Chapter 5: Distribution and ecology of trees in Eastern Africa drylands

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In this chapter, we first provide a description of the natural vegetation of the drylands of Eastern Africa. The reason for doing this is that there is little information on the distribution of individual tree species, a lacune which can be overcome however when using information on the distribution of vegetation types as an approximation of the distribution for individual tree species. Second, we provide an analysis of the principle natural factors that influence regional variation the structure or physiognomy of the vegetation, with particular attention for variation in tree cover and height. In the final section, we provide some reflection on the impacts of tree utilization on the distribution of trees.

5.1 Potential natural vegetation

The distribution of natural vegetation types provides a good approximation of the distribution of individual tree species at continental to national scales. The *Vegetation Map of Africa* developed by Frank White [13] delineates natural vegetation types such as the Somalia-Masai, Sudanian and Zambezian areas of endemism. Empirical distribution data for individual tree species were not available during the compilation of the vegetation map of Africa and this paucity of empirical species distribution data still holds today. In a situation like this maps of natural vegetation types can be used to infer the distribution of individual tree species [14] and generate maps that for example, discriminate where a particular species will be able to establish and provide, or alternatively fail to survive and provide desirable products and benefits. This inferential logic has been used to develop a species selection tool now available as an interactive map that can be used to select 'the right tree for the right place' throughout Africa [15]. Following this, a new higher resolution interactive vegetation map and species selection tool (the VECEA map, www.vegetationmap4africa.org) was produced for seven countries including four in the Eastern African region considered in this report (Ethiopia, Kenya, Malawi, Tanzania and Uganda [16]. Most of the descriptions of natural vegetation types given below were summarized from the documentation of the VECEA map.

The vegetation map of Africa was based on earlier vegetation maps of the 1960s and 1970s and it is possible that changes in temperature or rainfall that occurred since then may have shifted boundaries between vegetation types [17]. It would be possible in theory to adjust vegetation boundaries to climatic conditions today by calibrating the older map to the climatic conditions during production of the vegetation maps, and then predicting the adjusted boundaries based on more recent climatic conditions. Likewise it is theoretically possible for floristic studies to document recent vegetation shifts, although tree longevity may complicate analysis. However, ecotones or zones of gradual transition do exist between many vegetation types. It remains an open question whether widths of ecotones are substantially larger than the spatial shift in vegetation types due to recent climatic changes.

Somalia-Masai *Acacia-Commiphora* deciduous bushland and thicket (synonym: deciduous bushland) is the climax vegetation type of a large part of the arid and semi-arid lands of Eastern Africa (Figure 5.1b) where rainfall is low and bimodal. It characteristically is a dense bushland of 3 to 5m tall with scattered emergent trees up to 9m. Emergent species have well-defined trunks which carry the crown well above the main canopy; they are virtually absent from the driest areas. Most of the characteristic species of the main canopy underneath these emergents are multiple-stemmed bushes or small bushy trees branched near the base. In higher rainfall areas (especially on rocky hills), the emergent trees occur closer together and are somewhat larger (but only exceptionally taller than 10m). Some authors have categorized this physiognomic variant as woodland. Locally thickets are formed that are impenetrable.

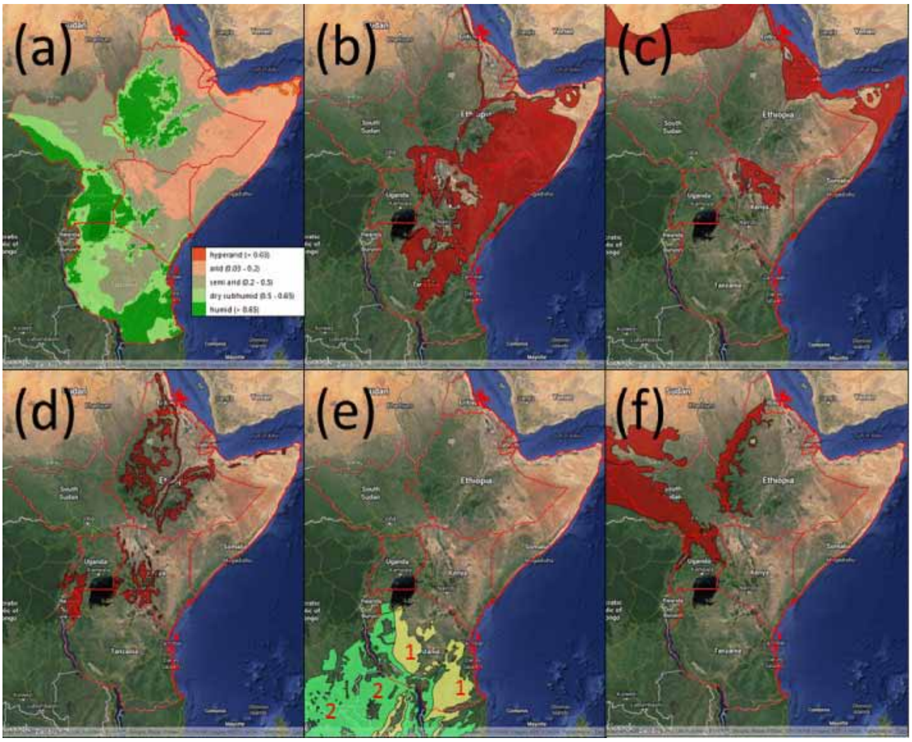

Figure 5.1 Aridity index (a) and major natural vegetation types in Eastern Africa: (b) Somalia-Masai *Acacia-Commiphora* deciduous bushland and thicket; (c) Somalia-Masai semi-desert grassland and shrubland; (d) mosaic of Somalia-Masai Eastern Africa evergreen and semi-evergreen bushland and thicket and secondary (biotic) *Acacia* wooded grassland; (e) Drier (1) and wetter (2) Zambezian miombo woodland; (f) Sudanian undifferentiated woodland and Sudanian woodland with abundant *Isoberlinia.* Aridity index derived from the CGIAR-CSI Global-Aridity and PET Database (http://www.cgiar-csi.org; [18] [19]. Distribution of vegetation types obtained from URL http://www.worldagroforestry.org/our_products/databases/useful-tree-species-africa, according to Kindt et al [15] [16] work by White [13]. Country boundaries obtained from the GADM database of Global Administrative Areas (URL http://www.gadm.org/). Map generated by R. Kindt in [20] with OpenLayers plugin to add the Google Hybrid layer.

There is appreciable variation in floristic composition within deciduous bushland and thicket, but species of Acacia, Commiphora, Grewia and various Capparidaceae species (e.g. Boscia, Cadaba and Maerua) are nearly always present. The dominant Acacia species and some of the Commiphora species are spinous. Most species are deciduous (losing their leaves simultaneously and usually for several weeks or months). Evergreen species occur, but never contribute more than 10% to the phytomass. Characteristic species of the main canopy include *Acacia bussei*, *A. mellifera*, *A. nilotica*, *A. reficiens*, *A. senegal*, *A. thomasii*, *Commiphora africana*, *C. campestris*, *C. edulis*, *C. erythraea*, *C. mollis* and *C. schimperi*. Emergent species include *Acacia tortilis*, *Adansonia digitata* (often only 8m tall with a short but massive trunk), *Delonix elata*, *Melia volkensii* and *Terminalia spinosa*.

Semi-deserts are areas where the differences in soil characteristics (such as soil colour) are more conspicuous than the vegetation itself, but where the plants are still sufficiently evenly distributed so that the vegetation can be further classified in physiognomic categories such as “semi-desert grassland” and “semi-desert shrubland”. In the Greater Horn of Africa, semi-desert vegetation occurs in areas that are more arid than those where Somalia-Masai *Acacia-Commiphora* deciduous bushland and thicket typically occur (Figure 5.1c). Where annual rainfall is between 100 and 200mm in the Somalia-Masai region, semi-desert grassland (dominated by grasses such as *Centropodia glauca*, *Eragrostis mahrana* and *Panicum turgidum*) occurs on deep sand. Under similar rainfall conditions, semi-desert shrubland occurs on stony soils.

Evergreen and semi-evergreen bushland and thicket occurs on the drier slopes of mountains and upland areas in Eastern Africa, which rise from the lowlands from the Somalia-Masai region all the way to central Tanzania. It often forms an ecotone between Afromontane single-dominant *Juniperus procera* forest and deciduous bushland. This vegetation type occurs in the dry sub-humid zone (Figure 5.1d) with mean annual rainfall of 500 to 850mm irregularly distributed throughout the year but with two main peaks. Evergreen bushland varies greatly in species composition and richness, but certain woody species that are nearly always present in the Somalia-Masai region include *Acokanthera schimperi*, *Carissa spinarum*, *Dodonaea viscosa*, *Euclea divinorum*, *Euphorbia candelabrum*, *Olea europaea* ssp. *cuspidata* (synonym: *Olea africana*), *Tarchonanthus camphoratus* (especially in disturbed areas) and *Vepris simplicifolia.* The Lake Victoria floristic region has a floristically poorer evergreen bushland variant.

Where domestic or wild animals are numerous, various *Acacia* species have replaced Eastern African evergreen bushland. It is therefore typical to find *A. drepanolobium*, *A. hockii*, *A. kirkii* and *A. seyal* occurring together with evergreen species. Evergreen bushland communities of the Lake Victoria region have been replaced by wooded grassland dominated by *Acacia hockii*, *A. gerrardii*, *A. kirkii*, *A. senegal* and *Euphorbia candelabrum*. In the documentation of the VECEA map, it was suggested that ‘biotic Acacia wooded grassland’ is an alternative steady state of potential natural vegetation (corresponding to disturbance by animals) to the steady state of evergreen bushland (corresponding to limited disturbance by animals). The degree of grazing pressure therefore determines the proportions of biotic Acacia wooded grassland compared to evergreen bushland in the Greater Horn of Africa.

Miombo woodland is floristically and physiognomically very different from other types of African woodland. It is nearly always dominated by species of *Brachystegia* either alone or with *Isoberlinia angolensis*, *Julbernardia globiflora* or *J. paniculata*. Most miombo woodlands are semi-deciduous, but some are completely deciduous and some are almost evergreen. Miombo woodland is the prevalent vegetation throughout the greater part of the Zambezian region (a region with unimodal rainfall rather than the bimodal rainfall experienced in the Somalia-Masai region), especially on the main plateau and its flanking escarpments. In the Greater Horn of Africa (especially in the countries that we focused on), Miombo woodland only occurs in Tanzania (Figure 5.1e), although a closely related type occurs in coastal areas of Kenya (this other type is 'Zanzibar-Inhambane transition woodland', a vegetation community that is intermediate between Zanzibar-Inhambane forest and Zambezian woodland and that is dominated by *Brachystegia spiciformis*). Miombo woodland generally occurs in dry sub-humid areas, and drier and wetter sub-types can be distinguished (Figure 5.1e). Whereas some authors (including White [13]) expected that, on moister and deeper soils in higher rainfall areas, Miombo had replaced Zambezian dry evergreen forest, the interpretation that all these areas previously supported forest is not generally accepted (P. Smith and J. Timberlake, pers. comm.).

In Eastern Africa*,* **Sudanian woodland** (as defined and mapped by White [13]) principally occurs in South Sudan, Ethiopia and Uganda. In a similar situation as with miombo woodland, Sudanian woodland generally occurs in areas that experience unimodal dry subhumid conditions (Figure 5.1f). Sudanian woodland was mapped as different vegetation types in the VECEA map: (i) dry *Combretum* wooded grassland; and (ii) *Vitellaria* wooded grassland. *Combretum* wooded grasslands are among the most widely distributed wooded grassland vegetation types of Eastern Africa. In wetter areas, various *Combretum* species are associated with larger-leaved species of *Terminalia* (especially *T. glaucescens* and *T. mollis*). In drier areas, *Combretum* species are associated with smaller-leaved *Terminalia* species: *T. brownii* in Kenya and Uganda and *T. sericea* in the "monsoon sector" of Tanzania (i.e. areas with a one-season summer rainy season typically). White [13] does not use the definition of *Combretum* wooded grassland, but the sub-type of "Ethiopian undifferentiated woodland" as described by White (1983 p. 107) is virtually equivalent to Combretum-Terminalia woodland and wooded grassland as described in the recent atlas of potential natural vegetation types of Ethiopia.

The shea butter tree *Vitellaria paradoxa* (synonym *Butyrospermum paradoxum*) is endemic to the Sudanian region [13]. *Vitellaria paradoxa* often replaces *Isoberlinia doka* in secondary grasslands where *Isoberliniadoka* dies out because of frequent cultivation.

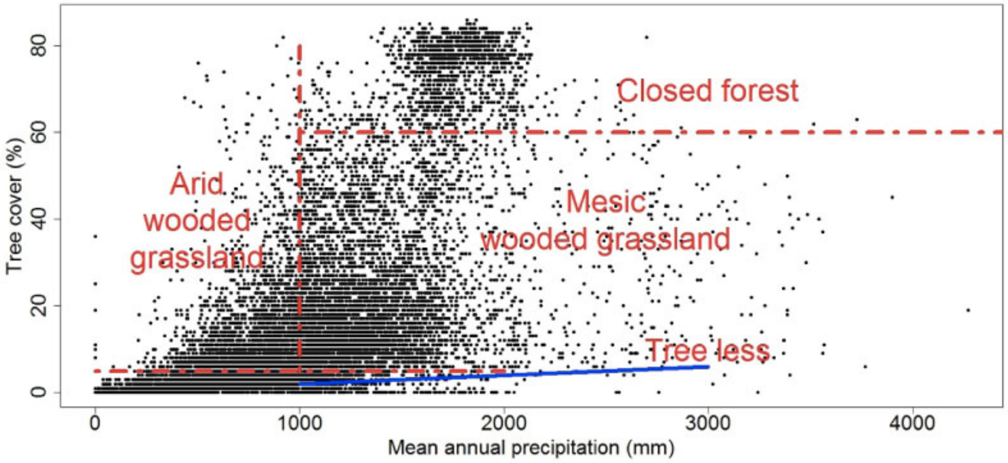

Figure 5.2 Relation for the African continent between tree cover (%) derived from MODIS[21] imagery and mean annual precipitation from WorldClim. Categories in red according to [22] and [23].

5.2 Ecology of trees and vegetation physiognomy

A number of factors affect the vegetation structure or physiognomy of dryland vegetation. This section focuses on tree cover and height, first because these are traits available from satellite-borne observations and secondly because many physiognomic studies consider these descriptors. Tree cover and height are also principal descriptors used in physiognomic classification schemes to differentiate between vegetation types such as forests, woodlands, wooded grasslands and bushland. Other parameters, such as stem diameter, density, age, biomass and species composition are equally important in the context of resilience for human use.

Abiotic factors including climate

Important abiotic factors that affect tree cover include soil properties and climatic factors such as rainfall (Figure 5.2) and temperature as these are 'direct environmental gradients' that influence resource gradients relevant to plant growth and plant development and therefore their potential distribution [24]. In general there is the notion that in arid systems resource limitations, especially water availability, are the major determinants of tree cover, while in more humid systems, disturbances such as fire determine the tree cover [25] [26] [22]. As a broad rule of thumb, systems with mean annual precipitation (MAP) below 1000mm are considered as drylands [23]. In drylands, nutrient limitation is hardly ever considered to be a limiting factor [27]. Empirical inference on tree distribution using either field based methods [25] or satellite derived information [23] have shown that MAP sets an upper limit to the tree cover that can be found up to approximately 1000mm of mean annual rainfall (Figure 5.2). This means that the maximum tree cover that can be expected is a function of MAP, but that the actual tree cover could be much less due to other factors (*i.e.*, factors leading to changes between potential vegetation [described under "Potential natural vegetation"] and actual vegetation).

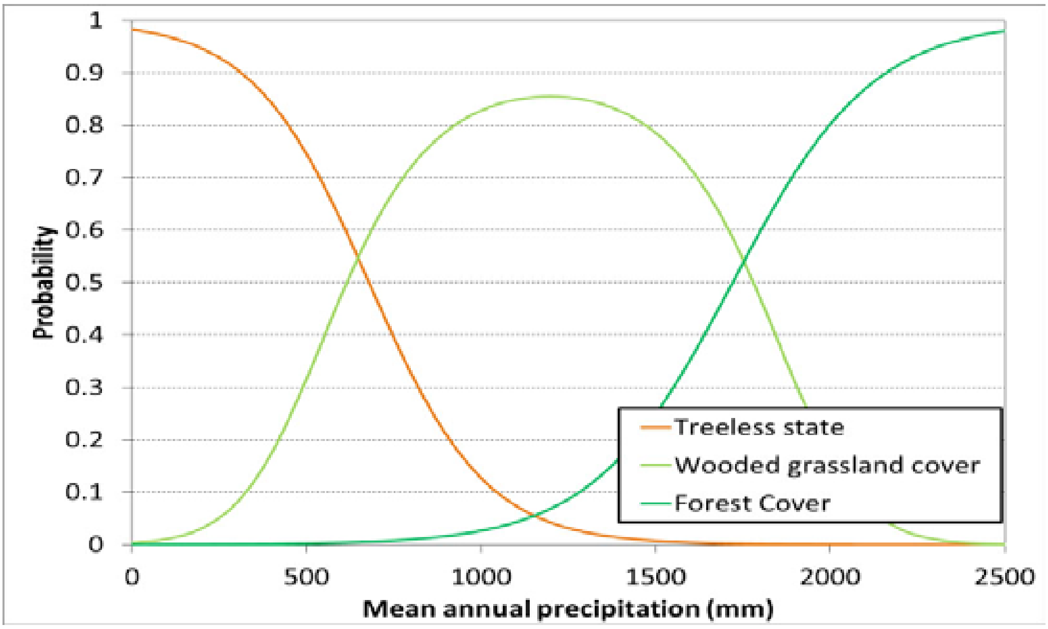

Figure 5.3 The probability of occurrence of three physiognomic vegetation classes in Africa as a function of rainfall on the African continent: a treeless state, a sparsely woody to intermediate density wooded state and a forested state. Probabilities from [22]

Given a certain amount of rainfall (MAP), several states of tree cover can exist: (i) a tree less state; (ii) a wooded grassland state; and (iii) a closed forest state [22]. In Figure 5.2 we can clearly see that under a given amount of rainfall (MAP), different types of tree cover can be found. For example at 500mm MAP, both a treeless and a wooded grassland state are almost equally likely (see also Figure 5.3). Which of the two states is actually found therefore depends on other factors.

As an alternative to MAP, Aridity indices combine both rainfall and evapotranspiration to provide a better representation of the available moisture for plant growth. Combining aridity with other relevant factors such as length of growing period provides a reliable set of parameters describing conditions that can distinguish between important biomes at the continental scale [28]. This can also be observed when plotting tree cover and height against aridity indices rather than MAP (Figure 5.4) displaying similar trends as described above. We also observe a generally lower tree cover for Eastern Africa. Around 99% of the Eastern African region has less than 60% tree cover and would be classified as Wooded Grassland in some vegetation classification schemes. This coincides with lower rainfall levels, a regional median MAP around 548mm against 740mm for the whole of Africa. Clearly high rainfall zones overlap with tall and closed forests (Figure 5.5).

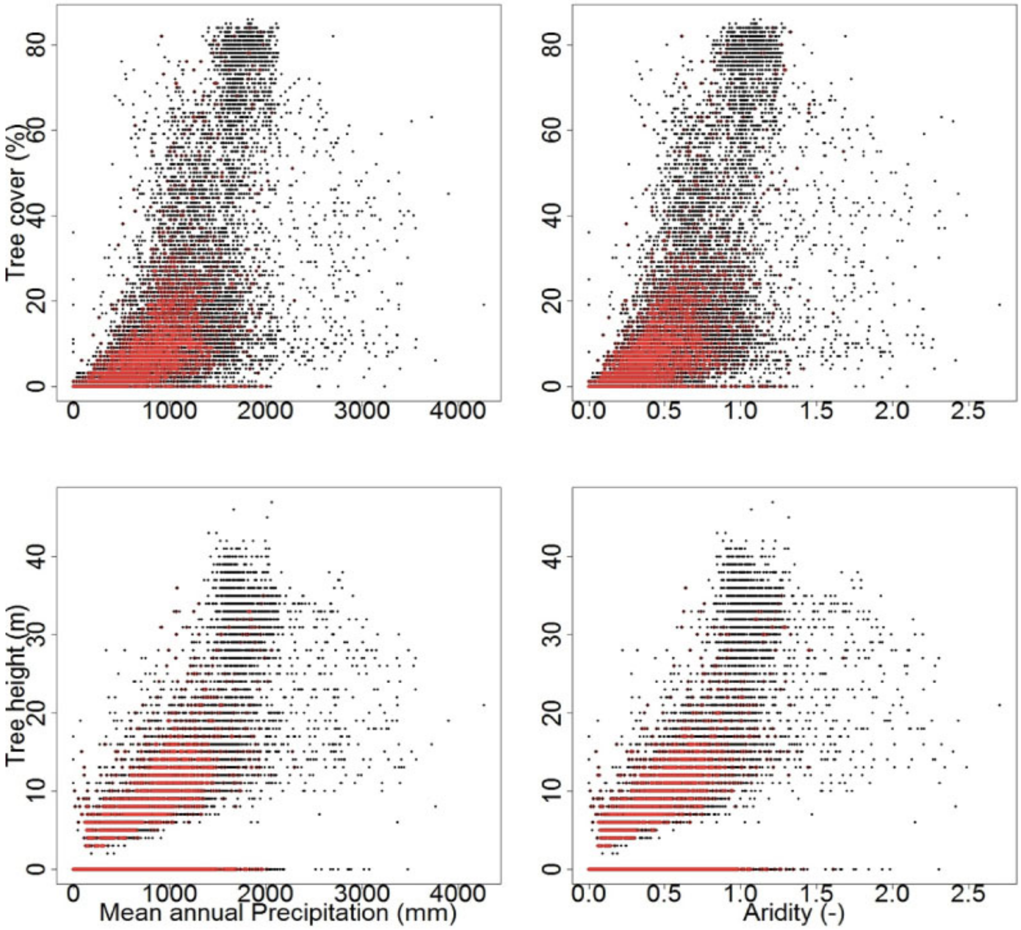

Figure 5.4 Tree Cover [29, 30] and height [31] as a function of mean annual precipitation (Worldclim) and aridity [19]. Red dots indicate plots in Eastern Africa.

Biotic factors and fire

Biotic factors include biotic interactions such as herbivory [32], competition with grasses [30] and fire [33] [34]. Fire itself is not a biotic process, but a mixture of biotic and abiotic factors influence its impact on trees. It is the biomass of grasses rather than trees that fuel most dryland fires. Only when grasses form a continuous layer of fuel with a fuel load of above 1500kg dry matter per ha is capable to carry the fire [35]. This is a situation occurring in the wetter drylands with annual rainfall above 1000 mm. The flammability of this biomass goes up at the start of the dry season when biomass is plenty and desiccating, which results in hot fires, which may damage trees [33]. Most savanna tree species are not really killed by fires, but we do speak of top-kill when trees are reduced to their belowground organs from which they have to resprout after a severe burn.

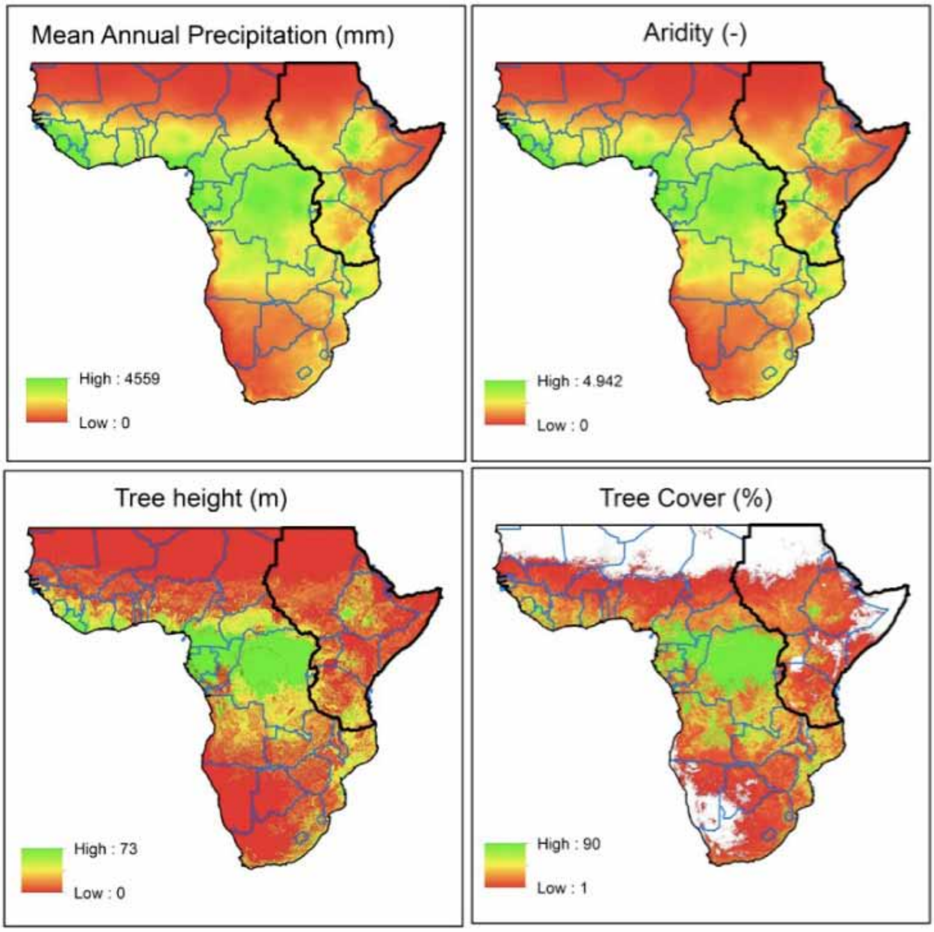

Figure 5.5 Maps showing the distribution of mean annual precipitation, aridity, tree cover and tree height for Sub-Saharan Africa. The black line indicates the subset of Eastern Africa that was included in the above figures.

Herbivore effects on tree cover and height are also complex and depend on the nature of the trees, the herbivores and the environmental setting. Firstly, herbivory can be broadly defined using two distinct approaches, browsing, related to the consumption of shrub and tree leaves, and grazing, referring to the consumption of the herbaceous layer [36]. Most dryland herbivores can be grouped into either of these two guilds, although some animals, such as goats or elephants, are so adaptable in their feeding strategy that they are referred to as intermediate feeders. Browsing clearly has a direct effect on trees in drylands as it reduces the leaf area of the plants, and through that, its photosynthetic activity and evapotranspiration. The extent to which browsers exert an effect on trees depends on the palatability, thorniness and height of the species. Taller trees are less susceptible to browsing than shorter trees [37], although not immune. For example, elephants are well known for their ability to tear down tall trees, giraffes (*Giraffa camelopardalis*) are clearly capable of accessing high positioned canopies, and even goats (*Capra spp.*) are well known for climbing into multi-stemmed trees to access higher located leaves. Grazing indirectly affects trees, as it reduces the fuel load, and thus the impact of fires on trees [33]. It also reduces competition for resources between trees and grasses [30]. However, this latter point is mainly an issue in the wetter systems that are more expected to be nutrient-limited rather than water-limited.

Clearly the above-mentioned factors that influence tree cover and height within the boundaries set by climatic and a-biotic effects are highly system specific, or apply to the wetter systems that have been discussed. An important aspect that relates to this is the human exploitation that to a large extent mediates these factors, such as control on burning, managing both the livestock and wildlife and the harvesting of plant organs. The lower than expected tree cover that can be observed in some parts of Eastern Africa such as the Ethiopian highlands or Uganda is partly attributable to the high population densities in these regions and subsequent exploitation.

5.3 The effect of tree management on tree cover

The above described factors thus set a maximum tree cover and height. Figure 5.2 shows that the maximum (threshold) achievable under certain rainfall conditions is not achieved in many situations. Exploitation and management of trees forms an important factor explaining why this maximum is not achieved. Within the potential and limitations to tree cover set by the factors described in section 5.2 actual tree will be dominantly determined by the way people exploit and manage trees. This section reviews the effect of tree management and exploitation on the actual density of trees in man-made landscapes.

Throughout the drylands of Eastern Africa there are several factors, which affect the intensity of management of trees. The first is a gradient going from systems where trees are not planted and exploited as they appear as a result of natural regeneration to systems where trees are planted for the benefits that they provide; mixed systems exist with naturally regenerated trees interspersed with planted trees. Tree ownership is an important factor determining the management beyond the seedling phase. While having planted a tree is an important factor, it does not always suffice to guarantee that the one managing a tree will be the (sole) beneficiary of this effort. Formal or informal land tenure arrangements are crucial to support tree tenure and the authority to determine, who profits from the benefits that managed trees provide. Land tenure is thus an important factor determining the intensity of tree management, and some relation exists between intensive tree management including planting, forcing of seedlings and managing of adult trees on lands with secure tenure, and less intensive or absence of management on open access lands. The relation is imperfect because private lands exist where trees are not managed while there are also many public lands where the use of land and trees is regulated by customary law and other institutional arrangements. However, tenure remains a crucial condition to create the environment, which makes investment in tree farming a viable option.

People exploit trees in drylands to derive various benefits from the various goods and services they provide. Some of these uses do not affect the production or survival of trees whereas other may have the effect of depressing the production and/or destroying the tree altogether. There is thus a gradient forcing uses with neutral effect to less or more intrusive tree uses, and below we provide a narrative describing the level of intrusiveness of tree uses, which are further described as the various ecosystem services in chapter six.

The harvesting of food from trees may range from harmless to intrusive depending on the intensity. The collection of fruits and nuts affects the reproductive strategy of trees and although many trees have an ability to also disperse through stoloniferous growth, seeds remain important to reproduce and to maintain genetic diversity. Broadly, two strategies can be defined in tree seed production. Some species produce many very small seeds, aiming at a high chance that some seeds will land in suitable locations to settle, but at the cost of providing these seeds with very little reserves. The second strategy is to produce very few bigger seeds that come with large reserves to make sure the seedlings get a good start at the beginning, but with the risk that these few expensive seeds all end up in unsuitable locations. Collection of fruits and nuts is likely to interfere more with tree reproduction in the second case. However, in harsh environments, such as arid and semi-arid savannas, the small seeds in high number - low survival strategy is adopted by many trees [38]. Overutilization and depletion of the seed bank may affect reproduction of trees in case of species with large seeds such as for example the shea butter tree. Where fruit trees are actively planted, this kind of extraction should have limited effects on the dynamics and persistence tree species.

The collection leaves from trees for human consumption (tree vegetables) or as a fodder for livestock reduces the trees' capacity for primary production. Depending on the season this can be more or less detrimental. When trees are (near) dormant (e.g. at the start of the dry period) removal of leaves will have little effect on the survival of a tree, as the leaves will have reached the end of their expected life time. However, defoliation during the growing period deprives the tree of its foliar tissue which it will try to compensate while mobilizing energetic resources. Repeated defoliation may deprive trees of these resources and lead to starvation and mortality. The provision of tree vegetables and livestock fodder should thus be managed carefully, and requires adequate tree tenure to allow this.

Harvesting of resins and gums may result in further decline of vegetation (tree) cover compared to what is expected naturally. We use the term "exploitation" to indicate that in this section the utilization of tree products is described from the perspective of tree ecology and its consequences for the difference between potential and actual distribution. The term "use of tree products" relates more to the perspective of providing services to human needs, which will follow in subsequent sections.

The collection of gums and resins may range from harmless to quite intrusive depending on the type of resins or gums (see section 6.2.7) harvested and the approach taken. Many resins and gums are harvested on an ad hoc basis from trees that are naturally oozing these substances, which would have low impact on the trees. Nevertheless, where commercial exploitation of gums and resins start to occur, caution has to be paid not to over-harvest these substances. Gums and resins play a vital role in the ecology of the trees in storage of essential elements, protection against insect attacks and transport within the stem. Examples are known of cases where resin extraction from *Boswellia papyrifera* for the production of Frankincense had clear negative effects on the survival and growth of trees [39].

Harvesting branches (e.g. for fuel wood) has a more distinct effect because a complete section of a tree is removed, including the leaves on the branches. This includes affecting the structural properties of the canopy. Also, breaking of branches creates a clear scar that makes a tree more vulnerable to insect and disease attacks. Complete harvesting the above-ground section of trees clearly resets the development of the above ground tree component completely. Harvesting complete stems may not necessarily kill the tree as many arid species can resprout after harvesting (essentially, being top killed by fire has the same result). Nevertheless, it has a profound effect on the state of a tree and in many cases it does require the re-establishment of a new tree that can take up to several years.

Roots are important organs for plants, allowing for access to sub-surface resources and providing stability. Although root harvesting normally happens after a tree has been chopped, it eliminates the possibility of re-sprouting, and also affects the structure of the soil, making it more vulnerable to erosion.

How the above mentioned exploitative uses of trees affect the tree population in an area depends on existing management systems by smallholder farmers and pastoralists, including aspects of usufruct, gender and tenure rights. Clearly, trees offer opportunities for use by people, but this can be done only sustainably when the multiple uses are coordinated. This poses a challenge in many drylands, because frequently trees do not belong to individuals but are a common good. Evaluation of management opportunities should therefore go beyond supporting current regeneration patterns and focus on active management, coordination of use and restoration.

Potential natural vegetation, and the abiotic conditions that set upper boundaries to tree cover, could be used as reference for restoration – both for understanding alternative restoration pathways and to actively promote useful, and therefore often over-exploited, dryland tree species. Above all however, secure tree tenure is required to stimulate an effective management of trees in the drylands of Eastern Africa.