Forest Ecology and Management 402 (2017) 166–176

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

A first look at the impediments to forest recovery in bracken-dominated clearings in the African Highlands

Fredrick Ssali*, Stein R. Moe, Douglas Sheil

Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, 1432 Ås, Norway

ARTICLE INFO

Keywords:
Afro-tropical forest
Arrested succession
Bwindi
Competition
Forest-bracken edge
Invasive species
Pteridium aquilinum
Regeneration

ABSTRACT

Areas dominated by bracken, *Pteridium aquilinum*, occur on every continent except Antarctica. These fern thickets appear to retard forest recovery and thus reduce forest diversity and carbon values. We examined how bracken inhibits forest recovery in the Bwindi Impenetrable National Park, Uganda. We established 40 50 × 5-m transects across the forest-bracken interface. On average, we recorded 596 ± 64 large trees (stems ha^{-1} ± 1 SE), 1440 ± 159 saplings, 33580 ± 8860 large seedlings and 31003 ± 8854 small seedlings in the forest and 45 ± 16 large trees, 114 ± 28 saplings, 7015 ± 2268 large seedlings and 6317 ± 2240 small seedlings in bracken. All bracken clearings had been affected by fire. The density of bracken was 4.9 ± 0.3 fronds m^{-2}. Our results suggest that distance limitation, lack of perches, damage by vertebrates and suppression by climbers all offer potential explanations of impeded regeneration in bracken. The sparser woody vegetation that occurred in bracken typically had smaller-seeded and thicker-barked tree species than the nearby forest and also included more pioneers and fewer animal dispersed species. Interestingly we detected a negative relationship between proximity to bracken plants and woody regeneration within the forest. Several key explanatory variables including canopy cover, litter depth, distance to forest and bracken density are correlated and hard to separate.

1. Introduction

Areas dominated by bracken *Pteridium aquilinum* (L.) Kuhn occur on every continent except Antarctica and appear to impede forest recovery (Der et al., 2009; Marrs and Watt, 2006; Marrs et al,. 1997, Page 1976). In the East African Highlands such fern thickets tend to result from droughts, fires and other disturbance processes (landslides, abandoned cultivation etc.), and already cover hundreds of square kilometres of previously forested habitat (DS pers. obs., Holm et al., 1997; TGC, 2011; Verdcourt, 1999). Bracken thickets are likely to expand in tropical Africa in future as droughts and fire are predicted to increase (IPCC, 2014).

Temperate studies indicate that common bracken, *Pteridium aquilinum* (L.) Kuhn, interferes with forest regrowth (Den Ouden, 2000; Dolling, 1996; Facelli and Picket, 1991; Gaudio et al., 2011; Priewasser, 2013). However, various interference mechanisms have been suggested and it is unclear which of these, if any, are involved in the highlands of equatorial Africa. In the Bwindi Impenetrable National Park (Bwindi), a UNESCO World Heritage site, bracken thickets are already locally abundant and appear persistent: retarding forest recovery and reducing forest biodiversity and carbon values.

There have been few ecological studies of how bracken and forest interact in the tropics. Most publications relating to bracken in Africa focus on taxonomy or control (Masozera, 2004; Thomson et al., 2005; TGC, 2011, but see Adie et al., 2011). Even outside Africa, forest boundaries adjacent to bracken-dominated clearings have received little attention despite a considerable literature on forest-edge dynamics (see Haddad et al., 2015; Harper et al., 2005; Porensky and Young, 2013 for reviews). In this paper, we examine how bracken interferes with forest recovery at the forest-bracken interface in and around Bwindi in the equatorial highlands of Western Uganda. To our knowledge, this is the first ecological study of bracken in tropical Africa.

Our objectives were to: (1) describe vegetation structure across the forest-bracken boundary, (2) determine the potential factors affecting the ability of woody species to re-colonise bracken, and thus (3) provide an initial exploration of mechanisms that might explain how bracken slows forest regrowth. Our observations and review of the literature suggested many mechanisms might be operating and that bracken might be both the cause or the consequence of impeded forest recovery (Fig. 1; see also Marrs and Watt, 2006 for a review). Crucially, these mechanisms might be operating alone or in combination so we sought to avoid misleading simplifications (see Evans et al., 2013; Hilborn and Stearns, 1982). For this exploratory investigation, we developed simple hypotheses, and predictions, associated with a subset of the candidate

* Corresponding author.
E-mail addresses: fredrick.ssali@nmbu.no, ssalifb@yahoo.co.uk (F. Ssali).

http://dx.doi.org/10.1016/j.foreco.2017.07.050
Received 20 March 2017; Received in revised form 23 July 2017; Accepted 28 July 2017

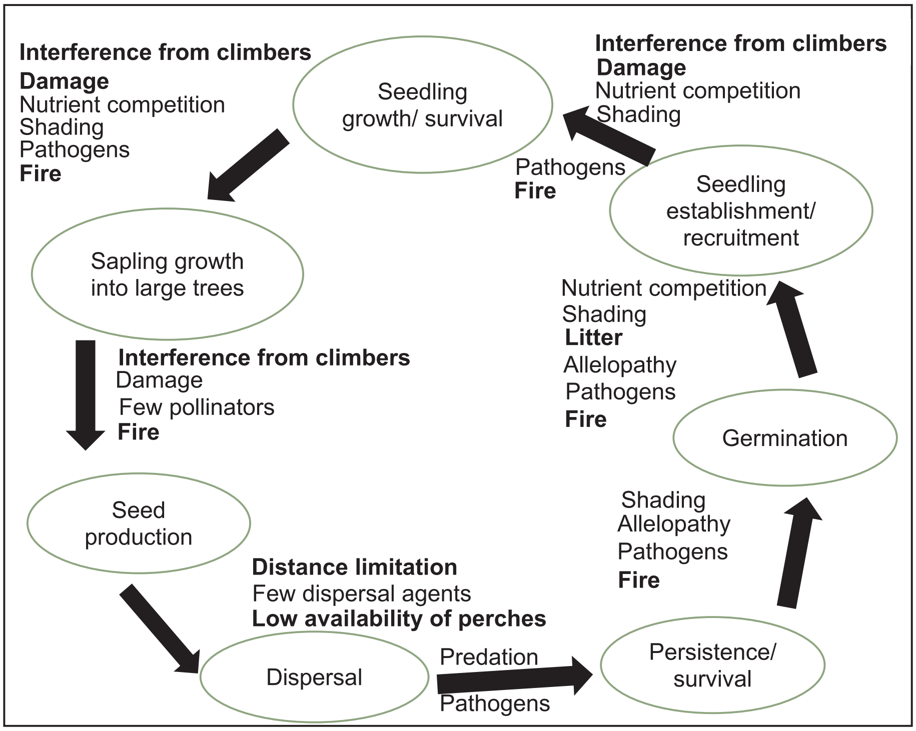

Fig. 1. Mechanisms and factors that might explain the influence of bracken on tree regeneration at different life stages. The mechanisms and factors examined in this study are denoted in bold.

mechanisms. If seed dispersal (seed limitation i.e. failure of seeds to arrive in bracken) is involved we expect a decline in regeneration with distance from seed sources, while if this limitation reflects perching animals as dispersal agents, regeneration will vary with perch availability (Saavedra et al., 2015). If bracken plants directly interfere with seed survival or germination, or with seedling establishment and growth, then we expect a negative relationship between the density of bracken and the density of woody species (den Ouden, 2000; Priewasser, 2013). If a thick litter layer impedes seedling establishment and survival (Xiong and Nilsson, 1999), we expect larger-seeded species to be relatively better represented than smaller-seeded species in the seedling population in bracken. We knew that some bracken areas had burned previously and wondered if fire was responsible for generating these areas and for keeping them open. If fire generates these areas we expect confirmation that they had all burned. If it maintains them we would expect that time since the last fire would be positively correlated with the density of woody species, and that given this rate of recovery fires would be sufficiently frequent to explain the low abundance of woody stems. Furthermore if fire plays a major role we predicted that it would be selective and that thicker-barked species would be relatively more common than thinner-barked species in affected areas due to their better survival (Pausas, 2015; Pellegrini et al., 2017). If stem damage is involved, we expect greater damage (per stem) in bracken than in forest due to higher incidence of damage in more open habitats (Ssali et al., 2012). If interference from climbers is involved (Schnitzer et al., 2004; Tobin et al., 2012), we expect stems in bracken to suffer a greater burden of climbers than those growing in forest.

2. Methods

The study took place in the Bwindi Impenetrable National Park a UNESCO World Heritage site "Bwindi" in South-West Uganda. The park is one of the most important forests for biodiversity conservation in East Africa, containing many endemic and threatened species (Butynski, 1984; Hamilton et al., 2000). Bwindi spans a range of elevations (1160–2607 m asl) and is located 0 °53′–1 °08′ S, 29 °35′–29 °50′ E near the equator and has been included in various larger regions including the "Kigezi Highlands", the "Greater Virunga Landscape" and the "Albertine Rift Valley" (Butynski, 1984; Butynski and Kalina, 1993; Plumptre et al., 2007; Taylor, 1990). Bwindi's vegetation is classified as moist lower montane forest (Hamilton, 1982; Howard, 1991). The forest is home to half of the world's critically endangered mountain gorillas *Gorilla beringei beringei* Matschie. The objective of park management is the protection, restoration and improvement of the forest's conservation value, which was affected by logging, fire and mining before it became a National Park in 1991 (Uganda Wildlife Authority: BINP General Management Plan 2014-2024).

Fieldwork was conducted between July 2015 and January 2016. We selected 40 bracken-dominated clearings with abrupt and noticeable changes in woody vegetation along the forest-bracken boundary and accessible from the ITFC research station at Ruhija (2355 m asl, see Fig. 2). To select a clearing, we searched for open areas within a day's travel from the research station using satellite images and experienced local guides. In total we surveyed 40 bracken patches and in each we placed one 50 × 5-m transect across the forest-bracken boundary with the 25-m point at the interface and 25 m extending into both the bracken patch and forest.

In each transect, we recorded all woody stems and the number of bracken fronds in 1-m^2 quadrats established every 5 m along the transect. We also measured site data and interviewed local informants who had worked in these forests for many years about the history of each site. The site data measured were: (1) litter depth (cm, using a ruler in the centre of a 1-m^2 quadrats placed every 5 m along the transect), (2) canopy openness (%, using a densiometer in the middle and at each end of the transect), (3) basal area (m^2 ha^{-1}, using a 'relascope' in the middle and at each end of the transect), (4) density of herbaceous plants (number m^{-2}, visually estimated every 5 m along the transect), (5) elevation (m, using a GPS in the middle and at each end of the transect), (6) inclination (°, using a clinometer in the middle and at each end of the transect), and bracken patch size (ha, visually estimated for each transect). Site history data collected per transect were: occurrence of past logging, landslides and fire (we also asked the key informants to estimate the first and last years when each site was burnt).

In our initial exploration of the data, we determined the 25 most abundant tree species. For each of these species we subsequently