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# Invasive Plant Species and Biomass Production in Savannas

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## 1. Introduction

Savannas are the second largest biome accounting for c. 30% of terrestrial production. Tropical savannas are distributed largely in Africa, Australia and South America occurring between tropical forests and deserts. It is the coexistence of trees and grasses that make savannas unique. The structure of savannas or the ratio of trees to grasses which has important implications on ecosystem productivity is determined by resource availability (rainfall and soil nutrients) and disturbances (fire and herbivory) also referred to as 'drivers'. Resources influence the distribution and productivity of savanna vegetation while fire can alter vegetation structure via effects on the woody layer. Herbivory influences savannas structure and composition through its effects on nutrient cycling, seed dispersal and physical defoliation effects and may lead to expansion of the shrub layer. While ecologists agree the four drivers determine tree-grass balance the exact mechanisms are still debated with one school of thought emphasizing the importance of resources as 'primary determinants' in what are referred to as 'competition models' which basically invoke the classic niche separation mechanisms in resource acquisition. The other school of thought referred to as 'demographic bottleneck models' emphasizes the role of disturbances as the primary determinants through their effects on life history stages of trees. It's been shown however that at low levels of mean annual rainfall, precipitation governs the cover of trees and above a critical value disturbances prevent trees from forming a closed canopy.

Invasive species are considered to be non-native species that have been introduced outside their normal range and are expanding in range causing ecological and economic harm and can drastically alter the structure and composition of savannas. Most non-native species introduced in savannas were for well intended commercial and ecological purposes such as pasture and fodder improvement or rehabilitation of degraded areas. Even though patterns of invasion can not be easily generalized, a trend is that African C<sub>4</sub> grasses such as *Melinis minutiflora* and *Andropogon gayanus* make up the most obnoxious invaders in the South American and Australian savannas while in contrast neotropical trees and shrubs are among the most successful invaders of African and Australian savannas such as *Prosopis spp* and *Lantana camara*. Ecologists have persistently attempted to answer the question 'what makes a community susceptible to invasion'? Plant characteristics of the invader is an important factor, plants introduced in savannas for improvement of pasture/fodder are generally selected for aggressiveness/competitiveness compared to native species. Selected shrubs for example tend to have fast growth, easy to propagate and often N fixers while grasses

display aspects of higher resource use efficiency and greater tolerance to grazing. Ecological disturbances such as heavy grazing can destroy native vegetation and favor unpalatable invaders through effects on resource availability. Among other factors thought to enhance invasibility is climate change and its synergistic interactions with elevated CO<sub>2</sub> since most invasive species have traits that allow them to respond strongly to elevated CO<sub>2</sub>.

Productivity levels of savannas are on a broad scale related to the relative proportion of trees to grasses while precipitation is the most important factor with an almost linear relationship to biomass production. Gaps and inconsistencies in savanna Net Primary Productivity data collected over the years make spatial and temporal comparison difficult. This paucity arises from the 'evolution' of methodologies in Net Primary Productivity (NPP) determination from the earlier commonly used 'peak biomass' methods that grossly underestimated NPP, through improvements incorporated in International Biological Programme (IBP) studies in the 1970's to further refinements in the United Nations Environmental Programme (UNEP) grassland studies that made corrections for a wide range of losses during the growth phase previously unaccounted for. Further gaps in data are because most savanna productivity studies have focused on single species within the community of study or lumped several species and rarely included both tree and grass components. Comparison of non-native and native species prior to introduction was often made through screening trials where the fodder trees were largely evaluated for productivity, digestibility, nutritional value and soil amelioration among others. Selected non-native woody species invariably had superior performance in growth parameters e.g *Prosopis juliflora* produced up to 188% more in aboveground biomass than the valuable indigenous *Acacia tortilis* in Senegal. Many screening trials also showed that despite slow growth native tree species in most trials had other positive attributes and not all were outperformed by non-natives and moreover only a small proportion of selected non-natives became invasive. African C<sub>4</sub> grasses introduced in the neotropics and Australia on account of higher productivity have also altered fire regimes, hydrology and nutrient cycling for example *Andropogon gayanus* invasion in Australia which can lead to a biomass load of over 300% compared to native species but has resulted in fires eight times more intense on average. Invasive herbs just like grasses and trees can have negative impacts such as the bi-annual unpalatable *Ipomoea hildebrandtii* which depresses native grass biomass production in addition to changes in site hydrologic and nutrient dynamics patterns.

Can invasive species in savannas increase carbon sequestration? Given the rapid increase in coverage of invasive species e.g *Prosopis juliflora* is already estimated to cover 500,000 and 700,000ha in Kenya and Ethiopia while vast areas in Columbia, Venezuela, Brazil and Australia are dominated by higher yielding African C<sub>4</sub> invasive grasses. An assessment of several studies in forests, grasslands and wetlands showed that ecosystem productivity was higher in invaded ecosystems. In savannas above ground carbon (C) stocks increases as the proportion of trees increases relative to grasses. Soil carbon constitutes over two-thirds of the global carbon found in terrestrial ecosystems. Net soil carbon stock in savannas is regulated by inputs from primary productivity and heavy losses due to herbivory and fire. It follows alteration of the C and N cycles by invasive species can vary carbon sequestration. Alteration of the C cycle components in savannas is attributed to differences in ecophysiological traits between the invasive and indigenous species. Some invasive species traits that lead to increased sequestration include faster relative growth, deep rooting, herbivore defense traits, faster litter decomposition and N fixation. However not all invasive species have these traits some decrease sequestration by depressing N mineralization and

having lower litter decomposition, more studies to enable the quantification of this process in savannas are required.

## 2. Savannas

### 2.1 What are savannas?

Globally savannas the second largest biome, covering one-sixth of the land surface and accounting for c. 30% of the primary production of all terrestrial vegetation. Africa has the largest savanna occupying about 50% of the continent or about 15.1 million km<sup>2</sup> (Grace et al., 2006). Substantial areas of savanna also cover India, Australia, Southeast Asia, Central America and Pacific islands. Tropical savannas occur in the transition between the tropical rainforests and the deserts where rainfall is inadequate to support forests. Savannas are home to about a fifth of the global human population and a large proportion of the world's ungulates both wildlife and livestock (Foxcroft et al., 2010). The term neotropics or neotropical zone includes South and Central America, the Mexican lowlands, the Caribbean islands, and southern Florida, because these regions share a large number of plant and animal groups

The climate of savannas is warm year-round, and has two distinct seasons, wet (summer) and dry (winter). Most of the rainfall is received in the summer. The length of the rainy and dry seasons generally varies with distance from the equator. In savannas near the equator the dry season is 3-4 months while closer to the desert it's longer lasting 8-9 months. The annual average rainfall in savannas ranges from 500 to 1500 mm. Fires started are by lightning or pastoralists are a common and natural part of the savanna ecosystems.

The physiognomy of savanna vegetation consists of a diverse range of tree-grass mixtures, different species of perennial grasses and sedges, trees, woody plants and shrubs with the herbaceous cover relatively continuous and woody cover discontinuous (Frost et al., 1986). It is the coexistence and close interaction of herbaceous and woody species that makes savannas unique. Plants of the savanna biome have diverse mechanisms of adaptation to drought and fire. Some of these include drought evasion as annuals, dormancy in the dry season, small sizes, slow growth and extensive root systems. Most trees also have deep roots, thick fire-resistant barks while those in African savannas often have spines to protect them from browsing herbivores.

It is acknowledged that grazing ecosystems consisting of savannas and grasslands support more herbivore biomass than any other terrestrial habitat and that there is a long history of coevolution of plants and herbivores due to their coexistence of tens of millions of years from the late Mesozoic (Frank et al., 1998). The stability of such coexistence has been attributed to the regular migration of large ungulate herbivores in response to spatial and temporal variation in resources as well as the positive feedback of grazing intensity and fire on primary productivity and fertility (Holdo et al., 2007; Frank et al., 1998).

### 2.2 South American savannas

Savanna ecosystems in South America occur in Brazil, Venezuela, Colombia and Bolivia covering about 269 million hectares (ha.) Cerrados of Brazil are the largest (76%), about 11% (28 million ha) form the Venezuelan Llanos and remaining Colombian Llanos (WWF, 2007). The Llanos ecoregion covers a large elongated area beginning at the foothills of the Oriental Andes of Colombia and extending along the course of the Orinoco River. This ecoregion has a typical savanna climate characterized by two well-defined seasons a wet season between

April and November and an intense drought 3 to 5 months long between December and April. The Llanos have typical savanna physiognomy consisting of an open tree layer and a continuous herbaceous layer. The ratio of trees to grasses increases with soil water availability during the dry season. The Cerrado vegetation occupies more than 2 million km<sup>2</sup> in the central part of South America with formations ranging from open shrub savanna (campo sujo), through open *savanna* (campo cerrado) to tree dominated savanna (cerrado sensu stricto).

A major threat to South American savannas is conversion to croplands with most of it in the Brazilian Cerrados. Livestock production is the main activity and is responsible for changes arising from activities such as the regular use of fire and clearing of forests to increase native pasture coverage and quality. Invasive species are also an important threat especially C<sub>4</sub> aggressive grasses introduced from Africa that include *Melinis minutiflora*, *Hypparrhenia rufa*, *Panicum maximum* and *Brachiaria mutica*.

### 2.3 Australian savannas

Tropical savannas in Australia cover almost one-quarter of the continent ranging from Rockhampton on the East Coast, across the Gulf, Top End and over to the Kimberley in Western Australia (Tropical Savannas CRC). The climate consists of a distinct wet and dry season just like other savannas. The wet season occurs December to March while the dry season is May to August. The average rainfall declines from the coastal north to the inland south.

Vegetation composition and structure is strongly associated with soil attributes such as texture, the rainfall gradient and geological factors. However in general the vegetation is dominated by *Eucalyptus* species in the overstorey, a shrub layer of species such as *Acacia cinocarpa* and an herbaceous layer of annual and perennial C<sub>4</sub> grasses (Setterfield, 2002). Fires are an important modifier of vegetation structure and composition in the northern savannas. This because savannas further north are inherently predisposed to regular and frequent fires due to higher rainfall which allows higher cover and height of grasses and higher litter from woodland trees all providing more fuel. Further south fires are less common due to lower fuel loads due to the open landscapes, less rain fall and further reduction by grazing cattle.

The major land use of Australian tropical savannas is by the cattle industry other uses include mining, wildlife conservation and Aboriginal land. Among the major threats are invasive species including Mission grass (*Pennisetum polystachion*) and gamba grass (*Andropogon gayanus*) which have invaded vast areas, greatly increasing fuel loads and leading to more destructive fires. Changes in fire patterns in northern Australian have been linked to climate change and the spread of invasive grasses in particular *Andropogon gayanus* (Rossiter et al., 2003)

### 2.4 African savannas

Africa contains by far the largest area of savanna with some estimates at 65% of the continent (Huntley & Walker, 1982). Tropical savannas form a semicircle around the western central rainforest areas, bordered by the desert zones to the north and south. Several classification systems for savannas in African have been used, mainly based on climate and physiognomy. The bioclimatic classification mainly based on Phillips (1959 quoted in Ker 1995) presented by Ker (1995) distinguishes 4 broad savanna zones and shows the importance of the rainfall gradient on savanna physiognomy (Table 1).

Bioclimatic zone	Equivalent ecological region		Mean annual rainfall (mm)	Length of growing season (days)
	West Africa	Eastern and southern Africa		
Arid savanna	Southern Sahelian	Acacia woodland	300–600	60–90
Subarid savanna	Sudanian	Southern miombo woodland	600–900	90–140
Subhumid savanna	Northern Guinean	Northern miombo woodland	900–1200	140–190
Humid savanna	Southern Guinean	Derived savanna	1200–1500	190–230

Note: Adapted from Ker(1995)

Table 1. The bioclimatic zones of African savannas

In the context of invasion ecology African savannas show variation in two attributes from those of South America and Australia in respect to herbivory and its impacts. Firstly they have been characterized by high grazing intensity due to large herds of a variety of species including substantial numbers of mega-herbivores and bulk grazers in contrast to Australia where the largest indigenous grazers were the eastern grey and red kangaroos and South America which lacked large congregating grazers (Foxcroft et al., 2010; Klink 1994). As a consequence African grasses are hypothesized to have evolved traits that contribute to their higher competitive potential compared to native species of Australia or South American savannas. Some of which include greater compensatory re-growth after defoliation, higher carbon assimilation rate and nitrogen use efficiency and higher opportunistic water use (Baruch & Jackson, 2005).

Secondly the African savannas harbor vast pastoral tribes with huge livestock populations that coexist with wildlife. This is because even though protected areas such as National parks are the main vehicles of wildlife conservation they do not encompass all wildlife and their migratory patterns. As such the largest proportion of wildlife is outside the protected areas system in what is referred to as dispersal areas. In these areas wildlife, livestock and human settlements exist in interrelationships that create complex spatial variations in disturbance patterns. For example Mworio et al. (2008a) found that in areas occupied largely the Maasai pastoralists adjacent to Amboseli and Chyulu wildlife reserves in Kenya that wildlife movement and distribution was primary determined by vegetation type and distribution of seasonal water resources while important secondary modifiers were human settlement density, livestock density and cultivation intensity. Disturbances as we shall see below increase the vulnerability of communities to invasion.

## 2.5 Determinants of savanna structure

We have seen that savannas are characterized by two contrasting life forms, trees and grasses. How do they coexist without one eliminating the other? Ecologists agree that resources (rainfall and nutrients) and disturbances (fire and herbivory) are the key determinants or 'drivers' of savanna structure and function (Sankaran et al., 2004). But the mechanisms by which these drivers regulate tree-grass mixtures are still debated some theories emphasize the role of competition in niche separation for limiting resources. Others

models highlight the role of demographic mechanisms where dissimilar effects of the drivers on life-history stages on trees allow the persistence of tree-grass mixtures. As we shall see below the ratio of trees to grasses greatly influences savanna ecosystem productivity.

Rainfall determines the supply of water, but the amount that is subsequently available to plants is subject to aspects of drainage and storage such soil texture and compaction, topography, vegetation cover and losses due to evaporation and evapotranspiration. Spatial and temporal variation of rainfall in savannas is high and increases with aridity with many areas experiencing regular droughts which can be a primary cause of vegetation compositional changes (Ellis & Swift, 1988). In general linear relationships have been found between biomass and precipitation and productivity and days of water stress (House & Hall, 2001). Years of high rainfall favor tree recruitment and growth over grasses while drought periods limit tree recruitment and growth (Sankaran et al., 2004)

Soil nutrients are generally limiting since most tropical savanna soils are derived from old, highly-weathered acid crystalline igneous rock leading to leached sandy soils with low fertility and CEC. In particular Low nitrogen and phosphorous availability constrain many savanna ecosystems (House & Hall, 2001). Soil water influences the availability of nutrients to plants in that nutrient mineralization, transport and root uptake are all dependent on soil water content.

Fire has been traditionally used by pastoralists and ranchers as a management tool in savannas to increase pasture and combat bush encroachment. This is because woody meristems within the flame zone (< 5m) are generally more exposed to fire damage than grass meristems and the latter can recover more efficiently in the short term (Trollope, 1974 quoted in Scholes & Archer, 1997). Frequent fires therefore favour grasses and suppress the recruitment of mature woody plants. Fire and grazing can have interactive effects on savanna structure whereby low grazing pressure allows the accumulation of high grass biomass which can affect tree biomass and population by fueling intense fires. Heavy browsing helps to keep woody plants within the flame zone thus a strong grazer-browser-fire interaction influences tree-grass mixtures (Scholes & Archer, 1997).

Herbivory consists of grazing and browsing by wildlife and domestic herbivores. Herbivores influence structure and composition through selective feeding and physical effects of defoliation. Heavy browsing pressure especially by mega herbivores such the elephant may compromise the viability of some woody plant populations, resulting in community changes coupled with a possible loss of species diversity and structural diversity. On the other hand herbivory plays a significant role in nutrient cycling, seed dispersal and creation of microsites and space thus enhancing shrub recruitment.

## **2.6 Models to explain savanna structure**

Ecologists have hypothesized several models through which resources (moisture and nutrients) and disturbances (fire and herbivory) regulate savanna structure. Models that explain the co-existence of trees and grasses in savannas can broadly be divided into 'competition models' and 'demographic bottleneck models'. Competition-based models apply the classic niche-separation mechanisms of coexistence whereby differences in the resource-acquisition potential of trees and grasses is the fundamental process structuring savanna communities. Importantly in competition models the resources (water and nutrients) are considered the 'primary determinants', while the disturbances (fire and grazing) represent 'modifiers'. Some competition models include; the root niche separation

model, the phenological niche separation model and the balanced competition model. The root niche separation model is the classic equilibrium model of savannas proposed by Walter (1971). It assumes that water is the primary limiting factor and trees and grasses have differential access with trees having an almost exclusive access to that in the lower soil horizons due to deep roots while grasses have more access to that near surface. This model therefore predicts trees should be advantaged on sandy soils of low water-holding capacity and under wetter climates grasses would be favoured on soils of high water-retention such as clays and arid environments.

In demographic bottleneck models disturbances are the primary focus unlike competition models. The direct effects of these disturbances on germination, mortality and demographic transition in trees determine the structure rather than any post-disturbance competitive interactions. Effects of savanna drivers; herbivory, fire and moisture variability are incorporated in most demographic models with differences only in how the model results have been interpreted. For example one views the savannas as transitional 'disequilibrium' systems where pure grasslands or forests are believed to be the only equilibrium states with disturbances such as fire and grazing permitting savannas to persist in a disequilibrium state preventing complete shifts to either state (Jeltsch et al., 2000). An alternate view interprets savanna structure to be driven by rainfall variation where trees are assumed to be limited by drought at the seedling stage and by fires at the sapling stage (Higgins et al., 2000)

In comparing the models empirical studies show that support for and against both competitive and demographic mechanisms leaving definitive conclusion on the relative importance of resource limitation versus disturbances in controlling savanna structure unresolved (Scholes & Archer, 1997; Jeltsch et al., 2000; Sankaran et al., 2004). However using very extensive data on African savannas Sankaran et al. (2005) showed that rainfall was the most important factor in tree-grass balance below annual mean of 650mm with woody component increasing linearly with rainfall. Above a mean annual rainfall of 650mm disturbances played a greater role in the balance by preventing the woody canopy from closing and therefore allowing grasses to coexist.

### **3. Invasive plant species in savannas**

#### **3.1 Definition and distribution in savannas**

Physical barriers such as oceans, river valleys and mountains present boundaries to the movement of individuals of the same species populations. This eventually led to the formation of unique species from the separated populations through drift and selection thus the emergence of native populations. However since human beings developed the ability to move across continents they have enabled species breach geographical barriers hence introduced species. The history and socio-economic development of mankind is strongly associated with human-aided movement of plants and animals. Many of the crops that sustain the human race today are introduced species. In general most plant species have been introduced intentionally with good intentions such as food crops, medicinal plants, livestock fodder, forestry or agro-forestry species. Most of these species depend on humans for their continued propagation after introduction however some have become pests or invaders.

The term 'non-native' species is used for species that have been moved outside their normal geographic range regardless of their impact to native ecosystems. Non-native species also

includes those that have expanded beyond their native range via human actions even though still in their native continents but sometimes cause substantial harm to ecosystems they enter (Lockwood et al., 2007). The term 'invasive species' describes non-native species introduced from a different area, often a different continent which becomes established, increases in density and expands rapidly across the new habitat (Myers & Bazely, 2003) causing ecological and economic harm or what some scientists describe as 'large environmental impacts' (Davis et al., 2000). In invasion ecology literature several and often confusing terms are frequently used interchangeably such as non-indigenous, exotic and alien to refer to non-native species.

Over the course of human civilization thousands of plant species have been moved across geographic barriers however only a very small proportion of these non-native species have become invasive. Most non-native species depend on humans for their continued propagation after introduction while others have become naturalized. Naturalized species refers to non-native species that reproduce consistently and maintain their populations over many life cycles without direct intervention of by humans but do not necessarily invade natural ecosystems or become overly abundant and damaging (Richardson et al., 2000; Myers & Bazely, 2003). To illustrate the huge numbers of introduced plant species across the globe literature shows that 2100 or 50% in New Zealand are introduced, in South Africa 8750 or 46% are introduced, in Chile 690 or 15% are introduced to give just but a few examples from Myers & Bazely (2003). Most of these introduced species have spread very little, if at all, beyond their point of introduction and it can therefore not be said that all introduced species are potentially harmful. Indeed it has been estimated that only about 1% of introduced species become invasive (Groves, 1986 quoted in Binggeli et al., 1998).

While patterns of invasion in savannas can not be definitively drawn, a general trend is that African C<sub>4</sub> grasses are among very successful invaders of tropical savannas of Australia and South America. Conversely neotropical shrubs and trees are highly successful invaders of tropics and sub-tropics including savannas of Africa, Australia and pacific islands.

It is noted that in Africa with an exception of South Africa reports and publications on invasive species are few despite the range of potentially invisable habitats, many forms of anthropogenic landuse and high levels of frequent disturbances (Foxcroft et al., 2010). This is partly due to lack of extensive and intensive research and surveys of invasive species.

### **3.2 Factors that enhance invasibility in savannas**

Generally the success of a non-native species in establishing and spreading in a new community has been related to its propagule pressure, existence of ecological and anthropogenic disturbances, biological characteristics of the invader and role of climate change (Lockwood et al., 2007; Myers & Bazely, 2003). In savannas we noted above that the key determinants of structure are the disturbances fire and herbivory and the resources moisture and nutrients. It is therefore conceivable that a complex interaction is these factors determine the success of an invader in savannas.

Propagule pressure is an indicator that combines the propagule size (number of individuals released), the number of release events and physiological condition of released individuals. The probability of establishment of the invader increases as propagule pressure increases. The importance of this factor is particularly evident where non-native species are introduced in large scale agroforestry, fodder or pasture improvement programmes as compared to limited introduction for example in a botanical garden. High propagule

<b>WOODY SPECIES</b>	<b>Life form</b>	<b>Native region</b>	<b>Invaded region</b>
<i>Lantana camara</i>	Shrub	Neotropics	All tropics
<i>Prosopis juliflora</i> , <i>P. glandulosa</i> , <i>P. velutina</i>	Tree	Neotropics	Africa, Australia, Asia
<i>Acacia nilotica</i>	Tree	Africa-India	Australia
<i>Cecropia peltata</i>	Tree	Neotropics	Africa, Asia
<i>Chromolaena odorata</i>	Shrub	Neotropics	Africa, Asia
<i>Leucaena leucocephala</i>	Small tree	Central America	Pacific islands
<i>Maesopsis eminii</i>	Tree	Africa	East Africa
<i>Miconia calvoescens</i>	Small tree	Neotropics	Pacific islands
<i>Mimosa pigra</i>	Small tree	Neotropics	Australia, Africa
<i>Pinus patula</i>	Tree	Neotropics	East Africa
<i>Psidium guajava</i>	Small tree	Neotropics	Africa, Pacific Islands
<b>GRASS SPECIES</b>			
<i>Melinis minutiflora</i>	Grass	Africa	South America
<i>Hyparrhenia rufa</i>	Grass	Africa	South America
<i>Panicum maximum</i>	Grass	Africa	South America
<i>Brachiaria mutica</i>	Grass	Africa	South America
<i>Andropogon gayanus</i>	Grass	Africa	Australia, Neotropics
<i>Cenchrus ciliaris</i>	Grass	Africa	Australia
<i>Pennisetum polystachion</i>	Grass	Africa	Australia
<i>Themeda quadrivalvis</i>	Grass	Africa	Australia

\* Adapted from Binggeli et al., 1998, Foxcroft et al., 2010

Table 2. Some of the most invasive species in tropics and sub-tropics

pressure is thought to have been one of factors contributing the invasive success of African C<sub>4</sub> grasses introduced in Australia (Lonsdale, 1994) as well as Columbia, Venezuela and Brazil (Williams & Baruch, 2000) where in both cases they were used pasture improvement. Propagule pressure across habitats in an ecosystem can be enhanced if the invasive species has multiple dispersal agents. For example Mworio et al. (2011) observed that the invader *Prosopis juliflora* was dispersed by several wildlife and livestock species within the savanna of the upper Tana River floodplain resulting in a significant association between habitat type and disperser type indicating the importance of habitat preference and livestock herding patterns.

Characteristics of non-native species can be an indicator of its potential invasiveness in the new community. Scientists have attempted to find differences in biological characteristics between native and non-native invasive taxa in particular floras. In savannas and tropics in general most introduced plants have a commercial value mainly improvement of pasture and fodder and tend have a general set of characteristics. For example (Binggeli et al., 1998) in an assessment of woody plants introduced in tropics found to them to have fast growth, easy to propagate, often nitrogen fixers and resistant to a variety of biotic and abiotic agents such as pests, drought and fire. Grasses introduced in Australia were generally selected for aggressiveness (Lonsdale, 1994). Even though characteristics that distinguish invasive from

non-invasive plant are not totally consistent, some patterns are observed; for example fitness over a wide range environments, phenotypic plasticity to exploit new environments, efficient competitors for limiting resources, small and numerous seeds, small genome size, good dispersal ability and no specific mutualisms (Lockwod et al., 2007). In grazing ecosystems of savannas characteristics such as unpalatability, formation of thickets, production of spines and thorns, allelopathy, toxicity to animals and fire tolerance may confer particular advantages.

Ecological disturbance is an event that disrupts the ecosystem and communities leading to changes in resource availability or physical environment (Lockwod et al., 2007). In the 'fluctuating resources hypothesis' by Davis et al., (2000) disturbances may make a community more susceptible to invasion by causing an increase in the amount of unused resources such as light, nutrients, water or space. Fluctuation in resources could be due to a large influx of resources (e.g. unusually rainy years) or reduction in use by resident species (e.g heavy grazing of native species). It is important to note that disturbances create opportunities for both natives and non-natives and for the prevalence of non-natives to increase there must a source of non-native propagule (Lockwod et al., 2007). Lets again take the example of the *Prosopis juliflora* in savanna floodplain of upper Tana River in Kenya where Mworio et al. (2011) found that ecological disturbance manifested by rested crop fields not only enhanced the establishment of the invader but also had a positive effect on indigenous woody species. Rested crop fields have vegetation and soil disturbance and represent early stages of plant succession. Enhancement of regeneration in native woody species and the invasive *Prosopis juliflora* in rested and abandoned farms in floodplains in savannas has been reported however the invader eventually becoming dominant (Muturi et al., 2009; Stave et al., 2003; Oba et al., 2002).

Fire is a key ecological disturbance in savannas which can play a role either in suppressing potential invasive plant species that are not tolerant or promoting those that are tolerant. For example Masocha et al. (2010) found that in a long term burning experiment in the mesic savanna of Zimbabwe more non-native plant species became established in plots that had a higher frequency of burning. In the tropical savannas of northern Australia the increased incidence of destructive fires has increased over the last century as result of changes in fire regimes have been partly attributed to climate change and the spread of invasive species such Gamba grass which accumulates high fuel loads (Rossiter et al., 2003). This in turn reduces the recruitment and cover of woody plants and native grass species enhancing its further spread. Herbivory is also a determinant of savanna structure. Herbivory especially at high intensities creates soil disturbances characterized by negative shifts both in soil physical and hydrologic attributes and leads not only to compositional shifts of native plant species but may also increase invasibility by non-native species especially unpalatable ones (Mworio et al., 2008b).

Climate change promoted by increased atmospheric CO<sub>2</sub> is another factor thought to have the potential to enhance the proliferation of invasive species (Sala et al., 2000). The implications of changes in global heat balance on the hydrological cycle include increase in the frequency of heavy rainfall events in terrestrial precipitation, increased variability in relation to individual weather systems such has in El Nino-Oscillation (ENSO) whereby the warm episodes of ENSO have become more frequent, persistent, and intense (Grantz, 2000). This is of particular importance in tropical savannas since many are influenced by the ENSO regime. In East Africa for example the frequency of droughts is predicated to increase (Adger et al., 2003). Of concern to scientists is the possible interactive and synergistic effects

of climate change and elevated CO<sub>2</sub> in promoting the invasion and spread of invasive species (Sala et al., 2000). This is because invasive plants possess traits which allow them to respond strongly to elevated CO<sub>2</sub> creating the potential for enhanced dominance and range expansion (Smith et al., 2000 in Lovejoy and Hannah, 2006). Indeed Baruch & Jackson (2005) found that elevated CO<sub>2</sub> increased the competitive potential of invader African C<sub>4</sub> grasses (*Hyparrhenia rufa* and *Melinis minutiflora*) in relation to germination, seedling size and relative growth rate compared to the dominant native grass *Trachypogon plumosus* in northern South America.

## 4. Biomass productivity

### 4.1 Factors that influence savanna productivity

We have seen that certain factors referred to as drivers in savannas govern the proportion of tree to grass cover. It follows then that the structural diversity and different mixture of tree and grasses will influence overall ecosystem productivity. Studies in agroecosystems have shown that different combination of multi-species affects the level of NPP. It therefore conceivable that the same applies to savannas especially given that trees and grasses have access to different resources both spatially and seasonally.

The productivity of savannas is, largely attributed water availability occasioned by the generally low precipitation, with pronounced and prolonged dry season. Rainfall determines the amount of water received however infiltration hence the amount eventually available to plants depends on a number of factors including; the slope which is function of topography, soil texture which determines the drainage and water storage capacity, and vegetation cover which determines runoff following rains.

The relationships between biomass and precipitation in savannas, have been found to be almost linear (Scholes et al., 2002) just as that between productivity and days of water stress (House & Hall, 2001) although from place to place productivity will be strongly affected by biomass burning (Frost, 1996). Rainfall is mostly received in short durations with high intensity. Furthermore as aridity increases its variability also increases making it prime driver of vegetation compositional change. Indeed Ellis & Swift (1988) argued that in such rangelands also characterized by pastoral herd mobility, droughts are more important in triggering compositional change than herbivore pressure.

Soil attributes in particular the nutrient level and texture has also been related to variability in productivity. However nutrients have been found to account for greater variation in productivity while texture was related to the proportion of productivity related to variation in functional types. In coarse soils forbs and shrubs made up a larger proportion of total productivity as compared to fine-textured sites. Thus across a regional precipitation gradient, soil texture may play a larger role in determining community composition than in determining total ANPP (Lane et al., 1998)

### 4.2 Paucity in ecosystem productivity data

Net primary productivity (P<sub>n</sub>) is the total photosynthetic gain, less respiratory losses, of plant matter by vegetation occupying a unit area. Over any one period, this must be equal the change in plant biomass ( $\Delta W$ ) plus any losses through death (L), both above- and below-ground formula:  $P_n = \Delta W + L$ . Thus P<sub>n</sub> is the measure of amount of plant matter available to consumer organisms. Net primary productivity can be estimated at species or ecosystem level. Historically techniques for estimating biomass and productivity in savannas have

undergone refinement with time by an enhancement in the number of parameters taken into consideration to improve accuracy. The technique employed can lead to almost five-fold variation in the estimate of tropical grassland production (Long et al, 1989).

The bulk of studies especially prior to the extensive International Biological Programme (IBP) studies of the 1970's (Sigh & Joshi, 1979) based estimations of net above-ground production on the peak standing dry matter alone and can be referred to as 'peak biomass' methods. The peak biomass method grossly underestimates NPP because it does not account for below ground production neither does it make corrections for mortality during the growing season, growth after peak standing-crop and effects of grazing and trampling. The peak biomass method therefore assumes that no carry over of biomass from one growing season to the next. Milner & Hughes (1968 quoted in Long et al.,1989) proposed a method for the IBP which measures positive increments in aboveground live biomass referred to as the 'IBP standard method. Similarly in the 'minimum-maximum' approach the residual live material (R) which is measured before growth resumes after a dormant period, is subtracted from peak biomass ( $B_{max}$ ) thus accounting for carry over of biomass ( $P_n = B_{max} - R$ ). However like the previous method no correction is made for mortality and disappearance of biomass during the growing season and  $P_n$  is therefore underestimated. To account for the assumptions in both the peak biomass and IBP methods the UNEP study (Long et al., 1992) made corrections for change in biomass for losses due to death, decomposition, root exudation and herbivory. It is evident use of different approaches will lead to quite different estimates of  $P_n$ . For example Kinyamario & Imamba (1992) taking into account mortality and decomposition obtained an NPP ( $g\ m^{-2}\ y^{-1}$ ) of 1292 and found that the 'standard IBP method' and the 'maximum-minimum' methods both underestimated productivity by 52 and 69% respectively.

Further gaps in the estimation of savanna ecosystem biomass and productivity arise from the fact that most studies have focused on a single species or have not attempted to separate contributions of various species and few have measured both tree and grass components (House & Hall, 2001). This may be partly attributed to the difficult nature of conducting harvest based productivity experiments at ecosystem level. However in recent years advances in technology have eased the rigours of ecosystem productivity estimation for example the use of carbon isotopes to estimate the relative contributions of woody and herbaceous vegetation to savanna productivity (Lloyd et al., 2008). This is possible because while most savanna trees have a  $C_3$  photosynthetic pathway, savanna grasses have mainly of the  $C_4$  photosynthetic pathway allowing the comparison carbon isotopic compositions of the plant and carbon pools. Further paucity in ecosystem biomass and productivity data is due to the large heterogeneity in savanna types even within the same region due the wide range in soils and climatic conditions.

#### **4.3 Ecosystem productivity of savannas**

Approximately 20% of the world's land surface is covered with savanna vegetation and this biome is responsible for almost 30% of global net primary production (NPP) and up to 35% if considered as a grassland- savanna system (Grace et al., 2006). It is apparent from the estimates of total NNP compiled by Grace et al (2006) that tropical savanna and grassland ecosystems constitute the second most productive biome after tropical forests (Table 3).

Biome	NPP (t C ha- 1 year-1)	Area (million km <sup>2</sup> )	Total carbon pool (Gt C)	Total NPP (Gt C year-1)
Tropical forests	12.5	17.5	553	21.9
Temperate forests	7.7	10.4	292	8.1
Boreal forests	1.9	13.7	395	2.6
Arctic tundra	0.9	5.6	117	0.5
Mediterranean shrubs	5	2.8	88	1.4
Crops	3.1	13.5	15	4.1
Tropical savanna and grasslands	7.2	27.6	326	19.9
Temperate grasslands	3.8	15	182	5.6
Deserts	1.2	27.7	169	3.5

\*Data adapted from Grace et al., 2006,

Table 3. Variation in carbon fixed by vegetation of different biomes, as net primary productivity (NPP). The total C pool includes vegetation and soil organic matter.

So what makes the biomes vary in productivity? Churkina and Running (1998) quantified the relative importance of environmental factors (temperature, water availability and radiation) on NNP of various biomes using a modeling approach with ecosystem process model BIOME-BGC. They found that in the high latitudes temperature appeared to be the primary control on NPP while in the middle latitudes a combination of either temperature and radiation or temperature and water availability limited NPP. In the low latitudes where savannas fall, water availability became more dominant than the other environmental factors. LeBauer and Treseder (2008) found N limitation on NNP to be widespread among biomes except deserts. This is not surprising since climatic variables such as temperature and precipitation also influence nutrient availability through N mineralization rates and plant N demand through effects on enzyme activity.

Changes in savannas globally characterized by declining cover due to conversion to agriculture as result of increasing human pressure and encroachment of bush in many grasslands has significant implications on NNP trends. It is therefore surprising that a lot of attention and monitoring (both satellite and ground) is devoted to forests with very little to savannas despite their importance in global NNP (Grace et al., 2006).

#### 4.4 Comparison of invasive and indigenous species productivity

Many plant species are introduced into savannas to enhance the nutritional plane of pasture and fodder so as to increase livestock production the main form of land use. Other reasons include provision of fuelwood/charcoal, building material, soil conservation, windbreak, organic manure and others. Various fodder trees play an important role in human food security through their function as animal-feed resources, especially as drought reserves. A major drive to improve pastoral production systems in savannas in 1970-80's by introduction of high yielding fodder tree species aimed at providing a more permanent feed supply over seasons (Nair, 1989). This was informed by the observation that while grasses in savannas produce more edible plant material for livestock they are extremely variable in their production as a result of seasonal fluctuations in rainfall. Extensive trials especially of *Prosopis* and *Leucacena* species were subsequently carried in Africa and Australia. The screening of tree species for introduction was normally based on comparative studies between combinations of introduced species and native species for biomass productivity, nutritional value, digestibility,

soil amelioration and resource requirements. A review of comparative studies consistently indicated the superior performance of South American trees in African and Australia in terms of biomass production. Two examples of trials of non-indigenous and indigenous trees in African savannas are discussed below to illustrate the point.

Deans et al. (2003) working in semi-arid site in Senegal compared 10 year old indigenous and non-indigenous species with some of their provenances being included while Jama et al. (1989) compared growth rates of 29 multipurpose fodder species both indigenous and non-indigenous at 6 year old in a semi-arid savanna climate in Kenya (Table 4).

Species	Origin	Leaves (kg)	Total above-ground biomass (Kg)
<b>Senegal trials<sup>a</sup></b>			
<i>Prosopis juliflora</i>	South America	8.2	141
<i>Acacia aneura</i>	Australia	14.3	107
<i>Azadirachta indica</i>	India	8.6	97
<i>Eucalyptus camaldulensis</i>	Australia	15.1	86
<i>Acacia tortilis ssp. raddiana</i>	Native	2.8	84
<i>Acacia nilotica</i>	Native	8.4	82
<i>Prosopis cineuria</i>	Australia	10.7	68
<i>Acacia tortilis</i>	Native	2.3	49
<b>Kenya trials<sup>b</sup></b>			
		Height (cm)	Diameter (dbh in cm)
<i>Grevillea robusta</i>	Australia	6.1	9.8
<i>Leucaena leucocephala (Peru)</i>	South America	5.3	5.2
<i>Casuarina equisetifolia</i>	Australia	4.4	4
<i>Acacia saligna</i>	Australia	3.9	4.5
<i>Acacia holosericeae</i>	Australia	3.4	3.2
<i>Prosopis juliflora</i>	South America	3.4	3.5
<i>Acacia albida</i>	Native	2.9	5.7
<i>Acacia salicana</i>	Australia	2.6	3.6
<i>Acacia stulmanii</i>	Native	2.3	4.1
<i>Zizyphus mauritania</i>	Native	2.3	1.8
<i>Tamarindus indica</i>	Native	1.5	1.7
<i>Balanites aegyptica</i>	Native	1.4	0.9
<i>Acacia tortilis</i>	Native	1.3	1.6
<i>Prosopis nigra</i>	South America	1.3	1.2
<i>Prosopis pallida</i>	South America	1.3	1.2

Data adapted from;

<sup>a</sup> Senegal data adapted from Deans et al. (2003). Only species for which above ground and leaves biomass was available were included

<sup>b</sup> Kenya data adapted from Jama et al. (1989). Only woody perennials and one provenance of *leucaena leucocephala* were included

Table 4. Estimated growth parameters for trials on native and non-indigenous species in Senegal and Kenya

From their results a number of conclusions can be drawn.

- a. Non-native species largely neotropical ones had superior performance in growth parameters (above ground biomass, height, bole volume, and leaf biomass) than the indigenous ones tested. As shown by the higher above ground biomass of *Prosopis juliflora*, *Acacia aneura* and *Azadirachta indica* as compared to native *Acacia tortilis*, *Acacia raddiana* and *Acacia nilotica* in Senegal while in Kenya the non-native *Grevillea robusta*, *leucanea leucocephala* and *Casuarina equisetifolia* attained the highest maximal height and the indigenous species such as *Acacia tortilis*, *Balanites aegyptica* and *Tamarindus indica* showed the minimal growth
- b. Not all non-native species out perform native species, for example the *Prosopis cineuria* and *Prosopis pallida* in Senegal and Kenya respectively. This could be due unsuitable ecological conditions thus even though *Prosopis pallida* is regarded to be amongst the most productive species in arid and semi-arid zones in biomass (Pasiiecznik 2001) the Kenya site was way above its altitude and rainfall range.
- c. Despite slow growth some native species had some positive qualities in comparison to non-native e.g. the indigenous *Acacia tortilis* and *Acacia raddiana* had the highest concentrations of N in their leaves while the non-native species *Eucalyptus camaldulensis* and *Acacia aneura* had the least
- d. Only a small fraction of non-native species are actually invasive, e.g. of the species tried in these two examples only *Prosopis juliflora* and *Prosopis pallida* are invasive.

African grasses introduced in the South American and Australian savannas and turned invasive have altered biomass production patterns, fire regimes, hydrology, nutrient cycling, native community composition and structure. Ecological disturbances that minimize the competitive ability of native grasses or cause soil disturbances are important at some stage of invasion in most cases. Non-native grasses can depress biomass and cover of native species if they have rapid growth thus diminishing light at the soil surface and consequently reducing the photosynthetic ability of competitors. Efficient water use is also another way non-native grass species can out compete native grasses while others have also been shown to compete effectively with native species for soil nutrients (D'Antonio & Vitousek, 1992). For example the non-native gamba grass (*Andropogon gayanus*) in northern Australia tropical savannas grows faster, forms taller and denser stands than native grasses resulting in an accumulation of biomass to the range of 11–15 tonnes/ha and may be as high as 30 tonnes/ha compared to 2–4 tonnes/ha of native species (Rossiter et al., 2003; Williams et al., 1998). This indicates a more than 300% production by the invasive species compared to native species. This high biomass accumulation greatly alters the fire regimes supporting fires that are about 8 and almost 25 times more intense in the early dry season and late dry season respectively (Rossiter et al., 2003). More intense fires have consequences on native species composition and abundance. In South America cerrado region the African grass, *Melinis minutiflora*, a C<sub>4</sub> stoloniferous grass, is one of the most problematic aggressive invaders forming dense mats that exclude many other herbaceous species. A manipulative experiment by Barger et al (2003) to test effects of disturbance showed that soil disturbance strongly enhanced its growth increasing biomass 7 fold while clipping to simulate grazing increased biomass 13 fold.

It is not only invasive grasses that depress biomass production of local grasses, in Africa Mworira et al. (2008b) found that the invasive herb *Ipomoea hildebrandtii* led to a decline of 47% in absence of grazing and 28% in the presence of grazing. Invasibility by *Ipomoea hildebrandtii* increases when lowered competition from indigenous grasses was accompanied by

increases in soil resources. Hence establishment of *Ipomoea hildebrandtii* was higher in conditions of low indigenous grass biomass, high soil moisture at a depth of 30 cm and higher soil N nitrification (Mworia et al., 2008b). Therefore in both the successful establishment of invasive grasses in South America and the invasive herb in Africa the important role of disturbance, grazing and resource supply changes are evident alluding to the applicability of the resource fluctuation hypothesis.

## 5. Carbon sequestering potential of invasive species

Carbon sequestering is the process of removing carbon from the air into reservoirs such as such as terrestrial ecosystems via photosynthesis. When carried out deliberately carbon sequestration it is a strategy for long-term storage of carbon dioxide released mainly by burning of fossil fuels hence mitigate or deferring global warming mainly. Invasive species have spread to large areas of savanna ecosystems and increased plant density and biomass in some degraded or disturbed areas and even in some cases undisturbed communities. For example in East Africa *Prosopis juliflora* is already estimated to cover 500,000 and 700,000ha in Kenya and Ethiopia, respectively in mainly the arid and semi-arid savannas while in Venezuelan savannas invasive African grasses have increased biomass by up to 50% (Brooks et al., 2004). In Columbia, Venezuela and Brazil 4 million km<sup>2</sup> were transformed to pasture by using, to a large extent, African C<sub>4</sub> grasses (Williams & Baruch 2000). The question that arises is 'can invasive species in savannas play a role in carbon sequestering?'

The tropical savannas are important in carbon sequestration at the global scale because not only are they remarkably productive being responsible for almost 30% of global net primary production (NPP), they are also the second largest biome of the world extending over 15 x 10<sup>6</sup> km<sup>2</sup> (Grace et al., 2006; Long et al., 1989). The carbon sequestered in savanna ecosystems is estimated to average 7.2 t C ha<sup>-1</sup> year<sup>-1</sup>. The carbon sequestration rate reflected by the net ecosystem productivity may average 0.14 t C ha<sup>-1</sup> year<sup>-1</sup> or 0.39 Gt C year<sup>-1</sup>.

The above ground carbon stocks in savannas is strongly influenced by the ratio of grasses to trees, the higher the tree cover the higher the sequestered carbon with a range of 1.8 t C ha<sup>-1</sup> where trees are absent, to over 30 t C ha<sup>-1</sup> where there is substantial tree cover (Grace et al., 2006). The ratio of grasses to trees is subject to the rainfall gradient and modified by the herbivory, fire, soil nutrients and texture. Plant traits also have a bearing on carbon stocks since they differ in growth rate and lifespan as a result of evolutionary trade-offs between acquisition and conservation of resources in stressful environments such as low nutrients and precipitation (Deyn et al., 2008)

Soil carbon constitutes over two-thirds of the global carbon found in terrestrial ecosystems or c. 2100 Gt, with the savannas biome soils estimated to have 200–300 Gt or 10–30% of the world soil carbon (Scurlock & Hall, 1998). Furthermore native savanna soils on global average contain at least as much carbon as that stored in above- and below-ground biomass (Scholes & Hall, 1996). Soil carbon pools are the balance between carbon input from primary productivity, and output processes such as decomposition processes, leaching of organic compounds and erosion losses. Net soil carbon input in savannas is mainly limited by low water availability and large carbon losses to herbivory and fire. Plant traits determine the amount of soil pool carbon sequestered mainly by altering overall primary productivity and belowground carbon allocation. Plant traits that may promote soil carbon sequestration comprise deep rooting, production of woody structures and herbivore defense traits. A particularly important trait in savannas is N-fixation which enhances plant productivity thereby increasing carbon input to

soil. These are some of traits found in invasive species such as *Prosopis juliflora* (Pasiiecznik, 2001). Furthermore many of the woody species found in the savanna have ligno-tubers and deep roots, enhancing the root : shoot ratio while tropical grasses generally have a high capacity to accumulate below-ground carbon (Scholes & Hall, 1996).

Losses mainly through burning and soil erosion also determine the amount of carbon sequestered. As discussed above fire is an integral driver and determinant of tropical savanna function and structure with large areas seasonally burnt resulting in an efflux of carbon in the range of 2.4–4.2 Gt C year<sup>-1</sup> or 42% of global burned phytomass and as high as 5–8 Gt C year<sup>-1</sup> if other losses such as management for grazing and land-use change are taken into account (Hall & Scurlock, 1991) may influence the regional and possibly global energy. Plant traits that reduce carbon loss include fire resistance manifested by thick bark, dense wood and high lignin concentration others include fire resilience traits such as fire tolerant seeds and resprouting.

From the foregoing invasive species will significantly alter carbon pools depending on whether they have large enough effects on flux variables such as above-ground net primary production and litter decomposition, fire regimes, resources such as water and nutrients, this will depend on their traits of the invader. By alteration of the components of the Carbon (C) and nitrogen (N) cycles which are fundamental ecosystem functioning and processes invasive plants influence sequestration. Do introduced plant species that turn invasive have traits that augment carbon sequestration?

Many studies have shown that ecosystem net primary production (NPP) to have increased and C and N stocks to be higher in the invaded ecosystems relative to the native ecosystems (Ehrenfeld et al., 2001). However due to the wide range of effects of invasive plants on C and N processes and stocks the overall direction and magnitude of such alterations are poorly quantified. Liao et al (2007) using a meta-analysis approach of 94 experimental studies to quantify the changes found that plant invasion enhanced C and N pool sizes in plants, soils and soil microbes and stimulated ANPP by 83% in invaded ecosystems compared with native ecosystems grouped into forests, grasslands and wetlands. This attributed to ecophysiological differences between native and invasive species that lead to greater ANPP, plant and litter biomass, higher plant N concentration, and higher litter N concentration and lower litter C : N ratio.

In savannas Archer et al. (2002) reported that in southern Texas bush encroachment by mainly the leguminous tree *Prosopis glandulosa* resulted in higher root biomass, increased SOC and total N with a linear increase in SOC storage rate with tree age. Similarly in sodic soils Kaur et al (2002) found trees planted in silvopastoral systems the total net productivity was highest in those consisting of the invader *Prosopis juliflora* even though grass productivity was lowest in such mixtures. Increased ANPP leading to higher C sequestration has been attributed to differences in ecophysiological traits such as specific leaf area and net photosynthetic rate between native and invasive species. In addition invaded ecosystems in general have 117% higher litter decomposition rate in comparison with native ecosystems, explained by higher plant and litter N concentration, lower litter C : N and lignin : N ratio than the native species (Liao et al., 2007). Where woody plants invade grass dominated savannas they tend to be more productive above- and belowground and hence deliver more organic matter into soils, are seldom browsed by livestock or wildlife, suggesting high concentrations of secondary compounds hence a large fraction of the foliar biomass goes into the soil pool directly as litter, more lignified roots of shrubs also promote C and N accumulation compared to that of grass roots and shoots (Archer et al., 2000)

However not all studies have noted increased C and N sequestering, some have shown plant invasion can have negative effects. For example Jackson et al. (2002) observed a C loss from a grassland ecosystem invaded by woody plants. In a Kenyan savanna Mworio *et al* (2008b) found N mineralization was significantly lower under the canopy of the invasive herb *Ipomoea hildebrandtii* as compared to locally dominant grass *Chloris roxburghiana* even though it was higher than bare ground/eroded areas. *Ipomoea hildebrandtii* is non-legume that is unpalatable and generally compounds that reduce plant palatability also reduce litter decomposition rate which may explain the reduced nitrification.

In conclusion plant invasions have led to increased C and N pools with responses attributed to differences in ecophysiological traits between invasive and native species related to ANPP, plant N concentration and litter biomass. Also sequestering is higher for invasive N-fixing than for nonN-fixing plants and invasive woody than for herbaceous species.

## 6. Conclusions

Savannas are an important biome given their high total NPP which is second only to forests, 3<sup>rd</sup> highest sequestered carbon pool, highest ungulate herbivore populations and habitation of pastoral peoples. Savannas consist of mixtures of trees and grasses with the ratio largely determined by factors precipitation, herbivory, fire and soil nutrients however the mechanisms by which they operate is still debated with some ecologists emphasizing the role of competition for resources and others the effect disturbances regulating tree populations. There is need for continued research in savanna dynamics incorporating aspects of changing climate and land use patterns.

Over the history of human development large numbers of plant species have been moved across physical barriers for a wide range of reasons such as food, forage and ornamental, many have been naturalized and only a small proportion have become invasive. Ecologists have put great effort in trying to understand factors that make plant communities susceptible to invasion. Important factors identified are the characteristics of the invader mainly traits that allow greater resource use efficiency, ease of propagation and faster growth, secondly the vulnerability of communities to invasion largely ecological disturbances leading to resource fluctuations. There are still several gaps and grey areas in our understanding of invasive species in savannas. Firstly the implications of the current rapid land use changes in savannas and their interaction with the climate change effects such as increased frequency of ENSO induced drought on invasive species proliferation and impacts is poorly understood. Secondly given the importance of plant characteristics on successful invasion of a non-native species there is inadequate information on the distribution of non-native species in savannas, their autoecology and to the dynamics of host savannas in relation to variation of disturbances in time and space. In some savannas such as in Africa with an exception of South Africa few comprehensive surveys and studies on invasive species have been conducted.

The productivity of savannas is mainly regulated by rainfall and soil nutrients whose variability leads gradients of production and compositional change in savannas while soil attributes such as texture have larger effects on functional group composition rather than production. The spatial and temporal comparison and monitoring of productivity in savannas has been hampered by the wide array of methods historically used with many underestimating NPP or focusing on single species or life-form. In general savannas have been accorded far less attention in research, monitoring and database development as

compared to forests which are regularly censused using ground and satellite imagery methods which is a conundrum given their almost equal total NPP.

## 7. References

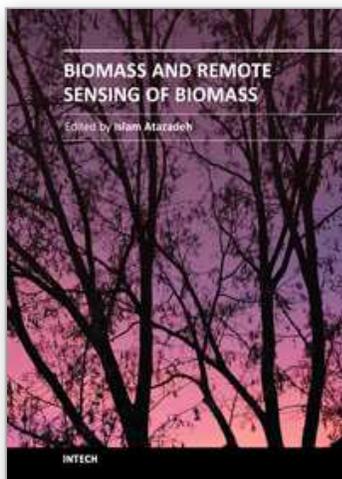
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## **Biomass and Remote Sensing of Biomass**

Edited by Dr. Islam Atazadeh

ISBN 978-953-307-490-0

Hard cover, 262 pages

**Publisher** InTech

**Published online** 06, September, 2011

**Published in print edition** September, 2011

Generally, the term biomass is used for all materials originating from photosynthesis. However, biomass can equally apply to animals. Conservation and management of biomass is very important. There are various ways and methods for biomass evaluation. One of these methods is remote sensing. Remote sensing provides information about biomass, but also about biodiversity and environmental factors estimation over a wide area. The great potential of remote sensing has received considerable attention over the last few decades in many different areas in biological sciences including nutrient status assessment, weed abundance, deforestation, glacial features in Arctic and Antarctic regions, depth sounding of coastal and ocean depths, and density mapping. The salient features of the book include:

- Several aspects of biomass study and survey
- Use of remote sensing for evaluation of biomass
- Evaluation of carbon storage in ecosystems
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### **How to reference**

In order to correctly reference this scholarly work, feel free to copy and paste the following:

John K Mworira (2011). Invasive Plant Species and Biomass Production in Savannas, Biomass and Remote Sensing of Biomass, Dr. Islam Atazadeh (Ed.), ISBN: 978-953-307-490-0, InTech, Available from: <http://www.intechopen.com/books/biomass-and-remote-sensing-of-biomass/invasive-plant-species-and-biomass-production-in-savannas>

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