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Factors affecting the production of fruitbodies of *Amanita muscaria* in plantations of *Pinus patula*

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Abstract. Monthly counts, in plantations of *Pinus patula* at Kodaikanal in southern India, during 1977 and 1978, indicate that fruitbody production by *Amanita muscaria*, a fungus forming sheathing (ecto-) mycorrhizas, was influenced by (i) the current month's rainfall and (ii) the age of the plantation.

Fruitbodies rarely appeared in the absence of rain. Average monthly numbers increased in rain-months from 11 to 320 per thousand trees when monthly rainfall increased from 40 to 640 mm.

During a period of 11 months (February/December 1978) numbers of fruitbodies per 1000 trees ranged from *c.* 150 to 10800 in plantations 5 and 16 years old respectively.

After rainfall-thresholds for fruitbody production had been exceeded—they were less in old, than in young, plantations—young plantations, judged by the production of *A. muscaria* fruitbodies, were more responsive to additional rainfall than older plantations.

Keywords. Fruitbodies; *Amanita muscaria*; *Pinus patula*; rainfall; plantation age.

1. Introduction

When observing plantation forests near Kodaikanal, Tamil Nadu, India, during December 1976, it was immediately obvious that the ages of different stands of *Pinus patula* Schl. and Cham., a native of Mexico (Wormald 1975), were strongly influencing the numbers of fruitbodies of *Amanita muscaria* (L. ex Fries) Hooker, the fly agaric. Because of the importance of this fungus which forms mycorrhizas with roots of many trees (Trappe 1962), including *P. patula* (Marais and Kotze 1975, 1977), and because very little is known of its ecology, counts of fruitbodies were made in May/June and October/November 1977 during the Southwest and Northeast monsoons respectively. In the event these observations were subsequently extended to monthly records taken from February–December 1978. As a result it has been possible to gain an insight into the effects of monthly rainfall in addition to those of plantation age.

2. Details of *P. patula* plantations

Plantings of *P. patula* were made in the Gundar experimental ' gardens ' having an organically rich gravelly soil (pH 5·8) above yellow clay which in turn overlies gneiss and charnockite, the gardens being at a height of *c.* 2200 m above mean sea level in the Palni Hills near Kodaikanal (lat. 10° 15′ N; long. 77° 31′ E). The different annual sowings with seed from Kenya and Mexico were usually made in September into unsterilised local soil mixed with (a) ' shola ' earth and (b) mycorrhizal soil from existing pine plantations. Seedlings, which emerged within 3 weeks of being sown, were transplanted when two months-old to polythene bags, ' polypots ', with shola earth and mycorrhizal soil before being transferred eight months later to cleared shola grassland sites with bracken in wet places [Champion's classification group 10 (a) i—' Southern montane temperate forest ']. At planting when saplings were arranged 2·5 m apart (both within and between rows), turves, 2 m square, were removed and pits 30 cm cube were dug. Combined NPK fertiliser (56 g) was mixed into each pit before planting. The different plantings spanning the period from 1962 to 1973 were located opportunistically to take advantage of available sites—they were not arranged systematically next to each other. At the onset of canopy closure, 5–6 years after planting, basal branches were pruned to a height of 2 m above ground.

3. Observations

Heights were recorded annually. Trees 5, 8 and 15 years-old in 1977 were 4·8, 11·0 and 20·9 m tall respectively. Trees 5 year-old in 1972 were 4·3 m. Observations made in 1977 indicated that the ages of *P. patula* plantations strongly influenced the production of *A. muscaria* fruitbodies with numbers, when counted in October/November, increasing from 15 per thousand trees planted 4 years previously, to 7,100 in plantations 11 years older (table 1). Earlier in the year (May/June), during the Southwest monsoon, the same relation was apparent, although fewer fruitbodies were produced, possibly because there had been less rain.

Table 1. Relation between age of plantation and numbers of *Amanita muscaria* fruitbodies per 1000 trees when counts were made during May/June and October/November 1977 in stands of *Pinus patula* at Kodaikanal, India.

	Ages of plantations (years after planting)											
	4	5	6	7	8	9	10	11	12	13	14	15
May/June	N.A.	..	N.A.	N.A.	160	110	450	440	320	1300	..	1300
October/ November	15	..	50	70	140	240	1500	970	1200	3500	..	7100

N.A. denotes that observations were not made.

The more detailed observations, made from February to December 1978 inclusive, confirmed that the monthly production of fruitbodies directly reflected the ages of the different plantations; they also suggested that amounts of rain were critical (figure 1). Numbers of *A. muscaria* produced during the 11-month period of observation ranged from *c.* 150 to 10800 per 1000 trees in plantations 6 and 16 years-old respectively. Before detailed analyses could be made of the data from the unreplicated plantations (duplicate stands of *P. patula* were planted in 1968), it was necessary to transform the fruitbody data because the standard errors of large means were larger than those of small means—they were not independent (Kleczkowski 1949). Square root transformations were rejected in favour of $\log_e (N + 1)$, where N is the number of fruitbodies per 1000 trees. Using this transformation it was found that the average monthly production of

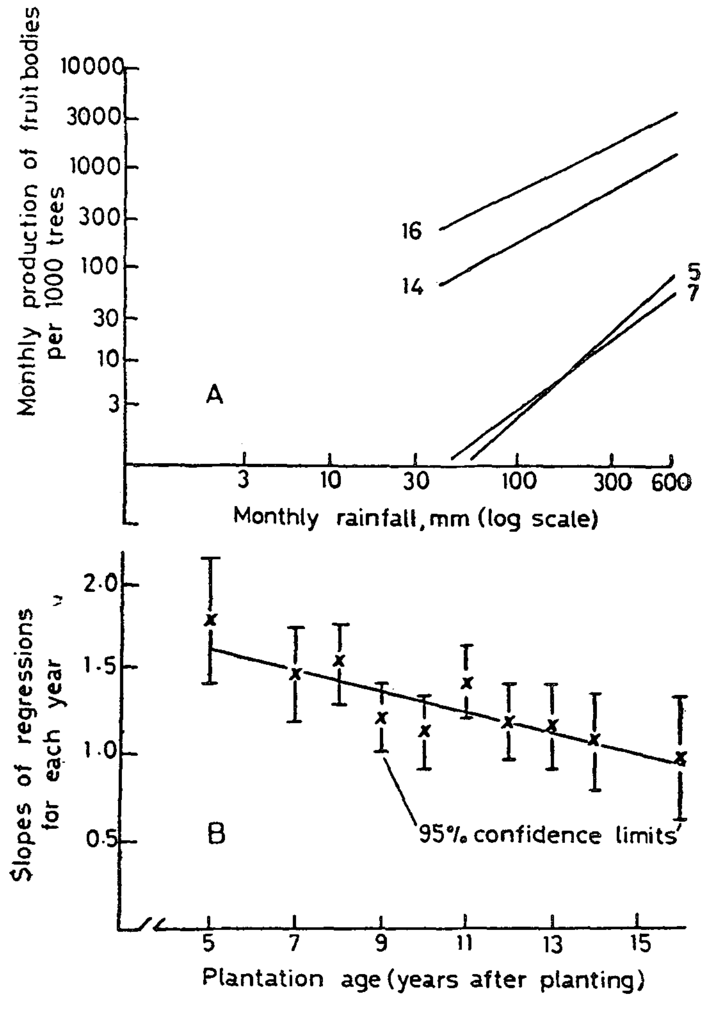

Figure 1. Association during 1978 between monthly rainfall (mm) and monthly mean production of *Amanita muscaria* fruitbodies in *Pinus patula* plantations from 6 to 16 years-old.

fruitbodies increased with increasing plantation age from 2·7 per 1000 trees to 310 in plantations 5 and 16-years-old respectively (figure 2). There was also a linear relation between numbers of fruitbodies and amounts (mm) of rain (R_e) when the latter, like the fruitbody data, were transformed to $\log_e (R + 1)$. Average monthly numbers of fruitbodies increased from 11, with 40 mm of rain, to 320 with 640 mm. By interrelating the effects of plantation age and rainfall it was calculated that:

$$\log_e (N + 1) = -3{\cdot}65 + 0{\cdot}37 A + 0{\cdot}75 \times \log_e (R + 1),$$

where A = age of plantation, years after planting. The effects of plantation age and rainfall accounted for 19% and 57% of the variation respectively (table 2). Additionally there was a significant interaction indicating that the response of *A. muscaria* to similar amounts of rain differed in plantations of different ages.

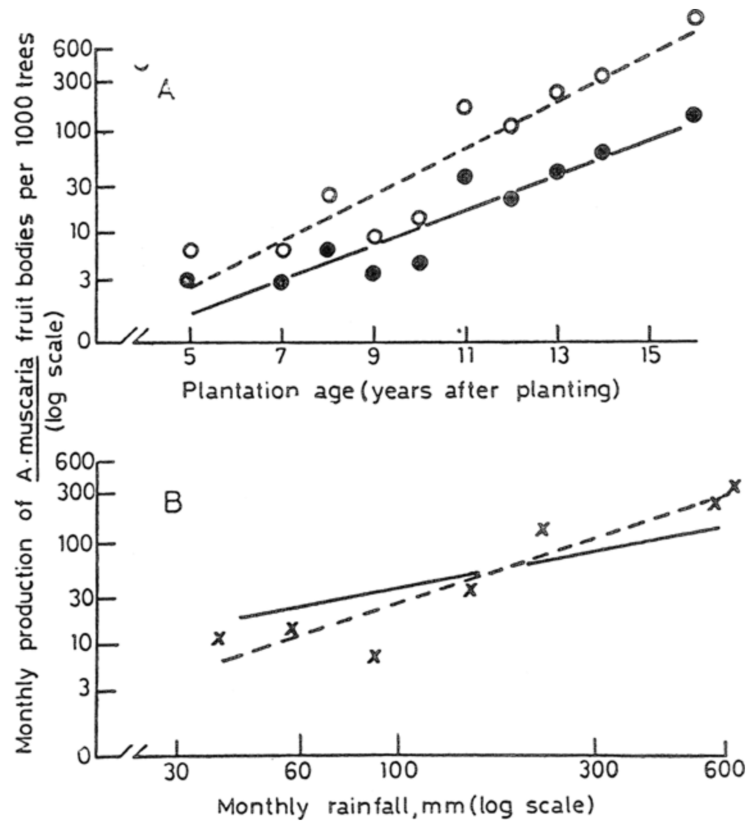

Figure 2. Relationships during 1978 between the monthly production of *Amanita muscaria* fruitbodies and *A*. the ages of different plantations of *Pinus patula* (●, — regressions calculated with data set February/December; ○, ... regressions calculated after excluding data for the months without rain, viz., February, March, June and August), and *B*. monthly amounts of rain (—, regression calculated with the inclusion of months without rain; - - -, regression restricted to the data (×) for the seven months with rain).

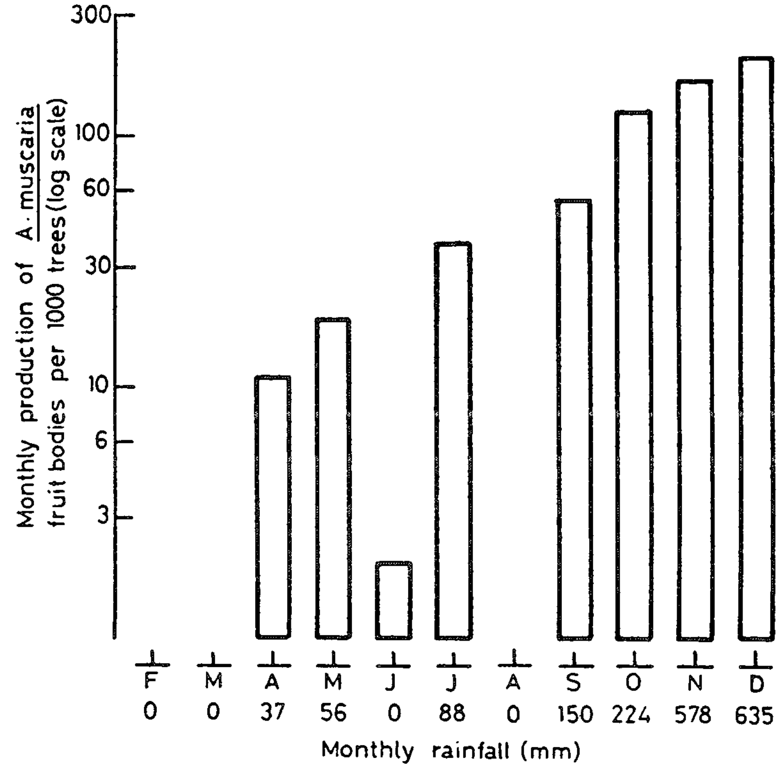

Figure 3. Interacting influences of plantation age and monthly rainfall on monthly production of *Amanita muscaria* fruitbodies in stands of *Pinus patula*. *A*. Fitted lines for plantations 5, 7, 14 and 16 years-old, and *B*. Best fit line linking the slopes, plotted on the vertical axis, of the curves showing how fruitbody production was affected in plantations of different ages by increasing amounts of rain—see section A.

Whereas detectable numbers of fruitbodies developed in old plantations with as little as 37 mm of rain per month, few were produced in young plantations unless amounts of rainfall exceeded 50 mm.

In determining these relationships, the calculations were heavily 'weighted' by the data for the four months without rain. No fruitbodies were recorded during three of them, February, March and August and in the fourth, June, the newly-emergent fruitbodies, possibly triggered by the rain that fell towards the end of May, were restricted to plantations 11 or more years old. When data for these months were omitted it was found, on recalculating, that

$$\log_e (N + 1) = -7{\cdot}95 + 0{\cdot}51\,A + 1{\cdot}30 \times \log_e (R + 1).$$

In this instance 47% of the variation is attributable to the effects of age and 34% to rainfall (table 2). In the months with rain the average monthly production of fruitbodies was 6·7 and 1060 in plantations 5 and 16 years-old respectively (figure 2). As before there was a significant age × rainfall interaction which accounted for 7% of the variation (table 2). Thus, with an increase in monthly rainfall from 100 to 300 mm monthly numbers of fruitbodies per 1000 trees

Table 2. Apportionment of variance when relating the monthly production during 1978 of *Amanita muscaria* fruitbodies per 1000 trees ($\log_e$), with (i) age, in years of different *Pinus patula* plantations and (ii) monthly rainfall (mm) ($\log_e$).

	A, all months			*B*, months with rain		
	Degrees of freedom	SS	MS	Degrees of freedom	SS	MS
Age of *P. patula* plantations	1	157·1	157·1	1	188·2	188·2
Monthly rainfall	1	450·7	450·7	1	132·8	132·8
'Interaction' between age of plantation and monthly rainfall (see footnote)	9	56·7	6·3	9	31·1	3·5
Residual	109	127·2	1·2	65	40·2	0·6

Interaction SS is equivalent to the variation removed when fitting separate lines to show responses to rainfall in plantations of different ages.
(*A*, using data for all months from February–December 1978 inclusive; *B*, using data for the seven months with rain (see figure 1).

increased by a factor of × 6 in young plantations, from 3·2 to 20·0, and by × 3·3 from 330 to 1100 in plantations 14–16 years-old (figure 3). Although these differences between plantations at opposite ends of the age scale were statistically significant the line relating the slopes of the rainfall responses of all plantations is not statistically significant. Nonetheless it supports the contention that the responses to rainfall lessened in ageing plantations.

4. Discussion

Understandably, forest microbiologists have been concerned with functional aspects of mycorrhizas such as their influence on forest establishment and the mediation of nutrient uptake, notably phosphorus. However, as forest technology becomes more sophisticated, with serious consideration being given to the possibly large-scale inoculation of forest transplants with 'effective' isolates of selected mycorrhizal fungi, it is time to seek a better understanding of their ecology. With many of the fungi forming sheathing (ecto-) mycorrhizas, much can be learnt from the distribution of their aerial fruitbodies, mostly toadstools typical of the Agaricales, but inferences should be made cautiously. It should not be assumed that the absence of toadstools necessarily reflects the similar absence of root-colonizing and/or soil-living cultures. At present the relation between them is virtually unknown.

Hora (1959) and Hall (1978) found that the occurrence of toadstools, some of them belonging to species known to form sheathing mycorrhizas, could be altered by the application of artificial fertilisers. At Kodaikanal the occurrence of *A. muscaria* fruitbodies was related to rainfall which, like fertilisers, could be acting directly on the fungus and/or indirectly by affecting its hosts (Wilkins and Harris 1946; Grainger 1946). It was somewhat surprising to find that more rain was needed to trigger the appearance of *A. muscaria* in young, than in old, stands of *P. patula*. Although this difference might possibly reflect changes in host physiology, it seems more likely to be attributable, notwithstanding increased losses by evaporation, to the greater diversion of rainfall in old stands where appreciable amounts of rain might be intercepted and channelled, by outward and downward-bending branches, to fall on ground directly beneath the fringe of the canopy—in effect rainfall may be concentrated into localised areas to reach the 'toadstool rainfall-threshold' sooner beneath old, than young, trees. The attainment of these thresholds in the older plantations may also be aided by their greater accumulations of moisture-retaining leaf (needle) litter whose own decomposition might conceivably influence, directly or indirectly, the appearance of *A. muscaria* fruitbodies.

Hacskaylo (1965) and Last *et al* (1979) have shown that fruiting of mycorrhizal fungi including *Thelephora terrestris* (Fr.), *Laccaria laccata* (Scop. ex Fr.) Cooke, *Hebeloma* spp. and *Peziza badia* Persoon ex Mérat can be stopped by shading, or removing, the foliage of Virginia pine (*P. virginiana* Mill) and birch (*Betula* spp.). Circumstantial evidence obtained at Kodaikanal suggests that the fruiting of *A. muscaria* is also host dependent, becoming more prolific in ageing plantations of *P. patula*. But the evidence is not unequivocal nor is it clear if differences in numbers of fruitbodies emerging above ground are good guides to comparable differences in the abundance of fruitbody primordia initiated below ground level.

In his Presidential Address to the British Ecological Society, Harley (1971) suggested that the prolific development of fruitbodies might, in some circumstances, minimize the benefit gained from mycorrhizal associations. Unfortunately it has not yet been possible to obtain the necessary dry weight data to compute the forest biomass annually diverted to the production of *A. muscaria* fruitbodies—it could be appreciable.

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