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Spatial distribution and species composition of tree seeds and seedlings under the canopy of the shrub, *Chromolaena odorata* Linn., in Ghana

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Abstract

The spatial distribution and species composition of tree seedlings and seeds under the canopy of the shrub, *Chromolaena odorata* Linn., were investigated at a 4 ha disturbed site that was surrounded by natural forests on two sides. For the seedling study, one hundred and eight 5 m^2 circular plots were established systematically (at 20 m intervals) with a random start point. For the seed bank study, soil samples were taken from 0.25 m^2 plots adjacent to 50% of the seedling plots at two depths (0–2 and 2–4 cm) and were germinated in a germination house. The study was conducted after the end of the seed dispersal season for tree species in the area. There were 11,780 seedlings ha^{-1} of 55 tree species growing under the woven canopy of *C. odorata* and 72% of the seedlings were economically valuable species. Tree seedlings as a whole were relatively uniformly distributed across the area but the distribution of individual species was very uneven. Some of the species were present only in 1% of the plots. Viable seeds of seven tree species were found in the soil seed bank with an average density of 46,000 seeds ha^{-1}. The spatial distribution of tree seeds was very uneven across the site and only 39% of the plots contained tree seeds. *C. odorata* seeds in the soil seed bank were over 1600 times more abundant than tree seeds. No clear relationships were found between the density and species richness of tree seedlings or seeds and the distance (up to 260 m) from adjacent forest stands in the direction of prevailing wind during the seed dispersal season. The data suggest that the stock of tree seedlings represented an accumulation of seedlings established over several years.

Keywords: Disturbed forests; Dry semi-deciduous forest; Natural regeneration of tropical forest; Forest restoration; Soil seed bank

1. Introduction

Ghana will need 200,000 ha of new productive forests by 2005 in addition to the existing forests to meet the increasing demand for forests and forest products. However, the total area of natural forests in Ghana has recently been declining at the rate of 22,000 ha per year (Repetto, 1988; Swaine et al., 1997; Avoka, 1999). The ecological and economic consequences of this decline are severe. For instance, the export revenue from forest products declined from 20% of the total export earning of the country in 1965 (Repetto, 1988) to 11% in 1997 (TEDB, 1997). Deforestation has contributed to the seasonal drying of some rivers (Prah, 1994).

The increasing demand for forest products and ecological functions of forests demands large-scale reforestation programs. Tree planting is presently the

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primary means of reforestation in Ghana, but it cannot meet the demand because of its high costs. Natural regeneration may provide a viable alternative that has been successful in some countries (Weetman and Vyse, 1990). Natural regeneration is generally much cheaper than planting (Weetman and Vyse, 1990). However, the natural regeneration of forests in Ghana is generally poor (Swaine et al., 1997) and not well understood. One of the possible explanations for the poor natural regeneration is the invasion of deforested areas by the shrub *Chromolaena odorata* Linn. (*Eupatorium odorata*; Asteraceae), but there is apparently no evidence to accept or reject this hypothesis (Hawthorne, 1989).

C. odorata is an aggressive, pioneer shrub species. The high production of light seeds allows the species to invade disturbed sites in a short period of time (Swaine et al., 1997). Once the seed germinates, the plants will grow to 2 m tall quickly and form a dense woven canopy that is almost impossible for tree seedlings to grow through (Riddock et al., 1991). The understory only receives about 7% of the full sunlight (Honu and Dang, 2000). However, tree seedlings have been observed under *C. odorata* canopy and the seedlings responded positively to the removal of the shrub (Honu and Dang, 2000), indicating that release treatments may be an effective way to restore *C. odorata* occupied sites back to forests. But the density, species composition and spatial distribution of tree seeds and seedlings under the *C. odorata* canopy must be known before a release treatment can be prescribed.

In this study we investigated: (1) the density, species composition and spatial distribution of seeds and seedlings of trees and competing vegetation on a *C. odorata* occupied site, and (2) the relationship of seed and seedling density and species richness to the distance to adjacent natural forests along the direction of prevailing wind in the season of seed dispersal. We hypothesized that there were enough seeds and seedlings of commercial tree species under the canopy of *C. odorata* to restore the area to productive forests after release treatments.

2. Materials and methods

2.1. Study site

The study was conducted in the Kabo River Forest Reserve in the Volta Region (8°50′N to 6°9′S, 0°20′W to 1°6′E) of Ghana. The area is characterized by the alternation of wet (major and minor rainfalls) and dry (hamattan) seasons with a total annual rainfall of 1250–1500 mm (Hall and Swaine, 1976; Jasikan Meteorological Rainfall Report, 1998; Internal Report). The area is flat and generally well drained. The soil is Orthic–Ferric Acrisols (Adu, 1992).

The experiment site was a 4 ha area that used to be occupied by a deciduous forest. A sever fire in 1983 destroyed the forest and the site was subsequently invaded by *C. odorata* (R. Kyekye, personal communication). The general area has since been set aside as a Forest Reserve and no further major disturbances have occurred. At the time when this project was initiated, the site was 95% (canopy coverage) covered by *C. odorata*. Plants distributed relatively evenly across the site. The flux density of photosynthetically active radiation under the woven canopy of *C. odorata* was 7% of the ambient level as measured at 20 random locations using a Li-Cor Li250 light meter at 12.00 h on an overcast day (Honu and Dang, 2000).

The site was adjacent to natural forest stands (see Honu and Dang (2000) for a description) on the northeastern and southwestern sides (Fig. 1). The southeastern and northwestern sides were bounded with farms (Fig. 1). The presence of trees higher than 2 m in the study site was minimal. The site was typical of severely disturbed forest sites in the region. Due to the limitation of time and funds available for the project, only one site was studied.

2.2. Assessment of seedling stocks

The density, species composition and spatial distribution of seedlings (plants < 2 m tall) were investigated using the systematic random sampling method with a random starting point (Cochran, 1997). A base line was established along the boundary with the adjacent forest stand at the southwest side (Fig. 1). Thirteen transects were established at 20 m intervals along the baseline. The position of the first transect was determined randomly. A total of 108 square plots ($5\ \text{m} \times 5\ \text{m}$) were established in the disturbed area and 34 in the adjacent forest stands along the transects at 20 m intervals. The position of the first plot on the first transect was also determined randomly. There were fewer plots in the forest on the northern side because of a river (River Anto in Fig. 1). Circular sampling

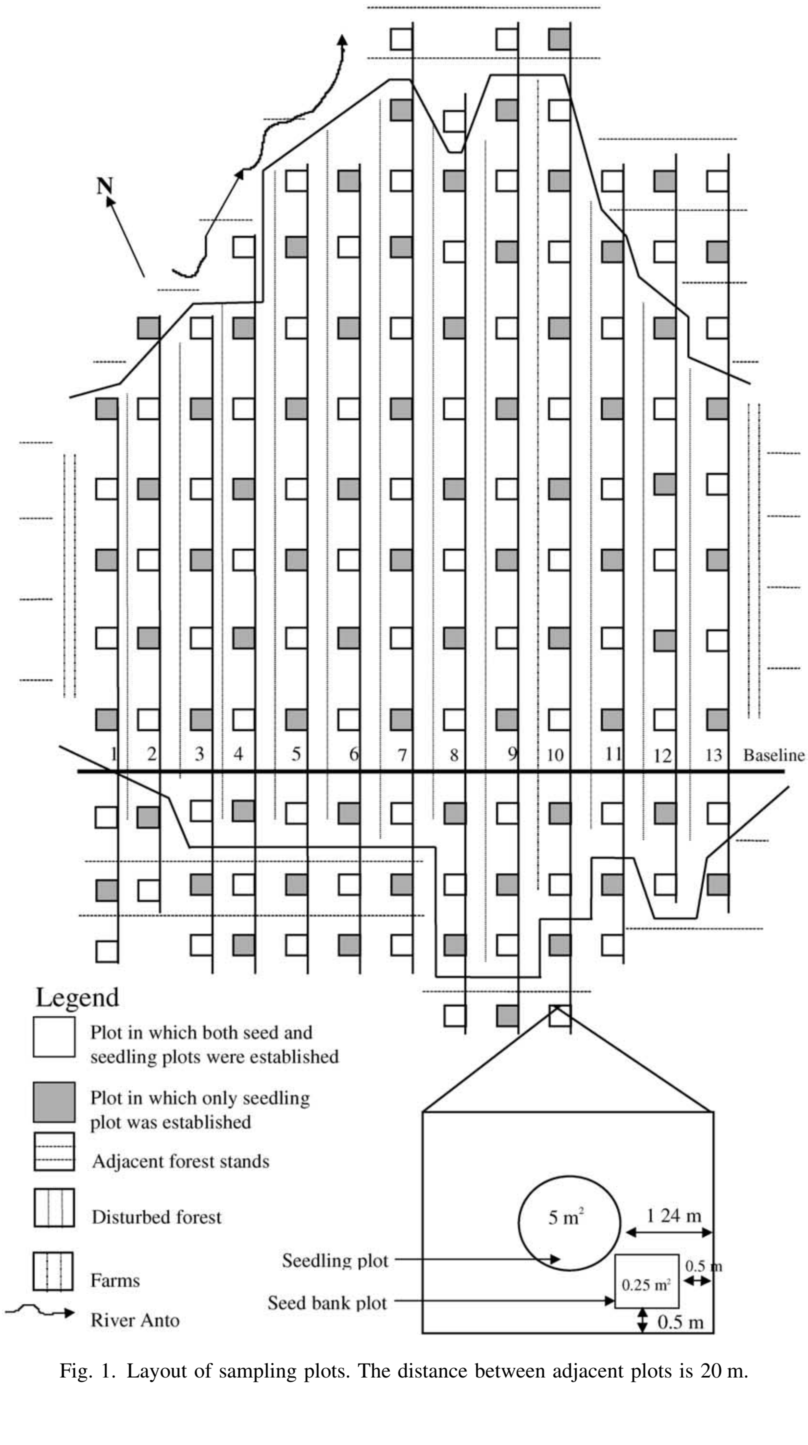

Fig. 1. Layout of sampling plots. The distance between adjacent plots is 20 m.

plots of 5 m^2 were established at the center of each square plot (Fig. 1). Tree seedlings within circular plots were identified based on Hawthorne (1990) and tallied in June 1998.

2.3. Assessment of viable seed stocks

Smaller square plots (50 cm × 50 cm) were established next to 50% (every other) of the circular seedling plots in the disturbed area and adjacent forests (Fig. 1). The first plot was selected randomly. Soil samples were taken at 0–2 and 2–4 cm layers on 2–3 June 1998, after the seed dispersal season for tree species in the area that generally occurs between November and March (Swaine et al., 1997). There is no information on the timing of seed fall of *C. odorata*, but no plants bore seeds or flowers at the time of sampling. Seed germination in the field is believed to coincide with the start of the rain season in March and April. However, the rain season was delayed in 1998 by an extended drought spell. Due to lack of available water, the experiment did not commence until 2 June.

The samples were transported in black plastic bags (to prevent light from reaching the samples) to Jasikan and kept in the bags overnight. The samples were placed into trays the next day for germination in a temporary germination house (18 m × 18 m × 1.2 m). The house was covered with fine-mesh net to prevent seed contamination from natural dispersal. The flux density of photosynthetically active radiation in the house was 32% of the ambient light level as measured at 12.00 h on an overcast day. Wooden boxes (50 cm × 100 cm × 6.5 cm) with perforated bottom were used as germination trays. A layer (5 cm) of washed river sand was spread at the bottom. The trays with sand were set up 25 days in advance to allow seeds in the sand to germinate and to be removed. Additionally, 16 trays containing sand only were used as controls. The controls were randomly located in the house.

Soil samples were spread evenly over the sand in the tray (about 1 cm thick) on 3 June 1998. The soil was carefully pressed with a smooth wood board to mimic field conditions. The trays were watered daily with 1.5–3.0 water per tray depending on the soil moisture condition. Hall and Swaine (1980) made weekly observations on seed germination in a test. However, it is very difficult to identify the species of young germinants. To avoid mis-identification, germinants were identified and tallied every 25 days in this study although casual observations were made each day. The germinants were removed after identification. The test lasted 100 days. Based on Hall and Swaine (1980), all tree seeds in the soil seed bank should germinate within 75 days. No mortality was observed during the experiment. The germinants were used as an index of viable seeds and will be referred to as such hereafter.

2.4. Seed production trees

Trees >20 cm dbh were considered as seed production trees in this study. Such trees were identified and counted in a 30 m wide strip along the edge and into the adjacent forests. Most of the trees were quite large, e.g. *T. scleroxylon* had a dbh of 1.6 m. Most of the tree species dispersed their seeds by wind (e.g. *T. scleroxylon*, *P. africanum*, and *T. sclerozylon*) and birds (e.g. *M. excelsa*, refer to Honu and Dang (2000) for silvics of tree species).

2.5. Data analyses

The density and species richness of tree seedlings were graphically examined for the normality of distribution using probability plots and for homogeneity of variances using scatter plots (Norusis, 1993). Regression analysis was used to describe the relationships between density and species richness and distance from adjacent natural forests in the direction of the prevailing wind during the seed dispersal season (SW to NE). The data showed that linear regression was appropriate for the seedling density and species richness. Analyses were done separately for each of the 13 transects.

The spatial distribution of three strong wind dispersal tree species, *C. pentandra*, *P. africanum*, and *T. sclerozylon*, were examined separately to avoid the interference of other species (Taylor, 1960; Jones, 1974; Swaine and Hall, 1983; Hawthorne, 1990; Richards, 1996).

The normality of distribution and homogeneity of variances for viable seeds of trees and *C. odorata* were examined as described previously. The tests showed that the data did not follow a normal distribution. Thus, a $\log_{10}$ transformation was applied. A paired *t*-test was used to test for differences between the two soil layers in seed density and species richness. *C. odorata* was analyzed separately from trees.

3. Results

3.1. Seedling stocks

Tree seedlings were present in 97% of the plots with an overall density of 11,780 seedlings ha^{-1} (Table 1). The number of seedlings per plot (5 m^2) ranged from 0 to 21. A total of 55 tree species were found in the disturbed area (Table 1). The species richness (number of species) ranged from 0 to 9 species per plot. *B. unijugata* was the most common species present in 30% of the plots (Table 1). Although the spatial distribution of tree seedlings was quite even across the site when all species were considered together, the distribution of each species was uneven, e.g. 14 out of the 55 species were present only in 1% of the plots. Sixty-four percent of the seedling species had no corresponding seed production trees within the 30 m wide sampling strip (Table 1).

The seedling density for all tree species together was not correlated to the distance from the adjacent forest in the direction of the prevailing wind in the seed dispersal season (SW to NE; Fig. 2; Table 2). The species richness of tree seedlings was also generally not significantly correlated with the distance from the adjacent forest in the direction of the prevailing wind during the seed dispersal season (SW to NE; Fig. 3; Table 2). The relationship was statistically significant in only 3 out of the 13 transects ($P \leq 0.04$; Table 2).

C. entandra seedlings were present in 14% of the plots and were scattered over the site (Fig. 4a). *P. africanum* and *T. scleroxylon* seedlings were present in 2 and 10% of the plots, respectively (Fig. 4b). The seedlings of *T. scleroxylon* were common only in the south eastern side of the site (Fig. 4c). The spatial distribution of these species did not show any clear pattern in relation to the distance to any side of the site (Fig. 4a–c).

3.2. Viable seeds

The germination of tree seeds started 5 days after the start of the test and finished in 75 days (Fig. 7). No germinants were observed in the 16 control trays. The 2–4 cm soil layer contained significantly more tree seeds than the top 0–2 cm layer ($P < 0.01$; Fig. 5) but the difference was not statistically significant at the first 25 days after the start of the test ($P = 0.852$; Fig. 7). The total number of viable tree seeds ranged from 0 to 16 per tray, with an average equivalent to 46,000 seeds ha^{-1} (Table 3).

Tree seeds were found in 39% of the plots (Fig. 6a). The total number of tree species ranged from 0 to 3 species per plot (Fig. 6b). At the end of the germination test, a total of seven species was recorded (Table 3). *S. erianthrum* was the dominant tree species (24,000 seeds ha^{-1}; 52% of all tree seeds) in both soil layers (Table 3). All tree species recorded in the seed bank were present in the seedling stocks (Tables 1 and 3) and 57% had corresponding seed production trees (Tables 1 and 3).

There were significantly more *C. odorata* viable seeds in the top soil layer (0–2 cm) than the deeper layer (2–4 cm, $P < 0.001$; Fig. 7). The total *C. odorata* viable seeds in the top layer ranged from 75 to 6336 seeds per plot with an average equivalent to 65,960,000 seeds ha^{-1}. The total *C. odorata* viable seeds in the deeper layer ranged from 36 to 2284 seeds per plot with an average equivalent to 7,960,000 seeds ha^{-1}. In other words, there were 1607 times more *C. odorata* seeds than tree seeds (Table 3). Two hundred and seven other herb and climber species (specific data not presented) were also recorded but were not included in the analysis (Table 3). The germination of *C. odorata* seeds was almost completed in 75 days but few germinants appeared afterwards (Fig. 7).

4. Discussion

The restoration of severely disturbed and degraded forest sites in Ghana is currently concentrated on converting disturbed areas to mainly teak plantations. Natural regeneration or human-assisted natural regeneration is generally not considered because of the lack of information on the density, spatial distribution and species composition of tree seeds and seedlings in disturbed areas. This study shows that there were 11,780 seedlings ha^{-1} growing under the canopy of *C. odorata* and the majority of the seedlings (72%) are

Table 1
Species composition and density of seedlings (seedlings ha^{-1}) and frequency of distribution (i.e. percentage of plots where a species was present) in a disturbed dry semi-deciduous forest site in Ghana

Species	Common name	Density	Frequency
Afzelia africana[a]	Papao	148	6
Afzelia bella[b,c]	Papao-nua	18	1
Albizia zygia[a,b]	Okoro	334	12
Antiaris toxicaria[a,b,d]	Kyenkyen	426	18
Bersama abyssinica[c]	Esonodua	38	2
Blighia sapida[e]	Akye	166	7
Blighia unijugata[e]	Akyebiri	1112	30
Buchholzia coriacea[b,c,d]	Esonobese	18	1
Celtis mildbraedii[a,d]	Prepresa	38	2
Celtis wightii[b,e]	Esa	186	6
Celtis zenkeri[a,d]	Esafufuo/Prempresa	112	4
Christiana africana[c]	Esakoko	18	1
Chrysophylum pruniforme[b,e]	Sesedua	38	2
Ceiba pentandra[a,b,d]	Duatadwe	334	15
Cola caricifolia[b,c]	Onyina	56	3
Cola gigantia[b,d,e]	Ananseaya	500	6
Cordia millenii[a,b,d]	Watapuo	38	2
Cynomentra ananta[b,c]	Tweneboa-nini	92	3
Daniella ogea[c]	Ananta	18	1
Distemonanthus benthamianus[a,b,d]	Senya/Hyedua	18	1
Duboscia viridiflora[b,e]	Bosamdua	56	2
Erythrina mildbraedii[c,d]	Akokoragyehini	18	1
Ficus exasperata[d,e]	Osorowa	852	26
Ficu sur[d,e]	Nwamdua/Domini	112	4
Greenwayodendron oliveri[b,c]	Nyankyerene	296	13
Hildegadia barteri[b,e]	Duabiri	74	3
Holarrhena floribunda[c]	Akyerekyewewa	38	2
Lecaniodicus cupanioides[b,c]	Sese	278	13
Lonchocarpus sericeus[b,e]	Dwindwera	556	16
Macaranga barteri[b,c]	Sante	18	1
Maesopsis eminii[c,d]	Opam	240	1
Mallotus oppositifolius[b,c]	Onwamdua	666	13
Maranthes chrysophylla[b,e]	Satadua	538	19
Margaritaria discoidea[d,e]	Kajabiri	18	1
Microdesmis puberula[c,b]	Ofema	74	4
Milicia exelsa[a,b,d]	Odum	352	13
Morinda lucida[a]	Konkroma	38	2
Nesorgodonia papaverifera[a,b,d]	Danta	612	13
Newbouldia laevis[b,c]	Sesemasa	92	4
Piptadenistrum africanum[a,b,d]	Dahoma	222	4
Ravolfia vomitoria[b,c]	Kakapenpen	592	20
Ricinodendron heudelotii[b,d,e]	Wama	18	1
Scytopetalum tieghemii[b,c]	Oprim	18	1
Solanum erianthrum[b,c]	Pepediawuo	112	4
Spathodea campanulata[b,c]	Akuakuo-ninsuo	92	5
Steculia rhinopetala[a,b,d]	Wawabima	166	6
Steculia tragacantha[e]	Sofo	482	8
Treculia africana[e]	Brebretim/Ototim	18	1
Trema orientalis[b,c]	Sesea	166	6
Tricalysia discolor[b,c]	Kwaekofi	278	7

Table 1 (*Continued*)

Species	Common name	Density	Frequency
Trichilia monadelpha[c]	Tanuro	18	1
Trichilia prieuriana[b,e]	Kakadikuro	462	12
Trilepisium madagascariense[b,d,e]	Ikure	148	6
Triplochiton scleroxylon[a,b,d]	Wawa	334	13
Vitex furruginea[c]	Otwentorowa	18	1

[a] Species being exported for the past 15 years.

[b] Seedlings found in the adjacent forest stands.

[c] All other tree species.

[d] Seed production trees in the adjacent forest stands (seed production trees were also present in the adjacent forest stands for *A. booni*, *A. leiccapus*, *A. micraster*, *C. perchrum*, *H. klaineana*, *M. bateri*, *P. marcrocarpa*, *S. glaucescence*, and *T. superba*).

[e] Non-exporting tree species that can grow up to 70 cm dbh.

commercial species, i.e. species that produce exportable products (i.e. Classes 1 and 2 species in Honu and Dang (2000)). This suggests that tree seedlings have the ability to survive the unfavorable conditions created by *C. odorata*. This density of tree seedlings is 10 times greater than the density of plantations in Ghana (3 m × 3 m spacing) and the trees were relatively evenly distributed across the site (Fig. 2). In an earlier paper (Honu and Dang, 2000) we found that those tree seedlings, particularly economically valuable species, responded very positively to the removal of *C. odorata* canopy. The species composition, high density and positive responses of the tree seedlings to release treatments suggest that the disturbed areas can

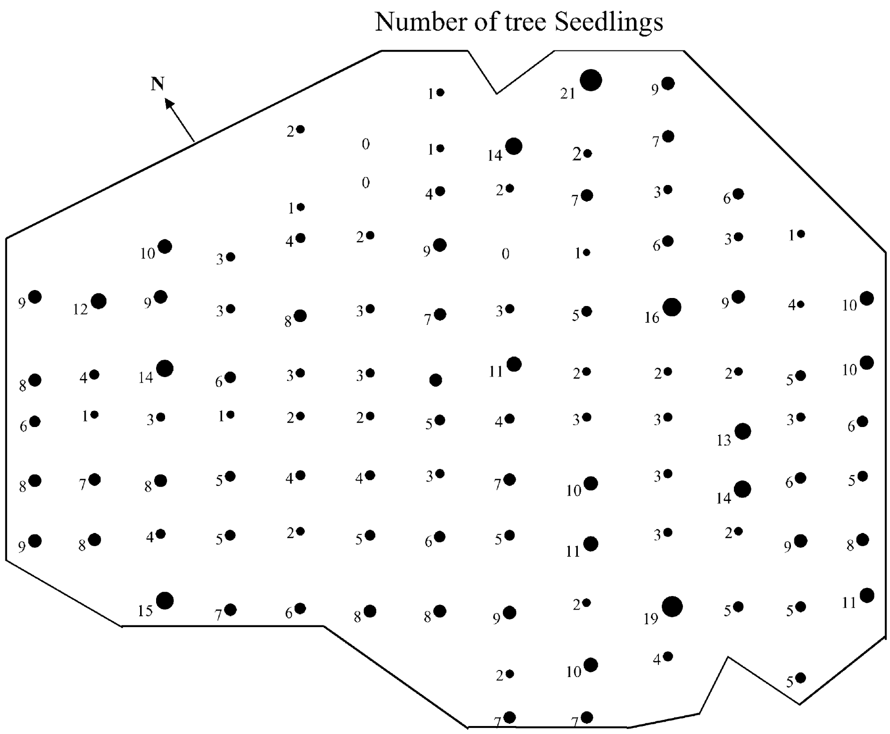

Fig. 2. Spatial distribution of tree seedlings in the disturbed site. The number of seedlings in each 5 m^2 plot is printed beside the dot "●". Here "0" indicates that no seedlings were present. The vertical and horizontal distances between adjacent plots are 20 m.

Table 2
Relationship of seedling density and species richness to distance to adjacent natural forest in the direction of the prevailing wind during seed dispersal season[a,b]

Transects	n	Seedling density						Species richness					
		a	P_a	b	P_b	r^2	S.E.	a	P_a	b	P_b	r^2	S.E.
1	5	8.00	0.04	0.00	1.00	1.00	1.41	5.00	0.11	−0.10	0.67	0.22	1.37
2	5	3.90	0.65	0.03	0.76	0.04	4.71	6.50	0.06	−0.04	0.19	0.49	1.30
3	7	8.75	0.17	0.01	0.92	0.00	5.42	6.32	0.04	−0.01	0.69	0.00	2.23
4	7	6.96	0.01	−0.03	0.19	0.32	1.87	5.49	0.00	−0.02	0.01	0.88	0.45
5	9	4.86	0.04	−0.01	0.49	0.07	2.31	4.78	0.00	−0.02	0.08	0.38	1.25
6	9	8.00	0.00	−0.04	0.00	0.83	1.09	6.24	0.00	−0.03	0.00	0.85	0.77
7	10	8.15	0.00	−0.02	0.11	0.28	2.46	5.13	0.00	−0.02	0.04	0.44	1.18
8	11	5.45	0.06	0.00	0.87	0.00	4.49	4.91	0.02	−0.01	0.71	0.02	2.97
9	11	5.77	0.11	−0.01	0.73	0.01	5.96	4.35	0.00	−0.01	0.51	0.04	1.91
10	11	7.04	0.10	−0.00	0.95	0.00	6.03	3.05	0.09	0.00	0.61	0.03	2.49
11	8	7.67	0.15	−0.00	0.84	0.01	5.13	3.29	0.22	0.01	0.80	0.01	2.59
12	8	7.32	0.00	−0.03	0.11	0.36	1.99	5.21	0.00	−0.02	0.10	0.38	1.28
13	6	8.08	0.06	0.00	0.93	0.00	2.71	5.00	0.12	0.00	1.00	0.00	2.24

[a] The model: $Y = a + bX$.
[b] P_a: probability for a; P_b: probability for b; r^2: correlation coefficient; S.E.: standard error of estimate.

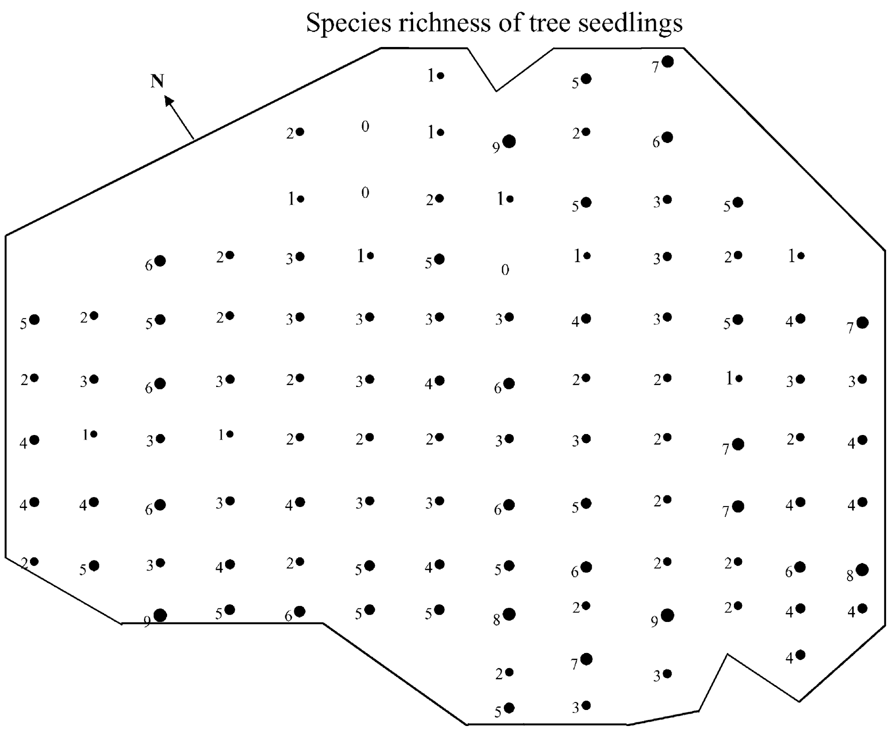

Fig. 3. Spatial distribution of species richness of tree seedlings in the disturbed site. The number of species in each 5 m^2 plot is printed beside the dot "●". Here "0" indicates no tree seedlings were present. The vertical and horizontal distances between adjacent plots are 20 m.

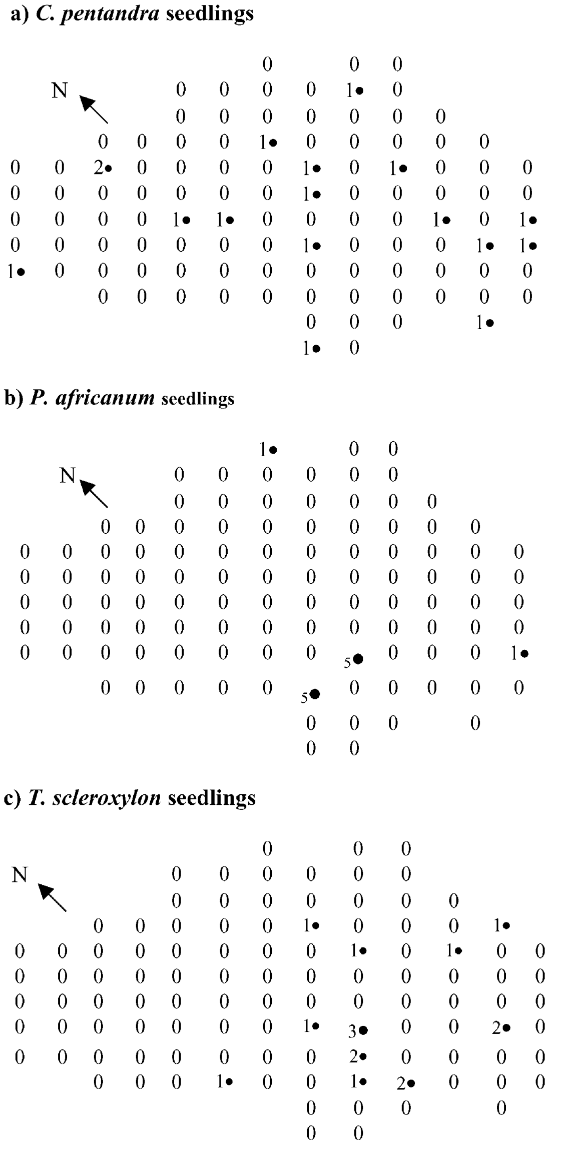

Fig. 4. Spatial distribution of *Ceiba pentandra*, *Piptadeniastrum africanum*, and *Triplochiton scleroxylon* seedlings in the disturbed site. See Fig. 2 for more explanations.

be restored back to forests by human-assisted natural regeneration.

This study provides further evidence to support the theory that *C. odorata* is the major factor hindering the regeneration of disturbed and degraded forest sites (Honu and Dang, 2000). Our seed bank data show that *C. odorata* can distribute over 7 million seeds ha^{-1} to

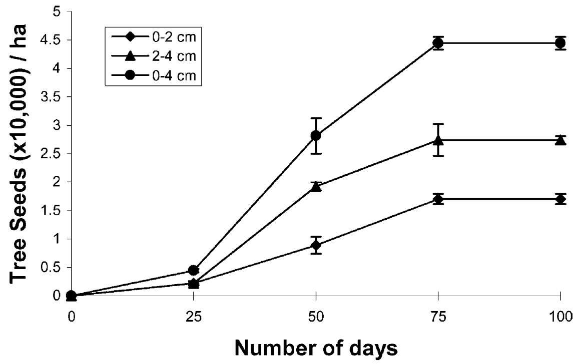

Fig. 5. Cumulative germination of tree seeds in the disturbed site. The number of viable seeds was estimated from the number of germinants in a 100-day germination test. Bars represent the standard error of the mean.

a disturbed site, i.e. over 1600 times the amount of tree seeds. Swaine et al. (1997) also found that disturbed areas contained more *C. odorata* seeds than tree seeds. The abundant light seeds and the fast growth rate allow this species to colonize a disturbed site quickly and form a woven canopy which greatly suppresses tree seedlings (Honu and Dang, 2000).

This study suggests that the tree seedlings growing under the canopy of *C. odorata* represents an accumulation of several years. This theory is supported by three lines of evidence: firstly the species richness was six times more in tree seedlings than in seeds; secondly seedlings were much more evenly distributed across the site (97% of the plots) than seeds (39% of the plots); thirdly, as reported in Honu and Dang (2000) there were substantial differences in size among seedlings of the same species as well as

Table 3
Density of viable seeds estimated from the number of germinants in a 100-day germination test of soil samples

Species	Viable seeds ha^{-1}
Celtis mildbraedii	1000
Ceiba pentandra	2000
Ficus exasperata	8000
Ficu sur	9000
Solanum erianthrum	24000
Trema orientalis	1000
Trichilia prieuriana	1000
Herb and climber species	153000
Chromolaena odorata	73920000

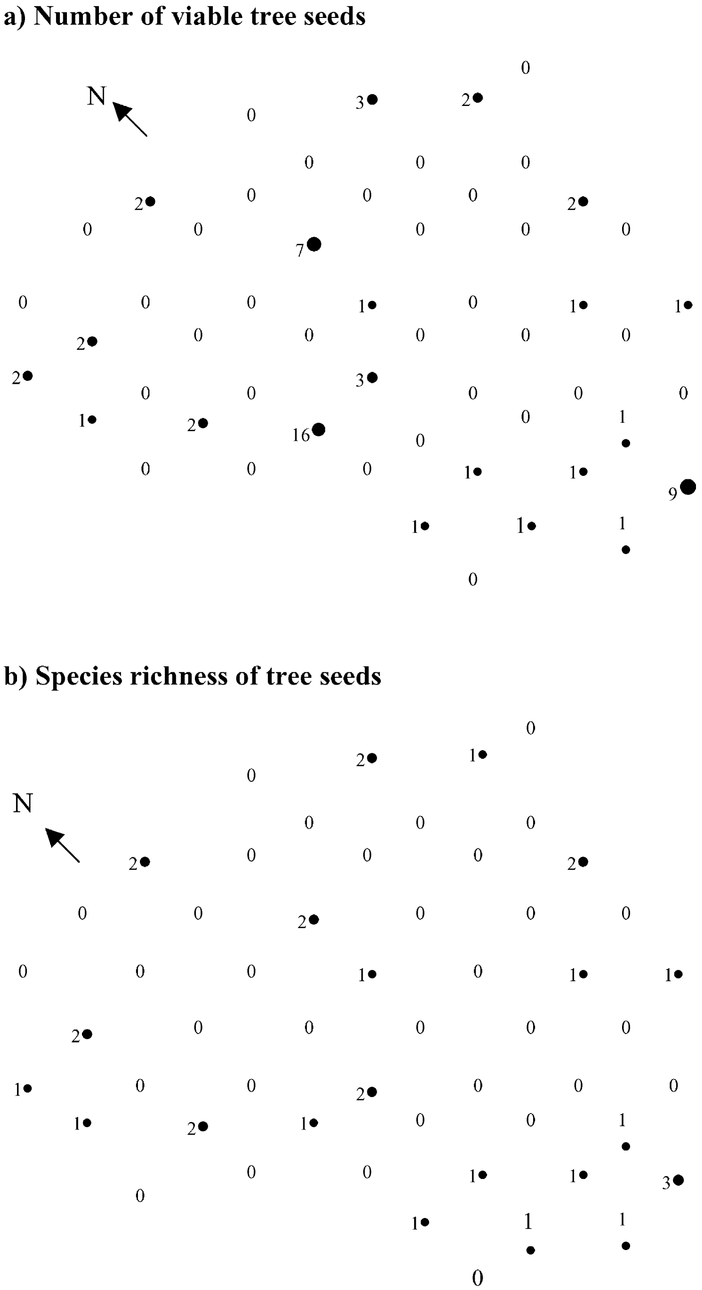

Fig. 6. Spatial distribution of tree seed density and species richness of tree seeds in the disturbed forest site. The relative size of the dot "●" indicates the number of viable seeds in a 0.25 m^2 plot. The actual numbers are printed beside the dots. Here "0" indicates no tree seeds were observed. The vertical and horizontal distances between adjacent plots are 40 m.

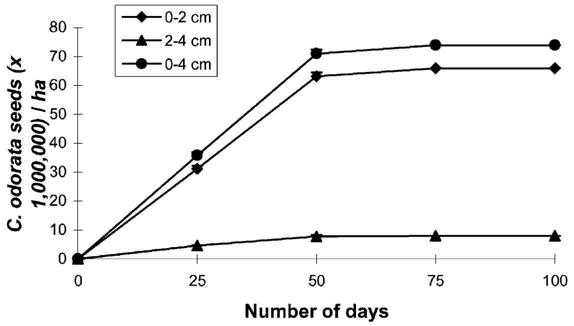

Fig. 7. Cumulative germination of *Chromolaena odorata* seeds in the disturbed site. The number of viable seeds was estimated from the number of germinants in a 100-day germination test. Bars represent the standard error of the mean.

between different species. Unfortunately the age of seedlings could not be determined because they do not form annual rings. Nonetheless, the data suggest that it will probably take several years to naturally regenerate a freshly disturbed area. Given the much greater seed production and aggressive invasion and faster growth of *C. odorata*, it is not wise to totally rely on natural regeneration for the restoration of disturbed areas. However, release treatments after enough seedlings have been established under the canopy of *C. odorata* represent a promising means to restore disturbed areas back to forests as an alternative to tree planting. Indeed, the positive responses of tree seedlings (Honu and Dang, 2000) demonstrate that this approach is effective and practical.

The species composition of tree seedlings shows that naturally regenerated forests contained a great diversity of tree species. A total 55 species of tree seedlings were found. Such a huge species diversity is probably beneficial for the health and functioning of the forest ecosystem but presents a challenge for the management of the forest, particularly when each species is so unevenly distributed. Many species in this study were present only in 1% of the plots although all the species together provided a relatively uniform coverage of the site.

Our data show that there were significant differences between different vertical soil layers in the amount of viable seeds. However, the trend was opposite for trees and *C. odorata*: the deeper soil layer (2–4 cm) contained more tree seeds but less *C. odorata* seeds than the surface layer (0–2 cm; Figs. 5 and 7). The pattern for tree seeds is in contrast to the finding of Enright (1978) that seed bank content generally decreases with increasing depth from the ground surface. It is not clear what caused the higher seed density at the deeper layer but it is possible that the deeper layer contained seeds from previous years or a greater proportion of the seeds in the surface layer geminated before the soil samples were taken. The differences in the trend between trees and *C. odorata* could be related to the timing of seed fall and germination but more detailed studies need to be conducted to examine factors influencing the vertical distribution of trees seeds and *C. odorata* seeds.

Our data have not shown any clear patterns of the spatial distribution of tree seedlings and seeds in relation to the distance to the adjacent forest and the distributions of individual species were very uneven across the site, for example, tree seeds were absent in 61% of the plots (Figs. 2 and 6). The density of tree seeds normally declines with increasing distance from the mother tree (Nyland, 1996). Such uneven spatial distribution of tree seedlings and seeds is difficult to explain. There might be several reasons for the irregularity: (1) seeds may have been dispersed into the area from more than one direction, (2) the small size of the area might have caused turbulence air flow, and (3) the seeds may have been dispersed by other agents as well as wind (Harper, 1977; Hall and Swaine, 1980). More studies are necessary to investigate factors influencing the spatial distribution of seeds and seedlings.

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References

Adu, S.V., 1992. Soil of Kumasi Region, Ashanti Region, Ghana. Soil Resource Institute, Memoir No. 8, Kwadaso-Kumasi, Ghana, 141 pp.

Avoka, C., 1999. Interview with He Mr. Cletus Avoka, Minister of lands and forestry, Ghana. In: Prebble C. (Ed.), ITTO Tropical update. ANUTECH, Pty Ltd., Canberra, Australia, pp. 16–17

Cochran, W.G., 1997. Sampling Techniques, 3rd Edition. Wiley, New York, 428 pp.

Enright, N.H., 1978. Effect of logging on regeneration and nutrient budget of *Araucaria cunninghamii* dominated tropical rainforest in Papua New Guinea. Malay For. 41, 303–318.

Hall, J.B., Swaine, M.D., 1976. Classification and ecology of closed canopy forest in Ghana. J. Ecol. 64, 913–951.

Hall, J.B., Swaine, M.D., 1980. Seed stocks in Ghanaian forest soils. Biotropica 12 (4), 256–263.

Harper, J.L., 1977. Population Biology of Plants. Academy Press, New York, USA, 892 pp.

Hawthorne, W.D., 1989. The flora and vegetation of Ghana's forests. In: Wong, J.L.G. (Ed.), Forest Inventory Project Seminar Proceedings, Accra, Ghana, 29–30 March 1989. Overseas Development Agency, London, UK; Ghana Forestry Department, Ghana, pp. 8–13.

Hawthorne, W., 1990. Field guide to the forest trees of Ghana, in: Ghana Forestry Series, Vol. 1. Natural Resource Institute for the Overseas Development Agency, London, UK, 278 pp.

Honu, Y.A.K., Dang, Q.L., 2000. Response of tree seedlings to the removal of *Chromolaena odorata* Linn. in a degraded forest in Ghana. For. Ecol. Manage. 137, 75–82.

Jones, N., 1974. Records and comments regarding the flowering of *Triplochiton scleroxylon*. K. Schum. Commonw. For. Rev. 53, 52–56.

Norusis, M.J., 1993. SPSS For Windows Base System Users Guide Release 6.0, SPSS Inc., MI, USA, 828 pp.

Nyland, R.D. 1996. Silviculture: Concepts and Applications. McGraw-Hill, New York.

Prah, E.A., 1994. Sustainable Management of the Tropical High Forest of Ghana. Commonwealth Secretariat Marlborough House, Pall mall, London, UK, 73 pp.

Repetto, R., 1988. The Forest for the Trees? Government Polices and the Misuse of the Forest Resources. World Resources Institute, Washington, DC, USA, 105 pp.

Richards, P.W., 1996. The Tropical Rain Forest, 2nd Edition. Cambridge University Press, Cambridge, 575 pp.

Riddock, J.C., Fasen, F.E., Riddock, B., Lapido, D.O., 1991. Photosynthesis and successional status of seedlings in a tropical semi-deciduous rain forest in Nigeria. J. Ecol. 79, 491–503.

Swaine, M.D., Hall, J.B., 1983. Early succession on cleared forests in Ghana. J. Ecol. 71, 602–627.

Swaine, M.D., Agyeman, V.K., Kyere, B., Ogle, T.K., Thomson, J., Veenendaal, E.M., 1997. Ecology of Forest Trees in Ghana. ODA Forestry Series No. 7, London, UK, 76 pp.

Taylor, C.J., 1960. Senecology and Silviculture in Ghana. Thomas Nelson and Sons Ltd., Edinburgh, UK, 418 pp.

Timber Export Development Board (TEDB), 1997. Ghana Hardwoods Trade Directory, 2nd Edition. TEDB, Unit 4, Granard Business Center, London, UK, 64 pp.

Weetman, G., Vyse, A.,1990. Natural regeneration. In: Lavender, D.P. Parish, R., Johnson, C.M., Montgomery, G., Vyse, A., Willis, R.A., Winston, D. (Eds.), Regenerating British Columbia's Forests. University of British Columbia Press, Vancouver, Canada, pp. 118–129.