Opportunistic vascular plant introductions in agricultural wetlands of East Africa

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ABSTRACT
The impact of wetland cultivation was investigated on species introductions using species functional traits. The roles of hydric regimes were assessed on two floodplains and two inland valleys in Kenya and Tanzania. Vegetation was assessed in 224 plots, each measuring 100 m². Land use gradients were categorised as unused, grazed, fallow and cultivated. Species presence and cover were recorded in each plot. Data on species functional traits including Raunkiaer’s life form were collected both in the field and from related literature. Indicator species analysis (ISPA) was done to classify weeds relative to land use gradients. Canonical correspondence analysis (CCA) was done on soil environmental variables in relation to weeds. Of the species recorded, 78% were classified as weeds. Fallow and cropped plots had higher weed species richness compared to both unused and grazed plots (p < 0.017). Therophytes constituted 70% of total weed presences. Five indicator weed species were identified: Cynodon dactylon ((L.) Pers)) on completely drained potassium rich plots; Leersia hexandra (Sw) on wet to moist with high organic C and N; Malva parviflora (L) on cultivated inland valleys; Oxalis corniculata (L) on fallow and cultivated inland phosphorous rich maize plots within inland valleys and Typha capensis ((Rohrb.) N.E.Br.) in saline and alkaline plots. Raunkiaer’s life forms, life history and growth forms are good indicators of disturbance in wetlands. Results demonstrated that while wetland disturbance from agricultural activity eliminates native species, a regime shift acts in favour of introduced weed species.

Keywords: obligate uplands, obligate wetlands, Raunkiaer’s life form, species additions, weeds

INTRODUCTION
Population growth, infertile upland soil and erratic climatic conditions are some of the reasons behind the increasing use of wetlands in eastern Africa for agriculture (Kyle and Leishman 2009; Schuyt 2005; Wood and van Halsema 2008). Consequently, many small wetland areas have been drained for subsistence and commercial agriculture; an action that has overstretched small wetland resources in eastern Africa, and now poses a real threat to their continued existence (Dixon and Wood 2003; Harper et al. 1990). Disturbances to wetlands, especially hydro-period alteration (Harper et al. 1990) from agricultural development and human settlement, create opportunities that are well matched by opportunistic wetland plant species (Howard and Chege 2007; Zedler and Kercher 2004). This is the situation in small wetlands currently used for agriculture.
in eastern Africa; they become devoid of native plant communities, even though they can still perform limited ecological functions. The majority of these wetland areas are characterized by the presence of introduced weeds such as sedges and grasses in old fallow or abandoned plots and herbaceous plants in cultivated areas (Handa 2011). These introduced plants that invade natural areas such as wetlands sometimes threaten local native communities and reduce the diversity of native species altering an ecosystem’s function (Daehler 1998). The ecological significance of species’ diversity within an wetland ecosystem used for agriculture has recently become a popular topic for related empirical studies (Pollnac et al. 2009). The current consensus among ecologists and conservationists in eastern Africa is that degradation of wetlands from agricultural activity is promoting a loss of biodiversity (Dixon and Wood 2003; Hall et al. 2009; Harper et al. 1990). Even though tropical sedge dominated wetlands are known to be species poor in flora (Chapman et al. 2001), most wetland vegetation in East Africa plays an important role as a habitat for fauna such as migratory water birds (Maclean et al. 2006). However, the fact that permanent wetlands are species poor makes them vulnerable to new species additions especially when a hydrological regime is altered (Van der Valk 1981; Zedler and Kercher 2004). The introduction of new species is what we call invisibility, the term describes the susceptibility of an environment and in this particular case a wetland environment to the colonization and establishment of individuals from species not currently part of the resident community (Davis et al. 2005). Traditionally, more diverse communities are less susceptible to invasion than species-poor communities (Lodge 1993). However, there is a widespread assumption that landscape modification such as wetland drainage can only lead to elimination, reduction or local extinction of species, thus promoting invasibility. On a global scale for example, there is a direct relationship between species decline and anthropogenic related stress on natural ecosystems (Perrings et al. 2010). Little research has focused on species additions due to landscape modification and ecological regime shifts arising from anthropogenic activities such as wetland agriculture in eastern Africa. Species gains have been observed especially at regional and local levels as range-expanding habitat generalists invade these disturbed environments (Hobbs and Mooney 1998). Such weeds invade new species’ pools, typically at the expense of rare and often endemic, native species that disappear (Hobbs and Mooney 1998; Rooney et al. 2007). This element of species additions in a modified landscape could at times be greater than losses, which might result in significant effects on ecosystems and some of the biotic components that they invade (Hobbs and Mooney 1998). In oceanic islands for example, the number of naturalizations has increased dramatically for vascular plants, with numbers of naturalizations greatly exceeding those of extinctions (Sax et al. 2007). The risk is that the impact of some of these introduced species (e.g. invasive species) may be irreversible if not detected well in advance (Doren et al. 2009; Gordon 1998). Despite the well known impact of non-native plants on ecosystems (Gordon 1998), their adaptive capabilities, especially in transition ecosystems such as wetlands, have not yet been well researched and remain little understood. Over time, these exotic species may alter a wetland ecosystem because of their ability to self rejuvenate and establish resilience. Understanding trends in the spread and density of weeds and exotic species, including the impact of control and
management activity, is therefore necessary to manage affective restorative strategies of affected ecosystems (Hulme 2006; Zedler and Kercher 2004).

Studying composition of weed species alone may not be adequate to understanding those ecosystems experiencing frequent perturbations (Richardson et al. 2007). One of the simplest yet underutilized tools is the use of plant functional traits (PFTs). PFTs are morphological, physiological or phenological traits that reflect plant performance. The study of PFTs may assist in making predictions relating to the dynamics of ecosystems such as wetlands (Violle et al. 2007). PFTs are important ecological tools as they provide an indication of a plant community’s response to variations in ecosystem attributes and processes that is largely independent of a taxonomic bias (Kyle and Leishman 2009). PFTs for example have been used in the past as a tool for the restoration and rehabilitation of ecosystems such as degraded wetlands (Kyle and Leishman 2009). Another advantage of the using PFTs is that they have also been extensively used to predict the invasiveness of species and the invasibility of habitats in the past (Pyšek and Richardson 2007; Richardson et al. 2007) and can thus be replicated in a wide geographical range. They have also been used to gauge ecological processes and to examine impacts of fire and grazing on plant communities (McIntyre et al. 1995). For instance there is a relationship between soil disturbed sites and spectrums of life-histories (McIntyre et al. 1995). The most common PFT used to classify species in relation to human disturbance has been growth or life form, as this trait tends to correlate with other physiological and morphological traits. Most of these life form traits respond differently to disturbance levels. In this paper we have used Raunkiaer’s life form traits (Raunkiaer and Gilbert-Carter 1937) to study the impact of biophysical changes on species establishment. For example, soil disturbed sites tend to have more weed vegetation that are predominantly therophytes (Lososová et al. 2004) and wind dispersed species compared to less disturbed sites that are often rich in geophytes, chamaephytes, phanerophytes with greater percentages of vegetatively reproducing species (McIntyre et al. 1995).

Hypothetically, weed vegetation that predominantly consists of annual plants shows a much higher degree of temporal dynamics than other vegetation types, such as those that operate both on the scale of seasonal changes (Lososová et al. 2004) and long-term and this corresponds to gradually increasing intensification of agricultural production (Andreasen et al. 1996). Thus agricultural activity in wetlands leads to loss of species and can also lead to establishment of additional weed species. Thus, weed functional traits can be used as indicators of regime shift from a natural wetland to a disturbed wetland used for agriculture. This paper therefore seeks to assess the impact of wetland regime change on introductions of weed species using species functional traits and changing hydrological conditions.

MATERIALS AND METHODS

Study sites

This study was done on two representative floodplains and two inland valleys (Fig. 1). The floodplains comprised one highland floodplain in Kenya (Ewasonarok swamp) and one lowland floodplain in Tanzania (Mkundi-Sangei swamp along the River Mkomazi). Highland inland valleys used in the study were the Tegu wetland on the foot slopes of Mt. Kenya and the Lukozi valley in West Usambara mountains. While Tegu and Lukozi were typical inland valley wetlands, Ewasonarok and Malinda were riverine-floodplains, with origins from the
rivers Ewasonarok and Mkomazi respectively. All these wetlands were under crop cultivation and livestock farming. The remaining undisturbed parts of wetlands were largely dominated by *Cyperus papyrus* (L.) in both highland and lowland flood plains in Kenya and Tanzania. The inland valleys however, were characterised by diverse species of Cyperaceae e.g. *Schoenoplectus corymbosus* (Roth ex Roem. & Schult.) and *Cyperus dives* (Delile). The land that was left fallow was dominated by upland weeds and permanently flooded sections with weeds such as *Azolla pinnata* (R.Br). In the floodplains, there was also intensive pastoral livestock activity as in the case of Ewasonarok wetland and River Mkomazi swamps in the Pangani basin.

**Vegetation sampling**

A list of all species introduced into the wetlands was made from an assessment of 224 plots each measuring 100 m² in two floodplains and two inland valley swamps in Kenya and Tanzania. Four land use gradients were identified, namely undisturbed plots as reference sites under either *Cyperus papyrus* (L.) or *Typha capensis* ((Rohrb.) N.E.Br.) strands, grazed, fallow and cropped (e.g. maize, cauliflower, tomatoes, and arrowroots). In each plot, species presence and percentage cover were recorded for herbs, sedges, grasses, vines, shrub and trees. Un-identifiable species were collected and placed in a plant press for further identification either at the National Museums of Kenya (NMK)’s East African Herbarium (EA) or at the University of Dar-es salaam’s herbarium by expert botanists.
Data on functional traits of all species including Raunkiaer’s (Raunkiaer and Gilbert-Carter 1937) life form, habit, duration and taxonomical group were collected. Raunkiaer’s life form subdivisions (Table 1) are based on the location of a plant’s growth point (bud) during seasons with adverse conditions (cold seasons, dry seasons), first proposed by Raunkiaer in 1934 (Raunkiaer and Gilbert-Carter 1937).

Based on floristic attributes, all weed species including potentially invasive species were recorded and described. Information on PFTs and species affinity to wetland was obtained from field collections and observations. Other sources from literature used for this research are as follows (Agnew and Agnew 1994; Haines and Lye 1983; Turrill and Beenjte 1952-2007) and East African herbarium collections at NMK, Nairobi. Online databases such as Aluka-Jstor (ALUKA 2010), PROTA 4U (Protabase 2010) and flora of Zimbabwe (Hyde and Wursten 2011). The indicator status (i.e. affinity to wetland) of each weed species was determined for obligate and facultative wetland species (Tiner 1999). Indicator status is a species probability of occurrence in a wetland as opposed to an upland habitat; for example Obligate wetlands (OBL) are species having a percentage of probability of occurrence in a wetland of > 99%; facultative wetland species (FACW), 67% - 99%; facultative species (FAC), 34-66%; facultative upland species, 1- 33%; and obligate upland species (UP), < 1% (Lopez and Fennessy 2002; Mack 2007; Tiner 1999).

**Soil sampling and analysis**

In every subunit, a composite sample of 9 top soil samples (2-15 cm) were collected (Mack 2007). Sampling was done in a ‘W’ shape using a 5 cm diameter-hand-held auger. The soil was air-dried, ground and sieved to pass a 2 mm sieve for subsequent laboratory analysis (Okalebo et al. 2002). Laboratory analysis was done on soil samples at the labs of Plant Nutrition, Department of the Institute of Crop Science and Resource Conservation of the University of Bonn (Kamiri 2010) using standard methods recommended for tropical soil samples. Total soil C and N were determined by an automated CNS elemental analyser (Euro EA 3000, manufacturer: Euro Vector SpA, Milan, Italy). Available phosphorus and exchangeable potassium were analysed by Modified Olsen P method (Olsen et al. 1954) using a 1:10 soil/solution ratio. The amount of potassium in the extract was measured on the Eppendorf Elex 6361 flame photometry and phosphorus was measured colorimetrically (molydenum blue) by an Eppendorf ECOM 6122 spectrophotometer. The volumetric soil moisture level was determined in every plot at the time of vegetation assessment (beginning of rainy season) using Time Domain Reflectometry (TDR) with 10 readings collected per plot 100 m² plot and later averaged. Soil salinity was represented as electrical conductivity (EC) and soil pH levels were determined in 1:2.5 soil water extract using EC and pH meters at room temperature (22° C).

**Data analysis**

**Weed diversity**

Introductions of new species were determined in terms of numbers of plant species not naturally occurring in wetlands of East Africa (Ervin et al. 2006b) and expressed as percentages. Comparisons of weed functional traits were made between wetland and non-wetland species, based on species-level traits, presence and percentage cover. Weed functional traits including Raunkiaer’s life form system, growth form and lifespan within each wetland and land use were compared using a non-parametric statistical analysis and PASW statistics version 18.1 where homogeneity of the
Table 1. Plant functional traits used to classify weed species including Raunkiaer’s life forms

<table>
<thead>
<tr>
<th>Traits</th>
<th>Attributes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growth form</td>
<td>herb, sedge, grass, shrub, tree, and duration</td>
</tr>
<tr>
<td>Lifespan</td>
<td>annual, perennial</td>
</tr>
<tr>
<td>Raunkiaer’s life form</td>
<td></td>
</tr>
<tr>
<td>Therophytes</td>
<td>Annual (monocarpic) plants, includes some facultatively perennial plants</td>
</tr>
<tr>
<td></td>
<td>(polycarpic) that were judged to be predominantly annual. They persist through seeds</td>
</tr>
<tr>
<td>Geophytes</td>
<td>persistent buds buried to a depth of 2-3 cm</td>
</tr>
<tr>
<td>Chamaephytes</td>
<td>persistent buds &gt; =1 cm and &lt; 20-30 cm above ground surface</td>
</tr>
<tr>
<td>Phanerophytes</td>
<td>persistent buds &gt;20-30 cm on stems above in the ground, includes twiners</td>
</tr>
<tr>
<td></td>
<td>and vines</td>
</tr>
<tr>
<td>Hemicryptophytes</td>
<td>persistent buds are in the immediate vicinity of the soil surface only,</td>
</tr>
<tr>
<td></td>
<td>maximum height, 1cm</td>
</tr>
<tr>
<td>Helophytes</td>
<td>not free plant: growing in water but attached to bottom</td>
</tr>
</tbody>
</table>

The rate of occurrence or relative frequency (f) of all weed species recorded in the four wetlands were evaluated according to the formula: \( f = \frac{ss}{ts} \), where \( ss \) is the number of sites in which the species occurred and \( ts \) the total number of sampling units (Goettsch and Hernández 2006).

**Indicator Species Analysis (ISPA)**

To determine indicator species, firstly, groupings of 330 weed species were identified using a hierarchical agglomerative cluster analysis using Bray-Curtis similarity indexes based on percentage covers. Only those species were recorded that had occurrence in more than three plots. A flexible beta linkage method with Bray Curtis as the distance measure, with \( \beta = -0.25 \) was employed in the program PC-ORD (McCune and Grace 2002). The group membership variable was set at five, given that there were four wetlands and four land use types used in the study. Indicator species analysis (Dufrène and Legendre 1997) was then used to choose an appropriate number of groups from results of the cluster analysis. ISPA calculates indicator values for each species in each group as the product of a species’ mean abundance in that group relative to other groups and the proportion of sites in that group where it is present. The indicator values thus represent the degree to which a species is distinguished between groups in terms of relative frequency and relative abundance (Flinn et al. 2008; McCune and Grace 2002; McCune and Mefford 2006). The significance of each indicator value was tested using multiresponse permutation procedures (MRPP) based on the Bray-Curtis index with 4,999 permutations at the random seed number of 5,768. Group definition, differences were determined using multiresponse permutation procedures (MRPP) based on Sørensen (Bray-Curtis) similarities using PCORD 5 (McCune and Grace 2002; McCune and Mefford 2006). Vegetation types were named according to the weed species with the highest indicator value. All analyses were done using PCORD version 5 (McCune and Grace 2002; McCune and Mefford 2006) and PASW version 18 (SPSS 2010).

**Ordination:** The spatial relationship between soil variables and introduced species was tested using Canonical Correspondence Analysis (CCA) (McCune and Grace 2002). Axis scores were standardized by Hill’s method (Hill 1979). All datasets were revitalised prior to statistical analysis (McCune and Grace 2002).
RESULTS

Weeds diversity

Out of the 425 species that were sampled, 78% (n=330) were classified as weed species representing 66 families. Highland floodplains had 159 weed species, whereas lowland floodplains of Malinda registered 154 weed species. The highland inland valley in Tegu registered 150 weeds while the mid-montane inland valley of Lukozi registered 133 species. There were no significant differences between floodplains with respect to introduced species composition (p > 0.05). However, the two flood plains were significantly different from the mid-montane inland valley (p< 0.05). Of the 330 weeds, 70% were dicots while the remaining 30% were monocots. The average weed species richness was 18 ± 9 species per 100 m² plots. There were dissimilarities in species composition among wetlands in inland valleys and floodplains; so there were differences along use gradients. Fallow and cropped plots had significantly higher weed species composition compared to either grazed or unused portions (p = 0.0177). Average weed diversity in all land uses had a similar pattern to fallow and cropped areas recording more weed flora compared to either grazed or unused areas of wetland (Fig. 2). Over 37% (n = 121) of all weed species recorded had relative frequency of occurrence below 1% i.e. many appeared in less than three plots sampled. Examples of common weeds encountered are shown in Table 2.

Potentially invasive species registered on fallow and cultivated plots were Vossia cuspidata (Griff.), Pistia stratiotes (L) and, Azolla pinnata (R.Br). Mimosa pigra (L) was common in fallow and seasonally flooded areas whereas Datura stramonium (L) was common in completely drained and cultivated plots.

Indicator species analysis

Results of the cluster analysis yielded five distinct cluster groups for indicator weed species in the four wetlands, with 15% of information retained in the dendrogram. There were significant differences (MRPP) among the five indicator groups with an overall T= -66 and within group agreement A=0.44, p = 0.000. From the indicator species analysis, five groupings were created as follows; Cynodon dactylon ((L.) Pers)) (group code 1), Leersia hexandra (Sw) (group code 31), Malva parviflora (L), (group code 54); Oxalis corniculata (L) (group code 56) and Typha capensis ((Rohrb.) N.E.Br.) (group code 85).

Cynodon dactylon ((L.) Pers)) indicator weed group was composed of 58 plots. The group registered 46 species associated to it. Some species associated with this group had high indicator values; Schkuhria pinnata ((Lam.) Thell.), Oxygonum sinuatum ((Hochst. & Steud. Dammer), and Tagetes minuta (L). This group was associated with high phosphorous and potassium contents but with lower moisture content levels in the soil. Land uses associated with this group were mainly intensively cultivated (cropped) patches, fallow plots in highland floodplains (Ewaso Narok) and a few plots under crops from inland valleys (Fig. 3). There was no contribution from lowland floodplains.

Leersia hexandra (Sw) indicator weed group was composed of 59 weeds in 53 plots, mainly from lowland flood plains of Malinda, Sangei and Mafuleta. A few plots from uncultivated portions in the highland inland valleys and highland floodplains were also skewed to this group and positively and negatively to axis 2. This group was closely associated with high soil moisture content, high total carbon and nitrate levels. Some group members included Azolla pinnata (R.Br), Ageratum conyzoides(L), Ethulia conyzoides (L.f. ), Boerhavia diffusa (L.), Basilicum polystachyon (L.), and Rotala fluitans (Pohnert).
Fig 2. Average numbers of weed species in relation to land use type in four wetlands. FP=Flood plain; IV= Inland valley.

**Table 2.** A list of cosmopolitan weed species in the four wetland areas. Species occurrence and frequency is shown. f = frequency.

<table>
<thead>
<tr>
<th>Weeds</th>
<th>Occurrence</th>
<th>f</th>
<th>Invasibility</th>
<th>gradients</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ageratum conyzoides (L)</td>
<td>88</td>
<td>39</td>
<td>Weed</td>
<td>Crops</td>
</tr>
<tr>
<td>Amaranthus hybridus (L)</td>
<td>115</td>
<td>51</td>
<td>Weed</td>
<td>Fallow</td>
</tr>
<tr>
<td>Bidens pilosa (L)</td>
<td>116</td>
<td>52</td>
<td>Invasive</td>
<td>Cropped</td>
</tr>
<tr>
<td>Commelina benghalensis (L)</td>
<td>168</td>
<td>75</td>
<td>Invasive</td>
<td>Cropped</td>
</tr>
<tr>
<td>Cynodon dactylon ((L.) Pers))</td>
<td>119</td>
<td>53</td>
<td>Weed</td>
<td>Grazed</td>
</tr>
<tr>
<td>Cyperus rotundus (L.) Palla</td>
<td>136</td>
<td>60</td>
<td>Weed</td>
<td>Cropped</td>
</tr>
<tr>
<td>Galinsoga parviflora (Cav)</td>
<td>130</td>
<td>58</td>
<td>Weed</td>
<td>Cropped</td>
</tr>
<tr>
<td>Harpagocarpus snowdenii (Hutch. &amp; Dandy)</td>
<td>67</td>
<td>30</td>
<td>Weed</td>
<td>Cropped</td>
</tr>
<tr>
<td>Leersia hexandra (Sw)</td>
<td>105</td>
<td>47</td>
<td>Weed</td>
<td>Fallow</td>
</tr>
<tr>
<td>Portulaca oleracea(L)</td>
<td>100</td>
<td>44</td>
<td>Weed</td>
<td>Cropped</td>
</tr>
<tr>
<td>Spilanthes mauritiana (A.Rich.) DC.</td>
<td>69</td>
<td>31</td>
<td>Weed</td>
<td>Fallow</td>
</tr>
<tr>
<td>Vernonia poskeana ( Vatke &amp; Hildebr.)</td>
<td>69</td>
<td>31</td>
<td>Weed</td>
<td>Fallow</td>
</tr>
<tr>
<td>Typha capensis((Rohrb.) N.E.Br.)</td>
<td>34</td>
<td></td>
<td>Invasive</td>
<td>Fallow</td>
</tr>
</tbody>
</table>
| Malva parviflora (L) indicator weed group was composed of 45 sampling units with 44 species, all from mid-montane inland valleys-the only distinct wetland group without a contribution from other wetlands. Other group members with high indicator values included Chenopodium album (L.), Chenopodium opulifolium (Schrad.), Chenopodium murale (L.), Taraxacum officinale (Weber), Setaria verticillata ((L.) P. Beauv.), Cyperus rotundus (L.) Palla) and Eleusine indica ((L.) Gaertn.). This group was positively skewed to axes 1 and 2 and strongly associated with pH and electrical conductivity. Oxalis corniculata (L.) indicator weed group had 39 plots all from the highland
inland valley of Tegu except two fallow plots from

**Fig 3.** Canonical correspondence analysis (CCA) biplot for weed species (n = 330) in four wetland types (n=201) categorized into five groupings from indicator species analysis (1= Cynodon dactylon ((L.) Pers)) group, 31= Leersia hexandra (Sw) group, 54 = Malva parviflora (L) group, 56 = Oxalis corniculata (L.) group and 85 = Typha capensis group). Soil environmental variables are represented by vectors. EC = Electrical conductivity; MO = percent moisture; C = Total carbon and P = available phosphorous and K = exchangeable potassium. The two axes together explained 34% of the variability among the five groups from analysis of indicator species.

The mid montane inland valley that was associated with this group. Other group members included Commelina benghalensis (L), Centella asiatica (L Urb)), Galinsoga urticifolia ((Kunth) Benth.), Vernonia poskeana (Vatke & Hildebr.), Kyllinga alata (Nees), and Stellaria media (L.Vill.). This group was dominated by highland inland valley sampling units; mainly from cropped areas and fallow plots. Other contribution was from the mid-inland valley. The group was associated with high phosphorous levels in soils but negatively skewed to axes 1 and 2.

**Typha capensis** ((Rohrb.) N.E.Br.) indicator weed group was composed of 6 sampling units all from mid-montane inland valleys and lowland floodplains and characterised by high electrical conductivity and
permanently inundated. Three other species were associated with this group, namely *Celosia trigyna* (L.), *Epilobium hirsutum* (L.) and *Paspalum vaginatum* (Sw.). This group was positively related to axes 1 and 2 of the biplot.

**Canonical Correspondence Analysis**

A 2-D CCA biplot shows the distribution of sampling units relative to species occurrences, abundance in various land use types in relation to soil parameters (Fig. 3).

**Lifespan**

With the exception of cropped subunits, there were significant differences between perennial and annual weeds across the wetlands relative to land use (p < 0.05). Cultivated and fallow plots within the wetlands had higher occurrences of annual weeds compared to either grazed or unused plots (Fig. 4).

**Growth forms**

The relationship between land use and growth form shows that herbs were the most abundant weeds across the wetlands with higher frequencies (Fig. 5). Fallow and cropped plots had significantly higher frequency of occurrences of herbs and grasses compared to either grazed or unused plots.

With respect to growth forms, a greater percentage of species additions were herbs and grasses, the majority of which were weeds (Fig. 5). Only 5% of herbs were classified as non weeds. Of all the herbs recorded, 82% were weed species, 13% of the herbs recorded were identified as potentially invasive. Sedges had no invasive species but constituted 57% of the species recorded as weeds. A greater percentage of the grasses within the wetland were upland grasses therefore qualified as weeds. There was a perfect negative correlation between weeds and non-weeds (p < 0.027) but a higher positive correlation between weed richness and herbaceous richness.

Facultative upland and obligate upland were the most dominant weed categories relative to flooding regimes (Fig. 6 and 7). Fallow and cultivated plots had greater percentages of species under either UP or FAC. Obligate wetland (OBL) and facultative wetland (FACW) categories however were associated with unused plots. Most plants species (77%) in the four wetlands surveyed were either facultative wetland (FAC) or upland (UP) weeds. Lowland floodplains had more species with high affinity to permanent inundation (i.e. FACW and OBL) compared to inland valleys, which had a bigger proportion of upland weed species.

**Raunkiaer’s life forms and land use**

There were significant differences in Raunkier’s life form traits between land use types (p=0.05). Weed species in cultivated lands were mainly therophytes with a higher affinity to completely drained areas. Helophytes and hydrophytes however were common in unused plots and mainly constituted perennial weed species in either permanently or seasonally inundated wetland areas. They were mainly associated with rice plots in lowland flood plains. Individual wetlands showed no significant differences relative to life form traits (p< 0.05). However, mid-montane inland valleys had a lower proportion of helophytes as weeds compared to the other three wetland areas (Fig. 8).

**DISCUSSION**

East Africa has experienced an unusually fast transformation of small wetlands from extensive subsistence cropping to intensive vegetable production (Wood and van Halsema 2008). Under this transformation crops have replaced emergent aquatic macrophytes in more than 70% of the wetlands (Dixon and Wood 2003; Schuyt 2005). Because they are drained, when left fallow these wetlands attract obligate upland (UP) species. One of the visible aspects of
this altered wetland structure is the addition of species to the flora. This has been documented in the uplands where a change from shifting to intensive/permanent agriculture in the tropics eliminates many woody, secondary species subsequently replacing them with aggressive, herbaceous pantropical elements (Kellman 1980). These species additions in most cases are agricultural weeds whereas others are considered environmental weeds by virtue of misplaced occurrences; in these cases in cultivated small wetlands.

Weed species additions
These results show that there has been immense species additions in the four wetlands selected for this study, which is in agreement with other research that has also concluded that agriculture in wetlands does indeed lead to an ecological regime shift (Folke et al. 2004). The high weed species richness of new additions recorded in used wetlands is indicative of a regime shift from permanently inundated, sedge dominated wetland to seasonally inundated annual herb-dominated wetland (Hobbs and Mooney 1998; Rooney et al. 2007). Related to new additions is the rich plant growth that is not indicative of high fertility of wetland areas but of quick nutrient recycling and high nutrient use efficiency (Junk 2002).

Wetland types
Despite the fact that these results show no significant differences (p > 0.05) on species traits between wetland type, floodplains were richer in introduced species in comparison to the inland valley wetlands. The replacement of native habitats by agricultural fields does indeed facilitate the easy movement of propagules (Tickner et al. 2001). Thus, species that are readily dispersed by water and whose seeds,
Fig 5. Frequency of weeds growth forms in relation to land use types in four wetlands: a) Highland and lowland floodplains (FP); b) Highland and mid-montane inland valleys (IV).

Diaspores or whole plants establish well on bare ground, are best equipped to invade bare spaces along stream banks and floodplains (Stromberg et al. 2007; Van der Valk 1981). The fact that inland valleys are perennially wet/or moist; cushions them against additional obligate upland introductions compared to floodplains,
whose seasonal flooding in combination with manmade drainage channels is conducive to establishment of these opportunistic species. Differences in weed diversity observed across wetlands in relation to land use type can also be attributed to different management practices that were specific and unique to every wetland type assessed in the study (Pyšek et al. 2005; Pyšek and Richardson 2007). This high diversity of weed species in used wetlands however does not indicate a healthy wetland but rather a reduced wetland quality due to an increased disturbance. The weed communities on wetlands contain neither the biodiversity nor the aggregate adaptive ability to coalesce into self-sustaining, self-replicating systems hence they have low resilience (Patchett and Wilhelm 1999). This low resilience therefore indicates that the destiny of many systems dominated by weeds is further destabilized, during which resources such as soil, nutrients and water are often lost at rates faster than they are replaced.

**ISPA and weeds**

The five indicator species groups that were generated were grouped on the basis of nutrient availability, moisture content or seasonality of flooding. The weeds were somehow biased towards those land uses based on existing cropping systems. *Cynodon dactylon* ((L.) Pers)) species-group was a representation of weeds accustomed to dry habitats with less moisture content, such as facultative upland (FC) species and obligate upland species. Other characteristics of this group included an affinity to maize and beans fields. *Tagetes minuta* (L), *Oxygonum sinuatum* ((Hochst. & Steud. Dammer)), *Bidens pilosa* (L) and *Schkuhria pinnata* ((Lam.) Thell.) were especially common species of this group. The common Raunkiaer’s functional trait of this group was therophytes, the
majority of which were annual upland species.

*Leersia hexandra* (Sw) species-group however was composed of species that were either facultative, facultative wetland or obligate wetland species. This group was also dominated by helophytes and phanerophytes and were predominantly perennial weeds. In most cases, they occurred in wet or moist parts of lowland floodplains such as Pangani in Tanzania and were related to the all season rice growing in Malinda Korogwe. Similar weed composition has been recorded in west African rice fields (Kent et al. 2001).

*Malva parviflora* (L.) species-group represented mid-montane inland valley weed species. These species were mostly exotic with the majority occurring as either cosmopolitan in distribution or either from a Mediterranean or a temperate zone. Examples were *Chenopodium album* (L), *Chenopodium opulifolium* (Schrad.), *Chenopodium murale* (L.), *Taraxacum officinale* ((L.) Gaertn.), *Setaria verticillata* ((L.) P. Beauv.), *Cyperus rotundus* (L.) Palla and *Eleusine indica* ((L.) Gaertn.). This group was related to vegetation and horticultural crops such as cauliflower, cabbage and, tomato plots within the wetland.

*Oxalis corniculata* (L) species-group were weed species skewed towards moderate moisture content. Together, they had group members including *Commelina benghalensis* (L), *Centella asiatica* (L Urb)), *Galinsoga urticifolia* ((Kunth) Benth.), *Vernonia poskeana* (Vatke & Hildebr.), *Kyllinga alata* (Nees) and *Stellaria media* (L.Vill.). This group was dominated by highland inland valley sampling units., mainly from cropped areas and fallow plots. Other contribution was from mid-inland valley. The group was associated with phosphorous rich soils and

![Fig 7. Frequency of weeds and non weeds in relation to their affinity to flooding regimes. FAC=facultative; FACU=Facultative upland, UP= obligate upland; FACW=Facultative wetland and OBL=obligate wetland](image-url)
Fig 8. Raunkiaer’s life forms of weeds in relation to land use gradients in four wetlands, a) highland and lowland floodplains and b) highland and mid-montane inland valleys. FP = floodplain; IV = Inland valley.

Weed functional traits relative to disturbance gradients

Plant community composition was biased towards species introductions that were herbaceous therophytes and facultative (FAC) wetlands (Fig. 9). The transition from a native sedge dominated wetland to one dominated by grasses and obligate upland associated with *Colocasia esculenta* (L.) Schott) and fallow plots.
Fig 9. A hierarchical cluster analysis of major land use types relative to Raunkiaer’s life forms, Hydrophytes, Geophytes, helophytes and therophytes.

annual herbs is indeed a pointer to ecological change that has occurred in the functional composition of a plant community within the small wetlands in East Africa. Unlike native species, introduced species exhibit a greater ability to adjust quickly to a regime shift in disturbed wetland ecosystems due to such activities as draining and partitioning that interfere with hydrology, soil and water quality (Ervin et al. 2006b). This is also due to the characteristically shorter canopy and short life cycle associated with therophytes/annuals that enable species to grow rapidly and complete their life cycles between disturbance events (Johnson 1997; Kyle and Leishman 2009). In contrast, perennials, typical of un-used or natural wetland
habitats may not complete a life cycle before the next wave of disturbance. For instance in mid-montane inland valleys of Lukozi, the average maximum fallow period was three months; a period that only annuals and biennial weeds can withstand. Soil disturbance also tends to favour therophytes as this opens up space for colonization through seed establishment. Therophytes are examples of species that are able to disperse effectively and exploit new resources rapidly (McIntyre et al. 1995)

**Effect of hydric regime on species additions**

Plants growing in water are technically called hydrophytes. However, not all plants grow in water or water logged soil but some also tend to grow in terrestrial habitats (Tiner 1999). It is noteworthy that reduced flooding induces new species introductions in cultivated wetlands. Facultative upland weeds completely dominated the drained sites that were studied, as opposed to permanently inundated areas that were dominated either by obligate wetland species or by facultative wetland species. A lower hydric regime is conducive for the survival of therophytes and geophyte upland plants that tend to have poor competitive ability in permanently flooded environments (McIntyre et al. 1995). Facultative weed species describe those species adapted to either seasonal conditions or wet conditions such as those between high moisture conditions and low moisture conditions (Ervin et al. 2006a). This is also in agreement with other investigations demonstrating that those species sensitive to permanently inundated conditions such as *Tagetes minuta* (L), *Oxalis corniculata* (L) and *Bidens pilosa* (L) are common in drier and nutrient-poor environments (Kercher and Zedler 2004). Related to this, introduced species and in most cases invasive plants, have been shown to benefit from changes in environmental conditions such as disturbance and nutrient enrichment, whereas native plants adapted to conditions prior to changes are less likely to benefit (McIntyre et al. 1995; Moles et al. 2008). Weed invasion threatens wetland biodiversity, leading to a decline in both species and habitat diversity. A loss of any functional group may severely affect the capacity of an ecosystem to reorganize after a disturbance (Diaz and Cabido 2001) The relative decline of other life forms might have been compensated for by an increased number of therophytes.

**CONCLUSION**

Regime shifts in the wetlands of East Africa favour species introductions, normally introduced weeds that present a potential threat to biodiversity (Hewitt and Huxel 2002). Weed species do increase diversity in a used wetland however, the fact that they play similar roles to existing flora creates a void in wetland functions that may serve to reduce the ecological integrity of these wetlands. Even though the study of invasive plants is important because they impact on ecological function and structure (Doren et al. 2009); their indicator capacity is only relevant to a specific ecological condition and future restoration success depends on the level of invasion and a good understanding of any adverse impact on an ecosystem. Therefore, there is a need to develop simple and cost effective tools to identify levels of disturbance in used wetlands for all-inclusive and informed management decisions.

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