Soil seed bank dynamics and above-ground cover of a dominant grass, Hyparrhenia confinis, in regularly burned savanna types in Gambella, western Ethiopia

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The spatial and temporal distribution of the soil seed bank of a dominant grass species, *Hyparrhenia confinis* (Hochst. ex A. Rich.) Stapf, was studied in regularly burned savanna in Gambella, western Ethiopia. The seedling emergence technique was employed to determine the density of the soil seed bank of six sites with different fire severity. The soil seed bank was largely dominated by graminoids as almost 90 % of the soil seed bank consisted of seeds of *Hyparrhenia confinis*. The seed density of *Hyparrhenia confinis* in the soil varied strongly between seasons, sites and depths and was not always closely correlated with the above-ground cover of *Hyparrhenia confinis*. This was high in the wooded grasslands and intermediate in the woodland, whereas the species, and other grasses, were absent from the more densely forested sites. The majority of the seeds were found in the uppermost 0.5 cm of the soil. Seed density was highest in the dry season and declined strongly in the beginning of the rainy season due to germination when conditions were favourable for plant growth. However, observations from the field suggest that sprouting from the base also may contribute to regeneration of the grass cover after the dry season. Our results show that the current fire regime of these savanna woodlands appears to maintain the dominance of *Hyparrhenia confinis* both as seeds in the soil and in the herbaceous stratum of the standing vegetation.

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Introduction

Vast areas of rangeland vegetation in many parts of the world are regularly cleared by natural and man-made fires, of which the latter play an increasing importance (Lock 1998). Fires are widespread in many African savanna woodland types and may result in open areas that may suppress the seed germination of some plant species, and stimulate that of other species. This is known to be an important phenomenon in forests (Swaine & Whitmore 1988), and probably also plays a role in woodlands. Thus, light-demanding species such as savanna grasses may benefit from burning. The gaps formed by slashing of vegetation or burning may quickly be colonized by plants recruited from the soil seed bank, from seed rain originating from the surrounding vegetation, as well as from pre-existing seedlings and sprouting shoots which may have escaped the disturbance (Demel Teketay 1997). Therefore soil seed banks are important as means of plant establishment after disturbance (Odgers 1996; Metcalfe & Turner 1998).

Soil seed banks enable plants to survive fire. Seeds buried in the soil are well protected from the direct effect of fire as the soil provides insulation from high surface temperatures during the course of fire (Whelan 1995). The mortality of seeds following burning depends on the intensity of fire and the depth of seed burial in the soil. According to Whelan (1995) seeds close to the soil surface could be killed by intense fire, whereas seeds in deeper soil layers may remain dormant. Water percolates into the soil and animal vectors such as small arthropods, *e.g.* insects, and other soil macro-organisms play major roles in the vertical and horizontal movement of seeds in the soil, facilitating the storage of seeds at deeper soil layers, and hence their survival in fires (Baskin & Baskin 1998).

The composition of a soil seed bank and its contribution to the restoration of a cleared or burned area depends on two important reproductive traits of the plants: (1) the capacity for seed dormancy, *i.e.* whether the species has persistent or short-lived seeds in the soil and (2) the potential for widespread seed dispersal (Dalling *et al.* 1997). The vegetation, particularly on disturbed sites, is often dominated by species that are abundantly represented in the site's seed bank (Uhl *et al.* 1981). Therefore, knowledge of the soil seed bank composition and dynamics in regularly burned sites may be used to predict the species composition of post-fire regeneration (Valbuena & Trabaud 1995). Species with large numbers of propagules already present in the soil seed bank, or dispersed to the site shortly or immediately after the fire disturbance have a great advantage over species arriving later, and over species with a small seed bank, or none at all (Swaine & Hall 1983). However, it has been questioned whether numerical dominance in the seed rain or seed bank puts the species at an advantage over others with few or no seeds in the soil seed bank (Swaine & Hall 1983; Uhl *et al.* 1981). This is because plants differ in their competitive ability, and competition for various resources among species also varies according to the timing of burning and the nature of the post-fire environment (Drake 1998).

Although grasses provide the major part of the primary production in savannas little is known about the regeneration strategies of some of the dominant species. This applies in particular to the importance of the soil seed bank for vegetation recovery after fire. The aim of this study was to reveal the spatial and temporal dynamics of the soil seed bank of *Hyparrhenia confinis*, and to compare the seed bank and above-ground cover of this species in vegetation types exposed to varying degrees of fire events. *Hyparrhenia confinis* is the dominant grass species in regularly burned savanna woodlands and grasslands in Gambella in western Ethiopia and is restricted to the border region between Ethiopia and Sudan from the Gamble region to Tigray (Phillips 1995).

Methodology

Study area

The study area is situated at about 500 m altitude on flat plains to undulating rocky areas with various types of savanna woodland in Gambella, western Ethiopia. The rainfall pattern in Gambella region is bimodal with a dry season from October to March, little rain in the months of April and May, and a main rainy season between July and late September, with a peak of rainfall in July. Annual rainfall recorded in 1991, 1992 and 1993 ranged from 700 to 1000 mm in the drier part of the area (at sites B, C and D, see below) and from 1000 to 1900 mm in the wetter part (at site A). The climate is hot tropical with mean monthly minimum and maximum temperatures of 18°C and 40°C respectively.

Four regularly burned sites (A, B, C, and D) representing different vegetation types and fire severity were selected in the Gambella region. At each site three replicate plots with the size of 20 meters by 50 meters maximally 2 km apart were selected for the study. Sites were selected on the basis of differences in their vegetation types and biomass compositions and hence, difference in burning intensities (see Jensen & Friis 2001). The wooded grassland sites C and D burn relatively intensively, the woodland-wooded grassland intermediate site A burns moderately, whereas the woodland (B) site burns infrequently or less intensively. Fire intensity was roughly estimated from the amount of grass biomass measured in each respective site, following the method used in DeBano *et al.* (1998). Finding a control site (*i.e.* a site which was unburned or burned less frequently) proved difficult as almost the whole region burns every year. However, two plots with dry forest within the local airport area (X1 and X2) and one forested site called Gog (G site) could serve as controls or unburned plots, with the same plot sizes as the burned plots.

Above-ground cover estimation of Hyparrhenia confinis

In order to estimate the above-ground cover of *Hyparrhenia confinis*, 20 quadrates each with an area of 1 m^2 were positioned within each plot at 5 meters intervals along a 100 m transect line. The presence of *Hyparrhenia confinis* rooted within each of the 20 quadrates per plot were recorded both in February and in June 1998 as the percentage cover of stems and leaves in each quadrate, estimated by visual inspection.

Soil collection and treatment

Soil samples for seed bank studies were collected from each of the 3 plots at sites A, B, C, D, X and G. Six replicate spots for soil collection were randomly selected within each plot. Soil samples were taken from 0-0.5 cm, 2.5-3 cm, 5.5-6 cm, and 8.5-9 cm. Each subsample covered a depth of 0.5 cm. Soils between successive subsamples were discarded to minimize the risk of soil mix or contamination. Samples were taken with a knife and a spoon within a wooden frame measuring 15 by 15 cm. Samples were collected three times in a year. The first soil sampling was in February 1997, which was in the hot and dry period, the second one was in June 1997, *i.e.* the beginning of the wet season and the last set was taken during November 1997, at the end of the rainy season. At each occasion a total of 342 soil samples (comprising 90 soil columns normally with sampling at 4 depths, from 15 plots at the 6 sites) were collected. Each sample was kept separate, air dried and then passed through a 4 mm sieve to remove vegetative plant fragments. Seeds larger than 4 mm would be removed by this treatment, but few seeds of this size class were observed, and those found were added to the soil sample.

After sieving the soil was spread out in a 10 mm thick layer over washed and sterilized river sand in circular plastic pots with a diameter of 12 cm and depth of 6 cm. Pots were incubated in a glasshouse and watered as required. Air temperature in the glasshouse during the study period ranged from 20 to 43°C, which is a typical temperature range between day and night and the hottest and coldest months of the study site in Gambella. The major part of the germination took place within a month and a half, but pots were kept for 3 to 6 months in the glasshouse to monitor later emergence of seedlings. Then all emerged seedlings were removed and the pots were stirred, watered and left for a further one month to stimulate germination of any remaining seeds in the soil. Emerging seedlings were identified, recorded and removed, or replanted for later identification. Identification was verified at the Royal Botanic Gardens, Kew.

Statistical analysis

Data were analyzed using analysis of variance (ANOVA) following the SAS General Linear Models procedure (Statistical Analysis Systems Institute 1997). The model used was a two way ANOVA with site and season (dates) as main factors.

Results

Seed bank sizes of Hyparrhenia confinis: effects of site and season

More than 90% of the soil seed bank in the burned sites was from a single graminoid species, *Hyparrhenia confinis*, whereas the remaining 19 taxa accounted for less than 10 % of the seed pool. The mean soil seed bank density of *Hyparrhenia confinis* as a function of site, depth and season is shown in Figure 1. Generally the number of seeds of this species varied greatly between sites, seasons and depths, whereas within sites the plots (which were at most 2 km apart and with similar vegetation) showed very similar patterns (Fig. 1). The two way ANOVA on effects of sites and seasons indicated that there was significant difference in the total soil seed densities of *Hyparrhenia confinis* between sites (Fig. 1, df.=3, F=13.40, $P<0.01$) and between seasons (Fig. 1, df.=2, F=41.49, $P<0.01$). No seeds of *Hyparrhenia confinis* were detected from the densely forested control plot (G) or from the dry forest control plots (X1 and X2). In contrast, seeds of *Hyparrhenia confinis* were abundant in the sites that burn more or less frequently (Fig. 1). At the beginning of the wet season (June) the soil seed pool of *Hyparrhenia confinis* was at a minimum in all burned sites. Thus, the soil seed banks were depleted during the wet season as a result of germination but were replenished in November and peaked in February, most markedly so in site A and site D. In November seeds of *Hyparrhenia confinis* were most abundant in site A followed by site B, C, D and X (in the order of decreasing seed abundance). However, in the dry period (February) the seed bank in site D was replenished too, resulting in relatively high seed numbers both in the woodland-wooded grassland intermediate (site A) and in one of the wooded grasslands (site D).

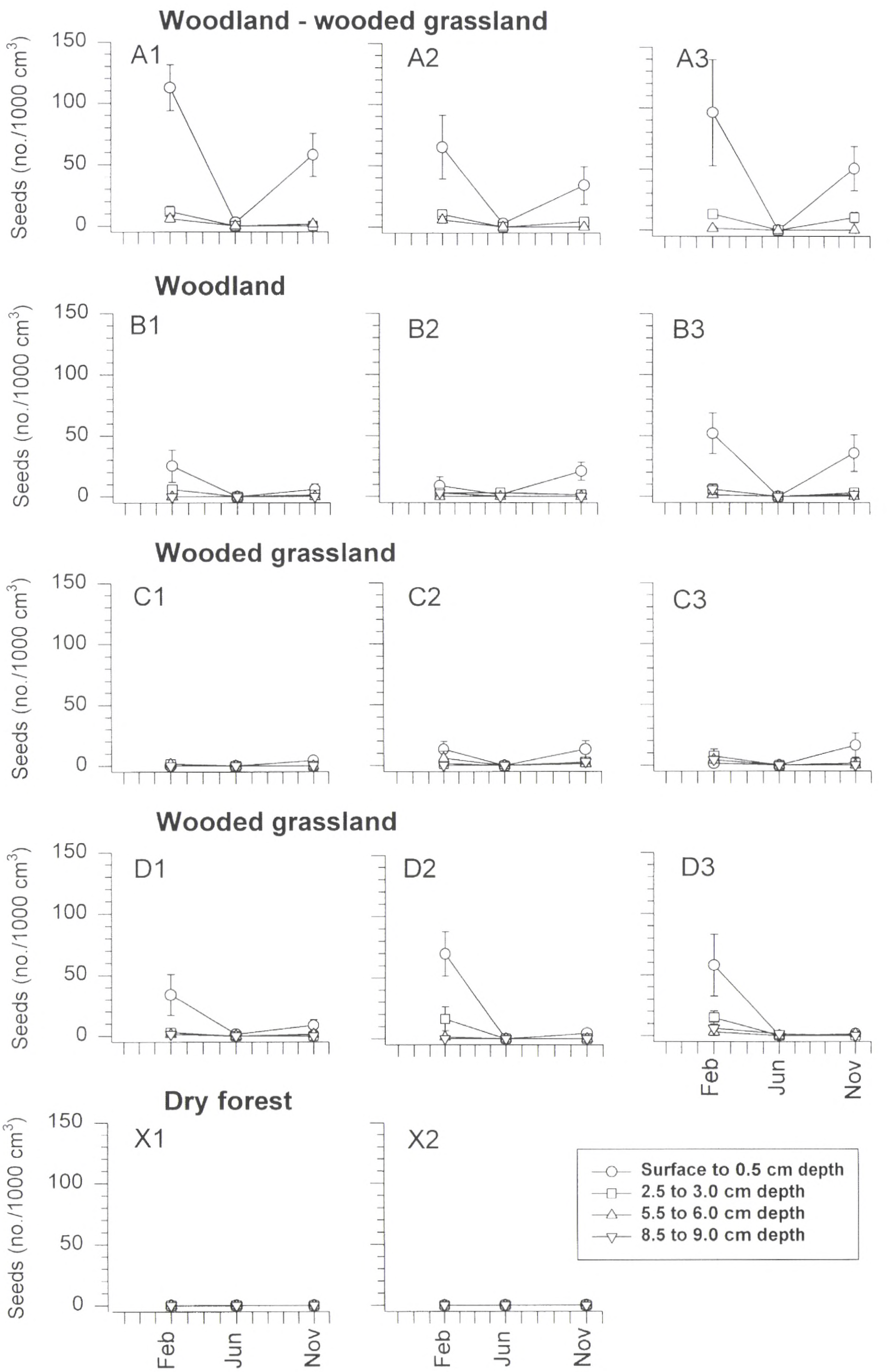
Vertical distribution of Hyparrhenia confinis seeds in the soil

Major changes in seed density of *Hyparrhenia confinis* with depth were observed. Most of the *Hyparrhenia confinis* seeds in the seed bank were found in the surface soil layer, *i.e.* between 0 and 0.5 cm depth (Fig. 1). The number of seeds at 2.5-3.0 cm depths was at most 20 % of that of the surface layer, with fewer seeds at even greater depth. A few viable seeds were found down to 9 cm depth in all burned sites.

Vegetation cover of Hyparrhenia confinis: changes with sites and season

Hyparrhenia confinis was absent from the densely forested and the dry forest sites. In the burned sites the cover of *Hyparrhenia confinis* was relatively higher in the wooded grassland sites A, C and D than in the woodland (site B) (Fig. 2). There were also significant differences in the cover of *Hyparrhenia confinis* between seasons (Fig. 2). In the plots of the wooded grassland sites C and D the cover of *Hyparrhenia confinis* was higher at the beginning of the

Fig. 1. Number of *Hyparrhenia confinis* seeds in February, June and November 1997 at four depths in soil profiles from three replicate plots of a woodland – wooded grassland intermediate site (A), a woodland site (B), two wooded grassland sites (C and D) and a dry forest site (X). Seeds of the grass were absent from the dry forest and densely forested sites (X and G). Each data point represents the mean of 6 replicate samples ±1 standard error.



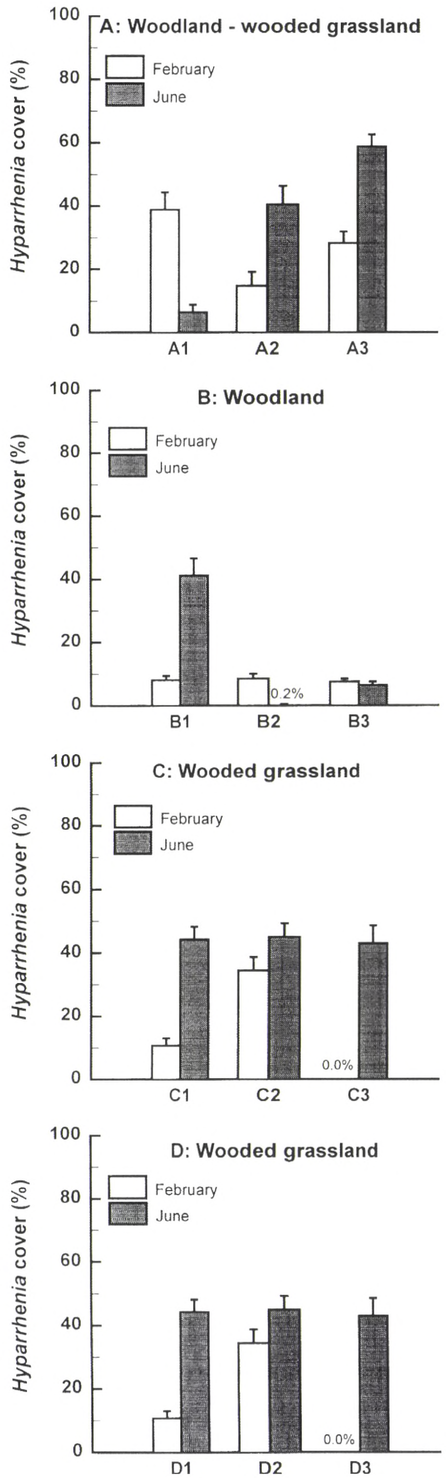


Fig. 2. Above-ground cover of *Hyparrhenia confinis* in February and June 1998 in a woodland – wooded grassland intermediate site (A), a woodland site (B), and two wooded grassland sites (C and D). The grass was absent from the dry forest and densely forested sites (X and G). Each bar represents the mean cover of *Hyparrhenia confinis* in 3 replicate plots per site, with 20 quadrats examined per plot, ±1 standard error.

rainy season (June) than in the dry season (February), at which time fire had removed the above-ground parts of *Hyparrhenia confinis* completely. In the woodland – wooded grassland intermediate (site A) and the woodland (site B) the variable grass cover in June between plots within sites was probably due to spatial differences in rainfall pattern right in the beginning of the rainy season.

Discussion

The soil seed banks of the regularly burned savanna woodland sites of the study area were almost entirely dominated by one grass species, *Hyparrhenia confinis*. According to Phillips (1995: 348) this species is an annual, and the high number of seeds recorded in the soil in the frequently burned sites in this study seems to support this notion. The herbarium specimens investigated for the Flora of Ethiopia pointed towards annual growth habit, although the material was scant when the account for the Flora was written (Sylvia Phillips, pers. com., 1999). However, our field observations of sprouting from stem bases in this species suggests that a large proportion of the individual grass shoots observed in the rainy season may actually come from perennial bases of individuals surviving light fires. These shoots were attached to the old stem bases and did not emerge from germinating seeds. Hence, the success of this species in the frequently burned savannas of the Gambella region could be ascribed to its dual modes of recovery after fires: by sprouts from the base and by germination from the large seed bank in the soil. More work is needed to elucidate the relative importance of the two means of regeneration of the *Hyparrhenia confinis* savanna after the dry season.

The major input to soil seed bank of *Hyparrhenia confinis* was largely in the beginning of the dry season, *i.e.* between November to January, similar to the seed dispersal of many other plants in the study area (pers. obs.). Consequently, *Hyparrhenia confinis* had the highest density of seeds in the soil in the dry season (February). Fire has usually taken place by this time (Jensen & Friis 2001), but there is still a high soil seed bank of this species to initiate growth after the fire when the rainy season begins and soil nutrient availability is increasing (*Jensen* et al. 2001). In addition, *Hyparrhenia* seeds from the study area tolerate temperatures up to 90°C for 1 and 5 minutes and 120°C for 1 minute (Menassie & Michelsen 2001). Seeds in the soil benefit from the scattered "small rains" in April and May, and by the end of June most of the *Hyparrhenia confinis* seeds have germinated and the seed bank is therefore exhausted. In the beginning of the dry season following the growing season, the grass dries up and disperses the seeds, leading to the restoration of the *Hyparrhenia confinis* seed pool in the soil between November and February. It follows that a late fire at the end of the dry season or beginning of the wet season (*i.e.* between May and June) which occurs with low frequency in the region (Jensen & Friis 2001) could be detrimental to this species as most seeds germinate during the "small rain" and the soil seed pool is very low in June.

The high cover of *Hyparrhenia confinis* in the wooded grasslands, the intermediate cover in the woodland and the absence of this and other grass species such as *Andropogon schimperianus, Hyparrhenia filipendula*, *Hyparrhenia rufa*, *Loudetia arundinacea* and *Penisetum polystachion* from the more densely forested control plots corresponds to the general pattern of grass cover in savannas across Africa (Menaut *et al.* 1995). The seed abundance in the soil partly reflects this pattern, with absence of *Hyparrhenia confinis* seeds in the densely forested control plots, relatively low seed density in the woodland, and high seed density in one of the grasslands and in the woodland-grassland intermediate. However, the seed density of *Hyparrhenia confinis* was very low in the one of the grasslands (site C), possibly because of absence of fire the previous year causing a relatively high fire intensity the next year due to high fuel load (which might have led to the observed wood fires and fire damage to trees in this particular site, and to high mortality of seeds in surface soil).

Seasonal changes in the size of the seed pool were large but easily explained. The high above-ground cover of *Hyparrhenia confinis* recorded in the rainy season (June) corresponds to the low seed density at the same time, at which most of the seeds stored in the soil have germinated and contributed to the high cover of the species. In contrast, in the dry season (February) the grass cover is low and the species survives, at least partly, as seed propagules in the soil, which are high in number at that time. The seasonal fluctuations in grass cover observed in these Ethiopian savanna types differ from the lack of seasonal changes in the amount of grass biomass in higher altitude forests of Ethiopia (Michelsen *et al.* 1993) which experience less changes in climate through the year and in which fires are rare or absent.

The input of seeds, their capacity for dormancy and the loss from the seed pool determines the density of seeds and the seasonal changes in the abundance of viable seeds in the soil (Enright 1985; Demel Teketay & Granström 1995; Dalling *et al.* 1997). The almost complete lack of germinating seeds in June suggests that the vast majority of the seeds has either germinated, or does not survive more than half a year of burial. However, seeds deep in the soil may be important for regeneration after late, strong fires that could be detrimental to the survival of individuals of *Hyparrhenia confinis*. The current fire regime of the study sites, high frequency and relatively low intensity, seems to maintain the dominance of *Hyparrhenia confinis* both as seeds in the soil and in herbaceous stratum of the vegetation as a whole.

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