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Importance of seedling recruitment for regeneration and maintaining genetic diversity of *Cyperus papyrus* during drawdown in Lake Naivasha, Kenya

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ABSTRACT

Drawdown-flooding cycles occur commonly in many water bodies and influence plant succession in many ways including the expansion of macrophytes through seedling recruitment. We investigated a regeneration event of *Cyperus papyrus* in Lake Naivasha and documented seed production, seedling recruitment, zonation progression, dispersal and establishment in relation to evidence from genetic relatedness between seedlings and mature stands using microsatellite loci. Seed estimate counts in five papyrus umbels reached high values between 98,000 and 337,000. The drawdown drying phase led to desiccation accompanied by cracking of mudflat soils, and the oxidation and demise of littoral aquatic plants. Reflooding led to distinct zones of young papyrus and hygrophilous ephemerals. In the final flooding phase when the lake reached normal water levels, hygrophilous ephemerals died off while papyrus survived. Young floating papyrus mats dispersed through wind and wave action joined existing mature stands or spread into formerly unoccupied shoreline areas.

Microsatellite analysis of seedlings in the drawdown zone and a neighboring stand of mature and juvenile shoots reveals high overall gene diversity ($Ho = 0.476$, $He = 0.576$, $Ae = 2.8$) reflecting an underlying sexual reproduction. A large overlap of genotypes was found in seedling and parent stands indicating a single gene pool. A total of 40 alleles were observed across 3 life stages (clonal juvenile, mature and seedlings), however, more private alleles and higher allelic diversity were detected in seedlings than in the parent individuals, showing their contribution to an increase in the local gene pool. Fine-scaled spatial genetic structuring was detected at about 100 m distance in parent stands for both juvenile and mature life stages indicating a potential influence caused by local seed rain.

1. Introduction

The Maasai historical local name, *Enaiposha* (meaning ‘receding water’) is an indication that throughout history Lake Naivasha has undergone large-scale water level fluctuations. Receding water resulting in drawdown (a drop of lake level), later followed by flooding, is a common feature of tropical wetlands and shallow lakes and has elicited the attention of many biologists (e.g. Gunn, 1973; Howard-Williams, 1975; Gaudet, 1977; Harper, 1992; Verschuren et al., 2000; van der Valk, 2005; Bond et al., 2008; Terer, 2011). For wetland plants that have evolved to live in alternately wet and dry habitats, drawdown can be a very positive event that promotes regeneration by seedling recruitment (Gaudet, 1977; van der Valk and Davis, 1978; Welling et al., 1988). *Cyperus papyrus* (Cyperaceae), the focus of the current study, is known to be adapted to normal climatic cycles of drying-flooding, and exhibits both sexual reproduction and unlimited clonal propagation (Gaudet, 1977; Terer, 2011; Triest et al., 2013).

The impact of drawdown-flooding cycles on hydrobiology especially in plant community succession is well studied (e.g. Gaudet, 1977; Wilcox and Meeker, 1991; Harper, 1992; Van Geest et al., 2005a,b), however, few studies relate such cycles to the role they

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play in genetic diversity of aquatic species by seedling recruitment (Shibayama and Kadono, 2007; Uesugi et al., 2007). Available ecological information on *Cyperus papyrus* shows that it has a persistent seed bank (Gaudet, 1977; Boar, 2006). One important factor that could be expected to influence the extent of *C. papyrus* establishment is intensity of the seed rain onto the lakeshore sediment seed bank, yet this information is unavailable. Identification of factors that determine the recruitment rates in aquatic plants and longevity of seed banks are fundamental to the understanding of population dynamics especially those in recovery after long drought events (Smith and Kadlec, 1983; Brock and Rogers, 1998; de Winton et al., 2000; Shibayama and Kadono, 2007).

Maintenance of high genetic diversity and high gene flow exhibited by *C. papyrus* in Lake Naivasha (Triest et al., 2013) imply that such diversity and flow can only occur when seeds/propagules are deposited on suitable microsites and are allowed to germinate and establish. In this process recruitment by seeds (hence successful sexual reproduction vis-a-vis clonal reproduction) is an indispensable mechanism to the long-term success of plant species (Santamaria, 2002). It is arguable that clonal propagation is not a substitute for sexual reproduction but merely prolongs the time to extinction when sex is absent for plant species (Honnay and Bossuyt, 2005; Silvertown, 2008). Making inferences on the life history survival strategies of *C. papyrus* can best be done during long drought events such as those experienced in the last ten centuries in eastern Africa (Verschuren et al., 2000). It is expected that as wetlands recede during such drought episodes, existing papyrus populations will be faced with severe water shortage so that some populations go extinct. In such circumstances, it is only the existence of a seed bank that will allow recuperation of the population after rewetting. In the event that these seed banks and seedlings are destroyed by human activities, the recovery of a population would have to rely on dispersal from other undisturbed populations.

In 1960s papyrus dominated the littoral zone of Lake Naivasha, but reduced 10-fold (from ca. 50 km^2 to ca. 5 km^2, Hickley et al., 2004) by 2005. The once continuous papyrus population is now highly fragmented due to processes driven by climate cycles and anthropogenic activities such as agricultural reclamation and grazing by domestic livestock (Hickley et al., 2004; Gichuki et al., 2006; Morrison and Harper, 2009), all of which impact negatively on regeneration by seedlings. An understanding of the connection between drawdown-flooding phenomena and papyrus population dynamics is crucial in putting in place conservation measures to reverse the loss of papyrus, which is known to provide the lake with an efficient and natural buffer against sediment and nutrient loading (Boar et al., 1999). Papyrus also provides for carbon sequestration, breeding grounds for fish and a habitat for threatened birds (Mnaya and Wolanski, 2002; Jones and Humphries, 2002; Terer et al., 2006; Owino and Ryan, 2006; Saunders et al., 2007; IUCN, 2010; Harper et al., 2011). In addition, papyrus is of great use to riparian people as a source of handicraft materials, and as fuel, fodder for livestock, medicine and roofing materials as well as socio-cultural uses (Jones, 1983; Gichuki et al., 2001; Simpson and Inglis, 2001; Terer, 2011; Terer et al., 2012a).

Seedling recruitment, dispersal and the subsequent areal expansion of the papyrus swamp in Lake Naivasha has been reported in the past (Gaudet, 1977; Harper, 1992; Boar, 2006). The current study explores the importance of drawdown-flooding cycles in regeneration of *C. papyrus* in relation to seed production, seed bank, seedling recruitment and the link between dispersal and maintenance of genetic diversity.

The aim of this study is to investigate the role of drawdown-flooding in the regeneration of *C. papyrus* and the contribution of seedlings in maintaining lake population gene pools. Specifically, we intend to: (1) provide information on seed production of *C. papyrus*; (2) describe the most recent drawdown-flooding progression including plant zonation; (3) document the natural regeneration of *C. papyrus* by seedling recruitment, and dispersal; and (4) provide genetic information on the seedlings vs. parent populations with a view of demonstrating the importance of seedling recruitment in enriching and maintaining lake population gene pools.

2. Methods and materials

2.1. Study site

Our study was carried out in Lake Naivasha (Kenya), a freshwater body on the floor of Eastern Great Rift Valley, occupying an endorheic basin with no surface outflow but underground seepage (Gaudet and Melack, 2006). The work was done between February 2008 and January 2012 in two papyrus shoreline swamps in the southern part of the Lake: Fisherman's Camp (0°49′ S 36°20′ E, altitude 1902 m) and Kamere Public Beach (0°48′ S 36°19′ E, altitude 1901 m). The Fisherman's Camp site was chosen because of its accessibility and undisturbed status on private land utilized for ecotourism (Terer et al., 2012b). The Kamere site, which is open to public access, was chosen because of its known population dynamics of local extinction and recovery (Terer, 2011). It should be noted that the Kamere site was devoid of papyrus during the drawdown period, thus it was not sampled for genetic analysis, although observations were made on the later colonization of that site by papyrus.

2.2. Seed production counts and data analysis

We estimated seed production from only five randomly cut mature umbels from the Fisherman's Camp site. The small sample size was chosen to avoid negative impacts on population size and deemed representatives. However the umbels were comparable in size, shape and form to most umbels at this and other sites on the lake. The cut umbels were packed tightly in polythene bags to avoid losing mature seeds. We counted the total number of rays (Fig. 1a) contained in an umbel, and then randomly selected 10 rays for further investigation from each umbel. From the selected 10 rays, we counted the number of spikes (Fig. 1b and c), spikelets (Fig. 1d), and the number of seeds (Fig. 1e) recovered from 50 spikelets from each umbel (total of 250 spikelets). The spikelet was randomly selected along the spike from top to bottom to account for their differences in length and hence the number of seeds contained in them. Fig. 1f and g shows the papyrus stand at this site and a representative papyrus umbel. The total number of seeds (S_T) for each umbel was estimated by average number of seeds recovered from 50 spikelets (S_M) multiplied by the average number of spikelets counted from 10 rays (SP_M), the obtained value was then multiplied by the total number of rays recorded for each umbel (R_T), simply expressed as:

$$S_T = (S_M * SP_M)R_T.$$

Images of general morphology of seeds and their position in a spikelet were taken with a Scion camera Model CFW-1310C mounted on an Olympus Stereoscope (Scion Corp.).

2.3. Drawdown succession and seedling density

Repeat photography was used to document the drawdown area at Fisherman's Camp starting with the dry phase (August 2009) until when it was reflooded (September 2010). At this site we also captured periodic regeneration of *C. papyrus* seedlings and the succession of aquatic and hygrophilous species (i.e., short-lived plants that die after re-flooding: Gaudet, 1977) until the *C. papyrus* seedlings had grown to maturity in September 2010. Observation