Tropical Ecology **46**(1): 91-98, 2005 ISSN 0564-3295

Forest site disturbances and seedling emergence in Kalinzu Forest, Uganda

HOSEA D.R MUHANGUZI[1], JOSEPH OBUA[2*], HANNINGTON OREYM-ORIGA[3] & OLE R. VETAAS[4]

[1]Department of Science & Technical Education, Makerere University P.O. Box 7062, Kampala, Uganda; [2] Department of Forest Biology & Ecosystems Management, Makerere University P.O Box 7062 Kampala, Uganda; [3]Department of Botany, Makerere University, University P.O. Box 7062, Kampala, Uganda; [4]Centre for Development Studies, Bergen University, Stomgt. 54, N-5007, Bergen, Norway

Abstract: The influence of forest site manipulations (loosening soil, weeding and removing topsoil) and forest light environment on emergence of seedlings of selected pioneer, canopy and understorey tree species were assessed in Kalinzu Forest in areas with different management histories. The species were *Craterispermum laurinum, Funtumia africana, Musanga leo-errerae, Parinari excelsa, Strombosia scheffleri* and *Trema orientalis*. Most seedlings (> 38 %) emerged where the soil was loosened and least (< 10 %) in the undisturbed plots. With the exception of the pioneer species (*T. orientalis* and *M. orientalis*), seedlings of other species emerged in all the manipulated plots. Seedlings of the pioneer species only emerged in plots with light intensity ≥90 % while those of the canopy and sub-canopy species (*P. excelsa, F. africana* and *S. scheffleri*) emerged in plots where light intensity ranged from 6 % to 100 %.

Resumen: Se evaluó la influencia de las manipulaciones locales del bosque (aflojamiento del suelo, desyerbe y remoción del suelo superficial) y del ambiente lumínico del bosque sobre la emergencia de plántulas de una selección de especies arbóreas pioneras, de dosel y de sotobosque en el Bosque Kalinzu, en áreas con diferentes historias de manejo. Las especies fueron *Musanga leo-errerae*, *Trema orientalis*, *Funtumia africana*, *Strombosia scheffleri*, *Parinari excelsa* y *Craterispermum laurinum*. La emergencia de plántulas alcanzó su máximo (> 38%) donde el suelo fue aflojado y su mínimo (< 10 %) en las parcelas sin disturbio. A excepción de las especies pioneras (*T. orientalis* y *M. orientalis*), las plántulas de otras especies emergieron en todas las parcelas manipuladas. Las plántulas de las especies pioneras sólo emergieron en parcelas con una intensidad luminosa ≥ 90%, mientras que las de especies del dosel y del subdosel (*P. excelsa*, *F. africana* y *S. scheffleri*) emergieron en parcelas donde la intensidad de la luz fluctuó de 6% a 100%.

Resumo: A influência das manipulações da estação florestal (revolvimento do solo, monda de ervas e remoção da camada superior do solo) e o ambiente luminoso da floresta na emergência das plântulas de pioneiras seleccionadas, o copado e as espécies de árvores no sub bosque foram determinadas em áreas com diferentes histórias de manejo na Floresta de Kalinzu. As espécies foram a *Musanga leo-errerae*, *Trema orientalis*, *Funtumia africana*, *Strombosia scheffleri*, *Parinari excelsa* e *Craterispermum laurinum*. A maior parte das plântulas (>38%) emergiram quando o solo foi revolto e foi menor (<10%) nas parcelas não disturbadas. Com excepção das espécies pioneiras (*T. orientalis* e *M. orientalis*), as plântulas das outras espécies emergiram em todas as parcelas manipuladas. As plântulas das espécies pioneiras só emergiram nas parcelas com intensidade luminosa ≥ 90% enquanto que as do

* *Corresponding Author*

copado e sub-copado (*P. excelsa*, *F. africana* e *S. scheffleri*) emergiram nas parcelas em que a intensidade luminosa se situou entre os 6% e os 100%.

Key words: Canopy, germination, pioneer species, seedling emergence, site manipulation, tropical forest.

Introduction

Seed germination, emergence, growth, survival and establishment of seedlings affect forest regeneration by influencing plant populations in tropical forests (Osunkjoya *et al*. 1992). These processes vary with species and forest habitat characteristics (Clark 1990; Pons 1992; Schupp 1988; Tripathi & Khan 1990). Habitat characteristics such as degree of canopy openness and nature of soil can be affected by various kinds of forest disturbances (Boot & Gullison 1995; Denslow 1995).

Soil disturbance can influence germination and seedling emergence because it exposes some of the formerly buried seeds to incident light, which may induce some of them to germinate (Denslow 1980; Jensen 1995; Pugnaire & Lozano 1997). For example, Putz & Appanah (1987) noted that pioneer tree species are most abundant in open forest areas where soil has been disturbed. Disturbance that loosens soil may enhance seed germination and seedling emergence because of improved aeration and temperature variation (Clark & Clark 1987; Denslow 1987).

Forest soil disturbance also affects the soil seed bank, which often contains dormant seeds (Riswan & Kartawinta 1991; Silvertown 1987). While seeds of many tropical trees have short longevity (Vasquez-Yanes & Orozico-Segovia 1996), seeds of some species, especially the pioneer species often lie dormant in the soil seed bank (Ellison *et al.* 1993; Thompson 1992). Soil disturbance can expose formerly buried and dormant seeds to the ground surface consequently promoting their germination (Everham *et al.* 1996).

Augspurger (1984) noted that light strongly influences regeneration of some tropical tree species. According to Martinez-Ramos & Soto-Castro (1995), pioneer species and secondary forest species usually germinate and establish in gaps. On the other hand, seedlings of many shade tolerant species can establish in either gaps or understorey (Forget 1991).

Whereas forest site disturbances can result from natural tree falls, logging is a major cause of forest disturbances (Whitmore 1992). This study was carried out in Kalinzu forest reserve in areas that experienced different logging levels. The objectives were to determine (1) the effect of different plot manipulations (loosening the topsoil, weeding out herbs and shrubs and removing topsoil) on seedling emergence, (2) the species composition and abundance of the tree seeds present in the forest soil seed bank and, (3) the effect of different forest light environments (under closed canopy, forest gap edge and gap centre) on seedling emergence. In this article, the term 'emerged seedling' refers to those very young seedlings that have just emerged above the ground surface.

Materials and methods

Study area and location of study plots

This study was carried out in Kalinzu Forest Reserve, which is located in southwestern Uganda between 0^0 17' S - 0^0 30' S and 30^0 00' - 30^0 07' E and has an altitudinal range of 1250 - 1827 m above sea level. It experiences two rainfall peaks from March to May and September to November. The annual rainfall ranges between 1,150 - 1400 mm (Howard 1991). Minimum and maximum temperature ranges are 14^0 - 17^0 C and 25^0 - 28^0 C, respectively. According to Howard (1991), this forest can be classified as a medium altitude moist evergreen forest and medium altitude moist semi-deciduous forest. Two hundred and sixty five tree species (more than 57 percent of the country's total) have been recorded in this forest (Howard 1991).

Study plots were located in three areas of the forest having different management histories (Howard 1991). One area was heavily mechanically logged between 1950 and 1975 and is referred to as forest type A (FTA). The second area was heavily pitsawn while the third was minimally disturbed, and these areas are referred to as forest types B (FTB) and C (FTC), respectively. In each of the three forest types, a 1 x 1650 m transect was established. Thirty-three study plots, each 20 x 20 m in size, were established in each forest type and laid out in an alternating fashion at 30 m intervals along each transect.

Seedling emergence was monitored in sub plots established within each of the big plots of 20 x 20 m size. The sub-plots measuring 2 x 2 m were located at a distance of one metre apart. In each forest type, 33 plots were manipulated in a particular manner e.g. some plots were manipulated by weeding out existing herbs and shrubs while others had their topsoil removed to a depth of about 10 cm so as to remove seeds already present in the soil prior to this study. Other plots were manipulated by loosening the topsoil and removing roots and any other plant remains. Some plots were left undisturbed while others were manipulated in order to simulate conditions often created by various types of forest disturbances such as logging, clearing for agriculture, natural tree falls and effects of landslides.

Plot manipulation and seedling emergence

Seedlings that naturally emerged in the manipulated plots

The species studied were *Musanga leo-errerae* R. Br. and *Trema orientalis* (L.) Bl. (pioneer and light demanding species), *Funtumia africana* (Benth) Stapf (second story species, Hamilton 1991), *Strombosia scheffleri* Engl. and *Parinari excelsa* Sabine (upper canopy species). The study plots were examined once a month for 18 months (from May 1998 to November 1999). During each visit, all newly emerged seedlings belonging to the selected species were enumerated and marked by fixing stakes in the ground against them. At the same time, any freshly dispersed seeds of the selected species encountered in the plots were also enumerated.

Seedlings that emerged from seeds sown in the manipulated plots

Seeds of *M. leo-errerae, T. orientalis, F. africana, S. scheffleri, P. excelsa*, *Albizia gummifera* (J.F. Gmel.) C.A.Sm. (a secondary forest and forest edge coloniser) and *Craterispermum laurinum* (Poir.) Benth. (an understory species, Hamilton 1991) were sown in the weeded and undisturbed plots. Other seeds were sown in plots where the soil was loosened and the topsoil removed. The location of each seed was mapped and ten replicates made for each type of manipulation. Before sowing the seeds, their viability was tested using a technique suggested by Burke (1970), whereby tetrazolium solution is applied to freshly exposed cotyledons of sliced seeds. Fresh and air-dried seeds were used because older seeds tend to be sensitive to light quality (Vasquez-Yanes & Orozco-Segovia 1996). Fifty seeds of *M. leo-errerae*, *T. orientalis*, *F. africana* and *C. laurinum* were sown in the replicate plots while only 30 and 20 seeds of *S. scheffleri* and *P. excelsa,* respectively, were sown because they had few fresh and viable seeds at the time. All seedlings that emerged were enumerated.

Soil seed bank analysis

Blocks of soil samples (50 × 50 × 10 cm in size) were collected from six points in each forest type. In FTA, soil was collected from heavily logged areas under open canopy (soil sample A). In FTB, soil was collected from areas under closed canopy of a secondary forest (soil sample B). In FTC, soil was collected from areas under a closed canopy (soil sample C).

The soil samples were thinly spread out (≤ 5 mm in depth) on a ground whose surface was cleared of vegetation and litter and then leveled. Its top 15 cm layer of soil was removed in order to eliminate seeds already present in the soil at the site. The surfaces and sides of the ground on which the soil samples were spread were covered by one millimeter white cotton mesh placed at a height of one meter above the ground. Soil samples from each forest type were placed in separate areas of about 1.5 x 3 m. The soil samples were watered twice a day during the dry season and once a day during the rainy season to ensure adequate moisture supply. The plots were monitored for six months and all the tree seedlings that emerged from the soil were identified and enumerated. The existence of any more dormant seeds, which, could have germinated after this monitoring period were not assessed because of the limited time of the study.

Forest light environments and seedling emergence

Midday light intensity (LI) for each 20 x 20 m plot in every forest type was measured using a light meter. All measurements were made on cloudless days from 1130 to 1330 hrs and one meter above the forest floor. The aim was to determine the relationship between LI and seedling emergence. In addition, seeds were sown in plots located at the center, edge of a forest gap and under a closed canopy and the locations of the sown seeds mapped. The plots at the center of the gap were cleared of herbs, shrubs and litter and the topsoil loosened. For each light treatment, the study plots were established in three sample sites. The selected gaps were relatively big (>150 m^2 in area) to allow 100% direct incident radiation during daytime. Fifty seeds of *M. leo-errerae*, *T. orientalis*, *F. africana* and *C. laurinum* were sown in the replicate plots. Thirty seeds of *S. scheffleri* and 20 seeds of *P. excelsa* were sown in each replicate because, as noted earlier, they had few fresh and viable seeds at the time. The plots were examined twice during the first month and, thereafter, once a month for six months. All newly emerged seedlings were counted.

Results

Plot manipulation and seedling emergence

Seedlings that naturally emerged in the manipulated plots

Most seedlings (n=1048) emerged in plots where the soil was loosened and least (n=205) in plots that were not disturbed (Table 1). Apart from those of *F. africana*, more seedlings of the other species emerged in plots with loosened soil than in any other site. *Trema orientalis* seedlings did not emerge in plots without topsoil and those of *M. leo-errerae* did not emerge in the undisturbed plots. Compared to other sites, few seedlings (3.3%) of the canopy species (*P. excelsa*) emerged in the plots where the topsoil was removed. For each species, time to initiation of seedling emergence was longest (≥ 6 months) among seedlings in sites where topsoil was removed (Table 1). The number of seedlings of different species significantly differed in the manipulated plots (χ^2 = 71.09, df = 4, P < 0.001)

In every forest type, large numbers of emerged seedlings of the sub-canopy and canopy species were recorded where a correspondingly high number of seeds were dispersed (Table 2). This was, however, not the case with seedlings of the pioneer species although many of their seeds were dispersed in FTA plots.

Strombosia scheffleri in FTC, *P. excelsa* in FTB and *F. africana* in FTB and FTC were the only species that had significant correlations between the number of dispersed seeds and the number of emerged seedlings in particular forest types (Table 3).

Table 1. Percentage of seedlings of target species that emerged in the manipulated plots in the three forest types in Kalinzu forest reserve.

Tree species	Percentage of emerged seedlings			
	Topsoil removed	Soil loosened	Weeded	Un-disturbed
Trema orientalis	0	80.2(1)	18.4 (1)	1.4 (1)
Funtumia africana	34.7(6)*	33.1(1)	25.3 (1)	8.9 (1)
Musanga leo-errerae	15.4(11)	46.2(2)	38.4 (2)	0
Strombosia scheffleri	17.1(6)	35.5(2)	21.7 (2)	25.7 (2)
Parinari excelsa	3.3(11)	56.7(2)	23.3 (3)	16.7 (2)
Σf†	814	1048	666	205

* Figures in brackets are the periods (months) it took seedling emergence to be initiated; †Σf= Total number of emerged seedlings.

Table 2. Number of emerged seedlings and dispersed seeds of different species in each forest type (area of each forest type was 1.32 ha).

Forest type	Species				
	Funtumia africana	*Parinari excelsa*	*Strombosia scheffleri*	*Trema orientalis*	*Musanga leo-errerae*
FTA	167 (115) †	3 (67)	7 (6)	263[	13[
FTB	1306 (691)	17 (56)	94 (552)	15	0
FTC	792 (2329)	10 (249)	48 (433)	0	0
Overall	2250 (3125)	40 (511)	147 (991)	263	13

† Figures in brackets are the number of dispersed seeds; [Means that the number of seeds were > 10000.

Seedling emergence from seeds sown in the manipulated plots

Of the emerged seedlings, most (> 38 %) were recorded in plots with loosened soil while about 13 % were observed in undisturbed plots (Table 4). Seedlings of the sub-canopy and understorey species were more abundant than those of the pioneer category. Seeds of *P. excelsa* did not germinate in any of the plots whilst *T. orientalis* seeds did not germinate in the weeded and undisturbed plots.

Table 3. Spearman's correlation coefficients showing the relationships between the number of dispersed seeds and number of emerged seedlings in particular forest types.

Species	Forest type	n	R
Musanga leo-errerae	FTA	4	0.4 ns
Strombosia scheffleri	FTA	5	0.304 ns
	FTB	9	0.876**
	FTC	15	0.643**
Parinari excelsa	FTB	5	0.918**
	FTC	4	0.4 ns
Funtumia africana	FTA	19	0.415 ns
	FTB	29	0.732**
	FTC	26	0.862**

n = the number of plots considered for this relationship analysis; ns = not significant at $P < 0.01$; and ** = the coefficient is significant at $P < 0.01$.

Table 4. Number of seedlings of species that emerged from seeds sown in the manipulated plots.

Species	Number of emerged seedlings*			
	Topsoil removed	Soil loosened	Weeded	Un-disturbed
Parinari excelsa	0	0	0	0
Strombosia scheffleri	38	36	22	26
Craterispermum laurinum	18	14	5	8
Musanga leo-errerae	6	16	4	1
Trema orientalis	6	7	0	0
Funtumia africana	32	17	6	0

* = the seedling counts of each species/site manipulation were made in a 40 m^2 area.

Soil seed bank analysis

Trema orientalis seedlings were the most abundant (> 85%) in the soil samples collected from each of the forest types (Table 5). While seedlings of most early colonizers (*Croton macrostachyus* Hochst. ex Del, *Macaranga schweinfurthii* Pax *and T. orientalis*) were observed in all the soil samples, their freshly dispersed seeds and fruiting individuals were not observed in the soil samples collected from secondary and undisturbed forests (Table 5). Even if present, the seeds of *M. leo-errerae* and *T. orientalis* were too small (< 2.0 mm) and could not easily be identified in the soil samples. The sizes of seeds of these species were determined from those seeds extracted from ripe fruits obtained from fruiting trees in other parts of the forest. Fresh seeds of *F. africana* and *S. scheffleri* were present in the soil samples collected from the three forest types.

Table 5. Number of seedlings that emerged in soil samples collected from different forest types.

Species	Seedling density (m^2) per soil sample		
	Soil sample A (from FTA)	Soil sample B (from FTB)	Soil sample C (from FTC)
Neoboutonia macrocalyx Pax	4.67 (7)+	0 -	0 -
Croton macrostachyus	0.67 (1)+	0.67 (1) -	1.87 (3) -
Macaranga schweinfurthii	2.01 (3) +	1.34 (2) -	2.01 (3) -
Funtumia africana	0 +	5.36 (8)+	3.35 (5)+
Trema orientalis	78.3 (117)+	57.6 (86) -	59.8 (89) -
Unidentified	1.34 (2) -	0 -	1.34 (2) -
Strombosia scheffleri	0 +	0 +	0.67 (1) -
Musanga leo-errerae	0.67 (1)+	0+	0.67 (1)+
Sapium ellipticum (Hochst. ex Krauss) Pax	0.67 (1) -	3.35 (5) -	0 -
Celtis africana Burm. f.	0 -	1.34 (2) -	0 -

*Figures in brackets are the total number of individuals per soil sample; + and – represent the presence and absence respectively of freshly dispersed seeds and/or fruiting conspecific individuals in the sites where the soil samples were collected.

Forest light environments and seedling emergence

Light intensity (LI) in the different forest types and its relationship with seedling emergence

The mean midday LI experienced in FTA, FTB and FTC were 51.35 ± 4.55 %, 37.82 ± 4.75% and 23.67 ± 4.01%, respectively. FTA had more plots (n = 9) experiencing 100% midday LI followed by FTB (n = 5) and least in FTC (n = 3). Seedlings of the pioneer species only emerged in plots with LI ≥ 90 % with those of *M. leo-errerae* only observed in FTA and in plots that experienced LI of 100%. On the other hand, seedlings of the canopy and sub-canopy species emerged in plots that had LI ranging from 6 % to 100 %. With the exception of *T. orientalis* in FTA, the other species showed no significant relationship between the number of seedlings that emerged in particular plots of any forest type and the corresponding light intensity (Table 6).

Table 6. Spearman's correlation coefficient (r) showing the relationship between the number of seedlings that emerged in particular plots per forest type and the corresponding light intensity.

Species	Forest type	N	R
Trema orientalis	FTA (263)[†]	9	0.814**
	FTB (15)	5	0.649 ns
	FTC (0)	-	-
Strombosia scheffleri	FTA (7)	5	-0.218 ns
	FTB (96)	19	0.112 ns
	FTC (49)	15	-0.058 ns
Parinari excelsa	FTA (3)	-	-
	FTB (17)	5	0.449 ns
	FTC (10)	4	0.2 ns
Funtumia africana	FTA (167)	21	0.069 ns
	FTB (1303)	29	0.087 ns
	FTC (790)	26	0.221 ns
Musanga leo-errerae	FTA (13)	-	-
	FTB (0)	-	-
	FTC (0)	-	-

** = correlation is significant at $P < 0.01$ and ns means not significant at $P < 0.01$; [†] Figures in brackets are numbers of seedlings of different species that emerged naturally in the different forest types.

Effect of different degrees of canopy openness on seedling emergence

The mean midday LI in the plots located in the forest gaps, forest edge and under closed canopy were 100%, 53.3 ± 2.76% and 6.67 ± 1.12%, respectively. Most seedlings (47.7%) emerged in the forest edge and least (10%) under closed canopy (Table 7). The number of seedlings significantly varied in the three different light treatments ($\chi^2 = 51.4$, df = 2, $P < 0.001$). Seedlings of the pioneer species did not emerge in any of the plots with closed canopy while the sub-canopy and understorey species emerged in each light environment. Seedlings of most species emerged in the forest gap plots.

Table 7. Number of seedlings of species that emerged in the different forest light environments**.**

Species	Abundance of emerged seedlings		
	Forest gap	Forest edge	Closed canopy
Musanga leo-errerae	18	11	0
Trema orientalis	40	33	0
Funtumia africana	9	5	5
Craterispermum laurinum	0	39	0
Strombosia scheffleri	21	0	14
Parinari excelsa	1	0	0

Discussion

Plot manipulation and seedling emergence

As noted by Pugnaire & Lozano (1997) and Osunkjoya *et al.* (1992), soil loosening during this study could have enhanced seedling emergence of most species of the different successional guilds by improving soil aeration and drainage. Loosening the soil probably stimulated the germination of some positively photoblastic seeds in the soil by exposing them to incident radiation (Jensen 1995). By removing the ground vegetation cover, weeding could have exposed some seeds to incident radiation, thus, promoting seedling emergence of otherwise dormant and shade intolerant species.

The absence of seedlings of *T. orientalis* and the long period (11 months) it took *M. leo-errerae* and *P. excelsa* seedlings to emerge in plots where the topsoil was removed suggest that their freshly dispersed seeds could have experienced innate dormancy. Other studies (Thompson 1992; Vasquez-Yanes & Orosco-Segovia 1996) have shown that such delays in seed germination result from innate dormancy, which, breaks down over time. This is also demonstrated by the fact that unlike their sub-canopy and canopy counterparts, few seedlings of the pioneer species emerged in FTA plots where many of their seeds were frequently dispersed. Furthermore, since they are shade intolerant species, their germination could have been inhibited by a cover of leaf litter, twigs, soil particles and the forest canopy (Molofsky & Augspurger 1992). In the case of *P. excelsa*, the hard seed testa could have contributed to the dormancy.

Lack of seed dormancy could have been the cause of the relatively short period of time between seed dispersal and germination of the canopy and sub-canopy species. This germination behaviour has also been reported among species belonging to these successional guilds (Vasquez-Yanez & Orozco-Segovia 1996).

Soil seed bank analysis

It was noted that seeds of several shade intolerant species, especially of *T. orientalis,* can remain dormant in the soil for some time. This was because seedlings of these species emerged from soil samples collected from forest areas where none of the conspecific trees was fruiting or where fresh seeds were deposited. Since these species are pioneer or early colonizers (Hamilton 1991), the exposure of their seeds to direct sunlight may have stimulated their germination (Orozco-Segovia & Vasquez-Yanes 1989; Osunkoya 1996). Previous studies on soil seed banks in other forests have also shown that seeds of early successional species account for most individuals in the seed-bank of different forest habitats (Quintana-Ascencio *et al.* 1996).

Forest light environments and seedling emergence

A higher mean light intensity and number of plots experiencing LI =100% observed in FTA than in the other forest types showed a higher degree of canopy openness in this forest type. This may have resulted from the heavy mechanical logging, which took place in FTA. The presence of seedlings of both pioneer species in FTA and their scarcity or complete absence in the other forest types could have been due to the low degree of forest canopy openness in most study plots of FTB and FTC. This observation agrees with the results of studies done in other tropical forests, which also noted that seedlings of pioneer species establish in forest areas with open canopies (Kitajima 1996; Turner 1990).

The emergence of seedlings of all considered species in forest gaps suggests that seedlings of different successional guilds could emerge in gaps. Furthermore, the emergence of seedlings of the sub-canopy and understorey species in all the forest types showed that different light intensity and quality in forest gaps, forest edge and under the canopy did not influence their seed germination and early seedling growth. Forget (1991) reported that many non-pioneer species can establish in understorey, forest edges and gaps. On the other hand, the failure of seedlings of the pioneer species to emerge under closed canopy is consistent with the findings of other studies which showed that seeds of early successional tree species usually germinate and establish in high light conditions such as clearings and big forest gaps (Augspurger 1984; Everham *et* al. 1996; Whitmore 1993).

Results of this study revealed that soil loosening can enhance emergence of seedlings of several tropical forest tree species of different successional status, most probably, because it exposes formerly buried seeds to incident radiation and improves soil aeration and drainage. Furthermore, forest gaps seem to favour the emergence of tree seedlings of more diverse tree species than do closed canopy habitats. In addition, the emergence of seedlings of pioneer tree species were restricted to forest gaps and forest edges because their seeds need direct light for germination. Otherwise, the seeds of these species may stay dormant in the soil until such forest light conditions prevail.

References

Augspurger, C.K. 1984. Seedling survival of tropical tree species: Interactions of dispersal distance, light-gaps, and pathogens. *Ecology* **65:** 1705-1712.

Boot, R.G.A. & R.E. Gullison. 1995. Approaches to developing sustainable extraction systems for tropical forest products. *Ecological Applications* **5:** 896-903.

Burke, M.A. 1970. *Plant Hormones*. Griffin and George, London.

Clark, B.D. 1990. The role of disturbance in the regeneration of Neotropical moist forests. pp.291-312. *In*: K.S. Bawa & M. Hadley (eds.) *Reproductive Ecology of Topical Forest Plants*. UNESCO and Panthenon Publishing Group, London.

Clark, B.D. & D.A. Clark. 1987. Population ecology and microhabitat distribution of *Dipteryx panamensis,* a Neotropical rain forest emergent tree. *Biotropica* **19:** 236-244.

Denslow, J. S. 1980. Gap positioning among tropical rain forests. *Biotropica* **12**: 47-55.

Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics* **18:** 431-451.

Denslow, J. S. 1995. Disturbance and diversity in tropical rainforests: the density effect. *Ecological Applications* **5:** 962-968.

Ellison, M.A., J.S. Denslow, A.L. Bette & B.M. Danilo. 1993. Seed and seedling ecology of Neotropical Melastomataceae. *Ecology* **74:** 1733-1749.

Everham III, M.E., W.M. Randal & E. Vandegenachte. 1996. Effects of light, moisture, temperature and litter on the regeneration of five tree species in the tropical montane wet forest of Puerto Rico. *American Journal of Botany* **83:** 1063-1068

Forget, P.M. 1991. Comparative recruitment patterns of two non-pioneer canopy tree species in French Guiana. *Oecologia* **85:** 434 – 439.

Hamilton, A.C. 1991. *A Field Guide to Uganda Forest Trees*. Makerere University Printery, Kampala.

Howard, P.C. 1991. *Nature Conservation in Uganda's Tropical Forest Reserves*. IUCN, Gland and Cambridge.

Jensen, P.K. 1995. Effect of light environment during soil disturbance on germination and emergence pattern of weeds. *Annual Applied Biology* **127:** 561-571.

Kitajima, K. 1996. Ecophysiology of tropical tree seedlings. pp. 559-596. *In*: S.S. Mulkey, R.L. Chazdon & A.P. Smith (eds.) *Tropical Plant Ecophysiology*. Chapman and Hall, New York.

Martinez-Ramos, M. & A. Soto-Castro. 1995. Seed rain and advanced regeneration in a tropical rain forest. *Vegetatio* **107/108**: 299-318.

Molofsky, J. & C.K. Augspurger. 1992. The effect of leaf litter on early seedling establishment in a tropical forest. *Ecology* **73:** 68-77.

Osunkjoya, O.O., J.E. Ash, M.S. Hopkins & A.W. Graham. 1992. Factors affecting survival of tree seedlings in North Queensland rainforests. *Oecologia* **91:** 569-578.

Pons, T.L. 1992. Seed responses to light. pp. 259-284. *In*: M. Fenner (ed.) *Seeds: The Ecology of Regeneration in Plant Communities*. CAB International, Wallingford, United Kingdom.

Pugnaire, F.I. & J. Lozano. 1997. Effects of soil disturbance, fire and litter accumulation on the establishment of *Cistus clusii* seedlings. *Plant Ecology* **131:** 207-213.

Putz, E.F. & S. Appanah. 1987. Buried seeds, newly dispersed seeds, and the dynamics of a lowland forest in Malaysia. *Biotropica* **19:** 326-333.

Quintana-Ascencio, R.F., M. Gonzalez-Espinosa, N. Rimirez-Marcial, G. Dominguez-Vazuez & M. Martinez-Ico. 1996. Soil seed banks and regeneration of tropical rain forest from milpa fields at the Sewa Lacandina, Chiapas, Mexico. *Biotropica* **28:** 192-209.

Riswan, S. & Kartawinta. 1991. Regeneration after a disturbance in a low land mixed dipterocarp forest in East Kalimantan, Indonesia. pp. 295-302. *In*: A. Gomez- Pompa, T.C. Whitmore & H. Hadley (eds.) *Rain Forest Regeneration and Management*. UNESCO, Paris.

Schupp, E.W. 1988. Seed and early seedling predation in the forest understory and in treefall gaps. *Oikos* **51:** 71-78.

Silvertown, J. 1987. *Introduction to Plant Population Ecology*. Longman, Essex.

Thompson, K. 1992. The functional ecology of seed banks. pp. 231-258. *In*: M. Fenner (ed.) *Seeds: The Ecology of Regeneration in Plant Communities*. CAB International, Wallingford, United Kingdom.

Tripathi, R.S. & M.L. Khan. 1990. Effects of seed weight and microsite characteristics on germination and seedling fitness in two species of *Quercus* in a subtropical wet hill forest. *Oikos* **57:** 289-296.

Turner, I.M. 1990. Tree seedling growth and survival in a Malaysian rain forest. *Biotropica* **22:** 146-154.

Vazquez-Yanes, C. & A. Orozco-Segovia. 1996. Physiological ecology of seed dormancy and longevity. pp 535 – 558. *In:* S.S. Mulky, R.L. Chazdon & A.P. Smith (eds.) *Tropical Forest Plant Ecophysiology*. Chapman and Hall, New York.

Whitmore, T.C. 1992. *Introduction to Tropical Rainforests*. Clarendron Press, Oxford.

Whitmore, T.C. 1993. Use of hemispherical photographs in forest ecology. Measurement of gap size and radiation totals in a Bornean tropical rainforest. *Journal of Tropical Ecology* **9:** 131 – 151.