Regeneration strategy and plant diversity status in degraded sal forests

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The degraded sal forests of north-eastern Uttar Pradesh were observed for the regeneration strategy of constituent woody perennials and the status of resultant plant diversity. The species showing poor sprouting were much greater in number at low disturbance. Conversely, the species showing rich sprouting and ramet formation were much more at high disturbance. The diversity index ($\overline{H}$) was always greater when a genet complex was treated as a single individual than in case when each ramet, distinct at soil surface, was treated as a separate individual. The value of $\overline{H}$, however, was lower at low disturbance. It is a moot point whether the diversity index should be based on the number of genets (biotypes) or superficially distinct shoots (including ramets) irrespective of their genetic status. The species like *Clerodendron infortunatum*, *Croton oblongifolius*, *Mallotus philippensis* and *Flacourtia indica* increased their ramet production with increase in disturbance level, but recurrent disturbance of high intensity affected ramet proliferation quite adversely. *Bridelia retusa*, *Casearia tomentosa* and *Holarrhena antidysenterica* produced comparatively much lesser number of ramets per genet. The inter-ramet distances or spacers on root-stock as well as the number of ramets per genet showed significant differences with respect to the level of disturbance. The age structure and spatial pattern of ramet population were also correlated with the level of disturbance. In a forest environment which is too harsh to allow regeneration through seed, a non-seed regeneration of a group of woody perennials may help maintain the minimal vegetation cover and considerable plant diversity. The non-seed regeneration strategy of prolific ramet producers, therefore, shows a promise to the quick recovery of forest ecosystems ravaged by anthropogenic perturbations.

SEED germination and vegetative propagation are the two major modes of regeneration in perennial plants. The morphological units in the form of vegetative offshoots, initially physically attached to the parent plant but capable of independent existence are called ramets, while a genet is a plant of seed origin irrespective of the number of sprouts and/or ramets originating from it[1]. All parts of the genet share exactly the same genes. As in many perennial herbs, a number of woody plants also show continuity of root-stocks in the form of inter-ramet connections which make the genet a physiologically integrated system. The phenomenon is well documented in several perennial herbs[2], but such reports are rare in case of woody perennials[3]. The connection between any two ramets may disappear after a few years of ramet growth or may persist for many years[4]. Species found in harsh environments are known to regenerate mainly by non-seed method, as evident from the studies on growth and regeneration of several clonal species[5,6]. In some cases, disturbance may cause significant changes in size and structure of plant populations, by influencing the regeneration of adult plants[7].

A few studies on Indian sal forest vegetation are available which have analysed the woody vegetation of *Shorea* communities[8,9] and have compared the *taungya* plantation with natural forest tract at Darjeeling Himalayas with greater emphasis on the alteration of landscape, loss of species and recovery of the system[10]. The architectural adjustment of common sal associates[11] and the changes in community and diversity pattern in relation to the degree of disturbance[12] have also been observed. Studies on several other Indian forests seem to indicate that prevalent disturbance, mainly from fire and grazing, severely affects the regeneration of most of the tree species[13–15]. The degree of proliferation of ramets from a genet and the size of ramet population of constituent species may alter the dominance and diversity of the forest community, but such observations are still lacking. The present study, therefore, attempts to observe the effect of disturbance on the diversity status of degraded sal forests of north-eastern Uttar Pradesh (UP), especially due to changes in genet versus ramet population. The significance of non-seed regeneration strategy of the constituent woody perennials which provide the minimum understorey vegetation cover to the disturbed forests, has also been discussed.

The study was conducted in Sohagibarwa Wildlife Sanctuary under Gorakhpur Forest Division, UP. The sanctuary is located between 27°05′ and 27°25′N latitude and 83°20′ and 84°10′E longitude and at 95 m altitude. The climate is seasonal and sub-tropical. The total average annual rainfall is about 1814 mm, 87% of which occurs during the wet summer or monsoon season. During the relatively dry period of about 8 months, i.e. January–June and November–December the monthly rainfall is less than 100 mm. The soil is old Gangetic alluvium. The texture is sandy loam and the soil reaction is circum-neutral. The regional forest of north-eastern UP is of subtropical semi-evergreen type with a number of deciduous elements. Of the total 428.2 km^2 forested area of the sanctuary, 2.32% is still under the natural, semi-evergreen forest vegetation[16]. The deciduous plantations of Gorakhpur Forest Division[17] consist mostly of sal (*Shorea robusta* Gaertn), planted mainly through *taungya* system. In this system, the clear-cutting of natural-growth forests follows the operations like ground-clearing by landless farmers (also called taungya), who plough the site and use the land

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for taungya cultivation. Freshly-collected sal seeds are sown in lines at intervals of about 10 feet between any two lines and the inter-line spaces are used to cultivate cereals, pulses and vegetables for 2–3 consecutive years. Once the sal saplings get established, their rows cast shade, rendering the site unsuitable for supporting any more agricultural crops. Now the site is abandoned, the sal saplings are left to grow naturally and ecological succession sets in. As the sal ages, the associated vegetation also develops naturally and gains considerable species diversity. Of these, several over- and understorey trees, a number of shrubs and some perennial herbs may grow as sal associates. The resultant plant community, developing in association with sal plantation, fairly mimics the composition of natural growth forests of the region[8].

Two stands of plantation forests of sal were identified, one within peripheral region facing high disturbance and the other within the interior of buffer zone of the sanctuary facing much lesser disturbance. The age of the stands was 50 ± 5 yr and they represented average conditions of their respective disturbance regime, species content and vegetation pattern. The degree of disturbance was measured through a disturbance index (DI) based on the per cent number of cut, damaged or mutilated individuals of associated plant communities[12]. A DI value of 60 was taken as the lower limit of high disturbance and a value of 30 as the upper limit of low disturbance for the observations on ramet population of different species. A brief description of study sites is given in Table 1. The requisite size of the sample plot for adequate sampling of forest vegetation was found to be 10,000 ± 1000 m^2 (Pandey and Shukla, unpublished data). Therefore one-hectare (100 m × 100 m) sample plots having average ground vegetation were marked in each of the above two stands. Each plot was divided into 4 quarters and each quarter was further sub-divided into 25 quadrats each of 10 m × 10 m size. Trees and undertrees of > 30 cm gbh were counted in all the 25 quadrats of each quarter. For accounting the individuals of < 30 cm gbh, only 10 random quadrats per quarter, i.e. a total of 40 quadrats (0.40 hectare) per hectare plot were observed. The data, however, were suitably multiplicated to represent them on per hectare basis.

In the presence of recurrent disturbance, most of the tree species remained as shrubs with no clear main axis. All the species encountered in both plots were categorized as sprouters and ramet-producers. The sprouter species were divided into least-sprouting, moderately-sprouting and highly-sprouting ones on the basis of their sprouting efficiency. Least-sprouter species generally produced one or two sprouts, moderate-sprouters produced 3–5 sprouts and high (prolific)-sprouters always had > 5 sprouts per plant (Table 2). After careful excavation of subterranean system, the vertical and lateral spread of roots of constituent species was traced. The individuals which showed separate identity at the soil surface were interconnected

Table 1. Species-specific characteristics of the forest vegetation at sites facing high or low disturbance

	High disturbance (DI > 60%)	Low disturbance (DI < 30%)
No. of herbaceous species	31	8
No. of woody species	137	246
Per cent evergreen species	33	28
Per cent deciduous species	67	72
Dominant trees (> 30 cm gbh)	*Mallotus philippensis* (Lamk.)	*Mallotus philippensis* (Lamk.)
	Holarrhena antidysenterica (Roth.) A. Dc.	*Schleichera oleosa* (Lour.) Oken.
	Flacourtia indica (Burm. f.) Merr.	*Bridelia retusa* Hook. f.
	Casearia tomentosa Roxb.	*Alstonia scholaris* (Linn.) R. Br.
	Bridelia retusa Hook. f.	*Dillenia indica* Linn.
	Bauhinia purpurea Linn.	*Semecarpus anacardium* Linn. f.
	Diospyros malabarica (Ders.) Kostel	*Careya arborea* Roxb.
Undergrowths (< 30 cm gbh)	*Clerodendron infortunatum* Gaerin.	*Moghania bracteata* (Roxb.) in Li
	Croton oblongifolius Roxb.	*Leea macrophylla* Linn.
	Moghania chappar (Ham.Ex.Benth.)Ktze.	*Cassia fistula* Linn.
	Antidesma ghaesembilla Gaertn	*Adina cordifolia* (Roxb.) Hook. f.
	Dalbergia lanceolaria Linn. f.	*Bauhinia purpurea* Linn.
	Bauhinia vahlii W. EA.	*Piper* sp.
	Leea sambusina Linn.	*Woodfordia fruticosa* (L.) Kurz.
Species of rare occurrence	*Bauhinia vahlli* W. EA.	**Abrus precatorius* Linn.
	Miliusa tomentosa (Roxb.) Sinclair	**Butea monosperma* (Lamk.) Taub.
	Mitragyna parvifolia (Roxb.)	**Desmodium latifolium* (Linn) Dc.
	Stereospermum suaveolens Dc.	**Ehretia laevis* Roxb.
	Streblus asper Lour.	**Rauwolfia serpentina* (Linn.) Benth.
	Terminalia chebula Retz.	**Kydia calycina* Roxb.
	Thespesia lampas Dalz & Gibs.	**Ougenia dalbergioides* Benth.

*These species were altogether absent from stands facing high disturbance.

Table 2. List of commonly occurring species with their natural habit

Plant species	Actual habit
Sprouting species	
Least-sprouting species	
Abrus precatorius Linn.	C
Acacia catechu Willd.	T
**Adina cordifolia* (Roxb.)Hook. f.	T
Alangium salvifolium (Linn. f.)Wang.	T
**Alstonia scholaris* (Linn.) R. Br.	T
Asparagus racemosus Willd.	C
Butea monosperma (Lamk.) Taub.	T
**Careya arborea* Roxb.	T
Desmodium heterocarpon (Linn.) Dc.	S
Desmodium latifolium Dc.	S
**Dillenia indica* Linn.	UT
Ehretia laevis Roxb.	T
Erythrina indica Lamk.	T
Gloriosa superba Linn.	C
Kydia calycina Roxb.	T
**Leea macrophylla* Linn.	UT
Moghania prostrata (Roxb.) Mukherjee	S
**Morus laevigata* Wall.	UT
Ougeinia dalbergioides Benth.	T
Pongamia pinnata (L.) Pierrc.	T
Pterocarpus marsupium Roxb.	T
Pterospermum acerifolium Willd.	T
Rauwolfia serpentina (Linn.) Benth.	S
Tinospora cordifolia (Willd.) Miers.	C
Moderate-sprouting species	
**Bauhinia purpurea* Linn.	T
**Bridelia stipularis* (Linn.) Blume.	C
**Carissa spinarum* Linn.	UT
**Colebrookia oppositifolia* Sm.	S
**Diospyros malabarica* (Desr.)Kostel.	T
Phyllanthus emblica Linn.	T
Piper sp.	C
**Schleichera oleosa* (Lour.) Oken.	T
**Semecarpus anacardium* Linn. f.	T
Shorea robusta Gaertn. f.	T
Smilax lamifolia Linn.	C
Smilax macrophylla (Roxb.)	C
**Stereospermum suaveolens* Dc.	T
**Thespesia lampas* Dalz & Gibs.	UT
**Woodfordia fruticosa* (L.) Kurz.	UT
High-sprouting species	
Bauhinia vahlii W. EA.	C
**Cassia fistula* Linn.	UT
Desmodium pulchellum (L.) Benth.	S
Leea sambusina Linn.	S
**Moghania bracteata* (Roxb.) in Li	UT
Ramet-producing species	
**Antidesma ghaesembilla* Gaertn.	UT
**Bridelia retusa* Hook. f.	T
**Casearia tomentosa* Roxb.	UT
**Clerodendron infortunatum* Gaerin.	UT
**Croton oblongifolius* Roxb.	UT
**Dalbergia lanceolaria* Linn. f.	UT
**Flacourtia indica* (Burm. F.) Merr.	T
**Holarrhena antidysenterica* (Roth)A.Dc.	T
**Mallotus philippensis* (Lamk.)	T
Moghania chappar (Ham.Ex.Benth.)Ktze.	S
Moghania lineata (L.) Ktze.	S

*Species occurring mostly in the habit of shrubs. T, tree; UT, under-tree; S, shrub; and C, climber or liana. The species have been categorized into sprouting and ramet-producing groups.

through subterranean horizontal root-stock in case of eleven species. The root-stock produced root-suckers (the adventitious buds formed on any part of the root system), which subsequently developed into ramets. These ramets were potentially independent, subsequently developing their own root system. In some species, however, the young ramets were devoid of any root system of their own. The position of emergence of every ramet was marked to draw the spatial distribution of ramet population of a single genet. The degree of ramet proliferation, however, varied for different species. It generally ranged from 60 to 90% of the total genets of a species. The size of the ramet population of a single genet and the inter-ramet distances (IRD) in different ramet-producing species were measured. The replication varied from 5 to 10, based on the availability of suitable genet and its ramet population. Generally, the most vigorous and old shoot of the complex happened to be the genet and all other superficially independent shoots were ramets. The number of ramets per genet and the IRD of different species at the two disturbance levels were compared. In another related observation, the ramet population of common ramet-producing species was identified at five different sites from periphery to the core of the sanctuary facing increasing level of disturbance. DI ranged as 5–20 (D_1); 21–40 (D_2); 41–60 (D_3); 61–80 (D_4) and 81–95 (D_5). The level of significance of the differences between the number of ramets per genet and inter-ramet distances with respect to high and low disturbance was also tested.

The dominance (C) for each community was calculated by Simpson's index ($C = \sum pi^2$) and diversity by Shannon's index ($\overline{H} = -\sum pi \ln pi$), where pi represents the proportional abundance of ith species in any given stand. The calculation of dominance and species diversity was made on two counts – first by treating the whole population of ramets along with their genet (genet-complex) as a single individual and second by taking each superficially distinct shoot as a separate individual. The structure of the ramet population of a single genet of different species was observed in sal stands facing high or low disturbance. Most of the identified genets which showed active ramet production with intact organic connections, were about 5 years old. The age of the genet was determined on the basis of annual growth pattern, number of branch tiers, short inter-node and the branch and leaf scars on the main axis of the individual of a species[18,19]. The ramets of each genet were sorted out into five vigour classes based on the average dry weight. The per cent number of ramets of different vigour classes was compared with respect to the two disturbance levels.

Disturbance acts as selection pressure and specializes species according to the conditions it creates, paving way to fugitivity even in closed communities[20]. At intermediate rates of disturbance, a range of sites becomes available which allow the full range of species traits to coexist, leading to maximal species diversity. Thus, diversity is expected to be maximum at intermediate frequencies or intensities of disturbance, as hypothesized by the 'intermediate disturbance hypothesis'[21,22]. In other words, periodically perturbed non-equilibrium systems are expected to have a higher diversity than 'equilibrium' ecosystems where competitive exclusion is probably higher[23]. Natural regeneration may occur even after large-scale disturbance by biotic and abiotic events[24], but the mechanism of regeneration may differ for different species as determined by their growth features and nature of disturbance. At low disturbance, all the ramet-producing species did regenerate through seeds showing little ramet-formation and maintained quite low ramet population among individuals mostly of seed origin. Thus, the disturbance as such was not essential for survival of these species. At moderate disturbance, a better ramet-proliferation resulted into a sizable genet-complex. At high disturbance, however, the species which depended exclusively on their seed for regeneration and could not propagate themselves vegetatively, were gradually pushed towards rarity. In such a situation, the ramet-producer species can utilize the niche space vacated by species being rarer. At very high disturbance, the recurrent perturbations of high intensities may alter the habitat to such an extent that even prolific ramet producers can hardly survive. In general, most of the ramet producers were also prolific sprouters. Least-sprouting species were maximum at low disturbance, while the moderate-sprouters as well as high-sprouters were more common at intermediate disturbance, as evident also from other observations[25].

Table 3. Density/ha of sprouting and ramet-producing tree, under-tree and shrub species in tree-form as well as in sapling form in sal forests facing high or low level of disturbance (HD/LD)

	Density/ha			
	Tree form (> 30 cm gbh)		Sapling form (< 30 cm gbh)	
Species group	HD	LD	HD	LD
Sprouting species				
Least-sprouting				
Trees	1	8	85	226
Under-trees	1	2	51	201
Shrubs	–	–	167	508
Total	2	10	303	935
Moderate-sprouting				
**Shorea* trees	252	319	3011	7621
Other tree species	1	24	3534	2596
Under-trees	2	18	821	511
Shrubs	–	–	9210	999
Total	255	361	16,576	11,727
High-sprouting				
Tree species	–	–	–	–
Under-trees	1	11	740	471
Shrubs	–	–	2003	516
Total	1	11	2743	987
Ramet-producing species				
Tree species	57	111	25,141	14,924
Under-trees	–	1	24,323	1,140
Shrubs	–	–	30,737	11,781
Total	57	112	80,201	27,845
Grand total	315	494	99,823	41,494

*Sal (*Shorea robusta*), a moderate sprouting species, has been mentioned separately as it is the planted timber with maximum number of individuals in tree form.

Less-disturbed hectare-plots had greater number of trees (> 30 cm gbh) than the highly-disturbed ones (Table 3). Of the 246 identified species, which were encountered at sites facing low disturbance, only 137 could survive at high disturbance. The number of species under different habit groups (trees, shrubs and perennial herbs), showing very poor or no sprouting, was much greater in less-disturbed stands. Conversely, the species showing asexual reproduction were much greater in number in sal stands facing high disturbance (Table 4). It may be argued that at a critical level of disturbance, the species lacking asexual regeneration strategy might have been pushed towards rarity or even disappearance[26].

Frequent small-scale disturbances have been hypothesized to be important events in structuring many forest communities by altering abundances and distributions of biotic and abiotic resources[27]. Here we calculate diversity and dominance indices in two ways: (i) by taking the genet as well as all its ramets as a single individual (genet complex), and (ii) by taking the genet as well as each of its ramets as separate individuals at the two disturbance levels. At high disturbance, in the first condition, the

Table 4. Total number as well as per cent number of species falling under different habit groups of sprouting and ramet-producing categories in sal stands facing high or low level of disturbance (HD/LD)

			Per cent number of species					
			Sprouters					
	Total number of species		Least-sprouting		Sprouting		Ramet producers	
Habit groups	HD	LD	HD	LD	HD	LD	HD	LD
Trees	34	72	3	23	76	74	21	3
Shrubs	86	141	2	12	93	87.3	5	0.7
Perennial herbs	17	33	6	38	88	62	6	0

number of rare species was low and the number of individuals per species was also not very high, resulting in high diversity and low dominance. In the second condition, the species represented by very few individuals, were very low in number and relatively fewer species had high number of individuals. In this condition, the community showed low diversity and very high dominance. At low disturbance, in the first condition, the number of rare species was more, but the number of individuals of different species was fairly high, resulting into higher values of diversity and dominance. In the second condition, however, the number of rare species as well as the individuals of these species was relatively fewer, leading to slightly lower diversity and dominance (Table 5). Irrespective of the level of disturbance, the value of $\overline{H}$ was greater whenever a genet complex was treated as an individual than in case when each ramet was treated as a separate individual. The dominance and diversity phenomena are based on the criterion that each individual is a biotype with a unique set of alleles contributing to the total heterozygosity of the community[28]. In disturbed environments, however, the number of superficially distinct individuals differs significantly from the number of biotypes. It is a moot point whether the diversity index should be based on genet (biotype) or on each superficially distinct shoot irrespective of its genetic status. High disturbance conditions species richness and allows only a small set of species which are able to withstand and perpetuate themselves in the community mainly through vegetative or asexual mode of reproduction. While moderate disturbance might result in a non-equilibrium, species-rich system, high disturbance interferes with the proper vegetative growth, successful flowering and fruiting of species, pushing them towards rarity. Thus, species which can regenerate efficiently by non-seed methods can withstand the vagaries of high disturbance. As Simpson's index is heavily weighed towards the most abundant species in the sample and is less sensitive to species having only a few individuals[28], the value of this index is always high at high disturbance provided that each superficially distinct shoot is considered as an individual.

Clonality is an important plant strategy found in many vegetation types and may play an important role in ecosystem recovery. Expansion of clonal plants is influenced by the degree of integration among sister ramets in a genet and the length of time they remain connected. The spread of genets, integration of patch types and response of clonal shrubs and trees to herbivory are still little understood[29]. The response of a plant species to the physical environment is conditioned by interaction with other species. In species where there is no need of below-ground storage, the rhizomes are replaced by foraging roots which explore the vacant microsites[30]. *Antidesma ghaesembilla*, *Clerodendron infortunatum*, *Croton oblongifolius*, *Flacourtia indica* and *Mallotus philippensis* were observed to be efficient ramet producers. The number of ramets per genet ranged from 1 to 28 and it varied with the degree of disturbance (Table 6). Disturbed sal-forest habitat witnessed more ramet production compared to less-disturbed stands. *Bridelia retusa*, *Casearia tomentosa* and *Holarrhena antidysenterica* had low number of ramets per genet even at high disturbance. Since sexual recruitment appears to be rare in clonal plants[31] and the sprouting as well as ramet-producing species generally show very low percentage of field germination and seedling establishment (Shukla and Pandey, unpublished data), a set of species, well adapted to proliferate asexually, may be able to provide a minimum vegetation cover to the fragile understorey of the recurrently disturbed forest. At moderate disturbance, the species which were efficient sprouters could do well but at high disturbance, the underground foraging of roots and production of root suckers sent ramets at varying intervals. In addition to sprouting, ramet production is a complementary strategy responsible to maintain at least a depauperate plant community in a hostile environment.

The two plots were different not only in their DI value based on per cent number of cut, severed or mutilated individuals per unit area, but quite often the peripheral stands also faced heat stress during dry summer. All the ramet-producing species showed highly significant differences in the number of ramets per genet with respect to the level of disturbance (t-test, $P < 0.01$) to which the communities were exposed. Similarly, the inter-ramet distance (IRD) or spacers on subterranean horizontal root-stock was significantly greater at low disturbance, except in case of *M. chappar* (t-test, $P < 0.01$). It is evident that, plant species that can propagate vegetatively through rhizomes or root-stock may spread over much larger distances than non-clonal species in a similar environment. They regularly encounter favourable and non-favourable patches, which accounts for their plasticity in ramet placement[32,33]. The spacers with shorter internodes and increased branching intensities may result in concentration of ramets in favourable patches, maximizing acquisition of resources[34] as evident in case of *C. infortunatum*, *C. oblongifolius* etc. Such a plastic response allows the plant to forage for the best microsites available within its environment[32]. Thus many plant species can respond to patchiness by concentrating root and shoot growth in resource-rich areas[35]. Both the disturbance and resource

Table 5. Values of diversity index ($\overline{H}$) and dominance index (D) for sal forests, based on the whole genet complex as a single individual and each superficially distinct shoot, irrespective of being genet or ramet, as separate individuals at two different levels of disturbance (HD/LD)

Disturbance level	Genets complex treated as single individual		Each genet and ramet as separate individuals	
	$\overline{H}$	D	$\overline{H}$	D
HD	2.620	0.103	2.060	0.256
LD	2.565	0.114	1.899	0.093

Table 6. The number (mean ± S.D.) of ramets per genet complex and the inter-ramet distances (given in parentheses) for different ramet-producing species in stands facing high or low degree of disturbance

Species	The number (Mean ± SD) of ramets per genet complex and inter-ramet distance (cm)	
	High disturbance	Low disturbance
1. *Antidesma ghasembilla* Gaertn.	6.9 ± 1.52 (22.1 ± 7.60)	1.6 ± 0.70 (77.0 ± 14.82)
2. *Bridelia retusa* Hook. f.	2.8 ± 0.63 (12.8 ± 2.86)	1.4 ± 0.70 (21.1 ± 3.64)
3. *Caesaria tomentosa* Roxb.	3.9 ± 1.0 (15.5 ± 2.80)	1.4 ± 0.70 (60.9 ± 12.9)
4. *Clerodendron infortunatum* Gaerin.	20.2 ± 8.11 (14.8 ± 5.94)	2.6 ± 0.87 (29.1 ± 8.2)
5. *Croton oblongifolius* Roxb.	19.7 ± 6.60 (16.8 ± 6.73)	1.7 ± 0.82 (32.3 ± 9.95)
6. *Dalbergia lanceolaria* Linn. f.	3.5 ± 1.43 (10.6 ± 2.37)	1.4 ± 0.70 (22.0 ± 5.7)
7. *Flacourtia indica* (Burm. F.) Merr.	4.5 ± 1.35 (14.1 ± 2.77)	1.6 ± 0.84 (21.1 ± 5.59)
8. *Holarrhena antidysenterica* (Roth.) A. Dc.	3.7 ± 0.95 (12.8 ± 3.88)	1.3 ± 0.48 (57.4 ± 12.9)
9. *Mallotus philippensis* (Lamk.)	9.3 ± 2.31 (13.4 ± 4.27)	2.6 ± 0.97 (34.8 ± 9.72)
10. *Moghania chappar* (Ham.Ex.Benth.) Ktze.	16.0 ± 3.00 (1.2 ± 0.42)	2.4 ± 1.35 (1.6 ± 0.52)
11 *Moghania lineata* (L.) Ktze.	2.6 ± 0.52 (2.0 ± 0.82)	1.3 ± 0.48 (8.5 ± 2.6)

The differences between the two disturbance levels with respect to the number of ramets and inter-ramet distance were significant at $P < 0.01$ (t-test) for all the above species except for *M. chappar*.

availability play important roles in plant community organization[36]. The capacity of established plants to capture resources, persist and avoid competitive exclusion ultimately determines their performance within communities[37,38]. Mallik and Gimingham[39] report that several Ericaceae are able to resprout quickly after cutting or burning because they invest shoot-stock photosynthates in their sprout growth. Fire can damage the meristematic tissue of the stump of those species where investment to root-stock is meagre[40]. Such species are not able to withstand the onslaught of recurrent disturbance. Many clone-forming plants have a fairly precise pattern of branching; hence, space is occupied in an economical and effective manner in terms of the amount of root-stock material needed to reach unoccupied sites. Clonal integration is expected to allow the genet as a whole to do well, even when parts of it may be found in less hospitable neighbourhood[41].

Quite often the spacer roots were branched up to III-order. Branching of spacers was less frequent in *F. indica. B. retusa* mostly produced primary and secondary ramets compared to that in *C. oblongifolius*, *C. infortunatum* and *M. philippensis*. Every genet and primary ramet of *C. oblongifolius* and *C. infortunatum* had clear tap roots going deep into the soil to provide anchorage (Figure 1). The phenomenon explains the patterns of abundance and distribution of species especially in the disturbed

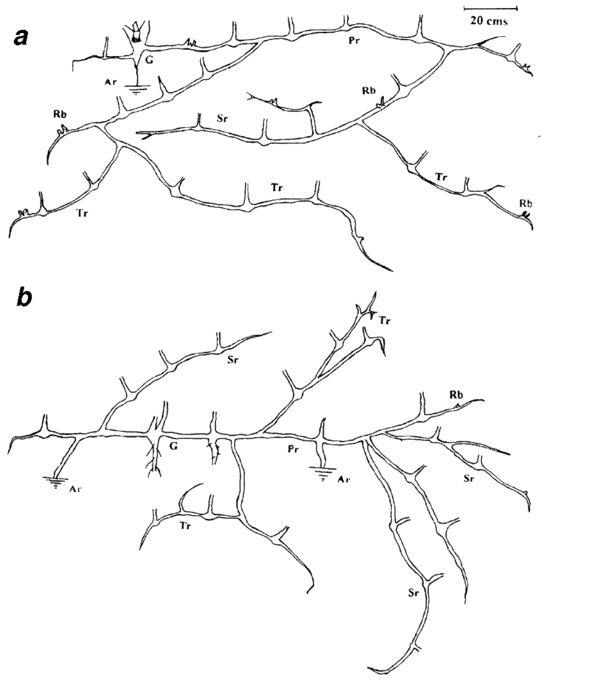

Figure 1. Spatial pattern of the subterranean spacers, ramet positions and the inter-ramet distance (IRD) on the root-stock of a genet complex of (***a***) *Croton oblongifolius* and (***b***) *Clerodendron infortunatum*. G, Genet; Pr, Primary or I-order ramets; Sr, Secondary or II-order ramets; Tr, Tertiary or III-order ramets; Rb, Adventitious bulb (root sucker) on root stock which grows into a ramet; Ar, Anchor root which goes deeper and fastens the root-stock to the soil.

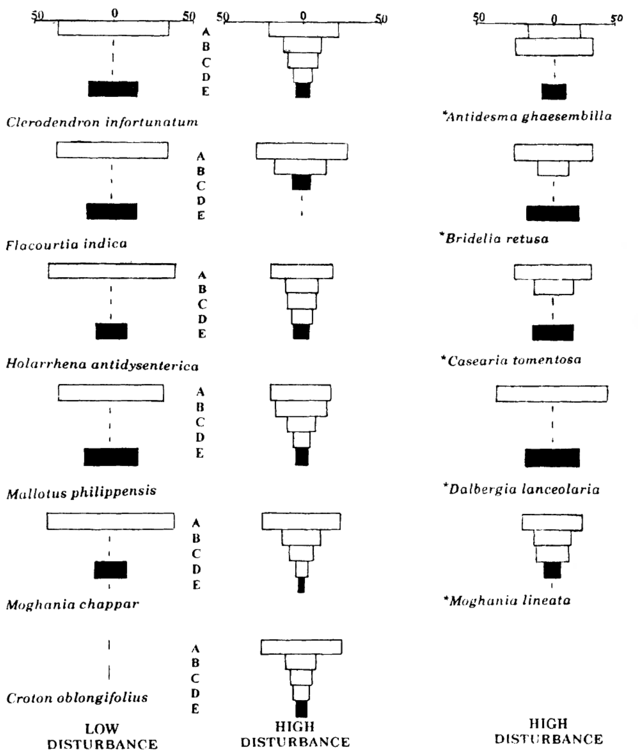

Figure 2. Age structure of genet complex (genet and its ramets) of common ramet-producing species at low or high levels of disturbance. Solid bars represent genet or original shoot and open bars represent ramets of different vigour. Vigour classes (A–E) are based on the average dry weight per individual. Class A, 1.0–5.0 g; Class B, 5.1–10.0 g; Class C, 10.1–15.0 g; Class D, 15.1–20.0 g; Class E, > 20.0 g. (Species marked with asterisks produced ramets only at high disturbance.)

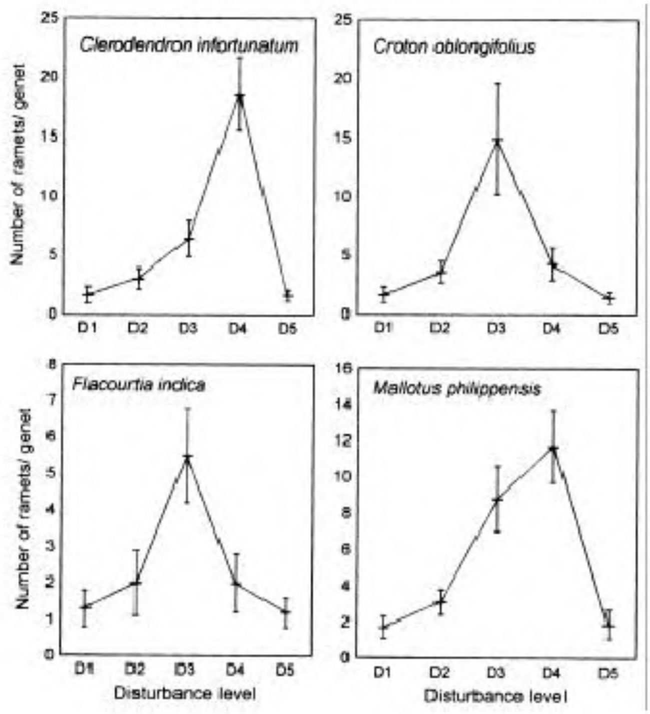

Figure 3. The number (mean ± SD) of ramets per genet complex of common ramet producers in stands facing different degrees of disturbance. [Disturbance levels (D_1–D_5) were based on the value of disturbance index (DI): D_1, 5–20; D_2, 21–40; D_3, 41–60; D_4, 61–80 and D_5, 81–95].

environment as to why some species are common whereas others are rare and why the species differ in their distribution range size. In such an environment, the ramet populations are known to show hierarchial structure which consists of ramets of different size[42]. A positive relationship between genet size and number of ramets has also been observed[43]. The structure and pattern of ramet population of the species may also be correlated with the level of disturbance. In general, the ramet populations of a genet of species like *C. infortunatum*, *C. oblongifolius*, *H. antidysenterica*, *M. chappar* and *M. philippensis* consisted of much greater number of young ramets, because in highly-disturbed stands, the older, more mature and woody ramets rarely escaped the onslaught of cutting for various uses. At low disturbance, however, most of the age classes of ramets remained unrepresented due to lesser ramet production which was more so for less-disturbed natural growth forest (Figure 2). Species like *F. indica, H. antidysenterica* and *M. philippensis* produced several ramets even after severe heat stress during summer as the root suckers in these species were situated on much deep-seated spacers. It has been found that reactivation of such meristematic tissue and suckers may give rise to new shoots even after high-intensity fire[44]. In general, the mean number of ramets per genet increased greatly with increasing level of disturbance. *C. infortunatum* and *M. philippensis* had maximum number of ramets per genet at D_4, while *C. oblongifolius* and *F. indica* did so but only up to D_3 level of disturbance. High intensity disturbance (D_5), however, severely affected the ramet proliferation (Figure 3).

Thus, in a hostile environment, regeneration through seed is quite unlikely. In such forests a modest layer of understorey vegetation may be maintained by the set of woody perennials, exhibiting non-seed regeneration strategy. Such a regeneration strategy potentially ensures considerable plant diversity and vegetation cover at the forest floor even under continual pressure of fuel-wood extraction and other severe perturbations. It suggests that the set of species possessing such mode of regeneration may be used to initiate the process of rehabilitation and ecosystem recovery of the degraded forests.

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Nature and composition of pyrite framboids and organic substrate from degraded leaf cuticles of Late Tertiary sediments, Mahuadanr Valley, Palamu, Bihar

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Detailed studies of pyrite framboids from degraded leaf cuticles have been carried out under scanning electron microscope (SEM) and energy-dispersive X-ray analyser system (EDAX). The investigations indicate that framboidal pyrites form in the cavities and cell lumen of degraded leaves and other plant entities under reducing conditions. They occur in clusters and as solitary spherules. The elemental analyses indicate that the carbon, nitrogen, oxygen, phosphorus, iron and sulphur are the main constituents of framboids developed on the organic substrate. The morphological characters of bacterial colonies are generally retained during mineral uptake to form framboids.

THE pyrite framboids associated with the biologically degraded organic matter from the carbonaceous shales of Upper Tertiary sediments, Mahuadanr Valley, Bihar (Figure 1) have been observed under scanning electron microscope (SEM). The presence of framboidal pyrites help in the interpretation of the burial history of the deposits and the diagenesis of organic matter found associated with the sediments.

Framboidal pyrites occur as solitary spherules or irregular masses on organic matter preserved in shales, carbonaceous shales, coal and other organic deposits. They fill pores or other empty spaces[1]. The single framboidal pyrites are irregularly or heterogeneously distributed, while their clusters are embedded in sheaths or in

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