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Environment-driven spatial pattern of tamarind trees in riparian forests

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Abstract: Domesticating indigenous agroforestry species is gaining interest as a potential option for conservation and production. Yet, spatial patterning of key species and how it is altered by environmental variations, which are important to design plantation schemes in forest and agroforestry systems, are still poorly documented. The pair-correlation function was used to assess spatial pattern of *Tamarindus indica* and its variation under contrasting environmental conditions (vegetation cover and soil degradation). Tamarind seeds being dispersed by zoochory and barochory, we hypothesized positive association within and among life stages (adults-adults, juveniles-juveniles, and adults-juveniles). Variations in environmental conditions did not significantly affect density and overall spatial pattern of either adult or juvenile trees. Adults and juveniles showed clumped patterns irrespective of environmental conditions. However, juveniles showed positive association with adults under low canopy cover and/or soil degradation, and independence from adults under dense canopy. This could be due to the shade intolerant status of this species and allelopathic effect of adults on juveniles under dense canopy. On the contrary, soil degradation favored attraction between adults and juveniles, presumably by inducing coppicing. Tamarind trees proved to withstand land degradation and could be used to restore degraded areas. To this end, we suggest introducing juveniles in patches of 40 m radius using a 10 m x 10 m planting grid, and at least 30 m from mature trees.

Key words: Vegetation cover, gully erosion, spatial point patterns analysis, Tamarindus indica, *Sudanian phytochorion*

Introduction

Recent FAO reports on state of world's forests, suggest dramatic reduction of forest land cover in Africa (3.5 million hectares per year; FAO, 2011). While many efforts are being invested to curve this trend, current forest and agroforestry management schemes in Africa are faced with many challenges including: (i) developing sylvicultural itineraries for over-harvested indigenous species; (ii) choice of best species and planting schemes for specific environmental conditions. To date, there is agreement that domestication of indigenous edible plant species for the diversification of subsistence agriculture could play a big role in the achievement of the Millennium Development Goals (Leakey *et al.,* 2007). A key advantage comparatively to their timber counterparts is that these species can be used to halt and reverse forest ecosystems degradation while providing multiple economic and job opportunities (Zomer *et al.,* 2009; Garrity *et al.,* 2010).

The tamarind tree, *Tamarindus indica* L. (Detarieae - Fabaceae) is a semi-evergreen tree species that grows pantropically but its precise origin remains debatable. On the one hand, its widespread distribution in the native vegetation of African savannahs and its presence in vestiges of orchards of ancient Egypt 400 B.C., suggest an Africa origin (Lefèvre, 1971). On the other hand, its presence in Buddhist sources 650 BC and in Brahmasamhitan sources 1200 BC (Aubréville, 1950) would suggest an Asian origin (mainly India). Nevertheless, fossil records for Detarieae are much older in Africa than Asia, *i.e.*, back to the late Maastrichtian or Palaeocene (Pan *et al.*, 2010). In addition, 90 % of the genus in the tribe Detarieae is endemic to Africa. This is rather congruent with an African origin for *T. indica*. Whatever its origin, tamarind is currently considered to be indigenous to Africa and Asia where it is a prominent Agroforestry Fruit Tree species.

In Sub-Sahara Africa *et alibi*, tamarind has nutritional, medicinal, cultural and economic importance for rural communities (Jama *et al.,* 2008; Fandohan *et al.*, 2010). It portrays a high economic value and has been identified as one of the top species for domestication programs in Sub-Sahara Africa (Akinnifesi *et al.,* 2008). Likewise, its other timber and non-timber counterparts, tamarind wild populations are being exploited in the absence of sufficient sylvicultural knowledge for reforestation or rejuvenation of agroforests. Sustainable use of such an important resource however needs a twofold strategy including conservation of viable wild populations and domestication (i.e., through forest enrichments and plantations).

The extensive literature on forestry and agroforestry species indigenous to Africa has yielded a huge body of knowledge. However, with respect to sylvicultural dimensions, most of the studies focused on seed dormancy and propagation techniques. To our knowledge, studies addressing spatial patterning of these species are scarce. Previous endeavors diversely used either the Ripley's K function (Diggle, 2003) or the O-ring Statistic (Wiegand and Moloney, 2004) to test the original hypothesis of complete spatial randomness (CSR) of the spatial pattern of trees (i.e., Couteron and Kokou, 1997; Fonton *et al.,* 2012). However, testing the CSR hypothesis does not provide any further information explaining the observed pattern. Recent developments in spatial pattern modelling have illustrated their relevance for explaining biological or environmental factors underlying a given point process (see Baddeley and Turner, 2005). In this respect, spatial patterns analysis has been used to test for association or repulsion between life stages as an indicator of anthropogenic disturbances (Djossa *et al.,* 2008), and to check for gender-specific spatial patterning of trees in dioecious species, that could have resulted from gender-specific environment requirements (Gouwakinnou *et al.,* 2011). Understanding natural spatial patterning of individual timber or non-timber forest product tree species and how this is influenced by environmental conditions is important not only to account for this effect when designing forest/agroforest enrichment plans but also for decision making towards intervention or specific conservation actions/strategies (i.e., *ex situ*, *in situ*). This is even more important in arid or semi-arid areas where competition for access to water is particularly high (Fonton *et al.,* 2012). Finally, spatial patterning of trees can also be used to unfold any negative effect of adult individuals on juveniles, which will further also improve plantation and enrichment designs (Dale, 1999).

The present study examined at fine scale the spatial pattern of tamarind trees in the wild and its variation under contrasting environmental conditions. Tamarind seeds being dispersed mainly by zoochory (monkeys) and barochory (Blumenfeld-Jones *et al.,* 2006), we hypothesized positive association (attraction) within and among life stages (adults-adults, juveniles-juveniles, and adults-juveniles).

Material and methods

Study system and data collection

The study was carried out in the Sudan phytochorion of Benin. Riparian habitats (i.e., forests that are adjacent to rivers) are the only habitat hosting tamarind stands (Fandohan *et al.*, 2011). The Pendjari and W National Parks, hosting the two major refuges of the species along Pendjari and Alibori rivers in Benin were considered for data collection. Sequel to scarcity of tamarind stands (see Fandohan *et al.*, 2011), explored stands were subdivided into vegetation types and those hosting a tamarind population were considered in full size for systematic counting and mensuration of tamarind individuals. It is expected that considering stands in full size will result in a more consistent and reliable description of the patterns than the conventional use of small plot replicates (see Fonton *et al.*, 2011; 2012). Three study sites were finally considered. Table 1 summarises environmental characteristics of each site, hereafter named as the stands. The three stands differ with respect to vegetation type and cover, and soil erosion. (1) Stand 1 is a dry semi-deciduous forest with a dense canopy, and faces no soil erosion (in the Pendjari National Park). (2) Stand 2 (in the Pendjari

National Park), is a tree savannah with an open canopy, also with no visible soil erosion. (3) Stand 3 is a dry semi-deciduous forest (in W National Park). It portrays the lowest canopy cover and is faced with gully erosion (Figure 1). Gully erosion is a type of soil degradation often observed in riparian forests, river banks or flood plains (Toko and Sinsin, 2008). Its results from accumulation and recurrence of runoff water in narrow channels from which the soil is removed to considerable depths and at large spatial scale (Poesen *et al.*, 2003). In the tropics, gully erosion is associated with either severe aridification of lands with alternating clay and concretionary gravel layers or anthropogenic disturbances such as land mismanagement, overgrazing, fire, etc. (Valentin *et al.*, 2005).

Within each plot, the position of each tamarind tree was recorded. Starting from a first randomly chosen tamarind tree, azimuth and distance between successive con specimen were measured up to the last one. Tamarind with diameter at 1.3 m above ground, D130 ≥ 10 cm were grouped in the adult life stage and individuals fitting 1 cm < D130 < 10 cm were grouped in the juvenile life stage sensu Rondeux (1999).

Table 1 - Environmental characteristics of the study stands.

ECOLOGICAL REGION	STAND	COORDINATES	VEGETATION TYPE	AREA (HA)	SOIL TYPE	OFFICIAL PROTECTION STATUS	VEGETATION COVER (%)	PRESENCE OF GULLY EROSION
Sudan	Stand 1	11°25′N–1°30′E	Dry semi-deciduous forest	25.92	Cambisols	Pendjari National Park	80	No
Sudan	Stand 2	11°25′N–1°30′E	Tree savannah	15.68	Cambisols	Pendjari National Park	50	No
Sudan	Stand 3	12°06′N–2°54′E	Dry semi-deciduous forest	19.14	Cambisols and Gleysols	W National Park	20	Yes

Figure 1 - Gully erosion in the W National Park.

Count data were used to compute first order intensity (density) of trees per life stage and stand. Azimuth data were first transformed to Cartesian coordinates to yield a map of tamarind individuals on the ground. The obtained spatial pattern was assumed to be the result of a stochastic process that generates point sets on a plane under the hypotheses of stationarity and isotropy, i.e. invariance by translation and rotation (Cressie, 1992; Penttinen et al., 1992).

The pair-correlation function (Stoyan and Stoyan, 1994) was used to test (1) whether observed samples can be considered as having a regular, random or aggregated pattern; and (2) whether the relationship between adults and juveniles suggests spatial association, repulsion, or independence.

The pair-correlation function is a normalized measure of how, on average, a plant perceives the density of other plants as it "looks out" over increasing distance r into the community in which it is living: "the plant eye view" sensu Law *et al.* (2009). The pair-correlation function of a stationary point process is:

$$g(r) = \frac{K'(r)}{2\pi r} \qquad (1)$$

where $K'(r)$ is the derivative of $K(r)$, the reduced second moment function ("Ripley's K function"; Ripley, 1988) of the point process. For a stationary Poisson process, the pair-correlation function is identically equal to 1.

The cross-type pair-correlation function is a generalisation of the pair-correlation function to multitype point patterns. For a stationary multitype point process, the cross-type pair-correlation function between marks i and j is formally defined as (Baddeley and Turner, 2005):

$$g_{i;j}(r) = \frac{K'_{i;j}(r)}{2\pi r} \qquad (2)$$

where K'_{ij} is the derivative of the cross-type K function $K_{ij}(r)$ of the point process. For any marked point pattern in which the points of type i are independent of the points of type j, the theoretical value of the cross-type pair-correlation function is $g_{ij}(r) = 1$.

The tests of spatial pattern/association were all constructed in the same way. To test for statistical significance of the observed spatial patterns, 95% confidence limit simulation envelopes of the null hypothesis (complete spatial randomness for spatial pattern tests or spatial independence for spatial association tests) were generated by 500 replicate Monte Carlo simulations of the null model. In case that $g(r)$ was for a given scale r outside the simulation envelopes, the null hypothesis was rejected at this scale. For a univariate point patterns, $g(r) = 1$ indicates randomness (i.e., adults or juveniles were randomly distributed over the study site), while $g(r) > 1$ and $g(r) < 1$ respectively indicate clumping and regularity (i.e., adults or juveniles showed aggregative or regular spatial patterning over the study site). For a multitype point pattern, $g_{ij}(r) = 1$ indicates a spatial independence (e.g., spatial patterning of juveniles is independent from that of adults), whereas $g_{ij}(r) > 1$ and $g_{ij}(r) < 1$ respectively indicate a positive association (attraction, e.g., juveniles were mostly observed in the vicinity of adults) and a negative association (repulsion, e.g., juveniles were mostly observed away from adults' location). Statistical analyses were performed in R (R Core Team 2015) using the spatstat package for spatial analysis of point patterns (Baddeley and Turner, 2005).

Results

Relative abundance of tamarind stems

Density of tamarind adult trees was 4 to 6 times greater in dense forest stands than in tree savannah stand (Table 2). Density of juveniles showed the opposite trend with 1.3 to 5 times more stems in the tree savannah as compared to the other stands. Similarly, juvenile to adult ratio seemed to be inversely proportional to canopy cover in absence of any other disturbance (e.g. Gully erosion). It seemed that tamarind could maintain a relatively high density even under extreme disturbances such as gully erosion. Furthermore, in dense forests, the juvenile to adult ratio was greater in the stand affected by gully erosion.

Table 2 - First order intensity of stems per life stage and stand.

Stand	Vegetation type	Juveniles (stems/ha)	Adults (stems/ha)	Juvenile-Adult ratio
Stand 1	Dry semi-deciduous forest	0.39	11.27	0.03
Stand 2	Tree savannah	3.32	3.06	1.08
Stand 3	Dry semi-deciduous forest	2.04	9.03	0.22

Environmental conditions and spatial patterning of tamarind trees

Spatial patterning of adult and juvenile tamarind trees using the pair correlation function apparently showed no important differences between stands conditions (Figure 2). Irrespective of life stage and environmental conditions, g(r) was positive and greater than 1 for radius smaller than 40 m suggesting strong aggregation under all tested environmental conditions. The complete Spatial Randomness null model was thus rejected for all life stages and stands.

On the contrary, spatial relationships between juveniles and adults unfolded some differences between stands. Under dense vegetation cover juveniles showed spatial independence from adults (Figure 3 - plot 1), while strong positive association (attraction) was observed at radius smaller than 60 m under open canopy and in presence of Gully erosion (stand 2 and stand 3; Figure 3 - plot 2 and plot 3).

Close analysis of the mapping of trees and distance to the nearest neighbor revealed some additional information on the stands. Except for Stand 3, there seemed to be more juveniles in patches were adults are sparse (Figure 4 - Stand 1 and Stand 2). The opposite trend was observed in Stand 3 where trees were faced with gully erosion (Figure 4 - Stand 3).

On average, tamarind trees had a more clumped pattern under dense canopy, with adult-to-adult distance being two to three times smaller in dense forest stands as compared to the tree savannah one (Table 3). Juvenile-to-Juvenile distance showed the reverse trend (higher aggregation under open canopy). Similarly, juveniles were on average far from adults under dense canopy (more 150 meters apart) while they were much closer under open canopy (more or less 30 meters apart).

One obvious contrast in the outputs, especially under dense canopy (Stand 1) is that average juvenile-to-adult distance is dramatically lower (about 13 times) than average adult-to-juvenile distance. This indicates that few adults did have juveniles in their vicinities and for those having, the distance is much smaller (less than 15 m). In addition, juvenile-to-adult distance appeared to be greater under dense canopy (Stand 1 vs. Stand 2) but much shorter in presence of gully erosion (Stand 3) with the lowest vegetation cover.

Table 3 - Distance to the nearest neighbor (meter: means and standard errors).

Stand	Vegetation type	Adults	Juveniles	Adults x Juveniles	Juveniles x Adults
Stand 1	Dry semi-deciduous forest	4.72 ± 0.34	24.06 ± 9.58	154.32 ± 4.73	12.31 ± 2.92
Stand 2	Tree savannah	14.91 ± 1.80	8.20 ± 1.33	25.88 ± 3.74	9.32 ± 0.84
Stand 3	Dry semi-deciduous forest	8.05 ± 0.74	20.51 ± 6.13	31.55 ± 2.17	5.59 ± 0.76

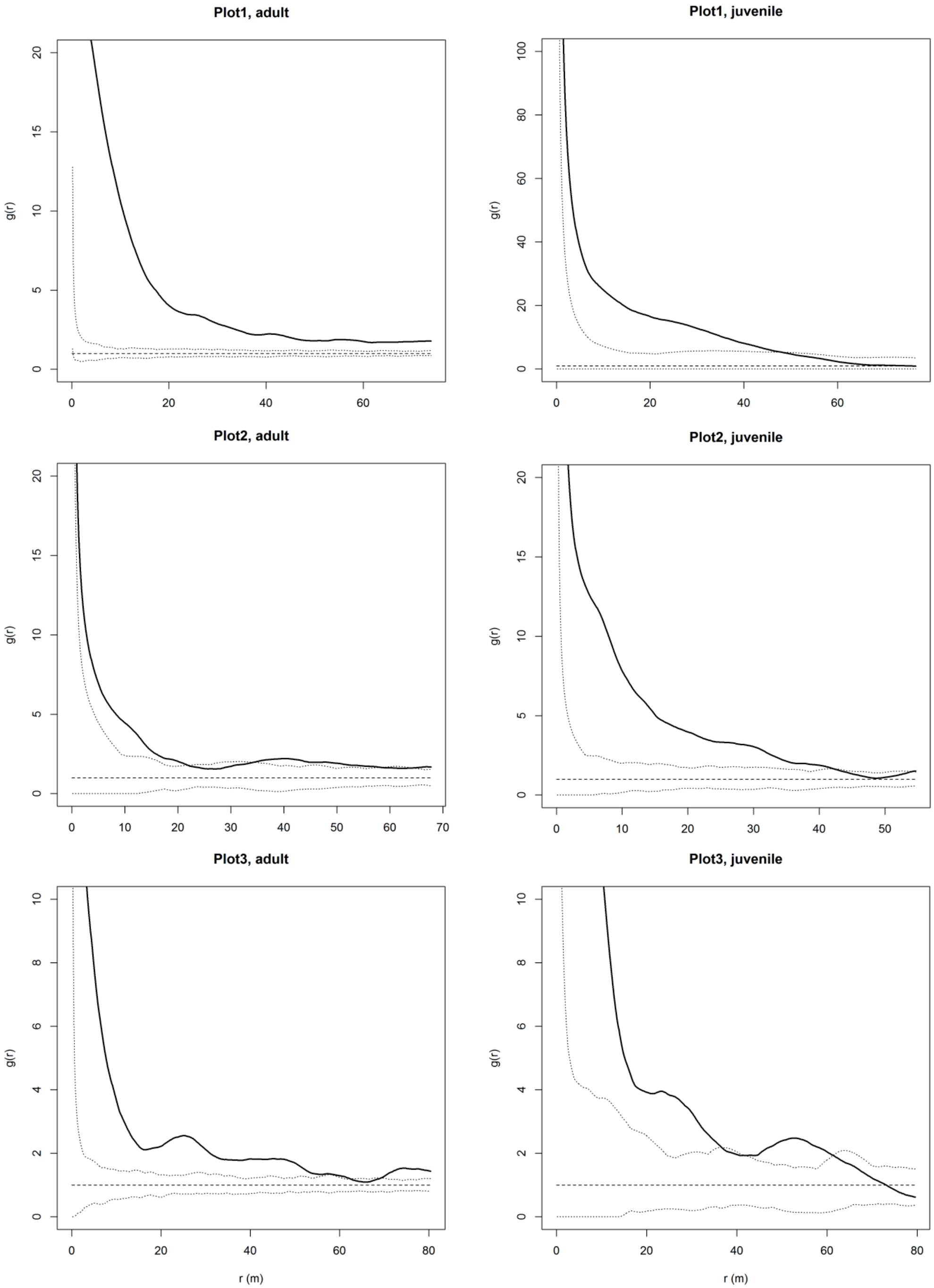
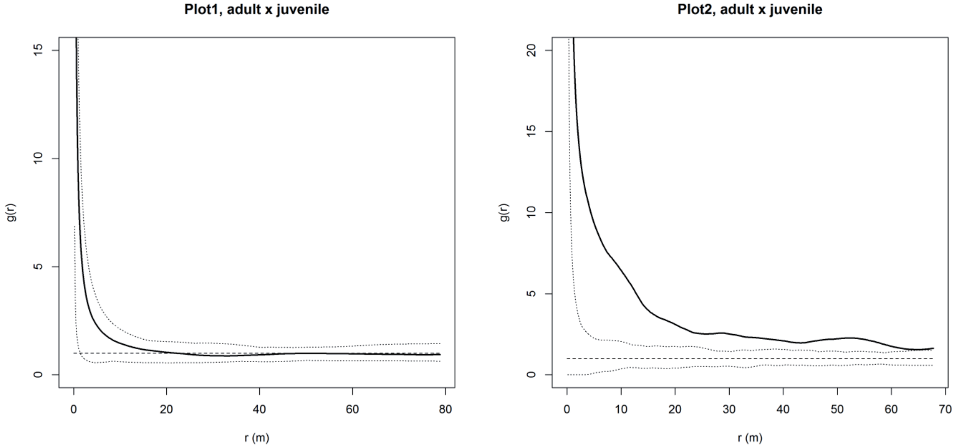


Figure 2 - Univariate spatial analyses of adults and juveniles.

Legend: Solid lines are the functions calculated from the data. The horizontal dashed line shows the pair-correlation function expected from a Poisson process. Dotted lines are approximate 95 % confidence envelopes for the null hypothesis, obtained from 500 independent simulations. Radius (r) is in meter.



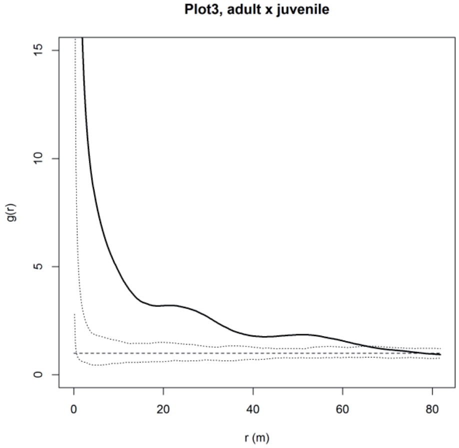


Figure 3 - Bivariate spatial analyses of juveniles around adults.

Legend: Solid lines are the functions calculated from the data. The horizontal dashed line shows the pair-correlation function expected from a Poisson process. Dotted lines are approximate 95 % confidence envelopes for the null hypothesis, obtained from 500 independent simulations. Radius (r) is in meter

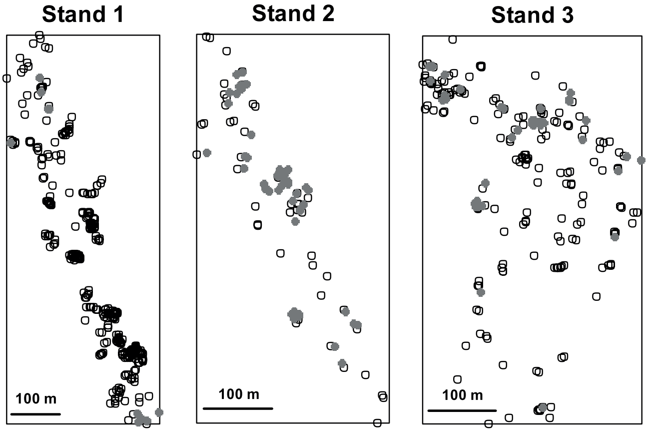


Figure 4 - Plots showing the patterns of adults (cycles) and juveniles (grey dots) of T. indica *in the three stands.*

Discussion

The main goal of this study was to examine influence of soil degradation and vegetation cover on spatial patterning of tamarind so as to yield data that could guide future forest or agroforestry park enrichment using tamarind trees. The results suggested clumped patterning of trees across life stage and stands. Clumped distribution of trees is typical in tropical forests (Clark and Clark, 1984; Boll *et al.,* 2005) and savannah woody vegetations (Couteron and Kokou 1997), and was reported to be highly linked with seed dissemination processes (Condit *et al.,* 2000; Svenning and Skov, 2005; Klimas *et al.,* 2007) and/or edaphic conditions (Couteron and Kokou, 1997).

We hypothesized that there should be an attraction between adults and juveniles in absence of critical disturbances, based on the assumption that juveniles originate from seeds dispersed through zoochory (monkeys) and barochory (Blumenfeld-Jones *et al.,* 2006). Our results evidenced case specific outputs. Under dense canopy, the pattern of tamarind juveniles was independence from adults. In addition, bivariate nearest neighbor distances analysis revealed that juvenile trees were often found far from adult individuals. Independence of juveniles from the adults could be explained by a set of previous observations on *T. indica*. Some recent studies revealed biologically active growth regulators to be present in the roots, leaves, bark, and seeds of *T. indica* adults (Parvez *et al.,* 2003; 2004). Water-soluble exudates of these plant parts were thus reported to have a strong inhibitory effect on the growth of a variety of agricultural crops and weed species. These works illustrated that adult individuals induce a hostile chemical environment under their canopy that inhibits the growth of many species including their own seedlings, i.e. tamarind adult trees limit their own reproductive success under their canopy. A more recent work concluded that tamarind recruits are shade-intolerant, usually do not have tamarind adults' canopy overhead and are seldom found near adults (Blumenfeld-Jones *et al.,* 2006). This corroborates the Janzen-Connell model which predicts that the probability of survival of seedlings to adulthood should increase with distance from the parent plant (Janzen, 1970; Connell, 1971). Many agroforestry species [including *Leucaena leucocephala* (Lam.) de Wit, *Acacia erubescens* (Welw. ex Oliv.), *Combretum imberbe* Wawra, *Sclerocarya birrea* (A. Rich.) Hochst. and *Terminalia sericea* (Burch ex DC.) among others] have been reported to have negative allelopathic effects (e.g. yield suppression) on food and fodder crops (Nakafeero *et al.,* 2007). Moreover, concentrations of allelopathic compounds can become particularly high in semi-arid soils because of low leaching and high evaporation rates, leading to a reduction in sub-canopy vegetation biomass (Nakafeero *et al.,* 2007).

Conversely, under lower canopy cover, juveniles were often in the vicinity of adult trees and showed positive association (attraction) with adult trees. This may be imputable to increased light availability under sparse canopy and is in agreement with the light-demanding species status of tamarind (Blumenfeld-Jones *et al.,* 2006). In addition, in the stand faced with gully erosion, juvenile-to-adult distance was nearly halved (9.32-12.31 versus 5.59). This could result from the fact that progressive ground sinking caused by gully erosion bares adult trees' roots, leading to coppicing and multi-stem trees (Fandohan A.B., field observation; Figure 5).

Figure 5 - Tamarind root sucker-originated young tree (on the left) in the stand facing gully erosion.

Conclusion and implications

Elucidating the spatial relationship between trees across life stage and under specific environmental conditions could help better guide forest enrichment and planting schemes. Variation in environmental conditions did not significantly affect density and overall spatial pattern of either adult or juvenile trees. Adults and juveniles showed clumped patterns irrespective of environmental conditions. However, juveniles showed positive association with adults under low canopy cover and/or soil degradation, and independence from adults under dense canopy. This could be due the light demanding status of the species on the one hand, and allelopathic effect of adults on juveniles under dense canopy, on the other hand. On the contrary, soil degradation favored attraction between adults and juveniles, presumably by inducing coppicing.

Bases on outputs of this study, the following suggestions could be made. As tamarind proved to maintain relatively high density under severe soil degradation such as gully erosion, it could be used to restore degraded areas. Our results would however indicate that restoration activities using tamarind would be more effective if young plants are introduced into open canopy away from adults rather than dense forests (shade intolerant species). Concurrently, for enrichment and/or planting activities using this species, small patches of more or less 40 m radius could be used. Within these patches a minimum between-stem-distance of 10 m (among juveniles) and 30 m (between juveniles and adults) could be sufficient to ensure normal growth of introduced young stems.

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