ADDIS ABABA UNIVERSITY
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SURVIVAL STRATEGIES AND ECOLOGICAL PERFORMANCES OF PLANTS IN REGULARLY BURNING SAVANNA WOODLANDS AND GRASSLANDS OF WESTERN ETHIOPIA, GAMBELLA

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Abstract:

The survival mechanisms of plants in response to fire were investigated to understand the ecological performances of plants in frequently burning plots of savanna woodlands and grasslands. These studies included: strategies of post-fire regeneration and resistance of tree-bark to fire; plant cover, leaf nutrient and condensed tannin concentrations following experimental burning treatments and relationships between fire and seasonal variations in leaf condensed tannin; soil seed bank dynamics; influence of heat on seed germination.

Regeneration mechanisms of vegetation were studied along a transect line by quantifying foliar cover and frequency of individual plant species regenerating by resprouting, by seedlings or both, during the dry season and the early wet season. Resprouting plants (both facultative and obligate) significantly contributed to post-fire recovery, comprising 98.5 % of total vegetation cover. The contribution of seedlings to cover and abundance immediately following fire was negligible, but seedling density increased in the early rainy season, 4 to 5 months after fire. The vigour of resprouting and seeding among species in different plant growth forms was discussed in relation to fire regimes. The role of tree bark thickness to survival was studied. Results indicated that tree bark resistance to fire varied interspecifically related to bark thickness, other characteristics and age of the plant.

The effects of three treatments: fire, biomass additions and ash fertilisation on plant cover, leaf nutrient (N, P, K) and condensed tannin concentrations were examined prior to experimental burning and after 90 and 210 days. There was a strong effect of fire on the cover of grasses and tree seedlings ($P<0.05$), whereas the effect of fire and other treatments was not significant on the cover of broadleaved plants and shrubs/trees. There was a significant effect of fire on the plant species richness after 90 days. The concentrations of N, P, and K and leaf condensed tannins were higher in broadleaved plants than in grasses. The effect of the different treatments on the level of N, P and K and condensed tannins are discussed. The changes in vegetation composition and herbage quality with fire, biomass and ash treatments are small compared to the changes between seasons. Therefore, the current fire regime (i.e. a regime with early annual burning of relatively low intensity) appears to maintain the present balance between the various plant forms.

The levels of leaf condensed tannin and the relative amount of tannin to nitrogen of 11 plant species were compared between seasons and between vegetation types. Mean condensed tannin concentrations varied between seasons, plant species and different plant growth forms, but seasonal variations and concentrations in single plant species were in most cases independent of vegetation type. Seasonal differences are probably due to leaf phenology, i.e. concentrations are high in new leaves emerging right after fire, and decrease during leaf expansion. Condensed tannins for individual species ranged from 2 to 400 mg catechin per g leaf dry weight. Trees contained higher amounts of condensed tannins and showed higher rates of tannins to nitrogen than grasses, with shrubs having intermediate concentrations. Facultative browsers may avoid tree foliage during the dry season when concentrations of tannin are high, while concentrations of tannins in the different life forms are more similar in the rainy season. Fire disturbance results in nutrient mobilisation and evolution of resprouting traits, and hence reduced selection pressure for the production of carbon-based defence chemicals by rapidly growing species.

In the study of soil seed bank dynamics, soil samples were collected from different sites at different seasons from different soil depths. The seedling emergence technique was used to determine the size and taxonomic composition of the soil seed bank. Results indicated that even if establishment of a soil seed bank is one of the strategies of fire escaping mechanism, it is only an alternative pathway used by few species, mainly graminoids.

The influence of exposure of seeds to heat treatments on the subsequent germination of 21 plant species was analysed, to reveal the response of seeds to fires and the plant regeneration after fires. Seeds were subjected to five different heat intensities (60, 90, 120, 150 and 200°C) for 1 and 5 minutes to simulate the situation during fires. Germination performance of the 15 species after different heat intensities and duration of heating were compared. Frequent and light burning of the savanna in the study area seems to enhance germination of most of the studied plant species.

This thesis is based on the following six original papers submitted to or accepted by international journals. The titles and names of the authors are as listed below:

Paper 1. Menassie Gashaw, Michelsen, A., Jensen, M., Friis, I., Sebsebe Demissew & Zerihun Woldu. (Under submission). Soil seed bank dynamics of regularly burning savanna woodland and grassland in Gambella region, western Ethiopia.

Paper 2. Menassie Gashaw & Michelsen, A. (In press). Soil seed bank dynamics and aboveground cover of a dominant grass, Hyparrhenia confinis, in regularly burned savanna types in Gambella, western Ethiopia. *Biologiske Skrifter fra Det Kongelige Danske Videnskabernes Selskab.*

Paper 3. Menassie Gashaw & Michelsen, A. (Submitted). Influence of heat on seed germination of plants from regularly burning savanna woodlands and grasslands in Ethiopia. *Journal of Plant Ecology.*

Paper 4. Menassie Gashaw, Sebsebe Demissew, Zerihun Woldu, Michelsen, A., Friis, I. & Jensen, M. (Under submission). Strategies of post-fire regeneration and resistance of tree-bark to fire in regularly burning savanna woodlands and grasslands of western Ethiopia.

Paper 5. Menassie Gashaw, Michelsen A. & Jensen, M. (Under submission). Plant cover, leaf nutrient and condensed tannin concentration following experimental burning of tropical savanna woodland.

Paper 6. Menassie Gashaw, Michelsen A. & Jensen, M. (Under submission). Seasonal variation in leaf condensed tannins to Nitrogen quotients in dominant trees, shrubs and grasses in regularly burning savanna woodlands and grasslands.

1. Introduction

Survival strategies of plants to fire-stress was defined in DeBano *et al.* (1998) as the inherent abilities of plant's tissue to withstand high temperatures (i.e. heat tolerance) and the ability of vegetative parts to survive the passage of fire (heat resistance). Grime (1977) identified three primary strategies in plants; i.e. the competitive, stress-tolerant and ruderal strategies in habitats with all the possible interactions between high and low stress with high and low disturbances. In fire-prone ecosystems, one could find all forms of the different primary strategies identified by Grime (1977). A plant is killed directly by fire when the temperature of internal living cells is raised to the lethal level. Plants escape the direct heating effect of fire spatially by withdrawing their sensitive parts to sheltered positions (e.g. underground organs or lignotubers, soil and canopy seed banks), and temporally by adjusting the timing of seed dispersal, flowering, fruiting, leaf and bud formations with fire seasons. The production of lignotubers and other adaptive traits such as soil seed banks and protected seeds or buds require considerable allocation of nutrient resources by the plant. Larcher (1995) for instance indicated that the survival strategy of plants in regularly stressed habitats is not directed at maximising productivity, but rather at achieving a compromise between productivity and survival.

Response of plants to the effect of fire differs from plants to plants and is different for different parts of a plant such as seed, root, flower, fruit, bark and foliage. This is due to differences among plants in their capacity to tolerate and resist heat. According to Larcher (1995) and DeBano *et al.* (1998) heat tolerance of plants is related to tissue moisture content, presence of sugars, pectin, and other plant tissue substances. There is consensus that stress as a constraint and as a stimulant, apart from affecting the individual, also promotes the development of better-adapted genotypes, as it is clearly seen along a stress gradient. Therefore, the different plant adaptive traits confer the existence and perpetuation of the species in fire-prone environments and enhance its ecological performances, such as increases plant abundance and richness, levels of plant nutrients and defence chemicals.

Savanna woodlands and grasslands are always in a dynamic state in which vegetation structure and composition vary spatially and temporally in response to climate, fire, herbivory, plant available water and soil nutrients. These ecosystems have been studied by various people to indicate that fire regimes (such as intensity, velocity, frequency, season and type of fire) and the successional stage of individual plants at the time of burning determine the degree by which fire can alter the structure and composition of plant communities (Bilbao *et al.* 1996, DeBano *et al.* 1998, Baruch & Bilbao 1999). Fire regimes according to Braithwaite (1996) are characteristics in turn determined by weather conditions, topography, fuel type, characteristics and load. Plant species composition is also an important, independent variable affecting fire characteristics and impacts. Equally important, the various fire adaptive traits of individual plant species determine changes or shifts in post-fire species composition and dominance in fire-prone ecosystems. This is further explained in DeBano *et al.* (1998), who pointed out that the study on plant's survival strategies to fire is important to determine the impact of fire on vegetation. The method of persistence in fire-disturbed environment, conditions of establishment and the life history characteristics of plant species are important attributes that provide information on post-fire successional patterns. Fire can alter vegetation composition by either elimination or introduction of new species in the burning habitat, or by changing the relative frequencies and cover of plant species. The balance of the different plant growth forms (grass, herbs, shrubs and trees) will then be affected.

Many plants in fire-prone ecosystems survive fire by storing their seeds either in the soil or in the canopy, commonly referred as soil seed banks or canopy seed banks, respectively. Simpson *et al.* (1989) defined soil seed bank as viable seeds present on the soil or in the soil or in association with the litter layer. Storage of seeds in the canopy for more than a year in order to escape fire, i.e. serotiny, is not observed in our study area. Serotiny is common for some trees in Mediterranean climate, where according to Enright *et al.* (1996), plants store their seeds in the canopy for longer period until the fire season passes, and such seeds germinate after they fall to the ground triggered by changes in environmental factors.

Some species use entirely sexual reproduction, from soil or canopy seed banks that are protected by hard seed coats or insulating pods or fruits. In addition to these protective tissues, 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. Therefore, soil seed banks considered by many authors as one of the survival strategies of plants, which reduces mortality of seeds by fire. The mortality of seeds following burning according to Arianoutsou & Margaris (1981), Keeley (1992) and Whelan (1995) depends on the intensity of fire and depth of seed burial in the soil.

The seed bank input is determined and contributed by both local and long-range seed dispersal. Fire as an external factor aids seed dispersal by triggering ejection of seeds from the fruit or pod (e.g. seeds of *Tylosema fassoglensis* and *Entada africana*, in our study area). Water percolates into the soil and animals such as small arthropods, insects and other soil macro-organisms play major roles in vertical and horizontal movement of seeds in the soil, facilitating the storage of seeds at deeper soil layers, and hence, according to Baskin & Baskin (1998) their survival of fires. The inputs and outputs of seeds directly control seed density, floristic composition, species diversity and genetic reserve; life history processes indirectly influence all these parameters. Simpson *et al.* (1989) noted that changes in the direction and speed of seed input and output processes over time govern soil seed bank dynamics.

Seed banks may be either transient, i.e. seeds that germinate within a year of initial dispersal, or persistent, with seeds that remain in the soil for more than 1 year. Persistent component of the seed bank according to Simpson *et al.* (1989) and Trabaud (1994), embodies a reserve of genetic potential accumulated over time that represents proximate genetic diversity for the population and ultimate genetic expression on which natural selection can act.

Ethiopian dry afromontane forests and woodlands have been explored for their seed bank characteristics and germination ecology in relation to the study of land degradation, forest clearing and rehabilitation (Demel 1992 & 1993; Demel & Granström 1995, 1997a & 1997b, Kebrom & Tesfaye 2000). However, information on the role of seed banks is lacking from fire–prone savanna woodlands in Ethiopia as well as from such woodlands elsewhere in Africa. Therefore, the study on soil seed banks in fire-prone ecosystems provide information on the role of the soil seed banks in the regeneration of plant communities that ensures community conservation and restoration.

Vegetation in the study areas often burns at least once a year. After the onset of the dry season, fire sweeps the aboveground vegetation. The next fire generally occurs in patches, because of the discontinuity of fuel, which enable plants to escape at least the occasional second and subsequent fires. During the course of these fires, plants and their seeds are exposed to different temperature ranges due to variable amounts of plant biomass, differences in relative moisture and wind intensity. Martinez-Sanchez *et al.* (1995) observed variable effects of fire on seed germination that on one hand high fire temperature kills seeds (Baskin & Baskin 1998) and on the other hand, stimulation of seed germination is observed by Thanos & Georghiou (1988) in fire-prone ecosystems by the strongly increased post-fire seedling densities of certain species.

Vegetative sprouting is another alternative means of reproduction, which is a common regenerative strategy of plants in diverse ecosystems, particularly in ecosystems, which experience long summer droughts and frequent fires. According to James (1984), Flinn & Wein (1977), the deeper these subterranean plant parts are located in the soil, the greater the survival rate. Sprouting structures serve as a source of dormant buds and may provide nutrient and water reserves for plants.

A combination of both modes of reproduction, i.e. sprouting and seeding may be found in a single species, but Keeley & Zelder (1978) noted that often reproduction after fire is exclusively by either seeding or sprouting. Moreover, sprouting in fire-prone environment could possibly be coupled with rare opportunities for seeding, which is aided by various forms of seed dispersal, particularly long distance one, and hence enable plants to have a wide distribution and genetic variability. This is further explained by James (1984) that the "K" mode of reproductive selection, which is vegetative reproduction, increases fitness of the genet, in like manner the "r" selection, which is sexual multiplication, yields genetic flexibility and hence greater potential fitness of offspring in an environment with many microsites. In a related study, Larcher (1995) noted that in populations exposed to long-term stress, selection gradually brings about a transition from a reproductive strategy (r-strategy) to a conservative survival strategy (K-strategy). Various reports from sites frequently exposed to harsh conditions indicated that selection favours plant types reproduce mainly by vegetative means.

In addition to these adaptations, barks of trees are important to resist fire. A number of authors like Fahnestock & Hare (1964), Hare (1965), Gill & Ashton (1968) and Gill (1980) have contributed in this field to indicate that sensitive parts of trees such as phloem, cambium, sapwood and meristematic tissues are protected from radiant heat by insulating bark. However, if fire is intense and of long duration these sensitive parts could successively be killed, which ultimately resulted in death of the whole individual. According to the results of all these authors, the time taken for the cambial cells to reach lethal temperature of 60°C (sufficient to coagulate proteins, Precht *et al.* 1973) when heat is applied to a tree trunk is a function of both bark thickness, size of tree diameter and thermal properties of the bark. Hence, bark resistance to fire varies with plant size and among species.

The significance of the various adaptive strategies of plants to fire is to improve their ecological performances such as cover, species richness and forage quality. DeBano *et al.* (1998) for instance has made a number of studies and compiled works from various authors to show that fire can affect forage quality by altering the phenological profiles of plant communities. Riggs *et al.* (1996) supported the studies by DeBano *et al.* (1998) in that they also showed change in vegetation composition as a result of burning may alter the post fire phenologies of the communities. DeBano *et al.* (1998) further noted that the importance of fire-induced phenological shifts to nutritional limitations depends largely on fire severity, extent of burning, and the seasonal pattern of nutritional constraints on the herbivores involved. Through its effect on nutrient availability, fire could determine the quality of herbage. The studies of plant defence strategies to herbivory as a function of nutrient availability has been well documented in Bryant *et al.* (1988, 1991a & 1991b) and Palo *et al.* (1993). These authors remarked that shortage of nutrients and nitrogen (N) in particular might result in a high production of carbon-based defence compounds (such as phenols and isoprenoids) at the expense of growth. In contrast, high availability of nutrients may result in a lower investment in carbon-based defences and increased growth, but alternatively high production of nitrogen-based defence chemicals such as alkaloids and cyanogens. There are evidences showing seasonal variations in the acceptability of foliage of savanna vegetation to herbivores, and according to Cooper *et al.* (1988) and Cooper & Owen-Smith (1985) unpalatability to browsing ruminants among plant species is associated primarily with their contents of condensed tannins. Condensed tannins play major role to protect plant cell walls against microbial and fungal attack; as a consequence, they inhibit fermentation of cell wall components by symbiotic microflora in the digestive tracts of mammalian herbivores, thereby deterring the nutritional quality of plant species with relatively high contents of these tannins. Hence, such species tend to be rejected as food by ungulates.

Considerable interspecific variations in condensed tannin content have been observed in many studies, Coley *et al.* (1985) and Coley (1986) accounted these changes presumably to environmental and ontogenetic effects, i.e. young fresh leaves are the plant's most valuable foliage and are, therefore, defended to higher extent by chemical defence than senescent leaves. However, high level of defence chemicals in young leaves is not always correlated with low herbivore pressure as some insects, fungi and microbes even prefer damaged leaves with high amounts of condensed tannins (Hartley & Lawton 1987). Macauley & Fox (1980) further noted that variations in condensed tannins could be due to both seasonal trends and leaf phenology, if the species produces new cohorts of leaves several times during the year. In contrast, if leaves are produced only once a year, seasonal trends cannot be separated from the effects of leaf ageing.

In Africa, the knowledge about the quality of leaves of dominant trees, shrubs and grasses in wooded grasslands and woodlands for grazers and browsers is restricted to certain well investigated ecosystems such as the Serengeti and the southern African plains (Bryant *et al.* 1989, McNaughton *et al.* 1985, du Toit *et al.* 1990, Tietema *et al.* 1991, Palo *et al.* 1993). We hypothesised that fire may affect the nutrient supply to dominant vegetation and thereby influence the plant nutrient concentrations and the production of grazer deterrents such as condensed tannins. Therefore, we studied the leaf condensed tannin and the tannin to nitrogen concentrations of dominant plants of the savannas of western Ethiopia, its seasonal changes and the possible difference between the tannin level of specific plant species in vegetation types ranging from woodlands to wooded grasslands.

In order to understand the influence of the existing fire regime on vegetation structure and composition of the woodland and savanna grasslands in Gambella region, western Ethiopia, this study is aimed at the investigation of the survival strategies and ecological performances of plants, and to provide information for the management and conservation of natural and biodiversity resources.

2. Literature review

2.1. State of the problem

Natural and man-made fires regularly clear vast areas of rangeland vegetation in many parts of the world, the latter accounting for most of the fires (Trabaud 1994, Lock 1998). The impact of fire on vegetative resources such as timber, forage and wildlife habitats is diverse and may be beneficial or detrimental to the sustainable use of the resources. Currently 40 % of the tropical lands are occupied by savannas, where 80 % of fire incidents are occurring in savannas, and hence Solbrig (1996) remarked that changes in vegetation composition and loss of biodiversity as a result of fire disturbances are intensifying. Therefore, there is a need to assess, study and understand changes in vegetation structure and ecosystem functions as a result of changes in fire regimes, and to make this information available for management and conservation of tropical savanna ecosystems.

2.2. Background

In the following paragraph fire effects on natural and biodiversity resources are discussed briefly:

2.2.1. Effects of fire on soil and water system

Effects of fire on soil physical, chemical and biological properties are complex and vary depending upon the fire regime, i.e. severity of fire, amount of aboveground and understorey vegetation burned, proportion of area burned and frequency of fire intervals. DeBano *et al.* (1998) reported from various studies that fire affects the soil physical properties mainly by destroying organic matter, which is essential for maintaining soil structure. Destruction of organic matter by fire destroys the soil structure and reduces bulk density and porosity, which decreases infiltration and increases runoff and erosion. The chemical soil system contains both organic and inorganic components that interact with each other continually, and could also be affected by fire. Various studies have shown the fate of nutrients contained in plant biomass and soil organic matter during and following fire. Some of these effects are (1) direct gaseous volatilisation into the atmosphere during fire. (2) Particulate loss in smoke. Phosphorus and cations are frequently lost into the atmosphere as particulate during combustion (Raison *et al.* 1985). (3) Deposition in ash on the soil surface. According to Christensen (1973) and Kauffman *et al.* (1993), these highly available nutrients can subsequently be leached into the soil or lost by surface runoff and wind erosion. The effect of fire on soil biological properties or composition is reported by various authors, DeBano, *et al.* (1998) for instance, indicated the effect of fire on various forms of soil organisms, range from microbiota (such as algae, protozoa, fungi, bacteria, and cyanobacteria) to macrobiota (including insects, earthworms, and plant roots). According to these authors, the effects of fire on soil organisms could be directly by killing or injuring the organisms, and indirectly by its effect on plant succession, soil organic matter transformations, and microclimate.

There is very little study on the effect of fire on water budgets compared to the study on the effects of fire on soil. Similar to the effect of fire on soil resources, the effects of fire on water resources are determined largely by the severity of the fire. When vegetation and litter accumulations and other decomposed organic matter on the soil surface are destroyed by fire, reductions in interception and evapotranspiration can result, along with decreases in infiltration and increases in overland flow and subsurface flow. Increases in runoff often translate into increases in stream-flow discharge. Fire in addition to affecting the quantity of water it also affects water quality, by affecting the water physical, chemical and biological characteristics.

2.2.2. Effects of Fire on ecosystem flora and fauna

The effects of fire on vegetation are broadly explored to indicate fire has obvious impacts to vegetation. Fire affects natural ecosystems by consuming plants, altering successional patterns, and changing vegetative resources such as timber, forage, and wildlife habitats. Based on the results of the various studies, Hanes (1971), Naveh (1975), Purdie & Slatyer (1976) and Young & Evans (1978) noted that patterns of vegetation development in the fire-prone ecosystems differs from the classical concept of vegetation succession that was first developed by Clements. According to the Clementsian concept, fire is an external force disrupting the natural stability of the original climax community (Abrahamson 1984 a, b). However, now fire is rather seen as an integral part of the ecosystem acting on vegetation to result in the evolution of various forms of adaptive traits, therefore enhances genetical and ecological diversity.

These evolutionary traits, such as the presence of soil seed banks or canopy seed banks, that are protected by hard seed coats or insulating pods or fruits (Arianoutsou & Margaris 1981, Keeley 1992, Whelan 1995 and Enright *et al.* 1996), lignotubers, bulbs, stolons, rhizomes, and the ability to sprout from remnant stems and root parts (Vines 1968, Hanes 1971, Flinn & Wein 1977 and Zammit 1988), allow plants to regenerate rapidly after fires.

Fires are widespread in many African savanna woodland types. According to Swaine & Whitmore (1988), fire may result in canopy gaps, which suppress the seed germination of some plant species not favored by canopy gaps, and stimulate that of other species. Thus, light-demanding species such as savanna grasses may benefit from burning. Demel (1997) reported that 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. Odgers (1996) and Metcalfe & Turner (1998) have shown that soil seed banks are important as means of plant establishment after disturbance.

According to Dalling *et al.* (1997), the composition of a soil seed bank and its contribution to the restoration of a cleared or burned area basically 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. The composition of vegetation, particularly on disturbed sites, is often dominated by species that are abundantly represented in the site's seed bank. Valbuena & Trabaud (1995) noted that knowledge of the soil seed bank composition and dynamics in regularly burned sites may be used to predict the potential composition of post-fire regeneration. 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 small seed bank or none at all. Swaine & Hall (1983) and Uhl *et al.* (1981) questioned whether the numerical dominance in the seed rain or seed bank could put the species at an advantage over others with few or no seeds in the soil seed banks. This is because, according to Drake (1998) 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 subsequent post-fire environment.

Although there has been much focus on the study of soil seed banks and about 1000 papers have been listed from temperate areas alone (Vyvey 1989, in Skoglund 1992), there is very little work on soil seed banks of tropical ecosystems. Furthermore, this fraction mainly consists of studies of arable lands and wet forests (Skoglund 1992). In a review of soil seed bank studies from the tropics Garwood (1989) cited only 43 papers, of which most are on tropical rainforests. From the scant studies, it is therefore difficult to establish general principles regarding the role of soil seed banks in vegetation dynamics in dry tropical ecosystems, particularly in the fire prone ecosystems.

Some plants in fire-prone habitats have evolved hard seed coats to survive and regenerate after fire. Many effects have been proposed in the enhancement of seed germination by fire, among these: fracturing of hard seed coats, stimulation of seed embryos, desiccation of seed coats and release of ethylene, ammonia and other substances in the plant-derived smoke (Keeley 1987, Brown 1993, Brits *et al.* 1993, Baskin & Baskin 1998). Martin *et al.* (1975) noted a number of methods, which have been developed to artificially break down or remove dormancy caused by impermeability of seed coats. These methods include scarification with sandpaper, soaking seed in sulphuric acid or in hot water, or treating seeds with dry heat, which is analogous to heating by burning of vegetation. In similar studies, Keeley *et al.* (1985) and Gonzalez-Rabanal & Casal (1995) reported that fire resulted in increased post-fire germination; this was attributed to reduction of inhibitory substances in soil and litter produced by plants or microorganisms, and to chemical stimulation of seed germination from charred wood. Waxy or pectic materials associated with palisade cells in the seed coat are impermeable to water, but the effect of these substances is reduced when seeds are exposed to moist or dry heat, which probably removes these substances. Watson (1948), Mucunguzi & Oryem-Origa (1995) and Herranz *et al.* (1998) reported seed impermeability to water due to waxy coverings is a major obstacle to germination in some legumes. Baskin & Baskin (1998), Hanley & Fenner (1998) further explained that germination is promoted in legumes because cracks induced by dry heat make the strophiole permeable to water. Therefore, thermal pre-treatment scarifies hard-coated, water-impermeable seeds and thus may promote the germination of such seeds. Furthermore, seeds of some plants are enclosed within pods, which provide much more heat resistance than provided by the seed coats alone, and fire may be a prerequisite for the release of seeds from such fruits.

However, severe burning is reported to affect germination of seeds and reestablishment of post-fire vegetation negatively. As a direct effect, high temperatures kill seeds. The indirect effect of fire has been reported by Brits (1986) and Hodgkinson & Oxley (1990) who concluded that fire might inhibit germination by causing subsequent increases in the soil temperature and decreases in the soil moisture content. Knowledge of germination responses of seeds to high temperatures, charred wood and to smoke derivatives may help to employ fire as a management tool in maintaining plant diversity in fire-prone ecosystems (Brown 1993, Keith 1997). However, little is known about the influence of fire on seed germination in African savanna plants.

Many authors have proposed different models and patterns of vegetation development and succession in areas subjected to periodic disturbances. Noble & Slatyer (1980) described a set of species attributes, which are considered vital to the survival and perpetuation of species inhibiting regularly disturbed sites. They recognised three groups of vital attributes: (1) the method of survival strategies on the site during and after disturbance, (2) the ability to establish and grow to maturity in the developing community, (3) the time it takes for a species to reach maturation after perturbation. The three successional models of Connell & Slatyer (1977), which are the facilitation, tolerance, and inhibition models, explain rate of vegetation recovery after major perturbation.

of resprouters. In another study, Verdu (2000) suggested that since seeders allocate more resources to above ground parts (high shoot to root ratio unlike sprouters), it is expected that seeder seedlings grow faster than sprouter seedlings. Seeders in South Africa were found to grow faster than resprouters and colonise tall forests acquiring an advantage in the light limited habitat (Kruger *et al.* 1997) and tended to be taller than congeneric resprouters. Similarly in the Mediterranean Basin, higher seedling growth rates allow seeders to establish rapidly after fires, behaving as 'disturbance-dependent recruiters' (Lloret 1998), whereas resprouters recruit independently of fire behave as 'disturbance-free recruiters'.

Many authors such as Trollope (1984), Fox (1998) and Bilbao *et al.* (1996) considered that fire and grazing are the major environmental factors determining the structural and functional organisation of savanna ecosystems. There is a general consensus that fire favours the development and maintenance of the wooded grasslands by preventing growth and maturity of shrubs and trees to a taller fire and grazing-resistant stage. However, once the tree/shrub strata have become dominant and suppressed the grass cover, fire does not produce a pronounced effect because of insufficient grass fuel for intense fires. Trollope (1984) has studied fire in the wet savanna regions, and he indicated that rainfall is adequate (above 600 mm yr^{-1}) to produce a large amount of fuel biomass under grazing conditions. As a result, the high fire frequency may control coppice growth of woody plants. In contrast, in more arid savanna ecosystems rainfall is too low and erratic to support frequent fires under grazing conditions, and fires may therefore not prevent the regeneration of woody plant cover from coppice and seedling recruitment.

Various studies indicated that disturbances such as cutting, fire and heavy grazing exert powerful selection pressures on plant communities and trigger different adaptive responses, such as physical and chemical defence mechanisms or rapid growth to replace the lost parts and utilise the available resources competitively. Perevolotsky & Haimov (1991), Moreno & Oechel (1991) and Grime (1977) for instance explained that fire opens the canopy, provides transient flushes of nutrients and plays a major role in nutrient recycling. As a result, rapidly growing species are selected for traits, which enable rapid regrowth of aboveground parts. The sprouting mode of regeneration strategy in plants according to Bryant *et al.* (1991b) therefore might further reduce the intensity of selection for defences that deter herbivory. Riggs *et al.* (1996) and DeBano *et al.* (1998) have noted that the change in vegetation composition as a result of burning basically alters the post-fire phenologies of plant communities. That means burning can substantially alter the quantity of herbage production and quality of food resources that are available to herbivores. According to these authors, the importance of fire-induced phenological shifts to nutritional limitations depends largely on fire severity, extent of burning, and seasonal pattern of nutritional constraints on the herbivores involved.

Fire removes old and poorly digestible plant parts with low concentrations of proteins and minerals. As a result of burning, ash and unburned plant residues are deposited and increase availability of nutrients in the soil (Daubenmire 1968; Raison 1979; Kellman & Sanmugadas 1985 and Kellman *et al.* 1985; Abbadie *et al.* 1992; Dumontet *et al.* 1996). This facilitates increased nutrient uptake by surviving forage plants and therefore livestock and other herbivores benefit from the resulting post-fire changes in forage quality. Christensen (1977) has supported this result, and he reported that during the first post-fire growing season the content of crude protein, fibre and nutrients such as N, P, K, Ca and Mg are higher in forage plants growing on burned sites than in plants growing on unburned sites. Therefore, according to Bergström (1992), the quality of browse can be described mainly in terms of nutrients, fibre and digestibility.

Fire, grazing stress and physical damage on leaves has been reported by many authors to induce chemical responses, most prominently the production of condensed tannins. Tannins are members of a large group of polyphenol compounds, which contain two distinct classes of chemicals, hydrolysable and condensed tannins. This study has analysed leaf-condensed tannins from dominant plants of the study sites, since condensed tannins are known for their effect as defence chemicals from herbivory. Structural and functional groups of condensed tannins are described in Swain (1977), Haukioja & Niemela (1979), Zucker (1983) and Hagerman & Butler (1991), in which condensed tannins are polymeric compounds formed by the acid-catalysed condensations of the precursors proanthocyanidins. Flavans are the monomeric precursors of condensed tannins in which either the 3 position alone, or positions 3 and 4 of the heterocyclic ring are hydroxylated.

Condensed tannins occur almost universally (Harborne 1984, Glyphis & Puttick 1988), for example in ferns and gymnosperms, and are found widespread among the angiosperms, particularly in woody species. They form complexes with a variety of target molecules such as structural proteins, starch, pectic substances and cellulose through multiple hydrogen bonds between the phenolic hydroxyl groups of tannin and the target molecules. In the plant cell, tannins are located separately from the proteins and enzymes of the cytoplasm, but when plant tissue is damaged, the tannin reaction may occur, making protein less accessible (Wisdom *et al.* 1987). Due to this effect, Fox & Macauley (1977), Zucker (1983), Glyphis & Puttick (1988) and Tuomi *et al.* (1988) considered condensed tannins as a non-lethal feeding deterrent against a wide range of organisms from microbes to mammals. Furthermore, tannins impede plant litter decomposition.

However, lack of induced chemical defence in response to simulated browsing was reported by Chapin *et al.* (1985). They further noted that the high tannin concentration in juvenile seedlings and stump sprouts which are established after fire, or resprouting after intensive browsing might be explained as a reversion to the physiologically juvenile growth stage rather than an induction of a specific defence. Hence, the inducible chemical responses of plants to herbivores may not be direct defensive responses, but according to Tuomi *et al.* (1984) it is a reflection of mechanisms, which alter the plant carbon/nitrogen balance in response to stress caused by defoliation.

Therefore, according to Bryant *et al.* (1983) and Bryant *et al.* (1988), plant defensive chemistry may also be determined by plant physiological responses to resource availability. These authors explained that the carbon to nitrogen balance determines carbon allocations either to growth or to chemical defences. Hence, particularly in nitrogen deficient sites, plants may have excess carbon, which is then available for production of carbon-based defences such as tannins. Through its effect on nutrient availability, fire could determine the quality of herbage. Any factors that influence the carbon to nitrogen balance such as symbionts, respiration and photosynthesis may also control production of condensed tannins. Furthermore, Owen-Smith & Copper (1987) noted that plants with structural defences are common on fertile soils, whereas those that are protected by carbon-based chemical defences against vertebrate herbivory are prominent on nutrient-deficient soils. However, Prudhomme (1983), Coley (1986) & Briggs (1990) reported that if carbon is limiting growth, the production of chemical defences is costly for plants due to competitive interactions among metabolic pathways involved in growth and defensive chemical production.

Fire in addition to its effect on forage quality, injures and kills wildlife directly by burning and suffocation, however, according to Riggs *et al.* (1996) and DeBano (1998), these losses are negligible in most instances. The indirect influences of fire on wildlife populations are largely important and common such as the changes in food, cover, and structural diversity. Mosaics of food resources and cover create structural diversity, an important element in wildlife habitat quality. A large fire of high severity often reduces interspersion of food and cover, producing uniformity in habitat condition. The effects of fire on wildlife food, cover and diversity components of wildlife habitats depend on long-term, landscape-scale interactions among the affected plant communities and wildlife populations. Interactions of morphological, physiological, and behavioural patterns of wildlife species with the plants and climate of post-fire environments define capacities of the wildlife species to adapt to the habitat changes brought about by fire.

2.2.3. Impacts of fire on the atmosphere

Various compounds are produced during the exothermic reactions of combustion and these compounds are either oxidised further or released into the atmosphere. DeBano *et al.* (1998) have reviewed studies from various authors on the effects of fire on atmosphere, and they reported that the effects of smoke and its constituents on the environment could range from localised visibility impairment to possible changes in the global climate. The effects of fire on air quality and chemistry are largely a result of the primary chemical products and secondary emissions of combustion (secondary emissions are air pollutants emitted into the atmosphere as a result of photochemical transformation of primary emissions from fuels). Primary chemical products of combustion include chemical products volatilised (but not oxidised) during combustion process, compounds formed by partial or complete oxidation of organic fuels, and compounds pyrosynthesised during combustion. Some of these products such as CO_2, water vapour, CO, SO_2, N_2O, and O_3 are reported in Larcher (1995) and DeBano *et al.* (1998).

The largest contribution of atmospheric emission from fire is CO_2. Although CO_2 is not an air pollutant, it is a greenhouse gas and, therefore, has a potential to impact the global climate by contributing to greenhouse gases. Fire accelerates the rate of CO_2 return to the atmosphere. This addition of CO_2 into the air is a concern where large tracts of forests are being cleared, burned, and converted into agricultural crop production. The second largest chemical product of fire is water vapour. The main concern about emissions of water vapour from fire is generally their contribution to smoke and visibility reductions in areas near to fire. Particulate matter is one of the more important groups of chemical products emitted by fire because of its importance to human health (aggravating respiratory problems) and its effect on visibility. Hydrocarbons released by combustion are a diverse group of compounds. Hydrocarbons that are a concern to air quality and human health are aldehydes and polynuclear aromatic hydrocarbons (PAH_s). Aldehydes found in smoke that can cause eye, throat, and nose irritations of mucosal membranes are formaldehyde and acrolein. DeBano *et al.* (1998) reported that aldehyde-production in fire ranges from 0.6 to about 2.5 percent of the fuel weight. Methane is the third most abundant greenhouse gas contributing to global warming. According to DeBano *et al.* (1998), about 10 percent of the methane released into the atmosphere annually comes from the combustion of biomass.

Bearing in mind that fire has all these diverse effects on the ecosystems' natural and biodiversity resources, this study has focused and aimed at the investigation of the survival strategies of plants and its implications to their ecological performances in regularly burning areas of western Ethiopia, Gambella. In the following objectives, the first three are designed to explore the different regeneration mechanisms of plants after fire disturbances, and the last two objectives are to investigate ecological performances of plants to the effects of experimental and wildfires.

3. Objectives of the study

The objectives of this study were:

(1) To identify the regeneration strategies of plants after fire disturbances, and to study the relationships between bark thickness and fire resistance among the dominant tree species and to relate this to the recovery strategy of tree species.

(2) To reveal the influence of the existing fire regime on vegetation dynamics, and forage quality in experimental burning plots.

(3) To estimate the stimulation or inhibition of seed germination caused by high temperatures reached in savanna fires.

(4) To investigate the role of soil seed bank in the regeneration of plants in fire-prone ecosystems, with an aim of quantifying the spatial and temporal dynamics of the composition of the soil seed pools and to determine, to which extent the species composition of the soil seed bank reflects the existing vegetation.

(5) To study the relationships between fire and seasonal pattern in the quotients of leaf condensed tannins to nitrogen from different vegetation types exposed to different levels of fire severity.

4. Methodology

4.1 Study area

The study area is situated about 500 m above sea level (a. s. l.) between 7°48′N, 34°17′E and 8°17′ N, 34°57′E on flat plains to undulating rocky areas with various types of savanna woodland in south western Ethiopia, Gambella (Fig. 1). The vegetation is characterised by savanna woodland with high productivity in the grass stratum and long dry periods. As a result, the vegetation is susceptible to frequent fires. 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) 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 (Fig. 2) (Ethiopian National Meteorological Institute, personal communication).

Four regularly burning sites (A, B, C, and D), and one unburned site (X) representing different vegetation types and fire severity were selected in the Gambella region. The location of the sites was determined with a GARMIN 45 GPS navigator. At each site three replicate plots with the size of 20 meters by 50 meters, maximally 2 km apart, were selected for the study, except at site X where it was only possible to establish two replicates. 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) could serve as controls or unburned plots, with the same plot sizes as the burned plots. Sites were selected on the basis of differences in their vegetation types and biomass compositions and hence, differences in burning intensities. 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 less intensively. Fire intensity was roughly estimated from the amount of grass biomass measured in each respective site (Jensen & Friis, in press), and following the method used in DeBano *et al.* (1998). Additional subjective indicators such as fire scars on trees, amount and color of charcoal remains and ash depositions were used to determine fire severity differences among sites. Description of the study sites is presented in Table 1.

Figure 1. Map of Gambella Region. The region borders to the Sudan (west), the Oromia Region (north east) and the Southern Nation, Nationalities and People's Region (south east). Modified from Ethiopian Wildlife and Natural History Society: Important Bird Areas of Ethiopia.

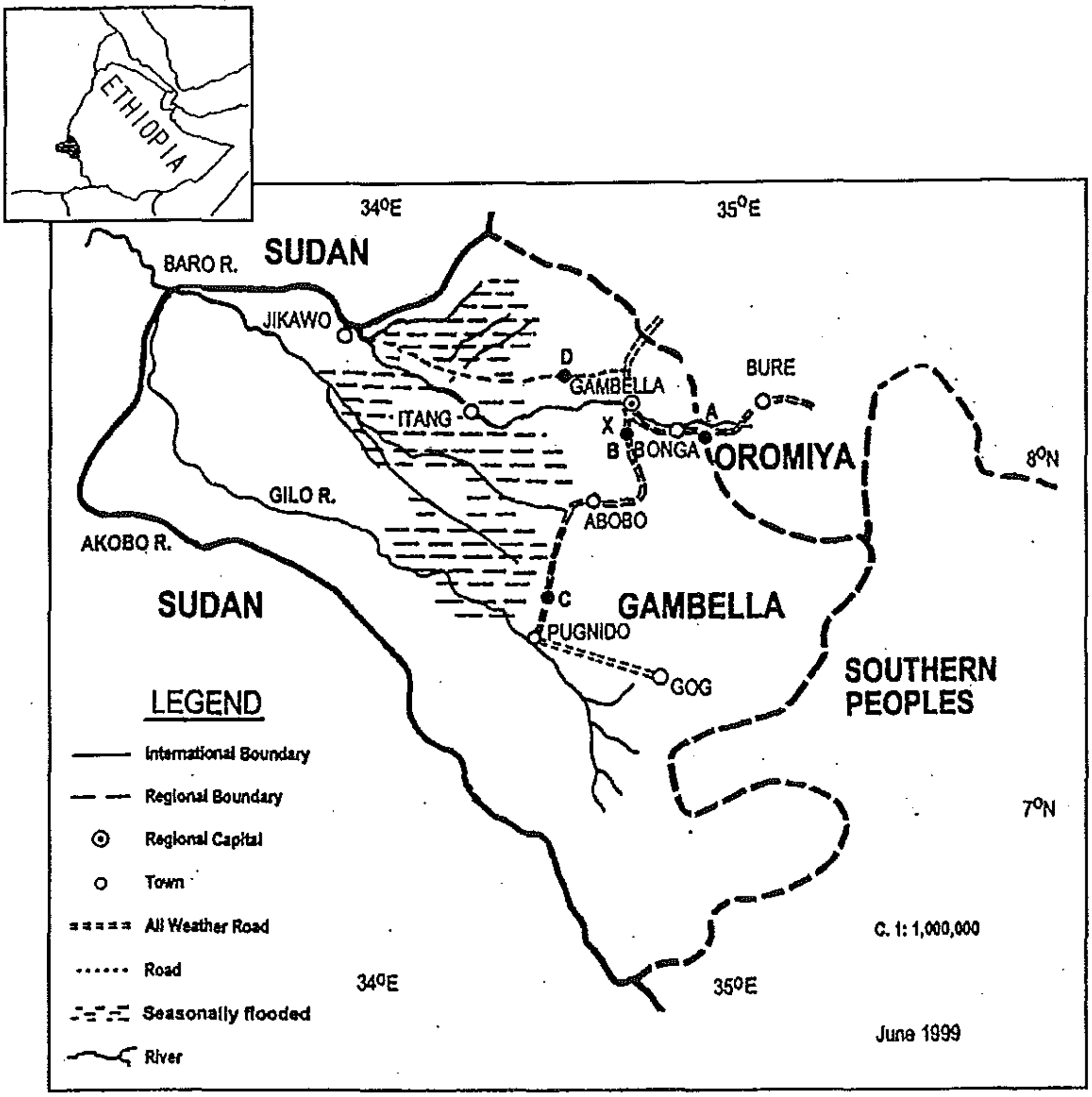
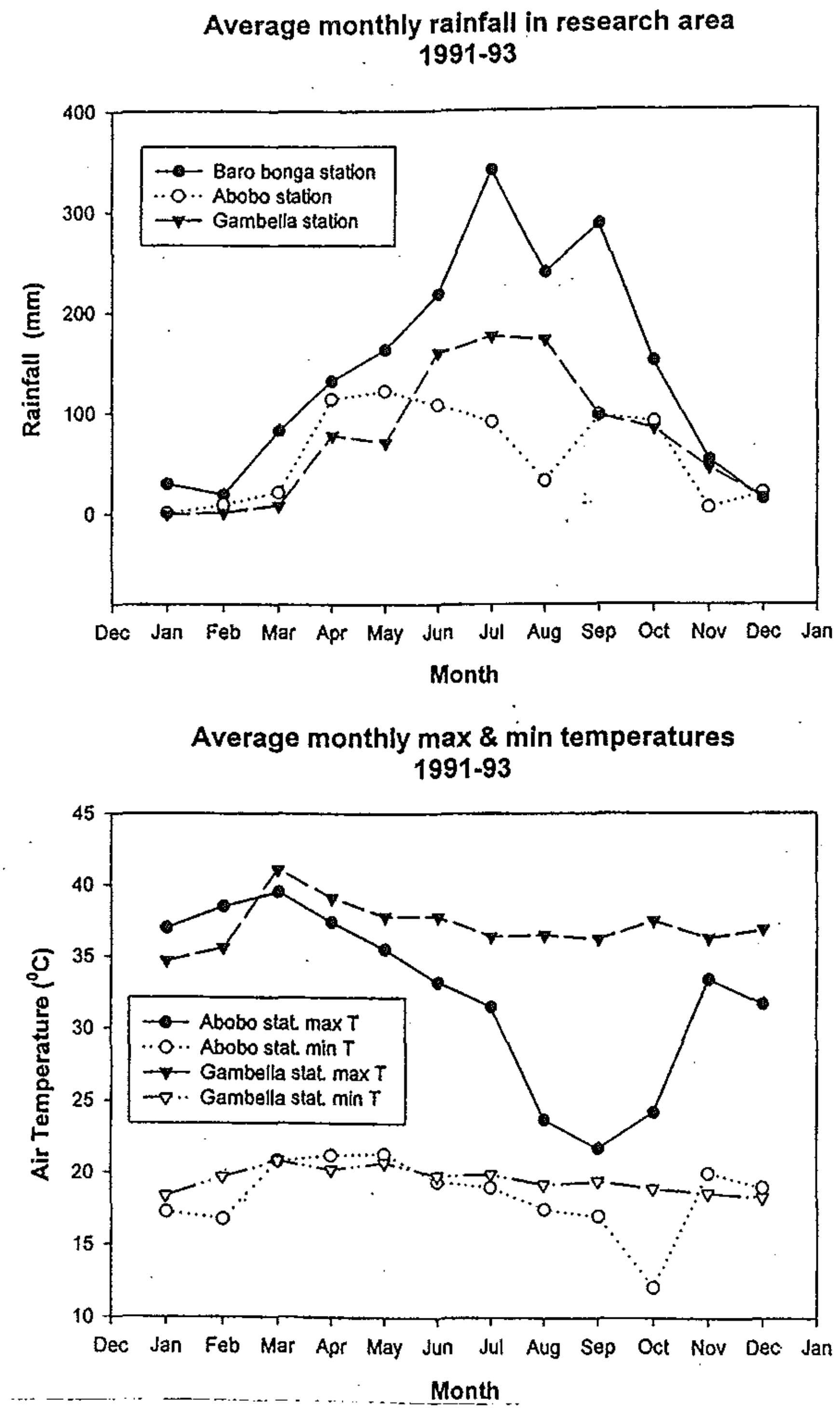


Figure 2. Annual monthly rainfall and maximum and minimum temperatures in the research area. Data obtained from the Ethiopian Meteorological Office in Addis Ababa, for the period of 1991-1993.



Average monthly rainfall in research area 1991-93

Average monthly max & min temperatures 1991-93

Table 1. Site description of

Sites	A
Position	8° 12' N, 34°
Altitude	c. 650 m
Rainfall	1000-1900 m
Temperature	18° - 40° C
Vegetation	Woodland - grassland (inte
Dominant trees	*Sterculia africa* *Pterocarpus luc* *Lonchocarpus* *Acacia senegal,* *Combretum co*
Crown cover (%)	29%
Density of trees (trunks/1000 m²)	160
Maximum tree height (m)	10-15
Dominant Grass	*Hyparrhenia c* *Loudetia simpl*
Grass biomass (t/ha)	7.0
Fire severity	Less intensive
Replicates	3 plots (20 x

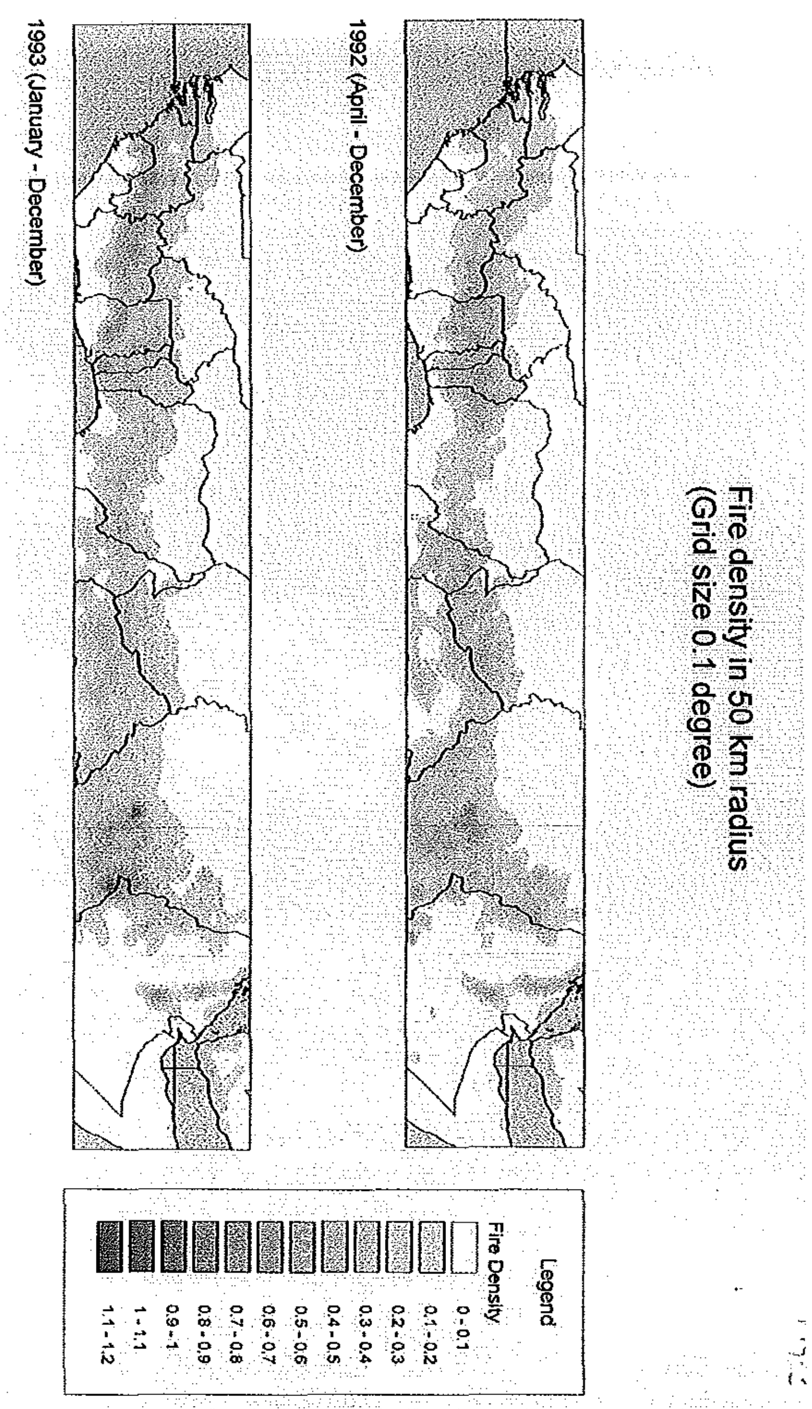
4. 2. Vegetation fire in the study area

Fire is largely anthropogenic and a deliberate action in the study area, i.e. to gain easier access into the bushes and woodlands for hunting, honey and fuel wood collection and to facilitate travels from one village to another. Our observations as well as local information suggests that the vegetation of the area burn at least once a year, and fire is common along major roadsides and around towns. Setting fires to encourage re-growth of fresh and palatable forage is not a common practice in the study area because of the prevalence of tsetse flies. A study of the effects of fire on plants, soil and local communities at Gambella has recently been published (Mengistu Woube 1998) with an emphasis on the geographical and sociological aspects.

The region is one of the most important biomes for wild fauna such as Elephants, Giraffe, Buffalo, Lelwel hartebeest, Waterbuck, Roan antelope, White-eared kob, Oribi, Topi, Reedbuck, Hippopotamus, Ostrich, Duiker, and Nile Lechwe and Warthog, although the present number and diversity of these faunal resources are much reduced and threatened.

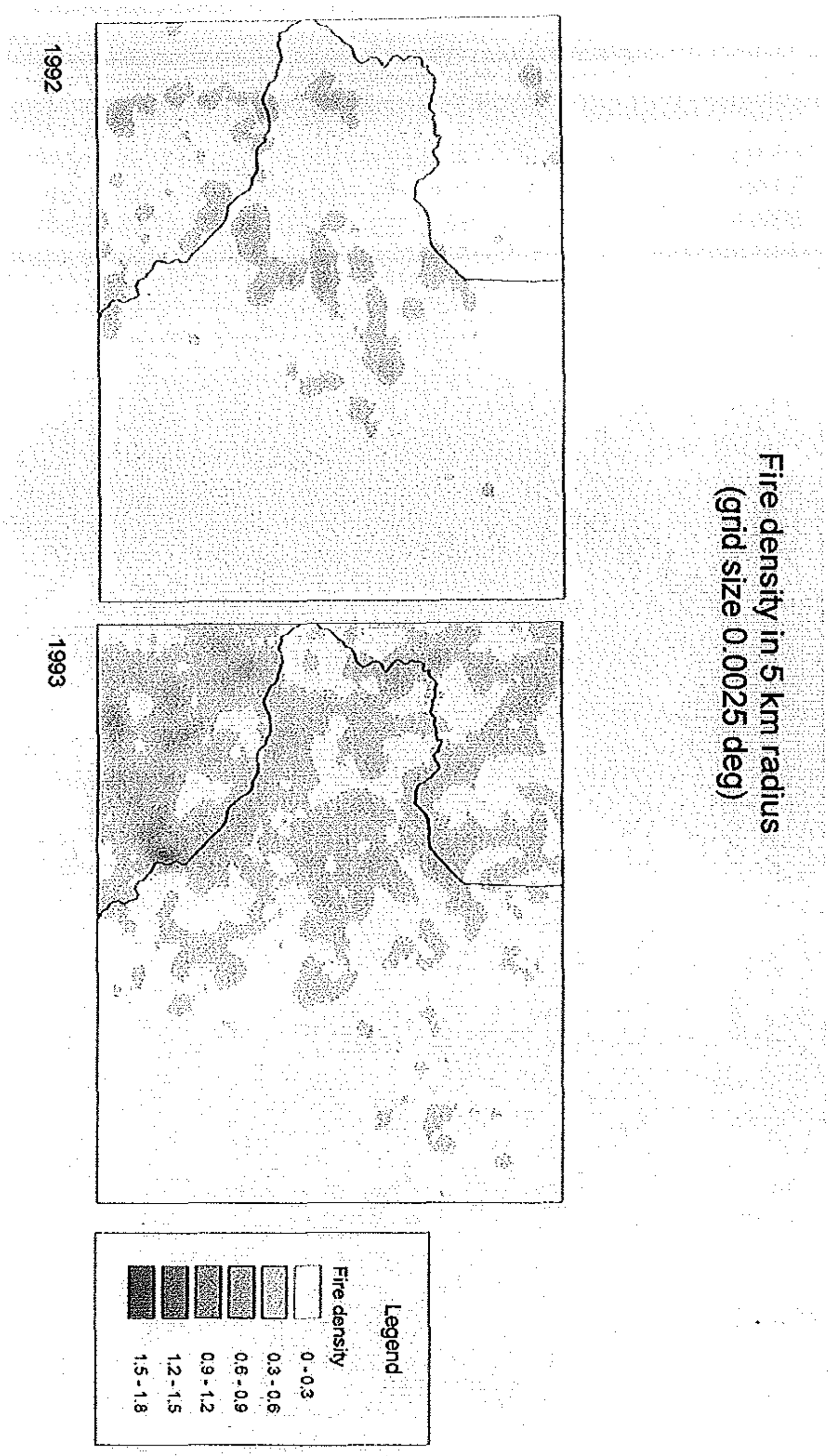
Processed satellite data on fire densities were obtained from the archive files of the Global Vegetation Monitoring Unit's Fire project at Space Application Institute, Ispra. The data was derived from daily satellite observations over the period from April 1992 to December 1993. Fire is wide spread right across the belt of Africa from Atlantic coast to Ethiopia (Fig. 3). The continental seasonal fire pattern is constant in Africa, where the grass biomass is large enough and dries out well enough to produce severe fires (Jensen & Friis, in press). The whole of the western lowlands of Ethiopia have fire densities comparable to the general pattern of fire across Africa and the highest fire densities in Western Ethiopia are found in Gambella Region (Fig. 3). Fire densities are lower in the areas to the north and south of Gambella, areas that are in the Oromia, Beni-Shangul-Gumuz and Southern People's regions (Fig. 4). Figure 5 and 6 shows zooming, in increasing resolution power of the fire densities of the Gambella Region. The major fire seasons in Gambella are between December and May. Fire incidence and density increased from December to April and declined in May, and no fires in the Gambella region have been detected from July to October (Fig. 7).

Figure 3. Fire density across Africa in April-December 1992 and January-December 1993. Fires have been recorded within an area of 50 km across; the scores have been marked on the map with a grid size of 0.1 degree. The maps are based on data from the archive files of the Global Vegetation Monitoring Unit's FIRE project at Space Application Institute, Ispra.



FIRES

Figure 4. A close up of fire density in Gambella, western Ethiopia in April-December 1992 and January-December 1993. Fires have been recorded within an area of 25 km across; the scores have been marked on the map with a grid size of 0.01 degree.



FIRES

Figure 5. Fire density of western Oromia and Gambella Regions in April-December 1992 and January-December 1993. Fires have been recorded within an area of 10 km across; the scores have been marked on the map with a grid size of 0.005 degree.

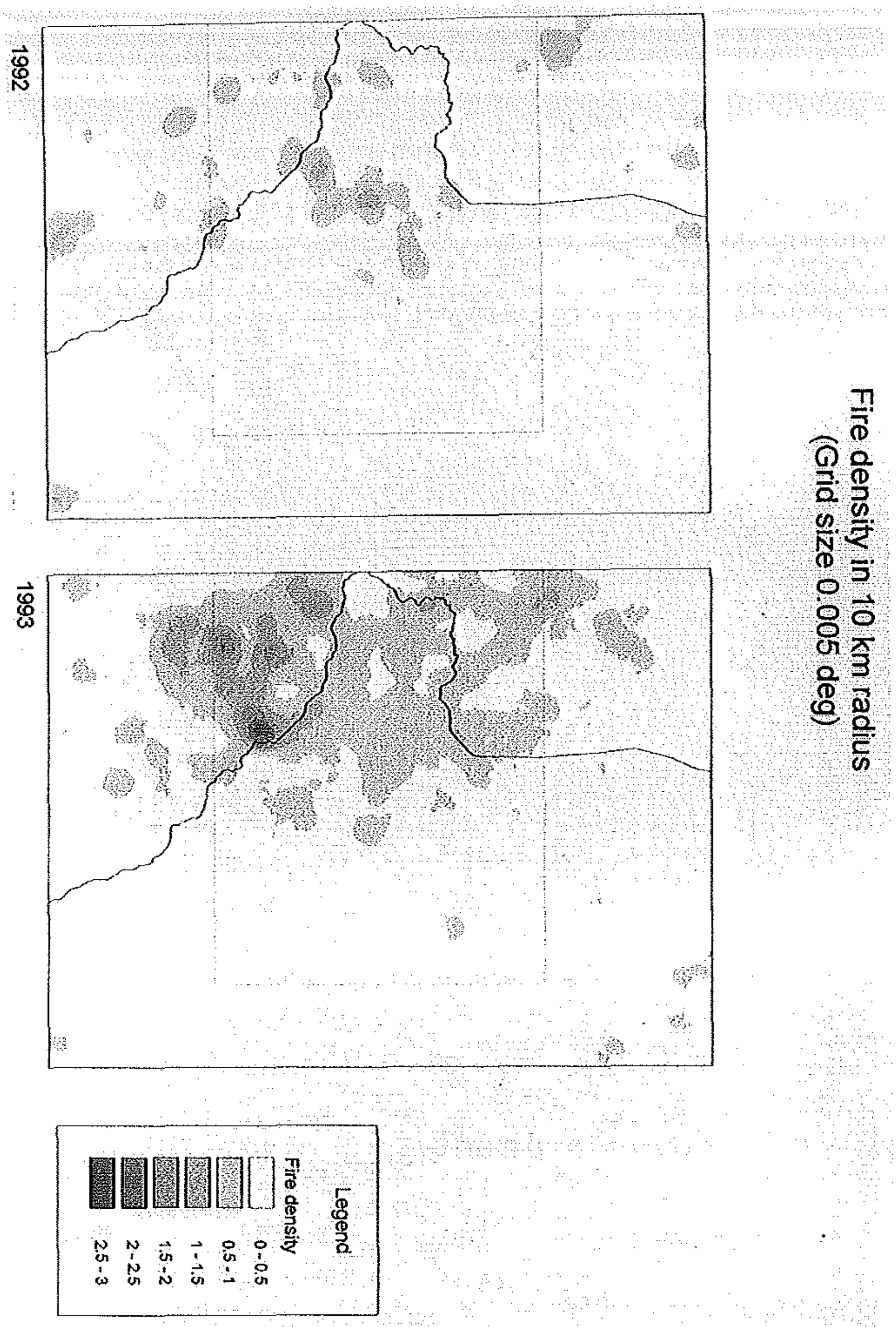
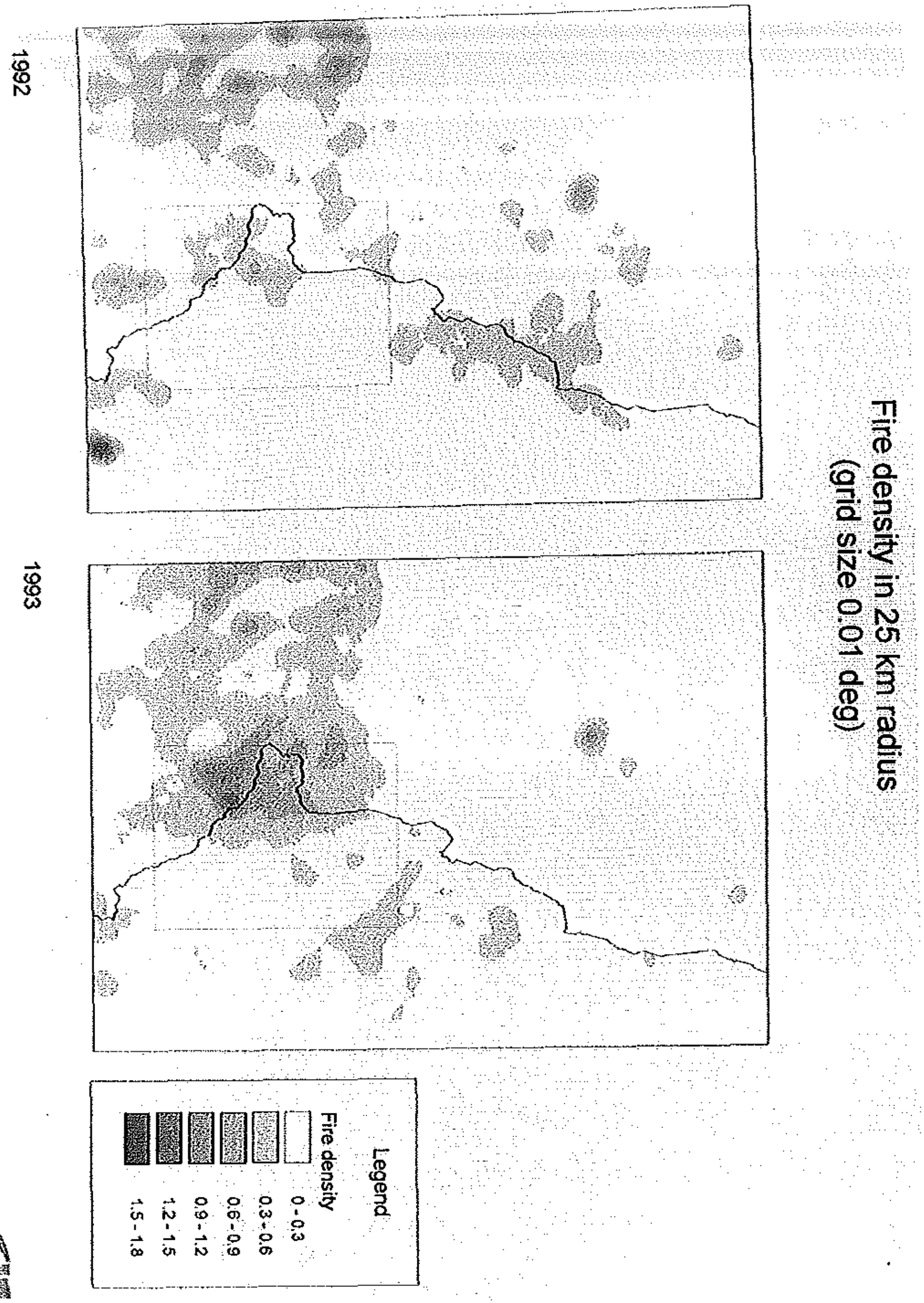
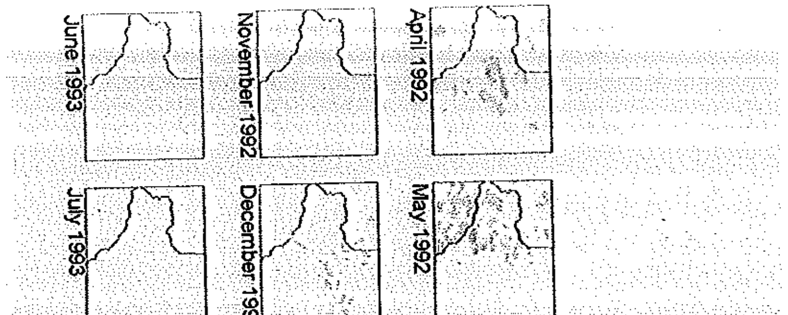


Figure 6. Fire density of Gambella region in April-December 1992 and January-December 1993. Fires have been recorded within an area 5 km across; the scores have been marked on the map with a grid size of 0.0025 degree.



FIRES

Figure 7. Monthly fire density of Gambella Region from April 1992 to December 1993.



4.3. Collection of samples

4.3.1. Collection of Soil samples

Soil samples for seed bank studies were collected from each of the 3 plots at sites A, B, C, D, and from X1 and X2, and from an unburned forest site, Gog (G). Six replicate spots were randomly selected for soil collection 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 for sites B, C, and D. For site A soil samples were taken from all depths except the deepest layer, i.e. 8.5-9 cm, because of stones and rocks obstructing digging any further below 6 cm depth. Each subsample had 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 from all sites were collected three times in a year, except site X and G, where samples were collected from one season only. The first soil sampling was in February 1997, which was in the hot and middle of the 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.

4.3.2. Collection of Seed samples

The seed samples for the experiment on the influence of heat on seed germination were collected in February and late October 1998 from wild plants growing in the regularly burning woodlands and wooded grasslands in the study area. Seeds were obtained from 21 species, mostly woody shrubs and trees, a climber, broadleaved herbs and grasses. Seeds of each species were collected either on the ground or from the canopy at different localities within the study area, and hence seeds originate from more than a single maternal parent, most frequently about 5-20 mother plants. Selection of species was based firstly on the dominance of the species in the study area and secondly on the availability of plants with mature seeds. In addition, seeds of one tree species (*Acacia albida* Del.), which is frequent in dry savannas across Africa, were obtained from outside the study area, and seeds of the grain crop *Eleusine coracana* (L.) Gaertn., which also can be found on disturbed soils in the area, were obtained from the market in Gambella town. Most of the species develop their seeds in the canopy or on shoots well above ground before the beginning of dry season (late October or early November). Most frequently, the seeds remain on the plants, and are dispersed in the first part of the dry season, between January and March. Fires are frequent between January and May, until the onset of the rainy season. During seed dispersal, some species predominantly release intact fruits such as pods to the ground, but in most cases, individual seeds are released from the fruits, and are directly exposed to fire. Furthermore, some plant species in the study area do not have pods (see table 6). For this reason, seeds from pod-bearing species were treated with their pods removed. In addition to these reasons, pods provide additional fire resistance to seed coats and depicts the fire resistance value by the seed coats alone. Also, the wings of *Combretum collinum* Fresen. and *Entada africana* Guill. & Perr. were removed prior to treatment. The seeds used in the treatment in *Ziziphus mauritiana* Lam. and *Clerodendrum capitatum* Hook. were in drupaceous fruits (the paired seeds in each drupaceous fruits taken as one seed unit) and within intact mericarps, respectively. Hence, the study focuses on the role of seed coats and any other tissues such as lemmas, glumes and waxy layers which protect the seed embryo from heat damage by fire. The working unit for the propagules of each of the studied species is defined in table 6.

Seeds were cleaned and sorted out by selecting the ones without evidence of insect and fungal attacks. The seeds were then stored for about three weeks in paper bags at 20-30°C before the treatments and germination experiments. Nomenclature follows Flora of Ethiopia and Eritrea (Edwards & Hedberg 1989—).

4.3.3. Sampling of plant samples

Aboveground plant biomass was collected for plant nutrient and condensed tannin analysis, 210 days (June 1998) and 1 year (December 1998) after the initiation of the experiment with fire, ash and biomass additions, i.e. at the beginning and the end of the growing seasons, respectively. Shrubs and tree saplings were not included in the sampling for plant forage quality determination because of their low frequency and clumped distribution. Grasses and broadleaved herbs were separated and air-dried in the field. The samples included senescing, yellow leaves.

4.3.4. Collection of leaf samples

In order to determine the relationship between fire and the seasonal variations of condensed tannins, leaf samples of 11 dominant trees, shrubs and grass species were collected from all the study sites, at four occasions, i.e. immediately following fire (February 97), and after four months (June 97), nine months (November 97) and 12 months (February 98). Tree leaves were collected 2 m above the ground, from the outermost part of the tree branches. Leaves of shrubs and grasses were collected at ½ - 1 m height. Within each plot, at least four replicate samples were collected from shrubs, trees or grass swards more than 5 m apart. Because of logistic constraints and restricted number of plant specimens in some sites, leaf material of all species was not sampled in all plots at all four sampling times. Samples in February appeared very fresh and green compared to the leaf samples collected in the other months or seasons as they had just emerged after fire events. The exception was *Acacia senegal*, which sprouted later than the February sampling.

4.4. Field experiment

4.4.1. Description of the vegetation and estimation of cover

In order to describe the vegetation and estimate cover, 20 quadrats, each with an area of 1 m^2, were positioned within each plot at 5 meters intervals along a 100 m transect line. Species rooted within each quadrat were identified and recorded, as the percentage cover of stems and leaves in each quadrat, estimated by visual inspection. Plants that proved difficult to identify in the field were collected for identification in the National Herbarium, Addis Ababa University and later sent to the Royal Botanical Gardens, Kew, UK and Botanical Museum, Copenhagen University, Denmark for further identification and verification. Check list of plant species collected from the research sites is attached as Appendix 1.

4.4.2. Analysis of plant regeneration

In order to classify the vegetation according to its regeneration strategy after fire, 20 quadrats each with an area of 1 m^2 were positioned within each plot of the four sites (A, B, C, D) at 5 meters intervals along a 100 m transect line. Data were collected from the four sites with different vegetation types and fire severity. At each site, three replicate plots with the size of 20 meters by 100 meters and maximally 2 km apart were selected (this time the size of each plot was changed from 20 m by 50 m to 20 m by 100 in order to fit the 100 meter transect line). Vegetation classification followed the terminology used in Keeley (1977), Keeley & Zedler (1978) and Trabaud (1987): (1) obligate seeders (species regenerating only from stored seeds), (2) obligate sprouters (species regenerating only from resprouting plant organs) or (3) facultative sprouters (species which show both types of strategies). Plant species rooted within each of the 20 quadrats per plot were recorded in late February 1998 (during the dry season) and in late June 1998 (beginning of rainy season), that is, a few weeks after fire and 4-5 months after fire, respectively. Species presence and estimation of foliar cover was recorded for individuals regenerating by sprouts or seed separately, and mean cover and frequency of regeneration in broadleaved herbs, grasses, trees and shrubs calculated. Cover was defined as the perpendicular projection of the live parts of each species rooted within each quadrat. Resprouts were defined as vegetative parts regenerated from underground sprouting structures with sign of fire scars in the dead stem bases, and similarly, seedlings were defined as independent plants with small root systems and no sign of pre-fire biomass, i.e. no charred stem bases. Trees above 3 m encountered in the transect were not included in the regeneration strategy study, instead measured for their bark thickness and diameter. In some doubtful cases, we excavated plants using hand tools or bare-hands to check for regeneration modes. Vegetation data were not collected from site C in February, because this site was burned while data were collected from the other sites.

4.4.3. Measurements of bark thickness and lethal temperature

The relationships between bark thickness and the time taken for the cambial tissues to reach an assumed lethal temperature of 60°C was measured on a range of size classes of live trees of 12 different species. Data from all sites were recorded in June 1998. The resistance of cambium to heating was measured for each tree species following the techniques used in Hare (1965) and Vines (1968). In all cases, diameter at breast height (DBH) and thickness of the bark were measured for each tree prior to the application of heat on the bark. An incision was made at 1 meter height of the tree and the sensor of the thermocouple was buried to a depth of 4 cm horizontally, beneath the bark or cork at the cambium. The cut was filled with a wooden plug after marking the exact position of the sensor of the thermocouple. Heat was then applied with a flame torch in the direction of the thermo-sensor with an intensity that could make the bark surface reach 100°C in one minute. Time was recorded at which the temperature of the cambium rose to 60°C (T_{60}). There were three replicate trees per species and size class.

4.4.4. Experimental block set up

This experiment is designed to study the effects of three treatments, i.e. fire, biomass and ash additions to plant cover, species number and plant forage quality in experimental burning plots.

Six replicate blocks each with the size of 10 m by 18 m were randomly selected. Each block was partitioned into 8 plots with the size of 2 x 2 m. The effect of three factors: fire, biomass addition (before burning) and ash fertilisation (after burning) were investigated with each of the eight possible factorial combinations repeated in six replicate blocks, i.e. with a total of 48 plots. The treatments were applied randomly within each of the six replicate blocks. Sampling from each plot was carried out in the central 1 x 1 m thus leaving a 0.5 m wide border zone around the sampling area. Vegetation around each block was cleared as firebreak in 2-m wide bands. The experiment was started in late November 1997 at the beginning of the dry season.

At day 0, extra fuel load in the form of grass biomass was added to 24 of the plots. An average of 480 g m^{-2} of biomass was added to each plot, which was equivalent to the standing aboveground grass biomass, hence leading to a doubling of the biomass in the treated plots. Following the addition of biomass, 24 of the 48 plots were burned at day 0. After burning, the 24 plots had ash added in an amount equivalent to that found in a burned area of the same size (roughly 15 g m^{-2}). During the fire, soil temperatures from two soil layers (1 cm and 5 cm) were measured in plots with added biomass (i.e. with a total of 960 g m^{-2}) and in plots with normal biomass (480 g m^{-2}). Temperature from the biomass added plots increased to an average of 48° C at 1 cm depth and 32° C at 5 cm depth from an initial level of 25° C and 20° C respectively, whereas temperature from the plots without biomass added increased to an average of 37° C at 1 cm depth.

4.4.5. Estimation of plant cover and species richness following experimental burning treatments

Presence and absence of plant species and cover of their green leaves in each experimental plot were initially recorded with visual estimation before burning, November 1997, i.e. in the end of the growing season. The same recordings were subsequently made on February 1998 (dry season) and June 1998 (first rain of wet season), i.e. 90 and 210 days after initiation of the experiment, respectively. It was not possible to record plant cover after 1 year because fires surrounding the plots were frequent and it was decided to give priority to harvest of biomass in blocks 1-3 before the approaching fire would burn all experimental plots.

4.5. Glasshouse experiments

4.5.1. Dynamics of the soil seed bank

The experiment on the role of soil seed banks to the recovery strategy and restoration of plants in frequently burning plots were carried out in the glasshouse of Addis Ababa University. Samples, which were collected for the study of soil seed bank dynamics, were kept separate, air-dried and then passed through a 4 mm sieve to remove vegetative 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. The soil was then 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. The pots were incubated in a glasshouse to a natural photoperiod and watered as required. Air temperature in the glasshouse during the study period ranged from 20 to 43°C, which is closer to a typical temperature range between day and night and the hottest and coldest months of the study site in Gambella.

The soil seed banks from the different sites were studied following the seedling emergence method (Kropac 1966, Roberts 1981). The major part of germination of seeds 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. Emerging seedlings were identified, recorded and removed, or replanted for later identification. Almost all seedlings were identified to species level, except one species that was identified only at the genus level (*Bulbostylis* sp.). Then all emerged seedlings were identified, counted and recorded before they were removed. The pots were then stirred, watered and left for an additional one month to stimulate germination of any remaining seeds in the soil.

4.5.2. Influence of heat on seed germination

The effect of savanna fires on seed germination of dominant species of the study area was carried out in the glasshouse experiment at the University of Copenhagen, Denmark. The experiment was done in two batches, i.e. seeds collected during February 1998 were used first, and the ones collected during October 1998 were used later. About three weeks after collection, seeds from each species were subjected to heat treatments according to ten different prescriptions: 60, 90, 120, 150, and 200°C, for 1 and 5 minutes duration. These are temperatures, which are likely to be reached at the soil surface or the first few centimetres below ground in savanna fires (DeBano et al. 1998). Dry heat treatments were accomplished using an oven with rapid insertion and removal of a wire tray containing the seeds. For each species, a total of 1,320 seeds in six replications of sets of 20 seeds were used for the heat treatments and duration of exposure. Untreated seeds were used as control (20°C), with the same number of replications and seeds as that of the heat-treated ones. For two species, *Entada africana* and *Tylosema fassoglensis*, 15 and 4 seeds per pot were used in 6 and 3 replicate pots per treatment, respectively, due to shortage of seeds. Treated and untreated seeds were soaked in water for 1-3 hours, and then sown individually by burying them at 1 cm depth in pots with heat-sterilised soil and sand. The pots were placed in a glasshouse with an average temperature of 20°C during the day and 15°C during the night and daylight of 12 hours. Pots were watered daily for the first week and then every second day until the end of the experiment. Germination, defined as the radicle emerging out of the seed coat, was recorded weekly. The experiment was completed within two and a half months after the last new seedling was recorded and new germination had ceased.

Seeds from six species, which failed to germinate with heat treatments, were additionally treated with charred wood or ashes on petri dishes in the laboratory. The same number of seeds and replicates were used as in the heat treatments. On each petri dish, five grams of ash from the field was spread and watered regularly to keep the filter paper moist. Seeds treated without ash were used as controls.

The mean seed size (length) and the weight of 20 seeds per species was measured in order to relate the maximal treatment temperature which was followed by germination to the average seed size and seed weight of the species.

4.6. Laboratory experiments

Laboratory experiments were conducted at the University of Copenhagen, Denmark. In order to study the relationship between fires and forage quality, laboratory experiments on plant nutrients and condensed tannins were undertaken for samples collected both from the experimental blocks and from the regularly burning sites (A, B, C and D). After the set up of the experimental block, plant N, P, K and condensed tannin concentrations were determined in experimental fire plots for a period of 1 year. Similarly, for samples collected from the different sites plant nitrogen and condensed tannin concentrations were also analysed and compared between the different vegetation types (sites) and the different seasons.

4.6.1. Determination of leaf N, P, K following experimental burning treatments and leaf nitrogen from the regularly burning sites.

The plant samples collected from the grasses and broadleaved herbs from the experimental blocks were milled and analysed for N, P and K. The same number of replicates per species and months, from the regularly burning sites (A, B, C and D) was also used for leaf nitrogen determination in the laboratory. The ground plant material was digested in concentrated sulphuric acid with Selenium as a catalyst (Kedrowski 1983). Nitrogen and phosphorus were subsequently measured with spectrophotometer using the salicylate method and molybdate method respectively. Potassium was measured by atomic absorption spectrometry.

4.6.2. Analysis of condensed tannins following experimental burning treatments and from the regularly burning sites

The concentration of condensed tannins in plant leaf material collected from the experimental burning blocks and from the regularly burning sites (A, B, C and D) was determined by the vanillin assay following the method outlined in Price *et al.* (1978). From each dried and ground leaf sample, 200 mg was extracted in 10 ml 100% methanol. Five millilitres of the vanillin reagent was then added into one millilitre aliquots of the extract. The red colour complex (anthocyanins) formed as a result of the reaction between the vanillin reagent and the condensed tannin polymers (acid hydrolysis of proanthocyanidins) were measured by spectrophotometer at 500 nm, with catechin as the condensed tannin standard.

4.7. Data analysis

The data were analyzed using analysis of variance (ANOVA) in the SAS statistical procedure (SAS Institute 1997). Plants from the soil seed bank and standing vegetation were grouped according to their respective habits of graminoids, broadleaved herbs, shrubs and trees and the model used was a 2 way ANOVA with site and season (dates) as main factor. Plant species richness in the aboveground vegetation stand and in the soil seed bank was compared at the level of 14 sampling points using the Spearman's rank order correlation coefficient. Compositional correspondence between the standing vegetation and the soil seed bank species at the sampling point level was compared with Sørensen's similarity coefficient.

To evaluate percent germination at week nine, a two-way analysis of variance (ANOVA) with the main factors duration (1 and 5 min) and temperature treatments (20, 60, 90, 120, 150, and 200°C), and the interaction between duration and temperature were employed for each individual species separately. Furthermore, a one-way ANOVA followed by Tukey's test was used for multiple comparisons of means (means from the final date, i.e. week 9) for each species and duration separately. Correlation between seed size and weight and the maximal temperature tolerated by seeds was evaluated by Spearman's rank correlation.

To assess the effect of plant survival strategies on plant cover and frequency three-way analysis of variance (ANOVA) with the main factors plant growth form, strategy and site, and all interactions were employed. This was followed by Tukey's test to compare means of plant growth forms and sites, for each strategy separately. To evaluate the contribution of tree bark to heat resistance, a two-way analysis of variance (ANOVA) with the main factors bark thickness and DBH was employed. Correlation between bark thickness, DBH and time taken for cambium to reach 60°C (T_{60}) was tested by Spearman's rank correlation.

To reveal the effect of fire, biomass and ash treatments on vegetation cover and forage quality in experimental plots, data were analysed using a 4 way ANOVA with fire, ash, biomass and block as main factors, and with all interactions between fire, ash and biomass included. Data were in some instances transformed to meet assumptions of homogeneity of variance. The significance level was $\alpha=0.05$. Tendencies ($0.05<P<0.10$) towards significant effects were also reported.

The level of condensed tannins in each species was compared using a two-way analysis of variance (ANOVA), with main factors date and plant species. Differences in the concentration of condensed tannins between plant growth forms were evaluated with Tukey's test, with $\alpha=0.05$.

5. Results

5.1. Strategies of post-fire regeneration and tree bark resistance to heating

5.1.1. Foliar coverage by the different strategies

Generally resprouting plants made the greatest contribution to foliar cover and abundance of the vegetation in the frequently burning savanna woodlands. Only 8 of the 56 species were found to be obligate seeders and contributed only 1.5% of the foliar cover compared to a cover of 98.5% made up by resprouters (both obligate and facultative). The proportion of individual species occurring as seeder or sprouter or in both strategies, the frequency of species encountered along the transect lines and their life forms are given in Appendix 2. A large number of species recorded as obligate resprouters of broadleaved herbs and trees/shrubs, were as frequent as the facultative sprouters, but their contribution to foliar cover was less (Table 2). Few species were facultative sprouters. Unlike obligate seeders and obligate sprouters, populations of the same species in facultative sprouters regenerate either by seedlings or sprouting, following fire. All grass species recorded were facultative resprouters, and they contributed to most of the foliar cover (54%) compared to facultative resprouters among the broadleaved herbs and trees/shrubs (13.3%) (Table 2).

Table 2. Species abundance of the three regeneration strategies in respect to the different growth forms.

Number of species calculated in percent out of a total of 56 species.

Strategy	Growth form	Number of species	Frequency (%)	Cover (%)
Obligate seeder	broadleaved herb, tree/shrub	14	12.2	1.5
Obligate sprouter	broadleaved herb, tree/shrub	66	42.5	31.3
Facultative resprouter	grass, broadleaved herb, tree/shrub	20	45.3	67.3

5.1.2 Effect of growth forms and reproductive strategy on plant cover and frequency

The different plant growth forms and strategies and the interaction between growth forms and strategy significantly affected plant cover (Table 3). Seedlings of broadleaved herbs and trees/shrubs were totally absent in February and the cover of obligate seeders in June was significantly lower than that of the obligate and facultative resprouters (Fig. 8). Seven of the eight species recorded as obligate seeders were annual broadleaved herbs and only two were trees. Broadleaved herbs and tree/shrub species had relatively higher cover when they reproduced entirely by sprouting than by both sprouting and seedling. The cover of obligate sprouter tree/shrub species was significantly higher than the broadleaved herbs in February, but lower in June. Species capable of regenerating both by seedlings and by sprouting were recorded in all plant growth forms with the highest contribution of cover by grass species and no significant difference between the broadleaved herbs and trees/shrubs. The cover of grasses was in both seasons significantly higher than that of broadleaved herbs and trees/shrubs, with more than 50% of the foliar cover contributed by grass species alone in June (Fig. 8).

The frequency of plants depended upon the growth form and plant strategies but not on the interactions between growth form and strategy (Table 3). Broadleaved herbs, which after fire regenerated by seedlings only, were significantly more frequent than trees/shrubs in the wet season (Fig. 9). Moreover, there was no significant difference in the frequency of the two growth forms when both regenerated by sprouting only. Regeneration after fire by both sprouting and seed germination was significantly more frequent in grasses than in broadleaved herbs and trees/shrubs (Fig. 9).

Table 3. Analysis of variance (ANOVA) F values and probability values (superscript) for the effect of growth forms, site and strategy, and the interactions between main factors.

Degree of freedom (df) for the error was 39.

	df	Cover	Quadrat frequency
Growth form	2	$51.71^{0.0001}$	$36.78^{0.0001}$
Site	2	$23.54^{0.0001}$	$0.94^{0.4011}$
Strategy	2	$27.22^{0.0001}$	$71.42^{0.0001}$
Site*strategy	4	$4.29^{0.0057}$	$4.43^{0.0048}$
Growth form*strategy	2	$3.59^{0.0370}$	$2.78^{0.0744}$
Growth form*site	4	$15.40^{0.0001}$	$4.56^{0.0041}$

Fig. 8. The effect of reproductive strategies to cover immediately following fire (February) and in the beginning of the wet season (June)

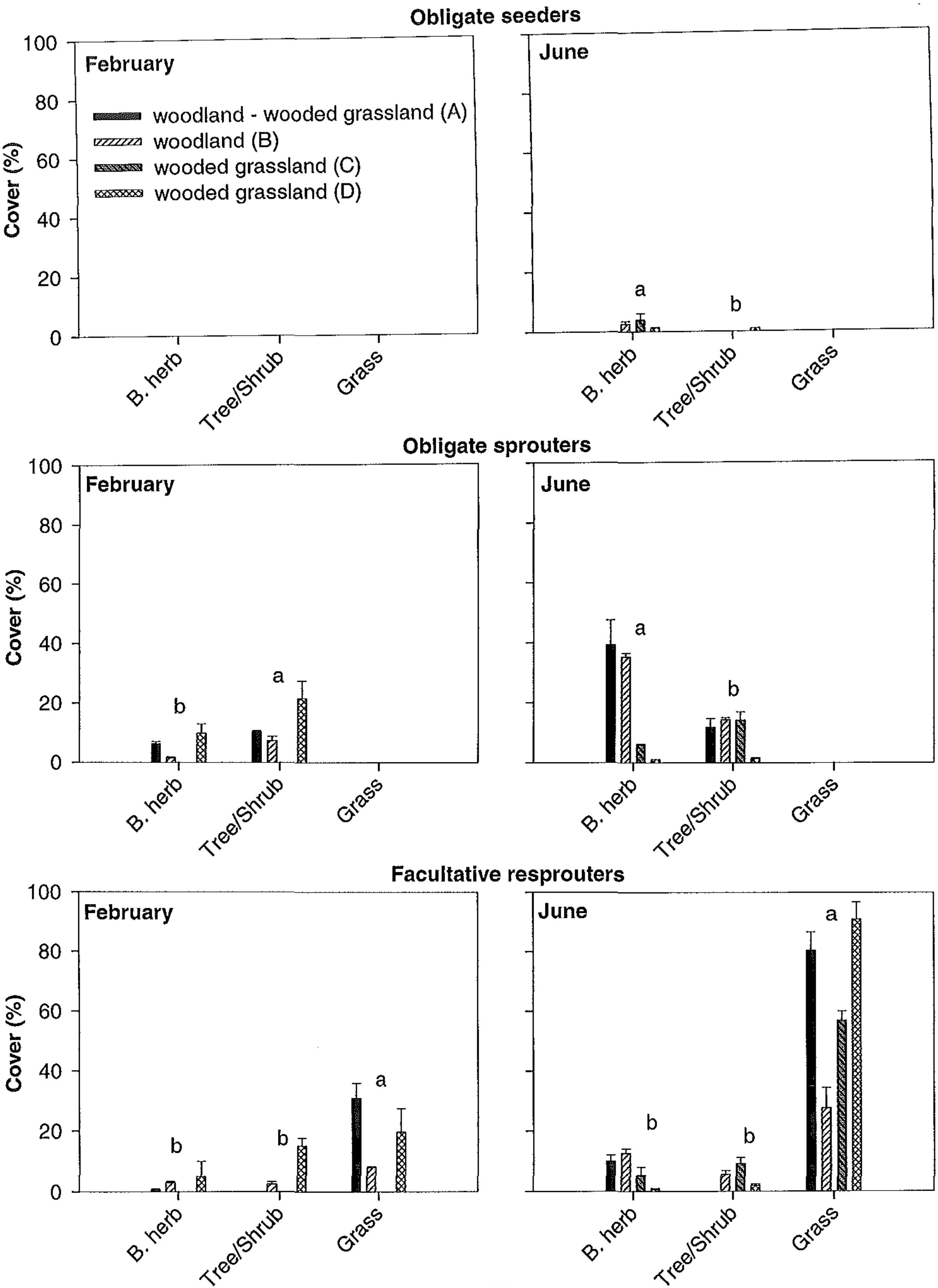
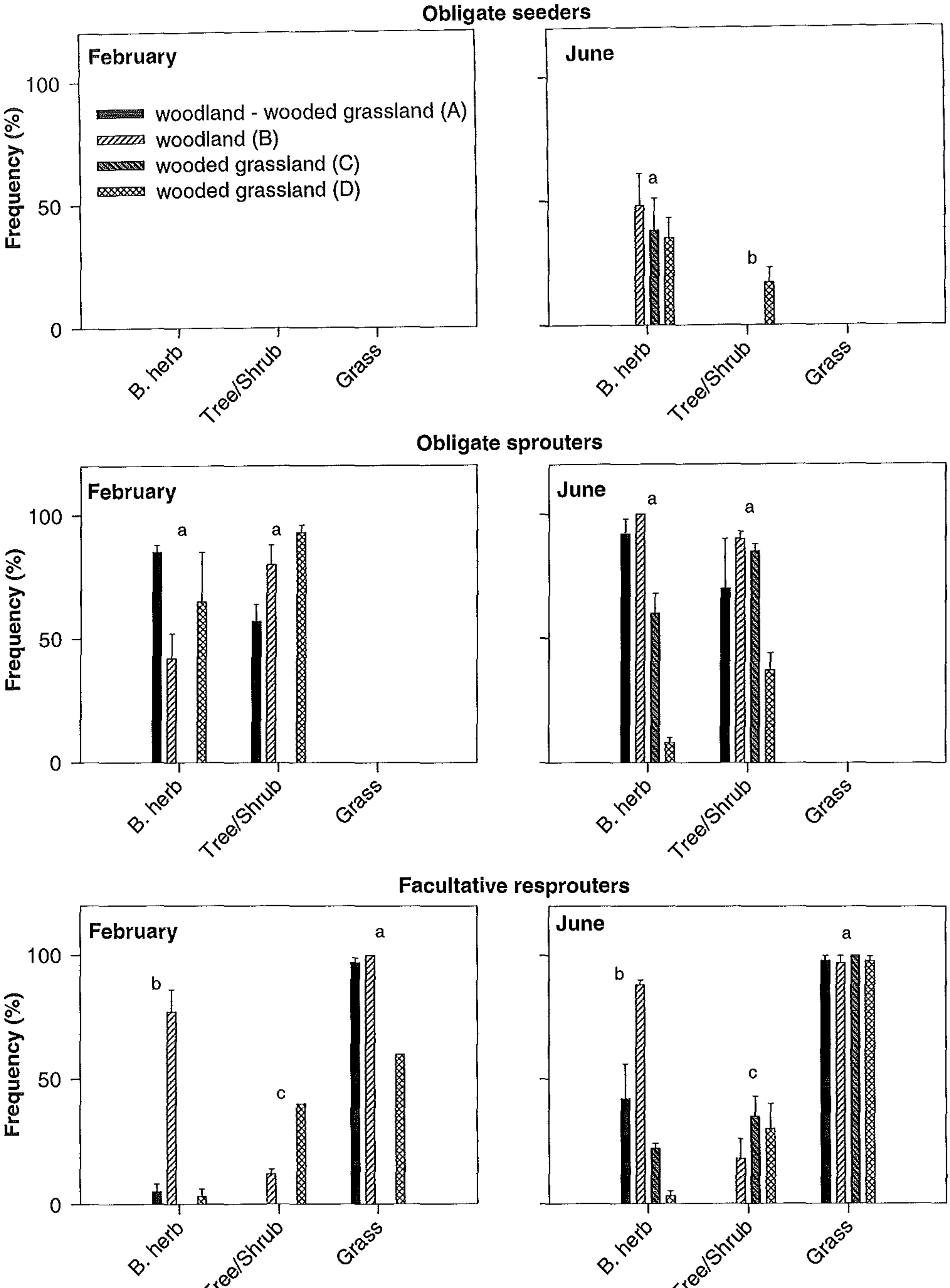


Fig. 9. The effect of reproductive strategies to plant frequency immediately following fire (February) and in the beginning of the wet season (June).



5.1.3 Site differences in cover and frequency

The cover of plants was significantly different between sites. However, frequency did not show significant difference between sites. The interactions between site and strategy, and between growth form and strategy showed significant changes both in cover and frequency of plants (Table 3). Differences between sites in their contribution to cover among the different strategies are given in Table 4. There was no difference between sites in February as no seedlings were recorded at this time, and in June site D only contributed to seedling cover. Moreover, obligate resprouters in broadleaved herbs and trees/shrubs were more dominant in site D than in site B in February. Site A was intermediate but not significantly different from site D. In June the contribution was much lower than site A, B and C and not significantly different from site C in the broadleaved herbs (Table 4). Facultative sprouters in broadleaved herbs and trees/shrubs were not different in their cover in all sites except in site D, which significantly contributed most of the tree/shrub cover in February. Most of the grass cover in facultative species was found in site A, C and D, but site A was not significantly different from site D in February, and from site C and D in June (Table 4).

Table 4. Between-site differences in the cover of plants with the different regeneration strategies and growth forms, tested with Tukey's test after one-way analysis of variance.

For each plant growth form and each date, sites with the same letter are not significantly different (*P*<0.05). In each site "." indicates missing values.

Date	Strategy	Broadleaved herb				Tree				Grass			
		A	B	C	D	A	B	C	D	A	B	C	D
February	Seeder	a	a	.	a	k	k	.	k	q	q	.	q
	Sprouter	ab	b	.	a	kl	l	.	k	q	q	.	q
	Facultative	a	a	.	a	l	l	.	k	q	r	.	qr
June	Seeder	a	a	a	a	l	l	l	k	q	q	q	q
	Sprouter	a	a	b	b	k	k	k	l	q	q	q	q
	Facultative	a	a	ab	b	m	kl	k	lm	qr	s	r	q

5.1.4 Tree bark resistance to fire

Figure 10 suggests that the time required to reach the assumed lethal temperature of 60°C in the cambium was exponentially related to bark thickness for all tree species. Species such as *Anogeissus leiocarpa*, *Sterculia africana*, *Strychnos innocua*, *Ficus sycomorus* and *Ziziphus mauritiana* had thin bark (i.e. less than 0.5 cm). Their cambium reached the lethal temperature in less than 5 min. In contrast, it took more than 5 min in species with bark thicker than 0.5 cm: *Combretum collinum*, *Entada africana*, *Lonchocarpus laxiflorus*, *Pterocarpus lucens* and *Terminalia laxiflora*. *Lannea fruticosa* and *Bridelia scleroneura* were intermediate in their resistance to the applied heat. However, for a given bark thickness the relationship between bark thickness and cambium resistance to heat varied among species. At bark thickness of 0.4 cm, it took three times longer to reach 60°C in cambium temperature in *Lonchocarpus laxiflorus*, *Pterocarpus lucens* and *Ficus sycomorus* than in *Strychnos innocua*, *Anogeissus leiocarpa* and *Ziziphus mauritiana* with the same bark size of 0.4 cm.

Table 5 shows that there is a strong positive correlation between bark thickness, tree diameter and the time taken for the cambium to reach 60°C in all tree species studied. The exceptions were *Anogeissus*, *Lonchocarpus* and *Terminalia*, which showed negative correlation between tree diameter and bark thickness, tree diameter and the time for cambial temperature to reach 60°C.

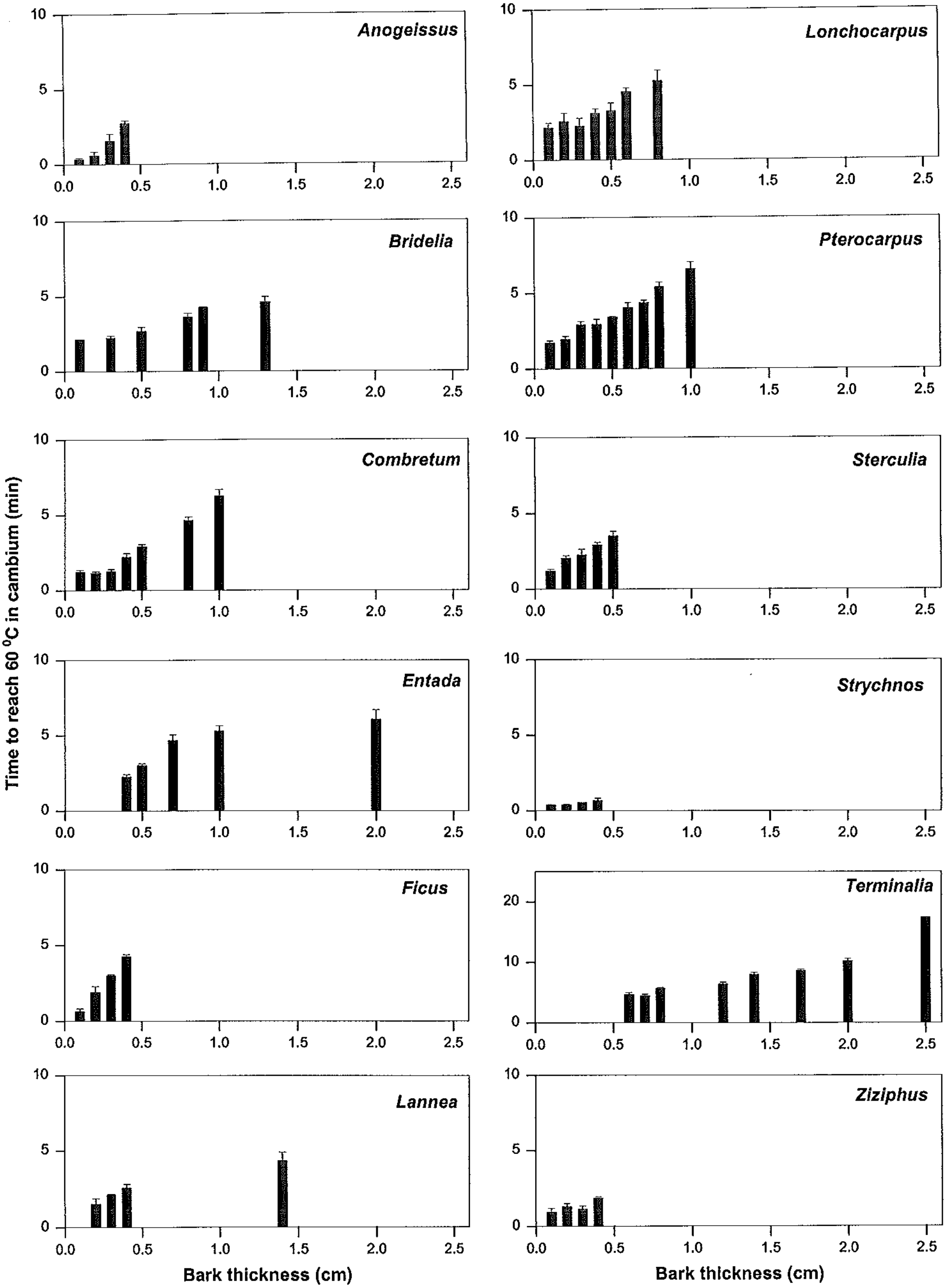


Fig. 10. Bark resistance to heating as a function of time taken by cambium to reach an assumed lethal temperature of 60^{0}C.

Table 5. Spearman's rank correlation coefficient (r_s) and significance for the relationship between bark thickness, tree diameter and time elapsed for the cambium to reach lethal temperature ($60^\circ C$) among the 12 tree species, based on a minimum of 12 and a maximum of 22 sampling points.

BT, DBH and T_{60} indicate bark thickness, diameter at breast height and time taken for cambial tissue to reach $60^\circ C$, respectively.

Tree species	**BT*T_{60} ($r_s{}^P$)**	**BT*DBH ($r_s{}^P$)**	**DBH*T_{60} ($r_s{}^P$)**	**Bark texture**
Anogeissus leiocarpa	$0.88^{0.0002}$	$0.24^{0.4565}$	$0.35^{0.2584}$	smooth and yellowish white
Bridelia scleroneura	$0.92^{0.0001}$	$0.79^{0.0001}$	$0.68^{0.0001}$	coarse or rough
Combretum collinum	$0.93^{0.0001}$	$0.97^{0.0001}$	$0.92^{0.0001}$	stringy and corky
Entada africana	$0.92^{0.0001}$	$0.96^{0.0001}$	$0.87^{0.0001}$	coarse
Ficus sycomorus	$0.97^{0.0001}$	$0.92^{0.0001}$	$0.96^{0.0001}$	whitish & papery with latex
Lannea fruticosa	$0.86^{0.0003}$	$0.68^{0.0147}$	$0.50^{0.0945}$	rough to corky
Lonchocarpus laxiflorus	$0.80^{0.0001}$	$0.45^{0.0377}$	$0.47^{0.0288}$	stringy with sap or latex
Pterocarpus lucens	$0.97^{0.0001}$	$0.83^{0.0001}$	$0.87^{0.0001}$	stringy with sap or latex
Sterculia africana	$0.92^{0.0001}$	$0.84^{0.0001}$	$0.93^{0.0001}$	yellowish white & papery
Strychnos innocua	$0.74^{0.0016}$	$0.84^{0.0001}$	$0.65^{0.0084}$	yellowish white & smooth
Terminalia laxiflora	$0.97^{0.0001}$	$0.43^{0.0452}$	$0.46^{0.0312}$	stringy and corky
Ziziphus spp.	$0.61^{0.0352}$	$0.68^{0.0147}$	$0.77^{0.0033}$	rough to corky

5.2. Plant cover and species richness following experimental burning

The grass cover was 2.5 to 8 times higher than the cover of broadleaved herbs, shrubs and tree saplings (Fig. 11). Seasonal changes in green leaf cover were most clear for the grasses. In November, which is the end of the wet period, and in June, which is beginning of the new rainy season, the grass cover was considerably larger than the (very low) cover in the dry season in February. Similar seasonal trends were found for the broadleaved herbs, although with smaller fluctuations. Shrubs varied less between seasons, and tree seedlings did not at all show variation between seasons.

There was a significant effect of fire on the cover of grasses and tree saplings. Fire increased the grass cover significantly after 90 days, and there was still a tendency towards an increase after 210 days. Tree saplings also tended to increase their cover 210 days after the onset of fire as compared to unburned plots. There was no significant effect of fire on the cover of broadleaved herbs and shrubs. The total understorey cover increased by fire, although not in plots, which also had ash, added, as shown by the tendency towards a significant fire times ash interactions (Fig. 11).

There was also a tendency towards a significant effect of fire on the plant species richness of the experimental plots after 90 days (Fig. 12). However, there was no detectable treatment effect in plant richness after 210 days.

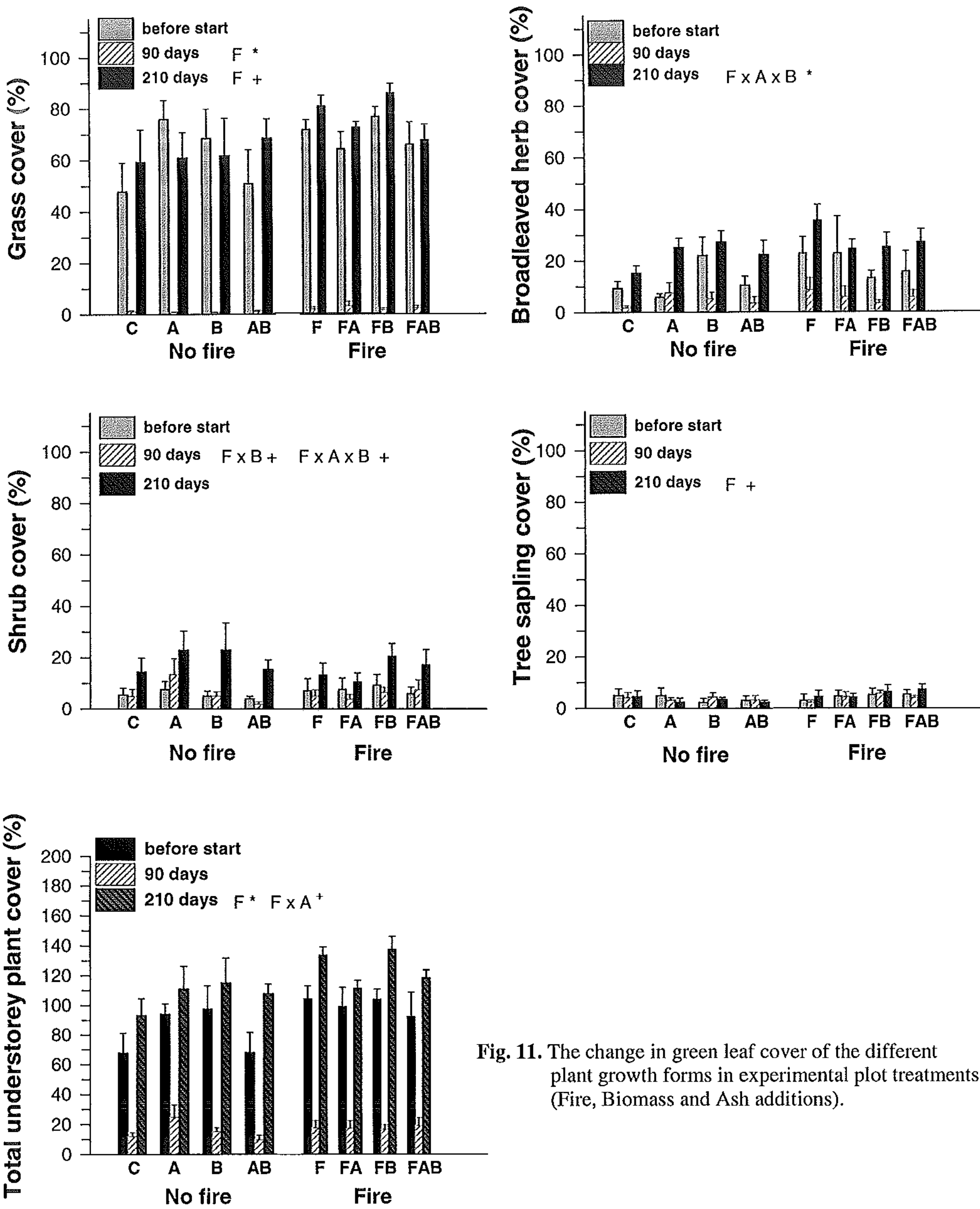
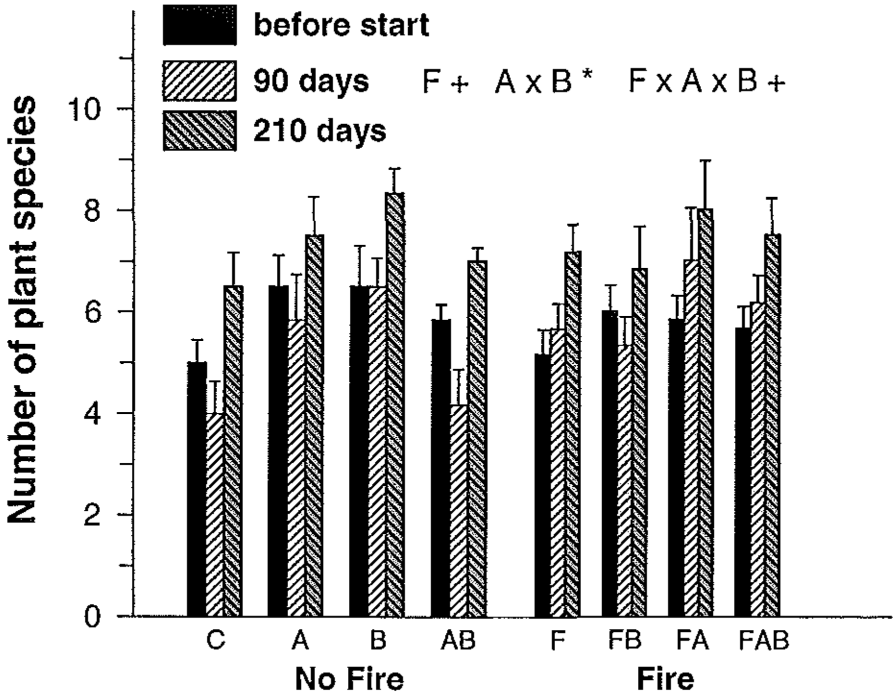


Fig. 11. The change in green leaf cover of the different plant growth forms in experimental plot treatments (Fire, Biomass and Ash additions).

Fig. 12. Total understorey plant species richness following fire (F), ash (A) and biomass (B) additions, with all possible combinations of their treatments, and in control plots (C).



5.3. Influence of heat on seed germination

Fifteen of the 21 plant species in the experiment had germinated (Table 6); nine species from Leguminosae, three species from Gramineae, and one species from each of the families Rhamnaceae, Combretaceae and Labiatae. Six species (*Lannea fruticosa* Engl., *Ziziphus abyssinica* Hochst. ex A. Rich., *Anogeissus leiocarpa* Guill. & Perr., *Strychnos innocua* Del., *Ficus sycomorus* L. and *Hibiscus cannabinus* Linn) failed to germinate for unknown reasons. All 15 species, which germinated, were significantly affected by the heat treatment (ANOVA, Table 7). Furthermore, in all but three germinating species the duration of the heat influenced seed germination, in almost all cases with an interaction between duration and temperature level (Table 7).

Table 6. Description of the life form, the diaspores and seeds of the germinating plant species, and the time required to reach maximum germination frequency (means ± standard error, n=20 per species, except for *Clerodendrum* and *Combretum* for which n=1).

Six species, of which the first five are trees and the sixth a broadleaved herb, viz. *Lannea fruticosa* Engl., *Ziziphus abyssinica* Hochst. ex A. Rich., *Anogeissus leiocarpa* Guill. & Perr., *Strychnos innocua* Del., *Ficus sycomorus* L. and *Hibiscus cannabinus* Linn., failed to germinate.

Species	**Life Form**	**Description of diaspores**	**Seed sizes (mm)**	**Seed weight (mg)**	**Max. germ. (weeks)**
Acacia albida	tree	seeds in pods	6.5±0.3	68.2±6.5	6
Acacia senegal	tree	seeds in pods	8.5±0.3	105±5.3	4
Acacia seyal	tree	seeds in pods	9.0±0.1	98.6±3.6	8
Cassia obtusifolia	herb	seeds in pods	5.5±0.1	26.9±1.0	9
Clerodendrum capitatum	herb	seeds in mericarp	11	274	7
Combretum collinum	tree	winged seeds	11	253	9
Desmodium sp.	shrub	seeds in pods	2.9±0.1	8.9±0.4	9
Eleusine coracana	grass	bare grains	1.1±0.04	1.9±0.1	2
Entada abyssinica	tree	winged seeds in pods	12.4±0.3	217±7.5	8
Hyparrhenia confinis	grass	grains within paleas, glumes and lemmas	7.7±0.2	1.9±0.2	8
Piliostigma thonningii	tree	seeds in pods	7.5±0.1	117±2.9	9
Sorghum arundinaceum	grass	grains within paleas, glumes and lemmas	6.2±0.1	6.4±0.3	6
Tamarindus indica	tree	seeds in pods	12±0.2	465±10.3	8
Tylosema fassoglensis	herb	seeds in flat pods	25.2±0.4	2908±132	7
Ziziphus mauritiana	shrub	seeds in drupaceous fruit	14.9±0.4	1015±51	9

Table 7. Analysis of variance F values and probability values (superscript) for the effect of duration and temperature, and the interaction between duration and temperature.

Degrees of freedom (*df*) are 1 for duration, 5 for temperature, 5 for the interaction and 55 for the error, except for *Tylosema* for which the *df* for the error was 22.

Species	**Duration**	**Temperature**	**Duration * Temperature**
Acacia albida	$17.38^{0.0001}$	$68.30^{0.0001}$	$5.2^{0.0013}$
Acacia senegal	$91.55^{0.0001}$	$333.21^{0.0001}$	$40.38^{0.0001}$
Acacia seyal	$21.25^{0.0001}$	$17.20^{0.0001}$	$33.55^{0.0001}$
Cassia obtusifolia	$117.46^{0.0001}$	$115.31^{0.0001}$	$55.12^{0.0001}$
Clerodendrum capitatum	$51.89^{0.0001}$	$77.90^{0.0001}$	$24.10^{0.0001}$
Combretum collinum	$16.29^{0.0002}$	$118.84^{0.0001}$	$14.41^{0.0001}$
Desmodium sp.	$5.59^{0.0216}$	$247.68^{0.0001}$	$2.13^{0.0898}$
Eleusine coracana	$161.70^{0.0001}$	$1448.70^{0.0001}$	$161.70^{0.0001}$
Entada abyssinica	$16.10^{0.0002}$	$15.09^{0.0001}$	$23.51^{0.0001}$
Hyparrhenia confinis	$11.33^{0.0014}$	$245.88^{0.0001}$	$69.05^{0.0001}$
Piliostigma thonningii	$1.04^{0.3118}$	$102.23^{0.0001}$	$23.69^{0.0001}$
Sorghum arundinaceum	$58.62^{0.0001}$	$464.03^{0.0001}$	$115.50^{0.0001}$
Tamarindus indica	$52.71^{0.0001}$	$15.26^{0.0001}$	$29.36^{0.0001}$
Tylosema fassoglensis	$0.68^{0.4195}$	$9.16^{0.0001}$	$2.26^{0.0949}$
Ziziphus mauritiana	$1.85^{0.1790}$	$15.99^{0.0001}$	$1.04^{0.3927}$

5.3.1 Germination of tree and shrub seeds

Nine species of trees and shrubs had germinated. They showed large variation in their tolerance of high temperatures, and in some species, germination was even promoted by high temperature.

Acacia albida seeds heated for 1 minute did not germinate after heating to above 120°C. Germination of seeds treated at 60°C was significantly higher than of seeds treated at 20, 90 and 120°C (Fig. 13). Five min of heating reduced the maximal temperature level followed by germination to 90°C. Germination following 20 and 60°C treatments was significantly higher than following 90°C when treatment was extended to 5 min.

Responses in *Acacia senegal* (L.) Willd. were similar to those in *A. albida*. Seeds heated at 20, 60 and 90°C for 1 min germinated better than at those treated with 120°C, and no seeds germinated after exposure to 150 and 200°C. Seeds heated at 120, 150 and 200°C for 5 min did not germinate (Fig. 13).

When treated for 1 min *Acacia seyal* Del. seeds germinated irrespective of the temperature treatments, with no significant differences between the levels. When exposed for 5 min A. seyal seeds showed lower germination at 20 and 60°C than at 90 and 120°C treatments. Higher temperatures (150 and 200°C) inhibited germination (Fig. 13).

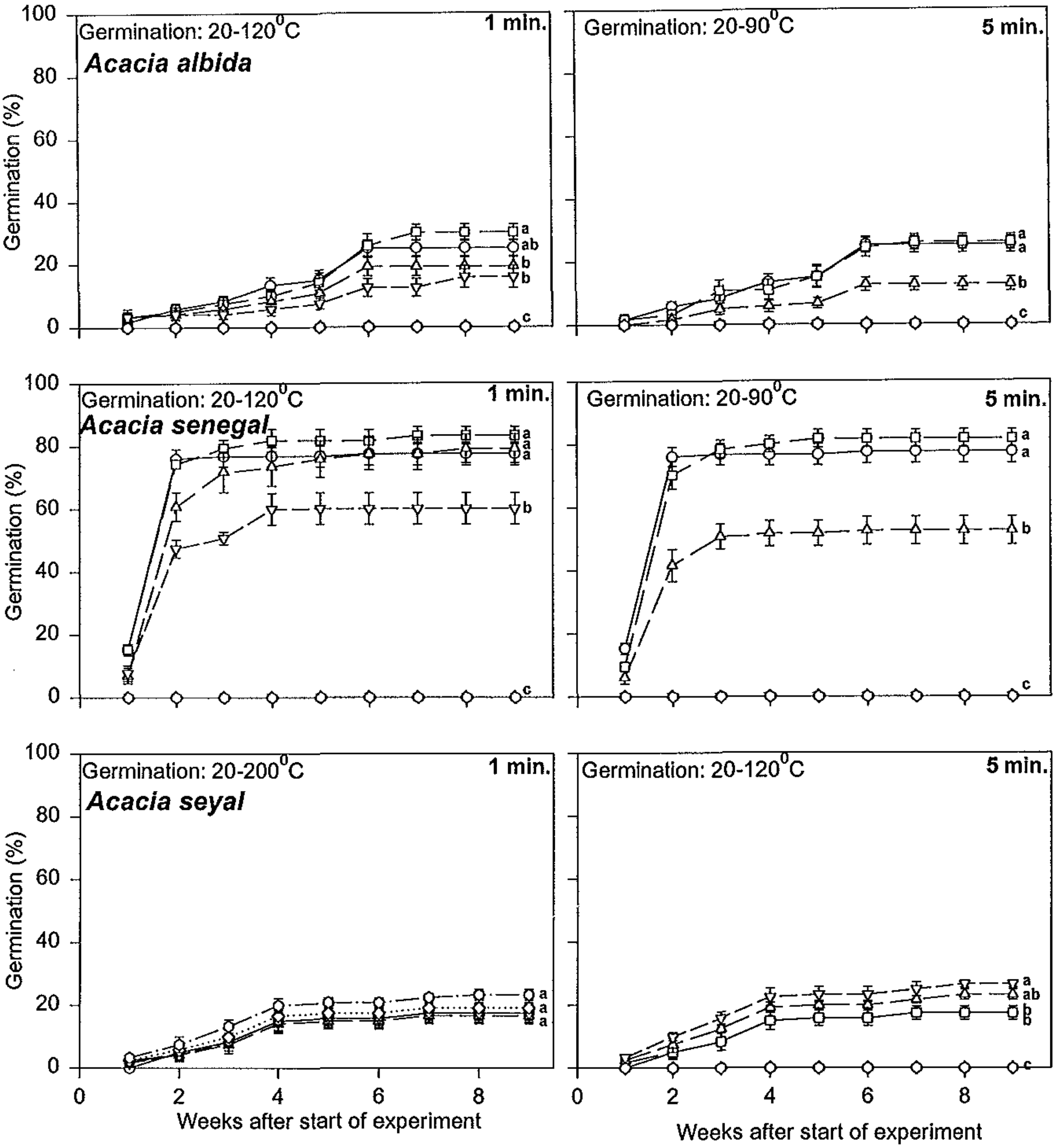


Fig. 13. Germination response of seeds of acacia trees exposed to 20⁰C and to heat shock of 60, 90, 120, 150 and 200⁰ C for 1 and 5 min.

Seeds of *Desmodium* sp. exposed to 1 or 5 min of 90°C heating germinated to a higher degree than those treated at 20 and 60°C, and no germination was recorded at 120°C or above, neither for seeds exposed for one or for five min heating (Fig. 14).

Seeds of *Piliostigma thonningii* (Schum.) Milne-Redh. did not germinate following exposure to more than 120°C for 1 min, or to 90°C for 5 min. There was no difference between the germination following treatment at the temperature levels below the critical level (Fig. 14).

Entada seeds resisted heating up to 150°C for 1 min and even germinated better after heating to 150°C than after 60, 90 or 120°C. After 5 min treatments maximal temperature that was followed by germination was 120°C, but germination frequency was much lower than at 20, 60 and 90°C (Fig. 14).

Seeds of *Combretum* treated for 1 min did not tolerate more than 90°C. The same was the case with 5 min exposure time but germination of seeds treated with 90°C was reduced by more than 50% compared to seeds heated at 90°C for 1 min (Fig. 15).

At least some seeds of *Tamarindus indica* L. treated for 1 min germinated in all temperature treatment classes, best after 120°C treatment. At 5 min duration, maximal temperature that led to germination was 120°C, but this treatment reduced germination compared to the lower temperature levels (Fig. 15).

Ziziphus mauritiana seeds resisted heating up to 200°C both for 1 and 5 min but germination was lowest in seeds treated with the highest temperatures (Fig. 15).

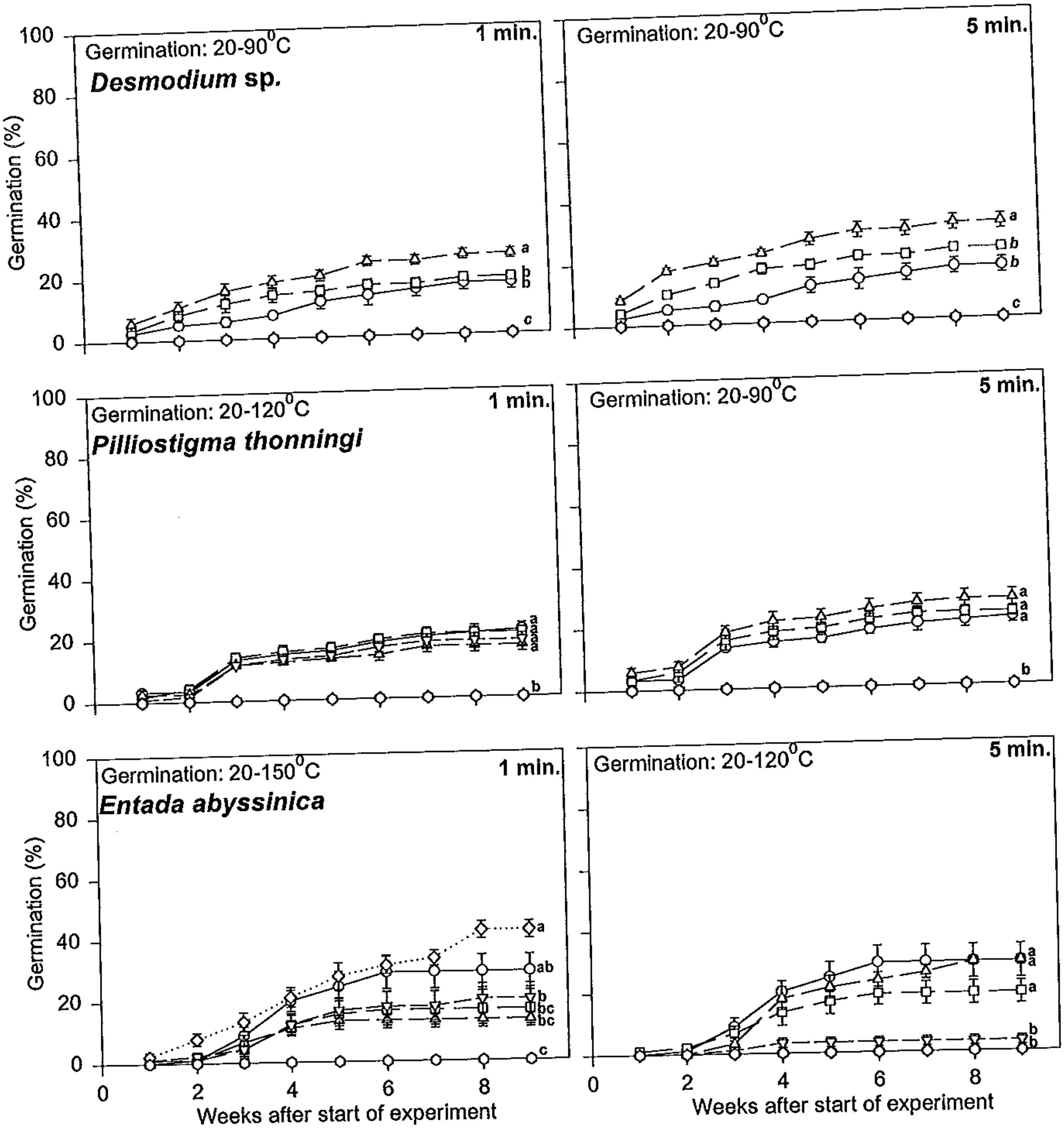


Fig. 14. Germination response of seeds of trees and shrubs exposed to 20°C (Control) and to heat shock of 60, 90, 120, 150 and 200°C for 1 and 5 min.

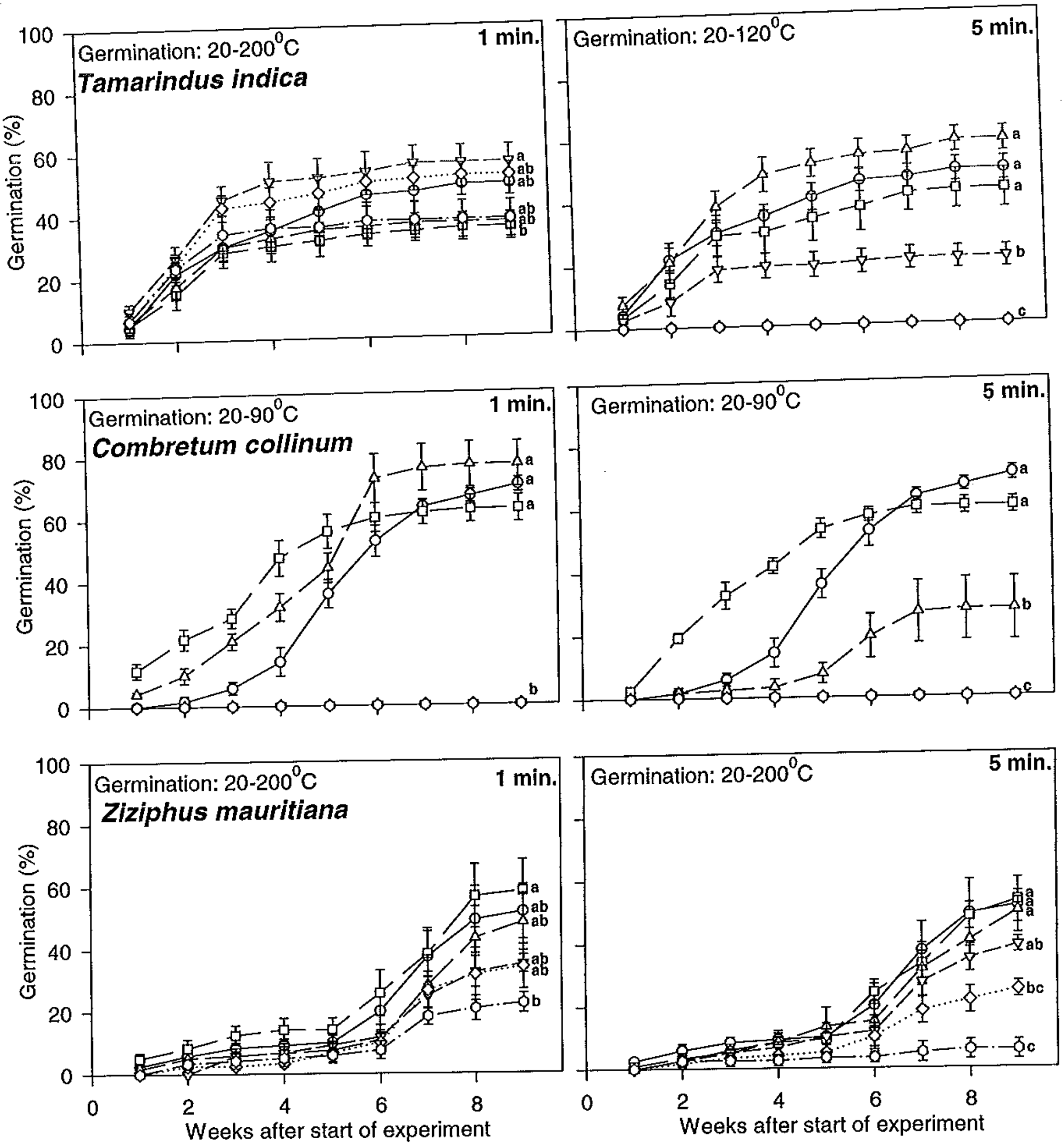


Fig. 15. Germination response of seeds of trees and shrubs exposed to 20°C (control) and to heat shock of 60, 90, 120, 150 and 200°C for 1 and 5 min.

5.3.2 Germination of grass seeds

The seeds of the two grass species *Hyparrhenia confinis* (A. Rich.) Stapf var. *nudiglumis* (Hackl.) W. D. Clayton and *Sorghum arundinaceum* (Desv.) Stapf. showed identical germination patterns (Fig. 16). The seeds germinated after treatments up to 120°C and 90°C for 1 and 5 minutes duration, respectively. The untreated (20°C) seeds of both species showed significantly higher germination than those treated with 60°C for 1 min. With 5 min treatment the maximal germination temperature was reduced to 90°C, and there was no significant difference between treatments at or below this temperature level.

Eleusine seeds germinated following exposure to 90°C when treated for 1 and 5 min. There was no difference between treatments at 20, 60 or 90°C for 1 min duration whereas at 5 minutes, germination following 90°C treatment was lower than at 20 and 60°C (Fig. 16).

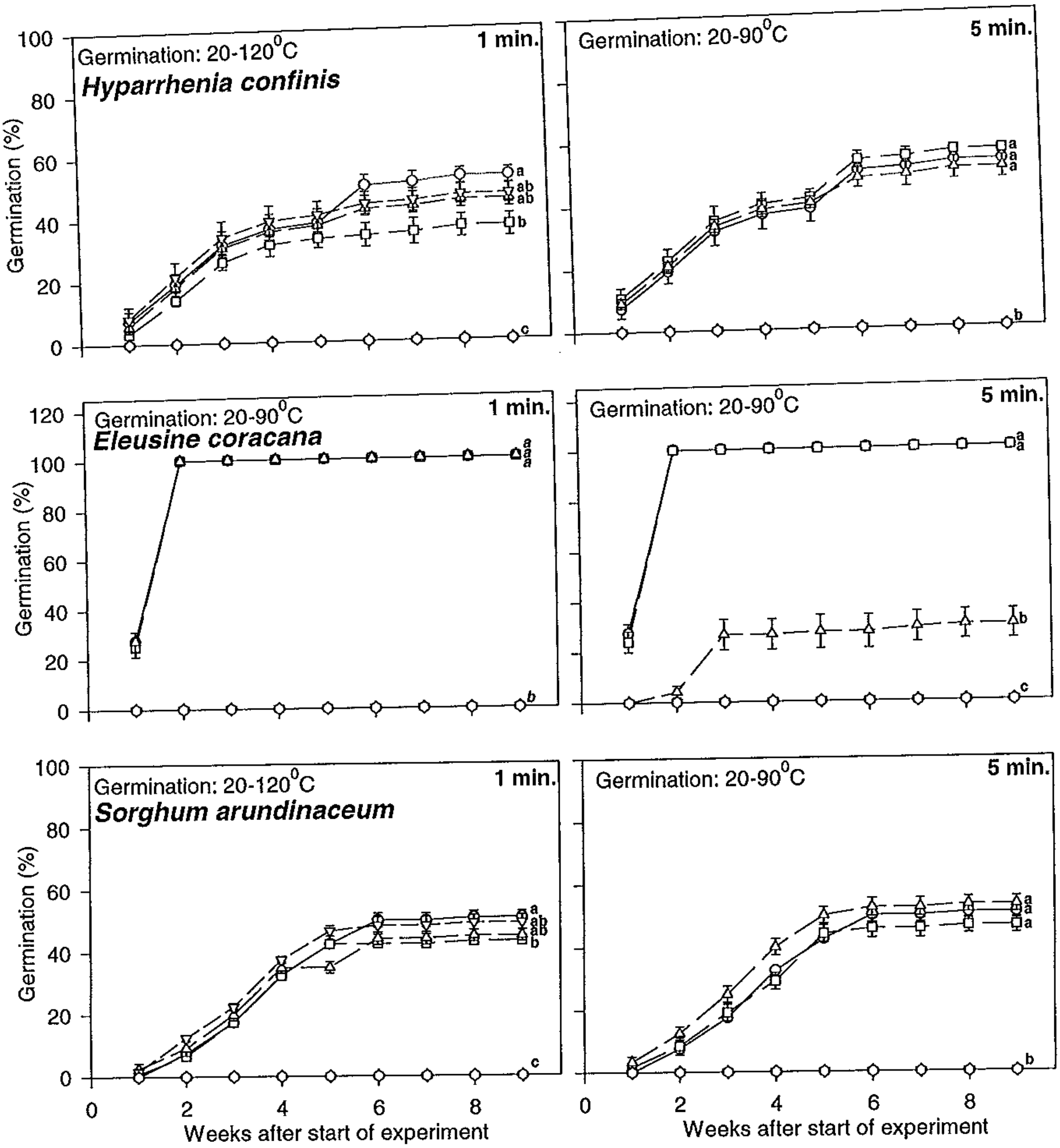


Fig. 16. Germination response of seeds of grasses exposed to 20^{0}C (Control) and to heat shock of 60, 90, 120, 150 and 200^{0}C for 1 and 5 min.

5.3.3 Germination of broadleaved herbs and herbaceous climbers

Seeds of the broadleaved herbs *Clerodendrum capitatum*, *Cassia obtusifolia* Linn. and the climber *Tylosema fassoglensis* tolerated temperatures of 120, 150 and 200°C, respectively, when treated for 1 min (Fig. 17). There was no significant difference between germination frequencies at temperatures below the critical level; in the case of *Tylosema,* this was probably because of the low number of seeds and replicate pots used. With an increase in the duration of treatment to 5 min, the critical level of germination in *Clerodendrum* was reduced to 90°C, and at this level germination was lower than following 20 and 60°C treatment. *Cassia* seeds treated for 5 min resisted 90°C, and germination was lower at 60°C than at 20°C or 90°C. Seeds of *Tylosema* resisted up to 150°C when treated for 5 min. Germination at 60°C was highest, followed by that at temperatures of 20, 90, 120, and 150°C. The frequency of germination at 150°C was lower than at 20°C and 60°C but it was still above 20% at this high temperature level (Fig. 17).

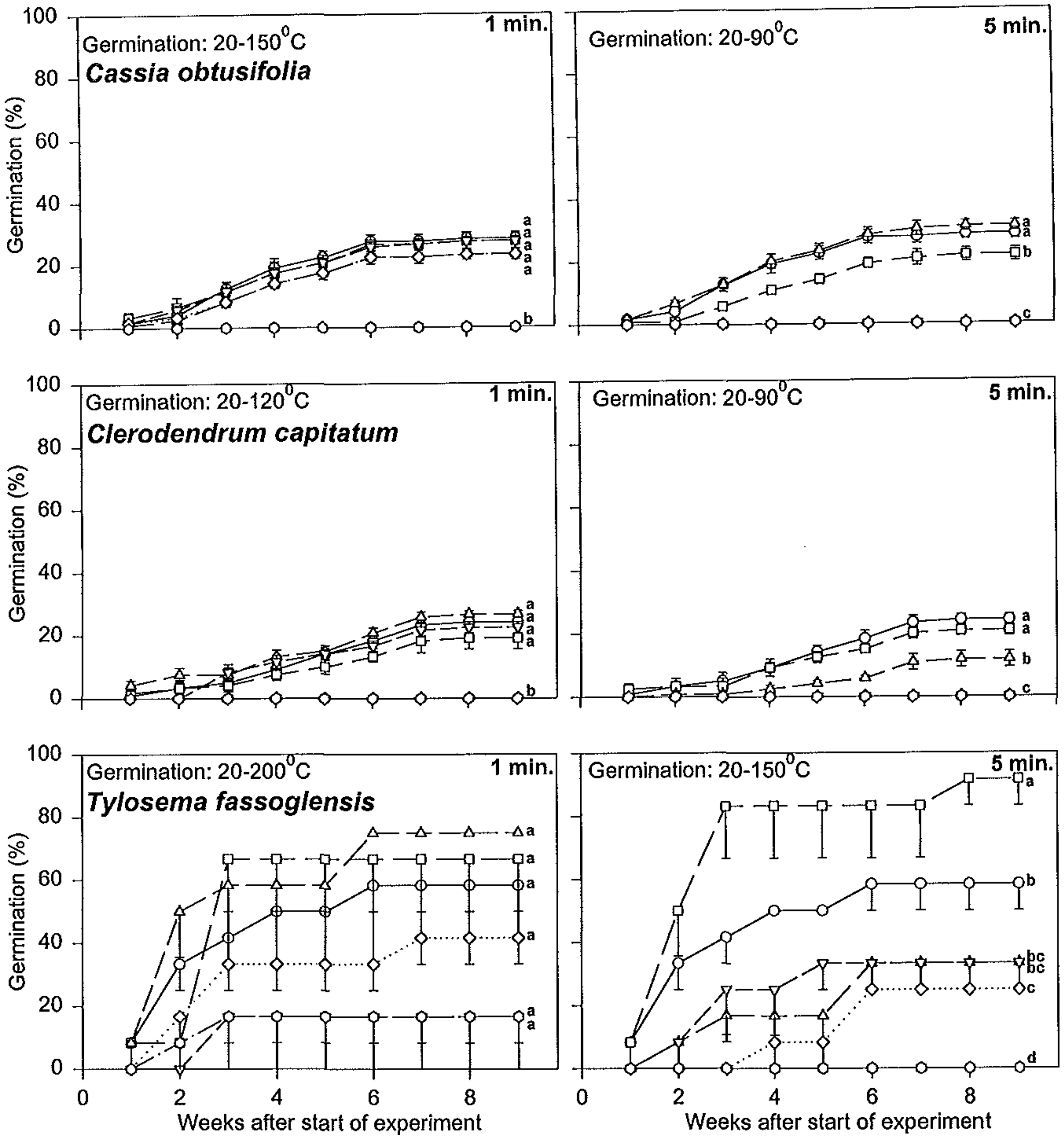


Fig. 17. Germination response of seeds of broadleaved herbs exposed to 20⁰C (control) and to heat shock of 60, 90, 120, 150 and 200⁰C for 1 and 5 min.

5.3.4 Relationships between seed weight, size, maximum germination period and temperature

Seeds from the different plant species varied greatly in terms of size and weight, in the presence of protective tissues (pods or fruits etc.), and in the time required to attain maximum germination frequency (Table 6). Most species required six weeks or more to reach their maximal germination frequency. However, *Eleusine* and *Acacia senegal* seeds reached full germination within 2 and 4 weeks, respectively. In most species the relative rate of germination was unaffected by treatment, but in Combretum seeds treated at 60°C germinated faster than those treated at 20°C.

There was a positive correlation between seed weight or size of the species and the maximum temperature level after which seed germination could take place (r_s=0.57, P=0.028 and r_s=0.65, P=0.009 for 1 min, and r_s=0.66, P=0.007 and r_s=0.78, P=0.001 for 5 min), for seed weight and for seed size, respectively (Fig. 18).

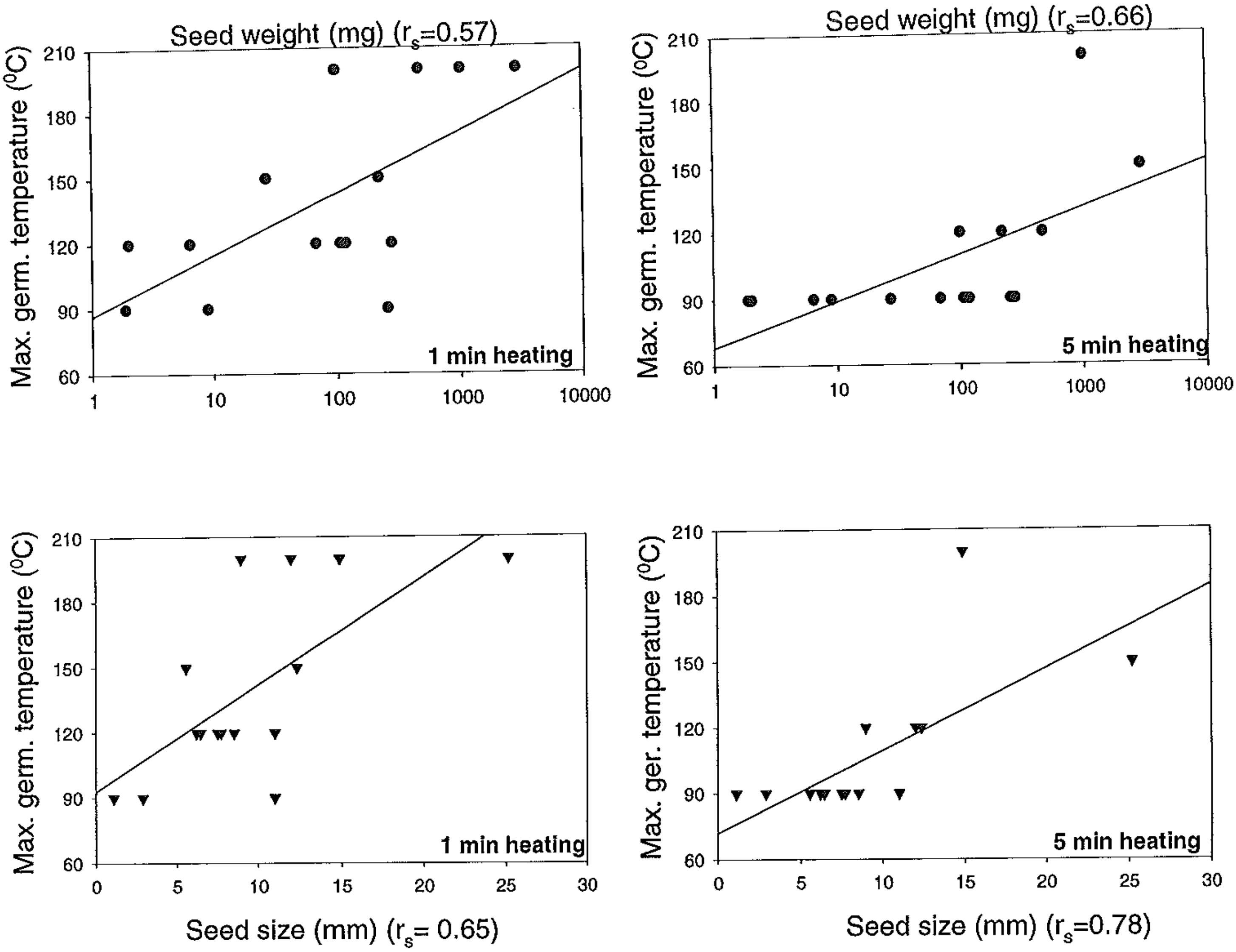


Fig. 18. Seed weight and seed size of each plant species plotted as a function of the maximum temperature which is followed by germination, after 1 or 5 min treatment, respectively.

5.4. Dynamics of soil seed bank

5.4.1. Species compositions of soil seed bank

A total of 20 plant species representing 14 families were recorded from all soil depths and sites in the study area. Of these 55% were broadleaved herbs, 25% were graminoids and 20% were trees and shrubs. 70% of the taxa were annuals whereas 30% were perennials (Table 8).

Table 8. Species composition of the standing vegetation and soil seed bank. The species present in the vegetation of the sites are listed in Appendix 1, to which can be referred.

Species present both in the seed bank and in the vegetation are marked with +, species present in the vegetation but not detected in the seed bank are not marked, and species present in the seed bank, but not in the vegetation are marked with *.

The growth form of the species are indicated as follows: AH (Annual broadleaved herbs), SA (Shrubby annuals), AG (Annual graminoids), PH (Perennial broadleaved herbs including herbaceous climbers), SP (Shrubby perennials), PG (Perennial graminoids) and T (Trees). GF (Plant growth form).

Plant species	**A**	**B**	**C**	**D**	**X**	**GF**		**Plant species**	**A**	**B**	**C**	**D**	**X**	**GF**
Abrus schimperi						SP		*Harrisonia abyssinica*						SP
Acacia senegal						T		*Hibiscus calyphyllus*						AH
Acalypha villicaulis					*	AH		*Hibiscus cannabinus*	+	+	+	+		AH
Achyranthes aspera						PH		*Hyparrhenia confinis*	+	+	+	+		PG
Allophyllus rubifolius						SP		*Hypoestes forskaolii*						PH
Ampelocissus abyssinica						PH		*Indigofera prieureana*		+	+			SA
Andropogon gayanus		+		+		PG		*Ipomoea heterotricha*	+	+	+			AH
Annona senegalensis						PH		*Jasminum streptopus*			+			SA
Anogeissus leiocarpa						T		*Justicia diclipteroides*						PH
Asparagus scaberulus						PH		*Lonchocarpus laxiflorus*						T
Aspilia kotschyi			+	+		AH		*Loudetia arundinacea*	+	+		+		PG
Astripomoea malvacea					*	AH		*Maerua triphylla*						T
Balanites aegyptiaca						T		*Maytenus senegalensis*						SP
Barleria grandicalyx						AH		*Meyna tetraphylla*						T
Blepharis maderaspatensis						AH		*Opilia amentacea*						SP
Bridelia scleuroneura						T		*Panicum comorense*						AG
Bulbostylis sp.			*			AH		*Pennisetum polystachion*						PG
Cadaba farinosa						SP		*Periploca linearifolia*						PH
Chlorophytum spp.						PH		*Phyllanthus pseudoniruri*					*	SA
Cissus petiolata						PH		*Piliostigma thonningii*						T
Clerodendrum spp.						PH		*Plumbago zeylanica*						PH
Combretum spp.						T		*Pterocarpus lucens*						T
Commelina benghalensis	+	+	+			AH		*Pyrenacantha kaurabassana*						PH
Conyza aegyptiaca	*		*	*		AH		*Sansevieria abyssinica*						PH
Corchorus tridens		+				AH		*Sida alba*					*	AH
Cyperus amabilis		+				PG		*Spermacoce sphaerostigma*			+			AH
Cyperus sp.						PG		*Sporobolus festivus*					*	PG
Cyphostemma adenocaule						PH		*Sterculia africana*						T
Desmodium sp.						SP		*Stereospermum kunthianum*						T
Dichrostachys cinerea						SP		*Strychnos innocua*						T

Plant species	**A**	**B**	**C**	**D**	**X**	**GF**		**Plant species**	**A**	**B**	**C**	**D**	**X**	**GF**
Echinops longifolius						PH		*Tacca leontopetaloides*						PH
Entada africana						T		*Tamarindus indica*						T
Ficus sycomorus	+		+	+		T		*Terminalia laxiflora*						T
Flueggea virosa						SP		*Tylosema fassoglensis*						PH
Gardenia ternifolia						T		*Vigna unguiculata*						AH
Grewia mollis						SP		*Ziziphus* spp.						SP

5.4.2. Seed bank sizes: variation of site and season

The input to soil seed bank is largely during the dry season i.e. between November and March, as most of the vegetation of the study area disperses seeds in this period. More than 90% of the soil seed bank was from a single graminoid species, *Hyparrhenia confinis*. 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 19. 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. 19). 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. 19). At the beginning of the wet season (June), the soil seed pool of *Hyparrhenia confinis* was at a minimum in all sites burned. 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). 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. 19). The number of seeds at 2.5-3.0 cm depth 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.

Generally there was a great variation in the seed pools of graminoids, broadleaved herbs, trees and shrubs between sites and between seasons (Fig. 20). The two way ANOVA on effects of sites and seasons indicated that there was significant difference in the soil seed densities of graminoids between sites (Fig. 8, df=3, F=13.40, P<0.01) and between seasons (Fig. 8, df=2, F=41.49, P<0.01), whereas no significant differences were found in the soil seed densities of herbs, or trees/shrubs between sites and between seasons. Seeds of graminoids decreased in abundance at sites in the order of A>D>B>C in the dry period (February). There was a slight increase in reverse order (but not significant) in the number of seeds of herbs, trees and shrubs in February. At the beginning of the wet season (June) the soil seed pool of graminoids reached a minimum level at all burned sites and there was also a decline in the seed densities of broadleaved herbs, trees and shrubs. The situation in the control site was different as relatively large seed densities of herbs, trees and shrubs were found at this time. However, no graminoid seeds were detected from the forested control site (G) and the graminoid species found in the control sites (X1 and X2) were uncommon in the burning sites (Fig. 19). In November graminoid seeds gradually decreased in the order of A>B>C>D, and the soil seed banks, which were depleted during the wet season as a result of germination, were replenished and peaked in February. Almost no seeds of herbs, trees and shrubs were detected in the soil during November (Fig. 20).

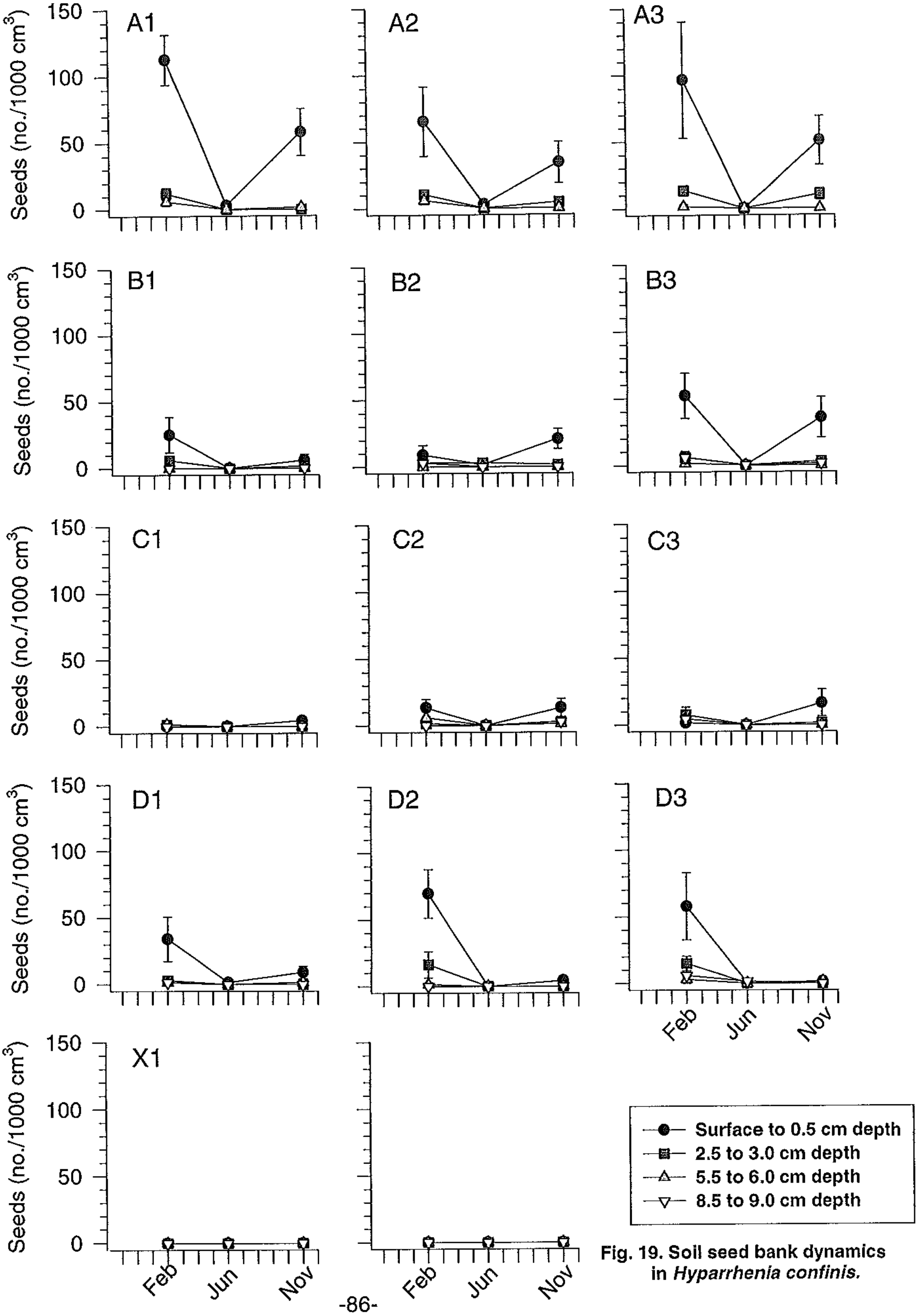


Fig. 19. Soil seed bank dynamics in *Hyparrhenia confinis*.

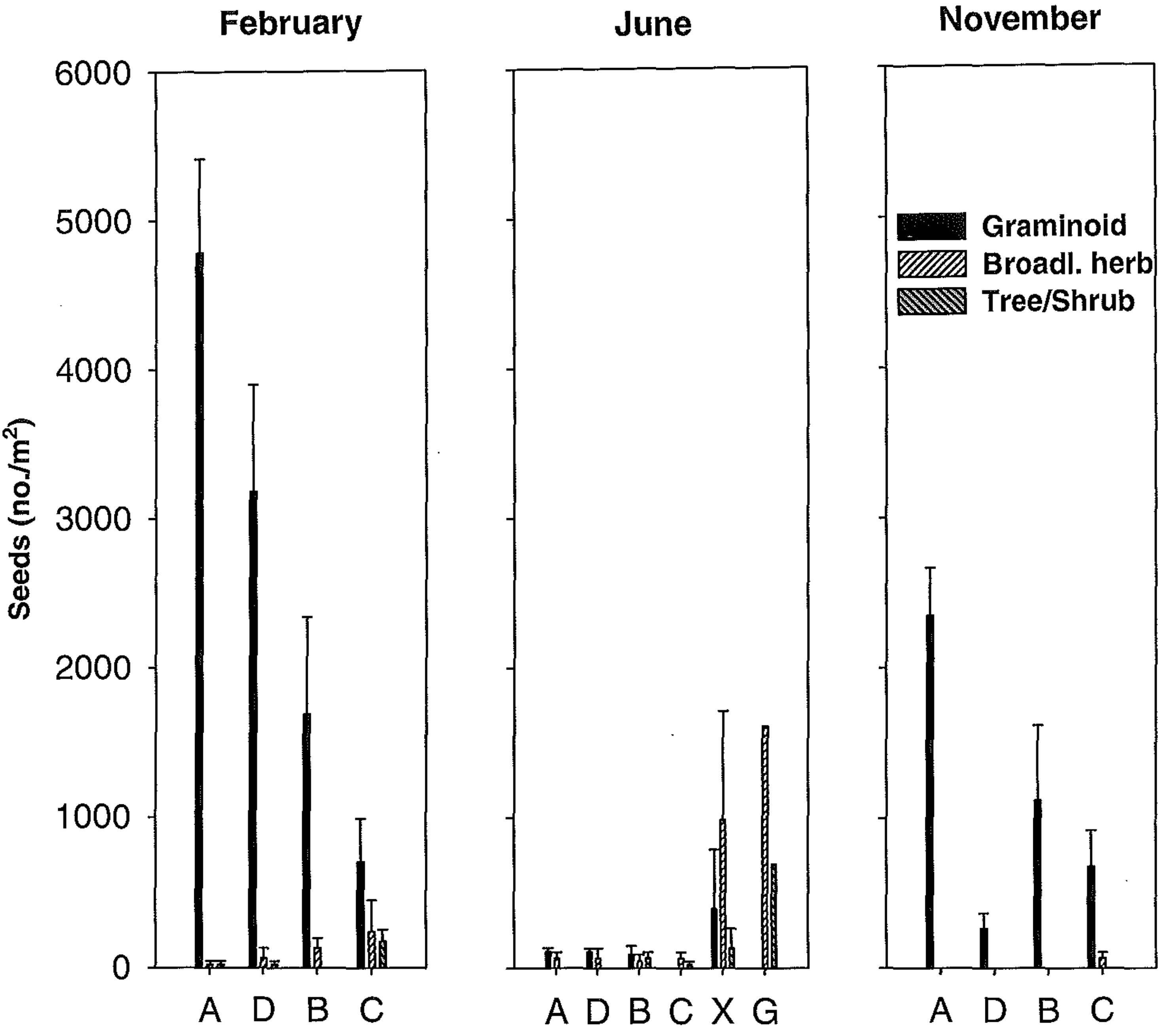


Fig. 20. Seasonal variation in soil seed pool density of graminoids, broadleaved herbs and shrubs/trees in each of the site.

5.4.3. Differences in the soil seed pools among the different plant growth forms.

Across all frequently burning sites and sampling times, a high percentage (about 90 %) of the seed pool stemmed from graminoids. The soil seed bank density of graminoids was significantly greater than that of trees/shrubs in all burning sites except site C, both in February and November. In June the seed banks of the various growth forms were equally low in the burnt plots (Table 9). However, seed densities of herbs, trees and shrubs were much higher in the unburned control plots than in the burned sites (Fig. 20, June). The density of seeds of broadleaved herbaceous plants was at most instances not significantly different from that of the trees and shrubs (Table 9).

Table 9. Differences in soil seed bank densities among plant growth forms tested with Tukey's test after one-way analysis of variance.

In each column, plant growth forms with the same letter are not significantly different ($\alpha=0.05$).

Plant growth forms		February					June					November			
		A	B	C	D		A	B	C	D		A	B	C	D
Graminoids		a	a	a	a		a	a	b	a		a	a	a	a
Broadleaved herbs		b	b	a	b		ab	a	a	ab		b	b	ab	b
Trees/shrubs		b	c	a	b		b	a	ab	b		b	b	b	b

5.4.4 Vegetation and soil seed bank comparisons

The mean value of species richness in the aboveground standing vegetation and soil seed pool at the level of the 14 sampling points was not significantly correlated using the Spearman rank order correlation coefficient ($r_s = 0.38$, $P = 0.18$, $n=14$). Similarly there was no close floristic compositional similarity between the total aboveground vegetation and the soil seed pool as measured by Sørensen's similarity index and many of the 14 sampling plots were characterized by zero correspondence. However, the floristic composition of graminoids of the standing vegetation strongly related with that of graminoids in the seed bank (Table 10).

Table 10. Sorensen's similarity coefficient for presence of species in the standing vegetation and in the soil seed bank based on the 14 sampling points.

Site	Grass	Broadleaved herb	Shrub	Tree	All vegetation groups
A	0.60±0.10	0.00±0.00	0.00±0.00	0.00±0.00	0.17±0.04
B	0.72±0.15	0.14±0.08	0.06±0.06	0.00±0.00	0.20±0.04
C	0.60±0.10	0.19±0.02	0.34±0.06	0.00±0.00	0.26±0.02
D	0.71±0.20	0.19±0.19	0.00±0.00	0.17±0.17	0.36±0.16
X	0.25±0.25	0.00±0.00	0.00±0.00	0.00±0.00	0.03±0.03

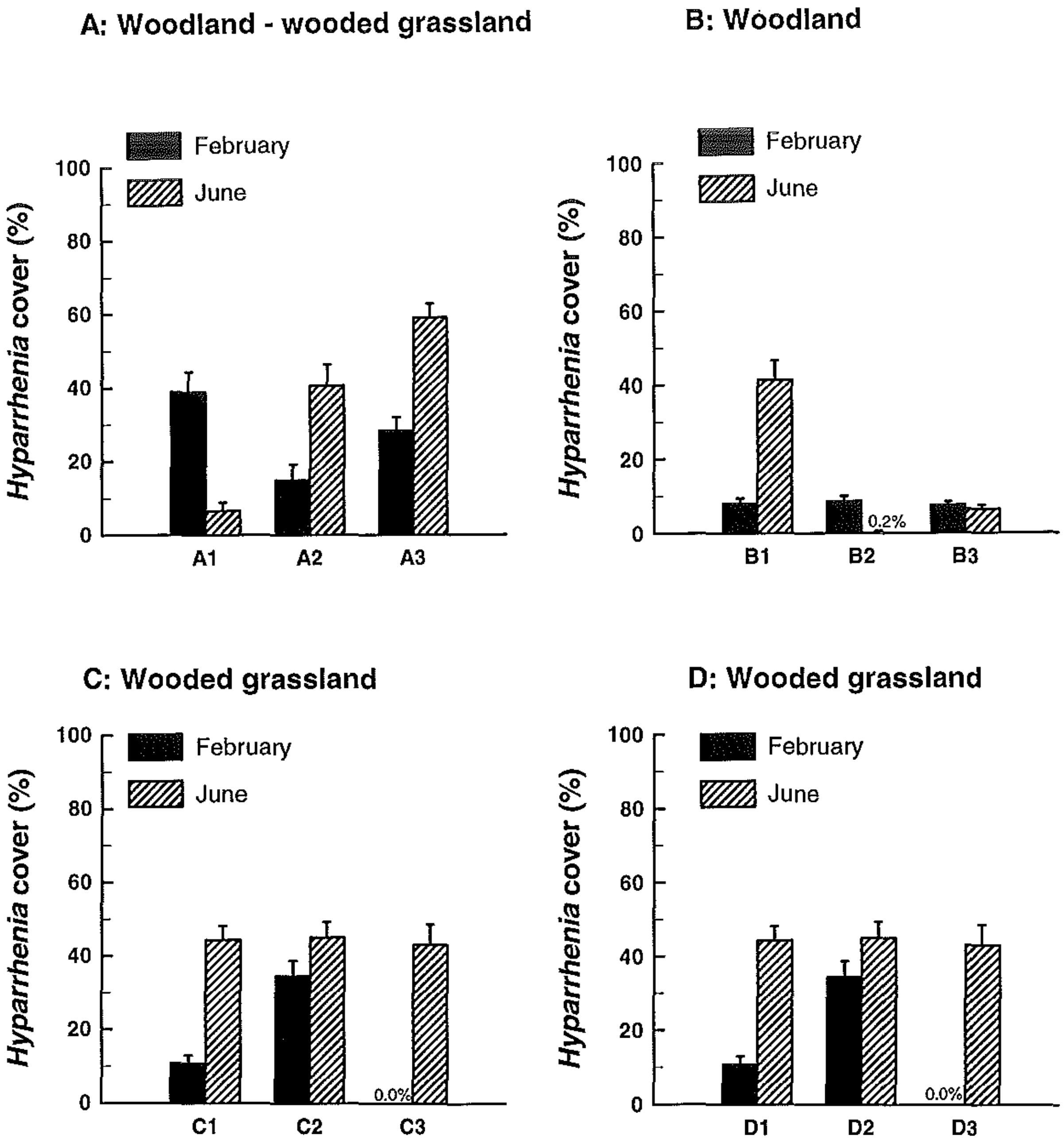
5.4.5. Vegetation cover of Hyparrhenia confinis: variation with sites and season

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. 21). There were also significant differences in the cover of *Hyparrhenia confinis* between seasons (Fig. 21). In the plots of the wooded grassland sites C and D the cover of *Hyparrhenia confinis* was higher at the beginning of the 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.

5.4.6. Vertical distribution of seeds in the soil.

The different plant growth forms differed in the vertical distribution of seeds in the soil. Generally major changes in seed density along the different depths were observed in graminoids, whereas in the woody vegetation seed density was more or less constant from the surface down to 8.5 cm. Most of the graminoid seeds in the seed bank were found in the surface soil layer whereas seeds of woody species were also localized at 2.5 to 8.5 cm depth (Fig. 22).


A: Woodland - wooded grassland

B: Woodland

C: Wooded grassland

D: Wooded grassland

Fig. 21. Above-ground cover of *Hyparrhenia confinis* in the dry (February) and in the beginning of the wet season (June).

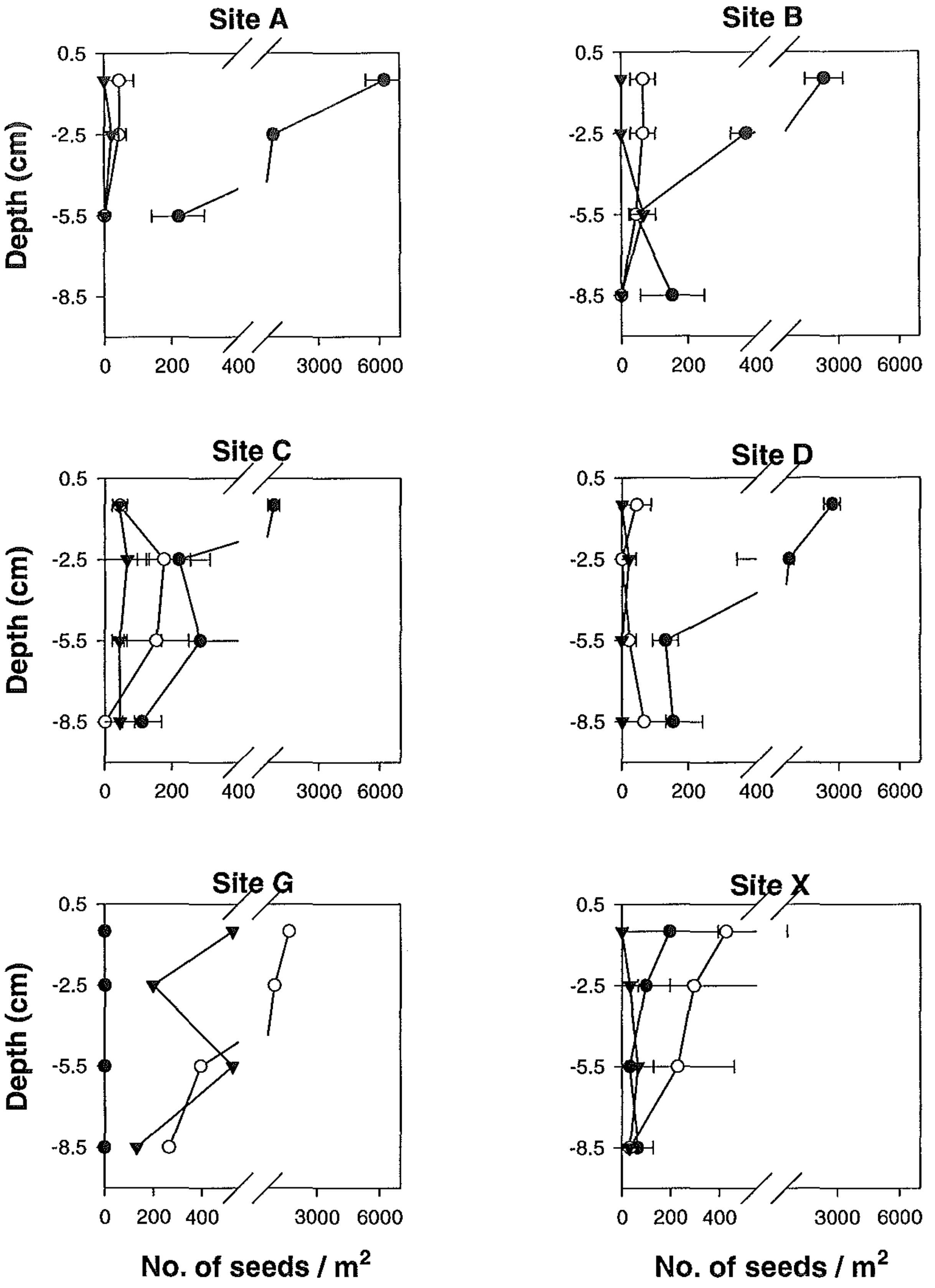


Fig. 22. Vertical distribution of seeds in the soil

5.5. Concentrations of plant nutrients and condensed tannins following experimental burning treatments

Generally, the N, P and K concentrations were higher in the broadleaved herbs than in the grasses (Fig. 23), but the seasonal changes in the concentrations of N, P and K were most pronounced in grasses. The reduction in plant nutrient concentration from the beginning (June) to the end (December) of the growing season in grasses was most pronounced for N, followed by K and by P. For broadleaved herbs, the reduction was clearly pronounced for K, whereas there were only smaller differences for N and P.

After 210 days, fire increased the concentration of K in grasses, whereas there was no effect on N and P concentration at this stage of grass growth. In contrast, after 1 year the P concentration of grasses in burned plots tended to be higher than in non-burned plots whereas N and K were unaffected. This effect of fire on grass P was most pronounced when ash was added too, as also shown by the tendency towards a significant fire times ash interaction term. In the broadleaved herbs fire, surprisingly, tended to decrease the concentration of P after 210 days, whereas there was no other significant main effect at this time. After 1 year, the depletion in P was no longer evident in the broadleaved herbs, and the concentration of K was higher in burned plots, and also tended to be so in plots that received ash. Hence, for both grasses and broadleaved herbs there was no main treatment effect on the N concentration whereas P concentration tended to be affected by fire, although in opposite direction and at a different time for the grasses and the broadleaved herbs. The clearest effect of fire was observed for K, although with increases at different times in the grasses and the broadleaved herbs.

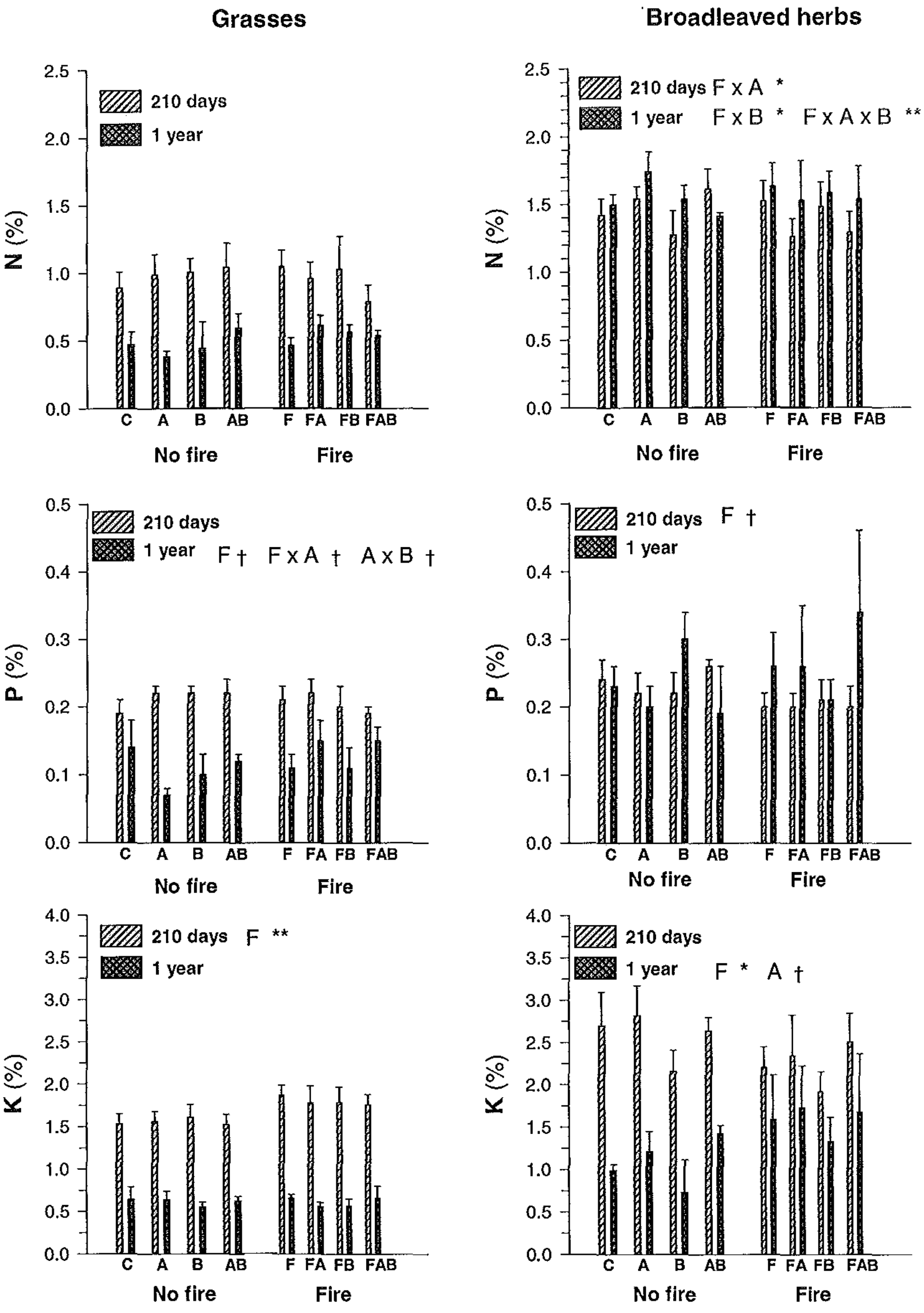


Fig. 23. Plant nutrient concentrations in leaves following fire (F), ash (A) and biomass (B) additions, with all possible combinations of their treatments, and in control plots (C).

Similar to the pattern of N, P and K in the leaves, the broadleaved herbs generally had higher concentration of condensed tannins than grasses (Fig. 24). In June, the condensed tannin concentration in the broadleaved herbs was 3 to 5 times higher, and in December, it was as much as 50 to 80 times higher than in grasses.

Fire significantly increased the concentration of condensed tannins in grasses after 1 year. Extra biomass (fuel load) seemed to increase the concentration of condensed tannins in grasses from burned plots after 210 days, whereas, in contrast, after 1 year the extra biomass addition led to a decrease in grass tannin concentration in burned plots, as shown by the significant fire times biomass interaction. In the broadleaved herbs, no main effect of fire or ash was observed, but fire tended to interact with ash yielding an increase in the concentration of tannins after 210 days.

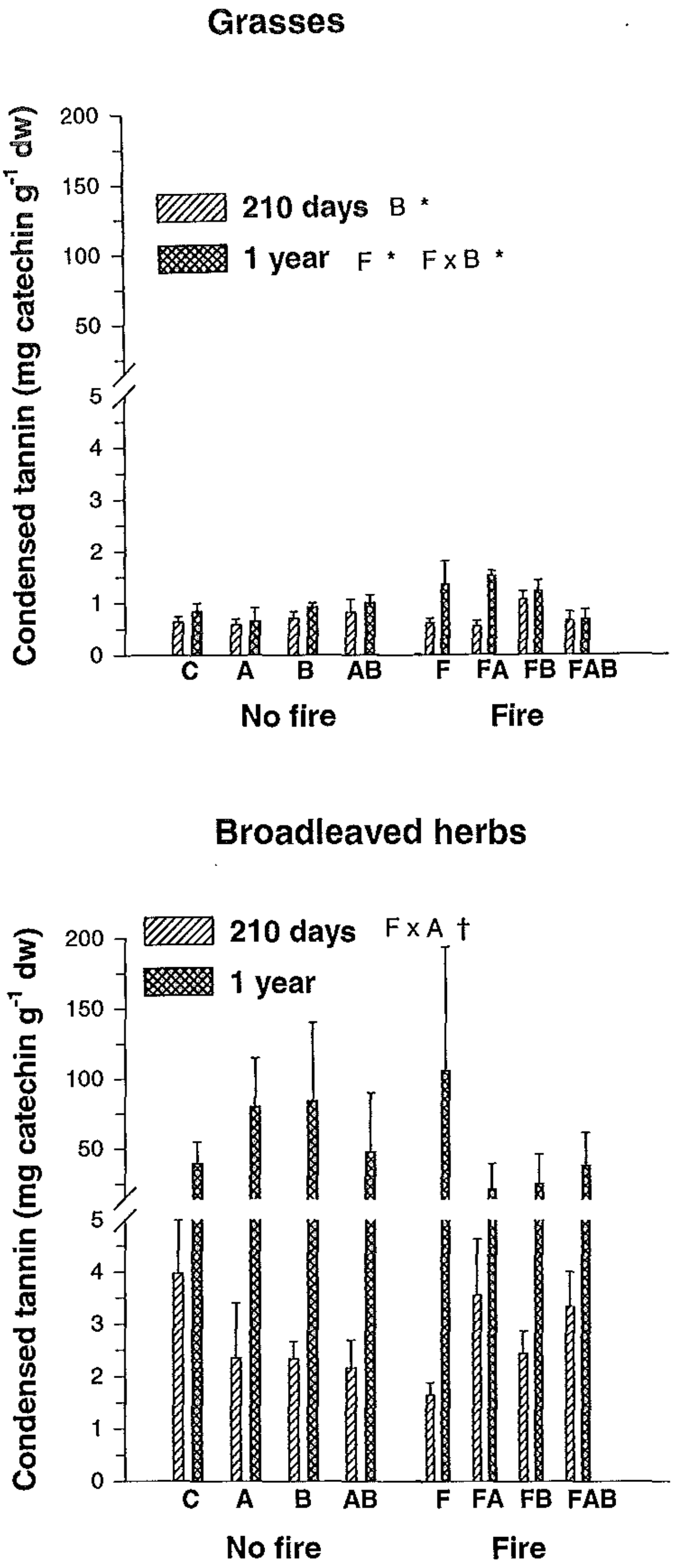


Fig. 24. Condensed tannin concentrations in leaves following fire (F), ash (A) and biomass (B) additions, with all possible combinations of their treatments, and in control plots (C).

5.6. Relationships between fire and seasonal variations in leaf condensed tannins to nitrogen quotients in dominant trees, shrubs and grasses

The concentration of condensed tannins in leaves varied widely among species, from 2 to 400 mg catechin per g leaf dry weight. There was a general trend of high concentrations of condensed tannins in February, i.e. immediately following fire, and a sharp decline in June and November (Fig. 25). This seasonal pattern was observed both for grasses (*Hyparrhenia* and *Loudetia*), shrubs (*Flueggea* and *Harrisonia*) and trees (*Combretum* and *Pterocarpus*). The exception was one tree species, *Acacia senegal*, which showed extremely low concentrations in February but a peak later, in June, and a shrub, *Ziziphus*, which did not show seasonal changes in condensed tannin concentrations (Fig. 25). The collections of three species, *Maytenus, Indigofera* and *Cadaba*, were insufficient to judge the seasonal changes.

Samples of the same species but from different plots within specific vegetation types were strikingly similar in condensed tannin concentrations (Fig. 26 & 27). The concentration of condensed tannins in tree species was significantly higher than in shrubs and grasses, i.e. 5-10 and 20-30 fold, respectively, (Fig. 25 and Table 11) ($P<0.05$). However, shrubs were not significantly different from grasses.

Furthermore, there were generally very small differences in tannin concentration between a plant species growing in different vegetation types (Fig. 26 & 27). However, the condensed tannin concentration in *Combretum* was higher in the woodland-wooded grassland intermediate site (A) than in the other sites, and seasonal changes were larger (Fig. 26).

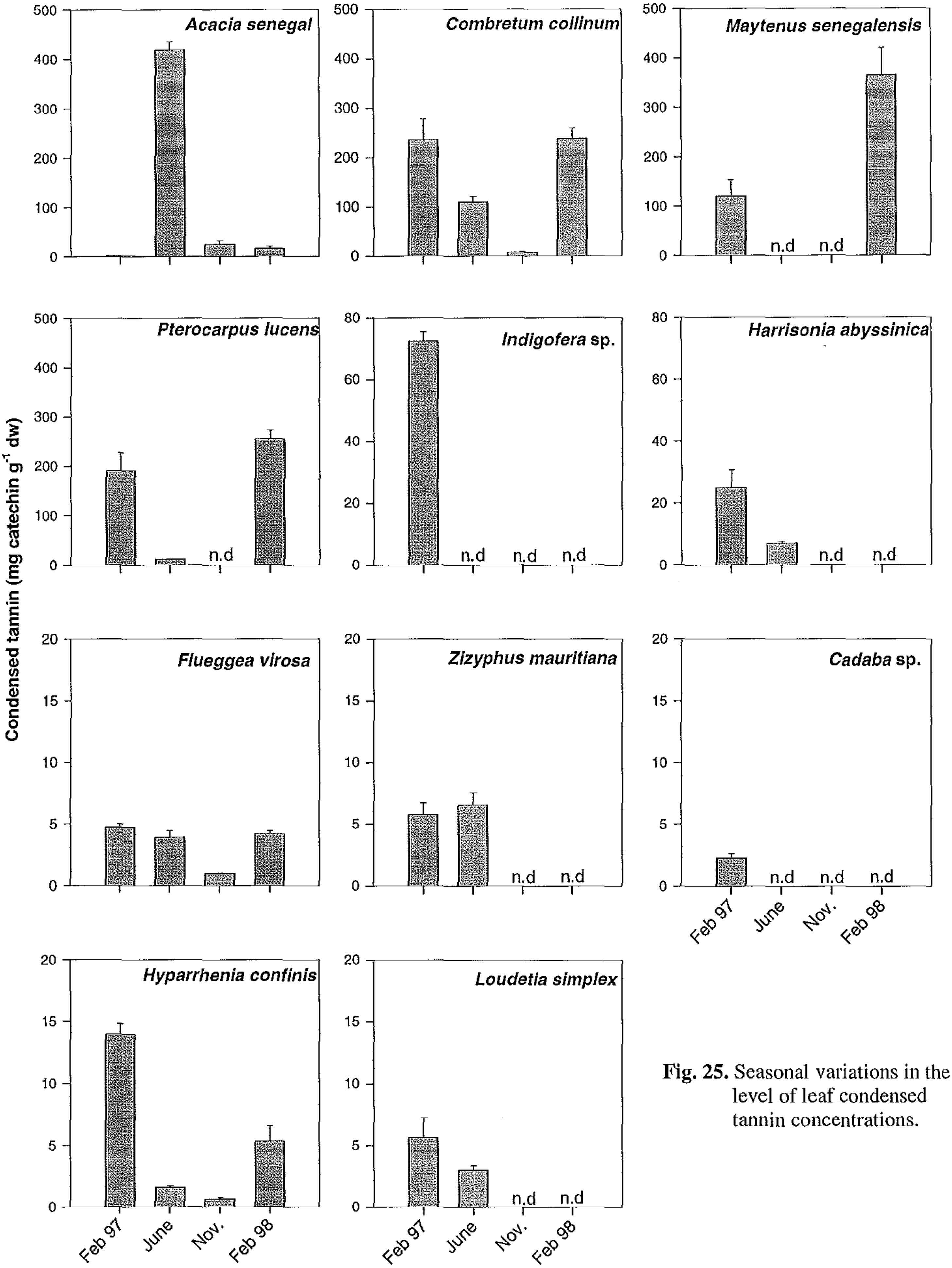


Fig. 25. Seasonal variations in the level of leaf condensed tannin concentrations.

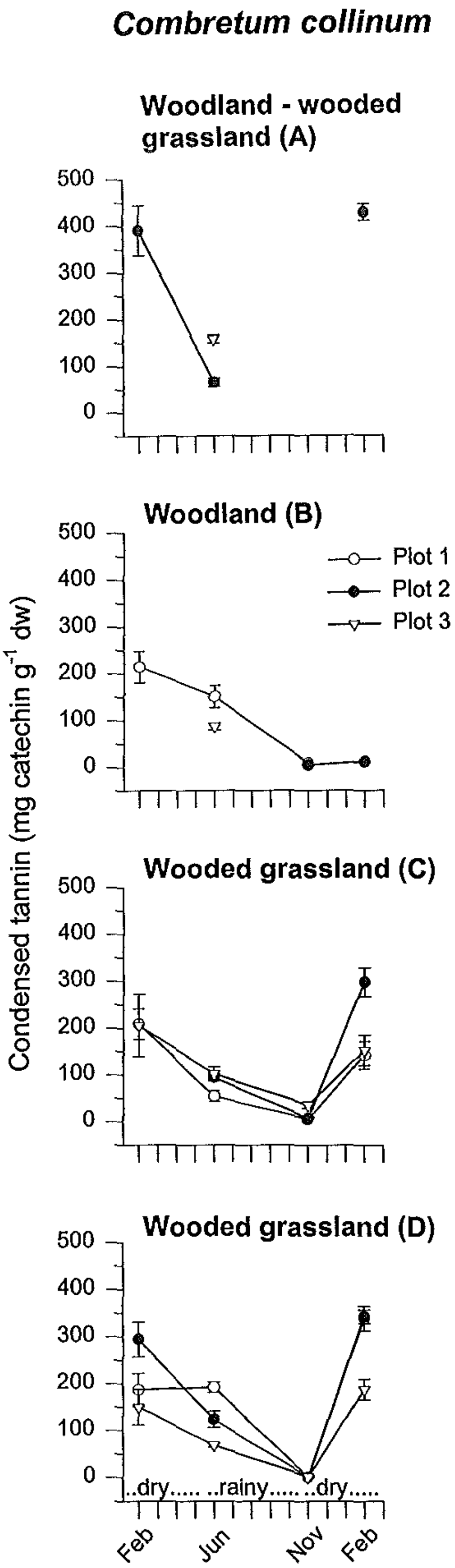


Fig. 26. Seasonal variations in leaf condensed tannin concentrations between the different vegetation types in *Combretum collinum*.

Hyparrhenia confinis

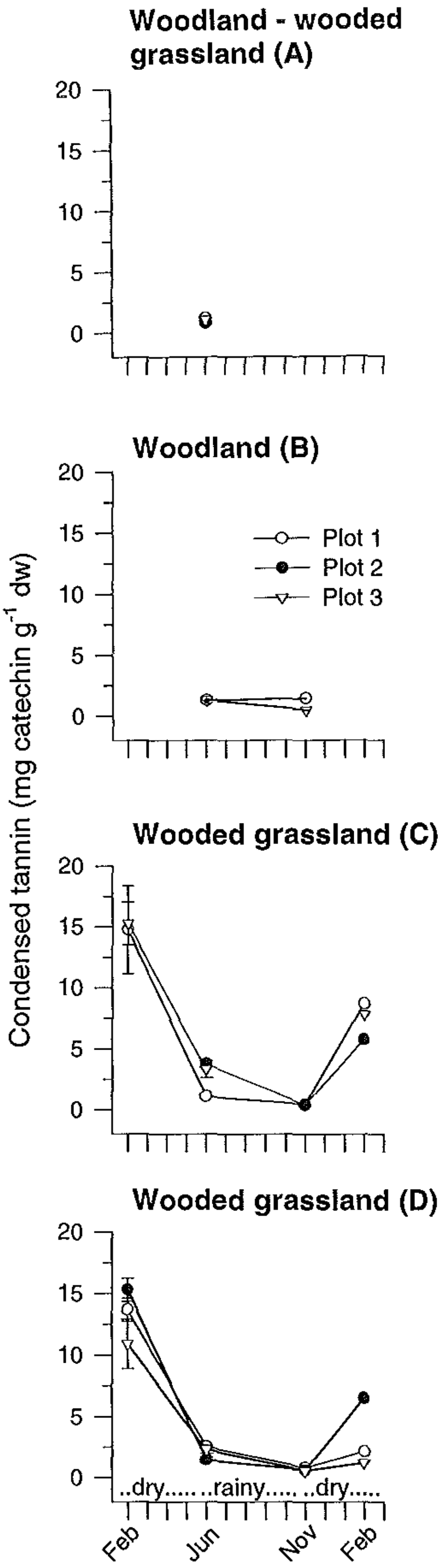


Fig. 27. Seasonal variations in leaf condensed tannin concentrations between the different vegetation types in *Hyparrhenia confinis*.

Table 11. Concentration of leaf condensed tannins (mg catechin g^{-1} dw) in the different plant growth forms, n = number of species in each group.

Effect of time and growth form on tannin concentration was analysed with two way ANOVA; F=4.62, P=0.03 for growth forms; F=0.33, P=0.81 for time and F=0.39, P=0.87 for the interaction between growth form and time, respectively.

Across dates, the difference between trees and grasses, and between trees and shrubs, was significant.

Growth form	February 97		June 97		November 97		February 98	
	n	0±SE	n	0±SE	n	0±SE	n	0±SE
Grass	2	9.9±4.2	2	2.4±0.7	1	0.7	1	5.4
Shrub	5	22±13	3	5.9±1.0	1	1.0	1	4.2
Tree	4	137±50	3	180±122	2	16.7±8.7	4	218±72.9

The ratio of condensed tannin to nitrogen varied between species and seasons in a similar pattern to that of the tannin concentration (Fig. 28, 29 and 30). Higher ratios were found in tree species than in shrubs or grasses. In many of the studied plants such as *Combretum collinum, Pterocarpus lucens, Harrisonia abyssinica, Flueggea virosa* and *Hyparrhenia confinis* the ratio of condensed tannin to nitrogen was very high in the middle of the dry season (February) and very low in the beginning of the dry period (November). The exception was again *A. senegal,* which showed high condensed tannin to nitrogen ratio in the beginning of the rainy season (June). Two species, *Loudetia simplex* and *Ziziphus,* did not show any seasonal changes in the ratio of condensed tannin to nitrogen.

Furthermore, there was no major variation in the ratio of condensed tannins to nitrogen among the different sites (Fig. 29). However, in the wooded grasslands sites (C and D) the ratio of condensed tannin to nitrogen in *Hyparrhenia confinis* was higher than in the woodland-wooded grassland intermediate site (A) and in the woodland site (B) (Fig. 30).

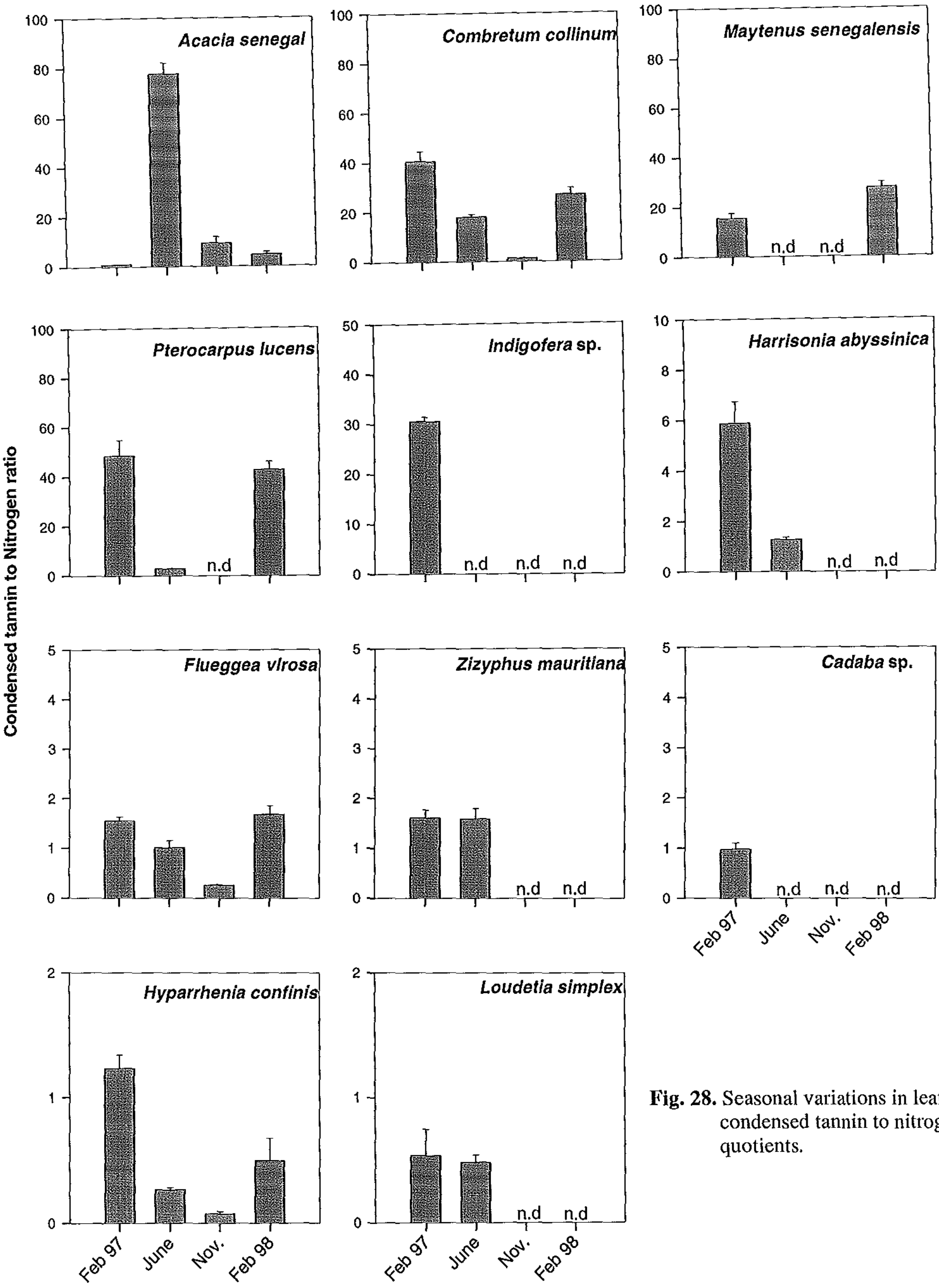


Fig. 28. Seasonal variations in leaf condensed tannin to nitrogen quotients.

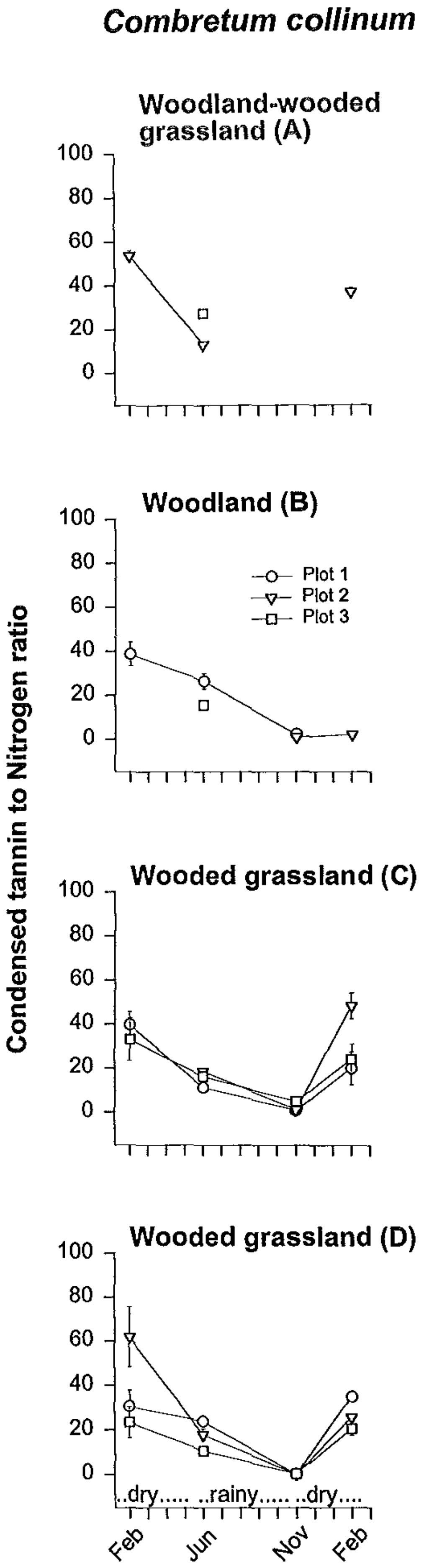


Fig. 29. Seasonal variations in the quotients of leaf condensed tannin to nitrogen between the different vegetation types in *Combretum collinum*.

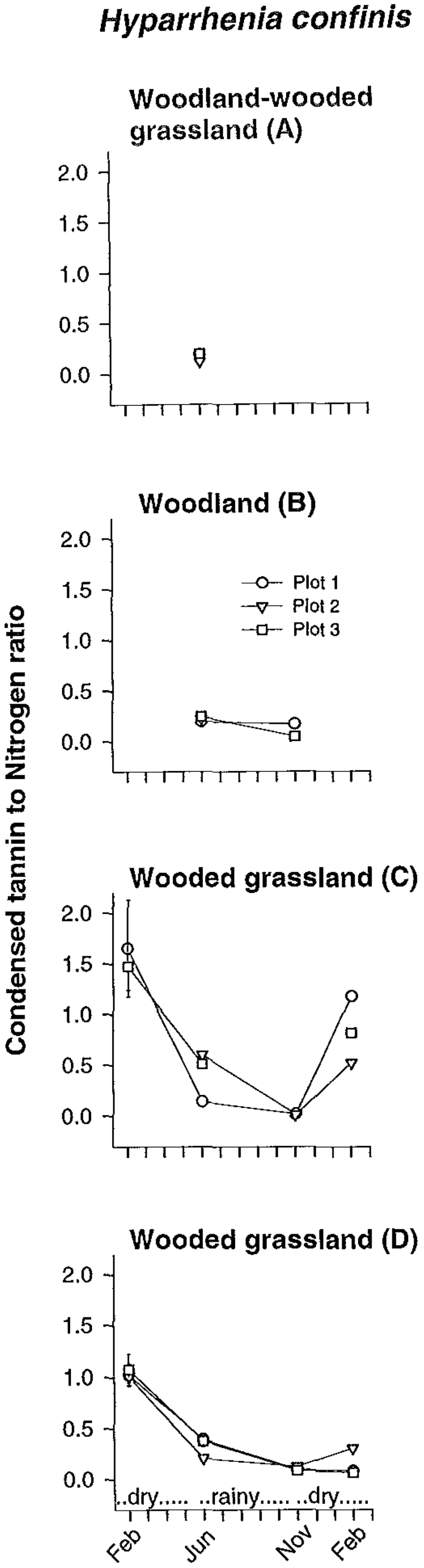


Fig. 30. Seasonal variations in the quotients of leaf condensed tannin to nitrogen between the different vegetation types in *Hyparrhenia confinis.*

6. Discussion

6.1. Strategies of post-fire regeneration and tree bark resistance to heating

The fact that the species under study occur in fire-prone environment does not necessarily imply that all have seeds that resist fire. Most of the species studied are able to regenerate by sprouting from protected buds on below ground stems (lignotubers) or above ground stems (epicormic buds), in addition to reproducing by seed. In a related study, seeds of many fire-resprouting dominant tree species did not germinate and those that did were less responsive to high temperature than understorey and obligate re-seeders (Bell *et al.* 1995). Plants with less heat resistant seeds may escape lethal temperatures of fires with the help of soil seed banks (Whelan 1995). The seed banks of the study area seem to be dominated by a single grass species, *Hyparrhenia confinis* (Menassie *et al.* in preparation and Menassie & Michelsen, in press), and this species only resisted up to 90°C heating for 5 min (Menassie & Michelsen, submitted). Likewise, *Combretum collinum* is a dominant tree in the frequently burning savanna of western Ethiopia, but its seeds showed low fire resistance compared to the other plant species studied. This species mainly survives fire by sprouting from unburned stem bases, and its cryptogeal type of germination further allows the species to escape fire and survive the post-fire conditions. In contrast, some species may survive the first fire due to resistant seeds but new seedlings might be killed during a second fire.

The main regeneration strategy in the frequently burning savanna woodlands of Gambella, western Ethiopia was by resprouting rather than by seedlings. Seed survival after fire has been found to be very low in many of the studies. For instance in Malanson & O'Leary (1982), 94.7 % the foliar cover was contributed by resprouts, and all the studied species were capable of sprouting after fire. The contribution to plant cover and frequency by obligate seeders was extremely low, probably due to the frequent fires that impede seedling growth much more than resprouting. This is in accordance with Keeley (1977) and the model proposed by Keeley & Zedler (1978). They found that with a very short fire cycle nonsprouting species could be eliminated, whereas an occasional long fire-free period (lasting 100 years or more) could be a very important evolutionary stimulus for the obligate seeding strategy. On the other hand, resprouters would not likely be affected by occasional short fire intervals as it relies on a lignotuber for recovery following fire (Enright & Goldblum 1999). Although there is little evidence to suggest how long genetic individuals of such resprouting species might survive in long absence of fire, lignotuber vigour may decline in old stands so that long awaited fires may cause high rates of plant mortality (Enright & Lamont 1992).

Furthermore, low seedling density under burned conditions could be caused by seed bank mortality due to very high temperatures, or by low germination percentage due to the high osmotic potential of the ash (Ne'eman *et al.* 1992) or ash water completely inhibits the germination process (Gonzalez-Rabanal & Casal 1995). With the exception of two tree species, obligate seeders in our study sites were all broadleaved herbs recruiting seedlings, though at low density, from the soil seed bank between fires. This is in agreement with the findings of Menges & Kohfeldt (1995). Although the obligate-seeding life history seems less advantageous, they maintain their population and coexist with resprouters through the fire cycle by allocating more resources to seed production and hence, recruiting numerous seedlings from seeds accumulated in the soil (Keeley 1977, Keeley & Zedler 1978). However, Thomas & Davis (1989) found that low density of seedlings recruited from soil seed banks and resprouting inability in obligate seeders is offset by high rate of seedling survivorship. The absence of obligate seeders and the low vegetation biomass in general during the dry season might be because of the reliance of the soil seed banks on the short rain, and the low soil moisture following fire which inhibited seedling establishment and resprouting. Low moisture level caused by intense burning was found to be one of the reasons for decreased number and biomass of resprouters at early stages of resprouting (Canadell *et al.* 1991).

There were major differences among the different plant growth forms in the mode of reproductive strategies. Broadleaved herbs and tree/shrub species mainly regenerated by sprouting alone, which indicated that large amount of energy is allocated for the production and development of sprouting organs, which may allow plants to recover quickly after fire disturbances. However, production of sprouts is not solely related to fire disturbances, as these structures may be considered pre-adaptation to fire, but could have developed under other conditions. Furthermore, continuous basal sprouting has also been observed in other disturbances such as drought, cold, cutting or grazing (Mesleard & Lepart 1989, del Barrio *et al.* 1999). Obligate resprouters in tree/shrub species and broadleaved herbs were abundant in the dry and the wet seasons, respectively, which indicates that trees and shrubs might have deep roots which provide better access to water and nutrient reserves than possible for more shallow-rooted broadleaved herbs. Instead, some of the obligate sprouter broadleaved herbs were equipped with burl or specialised lignotubers or roots buried deep in the soil. For instance, all geophytes were broadleaved herbs, *Tylosema fassoglensis*, *Pyrenacantha kaurabassana, Ampelocissus abyssinica, Chlorophytum* spp., *Tacca leontopetaloides,* could sprout many times after fire and survive without water for the long dry periods. This supports the findings of Bradstock & Myerscough (1988) that the growth habit alone does not determine the ability to persist under frequent fires, and hence, other characteristics such as rates of survival and development of lignotubers are crucial. Higgins *et al.* (2000) further noted that coexistence among the different plant growth forms should be considered from the long-term effects of life history-disturbance interactions, rather than from the fine-scale effects of shoot to root ratio and performances in resource competition.

All grass species were facultative sprouters and contributed to high foliar cover in the savanna grasslands, but the contribution from seedlings was much lower (5% and 27% in February and June, respectively). Facultative resprouters of broadleaved herbs and trees/shrubs were less abundant than the obligate sprouters due to the frequent fire preventing seedling establishments. However, facultative resprouters might have a greater chance of increasing genetic variability as these species reproduce sexually whenever conditions are prevailing.

The moderate fire intensity differences among the different sites might be the reason for some variations in the foliar cover and plant frequency by the different regeneration strategies. For instance, fire was relatively more intense in site D than in the other sites, which probably favoured sprouters of broadleaved herbs and trees/shrubs immediately after fire. Moreover, soil seed bank densities in site D and C were relatively lower than site A and B, and seedling densities from seed banks of unburned plots were higher than in burnt plots. However, Purdie (1977 b) found higher number of seedlings in burnt than in unburned quadrats, which was attributed to the direct heat stimulation of seed germination and removal of litter or germination inhibitors for seedling establishment. The grass cover in June was in site order of D>A and C>B, i.e. high cover with high fire intensity, and the absence of grass germination from soil seed banks of unburned plots might indicate that intense fire followed by rain promotes the dominance of grasses over the other plant growth forms. The largest contribution to foliar cover and abundance was from a dominant facultative resprouter grass species, *Hyparrhenia confinis*, which suggests that fire intensity and frequency probably determine plant regeneration strategy, and the potential for species dominance in savanna woodlands and grasslands of the study area. Purdie (1977 a) noted that although frequency and abundance of species related to fire intensity, the method of species regeneration following fire disturbances is important in determining floristic dominance. Moreover, Moreno and Oechel (1991) found very high intensity of fire decreased plant survivorship and the number of resprouts per plant, and delayed resprouting.

Resistance of individual trees to repeated fires was further enhanced by restoration of bark thickness. Although all the tree species tested for their bark resistance to heat showed similar patterns of increase in heat resistance with an increase in the thickness of bark, there was a considerable variation among species in the rise of cambium temperature for trees of a given bark thickness. This result supports the findings of Hare (1965) and Gill & Ashton (1968) but contradicts with the findings of Vines (1968) who found no interspecific variations. Such interspecific variations might be attributed to differences in the structure, composition and moisture content of the barks. Bark flammability is high in stringy, fibrous and rough bark, and, likewise, energy reflectance is high in the smooth and white barks, which were found to be the cause of variations among tree species in the Mediterranean type of climate (Whelan 1995). This also holds true in our investigation that the stringy barks of *Combretum collinum*, *Lonchocarpus laxiflorus*, *Pterocarpus lucens* and *Terminalia laxiflora* burns immediately on the application of heat but diffused heat very slowly due to their thick bark. The white and smooth barks of *Anogeissus leiocarpa*, *Ficus sycomorus* and *Strychnos innocua* may rely on heat reflectance to protect their cambium from fire, but heat also diffused at much higher rate than the stringy bark species. Dry bark serves as a good insulator, but the relatively low moisture content reduces heat capacity, therefore temperature rise could be significant (Vines 1968). For instance, the barks of *Lonchocarpus laxiflorus*, *Pterocarpus lucens* and *Ficus sycomorus* contained some moisture, sap or latex which might conduct heat better than the dry bark of *Strychnos innocua*, *Anogeissus leiocarpa* and *Ziziphus mauritiana*, but the rise in the effective cambial temperature decreased due to the high heat capacity.

The positive correlation that exists between bark thickness, tree diameter and the time elapsed for cambium to reach lethal temperature (60°C) indicated that small trees are more susceptible to fire damage than mature ones. In our study, the time taken for cambium to reach 60°C was unrelated to ambient temperature at the start of the experiment, which might be due to the constant ambient temperature prevailing at the study site ranging between 23 and 31°C. The results of Hare (1965) are in contrast to our findings, but his

with relatively low temperatures (60 and 90°C) but led to a significant decrease in the rate of germination following exposure to higher temperatures (120, 150 and 200°C). Therefore, a combination of a fire of medium intensities and brief exposure may result in high germination frequency. However, a combination of a low intensity fire and extended duration may also lead to high germination in some species, as also observed by Floyd (1966) and Hodgkinson & Oxley (1990). This indicates that species differ in their responses both to the cumulative heat and to the threshold temperature required to stimulate their germination. *Ziziphus mauritiana* was the only species that resisted the highest temperature (200°C) for 5 minutes of treatment; this is probably because the seeds are well protected by the fleshy and stony layers in the drupaceous fruit. Also, species with seeds in pods are more likely to withstand higher temperatures for longer duration than species protected by a seed coat only.

Similar studies have shown that the range of responses to thermic shocks could be related to seed size (Gonzalez-Rabanal & Casal 1995). In our study, small and light seeds resisted low heat intensity only. The smallest seed measured was that of *Eleusine coracana* (1.1mm and 1.9mg) that resisted heating up to 90°C only. In contrast, the heaviest and largest seed was of *Tylosema fassoglensis* (> 25 mm and 2900 mg) that resisted heating up to 200°C. Keeley (1977) proposed that a low seed surface to volume ratio contributes to the capacity of the seeds to tolerate high temperature, and our data seems to support this view. Likewise, in a related study, larger seeds of *Cistus laurifolius* required longer heat exposure in order to terminate germination than the smaller seeds of *C. ladanifer* (Valbuena *et al.* 1992).

The seeds of *Tamarindus indica, Hyparrhenia confinis, Sorghum arundinaceum, Cassia obtusifolia* and *Entada africana* showed a similar, bimodal pattern of germination: the seeds germinated with a high frequency both when heated at low and high temperature but germinated with reduced frequency at medium temperature level, most often 60°C. This indicates that there is variation in the germination requirement between seeds within the same species. The intraspecific germination differences among seeds could be due to genetic factors, to spatial and temporal variations in the environmental factors, or to interactions between both factors (Evans & Cabin 1995; Baskin and Baskin 1998). We cannot exclude that seed heterogeneity was caused by differences in seed age, maturity at collection, or depth of seed dormancy (Bell *et al.* 1995). However, the presence of two temperature tolerance optima of seeds ensures that at least some seeds germinate in the absence of fire, but also that viable seeds still remain if subsequent late fires kill emerging seedlings.

Germination failed in six species, irrespective of seed treatment. Charred wood or ash did not trigger germination in these species, but smoke treatment was not tried, although some reports suggest that smoke may induce germination in deeply dormant seeds (Keeley & Fotheringham 1998). Since seeds in all these six species were collected fresh from canopy or shoot, we can not exclude that the seeds might have had underdeveloped embryos. Morphological dormancy is due to underdeveloped embryos, which continue to grow slowly (for up to 3 months) after seeds are dispersed, and mainly occurs under tropical conditions (Baskin & Baskin 1998). None of these species germinated when germination potential was again checked after a year, which indicates that other types of dormancy such as physiological and physical dormancy might be combined with morphological dormancy to inhibit germination. Further investigations are required to study the causes of dormancy in these species.

6.4. Dynamics of soil seed bank

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) 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 scanty 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.

The rest of 10 % of the seed density was from other species of graminoids, broadleaved herbs and trees/shrubs. The density of graminoid seeds in the soil was much higher than that of broadleaved herbs, trees and shrubs, probably due to their high coverage compared to broadleaved herbs and woody species. The major input to soil seed bank of seeds from many of the species was largely in the beginning of the dry season, i.e. between November and January. Consequently, the plants studied had the highest density of seeds in the soil in the dry season (February). Fire has usually taken place by this time but there is still a high soil seed bank of species, particularly graminoids, to initiate growth after the fire when the rainy season begins. 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. Seeds in the soil benefit from the scattered "small rains" in April and May, and by the end of June most of the graminoid seeds have germinated and the seed bank is therefore exhausted. The period between June and October is the growing season. 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 graminoid 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 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 *Pennisetum 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 graminoid 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. 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 high altitude forests of Ethiopia (Michelsen *et al.* 1993) which experience little changes in climate through the year and fires are rare or absent.

Graminoids were abundant in the study sites because of the regular burning and seeds dispersed from the early successional post-fire vegetation are largely responsible for the abundance of seeds in the soil. Therefore, the two interdependent reproductive traits, i.e. high capacity for seed dormancy and widespread seed dispersal, will determine the density of seeds in the soil and the seasonal changes in the abundance of viable seeds in the soil (Enright 1985; Demel & Granström 1995, Dalling *et al.* 1997). In Venezuelan savannas, fire exclusion resulted in significant reductions in seed production and seedling recruitment of an annual grass (Canales *et al.* 1994), which is similar to our results, suggests that fire is an important factor for the maintenance of grass-dominance in savannas.

Seasonality in the soil seed bank richness and abundance of woody species was low in the sites that burn regularly. Unlike graminoid seeds for which restoration of the soil seed bank had already started by November, germination of seeds from broad-leaved herbs, trees and shrubs was still low at this time. This is because most broadleaved herbs and woody species are still growing in November and seed dispersal probably has not reached yet. The slower rate of seedling establishments, later appearance and longer growing season for herbs and woody species than for grasses may cause that fire in some years precedes seed dispersal, leading to severe reduction of the soil seed pool of herbs and woody species. In contrast grasses have a relatively short growing period but a fast seedling establishment (Tillman 1982) and hence compete well with woody plants by being able to benefit from improved growing conditions such as onset of rain and increased nutrient availability (Michelsen *et al.* 1999). Therefore, the abundance of woody plants and their seeds in fire prone ecosystems was small. Loss of seeds because of high fire intensities and predation, particularly by insects could also contribute to the low abundance of woody plant seeds in the soil. An additional explanation for the low species richness and abundance of seeds of herbs, shrubs and trees in the soil seed bank might be that the seeds remain in the soil following dispersal only for a short time. The formation of such a transient seed bank is common in woodland and primary forest species (Enright 1985, Young *et al.* 1987, Demel & Granström 1995, Dalling *et al.* 1997).

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 & Granström 1995, Dalling *et al.* 1997). The almost complete lack of germinating seeds in June suggests that the vast majority of the seeds have either germinated, or do not survive more than half a year of burial. The highest number of seedlings observed in the upper soil layer is according to the results of most studies (Valbuena *et al.* 2000). However, seeds deep in the soil may be important for regeneration after late, strong fires that could be detrimental to the survival of seeds in the soil surface. Successful germination of seeds from broadleaved herbs, trees and shrubs could be achieved with seeds from deeper soil layers (2.5 cm to 8.5 cm) because seeds here are better protected from the effects of fire.

Correspondence between species number and floristic composition of the seed banks and the standing vegetation was generally poor, however, there was a strong correlation in grasses indicating that soil seed banks are more important in grass species than in the broadleaved herbs and trees/shrubs to survive fire-disturbances. Soil seed bank study from degraded land in southern Wello, Ethiopia showed similar result that correspondence between species numbers and composition of the seed banks and the standing vegetation was poor (Kebrom & Tesfaye 2000). Other studies have also indicated a poor correlation between species in soil seed banks and those in standing vegetation (Major & Pyott 1966, Thompson & Grime 1979, Demel & Granström 1995).

6.5. Leaf nutrient and condensed tannin concentrations following experimental burning treatments

Broadleaved herbs contained relatively larger amount of N, P and K as compared to grasses. Moreover, less seasonal fluctuations in the concentration of these elements were observed in the broadleaved herbs than in grasses. This could be attributed to the longer time that the leaves remain green in the dry season, as compared to grasses. From an animal nutrition point of view, broadleaved herbs may be preferred by herbivores for their high nutrient content. However, the high concentration of condensed tannin in the broadleaved herbs may reduce their palatability compared to grasses. Therefore, the tendency in the broadleaved herbs (and shrubs/trees) to decrease palatability by high investment in the production of condensed tannins that affect nutrient uptake in grazing animals might be an evolutionary consequence of severe grazing by herbivores as well as a response to severe nutrient competition from the dense grass cover.

The differences in the amount of condensed tannins between grasses and broadleaved herbs are large. In the end of the wet season the concentration is 50 to 80 times higher in herbs than in grasses, because broadleaved herbs leaves are still green in December and, furthermore, seem to allocate resources to a chemical defence against herbivory. In contrast, at this time grasses already have passed their growing season. The yellow, senesced grass leaves retain similar concentrations of condensed tannins as that of the green leaves earlier in the season, and do not show massive increase in these compounds as seen in the herbs. The dominant grass species in the area have relatively large production of condensed tannins at the beginning of the growing season while leaves are still green, i.e. in February-March. This indicates that defence chemicals may play a role against herbivory at the early stage of the life cycle of savanna grasses, whereas at a later stage production of silica in grass species may be important for protection against grazing (McNaughton *et al.* 1985). The works of Macauley & Fox (1980), Prudhomme (1983), Palo *et al.* (1985), Menassie *et al.* (in preparation) show similar results in that plants allocate more resources to produce defence chemicals early in the growing season, when leaves are succulent and nutritious, and their susceptibility for herbivory is higher.

Fire increased the concentration of condensed tannins in grasses harvested one year after the treatment. This could be interpreted as physical damage imposed by fire, i.e. caused by removal of the aboveground part of the plants, similar to the effect of grazing. However, it could also be due to the increase in soil nutrient availability in the burnt plots, as shown by the increase of inorganic N up to 3 months after the fire (Jensen *et al.* submitted). This increased the growth of grasses in burnt plots, as shown by the high cover estimates 3 and 7 months after burning, and could have caused delayed senescence of grasses, evident from the tendency towards an increase in P concentrations in grasses after one year. Hence, in burned plots there was probably a slightly higher proportion of green, live leaf tissue than in non-burned plots. As young, green leaves and tips of growing branches are favoured by browsers, probably due to their high protein content, they contain more condensed tannins than senescing, yellow leaves (Macauley & Fox 1980, Prudhomme 1983, Coley *et al.* 1985, Palo *et al.* 1985, Hartley & Lawton 1987 and Perevolotsky *et al.* 1994). This could in part explain the higher condensed tannin concentrations in grasses 1 year after fire. Bryant *et al.* (1983) suggested that the level of chemical defence of a plant is less strongly influenced by herbivory than by the availability of soil nutrient resources, where plants increase their production of defence chemicals at the expense of growth in nutrient deficit conditions. However, this may not hold true for the broadleaved herbs in our experimental plots, as fire did not increase the level of condensed tannins in this plant growth form. In the broadleaved herbs the production of condensed tannins is probably controlled more by the level of grazing than by the availability of soil nutrients.

6.6. Relationships between fire and seasonal variations in leaf condensed tannins to nitrogen quotients in dominant trees, shrubs and grasses

The high level of condensed tannins in leaves in the middle of the dry season, i.e. following fire (February), with subsequent decreases in tannin concentrations from the beginning (June) to the end of the wet season (November) may be due to leaf phenology and physiology during seasonal growth. The high levels of condensed tannins in February seem to characterise new leaves emerging following fire. In June and November, leaves had expanded, with concomitant dilution of tannin concentrations, particularly in November. This is similar to results of Dement & Mooney (1974) and Meyer & Montgomery (1987), showing that the concentration of phenolics in general decreases with leaf age. This may have important consequences for herbivores. For example, leaf phenolics retarded larval growth at the early developmental stage of birch leaves, but were not effective when leaves had completed their growth (Haukioja & Niemela 1979). Prudhomme (1983) also reported that carbon allocation to total phenolics was greatest early in the season when leaf susceptibility to herbivores was highest. Such seasonal fluctuations in the concentrations of condensed tannins may, in leaves of species growing in Mediterranean climates in S. African, be caused by soil nutrient mobilisation during the rainy season, which is followed by strong growth (Glyphis & Puttick 1988). This is in agreement with our results showing low and high concentrations of condensed tannins during the rainy and dry season, respectively. However, leaf growth is probably more important than increased soil nutrient availability in explaining reduced tannin concentrations in the rainy season. For instance, the late emergence of leaves of *Acacia senegal* in the dry season explains the temporal shift in the peak concentration of condensed tannin to the month of June in this species. Furthermore, there were only small differences in tannin concentrations of single species when comparing collections from different vegetation types, although they differed strongly in soil nutrient availability (Jensen *et al.* in press, in preparation).

The wide difference in condensed tannin concentration between leaves of trees and leaves of grasses suggests that grasses may invest nutrient resources in rapid regrowth rather than in chemical defences, whereas trees which grow more slowly invest more carbon in the production of defence chemicals. This supports that species well adapted to massive disturbances such as fire (i.e. grasses) respond by rapid regrowth rather than by investing carbon into the production of chemical defences (Perevolotsky & Haimov 1991, Menassie *et al.*, in preparation). In contrast, nutrient limitation exerts a selection pressure for plants with inherently slow growth rates, characteristics of trees and shrubs which dominate in the woodland, over fast growing species, which in turn favours a large investment in defence chemicals by slow-growing plants (Coley *et al.* 1985).

Frequent Fires lead to release of nutrients right after fire (Raison *et. al.* 1985, DeBano *et al.* 1998, Jensen *et al.* submitted), and frequent fires favour grasses that are more palatable and become dominant over woody vegetation (Fox 1998). In the woodland, tree stem volume was 3-6 times higher than in the grasslands, while grass biomass was 3 times lower; with the woodland-wooded grassland is an intermediate position (Jensen et al. in press, in prep.). The trees with high tannin concentration, such as *Acacia senegal, Combretum collinum, Maytenus senegalensis and Pterocarpus lucens* are the most frequent trees in the woodland. The high content of defence chemicals in woody species, as found in the present study, explains why large herbivores in the African savannas show less food preferences for woody vegetation (Bryant *et al.* 1989).

The ratio of condensed tannin to nitrogen determines the quality of forage for herbivores, with high ratios resulting in low forage quality (Robbins *et al.* 1987, Bryant *et al.* 1989, duToit *et al.* 1990). The high ratio of condensed tannin to nitrogen in February indicates that although leaves in this month were fresh and soft most were highly deterrent and poor in food value to browsing herbivores. At this time of the year, facultative grazers and browsers may prefer the grasses and shrubs with low tannin to N ratio. In contrast, in the last part of the rainy season and the beginning of the dry season the ratios of condensed tannins to nitrogen were low, irrespective of the plant species and the tree foliage may be browsed to a much higher extent by facultative grazers/browsers. However, Palo *et al.* (1993) noted that low tannin to N quotient does not always imply low defence level because thorns, spines and N based defences such as alkaloids or non-nitrogen based chemicals such as silicon in the case of grasses (McNaughton *et al.* 1985) could increase species defence against herbivores. For instance, this may be important for the common shrub in the study area, *Harrisonia abyssinica,* which had relatively low tannin/N ratio but was well defended by thorns and a strong smell.

Palo *et al.* (1993) predicted that nitrogen-fixing species might be more palatable for mammalian herbivores. In our case two potential N_2 – fixing trees, *Acacia senegal* and *Pterocarpus lucens,* showed very high tannin to N ratio in the beginning of the wet season, which seems to contradict the latter hypothesis.

7. Conclusion

In the woodland and grasslands of western Ethiopia, Gambella, the three modes of reproductive strategies (obligate seeders, obligate resprouters and facultative sprouters) are considered to be important and coexist in forming the existing vegetation mosaic. This is determined by various interacting factors such as fire regime, means of survival, rate of recovery after fire disturbances and by the life-history or growth forms of plants. There were clear differences among the different plant growth forms in the strategy for regeneration after fire. Obligate seeding strategy was widely used by the short-lived broadleaved herbs, which relied on the short rain to recruit seedlings from the soil seed bank after fires. Trees/shrubs were largely obligate sprouters and were commonly sprouting immediately following fire in the dry season. Thick bark or cork layers further reinforced the survival of trees, once they reached adult size or when their reproductive tissues escaped the fire belt, whereas the thin barked trees might be susceptible to fire damage. The highest biomass production in the savanna woodlands and grasslands of the study area was made up of a dominant grass species, *Hyparrhenia confinis,* which reproduced both by seeds and by resprouting. Despite the fact that fire stimulates seed germination through direct heat effects and by removing litter or other inhibitors, the short fire cycle might impede seedling establishment, and hence low seedling density was recorded in all of our study sites. However, reduced fire frequency might constitute a high selection pressure for obligate-seeding strategy.

There is a distinct relationship between fire, vegetation dynamics and leaf chemistry of plants. A strong promoting effect of fire on plant cover was observed for the grasses. This suggests that fire is maintaining ecosystem stability by promoting the dominant species (grasses) and by suppressing the less frequent, such as woody species. Light burning has further increased plant richness immediately following fire, particularly in those species that are less competent.

The responses to the different levels of heat and duration were species specific. Five of 15 germinating species showed higher germination following treatments at 60°C or 90°C than at 20°C, and hence, benefited from heating. However, a combination of high temperature and prolonged exposure significantly reduced seed viability in most plant species. Also, five of 15 species showed two optima for germination, with peaks both following low and high temperature treatments. This mechanism ensures that at least some seeds germinate in the absence of fire, but also that viable seeds remain after late fires have killed emerging seedlings. Four of 15 species resisted temperatures of 200°C, and those can be considered as highly pyrophytic. High seed sizes and seed weights were correlated with high tolerance to heating. Seed resistance to high temperature alone may not assure the species abundance in the fire environments. Species with vegetative reproduction or with spatial and temporal fire escaping specialisations may add to the species richness and the plant biomass in fire-prone ecosystems. Examples in western Ethiopian savanna are the dominant grass *Hyparrhenia confinis* and the dominant tree *Combretum collinum*, which rely on a large soil seed bank and resprouting, and cryptogeal germination and resprouting survival strategy, respectively. The present fire regime, i.e. frequent burning with relatively low intensity, seems to be within the seed heat resistance range of most of the species.

However, if fires become less frequent and therefore more intense due to high fuel loads, a higher proportion of seeds may be killed in the less tolerant species, which will affect the plant species composition.

The amount of seeds in the soil and plant species composition of regularly burning savanna woodland in western Ethiopia varied spatially and temporally. Most of the seeds in the soil seed bank were annuals rather than perennial plants. A grass species, *Hyparrhenia confinis,* dominates the soil seed banks of frequently burning sites, but is rare or absent in the soil seed banks of the rarely burned plots. In contrast, the species abundance and richness of the soil seed banks of the woody plants are relatively higher in unburned plots. Grass species largely survive the mild fire by high seed input to the soil, and the strong floristic compositional similarity between the soil seed bank and the standing vegetation of graminoids shows that soil seed banks have important role in post fire regeneration and survival to fire. However, the soil seed bank of woody plants is low because of the few seeds produced and found in the soil and because of the small floristic compositional similarities between the standing vegetation and the soil seed banks. Therefore, soil seed banks of woody vegetation have less significance as a strategy to survive fire. The woody plants survive the fire by depositing seeds at deeper soil layer, and from coppice growth. The number of seeds of graminoids is high in the topsoil, which increase the possibility for survival of seeds after fire.

The soil seed bank of graminoids is highest during the early dry periods and lowest at the beginning of the wet seasons, whereas, in the woody vegetation it is highest in the late dry seasons and lowest at the beginning of the dry seasons. Hence, for graminoids the input of seeds in the soil or seed dispersal occurs ahead of the onset of the regular fire season, whereas for woody species and herbs some seeds may be killed by early fire prior to dispersal and incorporation into the soil. Late fires are detrimental to seeds of both graminoids, herbs and woody plants, and could affect the present grass dominance or the vegetation composition in general. However, the current fire regime of the study sites i.e. high frequency and relatively low intensity seems to maintain the dominance of graminoids, particularly, *Hyparrhenia confinis* both as seeds in the soil and in herbaceous stratum of the vegetation as a whole.

Fire is also playing a major role in controlling the level of plant nutrients and, in the grasses, the production of carbon-based defences against herbivory. For the less abundant broadleaved herbs, the tendency towards a high production of condensed tannins might be a strategy or evolutionary response to perpetuate in an ecosystem with severe competition. Trees allocate large nutrient recourses to the production of condensed tannins than to growth which implies that trees are highly defensive to herbivory than to the effect of fire at the early stage of their life cycle, and hence fire has caused high mortality of tree saplings than rapidly growing species such as grasses and annual broadleaved plants. The latter allocate much of their nutrient resources for rapid regrowth strategy than to defence, and are, therefore, able to complete their life cycle before the next fire. Generally, the changes observed in vegetation composition and herbage quality with fire are small compared to the changes observed between seasons. This indicates that the influence of the current fire regime is secondary in determining the vegetation pattern.

Fire, therefore, seems to maintain the present balance between the various plant forms under the current fire regimes in the study area i.e. with relatively low intensity and annual burning.

8. Recommendation

The extremely low density of woody species in the soil seed banks and its poor floristic correspondence with the standing vegetation, as well as the small number of seedlings encountered along the transect lines indicate that sprouting is more important than sexual means of reproduction after fire disturbances. The low seed bank density and seedlings of woody species may not balance adult losses from the matured stand, particularly if the current fire regime is changed. Therefore, it may be necessary to control fire in some parts of the frequently burning sites to increase cover and genetic heterogeneity of woody plants.

Further studies on germination ecology, specifically information on annual seed inputs by different plant growth forms, seed predation, type and period of seed dormancy are necessary to obtain a through understanding of the germination responses of plants in regularly burning savanna grasslands and woodlands. Moreover, in this study germination of six species failed under experimental conditions, therefore, studies on the effect of heating, smoking and charred wood treatments are required to investigate factors responsible in breaking or causing deep dormancy in these species.

Sprouters are common in the Sudanian type of woodland savannas in general and they might be more widespread than seeders. Research on geographical distribution of both types of regeneration strategies might be important to understand the general trend and vegetation structure on a large scale. Some ecological and evolutionary differences between seeders and resprouters, such as relative growth rates, pattern of resource allocation (either to shoot or root), leaf weight, life span, seed size, shoot to root dry weight ratio, root system and phylogenetic relationships should be considered to test the association between these morphological and functional characters and the regeneration strategy after fire. Moreover, demographic studies of obligate seeders and resprouters are necessary to understand future trend in vegetation structure and composition of the study sites.

Long-term studies are needed in order to understand fully savanna vegetation dynamics and herbage quality in relation to fire and other environmental factors.

Fire in the study site is frequent, most areas burn at least once in a year, and hence fire scars provides suitable spots for successful germination. Moreover, the intensity of burning is much reduced as a result of reduction of fuel load every year by fire, which implies less impact on the vegetation structure in general. Results indicated that the existing fire-regime is within the resistance limit of most of the studied plants, some species even benefited from the current intensity and frequency of fire prevailing at the study sites. However, the extent of fire in the study area is very wide, which has made nearly impossible to find unburned or control sites. Some of the study sites are located in the Gambella national park, which is under major fire attack and the faunal biodiversity resource is highly threatened. Gambella National Park needs an urgent rehabilitation programme. Regional and national efforts are necessary to demarcate the park's boundaries and fire should be controlled in the national park. Therefore, the park could be used as reference to evaluate the effect of fire-disturbances on biodiversity resources.

Furthermore, the $^{13}C/^{12}C$ isotope ratio in the soil (Michelsen *et al.*, in prep.) indicates that site A has experienced a shift in vegetation structure from a high frequency of C_3 plants (trees and shrubs) to a more open grasslands dominated by C_4 plants (grasses). It is important to determine the time scale of the change in vegetation composition, since there is already an indication that the current population pressure and fire regime have an impact on the processes of change from dry forest and dense woodland to open woodland and wooded grassland.

Regular fire monitoring and patrolling programmes in Gambella region has to be initiated, and encouraged to control and take measure before the onset of severe fire, such as late fire. Formulation of a fire policy at the national level is imperative to manage fire either for conservation purposes or to protect the natural and biodiversity resources from the negative effects of fire.

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Appendix 1. Species list from Gambella woodland research sites

The list includes species encountered during the research period (1996-1999).

Species	**Family**	**Site A**	**Site B**	**Site C**	**Site D**	**Site X**
Abrus schimperi Hochst. ex. Bak.	Leguminosae		*	*		*
Abutilon sp.	Malvaceae					*
Acacia senegal Willd.	Leguminosae	*	*	*		
Acacia seyal Del.	Leguminosae	*		*	*	
Acalypha villicaulis Hochst. ex A. Rich.	Euphorbiaceae		*			
Achyranthes aspera L.	Amaranthaceae					*
Allophylus rubifolius Engl.	Sapindaceae		*			*
Ampelocissus abyssinica (A. Rich.) Planch	Vitaceae		*			
Ampelocissus schimperiana Planch	Vitaceae	*	*			
Andropogon gayanus Kunth	Gramineae			*	*	
Annona senegalensis Pers.	Annonaceae				*	
Anogeissus leiocarpa Guill. & Perr.	Combretaceae		*	*		*
Asparagus scaberulus A. Rich.	Asparagaceae	*	*			
Aspilia kotschyi (Sch. Bip ex Hochst.) Oliv.	Asteraceae		*	*		
Astripomoea malvacea A. Meeuse	Convolvulaceae				*	
Azadirachta indica A. Juss.	Meliaceae			*		
Balanites aegyptiaca Wall.	Balanitaceae	*				
Barleria ventricosa Hochst. ex Nees	Acanthaceae					*
Barleria grandicalyx Lindau	Acanthaceae		*		*	
Biophytum umbraculum Welw.	Oxalidaceae		*			
Blepharis maderaspatensis Heyne ex Roth.	Acanthaceae					*
Boerhavia coccinia Mill.	Nyctaginaceae	*	*			
Boerhavia repens Rojas	Nyctaginaceae	*				
Bridelia scleuroneura Muell. Arg.	Euphorbiaceae		*	*	*	
Bulbostylis sp.	Cyperaceae			*		
Cadaba sp.	Capparidaceae	*			*	
Chlorophytum tordense Chiov.	Anthericaceae		*	*		
Cissus petiolata Hook. f.	Vitaceae				*	
Cissus sp.	Vitaceae		*	*		*
Clerodendrum alatum Gurke	Verbenaceae		*	*		
Clerodendrum capitatum Hook.	Verbenaceae		*			*
Clerodendrum cordifolium A. Rich.	Verbenaceae			*		
Coccinia adoensis (Hochst. ex A. Rich.) Cogn.	Cucurbitaceae		*			
Coccinia grandis Voigt.	Cucurbitaceae	*			*	
Coccinia megarrhiza C. Jeffrey	Cucurbitaceae				*	
Combretum adenogonium Steud. ex A. Rich.	Combretaceae			*		
Combretum collinum Fresen. subsp. binderiannum (Kotschy) Okafor	Combretaceae	*	*			
Combretum collinum Fresen. subsp. *collinum*	Combretaceae			*		
Combretum molle Engl. & Diels.	Combretaceae		*			
Commelina benghalensis Linn.	Commelinaceae		*			
Commelina sp.	Commelinaceae			*		*
Conyza aegyptiaca (L.) Ait.	Asteraceae	*		*	*	
Corchorus tridens Linn.	Tiliaceae		*			
Crossopteryx febrifuga Benth.	Rubiaceae			*		
Cucumis metuliferus E. Mey. ex Naud.	Cucurbitaceae		*			

Species	Family	Site A	Site B	Site C	Site D	Site X
Cyperus amabilis Vahl	Cyperaceae		*			
Cyperus subumbellatus Kukenth.	Cyperaceae					*
Cyphostemma adenocaule (A. Rich) Wild & R. B. Drumm.	Vitaceae	*	*			
Desmodium sp.	Leguminosae		*			
Dichrostachys cinerea (Linn.) Wight. & Arn.	Leguminosae		*			
Dioscorea praehensilis Benth.	Dioscoreaceae		*			*
Diospyros mespiliformis Hochst. Ex A. DC.	Ebenaceae					*
Echinops longifolius A. Rich.	Asteraceae				*	
Entada africana Guill. & Perr.	Leguminosae	*				
Erythroxylum fischeri Engl.	Erythroxylaceae					*
Ficus sycomorus L.	Moraceae			*	*	
Flueggea virosa (Willd.) Voigt	Euphorbiaceae	*	*			*
Gardenia ternifolia Schum. & Thonn.	Rubiaceae		*			
Grewia mollis Juss.	Tiliaceae	*	*	*	*	
Grewia tenax Aschers. & Schweinf. ex E. Christ.	Tiliaceae					*
Harrisonia abyssinica Oliver	Simaroubaceae	*	*	*	*	*
Hibiscus calyphyllus Cav.	Malvaceae					*
Hibiscus cannabinus Linn.	Malvaceae		*			
Hyparrhenia confinis (A. Rich.) Stapf var. *nudiglumis* (Hackl.) W. D. Clayton	Gramineae	*	*	*	*	
Hypoestes forskaolii (Vahl) R. Br.	Acanthaceae		*			*
Indigofera prieureana Guill. Perr.	Leguminosae		*	*		
Ipomoea eriocarpa R. Br.	Convolvulaceae		*			
Ipomoea heterotricha F. Didr.	Convolvulaceae			*		
Jasminum streptopus E. Mey. Ex DC.	Oleaceae		*	*		
Justicia ladanoides Lam.	Acanthaceae		*			
Justicia diclipteroides Lindau	Acanthaceae					*
Lannea barteri Engl.	Anacardiaceae	*		*		
Lannea fruticosa Engl.	Anacardiaceae	*			*	
Lippia sp.	Verbenaceae				*	
Lonchocarpus laxiflorus Guill. & Perr.	Leguminosae		*	*	*	
Loudetia arundinacea Hochst. ex Steud.	Gramineae			*		
Loudetia simplex (Nees) C. E. Hubbard	Gramineae				*	
Maytenus senegalensis (Lam.) Exell	Celastraceae		*	*	*	
Maerua oblongifolia A. Rich.	Capparidaceae		*			
Maerua triphylla A. Rich.	Capparidaceae					*
Meyna tetraphylla Robyns	Rubiaceae					*
Neorautanenia mitis (A. Rich.) Verdc.	Leguminosae		*	*		
Ochna leucophloeos A. Rich.	Ochnaceae			*		
Opilia amentacea Roxb.	Opiliaceae					*
Panicum comorense Mez	Gramineae					*
Pennisetum polystachion Schult.	Gramineae		*			
Periploca linearifolia A. Rich.	Asclepiadaceae					*
Phyllanthus sp.	Euphorbiaceae					
Piliostigma thonningii (Schum.) Milne-Redh.	Leguminosae				*	
Plumbago zeylanica Linn.	Plumbaginaceae					*
Psilotrichum sp. cfr. *P. elliotii* Bak.	Amaranthaceae					*
Pterocarpus lucens Lepr. ex Guill. & Perr.	Leguminosae		*			*
Pyrenacantha kaurabassana Baill.	Icacinaceae	*	*			*
Sansevieria sp.	Agavaceae					*
Solanum incanum Linn.	Solanaceae	*				

Species	**Family**	**Site A**	**Site B**	**Site C**	**Site D**	**Site X**
Spermacoce sphaerostigma Oliver	Rubiaceae		*	*		
Sporobolus festivus A. Rich.	Gramineae	*				
Sporobolus pyramidalis Beauv.	Gramineae		*			
Sterculia africana (Lour.) Fiori	Sterculiaceae	*				
Stereospermum kunthianum Cham.	Bignoniaceae	*			*	
Strychnos innocua Del.	Loganiaceae		*	*		*
Tacca leontopetaloides Kuntze	Taccaceae		*			*
Tamarindus indica Linn.	Leguminosae		*			*
Terminalia laxiflora Engl.	Combretaceae		*	*		
Tylosema fassoglensis (Schweinf.) Torre & Hillc.	Leguminosae	*	*			
Triumfetta pentandra A. Rich.	Tiliaceae		*			
Vangueria madagascariensis J. F. Gmel.	Rubiaceae					*
Vernonia turbinata Oliver	Compositae					*
Vigna ambacensis Welw. Ex Bak.	Leguminosae		*			
Vigna unguiculata Savi	Leguminosae		*			
Ziziphus abyssinica Hochst. ex A. Rich.	Rhamnaceae	*	*			
Ziziphus mauritiana Lam.	Rhamnaceae	*				

Appendix 2. Proportion of species occurring either as obligate seeder or sprouter, or in both regeneration strategies. The number of times species were encountered in the quadrats in percentage of the total amount of quadrats is shown under frequency (%). Life-forms of species are included, modified after Jensen and Friis (in press). Phanerophtes (Meso: 8-30m, Micro:2-8m, Nano: 0.25-2m), MEP, MIP, NAP, respectively. CHP: Chamaephytes (0-0.25). HEC: Hemicryptophytes. GEP: Geophytes. THP: Therophytes. SUC: Succulent. Lianas or vines has been separately indicated with "L"

Species	Life-form	Growth form	Seeder (%)	Sprouter (%)	Frequency (%)
Abrus schimperi Hochst. ex Bak.	NAP	Shrub	25.0	75.0	2.6
Acacia senegal Willd.	MIP	Tree	0	100	7.4
Acacia seyal Del	MIP	Tree	0	100	0.2
Acalypha villicaulis Hochst. ex A. Rich.	NAP	Herb	100	0	0.2
Allophylus rubifolius Engl.	MIP	Shrub	0	100	4.1
Ampleocissus abyssinica (A. Rich.) Planch.	GEP(L)	Herb	0	100	19.3
Andropogon gayanus Kunth	HEC	Grass	17.5	82.5	37.2
Annona senegalensis Pers.	MIP	Herb	0	100	0.7
Anogeissus leiocarpa Guill. & Perr.	MEP	Tree	25.0	75.0	0.9
Asparagus scaberulus A. Rich.	NAP(L)	Herb	10.7	89.3	6.1
Aspilia kotschyi (Sch. Bip ex Hochst.) Oliv.	THP	Herb	100	0	6.3
Astripomoea malvacea A. Meeuse	NAP(?)	Herb	0	100	3.7
Balanites aegyptiaca Wall.	MIP	Tree	0	100	2
Barleria grandicalyx Lindau	HEC(?)	Herb	0	100	0.4
Blepharis maderaspatensis Heyne ex Roth.	HEC	Herb	0	100	0.7
Bridelia scleuroneura Muell. Arg.	MIP	Tree	0	100	0.2
Cadaba sp.	NAP	Herb	0	100	16.7
Chlorophytum spp.	GEP	Herb	0	100	9.1
Cissus petiolata Hook. f.	MIP(L)	Herb	0	100	2
Clerodendrum alatum Gurke	GEP	Herb	0	100	3
Clerodendrum capitatum Hook.	MIP(L)	Herb	0	100	7.6
Clerodendrum cordifolium A. Rich	MIP(L)	Herb	0	100	4
Combretum collinum Fresen.	MEP	Tree	0	100	10
Commelina benghalensis Linn.	HEC	Herb	58.7	41.3	10
Corchorus tridens Linn	THP	Herb	100	0	1.5
Cyphostemma adenocaule (A. Rich) Wild & R. B. Drumm	GEP(L)	Herb	0	100	2.2
Desmodium sp.	NAP	Shrub	0	100	13.3
Dichrostachys cinerea (Linn.) Wight. & Arn.	MIP	Shrub	0	100	9.3
Echinops longifolius A. Rich.	HEC	Herb	0	100	0.4
Entada africana Guill. & Perr.	MIP	Tree	0	100	0.2
Ficus sycomorus L.	MEP	Tree	100	0	1.1
Flueggea virosa (Willd.) Voigt	MIP	Shrub	0	100	7.4
Gardenia ternifolia Schum. & Thonn.	MIP	Tree	0	100	1.7
Grewia mollis Juss.	MIP	Tree	0	100	4.6
Harrisonia abyssinica Oliver	MIP	Shrub	0	100	9.1
Hibiscus cannabinus Linn.	THP	Herb	100	0	2.4
Hyperrhenia confinis (A. Rich.) Stapf var. nudiglumis (Hackl.) W. D. Clayton	THP	Grass	10.1	89.9	84.1
Hypoestes forskaolii (Vahl) R. Br.	HEC	Herb	4.7	95.3	23.3
Indigofera sp.	NAP	Shrub	8.5	91.5	12.8
Ipomoea eriocarpa R. Br.	THP	Herb	49.1	50.9	12.4
Jasminum streptopus E. Mey. ex DC.	NAP(L)	Shrub	0	100	4.6
Lonchocarpus laxiflorus Guill. & Perr.	MEP	Tree	0	100	10.2
Loudetia arundinaceae Hochst. ex Steud.	HEC	Grass	9.4	90.6	23
Maytenus senegalensis (Lam.) Exell	MIP	Tree	0	100	3.7
Piliostigma thonningii (Schum.) Milne-Redh.	MIP	Tree	100	0	1.1
Pterocarpus lucens Lepr. Ex Guill. &. Perr.	MEP	Tree	0	100	3.5
Pyrenacantha kaurabassana Baill.	GEP	Herb	0	100	26.1
Sansevieria sp.	SUC	Herb	0	100	0.2
Solanum incanum Linn.	NAP	Herb	0	100	0.4
Spermacoce sphaerostigma Oliver	THP	Herb	100	0	7.4
Sterculia africana (Lour.) Fiori	MEP	Tree	0	100	0.2
Stereospermum kunthianum Cham.	MIP	Tree	0	100	0.2
Strychnos innocua Delile	MIP	Tree	0	100	20.7
Tacca leontopetaloides Kuntze	GEP	Herb	0	100	1.7
Terminalia laxiflora Engl.	MEP	Tree	33.3	66.7	0.7
Tylosema fassoglensis (Schweinf.) Torre & Hillc.	GEP(L)	Herb	0	100	33.3
Vigna unguiculata Savi.	THP(L)	Herb	100	0	2.4
Ziziphus mauritiana Lam.	MEP	Tree	0	100	2.6