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SPECIES COMPOSITION AND FIRE IN A DRY DECIDUOUS FOREST

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Abstract. A century of annual burning of the understory of otherwise fire-free deciduous tropical forest in central India has favored seven tree species that produce sprouts or suckers from root buds (root-sprouters) over 37 species that produce sprouts basally from root crowns (root-crown resprouters). Experiments over two years demonstrated that low-intensity ground fires killed seedlings (<1 year old), resulting in a 30% decrease in seedling diversity in burned relative to unburned plots. Overall fire-related mortality of seedlings was 74% for 17 root-crown resprouters, compared to 63% for six root-sprouters. Repeated-measures ANOVA showed that the number of juvenile (>1 year old) stems of root-sprouters increased in burned study plots but decreased in plots protected from fire. Annual burning by people favors species that repair damage by root sprouts. Root-sprouting offers a means of occupying new ground with clonal ramets away from the original parental base. Over time, forests may become dominated by clonal root-sprouters, in contrast to historical accounts of forest dominated by root-crown resprouters that do not spread by clonal growth. If this process continues in the Mendha Forest in India, >80% of its tree diversity could be lost within 100–200 years.

Key words: anthropogenic fire; dry deciduous forest; India; root suckers; species diversity.

INTRODUCTION

Seasonally dry deciduous forests of low latitudes are arguably the most threatened lowland tropical forest ecosystems (Murphy and Lugo 1986*a*, Janzen 1988, Lerdau et al. 1991). We hypothesize that a century of systematic annual burning by local people in tropical deciduous forests of central India (Gadgil and Guha 1992) favors dominance in advance regeneration in the forest by trees that resprout from multiple buds along the roots (root-sprouters) over trees that resprout from the base (root-crown resprouters). We project declines in the diversity of species in the forest understory, and ultimately in forest canopies, over successive years of annual fires set by local villagers. If annual anthropogenic fires continue, combined effects of greater fire-induced seedling mortality of root-crown resprouters and proliferation of root-sprouters should ultimately result in mature forests of low diversity, a process already well advanced elsewhere in South Asia.

Angiosperm tree species commonly resprout after damage from fire, herbivory, drought, wind, or other mechanical damage. Basal sprouting from root crowns is a widespread persistence strategy among tree species that experience disturbance (Bond and Midgely 2001; ''collar sprouting'' species sensu Del Tredici 2001 or ''root-crown resprouters'' of Drewa et al. 2002) . Such resprouting leads to replacement of a damaged trunk, but is not a common mechanism for occupying new ground. A smaller subset of tree species produce sprouts from roots or rhizomes. This is also often a reparative response, but it is additionally an evolutionary adaptation for occupying new ground with clonal growth (Williams 1975, Del Tredici 2001). Production of multiple stems from a damaged base could arguably be regarded as ''clonal'' (e.g., Molinas and Verdaguer 1993, Drewa et al. 2002). Because sprouts from root-crowns, rhizomes, root buds, and collar buds are not developmentally homologous (Zimmerman and Brown 1971, Bosela and Ewers 1997, Del Tredici 2001), and because rhizomatous spread and root suckering serve different ecological functions than basal repair, we follow Williams (1975) and Del Tredici (2001) in using the term ''clonal'' for the capacity to spread to new ground away from the original base of the parent plant, usually with rhizomes or root suckers. Aggressive clonal spread of root-sprouters is obvious in extreme cases (e.g., 1–40 ha clones of aspen, *Populus tremuloides*), but clonal spread away from the parental base is most likely in species that have re-

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generative meristems in roots or rhizomes up to several meters away from the parent trunk.

The central question of this study is whether anthropogenic fires reduce the diversity of tropical deciduous forests in which natural fires do not normally occur. Juvenile and adult tree communities in a deciduous forest of central India are dominated by species that resprout or sprout from root buds, but much more diverse seedling communities not exposed to fire are overwhelmingly of species that resprout only from basal root-crowns and rely on seed dispersal to occupy new ground. We hypothesize that annual fires set by people to supply markets for nontimber forest products convert a high-diversity seedling template of mostly root-crown resprouters to a low-diversity juvenile template of root-sprouting species that spread clonally after fires. We directly test two predictions: (1) fire-induced seedling mortality should reduce diversity, and (2) root-sprouting species capable of clonal spread should survive fire better than basal root-crown resprouters that hold the original parental site.

Methods

Study site and forest

We studied effects of annual anthropogenic fires in a seasonally deciduous tropical forest of central India (18°20–20°48′ N, 79°58–80°44′ E) within an 85-ha forest managed by the Mendha Village of the Gond Tribe. Approximately 17% of the state of Maharashtra (5 472 000 ha) is forested: the Mendha forest is part of a complex of woodlands that cover 60% (512 040 ha) of the Gadchirolli District. The area receives 1400 mm of rain annually during June to October monsoons, when the forest is wet and no fires occur. A severe dry season with no rain from December to May allows up to 1500 g leaf litter/m^2 to accumulate by March. Flammability in annual fires set by villagers in that month is low to marginal. Flame heights in 1999 and 2001 were 55 $\pm$ 12 cm and 60 $\pm$ 6 cm, respectively (mean $\pm$ 1 SE), with 25–30% of the area missed by a reticulate pattern of fire in any given year (Saha 2002*a*). Wet leaf litter decomposes completely several weeks into the monsoons, precluding fuel accumulation from one year to the next.

Field observations indicate that neither juvenile, sapling, nor adult trees are killed by these low-intensity fires. We examined the effects of fires on the transition from seedlings (<1 year old), which may be killed, to juveniles (≥1 year old, and <1.5 m in height), which are not. The forest has more species of root-crown resprouters (37) than root-sprouters (7), with all but one root-crown resprouter in low densities. Rank order abundance of species, based on 705 adult trees (≥5 cm dbh) in 1 ha within this area, can be found in the Appendix. Nomenclature follows Matthew (1983). No trees are harvested in this forest.

No published classification of these tree species as root-crown resprouters or root-sprouters exists (see Troup 1921 and references therein), but inspection allowed the distinction. Species were classified as root-sprouters (sprouts from axillary buds of roots) or root-crown resprouters (sprouts from the base of the collar or crown) based on excavations outside the study plots (see Kozlowski et al. 1997, Del Tredici 2001). Rhizomes are unusual in trees (Del Tredici 2001) and were not observed (cf. Drewa et al. 2002). Species that did not produce suckers from roots could resprout from stem bases (e.g., root-crown sprouters [Drewa et al. 2002]). Determination was straightforward for aggressive root-sprouters (e.g., *Wrightia tinctoria*, present as juveniles in the adult plot, *Diospyros melanoxylon*, *Stererospermum suaveolens*), and was possible for other species. Plots were censused in February 1999 and 2001 to record new seedlings and survivorship of seedlings and juveniles.

In rural India, fires are ignited intentionally from February to April to facilitate the collection of *Diospyros melanoxylon* leaves, which are used in cigarette manufacturing (Mahapatra and Mitchell 1997). Regional and national markets emerged after 1906 when industrial processing of *D. melanoxylon* leaves began. Dry-season fires have occurred annually in forests in which natural fire ignited by lightning is all but unknown (Shrivastava and Choubey 1968). We know of no fire-free years in the Mendha Forest since 1910.

Richness and diversity

To test the hypothesis that fires decrease seedling and juvenile diversity, 24 plots of 3 $\times$ 3 m were established in 1999 in a 4-ha Mendha forest. Twelve plots were allowed to burn by fires set by villagers in the study site in March–April of 1999 and 2000; the other 12 were protected from fire by raking leaves in a 1–1.5 m wide fire lane around the perimeter just before fires were set. Seedlings (<1 year old) and juveniles (>1 year old, <1.5 m in height) of all trees were marked and identified to genus.

Species richness was the number of species per plot. Stem diversity was estimated as Simpson's Diversity Index:

$$D = 1 - \sum_i p_i^2$$

where p_i is the proportion of plants represented by the ith species in a plot (see Pielou 1975). Calculations of D relied on counts of stems, and therefore overestimated juvenile diversity because some stems were ramets from the same genet. All stems of all species were counted regardless of whether sprouts were from seeds, root crowns, or roots. Seedlings (N = 101) and juveniles (N = 602) of all trees were marked and identified. A t test was used to compare the diversity between burned and unburned treatment plots.

Fire effects on seedlings

Do seedlings of root-sprouters survive fire more than seedlings of root-crown resprouters? A total of 251 seedlings of root-sprouters (6 species) and root-crown resprouters (17 species) were marked near the experimental plots in January 2000. The seedlings were burned or protected from fire (litter raked 1 m away). Survival was monitored 12 months later in the monsoons of 2001, following the dry season in which the fires occurred.

Fire effects on juveniles

Juvenile stems that experience fire may die or survive. All stems of all species were counted. Changes before and after fire were compared using repeated measures analysis of variance. Two root-sprouters, *Terminalia tomentosa* and *Diospyros melanoxylon*, occurred in all plots and hence were common enough for a statistical test. The dependent variable was the number of juvenile stems per plot in July 1999 and February 2001.

RESULTS

Composition of the forest

Our data show that fires or their absence indirectly influenced adult communities through their effects on seedlings and juveniles. Juvenile and adult trees were dominated by clonal root-sprouting species, but seedling communities were overwhelmingly of root-crown respouters (Fig. 1; $\chi^2 = 78.2$, df = 2, $P \lll 0.001$). Seedlings of 22 and juveniles of 30 species were found. Juveniles of 4 common species occurred in all plots; three were root-sprouters and 1 was a root-crown resprouter (Fig. 1). Pooled across all plots, the frequency of seedlings (20% root-sprouters, 80% root-crown resprouters) differed from juveniles (65% root-sprouters and 35% root-crown resprouters), with more root-crown resprouter than root-sprouter seedlings, and the opposite for juveniles ($\chi^2 = 22.171$, df = 1, $P < 0.0001$). A 95% confidence interval for the odds ratio was between 5.888 and 19.300. Since the confidence interval did not include 1, the true odds of finding root-crown resprouters were significantly different for the two groups (Agresti 1990).

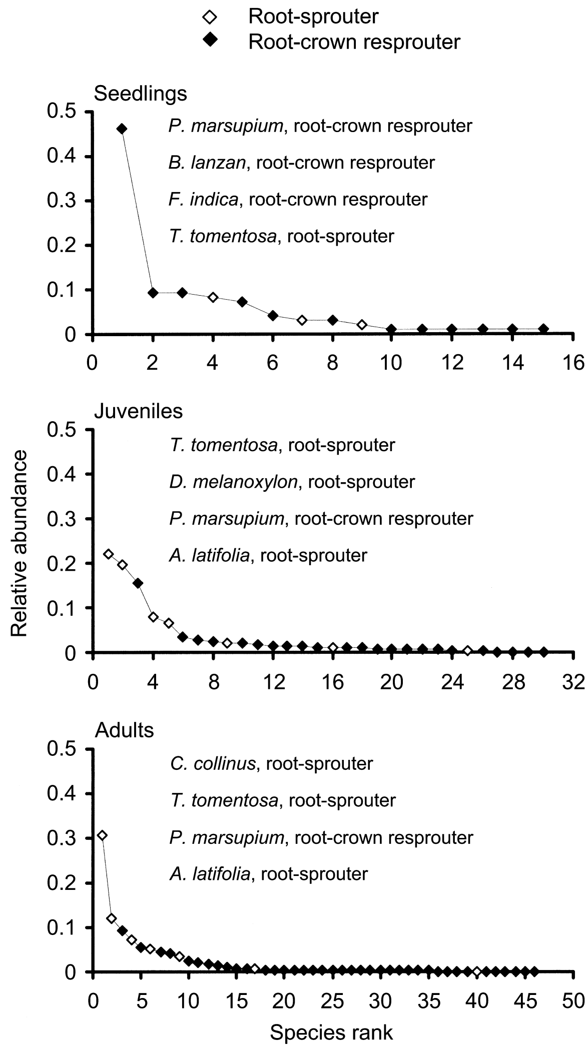

FIG. 1. Rank abundance of seedlings, juveniles, and adult trees. Binomials are given for the first four species, in rank order. Abundances of seedlings and juveniles are from 24 experimental plots at the beginning of the 1999 dry season, before fire was excluded from 12 plots. Abundances of 705 adults are based on a census in a 1-ha plot that had been burned annually by villagers for >40 years. Juveniles and adults are dominated by clonal root sprouters, while seedlings are dominated by root-crown resprouter species.

Richness and diversity

Fire treatment influenced richness and diversity. Plots burned in 1999 and 2000 averaged 2.1 ± 0.5 species of seedlings, whereas those protected from burning averaged 3.3 ± 0.4 species/plot (mean ± 1 SE); Fig. 2A). A one-tailed test of this predicted difference is significant ($P < 0.05$), amounting to a loss of one species in burned plots. Diversity was also significantly higher among seedlings in the fire-excluded plots than the burned plots, amounting to a 28% reduction in diversity (Fig. 2B). With no mortality from fire after the seedling stage, juvenile diversity in protected and burned plots was similar (mean ± 1 SE of the difference was 0.70 ± 0.003 in burned plots and 0.71 ± 0.004 for fire-exclusion plots).

Effects of fire on seedlings

Fires killed many seedlings of both root-crown resprouters and root-sprouters. We used a log-linear analysis to test responses of the seedlings of root-sprouters and root-crown resprouters exposed to or protected from fire. Using a saturated model fitted with three-way interactions, we found that seedling survival was low irrespective of the mode of propagation. Nine of 32 root-sprouters and 17 of 109 root-crown sprouters

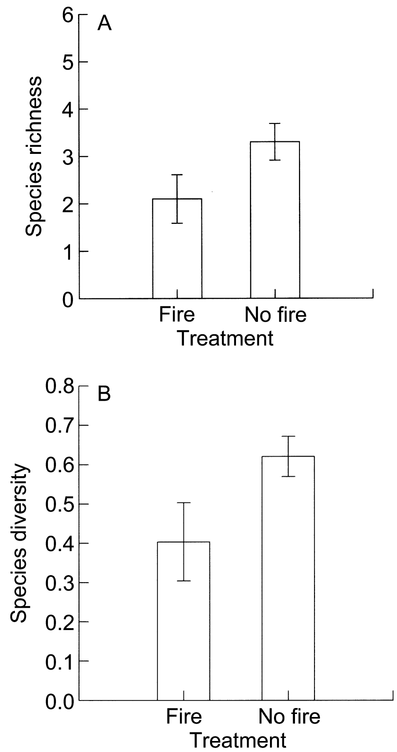

FIG. 2. Species richness and diversity of seedlings in burned and fire-excluded plots. (A) As predicted, richness was lower in plots burned for two seasons, as compared with plots from which fire was excluded ($t = -1.982$, df = 18, $P < 0.05$), amounting to a loss of one species per plot (>35%) over two years. (B) As predicted, diversity (Simpson's D) is lower (28%) in plots burned for two seasons by villagers, as compared with plots from which fire was excluded ($t = 2.062$, df = 13, $P < 0.025$). Simpson's index is $D = 1 - \Sigma(p_i^2)$, where p_i is the proportion of the ith species per plot.

survived fire; when fire was excluded, 12 of 29 root sprouters and 58 of 81 root-crown resprouters survived, a nonsignificant three-way interaction ($P > 0.05$).

We used Fisher's exact test to examine fire-induced mortality in four species sufficiently common for comparisons. Proportions of seedlings surviving were not affected by fire for two root sprouters, *Terminalia tomentosa* ($N = 13$, 0.63 ± 0.18 in burned and 0.50 ± 0.24 in fire-excluded plots, $P = 0.893$) and *Diospyros melanoxylon* ($N = 29$, 0.49 ± 0.17 in burned and 0.61 ± 0.001 in fire-excluded plots, $P = 0.270$). Seedling survival was reduced by fire in two root-crown resprouters, the common *Pterocarpus marsupium* ($N = 118$, 0.42 ± 0.12 in burned and 0.72 ± 0.09 in fire-excluded plots, $P = 0.0001$) and uncommon *Dalbergia paniculata* ($N = 15$, 0.17 ± 0.16 in burned and 0.55 ± 0.22 in fire-excluded plots, $P = 0.04$).

Fire effects on juveniles

Juveniles of all species survived low-intensity fires in 1999 and 2000 (0% mortality). Repeated measures ANOVA showed that the juveniles of species possessing the ability to produce root sprouts increased in number of stems per plot (each plot was 9 m^2) after fire between 1999 and 2001, while these same species declined in stem number in unburned plots during the same period. Overall, the number of juvenile stems of all root-sprouting species in burned plots increased from 19.5 ± 3.6 stems/plot in July 1999 to 22.1 ± 3.5 stems/plot (+13%) in February 2001, while the number of stems of these species in the unburned plots dropped from 29.0 ± 6.0 to 22.0 ± 4.0 stems/plot (−24%). There was a significant interaction of time and fire ($F_{1,19} = 18.666$, $P < 0.001$). The change in juvenile stem numbers was analyzed for two root-sprouting species occurring in all plots (*T. tomentosa* and *D. melanoxylon*). From 1999 to 2001 number of stems increased 13% in burned plots (15.4 ± 5.75 stems/plot in 1999 to 17.4 ± 4.26 stems/plot in 2001) and decreased 42% in fire-excluded plots (30.20 ± 5 stems/plot in 1999 to 17.4 ± 3.6 stems/plot in 2001, a significant interaction of time and fire, $F_{1,18} = 12.098$, $P < 0.005$). Juvenile stems of root-crown resprouters did not show a significant change in number between burned and fire-protected plots.

DISCUSSION

Annual, low-intensity anthropogenic fires in the Mendha Forest of central India reduce diversity of tree seedlings and shift juvenile composition by favoring proliferation of root-sprouters. These fires do not convert tropical deciduous forest to savanna, which happens elsewhere under regimens of frequent intense fires (e.g., Stott et al. 1990, Gadgil and Guha 1992). In the Mendha Forest grasses are sparse, and the nearest anthropogenic savanna is >1500 km away. What is clear is that stems of clonal root-sprouters increase in annually burned plots and decline sharply in fire-excluded plots. The net result of this process is that annual anthropogenic fires shift the template of regenerating seedlings and especially juveniles in the understory by suppressing the survival of common root-crown resprouters, thereby altering the potential recruitment of clonal root-sprouters and nonclonal root-crown resprouters into the canopy. The special concern in central India is that annual fires might result in conversion to low-diversity forests dominated by a few clonal species, in rapidly diminishing communities that are already at risk from other human activities. A prediction is that a greater fire-free interval would result in an increase in diversity among juveniles.

Resprouting after disturbance is an almost universal angiosperm trait (Bond and Midgely 2001). Basal sprouting from root-crowns is widespread, and is well documented as a response to disturbance in tropical deciduous forests of Puerto Rico (Murphy and Lugo 1986*b*), Mexico (Lott et al. 1987), Madagascar (Sussman and Rakotozafy 1994), and Ghana (Swaine 1992). The net effect of basal sprouting is regeneration that replaces damaged or killed shoots. Sprouting of suckers from root buds is less common than basal sprouting, but in frequently burned parts of Africa and South and Southeast Asia, domination by spreading suckers of root-sprouting species among the juvenile and adult communities is the rule, as reported in several observational studies (Lushington 1907, Trapnell 1959, Stott et al. 1990, Lieberman and Li 1992, Pandey and Shukla 2001). Our study is the first experimental confirmation that annual anthropogenic fires favor seedlings and juveniles of clonal root-sprouting species in tropical deciduous forests of India. This result is consistent with other experimental studies that show fire-induced shift to dominance by clonal species in Neotropical savannas (Hoffmann 1999), temperate forests that are dominated by *Populus* (Gom and Rood 1999), and forest understories that experience regular freezes (Olmsted et al. 1993).

Annual fires set by people indigenous to south Asian forests are now almost universal. We hypothesize that effects and potential consequences reported here operate on a scale of decades rather than centuries or millennia. Forest records from the 1860s indicate a greater abundance of such root-crown resprouters as *Santalum album* in the mature deciduous forests of south India (Morgan 1871*a*), which now lack regeneration classes of basal-sprouting species (Srivastava 2000). Similarly, forests of Mudumalai Wildlife Sanctuary in South India once had high densities of root-crown resprouting *Pterocarpus marsupium* in early forest inventories (Morgan 1871*b*), but today Mudumalai is dominated by such clonal root-sprouting species as *Kydia calycina*, *Lagerstroemia microcarpa*, and *Anogeissus latifolia* (Sukumar et al. 1998, John et al. 2002). In the Bori Wildlife Sanctuary of central India, juveniles and adults of clonal species are more abundant in sites most disturbed by forest people, with more root-crown resprouters where fires have been rare over the last 50 years (Saha 2001). Clonal domination is not a ''natural state'' for Indian tropical deciduous forests in areas where natural fires are rare.

How far along is clonal domination by root-sprouting species in the Mendha Forest? Historical differences between precolonial and contemporary forests are obvious, but the question cannot be answered definitively. No comparable forests exist nearby without a recent history of annual fires set by indigenous people. Tree diversity is maintained by adults, which die at a rate of ≤1% per year (e.g., Brokaw 1985 in Panama, Sukumar et al. 1998 in India), seedlings that survive fire, and patches of ground missed by fire (Saha 2002*b*). Seedlings that survive or are missed by fire in their first year are, as we experimentally show, unlikely to be killed by fire in their second or later years.

A feasible goal of restoration is to use a longer fire-free interval to promote higher seedling and juvenile diversities of nonclonal trees. We predict that reduction of fire frequency would enhance species diversity by increasing the survival of basal root-crown resprouting and nonsprouting species. We predict that a diverse template of young plants of root-crown resprouters, if allowed to pass through the transition to juvenile and sapling stages, would consistently yield diverse mature forests more like those of precolonial India than those that exist today. Like the clonal conversion of the regenerating understory, a reverse process of restoration could be rapid. Substantial losses of clonal stems in plots protected from fire for only two years suggest that with longer intervals between burns this restorative successional process would require decades, not centuries or millennia.

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Literature Cited

Agresti, A. 1990. Categorical data analysis. John Wiley, New York, New York, USA.

Bond, W. J., and J. J. Midgley. 2001. Ecology of sprouting in woody plants: the persistence niche. Trends in Ecology and Evolution **16**:45–51.

Bosela, M. J., and F. W. Ewers. 1997. The mode of origin of root buds and root sprouts in the clonal tree *Sassafras albidum* (Lauraceae). American Journal of Botany **84**:1466–1481.

Brokaw, N. V. L. 1985. Gap-phase regeneration in a tropical forest. Ecology **66**:682–687.

Del Tredici, P. 2001. Sprouting in temperate trees: a morphlogical and ecological review. Botanical Review **67**:121–140.

Drewa, P. B., W. J. Platt, and E. B. Moser. 2002. Fire effects on resprouting of shrubs in headwaters of southeastern longleaf pine savannas. Ecology **83**:755–767.

Gadgil, M., and R. C. Guha. 1992. The fissured land: an ecological history of India. Oxford University Press, New Delhi, India.

Gom, L. A., and S. B. Rood. 1999. Fire induces asexual sprouting of riparian cottonwoods. Canadian Journal of Botany **77**:1604–1616.

Hoffmann, W. A. 1999. Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. Ecology **80**:1354–1369.

Janzen, D. 1988. Tropical dry forests, the most endangered major tropical ecosystems. Pages 130–137 *in* E. O. Wilson, editor. Biodiversity. National Academy Press, Washington, D.C., USA.

John, R., H. S. Dattaraja, H. S. Suresh, and R. Sukumar. 2002. Density-dependence in common tree species in a tropical dry forest in Mudumalai, southern India. Journal of Vegetation Science **13**:45–56.

Kozlowski, T. T., S. G. Pallardy, and P. J. Kramer. 1997. Physiology of woody plants. Academic Press, San Diego, California, USA.

Lerdau, M., J. Whitbeck, and N. M. Holbrook. 1991. Tropical deciduous forest—death of a biome. Trends in Ecology and Evolution **6**:201–202.

Lieberman, D., and L. Li. 1992. Seedling recruitment patterns in a tropical forest in Ghana. Journal of Vegetation Science **3**:375–382.

Lott, E., S. H. Bullock, and J. A. Solis-Magallanes. 1987. Floristic diversity and structure of upland and arroyo forests of coastal Jalisco. Biotropica **19**:228–235.

Lushington, A. W. 1907. Some sucker produced forests of Kistna district. Indian Forester **33**:445–451.

Mahapatra, A., and A. P. Mitchell. 1997. Sustainable development of non-timber forest-products: implication for forest management in India. Forest Ecology and Management **1–3**:15–29.

Matthew, K. M. 1983. The flora of Tamil Nadu Carnatic. The Rapinat Herbarium, Tiruchirapalli, India.

Molinas, M. L., and D. Verdaguer. 1993. Lignotuber ontogeny in the cork-oak (*Quercus suber*; Fagaceae) II Germination and young seedling. American Journal of Botany **80**:127–131.

Morgan, H. R. 1871*a*. Survey of Mudumalai forests. Pages 104–106 *in* D. Lyttleton, editor. East India Forest Conservancy. Published with permission of The House of Commons, 1871. Her Majesty's Stationery Office, London, UK.

Morgan, H. R. 1871*b*. Memorandum of Mudumalai. Pages 131–132 *in* D. Lyttleton, editor. East India Forest Conservancy. Published with permission of The House of Commons. Her Majesty's Stationery Office, London, UK.

Murphy, P. G., and A. E. Lugo. 1986*a*. Ecology of tropical dry forest. Annual Review of Ecology and Systematics **17**: 67–88.

Murphy, P. G., and A. E. Lugo. 1986*b*. Structure and biomass of a subtropical dry forest in Puerto Rico. Biotropica **18**: 89–96.

Pandey, S. K., and R. P. Shukla. 2001. Regeneration strategy and plant diversity status in degraded forests. Current Science **81**:95–102.

Pielou, E. C. 1975. Ecological diversity. Wiley, New York, New York, USA.

Saha, S. 2001. Comparison of vegetation structure and composition between secondary deciduous forests and *Tectona grandis* (family Verbanaceae) plantations in Bori Wildlife Sanctuary of central India. Forest Ecology and Management **148**:159–167.

Saha, S. 2002*a*. Anthropogenic fire regime in a central Indian deciduous forest. Current Science **82**:1144–1147.

Saha, S. 2002*b*. Fire in an Indian deciduous tropical forest: effects on tree seedling and juvenile communities. Dissertation. University of Illinois at Chicago, Chicago, Illinois, USA.

Shrivastava, S. S., and L. K. Choubey. 1968. State trading in tendu leaves in M.P. Indian Forester **94**:39–45.

Srivastava, S. 2000. Forest fire causing poor stocking of *Santalum album* and *Terminalia chebula* in Southern India. International Forest Fire News **22**:28–30.

Stott, P. J., J. G. Goldammer, and W. L. Werner 1990. The role of fire in the tropical deciduous forests of Asia. Pages 32–43 *in* J. G. Goldammer, editor. Fire in the tropical biota: ecosystem processes and global changes. Springer-Verlag, Berlin, Germany.

Sukumar, R., H. S. Suresh, H. S. Dattaraja, and N. V Joshi. 1998. Dynamics of a tropical deciduous forest: population changes (1988 through 1993) in a 50- ha plot at Mudumalai, southern India. Pages 495–506 *in* S. Dallamier and J. Comiskey, editors. Forest biodiversity, research and modelling. Smithsonian Research Institution, Washington, D.C., USA.

Sussman, R. J., and A. Rakotozafy. 1994. Plant diversity and structural analysis of a tropical dry forest in southwestern Madagascar. Biotropica **26**:241–254.

Swaine, M. D. 1992. Characteristics of dry forest in West Africa and the influence of fire. Journal of Vegetation Science **3**:365–374.

Trapnell, C. C. 1959. Ecological results of woodland burning experiments in northern Rhodesia. Journal of Ecology **47**: 129–168.

Troup, R. 1921. Silviculture of India trees. Clarendon Press, Oxford, UK.

Williams, G. C. 1975. Sex and evolution. Princeton University Press, Princeton, New Jersey, USA.

Zimmermann, M. H., and C. L. Brown. 1971. Trees: structure and function. Springer-Verlag, New York, New York, USA.

APPENDIX

A table showing rank order of tree species in a 1-ha plot in the Gadchirolli District of Central India is available in ESA's Electronic Data Archive: *Ecological Archives* E084-082-A1.