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Ungulate herbivory overrides rainfall impacts on herbaceous regrowth and residual biomass in a key resource area

Francis K. Muthoni*, Thomas A. Groen, Andrew K. Skidmore, Pieter van Oel

Faculty of Geo-Information Science and Earth Observation (ITC), University of Twente, Hengelosestraat 99, P.O. Box 6, Enschede 7500 AA, The Netherlands

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Key grazing lands that provide dry season forage to both resident and migrating ungulates may experience heavy grazing impacts during the dry season, thereby jeopardizing future forage productivity. In this study a herbivore exclosure experiment was used to quantify the effects of grazing by large ungulates on herbaceous regrowth and residual aboveground biomass in a fragmented key resource area; the fringe zone around Lake Naivasha, Kenya. Top-down control mechanisms were prevalent in both the dry and wet seasons suggesting the existence of a high resident herbivore density. Intense grazing significantly reduced residual biomass that in turn reduced plant regrowth. An increased frequency of defoliation reduced regrowth during the dry season demonstrating the negative effect resulting from high herbivore densities during the dry season. This study indicates that grazing exerts a higher control on regrowth than rainfall as heavily grazed residual biomass did not recover during the following wet season.

1. Introduction

Savanna grasslands are abundantly inhabited by a diverse mix of wild and domesticated herbivores. Grassland productivity is key in providing forage for animals and contributes significantly to global carbon sequestration and stocks (Tanentzap and Coomes, 2011) and local nutrient cycling (Augustine and Frank, 2001). Despite benefiting from the available forage, herbivores have both positive and negative impacts on herbaceous productivity (e.g. Chase et al., 2000; McNaughton, 1985; Pandey and Singh, 1992). Positive impacts include stimulation of growth after grazing (compensatory growth) (McNaughton et al., 1996), nutrient cycling (Augustine and McNaughton, 2006) and enhancing species diversity (McNaughton, 1985). However they may negatively influence herbaceous productivity through reduction of photosynthetic area, loss of nutrients for growth stored in shoots or removal of apical meristems that produce new shoots (Noy-Meir, 1993). Herbivore grazing may also reduce survival fitness of the plant due to injury on the stolons or rhizomes (Anderson and Frank, 2003; Keya, 1997) and physical damage by trampling (Belsky, 1992). Moreover, overgrazing may promote bush encroachment (Coetzee et al., 2007; De Knegt et al., 2008) and favour growth of less productive annual grasses and forbs over perennial grasses (Keya, 1997).

The magnitude of herbivore effects on vegetation productivity in climatically variable ecosystems remains unresolved. There are no unifying hypotheses about herbivore impacts in African savannas, although several contradicting alternative hypotheses have been developed. The equilibrium hypothesis (DeAngelis and Waterhouse, 1987) postulates a density-dependent relationship between herbivores and vegetation productivity, where herbivore density increases with increasing forage productivity until a threshold is reached where competition for forage among herbivores suppresses vegetation productivity. Alternatively, the disequilibrium hypothesis (Ellis and Swift, 1988) posits that herbivores have no effect on vegetation productivity in ecosystems experiencing an approximately 30% variation in rainfall. Arguably, frequent droughts maintain herbivore densities at low levels below which they can exert significant top-down control on plant productivity (Derry and Boone, 2010; Vetter, 2005)

The non-equilibrium hypothesis (Illius and O'Connor, 1999, 2000) argues that both equilibrium and dis-equilibrium processes occur alternately in both the spatial and temporal dimensions. This is facilitated by the presence of key resource areas such as lakes, waterholes, marshes and salt licks in savanna landscapes. Particularly, key resource areas act as dry season refugia where herbivores from surrounding wet season ranges aggregate. During the dry seasons key resource areas experience higher top-down control

* Corresponding author. Tel.: +31 (0)53 4874524; fax: +31 (0)53 4874388.
E-mail addresses: fkmuthoni@gmail.com, k.muthoni@utwente.nl (F.K. Muthoni).

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due to aggregation of herbivores that potentially cause further decline in productivity (Illius and O'Connor, 1999, 2000). In contrast, the surrounding wet season ranges are driven by non-equilibrium forces but they experience higher grazing pressure in the wet season due to larger herbivore density that has been maintained in the key resource areas during scarcity (Illius and O'Connor, 1999, 2000). Therefore, monitoring herbivore impacts in key resource areas is not only important for their sustainable management, but also for the maintenance of diversity in the overlying rangelands.

In savanna landscapes, grazing lands fringing freshwater wetlands are key resource areas. Besides being critical watering points, their shorelines are abundant in high-quality forage. These resources attract high herbivore densities especially during the dry season. Nonetheless, some of these ecotones are prone to fragmentation from two directions (both landward side and lakeside) (Lachavanne and Juge, 1997). These include both natural and human perturbations from the landward side, as well as fluctuations in water and nutrient-levels on the lakeside that have direct impact on vegetation productivity. The fringe zone of Lake Naivasha, Kenya, is a typical example. Though the fringe zone was historically a nomadic pastoral area (Abiya, 1996), it now constitutes a unique and complex landscape mosaic centred around the Lake, comprising intensive horticulture, urban centres, ranches (wildlife and livestock), a national park and geothermal electricity generation.

Besides the prevalent natural and human induced fragmentation on the fringe zone itself (Onywere et al., 2012), the herbivores utilization of the fringe zone has increased due to a combination of (1) relatively high resident herbivore density (Harper and Mavuti, 2004; Smart et al., 2001; Douglas-Hamilton, unpublished) (2) land cover conversions in the surrounding rangelands that trigger immigration of wildlife and livestock (Morrison and Harper, 2009); (3) erection of electric fences on wildlife conservancies that lower habitat connectivity and concentrate high grazers densities in some zones and (4) the termination of a wildlife cropping programme since 2003. The combination of all the above has led to increased grazers densities, reduced grazing area, loss of habitat connectivity and probably deteriorated range conditions.

Despite all these documented changes, little is known about the herbivores' impacts on herbaceous vegetation productivity and aboveground biomass (AGB) accumulation in and around the fringe zone. Many studies have focused on productivity of a narrow band of the fringing *Cyperus papyrus* swamp (Jones and Muthuri, 1997; Muthuri et al., 1989). It has been shown that the papyrus stands are more degraded at sites that are more accessible to large ungulates, especially buffaloes (Harper and Mavuti, 2004; Morrison and Harper, 2009). Moreover, in the nearby Hell's Gate national Park, overgrazing was reported to promote encroachment by *Tarchonanthus camphoratus* bushes (Coetzee et al., 2007) that hinder herbaceous productivity as a result of competition for moisture, nutrients and light.

Information on herbaceous productivity and consumption levels by large herbivores on the fringe zone is required for monitoring the ecosystem health (Tappan et al., 2004) and designing appropriate management plans such as wildlife cropping quotas. This can promote sustainable grazing intensities (i.e. managing the proportion of the forage that is consumed relative to available aboveground biomass). Following the predictions of the non-equilibrium hypothesis (Illius and O'Connor, 1999, 2000), it has been hypothesized that top-down control mechanisms are prevalent only during the dry season when grazers aggregate in the key resource area. Therefore, significant impacts of grazing on regrowth and residual aboveground biomass (forage availability) would only be experienced during the dry season. Moreover, regrowth is hypothesized to significantly decline in areas where grazing has been persistently strong, because with increased grazing, the survival fitness of the herbaceous vegetation is lowered due to resulting injury to their meristems, stolons and rhizomes where new tillers sprouts (Keya, 1997). To test the above hypotheses, herbaceous biomass regrowth, the consumption by large ungulates and the resultant grazing intensities were estimated for different sites and seasons around Lake Naivasha. Inferences were drawn on the relative effects of both grazing and rainfall on herbaceous regrowth and residual aboveground biomass.

2. Methods

2.1. Study area

This study was undertaken on the fringe zone of Lake Naivasha (00 45′S and 36° 20′E) in an area covering approximately 500 km^2 (Fig. 1). Lake Naivasha is located at the floor of the Great Rift Valley at an altitude of 1890 m a.s.l. Annual rainfall is approximately 600 mm and is largely bimodal with two rainy seasons; the long rain (March to May) and short rains (October to December). The rainfall is characterized by high inter and intra-annual variability (CV $\sim$ 30%) as witnessed in 2011 when the long rains were below average but the short rains were above normal rainfall (Fig. 2). The mean temperature ranges from 20 to 26 °C. Soils range mainly from silt loam to clay soils with a humic topsoil that is relatively well drained (Hickley et al., 2004).

The land use on the fringe zone of the Lake has gradually evolved from pure nomadic pastoralism to sedentary farming and ranching (Becht and Harper, 2002). As described by Gaudet (1977), the vegetation composition changes gradually with increasing distance from the Lake. Vegetation ranges from aquatic macrophytes (*C. papyrus* and *Eichhornia crassipes*) to grasslands and shrublands dominated by *Tarchonanthus camphoratus* and climax into *Acacia xanthophloea* woodlands. Grasses are dominated by *Cynodon dactylon* (increaser II species) and *Pennisetum clandestinum*. Increaser II species are grass species that increase in overgrazed lawns (Danckwerts and Stuart-Hill, 1987). Herbaceous species in the woodlands are dominated by *Hypoestes forskaolii and Achyranthes aspera* which are invasive, unpalatable and shade tolerant. These characteristics enhance their ability to spread fast, eventually competitively excluding the palatable perennial grasses (Ng'weno et al., 2010). Bush encroachment, mainly by *Tarchonanthus camphoratus* (Coetzee et al., 2007), and *Psiadia punctulata*, poses a threat to the distribution and productivity of grasslands (Ng'weno et al., 2010). Common forbs include *Tribulus terrestris*, *Euphorbia inaequilatera* and *Euphorbia prostrata*. The abundance of these forbs is considered as a bio-indicator of overgrazing (Keya, 1998).

Common native grazers and mixed feeders include the hippo (*Hippopotamus amphibious*), buffalo (*Syncerus caffer*), common zebra (*Equus burchelli*), eland (*Taurotragus oryx*), impala (*Aepyceros melampus*) and defassa waterbuck (*Kobus ellipsiprymnus*).

2.2. Experimental setup

Herbivore exclosure experiments were utilized to measure the effect of large herbivores on herbaceous vegetation productivity. Six herbivore exclosures were erected on four ranches surrounding Lake Naivasha (Table 1, Fig. 1). Selection of the exclosure locations was based on vegetation type, ease of accessibility and security. The exclosures were 1.5 m tall and ringed with barbed wire with a spacing of 15 cm. Each exclosure measured 100 m^2 with two adjacent control plots of the same dimensions on either side. The exclosures and their control plots were subdivided into 25 lattice