THE SEASONAL FRUITING OF AGARICS IN MALAYA.

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There is no day in Malaya when the fruit-body of some agaric cannot be found in the high forest, but twice each year, in the south at least, there is a season of three months when a "run of fungus" develops like the autumn crop in temperate countries. Fruit-bodies, never seen at other times, then appear in great numbers with a succession of early, mid- and late seasonal forms. The forest may be so full of toadstools of all sizes, shapes and colours, in troops on the ground and on fallen wood and in myriads on dead leaves and sticks, that one cannot step without treading on them, and each kind has its season of but a few days or a week when it is in full fruit.

I learnt of these seasons first in the Gardens Jungle, over the few acres of which I searched almost daily in the year 1929, and then from repeated collecting in the forests of Singapore and south Johore and from occasional visits to more distant parts of the country. In the Gardens Jungle, also, I set myself to discover the exact times of inception of fruit-bodies and their periods of development and maturity so that I could determine the life of different kinds of fruit-body and the climatic stimulus to which their mycelia responded. I have collected much information on nearly a hundred species but only a few general facts can be mentioned in this place.

The Seasons.

In Singapore the first toadstool-season of the year extends from March to May and the second, less regularly, from some time in August or September, rarely October, to October or the beginning of December. From 1929 till the beginning of this year Boleti, for instance, fruited chiefly in March and August or September; *Hygrophorus firmus* B. and Br. fruited in April and October or November; *Amanita virginea* Mass. in May and November or the beginning of December. The lowlands of south Johore appear to have the same seasons though the dates may differ by two or three weeks through local variations in the weather. At Tembeling, in the centre of Pahang, a run of fungus was in mid-course at the beginning of November 1930, and one had just ended at the beginning of June 1931. On Fraser's Hill, at 4000′ in Pahang, a run had just ended in the middle of November 1930 and 1932. About 20 miles inland from Chukai, Kemaman, there was no run of fungus at the end of June 1932, though the forest was very wet. In Penang a run was starting at the beginning of March 1929. These dates agree with the seasons in Singapore. But in Perlis, in the north, a run was starting at the end of November 1929 : at Slim River, Perak, and

on Fraser's Hill, Pahang, a run was starting at the beginning of May 1930: round Kuala Pilah and on the lower slopes of Gunong Angsi, in Negri Sembilan, a run was starting in the last week of June 1930: at Cameron Highlands, at 5000′ in Pahang, a run was finishing at the beginning of August 1934. These dates disagree, yet one may be certain that, while there is a seasonal fruiting in all parts of Malaya following changes in the weather, the date of the season in each place depends on local conditions, for the times of the weather-changes vary considerably not only in the lowlands but from mountain to mountain.

The Succession.

Without a systematic account of malayan agarics, only an outline of the seasonal succession can be given. Briefly it has this order:—

1st Crop:—epiphyllous species of Marasmius, Androsaceus, Mycena, Collybia, etc. with small fruit-bodies: some horse-hair Marasmius: Coprinus, Psathyrella and Leucocoprinus.

2nd Crop:—developing 4–8 days after the first: most kinds with large fruit-bodies but especially Amanita, Amanitopsis, Lepiota, *Collybia radicata*, Laccaria, Lactarius, Russula, Volvaria, Pluteus, Clitopilus, Leptonia, Inocybe, Astrosporina, Cortinarius, *Hypholoma janus* (B. and Br.) Petch, *Psathyra trechispora* Petch, Psaliota, Boletus, *Paxillus, Lentinus giganteus* B.

3rd Crop:—about two weeks after the second: Hygrophorus, Cantharellus, Pleurotus, Entoloma, *Clitopilus flavidus* Mass. (really an Entoloma), *Lentinus connatus, L. blepharodes, L. hookerianus, L. similis,* and other horse-hair Marasmius.

4th Crop:—about two weeks after the third: *Hygrophorus firmus* B. and Br. and several miscellaneous species.

5th Crop:—about 2–4 weeks after the fourth: *Amanita virginea* Mass. and many species of Hygrophorus and Marasmius.

The crops are not actually distinct but peaks, rather, on a summation curve in which the number of species fruiting in a locality and the number of fruit-bodies would be plotted against time, and with fewer, less conspicuous species fruiting in the intervals. The succession is so constant under normal conditions that a few easily recognisable species serve as indicators:—

Crop.		*Indicator.*
1st	...	Epiphyllous Androsaceus and Filoboletus (=Poromycena)
2nd	...	Amanita, Russula, Boletus in great variety
3rd	...	*Clitopilus flavidus* Mass.
4th	...	*Hygrophorus firmus* B. and Br.
5th	...	*Amanita virginea* Mass.

Amanita virginea, like *Collybia velutipes* in England, signifies the end of the season.

The Cause of the Seasons.

In most of Malaya rain falls so frequently that the forest is nearly always damp. A week without rain scarcely affects the humus. But twice each year, after the wet weather of November and December and April to June or July, there comes a spell of several weeks with sunny, windy days and only occasional showers. The forest then dries; the humus becomes friable and brittle; streams shrink in their beds; and the leeches disappear. Mycelial growth in the soil gradually stops and the hyphæ remain dormant for a week or more. At the next rains the hyphæ revive and fruit. Thus spring the first two crops of toadstools which begin the succession.

It may be thought, now, especially from the evidence of fungi grown in culture, that a mycelium would fruit so soon as it had gathered enough food, but I am convinced direct fruiting is exceptional among forest fungi and pertains more to species of transient or confined habitats, like coprophytes and carbonicolous forms. This succession in the rain-forest shows that most forest-species need an external stimulus to fruit, which is primarily the check to vegetative growth given by mild drought. For, two or three days after the forest floor is soaked again, fine rhizomorphs begin to grow in the humus and there is the mouldy smell of active mycelium. A few days later the primordia of Russules, Boleti and Amanitas appear and these, I find, take only 8–10 days to mature. There is, therefore, no time between the onset of the rain and the fruiting for vegetative growth. Indeed, the first mycelial growths of these fungi after the soaking of the soil are slender rhizomorphs—somatic strands, not diffuse feeding hyphæ.

The relation between the dry weather, the onset of the rain and the crops of Boleti in the Gardens Jungle is shown in the following table. The period of the dry weather is taken from the daily rainfall record in the Botanic Gardens and measured from the end of continually wet weather to the heavy rain which caused the resumption of mycelial growth in the soil. Actually it is an interrupted period of dry rather than wet weather, and single storms and light rain on a few successive days I have reckoned in the dry weather because I found, by carefully digging in the humus where toadstools always grew, that such rain never penetrated or lasted long enough to evoke the development of primordia. By digging in the humus after each likely storm toward the end of the dry weather, I determined to a few days when mycelial growth was resumed.

Year	*Dry Weather*	*Rain begins*	*Mature Boletus-crop*
1929	7th Jan.–8th March	9th March	24th March
	29th June–23rd Aug.	24th Aug.	10th Sept.
1930	20th Jan.–6th March	7th March	22nd March
	23rd June–6th Sept.	6–14th Sept.	24th Sept.
	15–27th Sept.	28th Sept.	16th Oct.
1931	26th Jan.–28th Feb.	1st March	18th March
	10th June–18th July	19th July	7th Aug.
1932	1st –18th Jan.	19–26th Jan.	8th Feb. (small fruiting)
	27th Jan.–16th Feb.	17th Feb.	6th March (heavy fruiting)
	10th July–2nd Sept.	3rd Sept.	20th Sept.
1933	26th Jan.–23rd Feb.	24th Feb.	14th March
	No record in second half of year		
1934	20th Jan.–27th Feb.	28th Feb.	20th March
	4th Sept.–8th Oct.	9th Oct.	27th Oct.
1935	6–25th Dec. 1934	26th Dec. 1934 –21st Jan.	20th Jan.
	22nd Jan.–12th Feb.	13th Feb.	6th March
	9th July–9th Aug.	10th Aug.	31st Aug.

Two crops of toadstools immediately follow the rain because the fruit-bodies of the epiphyllous species of the first crop are small and develop more quickly than the larger ones of the second and, moreover, growing on the surface of the humus, their mycelia revive sooner than the more deeply situated and, perhaps, mycorhizal mycelia of the second crop.

The toadstools of the third crop, which mature about 4–5 weeks after the wet weather has returned, may need to vegetate before fruiting or they may be delayed merely because their mycelia recover more slowly or take longer to develop rhizomorphs than those of the early crops : in general, their primordia develop at the same rate as those of Boleti. The toadstools of the fourth and fifth crops must have a preliminary vegetative stage yet they do not fruit indiscriminately as shown by their constant sequence.

Heavy rain must follow the dry weather to revive the mycelia but rain in itself is no stimulus to fruit. In June and December, when the forest is wettest and mycelia have been growing during several months of rainy weather, fruit-bodies are scarce. Toadstools of the second crop, which fruit about August, do not fruit in December though they have been vegetating for four months.

Many epiphytic orchids, it is well known, flower after a heavy storm not because of the wetting but because of the sudden drop in temperature during the storm. There is no evidence, however, that agarics respond to this stimulus. The drop in temperature must be appreciably less, both in degree and severity, in the humus than on the boughs of trees and, were the stimulus effective, runs of toadstools would be as frequent as the flowering of pigeon-orchids (*Dendrobium crumenatum*). I have, moreover, grown lignicolous agarics in a cool frame, where the temperature varied very gradually from 73–78° F. daily, and found that by drying the logs for two weeks and then soaking them fruit-bodies would develop without any marked change in temperature. And it seems that, except the highest mountain tops, nowhere in Malaya is the temperature low enough to limit the fruiting or the distribution of toadstools. All the common lowland species occur in the mountains at 4000–5000′, where the soil-temperature in the forest is, on the average 60–70° F. and 10–15° below that in the plains.

Some of these agarics, especially the Russules, Boleti and Amanitas, must be mycorhizal. In forests which I have repeatedly visited they occur season after season in the same places under the same trees, among which dipterocarps, oaks and Castanopsis are prevalent, and not elsewhere. They should fruit, one might imagine, according to some general activity of their host yet, as they do so at the same time or in sequence with saprophytic species, their mycelia must react like the saprophytic. Most forest trees respond to one or both dry spells of the year by flowering or leafing so that a run of fungus coincides with a flowering season, but without exact knowledge of the habits of the trees or of their mycorhizal fungi the ways of the two cannot be related. A remarkable Russule, for instance, I found in fruit in the mid-weeks of April and October in 1930, 1931 and 1932 only in one small area, about 30 yards across, on the lower slopes of Gunong Panti in Johore; it is clearly a seasonal, mycorhizal species, but its host cannot be determined by inspection for some twenty kinds of tall tree grow in proximity.

The Shortness of each Season.

During a normal year in Singapore and, probably, in any one locality in Malaya, Boleti will fruit for two weeks, the first in March, the second about September, and a botanist visiting the forest at other times could have no inkling of their existence

apart from a few species which fruit sporadically. (I have collected about 60 species without particular search). So, too, with other forest agarics: their seasons are remarkably short. Unless one can visit the forest at least once a week during a run of fungi many species, if not an entire crop, may be missed not merely because each has its place in the succession but because the fruit-bodies develop rapidly, especially through the later stages of expansion when they emerge from the humus, and they are short-lived. Those of Boleti, Paxillus, Flammula, Inocybe and Hygrophorus last about 4–5 days at maturity; those of Entoloma, Cortinarius and Lentinus may last a week or ten days; those of Amanita, Lepiota, Collybia, Russula, Lactarius, Volvaria, Psaliota and Psathyra last only 2–3 days: though there are a few exceptions such as two Boleti which I find last nearly three weeks.

When Patouillard came to Singapore on August 21st 1917 (Journ. Straits Branch R.A. Soc. no. 78, p. 67), there was a Boletus season in the Gardens Jungle and he described sixteen new species, though only seven had not already been collected by Ridley and Burkill in the same place and described by Massee (Kew Bull. 1901, 1909, 1914). But it could never have befallen Westerdijk that he went into the forest during a toadstool-season, when he wrote of the malayan region "In the virgin woods.....even the flora of mushrooms on the ground .....is absent. Everything seems to point to the conclusion that conditions are unfavourable to fungus growth" (Ann. Miss. Bot. Gard. 1915, 2, 308).

Irregularities in the Seasons.

A run of toadstools in the forest in a sure sign of a climatic change. The weather must have been dry enough to have affected the humus and the ensuing rain heavy and prolonged enough to have soaked it. A dry week might stimulate trees to flower or change their leaves and a storm might cause the pigeon-orchid to flower but the effects of such would not penetrate the dense canopy of the forest. Nevertheless there are minor irregularites in the toadstool-crops, which appear to be caused more by topographical features than climatic. A small, isolated and deteriorated patch of forest, such as the Gardens Jungle or the Bukit Timah Forest Reserve in Singapore, is exposed and a short dry spell or single storm might affect the humus; the wind could blow through such forest and dry the soil in weather which would not affect the continuous virgin forest. Thus I have noticed that there may be two crops of Boleti at the beginning of a season. In the Gardens Jungle in 1930, after a dry July and August, a great many Boleti began to develop about the 16th Sept., following a rainstorm on the 6th with showery weather in the ensuing week. But from the 15–27th the weather turned dry and windy and the floor of the jungle soon dried out; most primordia shrivelled and only a very few

came to maturity. Rainy weather followed from the 27th, with a heavy storm on the 28th, and the normal run of fungi began in October with a second, rather feeble, crop of Boleti about 16th October. It is unlikely that the rain from the 6–14th September would have soaked the humus in virgin forest or, if sufficient, that the following dry spell would have checked the new growth of mycelia, and there would thus have been the one normal succession. For the same reason there were two crops of Boleti at the beginning of 1932 and 1935; and the first crop of 1935 was exceptionally early because the wet weather broke a month before usual. In each of these instances only the first two crops of the succession were repeated; presumably the dry weather which returned after the first heavy rain prevented the mycelia of species of the subsequent crops from reviving, and one might prefer therefore a late-seasonal species as *Hygrophorus firmus* to indicate the seasonal run. Similarly, the crop of epiphyllous agarics may occur out of order: in the Gardens Jungle there may be a small crop in June because the surface of the humus dries in a few windy days and a single heavy storm may penetrate the rather light canopy and soak it. But how often or at what short intervals of dormancy or vegetative growth the toadstools of the first two crops can be made to fruit under such circumstances I cannot state. Nor is it known how mycelia remain dormant in dry soil; few species have sclerotia.

Observations on crops of Boleti, as the most easily recognised indicators of a succession, would in the virgin mountain forest give a valuable clue to the climate. For instance, in the ridge-forest on Gunong Panti in S.E. Johore I have never seen a run of fungus though I have visited it in most months of the year and when there has been a run on the lower slopes: it is a long, narrow and disconnected mountain about 1600′ high and its climate, which must be intermediate between that of the East and West coasts, is generally wet.

Species in Secondary Habitats

The environmental factors controlling the growth of fungi are much more equable in the high forest than in the open or in secondary jungle, and the fruiting of agarics in such places may be irregular. All such places, in fact, as lawns, pastures, orchards, estates and other clearings, must be considered secondary habitats because the land was originally covered with high forest and malayan fungi are primarily forest dwellers. Agarics of secondary habitats fruit also in crops in response to the same stimulus as the forest species but, because of the openness of their habitat, their mycelial growth is checked more readily by short dry spells and promoted again by lighter and

less prolonged rain. Of this kind are several species of Hygrophorus related to *H. puniceus* and *H. conicus*, Lepiota, Marasmius, Clitopilus, Leptonia, Galera, Naucoria, Coprinus and Psaliota on lawns or pastures, and of Pleurotus and Pluteus together with *Schizophyllum commune, Collybia apalosarca, Flammula dilepis, Lentinus sajor-caju, L. subnudus,* and *L. Lecomtei* on logs in the open. They do not fruit continuously in wet weather nor will they fruit without an interval for vegetative growth after each crop. As already mentioned, I have proved this by growing several of the lignicolous kinds under equable conditions: no fruit-bodies grew when the logs were kept continuously damp during 3–6 months but, when they were dried for 10 days and then sprayed, an abundant crop was obtained. Indeed the best way to study lignicolous agarics is by collecting logs from the forest in the wettest weather, drying them gradually in a shady place for 10 days and then spraying them frequently: the variety of basidiomycetes which develop is often incredible.

The only agarics which I have found fruiting continuously under wet conditions are coprophilous ones, which grow and fruit till their habitat is exhausted, and some lignicolus species of Mycena, Collybia, Marasmius and Pleurotus with small fruit-bodies, yet even they respond to the stimulus of drying and wetting.

The Termite-Agaric, Collybia albuminosa (Berk.) Petch.

So irregular is the fruiting of this species that I can form no opinion about it. As Petch noted (A. R. B. Gdn. Perad. 1913, 5,323) it fruits from inhabited nests, but it seems not to fruit more than once from the same nest, at least in Singapore where, however, most nests are rather small, and so one cannot watch the same place repeatedly. It fruits at any time of the year, even in the dryest weather on lawns which are browning, and though there are many nests in the Gardens Jungle from which it could develop it gives no special crop in a seasonal run of toadstools.

The Fruiting of other Basidiomycetes.

It appears that all kinds of Basidiomycetes, fruit in Malaya according to their season exactly as the agarics, but I have few detailed observations on others. The rain which starts a run of agarics starts also the fruiting of the woody Thelephoraceæ, Hydnaceæ and Polyporaceæ, most of which become noticeable rather late in the succession because their fruit-bodies grow slowly, though a few, like Favolus and some Hydnums and Polypores, grow fast and come with the second crop of agarics. The dry weather

checks also the growth of the perennial fruit-bodies of Fomes, Stereum amd Hymenochæte and they form a new layer of tubes or hymenium in the wet weather: hence, in a normal year, these fruit-bodies develop two layers of tubes or hymenium, unless they have grown in secondary habitats when they may develop more numerous and narrower layers. Even the resupinate fruit-bodies of Poria, Corticium and Odontia become stratified in this way.

Most Clavarias fruit with the second or third crop of agarics, but the coriaceous fruit-bodies of Lachnocladium generally develop later with the fourth crop. There are Clavarias, however, which fruit late in the season.

Lycoperdon, Calvatia, Scleroderma, Mitremyces and the subterranean forms, as Hymenogaster, Hydnangium, Leucogaster and Dendrogaster, fruit with the second or third crop of agarics: the fruit-bodies of some develop as rapidly as those of Amanita. The Nidulariaceae, Geasters and *Tylostoma exasperatum* fruit later with the fourth or fifth crops, but I have not been able to watch them. In the forest at Tembeling, in Pahang, during the second and third weeks of November 1930, there was a remarkable fruiting of some ten species of Geaster: the fruit-bodies developed mostly on the deep humus between the buttresses of tall trees and at the base of some the humus was almost covered: yet most of these I have not seen elsewhere in Malaya or, indeed, another such crop at any time. The season of the phalloids I do not know. Dictyophora, in the Botanic Gardens, fruits irregularly with the toadstools of the lawns: other kinds I have found too seldom to generalise.

Most Auriculariaceae, Tremellaceae and Caloceraceae fruit early in the succession, with the second and third crops of agarics, but there are some which fruit late.

Comparison with Temperate Countries.

Of the genera of agarics common to tropical Asia and the north temperate region, those are best represented in the tropics whose species fruit chiefly in the late summer or early autumn in the temperate region. Dry weather in May or June in England, followed by rain in June or July, will the cause the fruiting in July or August of many species of the following genera:— Amanita, Amanitopsis, Lepiota, Hygrophorus, Laccaria, Russula, Lactarius, Marasmius, Cantharellus, Clitopilus, Leptonia, Entoloma, Pluteus, Inocybe, Astrosporina, Psaliota, Hypholoma (sect. *H. appendiculatum*), Psathyra. Boletus and Paxillus. And these genera are well represented in Malaya, there being, for instance, several species related to *Amanita caesarea* of southern Europe, and malayan toadstools in general resemble

those of the southern United States. In contrast, Tricholoma, Clitocybe, Collybia, Pholiota, Cortinarius, Hebeloma, Naucoria, Tubaria, Flammula, Stropharia, Hypholoma (sect. *H. fasciculare*), Gomphidius, Psilocybe and Panaeolus, whose species fruit mostly in late autumn and early winter in Europe, are poorly represented. I have not seen a single specimen of Tubaria or Gomphidius in Malaya———(*G. roseus* Mass. non (Fr.) Quel., described from Singapore, is probably *Paxillus lateritius* Petch and, certainy, no Gomphidius)———and only one Phlegmacium, one Hebeloma and one Psilocybe. Gomphidius, however, is typically associated with forests of Abietineæ and these are absent from Malaya.

It seems that the agarics of temperate countries can be divided roughly into two groups:—1. those which are related to tropical species and which fruit, like them, at relatively high temperatures in response to summer drought followed by late summer rain; 2. those which are truly temperate and fruit at relatively low temperatures in late autumn, winter or spring and perhaps only after night-frosts or prolonged cold rain.

Summary.

Each normal year agarics have two general fruiting seasons in south Malaya, perhaps over the whole country. A succession of species then develops for some three months. Each has its own short season of about a week in full fruit and most, especially Amanita, Russula and Boletus, fruit at the beginning of the succession.

The first season beings in March, the second about August or September. Both follow immediately the change from dry to wet weather. The stimulus to fruit is primarily the dry weather which checks mycelial growth, and ensuing rain causes the development of fruit-bodies. Seasonal species do not fruit in prolonged wet weather.

Observations on crops of Boleti in the forest would give valuable evidence of the local climate.

Agarics in open places fruit more often because their habitat is more exposed to alternate drying and wetting.

Most other basidiomycetes fruit in the same seasons. Perennial fruit-bodies normally develop two new layers each year.

Malayan agarics in their kind and manner of fruiting resemble the summer and early autumn agarics of temperate lands.