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The role of remnant forest trees in tropical secondary succession*

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Abstract

This paper emphasizes the contribution of remnant trees to the establishment of woody species during succession on abandoned fields and pastures in the Mexican rain forest area, Los Tuxtlas, Veracruz.

Remnant trees, original large forest trees left in the clearings by traditional farmers will become natural perching sites for both passing and resident birds. Frugivorous birds drop or regurgitate seeds and fruits which fall under the canopies of remnant trees during their stay, thus contributing to an accumulation of species, which make these remnant trees into 'regeneration nuclei'.

The species transported into these sites belong chiefly to older stages of successional development and reach these otherwise isolated areas, counteracting the depauperization of tropical land, brought about by both intensive and extensive clearing.

In a study of seven remnant trees, 29 woody species and two climbers were found, 86% of which are bird dispersed. The total number of species per tree varied from 6 to 15 and was higher under remnant trees with fruits attractive to birds.

Floristic variations of the understorey as detected by detrended correspondence analysis was correlated with the relative amount of shade-tolerant primary and late secondary trees versus light dependent pioneers and early successional trees.

Introduction

It is common practice in the humid tropical zones of Mexico to save some of the largest trees after forest clearance for agriculture or cattle raising. This meets both practical needs (shade, edible fruits), and cultural traditions (Guevara, unpubl.). Usually the entire vegetation even under the remant trees is removed. However, during the subsequent use of the clearing as a field or a grassland the area under the tree, which starts to be colonized, is left alone.

The remaining trees attract animals, mainly birds and bats because they provide facilities (protection, rest, food) for animals crossing a clearing while moving from one forest stand to another. The birds of forest ecosystems tend to avoid open spaces and if crossing them, they use perching sites.

Part of the birds and bats attracted are frugivorous. They may deposit seeds by defecation or regurgitation during their stays. In this way seeds from a rather large forest area may be funnelled into a small one. Hence such standing trees may serve as important nuclei of species establishment

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during secondary succession.

This effect has received little attention in the literature on succession. In many recent textbooks and review papers on forest succession in general or on tropical forest succession (Whitmore, 1984; Gomez-Pompa *et al.*, 1976; Hallé *et al.*, 1978; Longman & Jenik, 1978; Hall & Swaine, 1981; Golley, 1983; Holzner *et al.*, 1983; Sutton *et al.*, 1984; Miles, 1979; Packham & Harding, 1982), we found no direct references whatsoever. Only a few references mention the occurrence of remnant trees (Budowski, 1970; Hall & Swaine, 1981; Werger, 1983) but none of them say anything about their significance.

The following literature is known to us, however, that describes the possible effect of fruit trees or frugivorous birds on forest regeneration, and on the differences in environment between sites underneath and outside the canopy of (isolated) trees.

Uhl (1982) found a higher deposition of seeds of woody species under fruit trees in abandoned farms. He suggested the possibility that such trees may supply food and perching sites for birds.

McDonnell & Stiles (1983) emphasized the importance of seed distribution by birds in early secondary succession. However, they worked with artificial structures to attract birds and their simulation concerned a temperate and not a tropical forest.

Debussche *et al.* (1982, 1985) in their study of seed dispersal in relation to seed source, found peaks in the seed shadow around perching places, but this concerned abandoned orchards in the Mediterranean. Fleming & Heithaus (1981) studied the effect of seed-deposition by bats on the distribution patterns of plants in a dry tropical forest in Costa Rica.

The only general conclusion to be drawn from these few papers is the possible effect of clump distribution of species caused by bird and bat dispersion in secondary succession.

Kellman (1979, 1985; Kellman & Miyanishi, 1982) analyzed the effect of several trees on the invasion of tropical savannas by forest trees. They demonstrated a differential establishment of seedlings under and outside the canopy of such trees. The savanna trees may thus play a facilitative role (sensu Connell & Slatyer, 1977). This effect could not directly be attributed to soil enrichment beneath the canopy of the savanna trees but to a slower growth rate of intermediate species (not truly savanna or forest species) imposed by the low light levels beneath tree canopies, which allowed the persistence of species with the slow input of nutrients captured from atmospheric sources. Kellman (1979) even suggested that savanna trees are likely to be preferential resting and nesting sites for animals dispersing rain-forest seed into the savanna, but did not substantiate this supposition.

Remnant trees may thus operate as 'recruitment foci' (McDonnell & Stiles, 1983), especially for ornithochorous species and this recruitment forms a good example of the nucleation process as described for primary succession by Yarranton & Morrison (1974).

In this paper we present further evidence for the role of remnant trees in tropical secondary succession by presenting data on the occurrence of woody species underneath remnant trees in tropical pastures. We postulate the following variables to be important in determining the species composition of regeneration patches formed under and around remnant trees:

1) History of management, particularly the amount of disturbance during the clearance. If the site is severely disturbed, forest recovery will be considerably slower (Gomez-Pompa *et al.*, 1972).

2) The physical and chemical conditions existing under the canopy which promote or inhibit germination of species arrived at the spot.

3) The size of the tree (tree group). Apart from the general island ecological species-area relationship which will predict that larger trees will have more species underneath, there may be a more specific effect in that the length of the stay of frugivorous birds is correlated with the amount of shade (and protection) and therewith also the likelihood that seeds will be deposited. This has been demonstrated for temperate woodlands (Smith, 1975) and may also hold for the tropics.

4) Distance of the tree from the mature forest. Again this is a general island ecological relationship.

5) The nature of the remnant tree, particularly its function as a food source for birds. According to Snow (1981) we may distinguish between (1) trees which are attractive to unspecialized frugivorous birds (eating fruits which provide mainly carbohydrates), (2) trees attracting birds with a specialized feeding (eating high quality fruits rich in fats and

proteins), and (3) trees without any specific attraction to frugivorous birds.

Although our data set is small we think we can use it to discuss variables 3, 4 and 5.

Material and methods

The observations were made on grazed sites in the region of Los Tuxtlas, State of Veracruz, Mexico (18°36′ N, 95°02′-95°06′ W). In this area the rain forest which formerly covered the coastal plains of the Gulf of Mexico is subject to large scale clearing. The mean annual temperature in the area is 27 °C, the mean annual precipitation is 4900 mm. There is some seasonality in rainfall, with a relatively dry period extending from March to May.

We sampled the vegetation occurring under the canopy of seven isolated trees or small groups of maximally three individuals, in five open grasslands near to each other, which are actually used as such. For comparison we included two analyses from another study concerning regeneration of abandoned pastures (Purata, 1986) which regard vegetation developed after approximately 2 and 3 years of abandonment respectively. Here no remnant trees were left.

The information obtained for each individual remnant tree included: species, height, cover (canopy area), and distance to the nearest primary forest site. Exact information on the time of clearing was not available, but an estimation of age can be derived from the height of the vegetation that developed after clearing.

Species occurring underneath the remnant trees were recorded with the following scale:

scale	% cover
5	50 – 100
4	25 – 50
3	12.5 – 25
2	< 12.5, > 3 individuals
1	< 12.5, 1 – 3 individuals

In addition the ornithochory status of the observed species was noted and the successional status determined. Data on ornithochory were based on own observations on fruit type and reports by Trejo (1976), Snow (1981) and Van Dorp (1985). The common division into primary species and secondary species or pioneers was adopted. Primary trees occur in the mature forest, their seeds germinate under the full canopy and further growth of the sapling is dependent on the creation of a gap. Pioneers are colonizers of gaps and clearings germinating at high light intensities.

According to our own experience and other references (Budowski, 1965, 1970; Whitmore, 1978, 1982, 1984; Hartshorn, 1978, 1980; Vazquez-Yanes, 1980; Brokaw, 1985), we can further divide the first group into real primary species and late secondary species. The latter germinate in the shade as well but are not found in the undisturbed primary forest. The assignment of our species to either category was based on our own observations and is discussed by Guevara *et al.* (see Purata, 1986).

The vegetation data were subjected to Detrended Correspondence Analysis (DCA) (Hill & Gauch, 1980), agglomerative average linkage clustering with similarity ratio (SR) as a resemblance measure, and the table ordering program TABORD (Van der Maarel *et al.,* 1978), also with SR as resemblance measure, all in order to detect a floristic gradient and species clusters in the material.

Results

Results are summarized in Tables 1 and 2. The species list includes 29 woody species and 2 climbers, of which no less than 27 are dispersed by birds, or 86%. This figure can be compared with only 66% and 52% out of 21 and 23 species respectively in the two samples from treeless abandoned grassland. The figure is also higher than that of 66% ornithochorous species obtained for 170 species observed in secondary vegetation in the area, the fruits of which could be referred to a certain type of dissemination (Purata, 1986).

The total numbers of primary and late secondary species are 8 and 6 respectively, against only 3 and 1, and 2 and 2, respectively, in the two treeless abandoned grasslands.

The total number of woody species found under a tree canopy ranged from 6 in plot 5 to 15 in plots 3 and 6 (Table 1). Figure 1 suggests both a relation with the size of the canopy of the remnant tree, and with the food source character of the remnant tree: plots 2, 3 and 6 have each a fruit-bearing remnant

Table 1. Data on the seven remnant trees, col. 1 plot number; col. 2 species; col. 3 family; col. 4 food source type: – not edible, + fruits, specialized; + + fruits, non-specialized; col. 5 height (m); col. 6 canopy size (m²); col. 7 distance to the nearest rain forest site (m); col. 8 distance to the nearest remnant trees (m); col. 9 number of species found under the canopy.

1	2	3	4	5	6	7	8	9
1	Ceiba pentandra	BOMBACACEAE	–	25	250	15	150, 160	8
2	Zanthoxylum kellermanii	RUTACEAE	+ +	25	150	35	11, 12	13
3	Poulsenia armata	MORACEAE	+ +	20	50	30	6, 11	15
4	Nectandra sp.	LAURACEAE	+	25	50	30	6, 12	7
5	Pouteria sapota	SAPOTACEAE	+	25	120	35	50, 100	6
6	Pouteria sapota &	SAPOTACEAE		20				
	Ficus sp.	MORACEAE	+ +	18	200	50	100, 200	15
7	Ceiba pentandra	BOMBACACEAE	–	28	290	150	200, 240	13

Table 2. Species list with information on ornithochory (*), successional status: M = mature, S = late secondary, P = light demanding pioneer and early secondary species; cover-abundance value in the seven plots; and approximate height of vegetation under the tree.

		1	2	3	4	5	6	7	T
– P Acacia cornigera	MIMOSACEAE	3	3	3	2		4	2	6
– P Acalypha sp.	EUPHORBIACEAE		2						1
* M Anthurium pentaphyllum	ARACEAE	3	3	3	2	3			5
* M Brosimum alicastrum	MORACEAE			1					1
* S Bursera simaruba	BURSERACEAE		4						1
* P Citharexylum sp.	VERBENACEAE		1						1
– P Cnidoscolus sp.	SOLANACEAE				1				1
* P Coccoloba barbadensis	POLYGONACEAE		2				2	3	3
* P Conostegia xalapensis	MELASTOMATACEAE			1		1	2	2	4
* P Crataeva tapia	BIGNONIACEAE						1		1
* P Cupania dentata	SAPINDACEAE	1		2			3	2	4
* M Cymbopetalum bailonii	ANONACEAE		1						1
* S Eheretia sp.	EHERETEACEAE							3	1
* P Eugenia capuli	MYRTACEAE						1	3	2
* S Ficus sp.	MORACEAE		1						.1
* M Ocotea sp.	LAURACEAE						1		1
* M Orthion oblanceolatu,	VIOLACEAE			1					1
* M Paullinia pinnata	SAPINDACEAE			1		1			2
* P Piper hispidum	PIPERACEAE	1			1		4		3
* P Piper peltatum	PIPERACEAE			1				1	2
* P Piper umbellatum	PIPERACEAE			1				3	2
* S Pleuranthodendron mexicanum	FLACOURTIACEAE						1		1
* P Psidum guajava	MYRTACEAE							1	1
* M Psychotria sp.	RUBIACEAE						1		1
* P Sapium lateriflorum	EUPHORBIACEAE	4		2			2	5	4
– P Sida rhombifolia	MALVACEAE	3							1
* P Solanum ochraceo- ferrugineum	SOLANACEAE		3	3		3			3
* S Stemmadenia donnell-smithii	APOCYNACEAE	2	4	4	2	3	2	3	7
* M Syngonium sp.	ARACEAE	3	2	2	1	5	3	3	7
* P Tabernaemontana sp.	APOCYNACEAE		1	1	1		5	4	5
* S Zanthoxylum kellermanii	RUTACEAE		4	1			1		3
TOTAL SPECIES		8	13	15	7	6	15	13	31
TOTAL ORNITHOCHORES		6	11	14	6	6	14	12	27
TOTAL M		2	3	5	2	3	3	1	8
TOTAL S		1	4	2	1	1	3	2	6
TOTAL P		5	6	8	4	2	9	10	17
M + S %		37	54	47	43	67	40	23	45
HEIGHT OF VEGETATION m		1.5	8.0	1.5	1.0	1.5	6.0	8.0	

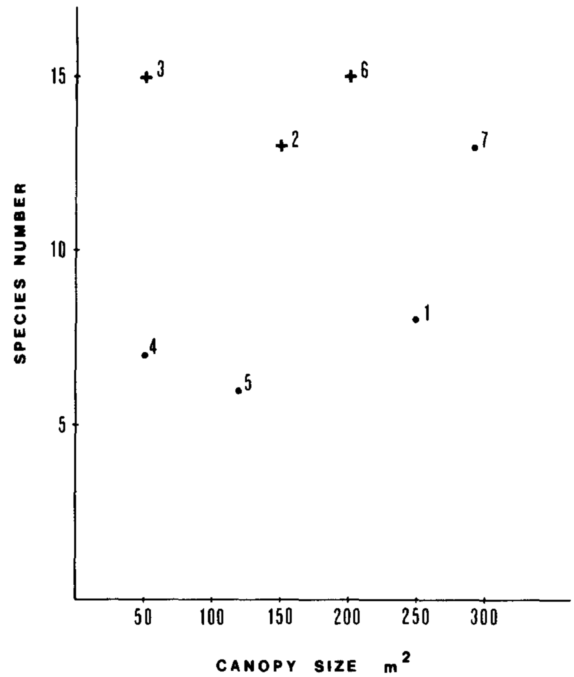


Fig. 1.

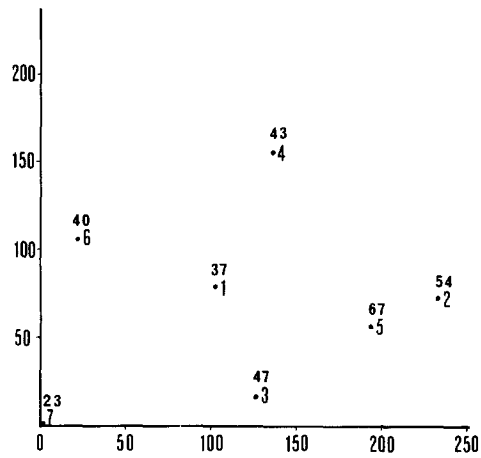


Fig. 2.

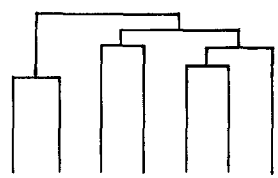
tree: *Zanthoxylum kellermanii, Poulsenia armata,* and *Ficus* sp. which are attractive to an unspecialized bird species assemblage.

A *t*-test showed that the average number of species under fruit-bearing trees, 14.3 is significantly higher than that under other trees, 8.4 ($p<0.05$). The Spearman rank correlation coefficient for the correlation between species number and canopy size for the four non fruit-bearing trees is high, $r=0.80$, but due to the few degrees of freedom the significance level is only at $p<0.20$.

Species number is not correlated with height of the remnant tree, neither with proximity to the nearest remnant trees or nearest primary forest site nor with height of the vegetation under the tree. In fact, while comparing the two samples under the same tree species, *Ceiba,* the more isolated site 7 (with an only slightly larger canopy size) has a larger number of species than the less isolated site 1.

The floristic variation in the plots is presented in the DCA diagram (Fig. 2), the dendrogram and the summarized TABORD-table in Table 3. The variation along axis 1 runs from plots 6 and 7 to plots

Table 3. TABORD-table of the seven sites, with 4 cluster solution from average linkage clustering at SR = 0.45, arranged according to Figure 2 with differentiating and common species. Dendrogram resulting from the cluster analysis is added.



PLOT NUMBER	7	6	1	4	3	5	2
CLUSTER CODE	4	4	1	3	2	2	2
Eugenia capuli	3	1	-	-	-	-	-
Coccoloba barbadensis	3	2	-	-	-	-	2
Tabernaemontana sp.	4	5	-	1	1	-	1
Sapium lateriflorum	5	2	4	-	2	-	-
Cupania dentata	2	3	1	-	2	-	-
Acacia cornigera	2	4	3	2	3	-	3
Stemmadenia donnell-smithii	3	2	2	2	4	3	4
Syngonium sp.	3	3	3	1	2	5	2
Piper hispidum	-	4	1	1	-	-	-
Zanthoxylum kellermanii	-	1	-	1	4	-	-
Sida rhombifolia	-	-	3	-	-	-	-
Anthurium pentaphyllum	-	-	3	2	3	3	3
Solanum ochraceo-ferrugineum	-	-	-	-	3	3	3
Paullinia pinnata	-	-	-	-	1	1	-
Acalypha sp.	-	-	-	-	-	-	2
Bursera simaruba	-	-	-	-	-	-	4

5 and 2. The first two plots form a cluster with *Tabernaemontana* sp. and *Eugenia capuli* as differentiating species. Plots 5 and 2 form a cluster together with plot 3, characterized by *Solanum ochraceo-ferrugineum.* Similarity values between plots are low however, clusters are loose and the main impression is one of variation. This variation is not related to species richness: the richest sites 3 and 6 are at opposite ends of axis 1. There is some indication for a relation with distance to the nearest forest site in that the two plots at one end of axis 1, nrs. 6 and 7 are the two most remote ones. Spearmans rank correlation coefficient is only 0.31 (non significant).

Regarding the successional status of the species involved, sites 7 and 6 have only one and two primary species of the mature forest (M-species) respectively, including the generally occurring climber *Syngonium.*

If we take primary (M) and late secondary (S) species as a group of 'shade-germinating' and follow their relative importance (Fig. 2) the *Solanum* type (sites 3–5–2) to the right has 56%, the *Sapium-Tabernaemontana* type (6–7) only 32%. The percentage of M+S species appears to be positively correlated with position on axis 1 (Spearmans $r = 0.89$, $p < 0.01$).

We could assume a relation between percentage of M+S species, and height of the understorey, as such an indication of age. However, the height of the vegetation under the tree is not correlated with any of the parameters involved.

Discussion and conclusions

Our results suggest the following:

1) The sites underneath remnant trees are rapidly colonized by woody species and the character of these species is different from comparable sites in early secondary succession.

2) The percentage of ornithochorous species under remnant trees is higher than on comparable sites in early secondary succession.

3) Relatively many species are mature primary forest and late secondary species and the floristic variation of the sites is related to the relative amount of those species.

4) The total number of species varies considerably, but this variation does not seem to be correlated with such obvious parameters as canopy size, distance of the remnant tree to primary forest stands and vegetation height under the tree. The only clear indication is that trees bearing fruits attractive to unspecialized birds have more species under their canopy.

These suggestions point to two hypotheses regarding the mechanisms involved in regeneration with the help of remnant trees.

a) birds are important vectors for the dispersal of seeds to sites under remnant trees.

b) conditions under remnant trees are favourable for the establishment of primary and late secondary forest trees.

A further hypothesis is that the speed of regeneration and the diversity of trees included in secondary succession will also be dependent on the density of remnant trees.

Regarding the attractiveness of remnant trees information would be needed on the categories and numbers of birds visiting them and on their feeding behaviour, as well as on changes in categories and numbers during secondary succession.

Regarding the germination and establishment conditions we would need experimental evidence on the effect of irradiance and light quality (R/RF ratio) in the germination and establishment of species with contrasting ecology (Guevara & Grime, in prep.).

The interesting variation in the relation between 'shade' versus 'light' species should be followed up by a study of real secondary succession. Purata (1986) had analyzed 40 sites under secondary succession which vary in age of abandonment from 1 to 30 years, and has found important differences, between the sites in relation to the availability of propagules, which is thought to be directly connected with the dispersal mechanisms of the species. Also some patterns of clumped species were found, presumably created by the differential deposition of seeds created by their dispersors.

One aspect of the results not mentioned so far deserves some discussion. It is intriguing that a few species occur under most or even all remnant trees. Either they have special advantages during dispersal or conditions under the remnant tree favour them.

The only special characters we have found so far are the presence of spines, in *Acacia cornigera* and *Solanum ochraceo-ferrugineum,* and the occurrence of latex in *Sapium lateriflorum, Stemmadenia donnell-smithii* and *Tabernaemontana* sp. These characters make them unpalatable for cattle. This would imply that cattle grazing is another important factor in selecting woody species in the early phases of regeneration.

The process of recolonization under remnant trees in grasslands can be summarized into three main stages:

1. Germination of seeds, either from the local seed bank or brought in through dispersal from the surrounding forest.

2. Grazing of palatable seedlings, persistance of species with chemical or mechanical protection which will form a first barrier for the cattle.

3. Successive recruitment of species dispersed by birds attracted to the tree either for food or shelter. Further development of shade tolerant trees is enhanced by the new conditions beneath the tree.

References

Brokaw, N. V. L., 1985. Treefalls, regrowth, and community structure in tropical forests. In: S. T. A. Pickett & P. S. White (eds), The ecology of natural disturbance and patch dynamics, pp. 53–69. Academic Press, Orlando.

Budowski, G., 1965. Distribution of tropical American rain forest species in the light of successional processes. Turrialba 15: 40–42.

Budowski, G., 1970. The distinction between old secondary and climax species in tropical Central American lowland forests. Trop. Ecol. 11: 44–48.

Debussche, M., Escarre, J. & Lepart, L., 1982. Ornithochory and plant succession in mediterranean abandoned orchards. Vegetatio 48: 255–266.

Debussche, M., Lepart, J. & Molina, J., 1985. La dissémination des plantes à fruits charnus par les oiseaux: rôle de la structure de la végétation et impact sur la succession en région méditerranéenne. Acta Oecol. Oecol. Gener. 6: 65–80.

Fleming, T. H. & Heithaus, R., 1981. Frugivorous bats, seed shadows, and the structure of tropical forests. Biotropica 13 (suppl.): 45–53.

Golley, F. D., (ed.), 1983. Tropical rainforest ecosystems. Ecosystems of the world, Vol. 11. Elsevier Amsterdam. 381 pp.

Gómez-Pompa, A., Vázquez-Yanes, C. & Guevara, S., 1972. The tropical rain forest: A nonrenewable resource. Science 177: 762–765.

Gómez-Pompa, A., Vázquez-Yanes, C., Amo Rodriguez, S. del & Butanda, A. (eds), 1976. Regeneración de Selvas. Compañía Editorial Continental, México. 677 pp.

Hall, J. B. & Swaine, M. D., 1981. Distribution and ecology of vascular plants in a tropical rain forest. Forest Vegetation in Ghana. Junk, The Hague. 383 pp.

Halle, F., Oldeman, R. A. A. & Tomlinson, P. B., 1978. Tropical trees and forests, an architectural analysis. Springer-Verlag, Berlin, 250 pp.

Hartshorn, G. S., 1978. Treefalls and tropical forest dynamics. In: P. B. Tomlinson & M. H. Zimmermann (eds) Tropical trees as living systems. pp. 617–638. Cambridge University Press, London.

Hartshorn, G. S., 1980. Neotropical forest dynamics. Biotropica 12 (suppl.): 23–30.

Hill, M. O. & Gauch, H. G., 1980. Detrended correspondence analysis, an improved ordination technique. Vegetatio 42: 47–58.

Howe, H. F. & Smallwood, J., 1982. Ecology of seed dispersal. Ann. Rev. Ecol. Syst. 13: 201–228.

Kellman, M., 1979. Soil enrichment by neotropical savanna trees. J. Ecol. 67: 565–577.

Kellman, M., 1985. Forest seedling establishment in neotropical savannas: transplant experiments with Xylopia frutescens and Calophyllum brasiliense. J. Biogeogr. 12: 373–379.

Kellman, M. & Miyanishi, K., 1982. Forest seedling establishment in neotropical savannas: observations and experiments in the Mountain Pine Ridge savanna, Belize. J. Biogeogr. 9: 193–206.

Longman, K. A. & Jenik, J., 1978. Tropical forests and its environment. Longman, London. 205 pp.

McDonnell, M. J. & Stiles, E. W., 1983. The structural complexity of the old field vegetation and the recruitment of bird-dispersed plant species. Oecologia (Berlin) 56: 109–116.

Miles, J., 1979. Vegetation dynamics. Chapman & Hall, London. 80 pp.

Packham, J. R. & Harding, D. J. L., 1982. Ecology of woodland processes. Edward Arnold. 261 pp.

Purata, S., 1986. Studies on secondary succession in Mexican tropical rainforest. Thesis Uppsala.

Smith, A. J., 1975. Invasion and ecesis of bird-disseminated woody plants in a temperate forest sere. Ecology 56: 19–34.

Snow, D. W., 1981. Tropical frugivorous birds and their food plants: a world survey. Biotropica 13: 1–14.

Sutton, S. L., Whitmore, T. C., & Chadwick, A. C. (eds), 1984. Tropical rain forest: ecology and management. Blackwell, Oxford. 498 pp.

Trejo, L., 1976. Diseminación de semillas por aves en 'Los Tuxtlas', Veracrúz. In: A. Gómez-Pompa, C. Vázquez-Yanes, S. del Amo & A. Butanda (eds), Regeneración de Selvas pp. 447–470.. Compañia Editorial Continental, S.A., Mexico.

Uhl, C., Clark, H., Clark, K. & Maquirino, P., 1982. Successional patterns associated with slash-and-burn agriculture in the upper Rio Negro region of the Amazon Basin. Biotropica 14(4): 249–254.

Van der Maarel, E., Janssen, J. G. M. & Louppen, J. M. W., 1978. TABORD, a program for structuring phytosociological tables. Vegetatio 38: 143–156.

Van Dorp, D., 1985. Frugivoria y dispersion de semillas por aves. In: A. Gómez-Pompa (ed.), Regeneracion de Selvas II. Compañía Editorial Continental S.A., México.

Vázquez-Yanes, C., 1980. Notas sobre la autoecología de los arboles pioneros de rápido crecimiento de la selva tropical lluviosa. Trop. Ecol. 21(1): 103–111.

Werger, M. J. A., 1983. Tropical grasslands, savannas, woodlands: natural and man-made. In: W. Holzner, M. J. A. Werger & I. Ikusima (eds), Man's impact on vegetation, pp. 107–138. Junk, The Hague.

Whitmore, T. C., 1984. Tropical rain forest of the Far East. Clarendon Press, Oxford. 352 pp.
Whitmore, T. C., 1978. Gaps in the forest canopy. In: P. B. Tomlinson and M. H. Zimmermann, (eds) Tropical trees as living systems pp. 639–655. Cambridge University Press, London.
Whitmore, T. C., 1982. On pattern and process in forests. In: E. J. Newman, (ed.), The plant community as a working mechanism, pp. 45–59. Blackwell, Oxford.
Yarranton, G. A & Morrison, R. G., 1974. Spatial dynamics of a primary succession: nucleation. J. Ecol. 62: 417–428.

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