

Diameter growth of trees in miombo and acacia woodland in an eroded landscape in NE Tanzania

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Abstract

Diameter increment of trees typical of miombo and acacia woodland was studied during a period of 20 years in Kondoa district, Tanzania. The study was performed in permanent plots in a severely degraded area subjected to considerable restoration efforts. A total of 15 species were selected from a database collected within a project for monitoring the landscape recovery. Growth performance of African woodland species was searched for in the literature for comparison, and a comprehensive list of citations was compiled. We found growth to fall within the range reported in earlier studies, although growth varied both between and within species. There are reports that the radial increments of trees are unimodal over their lifespan, but we found no clear support. In several species, the annual growth increased with stem diameter. Growth during the rainy ENSO year 1997/98 was pairwise compared with the preceding two years and was found to be significantly higher during the wet year, pointing to soil water as a limiting factor. We conclude that free development is an alternative to tree planting on marginal land.

KEYWORDS

acacias, *Brachystegia*, degraded ecosystem, limiting factors, rainfall, restoration, semi-arid, tree growth

Résumé

L'augmentation du diamètre des arbres typiques des forêts de miombo et d'acacia a été étudiée pendant une période de 20 ans dans le district de Kondoa, en Tanzanie. L'étude a été réalisée sur des parcelles permanentes dans une zone sévèrement dégradée soumise à des efforts de restauration considérables. Un total de 15 espèces ont été sélectionnées à partir d'une base de données collectée dans le cadre d'un projet de suivi de la restauration du paysage. Les performances de croissance des espèces forestières africaines ont été recherchées dans la littérature à des fins de comparaison, et une liste bibliographique complète de citations a été compilée. Nous avons constaté que la croissance se situait dans la fourchette indiquée dans des études antérieures, bien que la croissance varie à la fois entre et au sein des espèces. Nos résultats ne confirment pas que l'augmentation en diamètre des arbres est unimodale

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au cours de leur croissance. Chez plusieurs espèces, la croissance annuelle a augmenté en même temps que le diamètre du tronc. La croissance pendant l'année pluvieuse ENSO 1997-98 a été comparée par paires avec les deux années précédentes, et s'est avérée être significativement plus élevée pendant l'année humide, indiquant que la teneur en eau du sol est un facteur limitant. Pour conclure, la régénération naturelle est une alternative aux plantations forestières sur les terres marginales.

1 | INTRODUCTION

There is a lack of detailed information on species ecology of African trees. Knowledge of growth rate is crucial, but also regeneration and mortality, as well as other species-specific traits, such as tolerance to drought and possession of nitrogen fixation and mycorrhiza. This is also coupled with the need to find methods to restore degraded land in semi-arid Africa.

The lack of information on the growth of African trees outside the timber production systems has been pointed out by, i.a., Trouet et al. (2006), Winters et al. (2018) and Chidumayo (2019). In order to increase this knowledge, we extracted all tree stem growth data that we collected in a project on monitoring of vegetation development in an eroded landscape, and we here present an overview of growth of selected tree species for the period 1991–2010.

Stem increment of trees depends on species and species-specific traits and also varies with habitat conditions. In African woodlands, growth is generally correlated positively with water availability and negatively with high temperature, both within a year (Gourlay, 1995; but see Winters et al., 2018) and between years (Trouet et al., 2006). Stems may even shrink temporarily (Baker et al., 2002; Gerhardt & Todd, 2009) during drought. In arid and semi-arid regions, variation between years is likely to be important due to rainfall fluctuations.

Most soil nitrogen originally comes from the atmosphere and is accumulated by living organisms (Aerts & Chapin, 2000). Most eroded soils in the tropics have a shortage of nitrogen (Aweto, 1981; Long et al., 2012). This could lead to a larger diameter growth in nitrogen-fixing species than in others (Nasto et al., 2019). Also, most tropical trees have mycorrhiza, but the fungi may be rare in degraded soils with little soil organic matter, slowing down establishment and growth and reducing survival (Frost et al., 2001).

It has been suggested that the annual growth rate in a tree is unimodal over its lifespan, increasing with increasing diameter in small trees, reaching a peak and then declining (Bowman et al., 2013; Hérault et al., 2011). The peak may vary between species in age and diameter, giving rise to largely positive or negative relationships between tree diameter and stem increment.

Methods have varied in studies on tree diameter growth in African semi-arid areas (see Worbes, 1995). Measuring the width of growth rings, assumed to be annual, has been attempted by several researchers. A more reliable way is to measure repeatedly the stem circumference or diameter during several years on the same individuals (Baker et al., 2002; Gerhardt & Todd, 2009). Tree growth is slow,

and such studies need to be long-term (Chidumayo, 2019). The probably first published work of this kind was by Mugasha et al. (2017) who collected data over a period of fifteen years.

Our study took place in Kondoa Irangi Hills (KIH), Dodoma Region, in northeast Tanzania, a severely degraded area (Mbegu & Mlenge, 1984), where considerable efforts were made to halt soil erosion in the 1970s to 1990s. This study is a late contribution to the MALISATA research programme (Man–Land Interrelations in Semi-arid Tanzania) which included many disciplines and was active mainly in the 1990s (Kikula, 1999).

We report here on stem diameter growth in 15 selected woodland tree species. Our aims are (1) to present information on growth for the species as a possible basis for restoration work, (2) to use long-term data to test the effect of yearly variation in precipitation on tree growth and (3) to investigate possible differences in growth between species with or without nitrogen-fixing symbionts.

2 | MATERIAL AND METHODS

2.1 | Site description

Elevation of KIH extends to ca 2200 m above sea level (a.s.l.), but our sites are between 1280 and 1830 m a.s.l. (Supporting information S1). Kondoa town (4°54'14"S 35°46'56"E), at 1450 m a.s.l., has an annual rainfall of 652 mm (for 1931–1990; Ngana, 1996). Higher up, precipitation is higher. The rainy season is from November to April with peaks in December and April. KIH covers ca 125,600 ha surrounded by plains at about 1200 m a.s.l. Bedrock consists of highly weathered and erodible Precambrian gneiss.

Much of the hillslopes in KIH are believed formerly to have carried miombo (*Brachystegia-Julbernardia*) woodland (Backéus et al., 1994), still existing at less disturbed sites. Lower parts of the catena may have had acacia (the genera *Senegalia* and *Vachellia*) and other kinds of woodland. However, KIH is severely degraded. Most of the gullies were formed naturally more than 10,000 years ago (Eriksson et al., 2000). During the last millennium, trees have been cut for iron making (Lane et al., 2001). Further, there was intensive cultivation of cash crops for the 19th-century caravans (Mungo'ng'o, 1995). The appearance of the Rangi people about 200 years ago meant increased grazing (Christiansson, 1996). Finally, the colonial administration cleared trees in efforts to eradicate tsetse flies in the 1930s and 1940s (Eriksson & Sandgren, 1999). By then, much of the topsoil

had been lost over large areas. Residual soils were generally deficient in soil organic matter and, particularly, in nitrogen and boron. Further, also phosphorus, sulphur, manganese, zinc and copper were in low supply (Munkert, 2000).

Eight vegetation types were distinguished by Backéus et al. (1994). All were to various degrees affected by previous human activity. Apart from secondary mixed forest, found above 2000 m a.s.l., various types of woodland were distinguished, particularly *Brachystegia microphylla* at high elevations, *B. spiciformis* on lower levels, *Markhamia obtusifolia* on sites with strong disturbance and *Vachellia tortilis* on toe slopes. There are also a few types of grasslands, treeless or with scattered acacias (*Vachellia nilotica*, *V. seyal*). The correlation between the catena sequence and the vegetation types is weak and overshadowed by the degree of previous disturbance.

In 1973, the Tanzanian government launched a land restoration programme in Kondo District, known as HADO (Hifadhi Ardhi Dodoma, translated as the Dodoma Region Soil Conservation; Christiansson et al., 1991). At that time, parts of the KIH landscape were virtually without vegetation (Backéus, pers. obs. in 1975). Ongoing overgrazing by livestock was at that time assumed to be the main reason behind the precarious situation. All livestock were evicted from KIH in 1979 (Mungo'ng'o, 1995).

2.2 | Field methods

The data used in this study emanate from a project for monitoring of regeneration and succession in the absence of grazing and fire. With that purpose, 27 permanently marked 20 m × 20 m plots, representing different vegetation types and degrees of disturbance (Supporting information S1), were established in 1991.

Most plots were fenced, since trespassing herds of cattle occurred within KIH, despite bylaws intended to prevent this. Plots with no, or little, field layer vegetation were not fenced. Plot corners were marked. As fires were frequent, a firebreak was established around each plot. Fences and firebreaks were maintained until 1998.

Woody plants were monitored with a modified line intercept method (Canfield, 1941). Along five parallel line transects in each plot, 20 m long and 4 m apart, the stem diameters of all woody individuals >50 cm high, having vertical crown projections intercepting one or more of the lines, were measured at 30 cm above the ground. The lengths of the crown projections intercepting the lines were recorded. The sum of the 'intercept' lengths per species per plot expresses the percentage cover of the species (Supporting information S1).

The sampling was done in April, some years extending a few days into May. In 1991, all plots were recorded. Subsamples of plots were then recorded in 1992–1995, 1997 and 1998. Therefore, most individuals were not measured in all years. Also, individuals died during the period and new ones appeared.

At a final sampling in 2010, grazing had become widespread. Our plots had not been maintained and fences were broken. Full sampling was not attempted, but in 16 of the plots, we re-measured stem diameter of tree individuals that could be identified from previous

sampling with the help of field notes and remaining plot markings. The aim was now restricted to collection of data on growth of individual trees, intended for the study presented here.

2.3 | Data analysis

For this growth study, only individuals ≥50 cm high and with a stem diameter of ≥3 cm at measuring height (30 cm) were included and only individuals were identified and measured at least three times during the period 1991 to 2010. Only a limited number of individuals were present in the data set throughout the whole period from 1991 to 2010.

Some of our species are often referred to as shrubs, but the included individuals all had leading stems and are here called 'trees'. Trees were not tagged, and data were excluded when it could not be fully ascertained from the field notes that consecutive measurements referred to the same individual. In this reduced data set, only species with a minimum of six individuals were kept for further study. All in all, 15 species represented by 239 individuals and 1069 measurements were included.

Growth rate for each individual in cm yr^{-1} was calculated as the slope of a regression line with diameter against year, as this levels out irregularities in growth over time. Mean growth rate for each species with standard error was calculated.

Possible influence of stem diameter on diameter growth was analysed by regression on population level. For each species, we analysed whether growth was best described by simple linear or quadratic regressions, comparisons made with p - and R^2 -values (R^2 adjust for quadratic regressions) and residual distribution.

A regression of growth in all measured years against annual rainfall was not useful, because precipitation did not vary much between rainy seasons, except in the season 1997/1998, which had much rainfall due to El Niño Southern Oscillation (ENSO; Lyaruu, 1998). We performed paired two-sample t -tests of means for the actual growth data collected in the contrasting rainy seasons of 1996/97 and 1997/98. Species with at least 6 paired individuals were included.

Growth data collected by the end of the rainy season of 1996/1997 represent two years of growth, as no data were collected during the 1995/1996 season. The growth values were therefore divided by two. The rainfall in Kondo for the 1995/1996 rainy season was 749 mm and for 1996/1997 585 mm. The rainy season 1997/98 had 1131 mm of rain (Lyaruu, 1998).

3 | RESULTS

3.1 | Annual growth

The highest mean growth in diameter was found in *Vachellia tortilis* (0.95 cm yr^{-1}) (Table 1). Average annual growth of all other species was between 0.15 and 0.56 cm yr^{-1} . The lowest diameter growth was found in *Combretum zeyheri*.

Species	n	Diameter increment (cm y ⁻¹)				
		Mean	SE	Min.	Max.	Amplitude
<i>Brachystegia microphylla</i> all	40	0.364	0.076	-0.049	1.869	1.918
Plot 10 (big)	9	0.896	0.245	0.119	1.869	1.749
Plots 13-14 (small)	31	0.209	0.040	-0.049	1.010	1.059
<i>Brachystegia spiciformis</i>	23	0.559	0.103	0.081	1.931	1.850
<i>Combretum zeyheri</i>	7	0.149	0.036	0.059	0.338	0.279
<i>Dalbergia nitidula</i>	9	0.211	0.081	-0.017	0.781	0.798
<i>Dichrostachys cinerea</i>	13	0.250	0.051	0.047	0.774	0.728
<i>Euclea natalensis</i>	7	0.234	0.053	0.086	0.510	0.424
<i>Euphorbia candelabrum</i>	7	0.556	0.253	0.053	1.997	1.944
<i>Julbernardia globiflora</i>	27	0.355	0.048	-0.057	0.985	1.042
<i>Ormocarpum kirkii</i>	6	0.197	0.085	0.032	0.610	0.578
<i>Searsia natalensis</i>	22	0.272	0.047	0.062	0.800	0.738
<i>Senegalia senegal</i>	17	0.547	0.072	0.033	1.068	1.034
<i>Thespesia garckeana</i>	8	0.331	0.146	0.070	1.326	1.256
<i>Vachellia nilotica</i>	10	0.536	0.062	0.351	0.922	0.571
<i>Vachellia seyal</i>	18	0.334	0.035	0.040	0.650	0.610
<i>Vachellia tortilis</i>	25	0.950	0.175	0.071	3.550	3.479

Note: The measurements started in 1991. The investigated periods differed both within and between species. *Brachystegia microphylla* is reported separately for Plot 10 and Plots 13-14. For further explanation, see text.

Variation among and within species was considerable. The biggest average annual diameter increase was 3.55 cm in an individual of *Vachellia tortilis* and 2.00 cm in a *Euphorbia candelabrum*, and these two species also had the largest amplitude in diameter growth. A few individuals had a negative increment during certain periods (Table 1).

Differences between plots in diameter growth in individuals of all 15 species taken together were considerable (ANOVA, $p < 0.001$; plots with < 5 trees not included). Most species and individuals were fairly small, but a few were rather big (Table 1).

3.2 | Relation between tree size and diameter growth

The annual diameter increment increased with stem diameter in *Brachystegia microphylla*, *B. spiciformis*, *Julbernardia globiflora*, *Senegalia senegal* and *Vachellia nilotica* ($p < 0.05$; Figure 1a-e). *Combretum zeyheri* had a negative relation between growth rate and stem diameter (Figure 1f), which was significant in a quadratic function. For the remaining species, growth seemed to be independent of diameter, and their annual growth is best represented by their mean growth rate (Table 1).

Brachystegia microphylla occurred with big individuals in Plot 10 and small ones in Plots 13 and 14 (Table 1; Figure 1a). In line with the regressions, diameter growth was significantly higher in Plot 10 than in Plots 13 and 14 (Table 1; $t = 2.73$, $p = 0.013$). No other differences between plots in growth of individual species were found.

TABLE 1 Increment in diameter in fifteen woody species in Kondo Irangi Hills, Tanzania

3.3 | Relations between nitrogen fixation and diameter growth

We compared diameter growth rate (cm yr⁻¹) of species that potentially fix nitrogen with those that do not have this ability. In the former group, we have *Dalbergia nitidula* (0.21), *Dichrostachys cinerea* (0.25), *Senegalia senegal* (0.55), *Vachellia nilotica* (0.54), *V. seyal* (0.33) and *V. tortilis* (0.95), whereas *Brachystegia microphylla* (0.36), *B. spiciformis* (0.56), *Combretum zeyheri* (0.15) and *Julbernardia globiflora* (0.36) do not fix nitrogen. We found no difference between the groups.

3.4 | Differences between dry and wet years

We compared the mean growth of the two rainy seasons 1995/96 and 1996/97 with 1997/98. Growth for species with $n \geq 6$ was significantly higher in the wet year for *Julbernardia globiflora*, *Senegalia senegal*, *Thespesia (Azanza) garckeana*, *Vachellia nilotica* and *V. tortilis*, but not for *Dichrostachys cinerea* (Figure 2).

4 | DISCUSSION

4.1 | Growth rates

Our results substantially add to the number of diameter growth measurements in Africa and therefore need to be put into a general African context. The literature is summarised in Supporting

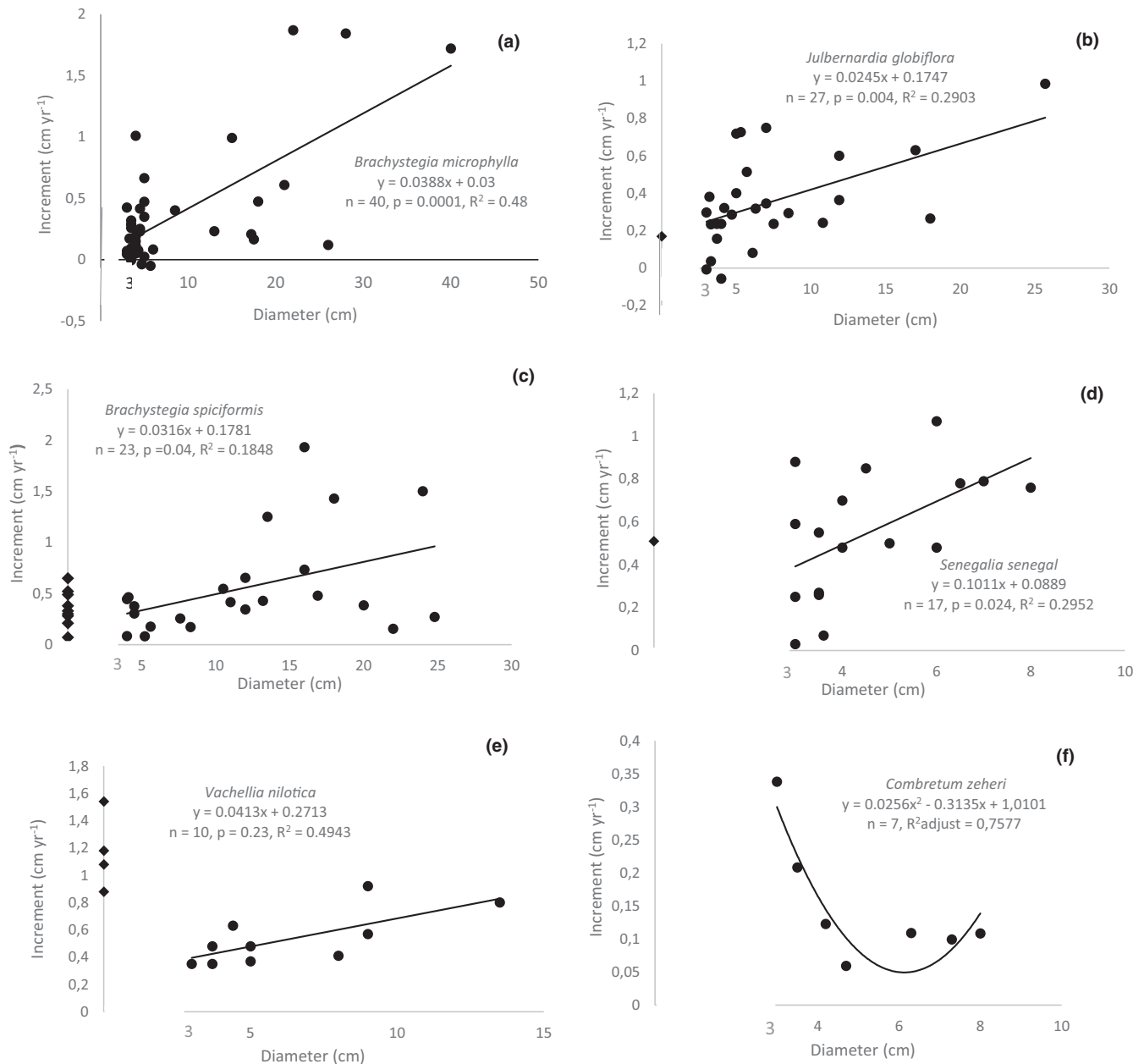


FIGURE 1 Annual diameter increment on stem diameter for six species. Points show actual values; trend line according to equation given. Symbols on the y-axis represent literature data on growth (not related to the x-axis). (a) *Brachystegia microphylla*, (b) *Julbernardia globiflora*, (c) *Brachystegia spiciformis*, (d) *Senegalia senegal*, (e) *Vachellia nilotica* and (f) *Combretum zeyheri*

information S2. Although studies on growth rates of trees in Africa are scarce (Chidumayo, 2019), we found more data than we expected, in several cases in studies not explicitly dealing with this topic. Several of the measurements in the literature were below 1.3 m (e.g. Mbow et al., 2013; Shackleton, 2002; Steenkamp et al., 2008), and in some cases, the researchers mixed, without comments, measurements at breast height and at lower height above ground (Sass-Klaassen et al., 2008; Therrell et al., 2007). According to Van Holsbeeck et al. (2016), ‘sampling ... at ... breast and stump heights were similar’.

Species and environments vary, but our results fall within the range of earlier reports. This applies both to the limited information

we have found on the species in our study and to other species in semi-arid Africa (Supporting information S2 and S3). Thus, there is nothing to indicate that the severely degraded environment in KIH has caused reduced growth. It should be emphasised that nutrient levels on the African Gondwanaland plateau are generally low and that trees are adapted to this environment. The highest mean diameter growth in our study was exhibited by *Vachellia tortilis*. It was sampled in a valley bottom close to a seasonal stream, where soil and water conditions were comparatively good.

Canopy cover in the plots varied largely (0.2%–199%; Supporting information S1). Our investigated species predominantly grew in plots with relatively high tree cover. Most studied

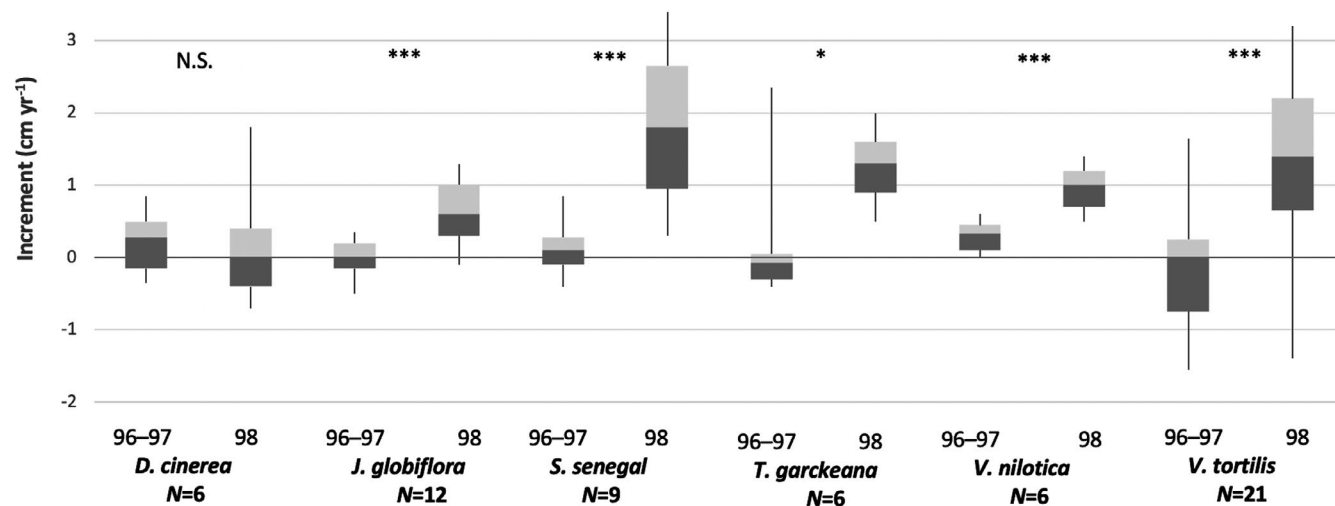


FIGURE 2 Comparison of yearly diameter growth as measured in April 1997 (mean for 1996 and 1997) and in April 1998. Boxes represent the interquartile range with the median value shown. Bars show the extreme values. Differences between the two measurements were tested by paired two-tailed t-test. *** $p < 0.01$; * $p < 0.05$; N.S. $p > 0.05$

species appeared in several plots (*Brachystegia spiciformis* and *Vachellia seyal* in 9 plots each; *Dichrostachys cinerea* and *Searsia (Rhus) natalensis* in 8 plots each). However, we failed to detect significant differences in growth rate between plots, except for *B. microphylla*.

The average diameter growth of our miombo trees (*Brachystegia microphylla*, *B. spiciformis* and *Julbernardia globiflora*) was $0.41 \pm 0.046 \text{ cm yr}^{-1}$ (all individuals of all three species together), which is within the range for regrowth of miombo trees ($0.34\text{--}0.50 \text{ cm yr}^{-1}$) given by Chidumayo (2019) from Zambia (*B. boehmii*, *Isoberlinia angolensis*, *J. globiflora* and *Uapaca kirkiana*). He found a higher growth rate in wet ($1000\text{--}1500 \text{ mm yr}^{-1}$) than in dry ($700\text{--}1000 \text{ mm yr}^{-1}$) miombo woodland. Higher parts of KIH have similar precipitation as his dry miombo woodland. Thus, the degraded state of KIH has not caused a reduction in growth compared with Chidumayo's sites.

Particularly rapid growth in several acacias based on studies of ring width was reported by Gourlay (1995) and Gourlay and Kanowski (1991) (Supporting information S2), in most cases above 1 cm yr^{-1} . Apparently, most of these trees had good water conditions.

There are several studies on growth rings in Africa (Supporting information S2). Most of these suggest that growth rings are reliably annual (e.g. Stahle et al., 1999; Therrell et al., 2007). Others disagree. Trouet et al. (2010) warn that the number of irregularities increases in old ages. Steenkamp et al. (2008) could recognise only 89% of the annual rings. Double rings (Gammadid, 1989; Gourlay, 1995; Martin & Moss, 1997) occur particularly in areas with two annual rainy seasons. Double rings, or no rings, can also occur in areas with erratic rainfall. February et al. (2006) concluded that 'without cross-dating, chronology development and precise age determination are not possible in our area'. Thus, data of this kind included in Supporting information S2 must be treated with care.

4.2 | Relation between growth rate and tree size

Brachystegia microphylla, *B. spiciformis*, *Julbernardia globiflora*, *Senegalia senegal* and *Vachellia nilotica* increased their growth rate with increasing stem diameter. Still, our results give no clear support to the hypothesis of unimodal growth. It is possible that most of our trees were too small to have reached the supposed peak, and still increased their growth rate with increasing diameter.

Combretum zeyheri, on the contrary, may have an early peak as suggested by Holdo (2006). It shows a significant negative trend in growth rate on stem diameter (significant in quadratic regression; Figure 1f). Other authors have found peaks at various diameters depending on species (Gourlay et al., 1996; Holdo, 2006; Mugasha et al., 2017). Although our study is long term, we cannot firmly refute any existing hypothesis.

Brachystegia microphylla was the only species showing a difference in growth rate between plots (Table 1). The plot with fast growth is on a traditionally protected rocky hill, where the trees obviously had not been cut. They had therefore reached a bigger stature than on the other two plots with recent establishment after protection.

4.3 | Nitrogen fixation and mycorrhiza

We hypothesised that trees with nitrogen-fixing ability would have higher growth rates than those without. The importance of nitrogen fixation for the tree itself, but also for its surroundings, is well known (e.g. Högborg, 1986; Bakhom et al., 2018; Nasto et al., 2019). Acacias have such ability (albeit variable within and among species), whereas miombo species do not. We found, however, no difference in growth rate between these groups. Högborg (1986) points out that nitrogen shortage may limit growth in non-nitrogen-fixing species, whereas shortage of phosphorus may be limiting in nitrogen

fixers. As mentioned above, there were large denuded areas in KIH up to the 1970s. It also had a general shortage of nutrients (Munkert, 2000). It is possible that the nitrogen fixers were limited by low supply of phosphorus.

4.4 | Growth and yearly variation in rainfall

Except for *Dichrostachys cinerea*, the measured diameter growth was significantly higher during the ENSO rainy season 1997/1998 than during the two preceding years with average rainfall (Figure 2). This expected result conforms to numerous other studies (e.g. Gammadid, 1989; Chidumayo, 2005; Gebrekirstos et al., 2008). The deviating result for *D. cinerea* may be due to its shrubby growth form, causing a weak reaction on precipitation in the leading stem we measured. A positive relation between growth and rainfall was found in Namibia for this species (Shikangalah et al., 2020), albeit in a drier climate. Years with extreme rainfall are not rare in KIH. Although the average precipitation in Kondoa is 652 mm, there were eight years with rainfall above 900 mm in the period 1932–1990 (Ngana, 1996). Such years appear to be important for the growth of woody plants.

A significant relation between rainfall and growth in species in miombo woodland was also found by Chidumayo (2005, 2019), and for some species, this correlation interacted with temperature. A positive correlation between diameter growth and rainfall was also found in acacias by Gourlay (1995) and Trouet et al. (2006, 2010), and for *Vachellia seyal* in the Sahel by Nicolini et al. (2010). Gourlay (1995) noted a few cases where correlation with mean minimum temperature was higher than with precipitation. Thus, if the yearly variation in rainfall is small, other factors may overshadow the effect of rainfall. The width of growth rings of *Brachystegia spiciformis* in Zimbabwe was found to depend on rainfall only in particularly wet or dry years (Grundy, 2006). Trouet et al. (2006) showed that 20 per cent of the variation in *B. spiciformis* chronology was accounted for by wet season rainfall.

A good relation between rainfall and diameter growth in *Pterocarpus angolensis* was reported by Shackleton (2002). However, the diameter growth of this species has been found to be particularly related to rainfall amounts 'during the heart of the wet season' (Stahle et al., 1999; see also Therrell et al., 2007; Trouet et al., 2010). Thus, not only amount but also distribution in time of rainfall appears to be important.

5 | IMPLICATIONS FOR RESTORATION

Interrelations between agriculture, livestock production and other forest use, as well as their consequences for nutrient conditions and erosion, are complex, not the least in KIH, where soils are eroded and nutrient-deficient. Restoration activities by HADO in the 1970s included, for example planting of fast-growing trees, particularly *Eucalyptus* spp. and *Grevillea robusta*. Decisions were taken without local involvement. Ca. 2000 ha were set aside for timber and

fuelwood, even amidst people's fields. A variety of tree seedlings were also produced for the rural people, for example fruit trees and for wood lots. Measures to improve infiltration and to slow down erosion were also taken (Mbegu & Mlengi, 1984). Burning of vegetation and cutting of trees were banned. These measures, although well motivated from a technical restoration viewpoint, were never accepted by the local people and conflicted with traditional land use and soil conservation (Östberg, 1995).

Planting of fast-growing trees may modify species assemblages in the natural vegetation, thereby affecting rural people's subsistence (Fleischman et al., 2020). Many reports confirm changes in tree cover following heavy grazing as well as grazing restrictions in semi-arid Africa, for example Kebrom Tekle (2001), O'Connor et al. (2014) and Demel Teketay et al. (2018). In the late 1970s, it was decided in the HADO project to abandon the planting of trees and leave the area for free development as it was considered too marginal for costly intensive management. In 1979, all livestock were evicted (Mungo'ng'o, 1995). This approach had positive effects on the natural environment with improved grass and tree cover (Mbegu & Mlengi, 1984). However, the restrictions of land use were enforced from above and unpopular among cattle owners. The ban on grazing was never fully adhered to.

When research in KIH started in 1991, KIH had already changed from a partly denuded erosion surface to a mostly well-vegetated landscape. However, species such as *Harpachne schimperii* and *Melinis repens* showed that it was still in an early stage of succession. The late successional *Themeda triandra* was rare. Woody vegetation cover increased with time in most of our sites. In the late 1990s, cattle once again entered KIH on a large scale, although still illegal (Kangalawe et al., 2008). In 2010, grazing was widespread and in practice uncontrolled.

Individual growth of indigenous, self-sown or re-sprouting trees was on a normal level for African semi-arid land even in this severely degraded area. Generally, trees can regenerate naturally even on quite degraded land (Fleischman et al., 2020). Our most severely eroded sites, however, improved far less and may be too marginal to motivate active measures. The seed bank in KIH has generally lacked woody species (Lyaru & Backéus, 1999), suggesting seed dispersal as a limiting factor.

Shortage of nitrogen will eventually be reduced through natural processes such as nitrogen-fixing plants and soil crusts (Aranibar et al., 2003; Dalton et al., 2004; Högberg, 1986). Regeneration outcome is affected by a great variety of interacting species, anthropogenic practices and environmental heterogeneity. Although tree planting may be undertaken in suitable areas, natural succession seems as a viable alternative to tree planting for heavily disturbed landscapes as long as there are remnants left of original vegetation.

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CONFLICT OF INTEREST

None.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in <https://doi.org/10.5878/5s6y-wv36>.

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