Disturbance impacts on the persistence niche of key species in the *Baikiaea–Guibourtia–Pterocarpus* woodlands of north-western Zimbabwe

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The persistence niche (studied through different modes regeneration) of three key species (Baikiaea plurijuga (Harms), Guibourtia coleosperma (Benth.) J. Leonard and Pterocarpus angolensis) (DC) under five different disturbance regimes (eight years after cessation of disturbance) was studied in the Baikiaea-Guibourtia-Pterocarpus woodlands of north-western Zimbabwe. The disturbance regimes were: protected area (no disturbance); timber concession area (timber harvesting); pole and firewood harvesting sites; abandoned crop fields (after clearing for agriculture); and burnt sites (fire disturbance). Influence of stump diameter and height on regeneration factors was investigated. For each disturbance regime, six main plots (100 m × 100 m) each were systematically laid out (20 m apart) to assess regeneration. In each main plot, 10 m wide transects (5 m apart) were surveyed for seedlings and saplings of the target species (at least 100 plants of each species), resulting in 7 transects per main plot, 42 transects in each study site and 210 transects in total. Number of seedlings with or without a rootstock (i.e., just grown from seed) was recorded. Diameter of stumps was measured at the cut surface. Shoot height was measured from their origin. Each target species was associated with mode of regeneration ($\chi^2 = 27$ 642, P < 0.001). Most plants regenerated from root suckers. Regeneration mode is dependent on disturbance regime (*B. plurijuga* γ^2 = 225.66, *p* < 0.001; *G. coleosperma* γ^2 = 158.62, p < 0.001; and *P. angolensis* $\chi^2 = 144.01$, p < 0.001). Stump diameter negatively influenced number of sprouts for *B.* plurijuga and P. angolensis, but positively influenced sprout height for all species. Stump height positively influenced sprout height for G. coleosperma and P. angolensis. The study therefore concludes that disturbances are necessary in facilitating sprouting and growth of suppressed shoots. Stump height and diameter influence the ability of stumps to regrow vegetatively through sprouting. Weak relationships between stump diameter/height and coppice density and shoot height suggest that there are other factors that affect vegetative regrowth through coppicing.

Keywords: coppicing, disturbance, recruitment, sprouting

Introduction

What can we do to improve the regeneration and population status of key species in indigenous woodland ecosystems where no silvicultural management systems are applied? In these ecosystems, we rely on natural regeneration (renewal of a tree crop by self-sown seed or vegetative regrowth) which may fail in some seasons. No silvicultural interventions are applied to enhance the growth of regenerated plants. We need adequate regeneration because the future of forest and woodland ecosystems and sustainable resource use are dependent on successful regeneration of key species. It is therefore important to assess the response (regeneration and growth) of key individual species so as to ascertain how the species persist in situ under different disturbance factors. Baikiaea plurijuga, Guibourtia coleosperma and Pterocarpus angolensis are the most harvested species in the Baikiaea–Guibourtia–Pterocarpus woodlands in north-western Zimbabwe (Chigwerewe 1996; JAFTA & Forestry Commission 2001). Therefore forest managers, harvesting

foresters and harvesting crews need to understand the most appropriate land management practices that prompt optimal regeneration of each species. The common mechanisms of regeneration of different species in the woodlands include advance regeneration (seedling banks); current-year seedlings; seedling sprouts that occur after seedling shoot dieback (including sprouts from underground rootstocks); coppice or sprouts from stumps of mature trees; and root suckers that arise from lateral roots (Timberlake et al. 2010).

Concerns have been raised over the future availability and possible extinction of some species, for example, *P. angolensis*, in Zimbabwe (Bradley & Dewees 1993; Clarke et al. 1996). Woodcarvers in South Africa indicated that *P. angolensis* is becoming rare (Steenkamp 1999). Also, low seedling recruitment rates during both germination and the suffrutex stage (Boaler 1966; Schwartz et al. 2002; Caro et al. 2005) and unsustainable harvesting rates (Schwartz et al. 2002; Caro et al. 2005) further threaten species populations. *B. plurijuga* regenerates adequately (Chigwerewe 1996; Gambiza 2001; Dube 2005). The species has taken over the woodlands after policy changed from controlled burning to total protection (Geldenhuys 2009). Vegetation changed from domination by *P. angolensis* to dense regeneration of *B. plurijuga. G. coleosperma* regenerates and grows slowly (Lemmens et al. 2008; Heita et al. 2019; Nott 2020).

Different disturbances influence regeneration, recruitment and persistence of individual species differently and treating them similarly might have adverse implications on the regeneration and recruitment of some species. The ability to sprout after severe injury from disturbances such as herbivory, fire, floods, logging or drought is vital, especially for the Baikiaea-Guibourtia-Pterocarpus woodland species which are subjected to frequent disturbances (Mudekwe 2007). Seedlings and sprouts face frequent and severe fire damage that can retard their recruitment into the tree layer. Between fires, seeds have to germinate and build enough root reserves to survive the next fire. However, given that fires usually occur frequently (Scholes and Walker 1993), sprouts would need to grow rapidly to escape damage. Lamont et al. (2011) highlighted that there are two ecomorphological properties required for successful resprouting after fire: presence of buds or pre-bud meristems; and the buds should be located in plant parts that are sufficiently insulated to escape death from the heat of fire. On cleared and abandoned land, regeneration often takes place but the speed of woodland recovery depends on the clearing methods used, sources available for regeneration and site history (type, frequency and intensity of stress and/ or disturbance) (Geldenhuys & Golding 2008). Furthermore, studies on regeneration of woodlands of north-western Zimbabwe concluded that competition for moisture and light from undergrowth makes survival beyond the first dry season very low (Calvert 1986). Moreover, the current utilisation of the woodlands ignores the natural disturbance-recovery processes of key species and their adaptation to survive these processes (Geldenhuvs 2009).

Regeneration in forest and woodland trees occurs through either sexual (reproductive) or vegetative means (Timberlake et al. 2010). Reproductive regeneration is the primary mode of regeneration which transfers the variation in genetic pools, resulting from reproductive processes of pollination (Wood 1986), seed dispersal, germination, seedling establishment and their recruitment into the tree phase. Vegetative regeneration is the secondary regeneration mode that developed as an adaptive response to damage or stress resulting from frequent fires, frost and browsing hence allowing the plants to persist in the ecosystems. Vegetative regeneration occurs through sprouting or resprouting (root suckers or stem suckers), with sprouting shoots developing into the tree phase from pre-existing trees damaged by fire, browsing, cutting, etc. (Timberlake et al. 2010). Such vegetative regeneration maintains the genetic pool of the parent plants (Wood 1986).

Many studies have investigated the regeneration of *B. plurijuga* (Calvert and Timberlake 1993; Gambiza 2001; Dube 2005) and of *P. angolensis* (Boaler 1966; Van Daalen 1991; Schwartz et al. 2002; Caro et al. 2005; Ncube and Mufandaedza 2013) after disturbances such as fire and logging. However, few studies have investigated the

regeneration of G. coleosperma (Lemmens et al. 2008) and other disturbance factors (clearing for agriculture and harvesting for poles and firewood) have not been considered. No study has investigated how disturbances hinder or promote regeneration of key species in the woodlands under different disturbance regimes. Such studies have been done in the Miombo woodlands of Zambia (Svampungani et al. 2010). Gambiza (2001) investigated the influence of fire, logging and herbivory on the growth of B. plurijuga while Dube (2005) only focused on the effects of logging at different periods on the growth and regeneration of *B. plurijuga*. Ncube and Mufandaedza (2013) studied the effects of fire on coppice shoot production and growth of B. plurijuga and P. angolensis. Chichinye et al. (2019) studied how different disturbance factors influence the composition and diversity of Baikiaea-Guibourtia-Ptercopus woodland species. It is therefore necessary to assess and analyse the regeneration mechanisms/modes that are set in motion in response to each type of disturbance.

Satisfactory regeneration of dominant species forms the backbone for sustainable forest management. The best harvesting techniques and management practices in the post-harvest area are those that promote regeneration and persistence of the harvested species. For example, adhering to optimum diameter classes within which particular species have high coppicing effectiveness would provide for enhanced coppicing ability for many woodland species. This study investigated how different disturbances, specifically timber harvesting, pole and fuel-wood harvesting, crop cultivation and burning influence the regeneration of the most harvested species (*B. plurijuga, G. coleosperma* and *P. angolensis*) in the woodlands (Chigwerewe 1996).

The following questions guided data collection and analysis:

- Under which form of regeneration does each key species perform best?
- How do the number of sprouts and sprout height vary amongst different regeneration modes, under different disturbance regimes?
- How does stump diameter (small to large) influence the number of sprouts and sprout height development for each of the key species?

Limitations of the study

The study was self-funded and hence other important variables (edaphic factors and moisture content) affecting regeneration of trees in the woodlands could not be investigated

Materials and methods

Description of study area

The study was conducted in the Gwaai and Tsholotsho *Baikiaea–Guibourtia–Pterocarpus* indigenous woodlands of north-western Zimbabwe (Figure 1). Gwaai forest (19°16′20″S and 27°56′36″ E) and Tsholotsho (19°46′00″S and 27°45′00″E) (JAFTA & Forestry Commission 2001) are both located in the Matabeleland North Province at an altitude ranging between 1 010 m and 1 055 m.

Kalahari sands (uniform, both physically and chemically) cover the bulk of the study area. They belong to the Regosol

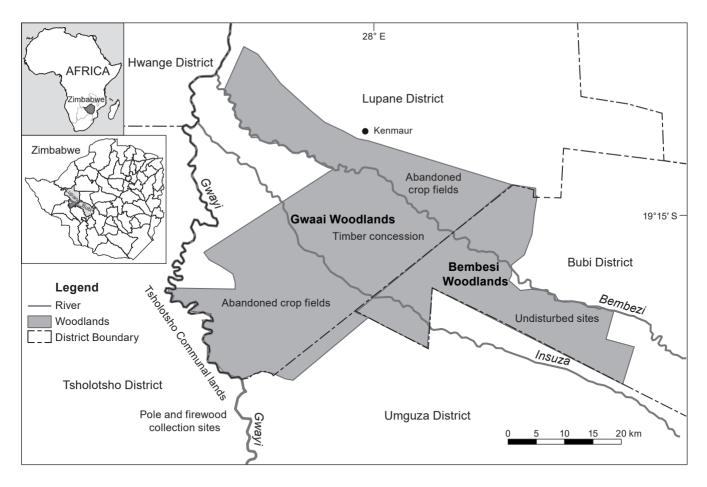


Figure 1: Location of the study area in Matabeleland North, Zimbabwe

group in the amorphic soil order (Nyamapfene 1991, as cited by Gambiza 2001). The underlying geology is of sedimentary rocks overlying Karoo basalt and sedimentary deposits (JAFTA & Forestry Commission 2001).

The short and erratic wet season is usually characterised by dry spells and sporadic droughts (Nemarundwe and Mbedzi 1999). Mean annual temperature is 21.5°C, with mean monthly temperature ranging from 15°C (June to September) to 25°C (October to December) (Nyamapfene 1991; JAFTA & Forestry Commission 2001). Ground frosts are experienced especially in the valleys in most years between May and September (JAFTA & Forestry Commission 2001).

The area is characterised by six main vegetation types (JAFTA & Forestry Commission 2001; Chichinye et al. 2019, 2020): open to closed *Baikiaea–Guibourtia–Pterocarpus* (Fabaceae) woodland occurs on the Kalahari sands; *Brachystegia* (Fabaceae) woodland occurs along the upper Bembesi river (shallower soils with more silt); *Colophospermum mopane* (Kirk ex Benth.) J Leonard woodland, dominated by either stunted or multi-stemmed *C. mopane* trees, occurs along rivers or river valleys on poorly drained and highly erodible alluvial soils; Vleis (a grassy or marshy wetland, mostly covered by water during the rainy season) are dominated by a single layer of grasses, with isolated trees occurring along vlei fringes; belts of *P. angolensis* (in association with *Burkea africana* Hook) occur as localised stands inside the *Baikiaea–Guibourtia–Pterocarpus*

woodland; and *G. coleosperma* woodland, characterised by the dominance of *G. coleosperma* and scattered *B. plurijuga* trees, occurs on the Kalahari sands.

Methodology

Sampling design and data collection

Five disturbance types (protected woodland, timber concession area, pole and firewood collection sites, abandoned crop fields and burnt sites) were selected for study. In each disturbance type, early development Stage 2 sites (i.e. where height was 2.1-5 m) of 8 years old (age since disturbance cessation) were identified (except in protected areas that only had mature stands). At each utilisation site, six main plots of 100 m × 100 m each (20 m apart; a total of 30 plots) were systematically laid for the assessment of regeneration. The distance between the main plots meant that the plots could be treated as independent samples (Geldenhuys and Van der Merwe 1988; Sullivan et al. 1995). The plots had no touching edges (as in Wong et al. 2001). In each main plot, 10 m-wide transects (5 m apart), were surveyed for seedlings and saplings of the target species, resulting in 7 transects per main plot, 42 transects in each study site and a total of 210 transects. At least 100 plants of each target species (B. plurijuga, G. coleosperma and P. angolensis) were sampled. The identified seedlings and saplings were excavated to record

the origin of the sprouts, that is, from seed (regeneration from seedlings), root (root sprout), swollen underground rootstocks (rootstock sprouts/root suckers), above ground at the base of the cut stem (basal sprouts) or from up the stem/trunk (stem sprouts). The numbers of sprouts and height of tallest sprout on each identified plant were recorded. Diameter of the identified stumps was measured at the cut surface. The height of sprouts was measured from the origin at the base.

Data analysis

Correspondence analysis in SPSS version 21 was performed to assess the mode of regeneration associated with each utilisation system. The chi-square test was used to test mode of regeneration associated with each of the target species. Differences in proportions were also tested using a *Z* test followed by a Bonferroni test. Differences in the number of sprouts and sprout height amongst regeneration modes were tested using one-way analysis of variance (ANOVA) at 5% level of significance. *Post hoc* analysis for variables with significant differences was carried out using Tukey's honestly significant difference (HSD). Regression analysis was performed to establish the relationship between different plant attributes (stump diameter and height, and number of sprouts and sprout height).

Results

Mode of regeneration for the three key species

The key species regenerated through four modes of regeneration: regeneration from seedlings, stem sprouts, rootstock sprouts and basal sprouts (Figure 2). Results showed a significant association between species and mode of regeneration ($\chi^2 = 27.64$, p < 0.001). Fewer than 10% of plants for each species regenerated from seedlings (Figure 2). Regeneration from stem sprouts was also low for the three species: 15%, 14% and 11% for *B. plurijuga*, *G. coleosperma* and *P. angolensis* respectively.

Seedling regeneration is located far from *B. plurijuga* and *G. coleosperma* in ordination space, suggesting that regeneration from seedlings is low for the species. The χ^2 test results showed that regeneration mode of the three target species is dependent on disturbance regime (*B. plurijuga*: $\chi^2 = 225.66$, p < 0.001; *G. coleosperma*: $\chi^2 = 158.62$, p < 0.001; and *P. angolensis*: $\chi^2 = 144.01$, p < 0.001). *B. plurijuga* regenerated in all disturbance regimes. The three species mostly regenerated from root suckers as compared to other modes of regeneration (Figure 3). As expected, basal sprouts were not recorded in the undisturbed sites.

Influence of mode of regeneration on number of sprouts and sprout height of targeted species

Different modes of regeneration showed significant differences in sprout density for the three species (p < 0.001) (Table 1). More sprouts were produced when the three species regenerated through root suckers and basal sprouts. The number of sprouts for the three species was statistically different when the species regenerated through basal sprouting. Different modes of regeneration showed significant differences in sprout height for *B. plurijuga* and *G. coleosperma* (p < 0.001) (Table 1) but not for *P. angolensis*. The tallest sprouts were produced when the species regenerated through root suckers. Significant

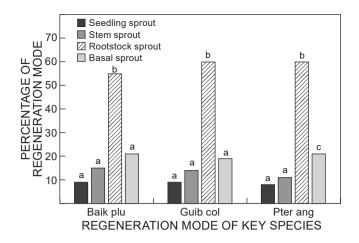


Figure 2: Percentage of total number of sprouts originating from (seedlings, stem or trunk = stem sprouts; rootstock = rootstock sprouts; and cut or damaged stumps = basal sprouts) for the key species (Baik plu = *Baikiaea plurijuga*; Guib col = *Guibourtia coleosperma*; and Pter ang = *Pterocarpus angolensis*)

differences in sprout height occurred when plants regenerated through seedlings, stem sprouting and basal sprouting for the three species studied. When regeneration occurred through root suckers, differences were not significant. *P. angolensis* produced the tallest shoots among the three species.

Influence of stump diameter and stump height on shoot parameters

Stump diameter has a significant negative influence on number of sprouts for *B. plurijuga* (p < 0.05) and an insignificant negative influence on *P. angolensis* (p > 0.05) (Figure 4). As stump diameter increases, the number of sprouts decreases, meaning that bigger stumps produce fewer sprouts in B. plurijuga and P. angolesis. The opposite is true for G. coleosperma where a significant positive relationship was shown (p < 0.05). Most sprouts are produced in the 5-20 cm dbh class. As stump diameter increases, sprout height also increases for the three species (p < 0.05) (Figure 4). Tallest sprouts are produced in the 5-25 cm dbh class for B. plurijuga and G. coleosperma, and 7-15 cm dbh class for P. angolensis. Weak positive correlations exist between stump diameter/stump height and different shoot parameters as shown by low R²-values. Stump height has a significant negative influence on number of sprouts for B. plurijuga and a positive significant influence on G. coleosperma (p < 0.05). An insignificant influence was shown on both parameters for *P. angolensis* (p > 0.05). Generally tall stumps produce fewer and shorter sprouts (Figure 5). High sprout numbers and tall coppices were shown on stumps of 5-20 cm height classes except for B. plurijuga (5-30 cm class).

Discussion

Mode of regeneration in each land use system and each targeted species

Piearce (1993) highlighted that the primary establishment of *Baikiaea–Guibourtia–Pterocarpus* woodland species is mainly from seed and thereafter the species maintain their populations by displaying vegetative regrowth from sprouting,

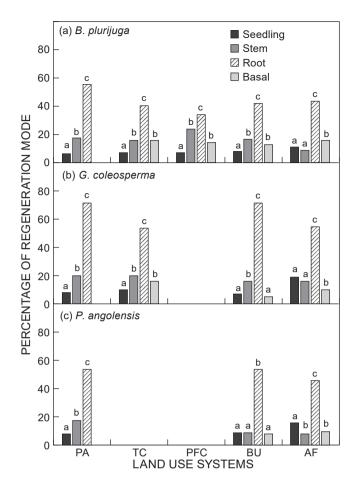


Figure 3: Modes of regeneration for the targeted species (*B. plurijuga, G. coleosperma* and *P. angolensis*) under each disturbance regime (PA = protected area; TC = timber concession area; PFC = pole and firewood collection sites; AF = abandoned crop fields; and BU = burnt areas). Each superscript (a, b, c) denotes a subset of regeneration mode categories whose column proportions do not differ significantly from each other at 5% level of significance

from roots, rootstock, stem or trunk or cut stumps. Sprouting therefore allows a species to persist in areas with a wide range of disturbances (Bond and Midgley 2001) and in areas with low seedling establishment (Vesk and Westoby 2004; Lamont et al. 2011). Regeneration by seedlings is therefore minor in relation to the vegetative regrowth modes (secondary mode of regeneration) that dominate the dynamics of these woodlands. Seedling germination may be good but subsequent survival can be very poor as a result of several factors affecting the growth of the seedlings. Tybrik (1991) concluded that fire, drought and browsing are the major constraints on survival of natural regeneration. Such disturbance factors restrict the recruitment of seedlings into tree stages. This might explain the low levels of regeneration from seedling in all disturbance regimes. Frequent fires would therefore result in death of seedlings and saplings and hence restrict seedling regeneration. In some cases dwarf vegetation (gullivers) may develop, as the seedlings cannot be recruited to the next height classes. The plants would develop underground rootstock storage systems through which they persist as

suppressed vegetation. When the area was cleared - by devastating fires, cropping or clearing of poles and firewood the rootstocks would sprout to produce fast-growing shoots. This might explain why heavily disturbed sites (pole and firewood collection sites, abandoned crop fields and burnt sites) had many root suckers. This mode of regeneration was also prominent in undisturbed and timber concession areas because of the considerable number of trees with large diameters. These trees can support rootstocks that are large enough to support sprouting in the undisturbed areas where there is no timber harvesting and in timber concession areas where the single tree selection harvesting system allows for some big trees to remain after harvesting operations so that they grow to harvestable sizes (Calvert and Timberlake 1993). The big trees in these sites also provide seeds for natural regeneration but, because of the shade from their canopy. there is reduced light penetration to the ground, reducing seed germination and shoot growth (Geldenhuys and Golding 2008). The shoots growing under the canopy of big trees may remain suppressed for years: their growth would increase when the canopy is opened through disturbances. Trees, shrubs and herbaceous plants may compete with delicate tree seedlings and shoots for sunlight and moisture (Jeffries 1997). Basal sprouting was evident in all disturbance regimes except the protected area because no cutting of trees is permitted in these areas. However, rootstock sprouting was high because of the extensive rooting system from large trees in undisturbed sites. Vegetative regrowth through sprouting from various means has therefore become an adaptation through which the indigenous species persist in the woodlands.

In this study, P. angolensis regenerated mainly from root suckers in the protected areas, burnt areas and abandoned crop fields. Low rates of germination, annual dieback of seedlings, competition from other trees over sunlight, effects of fire, slow rates of tree growth and delayed seed production have been reported to contribute to poor regeneration in P. angolensis (Van Daalen 1991). Low seedling recruitment rates during both germination and the suffrutex stage have been reported for P. angolensis (Boaler 1966; Schwartz et al. 2002; Caro et al. 2005). Caro et al. (2005) highlighted that seedling mortality was as a result of fire and high densities of browsing ungulates. In this study, the species only regenerated in the undisturbed sites, burnt sites and abandoned crop fields through rootstock sprouting. However, shoots produced in the undisturbed sites grow much slower than those that grow in the cleared areas. The observations in this study are consistent with those from other studies that concluded that the species regenerates and grows well in cleared areas (Graz 1996; Syampungani 2008) and burnt areas (Geldenhuvs 1977: Chidumavo 1988: Geldenhuvs 2009; Fillemon 2015). Exposure to light, and reduced competition for moisture and nutrients may contribute to the good performance of this species in opened up areas such as in abandoned crop fields and pole and firewood collection (Syampungani 2008). Occasional fires have been found to maintain good regeneration of P. angolensis (Geldenhuys 1977; Chidumayo 1988). However, repeated fires would result in death of seedlings if the intensity of the fire is high, and if dwarf seedlings and coppices are produced from stumps that are repeatedly burnt by fires. This can be attributed to the fact that P. angolensis has a lengthy suffrutex stage of

Table 1: Shoot attributes for sample plots across different regeneration modes (mean \pm standard error) and significance levels from one-way ANOVA with unequal sample size tests. Significance values are indicated in bold. Values with different superscript letters (a, b, c) within rows differ significantly and values with different superscript letters (A, B, C) within columns differ significantly (Tukey's HSD; P < 0.05). Regeneration modes are: SS = seedling regeneration; StS = stem sprouts; RS = rootstock sprouts; BS = basal sprouts)

Species	Regeneration mode				
	SR	StS	RS	BS	P value
	·	Sprout dens	sity (stems/ha)		
Baikiaea plurijuga	1.00 ± 0.0 ^{cA}	1.79 ± 0.1 ^{bA}	2.25 ± 0.0^{aA}	2.03 ± 0.1^{abA}	0.001
Guibuortia coleosperma	1.00 ± 0.0^{bA}	2.06 ± 0.2^{aA}	2.44 ± 0.1^{aAB}	2.28 ± 0.1 ^{aAB}	0.001
Pterocarpus angolensis	1.00 ± 0.0 ^{cA}	1.84 ± 0.4 ^{bA}	2.58 ± 0.1 ^{aB}	2.59 ± 0.1 ^{aB}	0.001
<i>P</i> value	0.05	0.44	0.05	0.001	
		Sprout	height (m)		
Baikiaea plurijuga	1.25 ± 0.0^{bdA}	1.34 ± 0.3^{bCA}	1.64 ± 0.0^{aA}	1.33 ± 0.0 ^{bA}	0.001
Guibuortia coleosperma	1.18 ± 0.1^{bdA}	1.20 ± 0.0^{bcB}	1.64 ± 0.0 ^{aA}	1.32 ± 0.1 ^{bA}	0.001
Pterocarpus angolensis	1.67 ± 0.1 ^{aB}	1.53 ± 0.1 ^{aC}	1.51 ± 0.1 ^{aA}	1.91 ± 0.21 ^{aB}	0.05
<i>P</i> value	0.001	0.001	0.07	0.001	

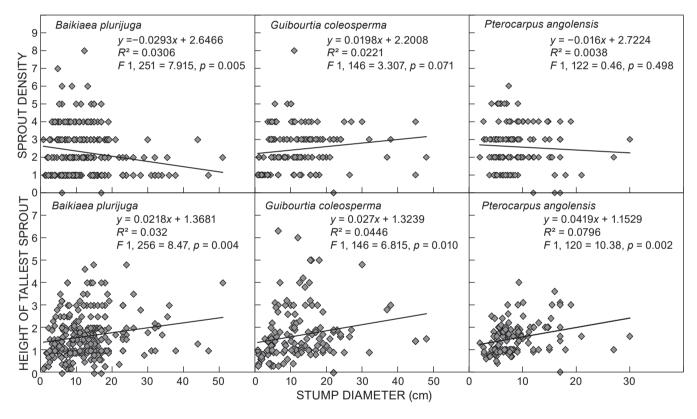


Figure 4: Influence of stump diameter on sprout density and sprout height for the three key species

about 10 years or more (Boaler 1966; Piearce 1993). During this stage, the leading shoot of seedling dies back annually, whilst the root system develops massively until it has sufficient vigour to support a permanent stem. This form of regeneration is commonly undervalued (Piearce 1993). Dieback may be triggered by water stress, fire, drought and browsing. Mortality has been shown to be high in natural regeneration of *P. angolensis* for which up to 96% of seedlings may die before succeeding the suffrutex stage (Vermeulen 1990). This would reduce or delay recruitment of seedlings to higher size classes as a result of mortality due to several factors such as fire and heavy browsing by animals (Caro et al. 2005). Influence of stump diameter on regeneration attributes Most dry forest species are able to regenerate vegetatively as reported in the South African savannah (Shackleton 2000; Kaschula et al. 2005); the Miombo ecoregion (Luoga et al. 2002; Chirwa et al. 2014); the Sudanian savanna–woodlands of West Africa (Ky-Dembele et al. 2007; Dayamba et al. 2011); and the Zambezi teak woodlands in Zimbabwe (Gambiza 2001; Dube 2005; Ncube and Mufandaedza 2013) because most tropical dry forest species generally have extensive vertical and horizontal root systems that facilitate recuperation after cutting (Mistry 2000). The number of sprouts decreased with increase in stump diameter for *B. plurijuga* and *P. angolensis*.

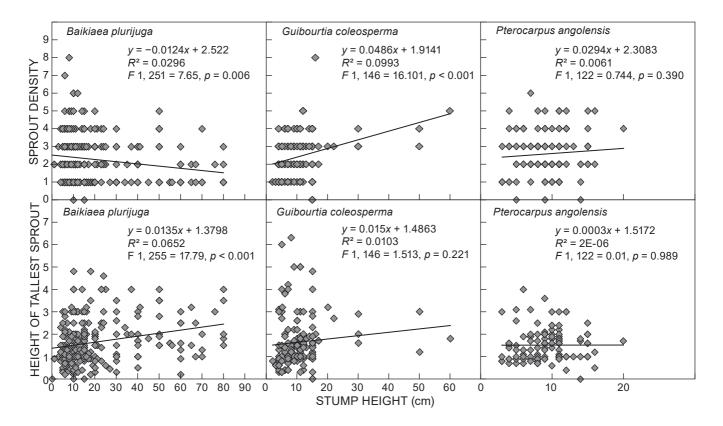


Figure 5: Influence of stump height on sprout density and height for the three key species

The number of sprouts per stump increased with increasing stump diameter for G. coleosperma. Sprouting is influenced by the amount of food reserves accumulated in the stump, and/ or the activity of underground buds, which in turn depends on stump diameter. Miura and Yamamoto (2003) and Knox and Clarke (2005) showed that larger stumps have much more food reserves and more extensive rooting systems, resulting in the production of more sprouts. Our study showed that the highest number of coppices was produced for stumps that had a diameter of between 10 and 20 cm and the number decreased as the stumps increased in diameter. This is in agreement with observations by Ncube and Mufandaedza (2013) in the same woodland type who found that the 10 to 20 cm stump diameter classes produced more sprouts. Hawley (1949) stated that the sprouting ability of trees decreases as they become older and larger in diameter. Kramer and Kozlowsky (1960) suggested that this could be because the number of sprouts per stump increases with diameter until the increase in bark thickness begins to hinder the emergence of dormant buds. Aaron (1956) revealed that cutting smaller trees induces the formation of adventitious buds that lead to the emergence of many small sprouts on the edges of the stumps. However, sprouts originating from adventitious buds are usually of poor quality and thus are not a reliable method of regenerating a forest stand (Evans 1992). In addition, many sprouts on a stump can reduce shoot vigour due to competition among shoots in a given stump (Khan and Tripathi 1989). This would therefore call for silvicultural interventions by forest managers, to thin coppicing stumps so that only those shoots with more vigour are left to develop on each stump. This ensures that resources

are not wasted on the shoots with less vigour. Although bigger diameters have a lower number of sprouts, they are preferred because in any case more sprouts self-thin themselves leaving one or two sprouts that will grow to become utilisable (Handavu et al. 2011). Coppice and sucker regrowth is, however, usually inferior (Chidumayo 1992). Most of the indigenous species growing in the woodlands are sun loving therefore the plants that regenerate in the patches created by disturbances would result in even aged stands; some trees, however, will grow faster than the others. During harvesting operations, the bigger stems would be selected for harvesting and the suppressed ones would be left behind to grow to harvestable sizes. Gonah (1994) pointed out that the current lower utilisable limit for the key species was 25 cm. Cutting more trees using the group felling system instead of single tree selection would enable the stems to sprout vigorously and grow faster as a result of better light conditions after the opening of the canopy.

A positive relationship between stump height and number of sprouts was also found for *G. coleosperma and P. angolensis*, which is consistent with the findings from several studies in the tropics and subtropics (Mishara et al. 2003). Within the Southern African savannahs, several studies reported the influence of stump height on resprouting ability of the Zimbabwean Miombo (Mushove and Makoni 1993) and South African (Shackleton 2001) and Zambian (Handavu et al. 2011) Miombo woodlands. The effect of stump height can be attributed to availability of more reserved food and dormant buds on longer stumps. Stump height influences the number of buds that will form on a stump. Stump surface area for sprout development increases with increasing cutting height (Huang 1990). Results from

our study are consistent with observations made by Ncube and Mufandaedza (2013) who concluded that the number of coppices decreases with an increase in stump height for *B*. plurijuga. Number of coppices and tallest sprouts were high for stumps that were between 10 and 20 cm high. The current stump height recommended by the Forestry Commission is 15 cm. Cutting too low on the stem of the tree may encourage fungal infection because of moisture from the ground or stump decay (Shackleton 2000). However, Shackleton (2001) cautioned that the positive effects of increased cutting height must be balanced against the loss of useful woody biomass that is left behind and also the low quality of coppices that results. The coppices that sprout on tall stumps are prone to wind and bird breakage (Gambiza 2001). These coppices form a bushy appearance and would not be commercially utilisable (Canadell and López-Soria 1991). The small branches that develop from these coppices are less vigorous and therefore produce fewer seeds, making them even more useless for regeneration (Chidumayo 1992). However, Kays and Canham (1991) suggest that it is the combination of all these factors that has a significant influence on the coppice shoot production. These authors state that the most vigorous sprouts arise from relatively young stumps cut close to the ground in late fall or winter when there are food reserves stored in the roots. As such, it is necessary to consider all the important factors to improve coppice shoot production key species in the woodlands.

Conclusion

Baikiaea-Guibourtia-Pterocarpus woodlands regenerate mostly from root suckers as compared to basal sprouts, seedling regeneration and stem sprouts in all disturbance regimes studied. We conclude that disturbances that cause the canopy to open and more light to penetrate to the forest floor are required to facilitate sprouting and growth of suppressed shoots in these woodlands. Weak relationships between stump diameter/stump height and sprout density suggest that there are other factors (external factors and practical management measures, such as cutting season, cutting method, site quality, rotation length and the density and spacing of the stumps) affecting successful vegetative regrowth of stumps. There is a need to maintain the 15 cm stump height, to reduce timber wastage and to allow adequate regeneration. We therefore conclude that different disturbances and regeneration from root suckers as compared to other modes of regeneration are important for the persistence of the key species in the woodlands. Therefore forest managers need to adopt disturbance regimes that promote regeneration of at least key species in the woodlands.

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References

Aaron I. 1956. Dormant and adventitious buds. Science 104: 329.

- Boaler SB. 1966. *The ecology of* Pterocarpus angolensis *D.C. in Tanzania*. London: Her Majesty's Stationery Office.
- Bradley PN, Dewees P. 1993. Indigenous woodlands, agricultural production and household economy in the communal areas. In Bradley PN, McNamara K (eds), *Living with Trees: Policies for Forest Management in Zimbabwe*. World Bank Technical Paper Number 210. The World Bank, Washington, DC. pp 63–153.
- Bond WJ, Midgley JJ. 2001. Ecology of sprouting in woody plants: The persistence niche. *Trends in Ecology and Evolution* 16: 45–51
- Calvert GM. 1986. The ecology and management of the Kalahari sand forest vegetation of south-western Zimbabwe. In: Pierce GD (ed.), *The Zambezi teak Forests. Proceedings of the first national conference on the teak forests of Southern Africa, March 1984, Livingstone, Zambia.*
- Calvert GM, Timberlake JR. 1993. Burning trials in *Baikiaea* woodland, Gwayi Forest, Zimbabwe'. In Piearce GD, Gumbo DJ. (eds.), *The Ecology and Management of Indigenous Forests in Southern Africa*. Proceedings of an international symposium, 27–29 July 1992, Victoria Falls, Zimbabwe. Harare, Zimbabwe: Forestry Commission and SAREC. pp 347–365.
- Canadell J, Lloret F, López-Soria L. 1991. Resprouting vigour of two Mediterranean schrub species after experimental fire treatments. *Vegetatio* 95: 119–126.
- Caro TM, Sungula M, Schwartz MW, Bella EM. 2005. Recruitment of *P. angolensis* in the wild. *Forest Ecology and Management Journal* 219: 169–179.
- Chichinye A, Geldenhuys CJ, Chirwa PW. 2019. Land-use impacts on the composition and diversity of the Baikiaea–Guibourtia– Pterocarpus woodlands of north-western Zimbabwe. *Southern Forests: a Journal of Forest Science* 81: 151–165.
- Chichinye A, Geldenhuys CJ, Chirwa PW. 2020. Analysis of growth rings to determine age and mean radial growth of selected Baikiaea–Guibourtia–Pterocarpus species from regrowth stands after pole/firewood harvesting and abandoned crop fields, north-western Zimbabwe. *Journal of Ecology and The Natural Environment* 12: 129–139.
- Chidumayo EN. 1988. A re-assessment of effects of fire on Miombo regeneration in the Zambian Copperbelt. *Journal of Tropical Ecology* 4(4): 361–372.
- Chidumayo EN. 1992. Effects of shoot mortality on the early development of *Afzelia quanzensis* seedlings. *Journal of Applied Ecology* 29: 14–20.
- Chigwerewe SK. 1996. The ecology and management potentials of naturally regenerated Teak forests of the Kalahari-Namib sandstone formations in Zimbabwe. In: Mushove PT, Shumba EM, Matose F (eds), *Sustainable management of indigenous forest in the dry tropics*. Proceedings of an International Conference, ZFC & SAREC-SIDA, 28 May–1 June, Kadoma, Zimbabwe. Wallingford: CAB International. pp. 148–154.
- Chirwa PW, Syampungani S, Geldenhuys CJ. 2014. Managing southern African woodlands for biomass production: the potential challenges and opportunities. In: Seifert T. (ed.), *Bioenergy from wood: sustainable production in tropics, managing forest ecosystems*. Dordrecht: Springer. pp. 67–87.
- Clarke J, Cavendish W, Coote C. 1996. Rural households and Miombo woodlands use, value and management. In Campbell B (ed.), *The Miombo in Transition: Woodland and welfare in Africa*. Bogor, Indonesia: Centre for International Forestry Research. pp 101–135.
- Dayamba SD, Savadogo P, Savadogo L, Zida D, Tiveau D, Oden PC. 2011. Dominant species' resprout biomass dynamics after cutting in the Sudanian savannah –woodlands of West Africa: Long term effects of annual early fire and grazing. *Annals of Forest Science Journal* 68: 555–564.

- Dube L. 2005. Patterns of regeneration of *Baikiaea plurijuga* in areas logged at different periods in Gwaai forest. Unpublished MSc thesis, University of Zimbabwe, Harare.
- Evans J. 1992. *Plantation forestry in the Tropics: Tree planting for Industrial, Social, Environmental and Agroforestry purposes.* Oxford Science Publication, Clarendon Press.
- Fillemon K. 2015. Natural regeneration potential of *Pterocarpus angolensis* (Kiaat tree) in the dry forests of northern Namibia. Unpublished MSc thesis, Stellenbosch University, South Africa.
- Gambiza J. 2001. The regeneration of Zambezi teak after logging, influence of fire and herbivory. Unpublished PhD thesis, University of Zimbabwe, Harare.
- Geldenhuys CJ. 1977. The effect of different regimes of annual burning on two woodland communities in Okavango. *South African Forestry Journal* 102: 32–42.
- Geldenhuys CJ. 2009. Managing forest complexity through application of disturbance recovery knowledge in development of silvicultural systems and ecological rehabilitation in natural forest systems in Africa. *Journal of Forest Research* 15: 3–13.
- Geldenhuys CJ, Van der Merwe CJ. 1988. Population structure and growth of the fern *Rumohra adiantiformis* in relation to frond harvesting in the southern Cape forests. *South African Journal of Botany* 54: 351–362.
- Geldenhuys CJ, Golding JS. 2008. Resource use activities, conservation and management of natural resources of African savannas. In: Faleiro FG, NetoALde F (eds), Savannas: desafios estrategiaspara o equilibrio entre sociedade, agrenegocioerecursosnaturais. Planaltina, DF: EmbrapaCerrados. pp 225–260.
- Gonah J. 1994. *Timber harvesting policy*. Forestry Commission, Bulawayo, Zimbabwe.
- Graz FP. 1996. Management of a *P. angolensis* under the influence of fire and land use. MSc dissertation, University of Stellenbosch, South Africa.
- Handavu F, Syampungani S, Chisanga E. 2011. The influence of stump diameter and height on coppicing ability of selected key Miombo woodland tree species of Zambia: A guide for harvesting for charcoal production. *Journal of Ecology and the Natural Environment* 3(14): 461–468.
- Hawley RC. 1949. *The practice of silviculture* (5th edn). New York: John Wiley & Sons.
- Heita HTN, Ham H, Mensah S 2019. Effects of seed viability and pre-treatments on seed germination of two indigenous species — *Strychnos cocculoides* Baker and *Guibourtia coleosperma* (Benth.) Leonard in Namibia. *Agroforestry Systems* 93: 2173–2180. https:// doi.org/10.1007/s10457-018-0333-4
- Huang S. 1990. Study on the effect stump diameter and height on sprout regeneration in mangium (*Acacia mangium* Wild). *Journal of Forest Research* 3: 242–249.
- JAFTA, Forestry Commission. 2001. The forest survey in the Gwaai and Bembesi areas in the Republic of Zimbabwe: final report, March, 2001. Japan Forest Technical Association (JAFTA), under the auspices of Japan International Cooperation Agency (JICA) and the Zimbabwe Forestry Commission, Harare. Tokyo: Kogyo Co Ltd. https://openjicareport.jica.go.jp/pdf/11623741_01.pdf
- Jeffries MJ. 1997. *Biodiversity and conservation*. Abingdon: Routledge.
- Kaschula SA, Twine WE, Scholes MC. 2005. Coppice harvesting of fuel-wood species of a South African Common: Utilising scientific and indigenous knowledge in community based natural resource management. *Human Ecology* 33(3): 387–418.
- Kays JS, Canham CD. 1991. Effects of time and frequency of cutting on hardwood root reserves and sprout growth. *Forest Science* 37: 524–536.
- Khan ML, Tripathi RS. 1989. Effects of stump diameter, stump height and sprout density on the sprout growth of four tree species in burnt and unburnt forest plots. *Acta Oecologica*. 10: 303–316.

- Knox K, Clarke P. 2005. Nutrient availability induces contrasting allocation and starch formation in resprouting and obligate seedling shrubs. *Functional Ecology* 19: 690–698.
- Kramer PJ, Kozlowski TT. 1960. Physiology of trees. New York: McGraw-Hill. pp. 388–390.
- Ky-Dembele C, Tigabu M, Bayala J, Ouedraogo SJ, Oden PC. 2007. The relative importance of different regeneration mechaisms in a selectively cut savannah woodland in Burkina Faso, West Africa. *Forest Ecology and Management Journal* 243: 28–38.
- Lamont BB, Enright NJ, He T. 2011. Fitness and evolution of resprouters in relation to fire. *Plant Ecology* 212: 1945–1957
- Lemmens RHMJ, Louppe D, Oteng-Amoako AA. 2008. *Plant resources of tropical Africa*. Wageningen: PROTA Foundation, Backhuys CTA.
- Luoga EJ, Witkowski ETF, Balkwill K. 2002. Harvested and standing woodstocks in protected and communal lands of eastern Tanzania. *Forest Ecology and Management Journal* 164: 15–30.
- Mishara BP, Tripathi RS, Tripathi OP, Pandey HN. 2003. Effects of disturbance on the regeneration of four dominant and economically important woody species in a broad-leaved subtropical humid forest of Meghalaya, north east India. *Current Science* 84: 1449–1453.
- Mistry J. 2000. *World savannas: ecology and human use*. Edinburgh: Pearson Education.
- Miura M, Yamamoto SI. 2003. Structure and dynamics of a *Castanopsis cuspidata* var. *sieboldii* population in an old-growth, evergreen, broadleaved forest: the importance of sprout regeneration. *Ecological Research* 18: 115–129.
- Mudekwe J. 2007. The impact of subsistence use of forest products and dynamics of harvested woody species populations in a protected forest reserve in Western Zimbabwe. PhD thesis, University of Stellenbosch, Stellenbosch.
- Mushove PT, Makoni JT. 1993. Coppicing ability of Colophospermum mopane. In: Pierce GD, Gumbo DJ (eds), Proceedings of the International Symposium on the Ecology and Management of Indigenous Forests in Southern Africa, Victoria Falls, Zimbabwe. Harare: Zimbabwe Forestry Commission and SAREC. pp 226–230.
- Ncube Z, Mufandaedza E. 2013. Effects of fire on coppice shoot production and growth in an African savanna woodland dominated by *Pterocarpus angolensis* and *Baikiaea plurijuga*. Academia Journal of Agricultural Research 1(2): 028–035.
- Nemarundwe N, Mbedzi D. 1999. Social development studies for the Gwayi-Mbembesi settlement option study. Forestry Commission, Harare.
- Nott K, Nott A, Newton D. 2020. A critical assessment of the economic and environmental sustainability of the Namibian indigenous forest/timber industry with reference to Zambia and Angola. Pretoria: TRAFFIC.
- Nyamapfene K. 1991. Soils of Zimbabwe. Harare: Nehanda Press.
- Piearce GD. 1993. Natural regeneration on indigenous trees: The key to their successful management. In Piearce GD, Gumbo DJ (eds), *The Ecology and Management of Indigenous Forests in Southern Africa. Proceedings of an International Symposium, 27–29 July* 1992, *Victoria Falls, Zimbabwe*. Harare: Forestry Commission and SAREC. pp 347–365.
- Scholes RJ, Walker BH. 1993. An African Savanna: Synthesis of the Nylsvley study. Cambridge University Press.
- Schwartz MW, Caro TM, Banda-Sakala T. 2002. Assessing the sustainability of harvest of *P.angolensis* in Ruhwa region, Tanzania. *Forest Ecology and Management Journal* 70: 259–269.
- Shackleton CM. 2000. Stump size and the number of coppice shoots for selected savanna tree species. *South African Journal of Botany* 66: 124–127.
- Shackleton CM. 2001. Managing regrowth of an indigenous savanna tree species (*Terminalia sericea*) for fuel wood: The influence of stump dimensions and post-harvest coppice pruning. *Biomass Bioenergy* 20: 261–270.

- Steenkamp C. 1999. South Africa's wood-carving industry. *TRAFFIC* Bulletin 18: 11–20.
- Sullivan S, Konstant Tz, Cunningham AB. 1995. The impact of utilization of palm products on the population structure of the vegetable ivory palm (*Hyphaene petersiana, areacaceae*) in North Central Namibia. *Journal of Economic Botany* 49(4): 357–370.
- Syampungani S. 2008. Vegetation change analysis and ecological recovery of the Copperbelt Miombo woodland of Zambia. PhD thesis, University of Stellenbosch, Stellenbosch, South Africa.
- Syampungani S, Geldenhuys CJ, Chirwa PW. 2010. Age and growth rate determination using growth rings of selected miombo woodland species in charcoal and slash and burn regrowth stands in Zambia. Journal of Ecology and the Natural Environment 2: 167–174. Timberlake J, Chidumayo E, Sawadogo L. 2010. Distribution and characteristics of African dry forests and woodlands. In Chidumayo E, Gumbo DJ (eds). *The dry forests and woodlands of Africa: Managing for products and services*. London: Earthscan. pp 11–39.
- Tybirk K. 1991. *Regeneration of woody legumes in Sahel*. AAU Reports 27. Botanical Institute Aarhus University/Danida Forest Centre, Denmark.
- Van Daalen JC. 1991. Germination of *P. angolensis* seed. South African Forestry Journal 158: 33–36.
- Vermeulen WJ. 1990. *Pterocarpus angolensis*. Monograph. Pretoria: SARCCUS Technical Publication. pp. xix, 124.
- Vesk PA, Westoby M. 2004. Sprouting ability across diverse disturbances and vegetation types worldwide. *Journal of Ecology* 92: 310–320.
- Wong JLG, Thornber K, Baker N. 2001. Resource assessment of on-wood forest products: Experience and biometric principles. Rome, Italy: FAO.
- Wood AP. 1986. Man's impact upon the *mukusi* forest of Zambia, with special reference to Sesheke District. In: Piearce GD (ed), *The Zambezi teak forest. Proceedings of the First International Conference on the Teak Forest of Southern Africa, March 1984, Livingstone, Zambia.*