapos, 1991; Kalapos et al., 1997; Keeley and Rundel, 2003; Krenzer et al., 1975; Kuoh and Chiang, 1991; Li et al., 2009; Prendergast and Hattersley, 1987; Sage et al., 2007; Sikolia et al., 2009; Stowe and Teeri, 1978; Vogel et al., 1986; Wang, 2003; Wentworth, 1985).

Data analysis

The relationship between weed vegetation and altitude were analysed using multivariate statistical ordination and classification techniques previously used for similar purposes (Hanzlik and Gerowitt, 2016). For data analyses and presentation purposes, scientific names of weed species were replaced by their respective five-character EPPO codes (European and Mediterranean Plant Protection Organization; Supplementary Information S1). Prior to data analysis, species scored on the abundance-dominance scale (220 weed species from 93 quadrats) in the main matrix were not transformed for preservation of original information, whereas topographic descriptors in the second matrix were relativized by standard deviate (column). This transformation represents each transformed value as number of standard deviations that it differs from the mean and considered very useful for environmental variables, putting them on the same footing.

First a Nonmetric Multidimensional Scaling (NMS; Kruskal, 1964) was done of the 93 quadrats by general patterns of all weed species using 'Medium' autopilot mode as setting, Kruskal's first approach for non-penalization for ties in the distance matrix and using the Euclidean distance method (McCune et al., 2002). NMS was selected because it does not require normality or linearity assumptions. We then correlated the topographic descriptors (altitude, longitude and latitude) with the NMS axes in the three dimensions that yielded a stable solution to our data set. Finally, the first axis of the NMS reflecting the principal dimension of the variation (showed a moderate positive correlation to altitude, $r = 0.55$) was examined as a proxy for altitude influencing weed vegetation. We tested whether the scores of the first axis of the NMS differed between altitudinal classes—hence have consistent weed vegetation according to altitude. Prior to the analysis of variance (ANOVA), Levene's test was used to assess whether the homogeneity of variance (homoskedasticity) assumption was met. As this assumption was not satisfied (with P<0.05, indicating variances are not equal and further parametric tests such as ANOVA are not suited), the non-parametric Kruskal-Wallis test was employed.

Second, to identify the indicators species at each altitudinal class, an Indicator Species Analysis (ISA; Dufrêne and Legendre, 1997) was performed. A Monte Carlo test with 1,000 randomization runs evaluated statistical significance of Indicator Values (IV) at a P<0.05 cut-off threshold. Indicator values (IV) are measures of faithfulness (closeness) of occurrence of a species in a particular group and ranges from zero (no indication) to 100 (perfect indication). The objective was to determine which species were characteristic of each altitude class. Names of three weed species with the highest IV were used to name vegetation type of each altitude class.

Third, to test the null hypothesis of no difference in community species composition between elevational classes, we performed the analysis of similarities (ANOSIM) through a one-way ANOSIM test (9999 permutations) of weed vegetation based on Euclidean distance where an R-value close to 1 indicates strongly dissimilar vegetation groups, and an R-value close to zero indicates that vegetation groups are barely distinguishable (Clarke, 1993). Next, a Similarity Percentages (SIMPER; Clarke, 1993) analysis concentrated on Euclidean distance (9999 permutations) was done to identify those species that contributed most to the observed altitude class distinction in community species composition. A threshold of 50% for cumulative percentage was chosen to identify abundant species with the highest dissimilarity contribution as good discriminators for comparison (Clarke, 1993) between altitudes.

Finally, after identifying abundant species that contributed most consistently to differences between altitudes, calculation of percentage abundance of each of those 24 species follows as mean coverage. A cut-off (superior to 4%) was chosen as threshold for dominant (or most abundant) species to each altitude class. In addition, five weed species with total high abundance values per country and rice production site between altitude classes were calculated as:

*% Coverage of spp. A = (# of quadrats cover class 1 * 5.5%) + (# of quadrats cover class 2 * 20%) + (# of quadrats cover class 3 * 45%) + (# of quadrats cover class 4 * 70%) + (# of quadrats cover class 5 * 90%) ÷ total number of quadrats* (1)

*% Mean coverage of ssp A = % Weed coverage of spp A * 100 ÷ ∑ of % Weed coverage for all species* (2)

Diversity of weed species was evaluated using Shannon Weiner Index (*H'*) (Shannon and Weaver, 1949):

$$H' = -\sum_{i=1}^{S}(P_i)(\ln P_i) \quad (3)$$

where Pi is the proportion of all observations in the i^{th} species, Ln = $\mathrm{logbase}_n$ and S is the total number of species within each altitude class or species richness. The minimum value of H' is zero —a value representing a community with a single species— and this increases as species richness and evenness increases.

In order to determine if species abundance correlated with altitude, a simple Mantel test (Mantel, 1967) using asymptotic approximation method was employed. Euclidean distance matrix was calculated both for species abundance data, and for altitude.

In order to investigate whether the occurrence of weed species could be explained by altitudinal gradient or photosynthesis pathway, a logistic regression model was fitted to our data, with occurrence (absent or present) as response variable and photosynthesis pathway and altitude variables as predictors. This relationship was examined at $P<0.05$ significance level.

The NMS, ISA and Mantel test were performed using MjM software design, PC-ORD program Version 6 (McCune and Mefford, 2011), while Kruskal-Wallis test, Levene's test, ANOSIM and SIMPER were performed using the PAleontological STatistics (PAST) software version 3.20 (Hammer et al., 2001). The logistic regressions using a logit link function "glm (formula = Occurrence~ PP + Altitude, family = binomial (link = "logit") data = dat.new)" were performed in the statistical software R version 3.6.3 (R Core Team, 2020).

Results

In the 93 quadrats used for the statistical analyses, 220 different weed species were observed. The NMS ordination shows a three-dimensional (3 axes) representation as best solution for our dataset (93 quadrats by 220 species) with a final stress value of 17.74. A final stress value between 10 and 20 is generally considered to be good and reliable when the NMS technique is applied to ecological community datasets (McCune et al., 2002). Proportions of variance represented by the three dimensions were 32.5%, 30.1% and 20.5% respectively (cumulative r = 83.2%). Only the graph presenting principal dimensions (NMS 1 and NMS 2 axes) with a high proportion variation of the altitude variable as joint plot is shown (Figure 2). The Monte Carlo test suggested a significant separation of weed vegetation across altitude (P=0.0196). The Kruskal-Wallis test, performed on the first NMS axis reflecting the principal ordination, showed a significant pattern of weed vegetation between altitude classes (H = 26.34, Hc = 26.34, n_{High} = 33, n_{Medium} = 30, n_{Low} = 30, $P<0.0001$) suggesting an important role of altitude in the variation of weed vegetation.

In the complete set of quadrats (201), a total of 286 weedy species were recorded, belonging to 156 genera and 59 families, with 127 monocotyledonous, 151 dicotyledonous and eight fern species (Supplementary Information S1). The Cyperaceae, Poaceae and Asteraceae were the most important families in terms of weed species numbers across altitudes. The Cyperaceae was the prevalent plant family at high and medium altitudes (23 and 26 species, respectively) whereas at low altitude the Poaceae family was most common (19 species). The Fabaceae, Commelinaceae and Onagraceae were also well represented across elevations (Table 2). The Shannon-Weiner index diversity (H') of weed species suggested that the medium altitudes had a higher diversity than the high and low altitudes. The high altitude, in turn, recorded greater diversity than the low altitude (Table 2).

The analysis of similarity (ANOSIM) in community species composition performed between altitude classes revealed significant differences (Global R_{ANOSIM}=0.1321; n_{High}=33; n_{Medium}=30; n_{Low}=30; $P<0.0001$; Supplementary Information S3c), with complete dissimilarity (SIMPER) of 80%. The high and low altitudes differ in species composition by a dissimilarity of 81% (R=0.165). Lowest floristic difference was observed between medium and low altitudes with a dissimilarity of 71% (R=0.116). The largest floristic difference was observed between high and medium altitudes with a dissimilarity of 89% (R=0.123) (Supplementary Information S3b). The high dissimilarity in species composition between altitude classes was mostly caused by 24 species that had a cumulative contribution of 50% (Supplementary Information S3a,c), reflecting the overall differences in community composition (i.e. *Crassula granvikii* Mildbr., *Echinochloa colona* L. (Link), *Leptochloa squarrosa* Pilg., *Eleocharis atropurpurea* (Retz.) J.Presl & C.Presl, *Crepidorhopalon hepperi* Eb.Fisch., *Sphaeranthus suaveolens* (Forssk.) DC., *Pycreus lanceolatus* C.B.Clarke, *Ageratum conyzoides* L., *Sacciolepis africana* C.E.Hubb. & Snowden, *Leersia hexandra* Swa, *Ludwigia adcendens* (L.) H.Hara, *Courtoisina assimilis* (Steud.) Maquet., *Pycreus* *flavescens* (L.) P.Beauv. ex Rchb., *Cyperus dichrostachyus* Hochst. ex A.Rich, *Ammannia auriculata* Wild., *Basilichum polystachion* (L.) Moench., *Cyperus* sp., *Fimbristylis littoralis* Gaudich., *Acmella uliginosa* (Sw.) Cass., *Cyperus difformis* L., *Cyperus esculentus* L., *Cyperus rotundus* L., *Marsilea crenata* C.Presl and *Kyllinga polyphylla* Willd. ex Kunth). The Mantel test showed a positive weak correlation between species abundance and altitude (t=0.49; r=0.15; $P<0.0001$). Most important weed species per country and rice production site between altitude classes are presented in the Supplementary Information section (Supplementary Information S4).

The logistic regression model indicates that altitude has significant influence ($P<0.05$) on occurrence of photosynthesis pathways at medium altitudes but not at high and low altitudes (Supplementary Information S5). Generally, the prepotency of the C_3 pathway dominated the flooded rice fields in East Africa. In medium altitudes, 66.9% of C_3 pathway were mostly represented by Cyperaceae, Asteraceae, Fabaceae, Malvaceae and Amaranthaceae, whereas 32.4% of C_4 pathway were mostly represented by Poaceae and Cyperaceae. The high and low altitudes were also dominated by C_3 pathway (72% and 66.7%, respectively) mostly represented by the family of Cyperaceae, Poaceae, Commelinaceae and Asteraceae. The proportion of species with the C_4 pathway increased at low altitudes (33.3%) compared to high and medium altitudes (Figure 3, Supplementary Information S5).

We identified 34 indicator species ($P<0.05$, Table 3): 16 species at high altitudes, 10 at medium altitudes and eight at low altitudes, reflecting significant indicators species with strong closeness/description to each altitude classes. Based on indicator species with a high Indicator Value (IV), the following species groups were distinguished for each altitude:

(1) The ***Sacciolepis africana* - *Cyperus* sp. - *Sphaeranthus suaveolens*** group (High-altitude; > 1,000 m a.s.l.) was dominated by six species: *E. colona*, *L. squarrosa*, *S. suaveolens*, *S. africana, E. atropurpurea* and *C. hepperi* (Supplementary Information S3d). Indicator species associated to this altitude were: *S. africana*, *Cyperus* sp., *S. suaveolens, Marsilea minuta* L., *L. adscendens*, *L. hexandra, Ammania auriculata, Azolla pinnata* subsp. *africana* Desv. R.M.K. Saunders & Fowler, *C. assilis, Pycreus niger* (Ruiz & Pav.) Cufod., *Hydrocotyle ranunculoides* L.f., *L. squarrosa, Acmella caulirhiza* Delile, *C. dichostachyus* and *Persicaria pulchra* (Blume) Soják (Table 3). Annual weed species were more frequently encountered than any other life cycle category. One parasitic weed species was observed: the facultative hemi-parasite *Rhamphicarpa fistulosa* (Hochst.) Benth. (Supplementary Information S2).

(2) The ***Crassula granvikii - Euphorbia hirta - Lipocarpha chinensis*** group (Medium-altitude; 200 - 1,000 m a.s.l) was dominated by three species: *C. granvikii, P. lanceolata* and *A. conyzoides* (Supplementary Information S3d). The indicator species were: *C. granvikii, Euphorbia hirta* L.*, Lipocarpha chinensis* (Osbeck) T.Tang & F.T.Wang*, M. crenata, Cyperus haspan* L.*, Fuirena angolensis* (C.B.Clarke) Lye ex J.Raynal & Roessler*, Spilanthes costata* Benth., *Thelypteris totta* var. *longipinna* (C.Chr.) C.V.Morton, *Acmella radicans* (Jacq.) R.K.Jansen and *Cyperus iria* L. (Table 3). Annual weed species were dominating. One parasitic weed species was observed: the obligate hemi-parasite *Striga asiatica* L. (Supplementary Information S2).

(3) The ***Imperata cylindrica*.- *Phyllanthus amarus*** - ***Fimbristylis littoralis*** group (Low-altitude; < 200 m a.s.l.) was dominated by six species: *E. colona, C. difformis, Cyperus esculentus, L. hexandra, K. polyphylla* and *A. uliginosa* (Supporting Information S3d). Eight indicator species were associated to this group: *Imperata cylindrica* (L.) Raeusch*, Phyllanthus amarus* Schumach. & Thonn.*, F. littoralis, Oryza longistaminata* A.Chev.*, Mimosa pigra* L.*, Stachytarpheta jamaicensis* (L.) Vahl and *Melochia melissifolia* Benth. (Table 3). Annual species were dominating this group (Supplementary Information S2).

Discussion

Weed species diversity in rice in East Africa

This study reveals a rich species diversity of the weed flora in seasonally flooded rice fields in East Africa. Overall, the proportion of dicotyledonous contributed more to the total reported flora than monocotyledonous (53% vs 45%). Species from two monocotyledons families, the Cyperaceae and the Poaceae, were the most frequently encountered. This confirms earlier reports on weeds of rice in sub-Saharan Africa, reviewed by Rodenburg and Johnson (2009). They calculated that 43% of the observed weed species were Poaceae, and 37% were Cyperaceae. Our findings are also in agreement with reports from rice fields in Brazil (Linke et al., 2014; Mesquita et al., 2013) and rice agroecosystems in Vietnam and the Philippines (Fried et al., 2017). Species of the Poaceae (grasses) and Cyperaceae (sedges) families are more important than others in rice because they are most adapted to the wet growing conditions and because grasses and sedges are most difficult to control, due to their resemblance (both physiologically and morphologically) to rice, in particular at the early phenological stages.

Weed species diversity at medium altitudes is relatively high in comparison to high and low altitudes. High diversity at medium altitudes, could be a result from a relatively high variability in landscape, climate and soil at this elevation, which in turn cause differences in water and nutrient availability. Gabriel et al. (2005) demonstrated that environmental heterogeneity promotes the diversity of plant species. Of the 286 observed species, 42 did not feature in any previous weed inventory from this region, including some recent reports (e.g. (Makokha et al., 2017). The majority of these species even represent new rice weed observations for the African continent.

Weed abundance along the altitude gradient in flooded rice in East Africa

The current study showed that altitude was correlated with species' abundance. Along the altitude gradient the abundance of certain species (e.g. *E. colona, L. adcendens* and *S. africana*) increased with increasing elevation, whereas the abundance of other species (e.g. *C. difformis*, *F. littoralis* and *A. uliginosa*) showed an opposite trend. In this study, *E. colona* was the most abundant species in high and low altitudes. It has been considered as the most serious grass weed of rice with a wide distribution in the subtropics and tropics (Holm et al., 1977) and a wide altitude range, as it was recorded from 0 to above 2,000 m a.s.l. (Lazarides, 1980). It is also the most cited weed species of lowland rice in sub-Saharan Africa (Rodenburg and Johnson, 2009). The two broad-leaved weed species *S. suaveolens* and *C. hepperi* were observed as most abundant at high altitudes. These species have previously been described as widespread in East Africa over a range of altitudes (Ivens, 1967). The grass *L. squarrosa* reported for the first time by Makokha et al. (2017)was determined as a major weed of rice at high altitude ranges (between 1093 and 1391 m a.s.l.) in the current study, while knowledge about the species' ecology and management is largely lacking. The broad-leaved weed *C. granvikii* and the sedge weed *P. lanceolata* were among the most abundant at medium altitudes (between 721 – 1,596 m a.s.l) in this study. *Crassula granvikii* grows along permanent streams up to 3,200 m a.s.l. from Central, East and Southern Africa (Exell and Fernandes, 1960; Troupin, 1983) while *P. lanceolata* was previously reported to thrive between 750 and 1,160 m a.s.l. in East Africa (Haines and Lye, 1983). In West Africa, *P. lanceolata* was reported as a common weed of rice on hydromorphic soils (Agyakwa and Akobundu, 1987; Johnson, 1997). In this study, we also observed the sedges *C. difformis* (4 – 1,596 m a.s.l)*, K. polyphylla* (0-40 m a.s.l.) and *C. esculentus* (0- 798 m a.s.l.) among the most abundant species at low altitudes. The species *K. polyphylla* and *C. esculentus* were reported to occur along streams in the forest zone of East Africa up to 1,200 m a.s.l. and 2,000 m a.s.l., respectively (Haines and Lye, 1983) while *C. difformis* has been widely reported as a common weed of rice over a range of altitudes (e.g. Ivens, 1967). Other grasses such as *L. hexandra* and *S. africana*, considered as important perennial grasses in lowland rice production systems in Africa (Rodenburg and Johnson, 2009), were reported in the current study between 5 and 1,596 m a.s.l and between 721 and 1,596 m a.s.l, respectively. In Asia, *L. hexandra* has been reported as moderately to highly competitive in lowland rice (up to 2,200 m a.s.l.; Caton, 2010).

Altitude effects on weed species composition in flooded rice in East Africa

The present study identified the weed species of flooded rice fields in East Africa and revealed that species composition of the weed vegetation in these environments is influenced by altitude. Despite a clear distinction in terms of weed species between altitude classes, the proportion of variance between the principal dimension (first NMS) was not very high in comparison to other two dimensions, indicating other ecological or management descriptors associated with altitude are important to explain the variation of weed species. These other descriptors, such as water depth and flooding period, weed management, crop rotation, climate, soil parameters and even topographic descriptors (latitude and longitude) were not considered in this context. The results presented in this study encompass however a very useful first step allowing the development of more tailored weed management strategies along elevation gradients. Follow-up research could refine the resolution obtained in this study. For instance, within each altitude class a further weed group differentiation could be made based on weed management practices, soil properties and climate as shown before (Pinke et al., 2012). Lososová et al. (2004) and Fried et al. (2008) have shown that significant changes in weed species composition are associated with a complex gradient of altitude, precipitation, clay content, texture and pH.

This study showed that some weed species were clearly restricted to a certain altitude. Floristic composition and distribution of weeds often serve as indicators of field conditions and environments (Moody, 1989). For example, results from indicators species revealed that species such as *P. niger*, *E. atropurpurea, C. assimilis, C. dichrostachyus, L. squarrosa* and *Hydrocotyle ranunculoides* are associated to high altitude in flooded rice fields in East Africa. Other species such as *F. angolensis*, *A. radicans* and *M. crenata* were restricted to medium altitudes, while *M. melissifolia*, *Agathisanthemum bojeri* Klotzsch*, S. jamaicensis* and *K. polyphylla* were associated to low altitudes.

Finally, the present study elucidated that in terms of their photosynthesis pathway, weed species followed a certain pattern of occurrence across altitude. The distribution of weed species exhibiting the C_3 pathway was remarkably prepotent at all altitude due to wet environments describing the flooded rice fields in East Africa. The composition of C_3 weeds mostly included species able to survive in water, and even under prolonged submerged conditions, such as the annual weeds *A. uliginosa*, *A. auriculata*, *B. polystachyon, C. hepperi, Eclipta prostata* (L.) L.*, Fuirena ciliaris* (L.) Roxb.*, Ipomoea aquatica* Forssk.*, Kyllinga pumila, S. suaveolens* and *Sphenoclea zeylanica* Gaertn., the perennial weeds *L. adscendens, Fuirena umbellata* Rottb., *L. hexandra*, and the annual/perennial weeds *Commelina benghalensis* L.*, Commelina diffusa* Burm.f. and *C. haspan*. Although the objective of the current study did not focus on factors such as flooding duration and water depth, water regime may exert an important effect on the structure of weed communities even within an altitude gradient. Several studies suggested the C_3 pathway to provide a higher degree of physiological flood-tolerance than their C_4 counterparts (Carmo-Silva et al., 2008; Ghannoum, 2009; Kalapos et al., 1996). In a situation of seasonally flooded rice fields, as in our study, species with the C_3 pathway might have a competitive advantage over those with the C_4 pathway. For example, a study by Kent and Johnson (2001) indicated that continuous flooding conditions to 2 – 4 cm in 2 – 4 days every week increased density of the annual C_3 *S. zeylanica* and decreased that of annual C_4 *E. colona* and *Echinochloa crus-pavonis* (Kunth) Schultes. According to Caudle and Maricle (2012) and Maricle and Lee (2007), tolerance of plants under flooded conditions is explained from the ability to maintain photosynthetic activity, high stomatal conductance and oxygen transport to submerged tissues in order to avoid shortage of oxygen to roots. The current study also revealed that species with the C_4 pathway have a relative higher representation at low altitudes, perhaps because of associated higher temperatures, than high altitudes. The composition of C_4 pathway at low altitude included annual grasses (e.g. *Echinochloa* spp., *Brachiaria lata* (Schumach) C.E.Hubb., *Leptochloa coerulescens* Steud., *Digitaria pseudodiagonalis* Chiov. and *Ischaemum rugosum* Salisb.), perennial grasses (e.g. *I. cylindrica,* and *S. consimilis*) and broadleaved species (*Portulaca oleracaea* L., *Chromolaena odorata* (L.) R.M.King & H.Rob and *S. jamaicensis* and *Euphorbia hypericifolia* L.). Species with the C_4 pathway predominate in hot, or arid regions (Ghannoum, 2009). In rice systems, C_4 weeds have been previously suggested to favour rainfed upland conditions over lowland conditions (Rodenburg et al., 2011).

The current study represents the first large-scale survey of species of weed vegetation of flooded rice in East Africa. The 24 most abundant species are known to exert a high level of competition to flooded rice across altitudes and should be prioritised in weed management strategies. The identified altitude-specific weed grouping will also enable the development of more tailored weed management strategies.

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Author contributions

J.R. and T.L conceived the project; R.I., J.R. and D.M. designed the research; R.I. and D.M. collected data; R.I. performed statistical analyses; R.I and J.R. wrote the paper, T.L., I.M. and A.C. contributed to the manuscript writing.

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Table 1. Description of study sites in East Africa: name of country, district/region and site, altitude range (ALT), altitude classes (AC: HA=High; MA=Medium; LA=low), latitude (LAT), longitude (LON).

Country	District/region	Site name	ALT	AC	LAT	LON
Rwanda	Huye	Rusuli	1596	HA	-2.47	29.74
		Rwasave	1584		-2.57	29.76
		Cyili	1391		-2.46	29.84
	Bugesera	Rwabikwano	1387		-2.29	30.06
	Ruhango	Mukunguli	1380		-2.15	29.93
	Kirehe	Rwabutazi	1338		-2.3	30.57
	Rwamagana	Cyaruhogo	1324		-2.03	30.43
Tanzania	Mbeya/Mbalali	Igurusi/Ruandamajenje	1256		-8.84	33.84
Uganda	Butaleja	Doho	1093		0.96	34.02
	Lira	Olweni	1068		2.2	33.03
Tanzania	Songea	Makomboni A	1017		-10.66	35.54
		Mtopesi	966	MA	-10.6	35.3
		Namatuyi	927		-10.92	35.49
	Moshi	Mabogini	815		-3.39	37.37
	Iringa	Luganga	798		-7.54	35.48
		Magozi	770		-7.46	35.47
	Songea	Namtumbo - Mtonya	721		-10.38	36.12
	Kyela	Kilasilo	527		-9.59	34.31
	Dakawa	Wami	382		-8.42	37.55
	Kilombero	Mkula	302		-7.8	36.91
		TAC/Ifakara	225		-8.16	36.68
	Zanzibar (Unguja)	Kiyanga	40	LA	-6.13	39.25
	Zanzibar (Pemba)	Kimbuni	30		-5.35	39.72
Kenya	Tana Delta River	Tana Delta irrigation project	26		-2.26	40.19
Tanzania	Pwani	Chauru/Ruvu	24		-6.75	38.68
	Zanzibar (Unguja)	Mwera	23		-6.15	39.27
		Mtwango	20		-6.19	39.24
	Zanzibar (Pemba)	Mangwena	20		-5	39.77
		Kinyakuzi	17		-4.95	39.75
		Tibirinzi	5		-5.22	39.77
	Bagamoyo	Jica/Bagamoyo	4		-6.48	38.83

Table 2. Taxonomic classes (Class), proportion of important families (only the ones with more than one species are shown) and weed species diversity indices (H'= diversity index of Shannon-Weiner per altitude (HA: High Altitude, MA: Medium Altitude and LA: Low Altitude) of lowland rice fields in East Africa.

Class Family	Genera	Species	Proportion (%)
HA			
Cyperaceae	10	23	22
Poaceae	12	19	18
Asteraceae	10	12	12
Commelinaceae	4	5	5
Onagraceae	1	4	4
Ammaranthaceae	2	3	3
Fabaceae	3	3	3
Rubiaceae	2	3	3
Acanthaceae	2	2	2
Lytraceae	1	2	2
Phyllantaceae	1	2	2
Polygonaceae	1	2	2
Tiliaceae	1	2	2
Species richness			*103*
H'			*3.94*
MA			
Cyperaceae	7	26	19
Poaceae	18	25	19
Asteraceae	12	15	11
Fabaceae	10	10	7
Malvaceae	1	6	4
Ammaranthaceae	5	5	4
Rubiaceae	4	5	4
Lamiaceae	4	4	3
Onagraceae	1	4	3
Commelinaceae	1	3	2
Euphorbiaceae	1	3	2
Acanthaceae	2	2	1
Convolvulaceae	1	2	1
Lytraceae	1	2	1
Marsileaceae	1	2	1
Orobanchaceae	2	2	1
Phyllantaceae	1	2	1
Polygonaceae	1	2	1
Species richness			*135*
H'			*4.47*
LA			
Poaceae	15	19	22

Cyperaceae	5	17	20
Asteraceae	7	7	8
Commelinaceae	4	7	8
Acanthanceae	4	4	5
Euphorbiaceae	1	3	3
Fabaceae	3	3	3
Lytraceae	1	3	3
Malvaceae	2	3	3
Onagraceae	1	3	3
Rubiaceae	3	3	3
Species richness			*87*
H'			*3.91*

Table 3. Indicator species of weed species for each altitude range (HA: High altitude, MA: Medium altitude and LA: Low altitude). Indicator value (IV = 0 no indication to IV = 100 perfect indication), level of significance of the IV value is indicates with probability (p-value). Names of the three species with high indicator values in each group were used for the group name. Only indicator species with *P<0.05* are shown in the table with their standard deviation.

Species	Altitude range	IV	Mean	S.Dev	*p-value*
SAEAF	HA	46	11.1	3.35	0.001
CYPSS	HA	37	9.7	3.28	0.001
SPSSU	HA	32	14.4	3.42	0.001
MASMI	HA	31	9.5	3.36	0.001
SPLAC1	HA	30	7.6	2.84	0.001
MAPAS	HA	27	7.5	2.96	0.001
LEFSQ	HA	27	7.4	3.04	0.001
AMMAU	HA	26	7.9	2.92	0.001
LUDAD	HA	26	11.2	3.46	0.003
ELOAT	HA	24	7.1	2.92	0.001
HYDRA	HA	21	6.3	2.82	0.001
CYPNI	HA	21	6.5	2.72	0.001
LIDHE	HA	21	10.3	3.29	0.01
AZOPI	HA	15	7.9	2.9	0.013
CYPDS	HA	12	4.7	2.3	0.034
POLPV	HA	12	4.7	2.29	0.031
CSBVA	MA	24	8.9	3.35	0.003
EPHHI	MA	21	8	3	0.005
LICCH	MA	20	10.8	3.36	0.009
MASCR	MA	15	4.9	2.42	0.005
CYPHP	MA	14	6.3	2.65	0.027
FUIAN	MA	11	4.1	2.16	0.013
SPLCO	MA	11	4.2	2.22	0.02
THETT	MA	11	4	2.14	0.018
SPIRA	MA	11	4.1	2.33	0.02
CYPIR	MA	11	4.3	2.26	0.022
IMPCA	LA	43	10.8	3.36	0.001
PHYLAM	LA	34	10.4	3.34	0.001
FIMLI	LA	21	8.4	3.2	0.001
KYLPO	LA	21	6.5	2.78	0.003
ORYLO	LA	17	7	2.84	0.012
MIMPI	LA	15	5.2	2.58	0.011
STCIN	LA	12	4.8	2.48	0.046
MEOME	LA	12	4.8	2.44	0.037

Figure 1. Map indicating the geographical locations of the study areas in East Africa (Rwanda, Uganda, Tanzania and Kenya): 1, Huye-Rusuli; 2, Huye-Rwasave; 3, Huye-Cyili; 4, Bugesera-Rwabikwano; 5, Ruhango-Mukunguli; 6, Kirehe-Rwabutazi; 7, Rwamagana-Cyaruhogo; 8, Mbeya-Igurusi/Ruandamajenje; 9, Butaleja-Doho; 10, Lira-Olweni, 11, Songea-Makondini A; 12, Songea-Mtopesi; 13, Songea-Namatuyi; 14, Moshi-Mabogini; 15, Iringa-Luganga; 16, Iringa-Magozi; 17, Songea-Namtumbo/Mtonya; 18, Kyela-Kilasilo; 19, Dakawa-Wami; 20, Kilombero-Mkula; 21, Kilombero-Ifakara/TAC; 22, Zanzibar (Unguja) -Kiyanga; 23, Zanzibar (Pemba) - Kimbuni; 24, Garsen-Tana Delta Irrigation Project; 25, Pwani-Chauru/Ruvu; 26, Zanzibar (Unguja) -Mwera; 27, Zanzibar (Unguja) -Mtwango; 28, Zanzibar (Pemba) - Mangwena; 29, Zanzibar (Pemba) -Kinyakuzi, 30, Zanzibar Pemba-Tibirinzi; 31, Pwani-Bagamoyo/Jica.

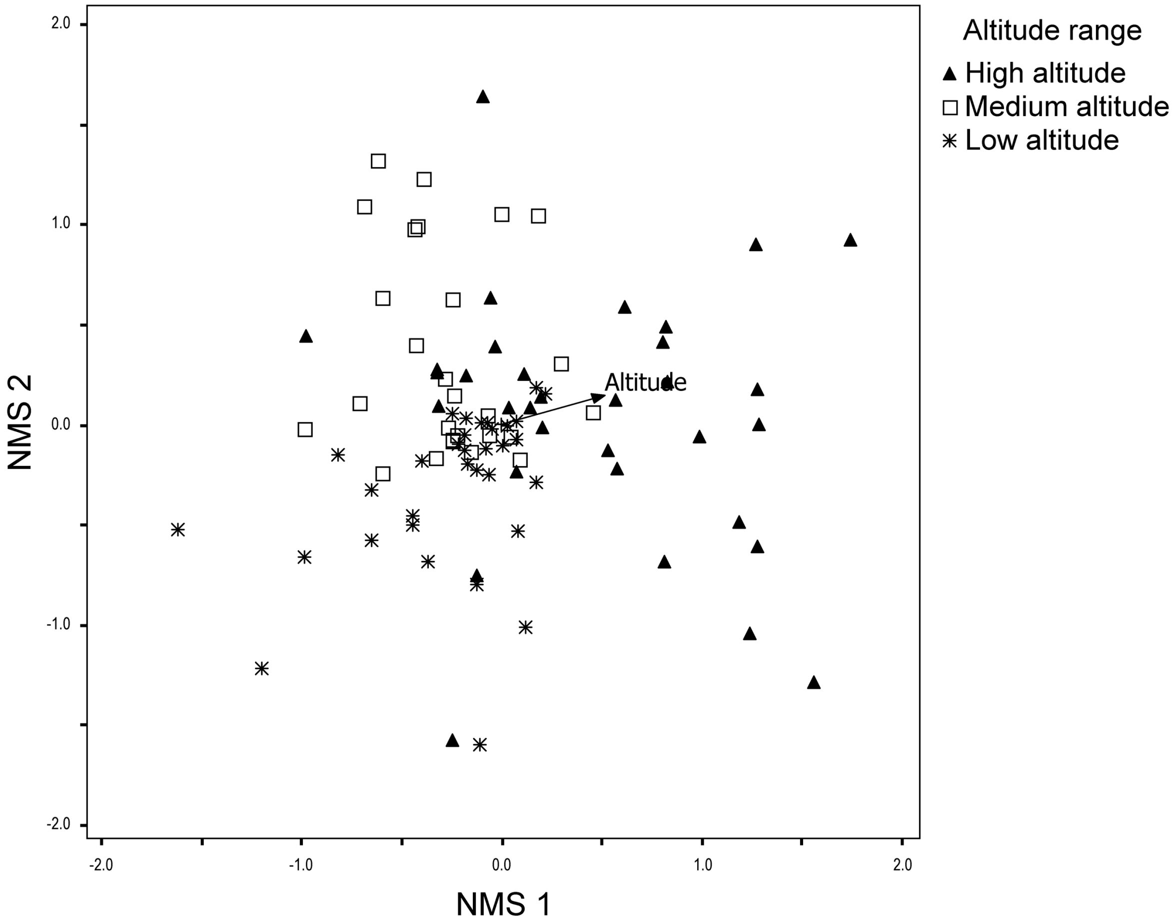

Figure 2. Nonmetric Multidimensional Scaling (NMS) ordination of abundance data from 220 species by 93 quadrats studied in East Africa showing the altitudinal gradient along the axis 1. Only graph for dimensionality (NMS1 and NMS2) with high proportion variation of altitude variable as joint plot is shown. Graphs for dimensionalities NMS1 & NMS3 and NMS2 & NMS3 are not shown.

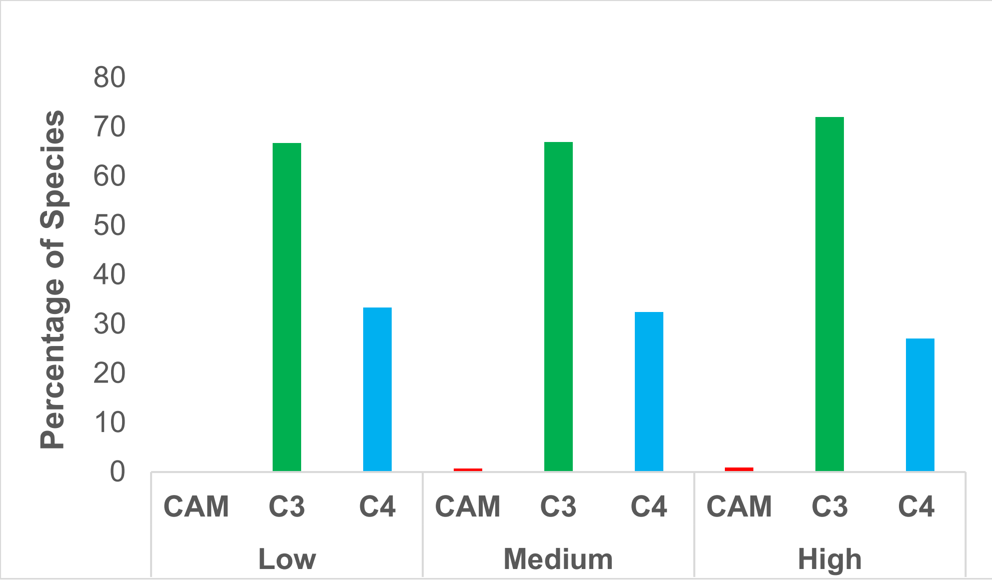

Figure 3. Frequency distribution of C_3, C_4 and CAM photosynthetic pathway (PP) of species along altitudinal gradients based on occurrence of 220 weed species, with known photosynthetic pathways, in seasonally flooded rice systems in East Africa. The data was reorganized to come up with three major variables with their corresponding categories; PP (CAM-0, C_3-1 and C_4-2), Altitude (Low-0, Medium-1 and High-2) and Occurrence (Absent-0 and Present-1). The occurrence variable was an indicator variable of the PP to show if the categories CAM, C_3 and C_4 were present or absent in the corresponding altitudes. Thus, the variable occurrence, becomes the response (dependent) variable to test for the independence of the presence of the PP categories across the three-altitude classes.