

Responses of agaric fruit-bodies to light and gravity: growth straight downward in response to light from below

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Fruit-bodies of Agaricales are known to show positive phototropism during the early stage of development, but negative gravitropism at the later stage after the onset of basidiospore formation. However, when exposed to light from below, the fruit-bodies of *Tephrocybe tesquorum* and *Coprinus* spp. grew downward through all stages of development, even after the onset of basidiospore formation. Primordium formation, fruit-body development and basidiospore formation were not disturbed under such conditions. In these downward-growing fruit-bodies, gills stood straight upward. In *T. tesquorum*, caps often became swollen and stipes sometimes became twisted anticlockwise, contrary to those in light from above, while such behaviours were not observed in *Coprinus* spp.

Key Words—*Coprinus* spp; fruit-body development; gravitropism; phototropism; *Tephrocybe tesquorum*.

Figure 1 shows the known responses of Agaricales fruit-bodies to light and gravity. The response marked ? is unknown. Many Agaricales fruit-bodies exposed to light from one side grow first toward the light by positive phototropism, and then upward by negative gravitropism (Buller, 1909, 1924, 1931; Gooday, 1985). The (negatively) gravitropic bending has been reported to take place when basidiospores begin to form (Badham, 1982). In Fig. 1, this bending was assumed to take place at the same distance from the centre, at the onset of basidiospore formation.

While agaric stipes show negative gravitropism, gills show positive gravitropism (Schmitz, 1842, 1843; Sachs, 1865, 1877). These tropisms have been considered as an adaptation for dispersing basidiospores successfully (Buller, 1909). Buller (1909) reported that all the gills grew downward when the pileus of *Agaricus campestris* L.: Fr. was tilted at an angle of less than about 30°, and that, when tilted beyond a certain degree, some of the gills became stuck together and only a few gills at the highest position grew downward to disperse basidiospores successfully. Buller (1909) also observed that gills of the *Coprinus* species did not show such gravitropism. Later, he called those *Coprinus* Type' and the other agaric species 'Non-*Coprinus* Type' (Buller, 1922). Gorovoj et al. (1987) classified hymenomyces into three types based on the gravitropic response: *Coprinus* species, other agaric genera and bracket fungi.

To elucidate the response marked ? in Fig. 1, we studied the growth of Agaricales fruit-bodies exposed to light from below. We also studied the developmental behaviours of their stipes, gills and caps under the same conditions.

Plunkett (1961) exposed the fruit-bodies of *Polypo-*

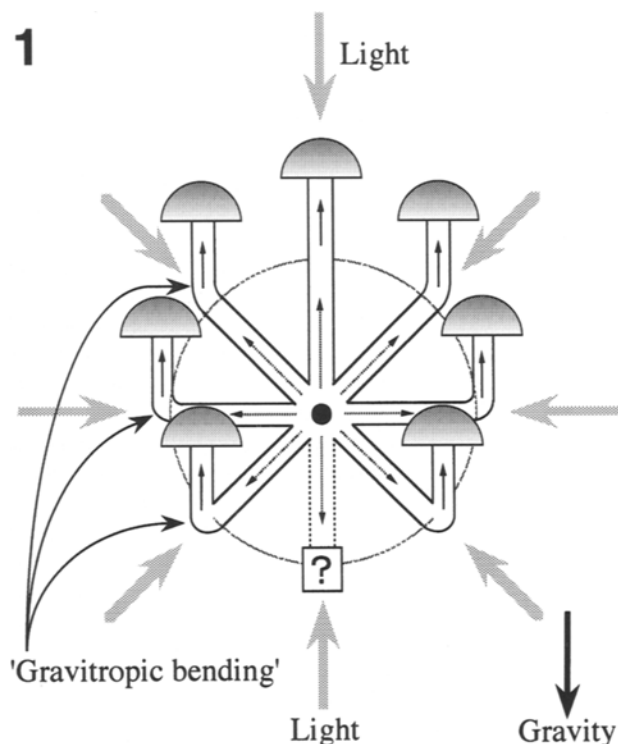


Fig. 1. Responses of Agaricales fruit-bodies to light from directions other than below. The mark ● at the centre: the position from which the fruit-bodies are assumed to have emerged. Circle: the position where basidiospores began to form. Dotted arrows: phototropic growth. Solid arrows: negatively gravitropic growth. The mark ?: lack of information.

rus brumalis (Pers.: Fr.) Fr. (Aphylophorales) to light from above first, then from the side and finally from below. As a result, the fruit-bodies grew toward the light source throughout their development, and eventually formed an inverted 'U' shape. In his experiment, however, the light from below was not given from the beginning (from before primordium formation), but only in the last stage.

As a new method to obtain agaric fruit-bodies to be exposed to light from below, we adopted an experimental system known to yield 'ammonia fungi' (Sagara, 1975, 1992, 1995). The system includes collecting raw humus from a forest and treating it with urea. The raw humus can be set afloat using a container with holes bored in the bottom, and fruit-bodies emerging through the holes can be exposed to light from below throughout development.

Materials and Methods

Fungal species used We used *Tephroclybe tesquorum* (Fr.) Moser (Tricholomataceae), *Coprinus neolagopus* Hongo & Sagara, *C. phlyctidosporus* Romagn. and *C. cinereus* (Schaeff.: Fr.) S. F. Gray (Coprinaceae), which fruited on the urea-treated humus. Nomenclature of the fungi follows Sagara (1992). They belong to the ammonia fungi, and fruit in the early phase of fungal succession on urea-treated forest soils (Sagara, 1975, 1992, 1995). According to the classification by Buller (1922), *T. tesquorum* should belong to the 'Non-Coprinus Type', and three *Coprinus* spp. to the 'Coprinus Type'.

Preparation of urea-treated humus Raw humus was collected from the mixed forest of *Pinus densiflora* Siebold & Zucc. and *Quercus serrata* Thunb. on Mt. Daimonji in Kyoto City, Japan. The amount of humus used was from 46 to 200 g in fresh weight (from 17 to 80 g in dry weight) depending on its water content; when water content was lower, a larger amount of humus was used.

Fresh humus from the forest was mixed well with urea dissolved in 50–100 ml of tap water, at the rate of 20 mg N per g dry humus. The humus thus prepared was packed into the container pot.

Apparatus To obtain light from below, we used an apparatus (Fig. 2) equipped with a rotator (Rotator RT-5, Taitec Co., Inc.; Fig. 2, g) with a vertical axis (Fig. 2, f) to cancel the effect of unilateral light. (Historically, a rotator or clinostat with a horizontal axis has been used, vertical rotation cancelling the effect of vertically-directed gravity and bringing about *simulated* zero-gravity.) Horizontal rotation (Fig. 2, arrow) made the unilateral light uniform and vertical, and, as a result, brought about *simulated* light from below (Fig. 2, arrow in halftone). Hereafter, such light will be called 'light from below'. One to four apparatuses, each with a pot containing the humus, were placed in an incubator, where light was provided from fluorescent tubes (FL40SEX-N, NEC) installed vertically on two walls. The top of the pot (a in Fig. 2) packed with humus was covered with a black vinyl sheet (b), and the bottom (c) with small holes (see below) was exposed to light from below. By rotating the

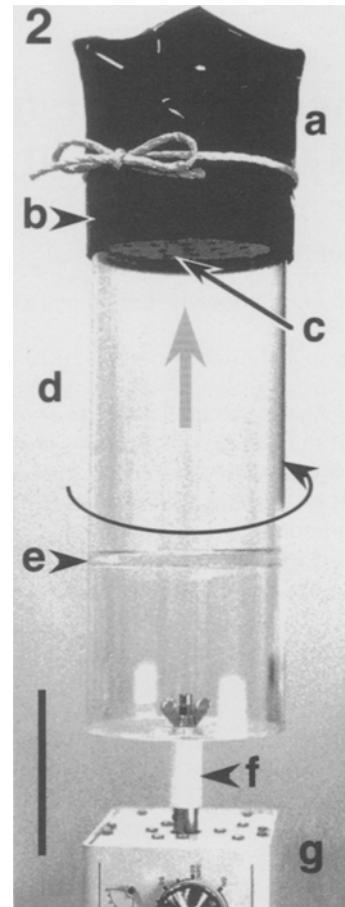


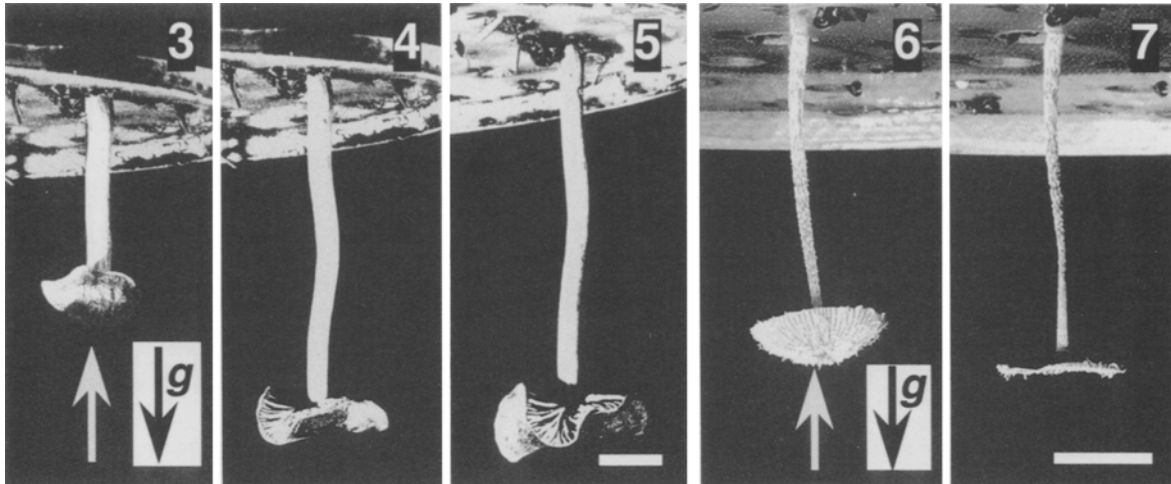
Fig. 2. Apparatus used in the present study. a: pot covered with vinyl sheet (b); b: vinyl sheet to block light; c: pot bottom with holes; d: transparent plastic cylinder; e: plastic partitioning plate in the cylinder; f: vertical axis; g: rotator. Pot (a) and transparent plastic cylinder (d) were rotated by the rotator (g) in the direction of the arrow, and hence unilateral light was made to be uniform, i.e., vertically upward (arrow in halftone). Scale bar = 10 cm.

pot, light from below was provided to the humus (Exp. 1); by placing, without rotating, the pot close to one fluorescent tube, light from obliquely below was provided (Exp. 2).

The pot was made of non-transparent epoxy resin and measured 13 cm in diam and 12 cm in height. From 20 to 37 holes, each 7 mm in diam, were made in its bottom for fruit-bodies to emerge through.

The pot was placed on a transparent plastic cylinder (d in Fig. 2) fixed on the vertical axis (f) of the rotator (g). Tap water was added to the upper part of the cylinder above its partitioning plate (e) to maintain humidity in the space below the pot, where fruit-bodies were to develop. Because the pot was rotated slowly at a rate of 2.0 rpm, centrifugal force (in the order of $10^{-4} \times g$ at most) is thought to have been negligible.

As the control experiment, the pot packed with the humus was placed in the incubator without connecting to the rotator. The upper part of the pot was covered with



Figs. 3–7. Fruit-bodies of *Tephrocybe tesquorum* (Figs. 3–5) and *Coprinus neolagopus* (Figs. 6, 7) exposed to light from below at successive stages of development (Exp. 1). Half-tone arrows: direction of light. *g*: gravity vector. Scale bar=1 cm. 3. *Tephrocybe tesquorum* 1 d after the onset of basidiospore formation (the beginning of gravitropic stage). 4. Three days later: the cap has begun to wave. 5. Further 2 d later: waving has increased. 6. *Coprinus neolagopus* with convex cap. 7. Nine hours later: the flat cap with gills and the whole appearance are similar to those in the control (see Fig. 11).

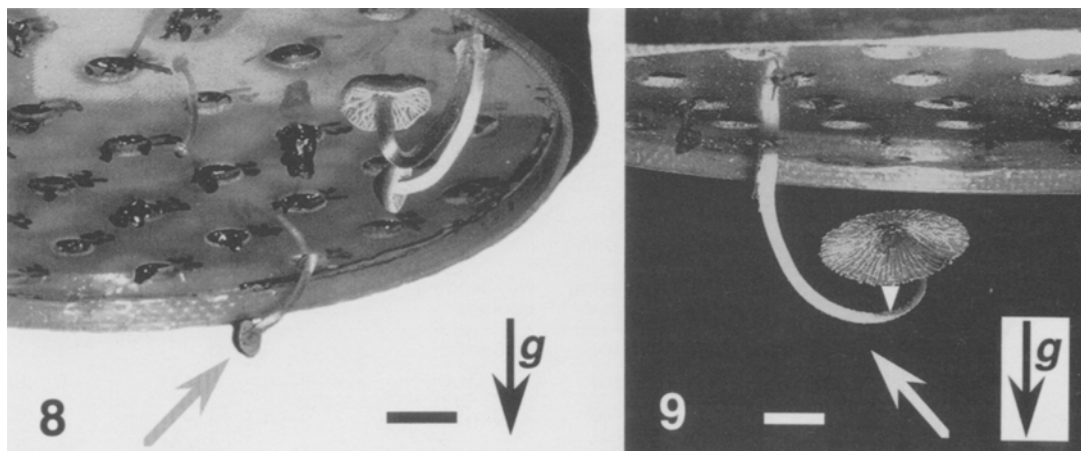
transparent polyethylene sheet to maintain humidity and thus the humus was exposed to light from above.

Incubation The pot packed with humus was incubated at 15 or 20°C and about 60% relative humidity. Light was provided for 12 h every day (12 h light/12 h dark), because such a diurnal light cycle is necessary for fruit-body maturation in some fungi, including *Coprinus* spp. (Cochrane, 1958; Manachère et al., 1983). Since the intensity of light reaching each pot differed with the position in the incubator, it was measured for each pot. The intensity of light from below, measured with a photometer with its sensor facing downward at the bottom of each pot, was ca. 1200, 1300, 1400, 1500, 1600, 1700, 1800 or 1900 lx; that in the experiment to study the effect of low-intensity light was ca. 100, 200, 400 or

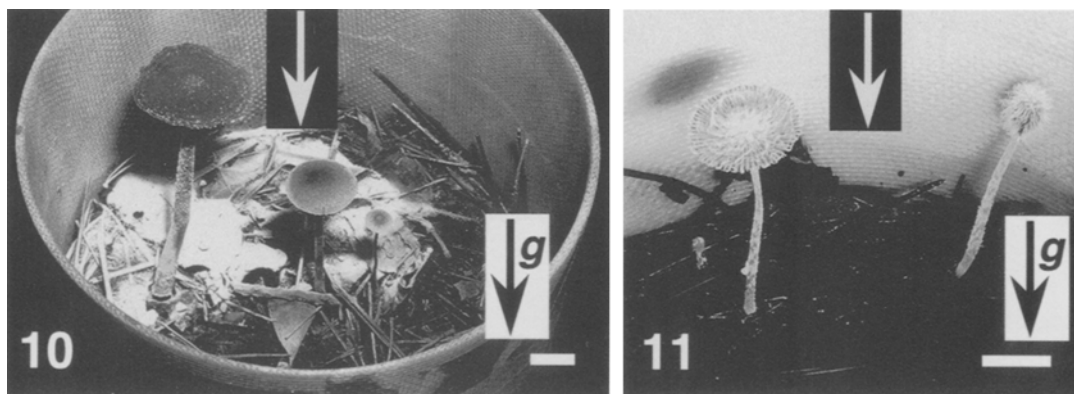
800 lx (here, 1 lx=0.00146378 W/m²). In the control, the intensity of light from above was ca. 800, 1200, 1300, 1400 or 1500 lx.

Since the urea-treated humus absorbs a large quantity of water during the initial period after urea treatment (Sagara, 1975), 1 ml of tap water per g of dry humus was spread on the humus every day during the first 6 d following the urea treatment. Fruit-bodies appeared mostly 3–10 wk after the urea treatment, and scarcely after 3 mo. Rotation was started 2 or 3 wk after the urea treatment, that is, shortly before the primordium formation.

Observations The elapsed times from the primordium formation to the beginning of stipe bending and to the onset of basidiospore formation were measured, since the



Figs. 8, 9. Fruit-bodies exposed to light from obliquely below (Exp. 2). Half-tone arrows: direction of light. *g*: gravity vector. Scale bar=1 cm. 8. *Tephrocybe tesquorum*. 9. *Coprinus neolagopus*. Black matter on the stipe (arrowhead): basidiospores dispersed from the fruit-body and accumulated on the stipe.



Figs. 10, 11. Fruit-bodies exposed to light from above (control). Half-tone arrows: direction of light. *g*: gravity vector. Scale bar=1 cm. 10. *Tephroclybe tesquorum*. White matter on the humus: basidiospores dispersed from the fruit-bodies. 11. *Coprinus neolagopus*.

gravitropic bending starts at the onset of basidiospore formation (Badham, 1982). The time of the onset of basidiospore formation was determined by microscopic observation. Here, the time when a primordium grew to ca. 5 mm high was regarded as the time of primordium formation.

Fruit-bodies which failed to mature were excluded from the following account.

Results

Development of fruit-bodies Most of the fruit-bodies exposed to light from below (Exp. 1) grew downward throughout all stages of their development (Figs. 3–7); they grew downward toward light in the early stage (Fig. 3), and even after the onset of basidiospore formation, i.e., in the presumed gravitropic stage, they continued to grow downward without bending upward (Figs. 4–7). Gills faced upward (Figs. 4, 5, 7). Basidiospores were formed normally and projected from basidia, but they accumulated between gills without dispersing abundantly.

All of the fruit-bodies exposed to light from obliquely below (Exp. 2) grew toward light (positive phototropism) in the early stage, but they bent and grew upward (negative gravitropism) after the onset of basidiospore forma-

tion (Figs. 8, 9). Their gills faced downward; basidiospores matured normally and dispersed as usual (Fig. 9, arrowhead).

In Exps. 1 and 2, no fruit-bodies developed from the upper surface of the humus which was under darkness covered by black vinyl sheet.

All of the fruit-bodies exposed to light from above (control) emerged from the upper surface of the humus, grew upward and dispersed basidiospores on to the humus as usual (Figs. 10, 11).

The above-mentioned responses were commonly observed in *Tephroclybe tesquorum* and the three *Coprinus* species.

The ratio of amount of stipe elongation during the phototropic stage to that during the (presumed) gravitropic stage was: in *T. tesquorum*, ca. 5:5 (compare Fig. 3 and Fig. 5) in light from below (Exp.1) and also from obliquely below (Exp. 2), and 8:2 in light from above (control); in *Coprinus* species, ca. 3:7 in all cases.

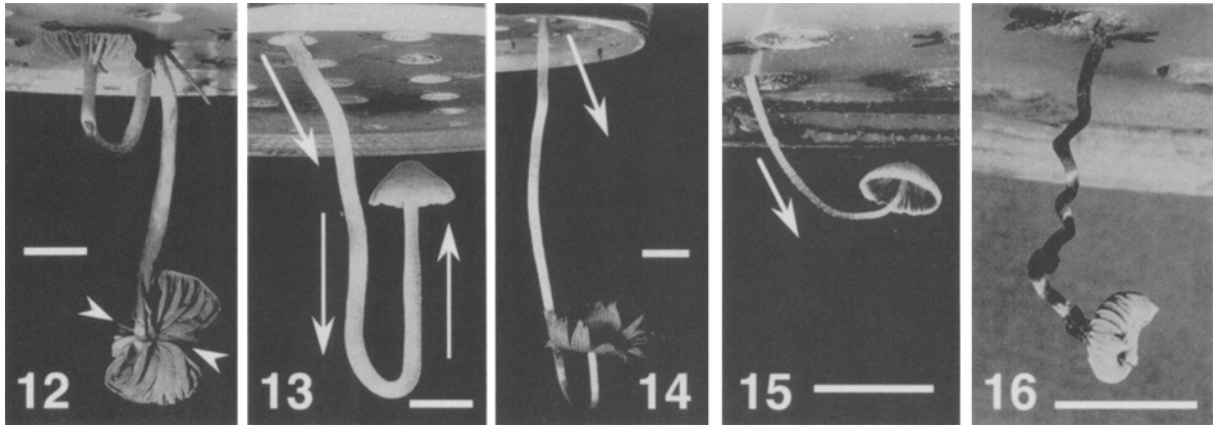
Response of the fruit-bodies exposed to light from below at different intensities Table 1 shows: (1) the higher the intensity was of light provided from below, the more fruit-bodies grew straight downward, especially in *T. tesquorum*; (2) *Coprinus* fruit-bodies bent more frequently than *T. tesquorum* ones, except at 1200 lx, where one

Table 1. Effect of light intensity on the development of fruit-bodies exposed to light from below (Exp. 1): the number of fruit-bodies which grew straight downward throughout development and of those which bent upward after downward growth.

Average light intensity (lx)	No. of replicates	<i>Tephroclybe tesquorum</i> fruit-bodies			<i>Coprinus</i> spp. ^{a)} fruit-bodies		
		Total no.	No. growing downward	No. bending upward	Total no.	No. growing downward	No. bending upward
Below 800	7	16	0 (0) ^{b)}	16 (100)	11	0 (0)	11 (100)
1,200	2	5	0 (0)	5 (100)	7	1 (14)	6 (86)
1,300–1,500	4	5	2 (40)	3 (60)	8	3 (38)	5 (62)
1,600–1,900	3	13	12 (92)	1 (8)	7	3 (43)	4 (57)

^{a)} Inclusive of three *Coprinus* species: *Coprinus neolagopus*, *C. phlyctidosporus* and *C. cinereus*, among which no distinct difference in the fruit-body development was observed.

^{b)} Values in parentheses show percentages.



Figs. 12–16. Atypical bending of the fruit-bodies exposed to light from below (Exp. 1). Scale bar=1 cm. 12. *Tephroclybe tesquorum* fruit-bodies having bent upward possibly due to mutual shading. The cap on the right is swollen and waved with gills tilting to lower positions (arrowheads) of the cap before bending; the right fruit-body did not bend completely upward, and it split its own stipe. 13. *Tephroclybe tesquorum* fruit-body having bent due to its oblique emergence from the rim of the hole and to low-intensity light (800 lx). It grew in the directions of the arrows, i.e., first obliquely downward due to oblique emergence, then nearly downward by phototropism and finally upward by gravitropism. 14. *Coprinus phlyctidosporus* fruit-body having bent due to its oblique emergence and to low-intensity light (100 lx). It first grew obliquely downward in the direction of the arrow due to its oblique emergence, then drooped under its own weight and finally bent upward by negative gravitropism. 15. *Coprinus phlyctidosporus* fruit-body having bent upward due to its oblique emergence. It first grew obliquely downward in the direction of the arrow and then bent upward by negative gravitropism. 16. *Tephroclybe tesquorum* fruit-body having bent upward due to strong twisting of the stipe. Having bent upward, its cap thereafter gradually drooped under its own weight and became swollen.

in seven *Coprinus* fruit-bodies grew straight downward while all five *T. tesquorum* fruit-bodies bent upward; (3) at intensities below 800 lx, all fruit-bodies bent upward. In low-intensity light, stipes tended to grow longer (see Figs. 13, 14), which may have given them a chance to bend during the gravitropic stage. These results (1) and (3) indicate that, for the fruit-bodies to grow straight downward, stronger light than that usually provided for mushroom cultivation (ca. 100–300 lx) is necessary.

Atypical upward bending in Exp. 1 (light from below) In Exp. 1, some fruit-bodies bent upward after growing downward (Figs. 12–16). The possible explanations are as follows.

(1) Sufficient light was not provided from below when it was partially blocked by neighbouring fruit-bodies (Fig. 12), or when light intensity was low (below 800 lx) as in the above results (Figs. 13, 14).

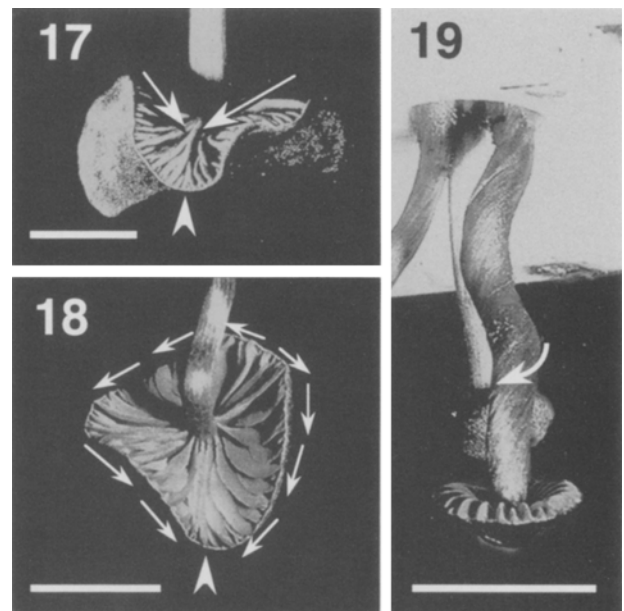
(2) The primordia were mechanically forced to emerge obliquely and fruit-bodies developing from them had a chance to bend (Figs. 13–15).

(3) The fruit-body developed asymmetrically due to internal factors and had a chance to bend (Fig. 16).

These atypical results will be discussed from a more general viewpoint in a separate paper (Kaneko, 2001).

Development of caps, gills and stipes in Exp. 1 (light from below) The caps of *T. tesquorum* growing straight downward were at first convex, then became flat (Figs. 3, 4) like those in the control (Fig. 10). Later, however, they often became swollen with wavy margins (Figs. 5, 17). The caps of *Coprinus* spp. were at first convex as in Fig. 6, then became flat as in Fig. 7 and finally repand; this growth pattern in *Coprinus* was commonly seen in all experiments.

The gills of *T. tesquorum* growing straight down-



Figs. 17–19. Unusual development of *Tephroclybe tesquorum* fruit-bodies exposed to light from below and growing straight downward (Exp. 1). Scale bar=1 cm. 17. Waving of the cap and tilting of the gills (photograph enlarged from Fig. 5). 18. Tilting of the cap and gills. 19. Twisting of the stipe. Gills in Figs. 17 and 18 tilted in the direction of the arrows, but the gills at the lowest position (arrowhead) stood upright, pressed by neighbouring gills from both sides. The stipe in Fig. 19 twisted in the clockwise direction (arrow).

ward often tilted toward the valleys of the waving cap (Fig. 17) or toward a lower position of the tilting cap (Fig. 18), while they remained standing upward when the cap was convex or flat without waving or tilting (Fig. 19). The gills of *Coprinus* spp. did not tilt.

The stipes of *T. tesquorum* often became twisted clockwise (when viewed from the base of the fruit-body; Fig. 19), or anticlockwise (Fig. 12, right; Fig. 16). Twisting was often much stronger than that in the control; these strongly twisted stipes rarely swung (Fig. 19) or spiralled (Fig. 16). The stipes of *Coprinus* spp. did not twist.

In the fruit-bodies of *T. tesquorum* that bent upward (Figs. 12, 13, 16), the cap rarely became swollen or wavy and the gills rarely tilted, except when fruit-bodies failed to bend completely upward (Fig. 12, right; Fig. 16). In the fruit-bodies of *Coprinus* spp. that bent upward (Figs. 14, 15), the caps were at first convex (Fig. 15), then flat and finally repand (Fig. 14) as in the control.

Development of caps, gills and stipes in Exp. 2 (light from obliquely below) The caps and gills of *T. tesquorum* that grew upward after growing downward in this experiment (Fig. 8) always showed the normal appearance, like those in the control; swollen caps and tilted gills were rarely observed. The stipes of *T. tesquorum* often became twisted; the predominant direction was clockwise (Table 2).

The fruit-bodies of *Coprinus* spp. that grew upward after growing downward showed almost the same appearance as those of the control (Fig. 9).

Development of caps, gills and stipes in the control (light from above) The caps of *T. tesquorum* were at first convex, then became flat (Fig. 10); they were rarely swollen. The caps of *Coprinus* spp. were at first convex, then flat (Fig. 11) and finally repand.

The gills of *T. tesquorum* grew downward and did not tilt. The gills of *Coprinus* spp. did not tilt.

The stipes of *T. tesquorum* often became twisted; the predominant direction was clockwise (Table 2). Stipe twisting was in most cases so weak that it did not disturb the straight growth of the stipe, unlike the examples in Exp. 1 (Figs. 16, 19). The stipes of *Coprinus* spp. did not twist.

Discussion

Fruit-bodies are considered eventually to grow upward

Table 2. Direction of the stipe twisting in *Tephrocybe tesquorum* fruit-bodies exposed to light from below (Exp. 1), light from obliquely below (Exp. 2) and light from above (control).

Kind of expts.	Total no. ^{a)}	No. twisting clockwise	No. twisting anticlockwise
Exp. 1	8	4 (50) ^{b)}	4 (50)
Exp. 2	11	7 (64)	4 (36)
Control	11	10 (91)	1 (9)

^{a)} Including the number of the fruit-bodies which developed under low-intensity light.

^{b)} Values in parentheses indicate percentages.

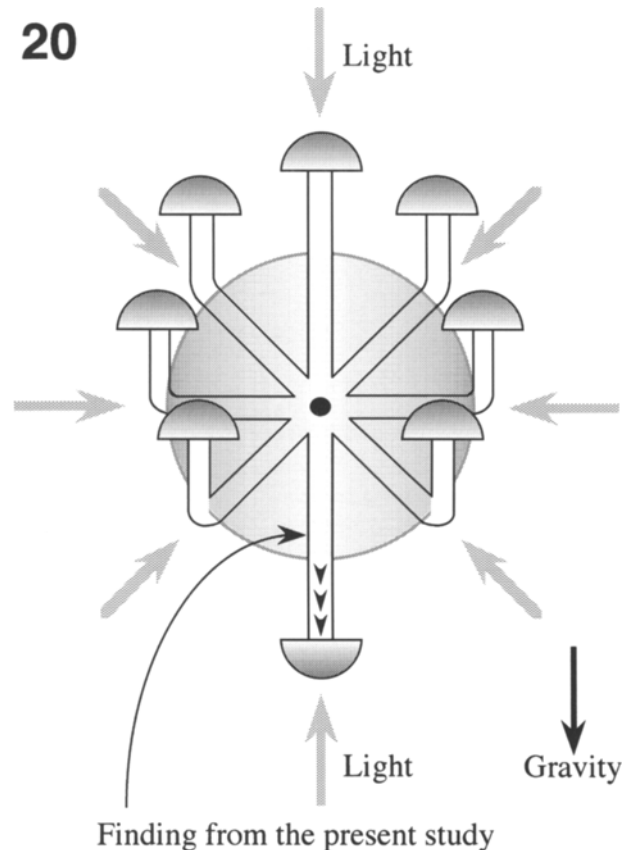


Fig. 20. Responses of Agaricales fruit-bodies to light and gravity in the Earth's gravitational field. After the onset of basidiospore formation on the circle, all fruit-bodies grow upward by negative gravitropism except that exposed to the vertically-directed light from below; it continues to grow downward, even through the presumed gravitropic stage (arrowheads) after the onset of basidiospore formation.

by negative gravitropism, with gills facing downward so as to disperse basidiospores efficiently. In the present study, however, the fruit-bodies exposed to light from below principally grew straight downward through all stages of development, with gills facing upward, and hence were unable to disperse basidiospores. To our knowledge, this is a new finding, which enables us to modify the diagram in Fig. 1 as in Fig. 20. This finding does not seem to be affected by whether the culture is pure or not, since the same result has been obtained also with other agaric species fruiting in pure culture (Kaneko, unpublished data).

Conditions that allow the straight downward growth In Fig. 20, vertically-directed light from below causes not only downward phototropic growth at the phototropic stage, but also further downward growth even at the presumed gravitropic stage after the onset of basidiospore formation (arrowheads in Fig. 20). During the latter stage, the stipe elongation did not stop: elongation during this stage constituted ca. 70% of the whole length in *Coprinus* spp. (the same as in the control), and ca. 50% in *T. tesquorum* [even more than in the control (20%)]. We consider that the downward growth at the latter

stage, although apparently phototropic or positively gravitropic, occurs despite a potential for gravitropic bending. It seems that fruit-bodies growing vertically downward had no chance to bend and were forced to grow downward, their bending being obstructed by their own bodies. Figure 20 shows that, under the unidirectional and sustaining stimulus of the Earth's gravity, only vertically-directed light from below does not allow fruit-bodies to grow upward in response to gravity.

Moore (1991) argued that the perception system of gravity may be adapted to recognise and correct for fairly small deviations from the vertical. Fruit-bodies growing straight downward must be unable to recognise 'deviations from the vertical' because their stipes themselves are also vertical; those having deviated from the vertical and bent upward (Figs. 12–16) must be able to. This consideration may be supported by Plunkett's description (1961): 'the gravitational response mechanism is unstimulated in vertical stipes and tubes' ['tubes' (of *Polyporus*) correspond to agaric gills in his context].

'Two null-positions for gravitational curvature' The fruit-bodies exposed to light from below grew straight downward, and those exposed to light from above grew straight upward (see Fig. 20). These two situations in which fruit-bodies grow downward or upward without bending would be equivalent to 'two null-positions for gravitational curvature' as reported for a polypore species by Plunkett (1961).

The two null-positions differ in whether or not fruit-bodies **have to** bend gravitropically for spore dispersal. Namely, fruit-bodies growing upward with their gills facing downward are able to disperse basidiospores; they do **not have to** bend upward to disperse basidiospores. On the contrary, fruit-bodies growing downward with their gills facing upward are unable to disperse basidiospores; they **have to** bend upward, but **are unable to** do so.

Gravitropism in gills The absence of the gill tilting in *Coprinus* spp. supports Buller's view (1922) that *Coprinus* gills are not gravitropic. We consider that this absence of gravitropism may partly be due to the characteristic structure of their cystidia firmly attached to the opposite hymenium and hence tying adjacent gills mechanically (Moore, 1998).

The upward growth of gills in *T. tesquorum* is another new finding. Fruit-bodies exposed to light from below grow downward with gills growing upward, whereas fruit-bodies exposed to light from any other direction grow upward with gills growing downward (Fig. 20). Thus, gills also seem to have two situations equivalent to the 'two null-positions for gravitational curvature' (Plunkett, 1961).

The downward tilting of the gills in *T. tesquorum*, which took place on the waving or tilting caps, may represent a positive gravitropism, corresponding to the upward bending of the stipes. However, the tilting gills never directed straight downward, being obstructed by neighbouring gills, and they were unable to disperse many basidiospores. This situation is in agreement with Buller's observation (1909) that, when the tilt of the *Agaricus campestris* pileus exceeded a certain angle

(more than 30°), some of the gills stuck together and basidiospores could not disperse there.

Fruit-bodies growing downward with gills facing upward are unable to disperse basidiospores. To disperse basidiospores, the stipes **have to** bend upward, or gills **have to** bend downward; however, they **are unable to** do so.

Cap swelling The absence of cap swelling in *Coprinus* spp. suggests that the *Coprinus* fruit-bodies do not absorb so much water from the humus as to cause cap swelling. This view may be supported by the fact that, in *C. cinereus*, fruit-bodies excised from the substratum continue to grow (Gooday, 1974), while in other agarics, e.g., *Flammulina velutipes* (Curt.: Fr.) Sing., excised fruit-bodies grow little without supply of water (Gruen and Wu, 1972a, b).

In *T. tesquorum*, caps did not swell when water content of the humus was low (Fig. 19). The water content of the humus in Fig. 19 was 16% at the time of collection (in other cases, 53–66%). Thus, we consider that the cap swelling might be caused by an excessive supply of water to the cap. In the fruit-bodies growing downward, water may flow downward by gravity, causing an excessive supply of water to the cap. This view may be supported by the result that the cap swelling was observed in fruit-bodies which did not bend completely upward, their caps remaining at lower positions (Fig. 12, right), but not in those which bent completely upward (Fig. 12, left).

The cap swelling in *F. velutipes* is visible in the photograph published by Kern and Hock (1996), although not mentioned by the authors themselves, and it may be due to the excessive water supply under weightlessness (microgravity) in space. The cap seems to swell when the fruit-body does **not have to** actively absorb water against gravity, i.e., under microgravity or when growing downward.

Stipe twisting in *T. tesquorum* In *T. tesquorum* fruit-bodies, the anticlockwise twisting of the stipes was seldom observed when they were exposed to light from above (control) (Table 2), but frequently when they were exposed to light from obliquely below (Exp. 2), and still more frequently when they were exposed to light from directly below (Exp. 1). This anticlockwise twisting may have resulted from certain unusual conditions brought about by the downward growth of the fruit-bodies. The stipe twisting may be caused by certain unusual magnitude and/or direction of gravity, since it is also observed under microgravity (Kern and Hock, 1996).

Comparison between *T. tesquorum* and *Coprinus* spp. Although *T. tesquorum* and *Coprinus* spp. responded somewhat differently to light and gravity, they both grew straight downward when exposed to light from below (Table 3). Namely, the behaviour of growing downward is common to both the '*Coprinus* Type' and the '*Non-Coprinus* Type' of Buller (1922). Further, if Plunkett's observation (1961) with Aphyllophorales is taken into consideration, this behaviour seems to be common to all three types classified by Gorovoj et al. (1987).

The frequency of atypical upward bending in light

Table 3. Comparison of *Coprinus* spp. and *Tephrocybe tesquorum* in growth direction of fruit-bodies and in behaviours of gills, caps and stipes in light from below.

	<i>Coprinus</i> spp. ^{a)}	<i>Tephrocybe tesquorum</i>
Growth direction	Straight downward	Straight downward
Frequency of upward bending	Higher	Lower
Gill	Not tilting (Non-gravitropic)	Growing upward or tilting downward (Positively gravitropic)
Cap	Not swelling	Swelling and waving
Stipe	Not twisting	Often twisting

^{a)} Inclusive of *Coprinus neolagopus*, *C. phlyctidosporus* and *C. cinereus*.

from below was lower in *T. tesquorum* than in *Coprinus* spp., except at 1200 lx (Table 1). This suggests a difference between *T. tesquorum* and *Coprinus* in the sensitivity to light or in the degree of dependence on light.

The occurrence of morphologically abnormal developments such as cap swelling and stipe twisting in *T. tesquorum* (Table 3) and in *F. velutipes* (Kern and Hock, 1996), but not in *Coprinus* spp. (Table 3), suggests that, for normal development, agaric fruit-bodies (other than *Coprinus*) need to be under the stimulus of gravity with an appropriate direction and magnitude. *Coprinus* differs from other Agaricales in this respect, as has been reported by other workers (Hasselbring, 1907; Reijnders, 1963), who studied the fruit-body development in *Coprinus* spp. by cancelling the effect of gravity on the clinostat and obtained normal fruit-bodies.

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