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Structure of mushroom casing soil and its influence on yield and microflora

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Summary

The more compact the structure of mushroom casing soil, the better the yield, provided much water has been given during vegetative growth and, especially, provided the upper layer of the casing is ruffled or raked up before the induction of the generative phase.

Expressed in terms of diffusion rate: the more the diffusion from gaseous metabolites from compost to air is hampered during vegetative growth, the better the yield, provided a good diffusion to air is restored just prior to fructification.

Many of the relevant phenomena can be attributed to CO_2, but the influence of other metabolites, such as acetone and ethylene, on fruitbody-inducing micro-organisms cannot be neglected, as may be seen in the above-mentioned experiments on structure, and in studies on the difference in behaviour on thin and thick casing layers, supplementation at casing with soybean meal, the difference in behaviour between slow- and quick-pinning mushroom strains and excess volatile components of the compost, applied at different times.

Introduction

Mushroom casing soils with a compact structure are usually considered as bad soils because of impeded diffusion from the nutritional base, the compost, through the casing soil, in which the mushrooms are formed, to the air in the mushroom house. This leads to harmfully high concentrations of CO_2 in the soil during fructification and as a result to yield depression (Sinden, 1973). By repeated watering during the culture the soil will become still more compact, for example by changes in soil aggregation (Flegg, 1954).

Edwards & Flegg (1953) working with cultures in pots or very small trays found that the larger the number of pores in soil, the better the diffusion and the better the yield. When more water was applied to the soil before casing, however, they found that yield was better. These findings seem to conflict since more water decreases the number of air-filled pores and therefore the diffusion rate (Flegg, 1953). Only Lambert & Humfeld (1939) remarked that in general heavy clayish soils yielded better than lighter sandy soils.

Table 1. Yield in kg/m² from 100 kg compost/m² after 5 weeks of picking. Soils ruffled before fructification. Water: given during vegetative phase. Basic ingredients of the soil: black peat 65 %, spaghnum peat or substitutes 25 %, marl 10 %. Four replicates.

Casing soil	Amount of water added	
	'standard' (4 litres/m²)	'wet' (7 litres/m²)
Standard loose	15.5	18.0
Standard adpressed	15.0	19.8
Hygromull 25 % loose	15.2	17.8
Hygromull adpressed	15.3	20.7
Styromull 25 % loose	16.9	19.4
Styromull adpressed	16.1	21.4
Hygromull 15 % loose + styromull 10 % adpr.	15.4 20.4	19.4 18.9

At the Mushroom Experimental Station at Horst preliminary experiments were started to study the influence on yield of a flattened, adpressed, i.e. more compact casing soil as one of the prerequisites for mechanical harvesting. The intriguing results led to a closer investigation into the structure of casing soil in relation to yield (Visscher, 1973, 1975). In this paper more attention will be paid to the microbiological aspects of the structure of casing soil.

Structure of casing soil in relation to CO_2

Three methods were applied or combined: compact or non-compact components of the casing mixture, e.g. clay versus spaghnum peat, adpressed or not-adpressed soils in different growing phases, and normal or extra water during the vegetative phase. The result of one of the experiments is given in Table 1.

From these and many other data we concluded that:

1. the more compact the structure of casing soil, the better the yield, *provided*
2. much water has been given during vegetative growth, *especially provided*
3. the upper side of the soil is raked up before fructification starts.

If we express this in terms of diffusion rate, only two statements remain:

1. the more diffusion through casing soil is hampered during vegetative growth, the better the yield, *provided*
2. a good diffusion is restored in the upper layer of the casing, i.e. where fructification occurs.

For this contention we needed CO_2 measurements in loose and adpressed soils during vegetative and generative phase, and also at 1 and 4 cm depth in the casing. We found the data given in Table 2, as measured with a Wösthoff apparatus.

Note in passing that the somewhat higher values at 1 cm depth in adpressed soil during 'pinning' are probably not dubious registrations but expression of the fact that at time and place of pinning there must be a considerable metabolism, registered only when diffusion was seriously hampered.

Table 2. CO_2 concentration in casing soil in % during vegetative and generative phase. First harvest: 8/2.

	Vegetative phase		Generative phase			
	loose	adpressed	raked up		adpressed	
	25/1	25/1	3/2	7/2	3/2	7/2
1 cm depth	0.35	0.75	0.13	0.14	0.30	0.43
4 cm depth	0.45	1.00	0.13	0.14	0.28	0.35

Since we make a clear distinction between the vegetative and generative phases, it is possible to find confirmation for our findings in recent literature. Long & Jacobs (1968), San Antonio & Thomas (1972) on a laboratory scale (see also Tschierpe, 1972, and earlier on a more applied scale Rasmussen, 1962, working with extra deep layers of compost) all found the benevolent influence of a high CO_2 concentration during vegetative growth, which we are applying by adpressing our casing soils.

Mushroom growers know from experience, moreover, that sparse mycelial growth in the compost looks much better a few days after casing, i.e. by hampering the diffusion, the same phenomenon as in our experiments, but encouraged by adpressing the soil.

The ruffling or raking up, moreover – apart from restoring the desired low CO_2 concentration during fructification up to about 0.1 % (Long & Jacobs, 1968; Tschierpe 1959, 1972; Tschierpe & Sinden, 1964) – disturbs the capillary evaporation occurring in undisturbed soils, thereby eventually giving better retention of the extra water given. It also gives rise to 'mountains' and 'valleys', the young 'pinheads' forming in the valleys where they suffer less from the air streams caused by ventilation and circulation.

The Dutch mushroom growers have been raking up or ruffling their rather compact casing soil long before our experiments led to the same conclusion. In the meantime they have developed methods to simplify the procedure. From the original ruffling the surface by hand they developed a small wooden plank with nails in it, employed as a kind of rake. More recently, some use a slowly-rotating drill, with a long axle fitted with side pins, disturbing the surface to the required depth.

Eger's bacteria

The discussion so far has been confined to the role of CO_2 during the vegetative and generative phases. Lockard & Kneebone, however, reported in 1962 that other volatiles are produced by the mycelium in the compost: acetone, acetaldehyde, ethylene, ethyl alcohol and ethyl acetate. In 1960 Eger introduced the 'Halbschalen' test in which compost and casing soil are placed alongside in a petri dish instead of casing on compost as is usual. She demonstrated that under sterile con-

ditions no fructification occurred. Unsterilized soil or soil from a cased mushroom bed, however, induced fructification; the longer the lapse of time after casing, the more 'pinheads' were induced by the soil sample. She concluded that, after casing, micro-organisms began to develop which, when present in sufficient quantities, induced fructification. The responsible organisms appeared to be bacteria (Eger, 1961). About at the same time Urayama (1961) reported that some bacteria isolated from *Psilocybe* mushrooms increased mycelial production and initiation of fruit bodies of *Agaricus bisporus*. Des Thomas et al. (1964) reproduced Eger's results, using petri dishes with bases divided into quadrants.

Hayes et al. (1969), also confirming Eger's results, postulated that *Pseudomonas putida* might be one of the responsible species. (See, however, Park & Agnihotri (1969a, b), but not substantiated by Eger (1972).) It is appropriate here to mention that Hayes identified the bacteria from his casing soil as *P. putida*, but is seems possible that in other countries, with other casing soils, other species of bacteria or perhaps other groups of micro-organisms may be involved in the induction of fructification. Indeed Eger (1972) observed a difference in behaviour between bacteria from her soil and strains of *P. putida*, though she did not substantiate the work by Park & Agnihotri (1969a) who tentatively idientified other active micro-organisms.

In accordance with Eger's ideas Long & Jacobs (1968) reported that under non-sterile conditions fructification occurred in an optimum CO_2 range of about 0.03 – 0.1 %. Under sterile conditions, however, no fructification started, whatever the CO_2 concentration. These results reconciled Eger's data and Tschierpe's opinion that variations in CO_2 concentration alone were responsible for fructification.

Eger (1961) reasoned that the bacteria are stimulated by volatile metabolites from the compost mycelium which are oxidized or converted before being present in excessive quantities at 'pinning'. She referred to earlier authors, who had concluded that compost volatiles other than CO_2 exercised no harm during vegetative growth but should be present during pinning in low concentrations only. (See Mader (1943), Schisler (1957) and Stoller (1952), who suggested an oxydation/reduction mechanism in the casing layer; see also in this context recent work by Hayes (1972, 1973) on the possibility that Fe^{2+} ions could play a prominent role in the mode of action of the bacteria.)

Other metabolites

After the discovery by Lockard & Kneebone (1962) of volatile metabolites from the compost other than CO_2, Hayes et al. (1969) observed that compost volatiles, including a partial 'Lockard-Kneebone' mixture of acetone, ethanol and ethyl acetate, stimulated their *P. putida* cultures when grown on a carbon-free liquid medium. Eger (1972) corroborated these findings, demonstrating that her bacteria could grow on a medium with acetone as the sole carbon source. Moreover, bacterial cultures supplemented with acetone seemed to induce more pinheads on 'Halbschalen' tests than not-supplemented cultures.

Tschierpe & Sinden had ascertained in the meantime (1965) that acetone is the

most important substance, liberated from the compost under aerobic conditions. They observed that after casing its concentration gradually decreased, interpreted by Eger (1972) as the result of increased consumption of acetone by the increasing bacterial population until some equilibrium had been reached.

Complications arise, however, since Tschierpe & Sinden (1965) and Richter (1967) found that many of the products reported by Lockard & Kneebone (1962) are mainly products of an anaerobic vegetative growth. Notwithstanding this, there was a 1940 observation by Stoller (1953), seldom cited, that compost volatiles worked out like ethylene-like products on tomato plants, present under bell jars on beds with growing mushrooms or in bottles of spawn, long before the identification of ethylene by Lockard & Kneebone. We do not know if acetone has a similar epinastic influence on tomato plants. If not, some more attention for the role of ethylene seems desirable, especially after a recent paper by Smith (1973) about the influence of 0.5-3 ppm ethylene on micro-organisms in soil. The absence of ethylene caused dense mycelia from various mould genera from which many species are known in mushroom culture as weed moulds, appearing usually after bad mycelial growth of *A. bisporus*. Its presence caused 'fungistasis, an inhibition of the germination of fungal propagules in soil under apparently favourable conditions'. It was produced as well under aerobic as anaerobic conditions.

Until now the important research into the microflora has been performed on a laboratory scale. It would be interesting to find a link with the practice of mushroom growing – for instance on an experimental station – as to the existence and action of the microflora for which we suggest the name 'Eger's bacteria' in honour to their discoverer. We leave undecided the exact way in which this flora exerts its influence. From the data by Eger, des Thomas, Hayes and Long & Jacobs we assume a causal relation between the presence of certain micro-organisms in the casing layer – say *P. putida* – and fructification. We modestly suppose to have found such links; we will give them below.

A. The structure of casing soil and metabolites other than CO_2

An impeded diffusion rate, as obtained in our experiments by adpressing the soil, not only leads to a doubling of the CO_2 concentration (Table 2) and a better yield under favourable conditions later on, but must lead to higher concentrations of all volatile metabolites, consumed later on or not. It is true that Eger (1962b, c; 1972, thesis 5) supposes that the casing must protect the microflora against too high concentrations volatile substances in the compost, since she found that the development of many micro-organisms was retarded by these products in petri dishes. However, she has never demonstrated, as far as we know, that precisely the fruiting-inducing bacteria were slowed down, but the reverse, i.e. stimulated by acetone. We are inclined from our experiments to support Schisler's view (1957) that the casing acts as a barrier to the release of some essential metabolite(s), consequently stimulating bacterial development, fructification and yield.

In a more open soil the volatile components will escape more readily, to the detriment of the bacteria which will be less stimulated, and consequently the yield

Table 3. Yield in kg/m² after 5 weeks of picking from 100 kg compost/m² in loose or adpressed casing soil with two mushroom strains; the compost was supplemented or not with 1 kg soybean meal/m².

Strain	Casing	Compost	
		— soybean meal	+ soybean meal
Sinden A 1	loose	18.3	21.9
	adpressed	18.3	23.0
Y 205	loose	17.9	20.8
	adpressed	16.8	21.5

will be lower. From Eger's findings we may tentatively conclude that the fungistasis just mentioned, caused by ethylene or something like that, played a role in her experiments. Moreover, we must remember that in a casing soil of which the surface has been raked up, the disturbed capillary evaporation gives a better holding of the water. In a wetter soil there is, besides perhaps more free water, a lower osmotic pressure and a higher moisture tension which may also favour bacterial development later on in the culture (see Section E).

B. Soybean meal in the compost

In one of our experiments the compost was supplemented at casing with soybean meal at a rate of 1 kg/m². The control had none. Two mushroom strains were used, Sinden A 1 and Y 205; the casing soil had been adpressed (or not) during the vegetative phase (see Table 3).

From the pattern in Table 3, considered in conjunction with Table 1, we conclude that soybean meal in the compost works out like much water during vegetative growth. Why? There is no extra restriction of diffusion through additional water. There is, however, a considerably higher metabolism in the compost as appears, for example, from the 2–4 °C higher compost temperature in supplemented series during the first 2–6 days after casing. This must inevitably lead to more volatile metabolites, and consequently – as argued earlier – to a stimulation of the micro-organisms and a higher yield.

Moreover, soybean meal does not yield larger, but more mushrooms, i.e. it has an influence on fructification (Gerrits 1972, in accordance with various data from Schisler). In our experiment the pressing of the soil must lead to still more volatile components held in the casing and, consequently, as we have said, to a still higher yield. Holz & Schisler (1972), studying lipid metabolism, suggest that the stimulatory properties of linoleic acid – a fatty acid also present in soybean meal – when applied subsequent to casing, are due to its breakdown to acetate units, which are synthesized then into sporophore lipids.

While admiring the studies in lipid metabolism, we must bear in mind that the whole process apparently does not work in a sterilized casing soil. We must assume, therefore, some role for the micro-organisms in the casing soil in this process, since

even on 'Halbschalen' tests with a Till substrate supplemented with rasped coconut – giving a much more abundant fructification in some cases than with soybean meal in a non-sterile casing soil – no fructification appeared under sterile conditions (Till, Eger, unpublished results).

At the moment we only have to suppose that soybean meal, or the linoleic acid in it, influences fructification, for instance, by the indirect pathway of stimulating the microflora by supplying a larger amount of mycelial volatile components from the compost – as well CO_2 as other break-down products from linoleic acid by the acetyl-CoA-acetoacetate pathway – converted by the microflora and to be built in, somehow, as sporophore lipids. (See also Section E, in which an indirect pathway is assumed, caused by application of excess volatile components.)

Bearing in mind also the studies by Rast and coworkers as for other volatile mycelial metabolites, such as isovaleric acid with its metabolic products acetoacetate and acetyl-CoA (Rast & Stäuble 1970), we have to leave open the possibility that diffusion and water streams upwards may carry non-volatile substances into the casing soil as a source for the micro-organisms.

C. Thin and thick casing layers

In one experiment two of our small growing rooms were filled, spawned (seeded with mycelium) and cased on the same day. In the first room all casings had a depth of 2.5 cm, in the second room of 5 cm. The first room could be cooled down after vegetative growth 5 days earlier than the second, due to the earlier appearance of the mycelium near the surface. Both rooms, notwithstanding, came into production on the same day (up to one day earlier for the thin casings). In the meantime it was clearly visible that on the thin casings fructification started after cooling down very slowly and hesistantly. Pinheads did not appear until about the moment when fructification started in the second room. The explanation may be that during vegetative growth in the thin casings – apart from having a less hampered diffusion, as suggested already by Schisler (1957), and consequently having less volatile substances at disposal – the micro-organisms had had insufficient time to build up a population large enough to induce fructification when the mycelium was already present. At the time that enough inducing influence had been built up, fructification started in a more normal way in both rooms simultaneously.

The foregoing paragraphs suggest that micro-organisms are at work in mushroom practice. They are no certain proof, since the existence of CO_2 as the most important volatile component, explained in the classic way without micro-organisms, might explain many of the phenomena.

The following paragraphs describe some observations that are even harder to interpret exclusively by the presence of CO_2 in the classic way.

D. Quick-pinning and slow-pinning mushroom strains

As a working hypothesis, we explain the difference in behaviour between slow-pinning and quick-pinning mushroom strains by assuming that the slow-pinning

strains need more micro-organisms (or their inducing influences) than quick-pinning strains to start fructification and usually give lower yields of mushrooms in the first flush(es) than the quick ones do.

When growing slow-pinning strains, we found the same slow way of pinning as when growing a quick-pinning strain on a thin casing layer (Section C). The slow pinners might therefore also lack bacterial influence, not by accident but as a kind of inherent property. Therefore we started a program to test this hypothesis. We have the results of the first experiment.

An impression which supports this hypothesis is that we have found good mushroom growers who have experienced the need for a slightly thicker casing layer with slow-pinning strains than is usual. So perhaps the mushroom mycelium needs more time to reach the stage to be cooled down in a thicker casing layer, and diffusion in a thicker layer is less. The microflora, stimulated to a larger extent, has more time to build up a population large enough to induce fructification reasonably for this particular type of spawn.

Also from Eger's data (1962a), fewer micro-organisms were needed to induce fructification in quick-pinning strains than in the slower-pinning ones.

Steaming of a soil thoroughly disturbs the microflora in that soil and, in mushroom culture, steaming may depress yield. By introducing live steam in a room where the soil in trays reached a temperature of 60 °C for about 6 h, a soil was steamed before casing. As a control the usual Dutch procedure was used, in which a formalin solution was sprinkled over the beds after casing, about 2 litres formalin in 100 litres water per 100 m².

If our hypothesis is correct, there would be a greater yield depression due to steaming in a slow-pinning strain than in a quick-pinning one, especially in the first weeks of picking, since the microflora needed to start again from near zero. In the experiment with Sinden A 1 as a 'quick pinner' and Somycel 53 as a 'slow pinner', the results of all treatments supplemented with 1 kg soybean meal per m² at casing seem to confirm our hypothesis in an extreme way (see Table 4). Expressed as a percentage of the control, the steamed soil produced a yield in the respective flushes of 37, 52, 135, 321 and 361 % in the quick-pinning strain and of 27, 23, 39, 107 and 275 % in the slow-pinning one. The essence of the experi-

Table 4. The influence of steaming of casing soil on yield of a quick-pinning strain (Sinden A 1) and a slow-pinning strain (Somycel 53). Yield in kg/m² from 100 kg compost/m². Supplemented at casing with 1 kg soybean meal/m². Four replications.

Strain	Casing treatment	Yield					
		1st week	2nd week	3rd week	4th week	5th week	total
Sinden A 1	not steamed	4.98	11.13	4.22	1.61	1.09	23.03
	steamed	1.83	5.81	5.71	5.17	3.94	22.46
Somycel 53	not steamed	2.34	6.98	6.99	4.01	2.30	22.62
	steamed	0.63	1.64	2.74	4.30	6.32	15.62

Table 5. Yield in kg/m² in 5 successive weeks of picking. Treatments: a stay in an unventilated climate box until the following charge. Cooled down at 27/1. Mean of two replications.

Intervention day	1st flush 7/2-12/2	2nd flush 13/2-19/2	3rd flush 20/2-26/2	4th flush 27/2-5/3	5th flush 6/3-12/3	total
A 29/1	3.15	6.00	2.81	2.56	1.37	15.89
B 31/1	3.56	6.14	0.30	2.78	1.89	14.93
C 2/2	3.26	5.19	2.74	2.44	1.44	15.08
D 5/2	2.56	5.56	3.30	1.81	1.15	14.37
E 9/2	3.59	5.04	2.20	2.74	1.78	15.37
F 19/2	3.00	4.93	0.96	2.33	2.26	13.49

ment is the slower recovery in the slow-pinning strain due to the steaming and, consequently, the lack of fruitbody-inducing micro-organisms.

E. Phenomena, caused by excess volatile components from the compost, applied at different times

In two experiments with nearly the same results in a climate box the same conditions prevailed as in one of the growing rooms, with only one exception: there was no ventilation in the box, only circulation. At various times after casing, two small trays were transferred simultaneously from the growing room to the box until they were replaced by another two trays (Exp. 1) or for two or three consecutive days (Exp. 2) and afterwards returned to the same room.

When trays were present, CO_2 concentration in the air of the unventilated box rose to about 0.2 – 0.3 (0.35) % in the first and to about 0.2 – 0.25 % in the second experiment.

This procedure resulted in excess volatile substances as demonstrated by the CO_2 concentration as a parameter, applied at different times.

The yield of the first and preliminary trial is given in Table 5. In the second ex-

Table 6. Yield in kg/m² (Y) and number of mushrooms/m² (N) in 5 successive weeks of picking. Treatments: stay in an unventilated climate box for 2-3 days. Cooled down at 27/10. By conversion and rounding off, additions can give slightly different data. Mean of two replications.

Intervention	1st flush 6/11-12/11		2nd flush 13/11-19/11		3rd flush 20/11-26/11		4th flush 27/11-3/12		5th flush 4/12-7/12		Total	
	Y	N	Y	N	Y	N	Y	N	Y	N	Y	N
A 26/10-29/10	5.06	530	7.82	1485	2.89	693	1.61	270	0.45	78	17.82	3056
B 30/10-1/11	3.80	270	9.02	1685	3.19	659	1.96	307	1.24	133	19.21	3052
C 2/11-5/11	3.65	244	8.21	1322	4.54	993	1.58	233	1.15	141	19.12	2930
D 6/11-8/11	4.50	393	5.96	1063	3.13	667	2.26	400	0.85	133	16.70	2648
E 9/11-12/11	4.54	363	7.82	1363	3.34	548	2.08	289	1.67	152	19.43	2707

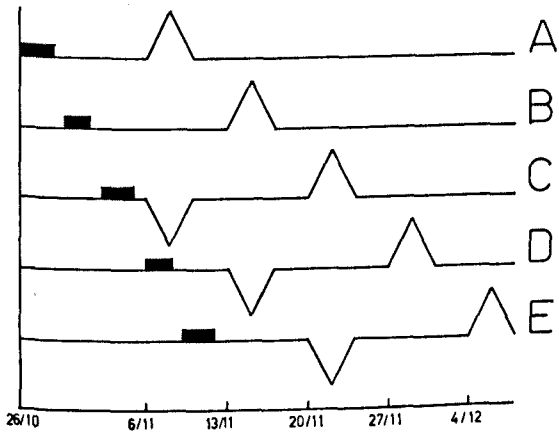

Fig. 1. Schematic reproduction of the data from Table 6 reflecting the ups and downs of relevant treatments after intervention (intervention periods are indicated as black rectangles).

periment (Table 6) not only was the yield recorded, but also the number of mushrooms harvested. Moreover, times of intervention were slightly modified. The data in both tables are given as a mean of two trays, each with a surface of 0.27 m^2 and filled with 27 kg compost. From the data we see (Tables 5 and 6, Fig. 1) that after a lapse of time, enlarging at later times of intervention, two phenomena become visible, in yield as well as in number of mushrooms harvested, meaning that the phenomena are mainly due to some factor(s) affecting fructification.

Phenomenon A. About two to four weeks after the stay in the climate box the relevant treatment gives the highest yield in a flush of all treatments in that flush. The later the intervention the more delayed the appearance of the phenomenon.

Phenomenon B. About two weeks before phenomenon A appears, the relevant treatment gives the lowest yield in a flush of all treatments in that flush, the phenomenon appearing only when mushrooms are present or in development. Since only A appears after the first interventions and B only from the third intervention onward, we must conclude that A appears independent of B and not that A, though later in time, is a reaction on B.

We are inclined, therefore, to look for a different cause for both phenomena. For B we suppose a direct temporary self-poisoning effect on mushroom induction by excess volatile substances during the stay in the climate box, according to Tschierpe's results with CO_2.

The most reasonable explanation for A seems that the larger amount of volatile substances during the stay causes a temporary stimulation of the micro-organisms, consequently – as argued earlier – leading to a better yield afterwards. So A can be seen as the result of an indirect pathway and therefore appearing later than B. (See also Section B, in which an indirect pathway caused by linoleic acid is assumed.)

The delayed reaction in both cases at later intervention times we tentatively attribute to the ageing of the mycelium coupled with a lower metabolism reacting more slowly on the bacterial impulse and on the self-poisoning effect. If our inter-

pretation is correct, we have segregated the effects of CO_2 from those of other metabolites, again reconciling Eger's (new) data (and those of Mader, Schisler, Stoller and others) and Tschierpe's ideas about CO_2 concentrations.

These kinds of experiment, part of a system of splitting up the time after casing into defined phases, may offer a better understanding of what is exactly required, not only 'after casing', or even in the vegetative or generative phase, but much more exactly, perhaps up to hours instead of days or weeks, in which decisions are made about fortune or crop failure, as has been demonstrated already by Tschierpe (1972) for the time between cooling down and first flush. We may learn, for instance, from the box experiments that stimulation of the microflora may be of a temporary nature, so that also during the harvest period the microflora needs a constant flow of volatile metabolites.

Otherwise phenomenon A would be a lasting one, appearing also in later flushes after its first appearance. In the undisturbed part of a wet, adpressed soil, raked up before fructification, the benevolent conditions for bacterial development are still present, as pointed out in Section A, for example, for higher moisture tensions. Our approach may have tentatively shown, moreover, that it is possible to bring the results of laboratory workers to growers 'in the field'.

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