Mycoscience 42: 75–82, 2001

Application of the equilibrium concept to the development of agaric fruit-bodies, with special reference to their straight downward growth in light from below

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Accepted for publication 20 November 2000

Equilibrium, a concept of dynamics, is found to be applicable to the phototropic and gravitropic growth in agaric fruit-bodies. The fruit-bodies exposed to light from below grow straight downward without bending upward, and those exposed to light from obliquely below grow first downward and then upward by negative gravitropism. The fruit-bodies exposed to light from above grow upward. Fruit-bodies growing straight downward or upward do not change the direction of growth; they are in 'equilibria'. The straight downward growth can be regarded as an 'unstable equilibrium' having a higher potential, and the straight upward growth as a 'stable equilibrium' having a lower potential. The change in the direction of growth can be explained by the change in the potential; the upward bending in fruit-bodies that have grown obliquely downward can be regarded as a 'transition' from the unstable equilibrium to the stable one.

Key Words——Agaricales; equilibrium; gravitropism; modelling; phototropism.

Kaneko and Sagara (2001) found that agaric fruit-bodies exposed to light from below grew straight downward throughout their developmental stages, i.e., not only at the phototropic stage but also at the otherwise gravitropic stage after the onset of basidiospore formation (see Fig. 1). This downward growth was observed only in light from below; light from obliquely below or any other direction eventually allowed upward growth by negative gravitropism. Based on these observations and on a review of literature, I try to apply the physical concept of 'equilibrium' to the development of agaric fruit-bodies.

Fruit-bodies may change the direction of growth by phototropism and gravitropism in the course of their development, but those growing straight upward or downward never do. I will apply (in Results) the concept of equilibrium to this straight upward and downward growth in terms of the direction of growth. By this, the straight upward growth will be regarded as a 'stable equilibrium' and the straight downward growth as an 'unstable equilibrium'. These two states will then be considered to be equivalent to the 'two null-positions for gravitational curvature' proposed by Plunkett (1961) for *Polyporus brumalis* (Pers.: Fr.) Fr. Subsequently, I will present a model of the development of agaric fruit-bodies and a graph of potential corresponding to their growth directions.

To confirm the validity of the model presented, I will discuss (in Discussion) some other aspects of the development of fruit-bodies using the potential graph. For instance, I will examine patterns of their growth under light from all possible directions including above and below. Also, I will explain gravitropic bending of the fruit-bodies that have grown obliquely downward in terms of

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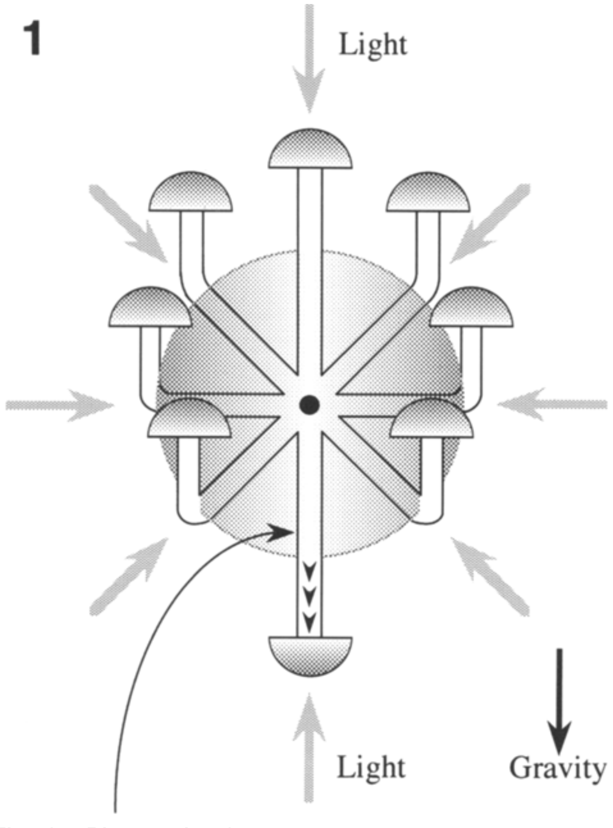

Fig. 1. Diagram showing responses of Agaricales fruit-body to light from different directions and to gravity (information from Buller (1909) and Kaneko and Sagara (2001)). Arrowheads indicate the downward growth at the presumed gravitropic stage after the onset of basidiospore formation.

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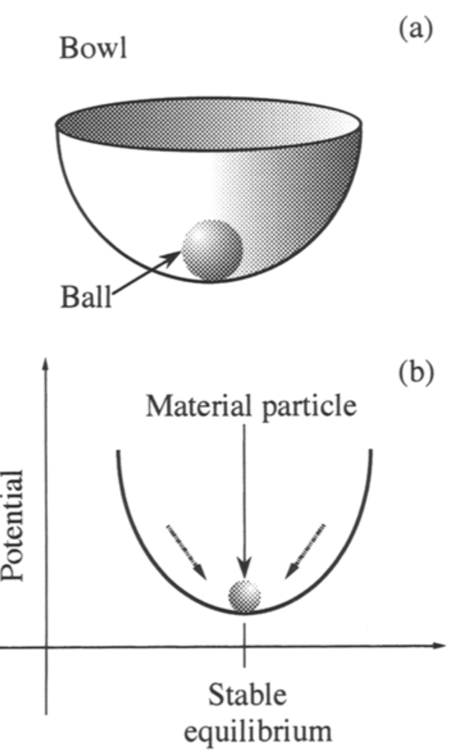

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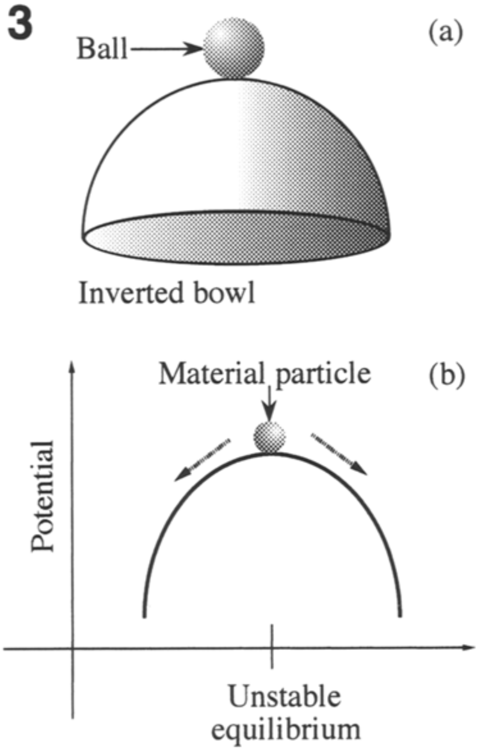

Figs. 2, 3. Diagrams illustrating the concept of equilibrium in dynamics. 2. Stable equilibrium. (a) A system in stable equilibrium, represented by a ball located at the bottom of a bowl. (b) Potential graph for the system in (a), with a small ball (material particle) representing the ball in (a); even if displaced away from the equilibrium point, it will return there in the directions of the dotted arrows. 3. Unstable equilibrium. (a) A system in unstable equilibrium, represented by a ball located at the top of a bowl. (b) Potential graph for the system in (a); if displaced from the equilibrium point, the small ball will move further in the directions of the dotted arrows.

the change in the potential from an unstable equilibrium to a stable one (this change will be regarded as a 'transition'). Finally, I will apply this model to various axial organs other than agaric fruit-bodies.

For studying responses of axial organs to external stimuli, e.g., light and gravity, measurement of their growth direction or bending angle has often been employed, e.g., for basidiomycete fruit-bodies (Monzer et al., 1994; Kher et al., 1992), for *Phycomyces* sporangiophores (Galland and Russo, 1985; Ootaki et al., 1991) and for plant shoots (Neumann and Iino, 1997; Kiss et al., 1997; Tarui and Iino, 1997). In these past studies, the term 'equilibrium' was often used to mean vectoral balance among plural tropisms. This usage, which differs from that proposed here, will also be explained by the present model. Some mathematical models to explain gravitropic bending of fungal fruit-bodies and plant shoots have been presented, e.g., by Meškauskas et al. (1999a, b), but these models are concrete and therefore different from my abstract one presented here.

Materials and Methods

Fruit-body development As the material for modelling fruit-body development, I used the experimental results reported by Kaneko and Sagara (2001; abbreviated as KS2001 hereafter). The results are summarised as follows.

Many of the fruit-bodies exposed to light from below grew straight downward (Figs. 3–7 in KS2001). Some of them, however, grew first downward and then upward by bending their stipes (Figs. 12–16 in KS2001). This bending was caused by: (1) exposure to light from obliquely below, which resulted from shading by neighbouring fruit-bodies; (2) oblique emergence of the fruit-bodies; (3) some internal factors of the fruit-bodies, as was exemplified by stipe twisting. When exposed to light from below, *Coprinus* spp. bent upward more frequently than *Tephrocybe tesquorum* (Fr.) Moser.

All fruit-bodies exposed to light from obliquely below grew first obliquely downward toward the light, and then upward (Figs. 8, 9 in KS2001). All fruit-bodies exposed to light from above grew straight upward (Figs. 10, 11 in KS2001).

Figure 1 summarises the patterns of development of fruit-bodies exposed to light from different directions: only the fruit-body exposed to the vertically-directed light from below grows downward throughout the developmental stages, even at the presumed gravitropic stage; the others eventually grow upward.

Introduction of the equilibrium concept 'Equilibrium' in dynamics means a physically-balanced state. If a system is in equilibrium as its initial condition, it continues to be 'static' forever. 'Static' refers to a state without movement or change. The concept of equilibrium is schematically shown in Figs. 2 and 3. When a ball is located at the bottom of a bowl (Fig. 2a), this state can be regarded as a 'stable equilibrium'. If the ball is displaced to the side, it will oscillate around its original position, and eventually come to rest at the bottom. The stability of this system is represented by a graph of potential (positional energy) (Fig. 2b). When the ball is located at the top of the inverted bowl (Fig. 3a), this state can be regarded as an 'unstable equilibrium'. In this condition, displacement of the ball will cause it to fall off the top of the bowl. Instability of this system is represented by another graph of potential (Fig. 3b).

When the system reaches a stable equilibrium, the potential reaches an energetically low and stable point (the minimum in Fig. 2b); and when the system reaches an unstable equilibrium, the potential reaches an energetically high and unstable point (the maximum in Fig. 3b). Disturbance of a system may result in 'fluctuation', i.e., deviation from a mean value. If a system in stable equilibrium is disturbed, the fluctuation will be damped with time, and the system will regain the original state of equilibrium; but if a system in unstable equilibrium is disturbed, the fluctuation will grow and destroy the equilibrium. For a system to remain in unstable equilibrium, certain conditions are necessary: the system must be in this state from the beginning; it must be static forever; it must not be disturbed even slightly.

Results

Application of the equilibrium concept to the fruit-body development If the agaric fruit-bodies growing straight upward or downward are viewed from the equilibrium concept described above, they are in an equilibrium in terms of the direction of growth, since they never change their growth directions (see Fig. 1). The straight upward growth can be regarded as a 'stable equilibrium' since, when a fruit-body growing straight upward is turned horizontally, it bends upward by gravitropism (e.g. Buller, 1909) and regains its original growth direction. On the other hand, the straight downward growth can be regarded as an 'unstable equilibrium' since, when a fruit-body growing straight downward in light from below is slightly tilted, it bends upward by gravitropism (Figs. 12–16 in KS2001) and the original state is destroyed even by a slight tilting of the stipe. Hence, the exposure of fruit-bodies to light from below can be regarded as a necessary condition for the unstable equilibrium.

Straight downward growth represents 'unstable' equilibrium Figure 4 shows the graph of potential corresponding to the development of a fruit-body. Here, two equilibria are assumed to be connected by a smooth curve, which is assumed to be symmetrical, because many fruit-bodies grow symmetrically.

The potential of the fruit-bodies growing downward should have a maximum (Fig. 4a), since the downward growth can be regarded as an 'unstable equilibrium' (see Fig. 3b). Figure 4a shows that fruit-bodies growing obliquely downward will bend upward even if the tilt of their stipes is only slight; in actuality, fruit-bodies which are only slightly tilting cannot bend upward due to obstruction by their own volume or weight, and hence will continue growing downward. This suggests that the potential for the actual system should have a local minimum (minor trough in Fig. 4b), as in the 'metastable' equilibrium in thermodynamics. However, I still regard the straight downward growth as an 'unstable' equilibrium, since, in the ideal system where fruit-bodies have no volume and no weight, the potential curve should take the form of Fig. 4a.

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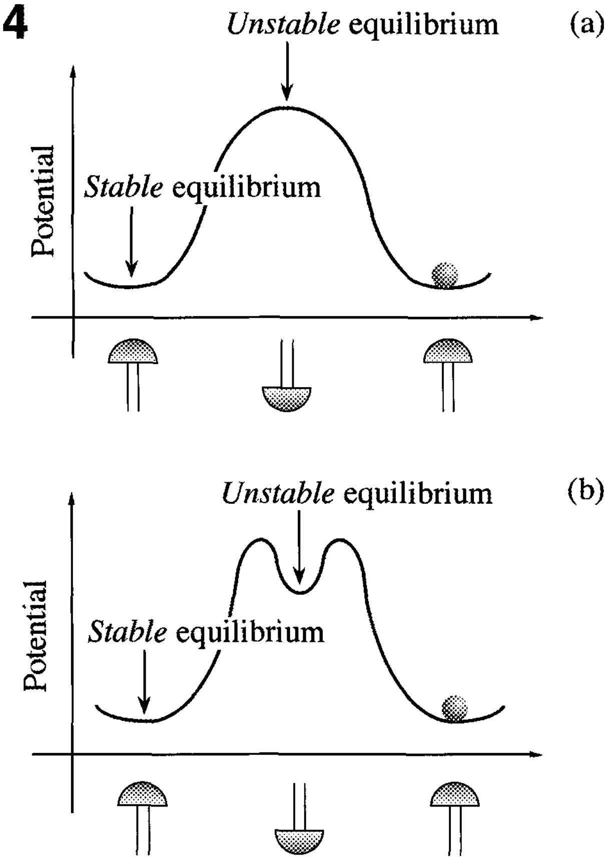

Fig. 4. Graphs of potential corresponding to the direction of growth in the fruit-body as shown in the abscissa. The fruit-body growing straight downward corresponds to the unstable equilibrium, and that growing straight upward to the stable equilibrium. (a) The basic potential graph with the maximum at the unstable equilibrium. (b) Modified potential graph with a local minimum at the unstable equilibrium (the potential curve around the unstable equilibrium is exaggerated for clarity).

Variable of potential To analyse further the development of fruit-bodies, I used the direction of growth as the variable of potential. The growth direction is shown by the angle θ in Fig. 5, i.e., deviation from the vertically downward direction. For example, $\theta=0$ when a fruit-body grows straight downward; $\theta=\pm180$ when it grows upward (after gravitropic bending; the symbol + is for the fruit-body bending toward one side and the symbol − for one bending toward the other side). All fruit-bodies will eventually grow upward or downward (Fig. 1), when

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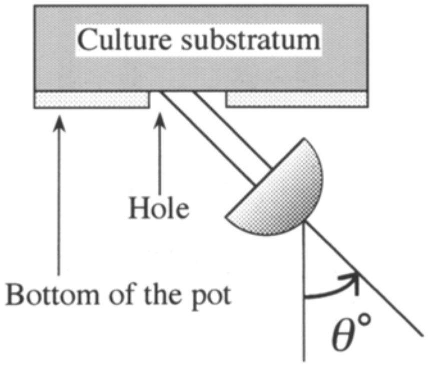

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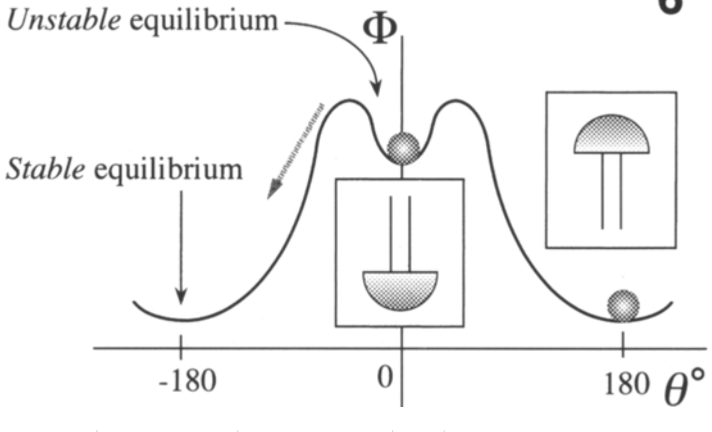


Figs. 5, 6. Definition of the variable: growth direction θ. 5. Angle θ showing the direction of growth of a fruit-body developing through a hole in the bottom of a culture pot. 6. Diagram showing relationship between the potential Φ (positional energy of the ball) and the growth direction θ. The ball at the unstable equilibrium point ($\theta = 0$) represents the fruit-body growing straight downward, and that at the stable equilibrium point ($\theta = 180$) represents the fruit-body growing straight upward. The dotted arrow indicates a 'transition' from the unstable equilibrium to the stable one, which corresponds to the gravitropic bending of the fruit-body.

$\theta = \pm 180$ or 0, respectively.

Figure 6 shows a graph of potential as a function of angle θ, in which the potential has a major trough (minimum at $\theta = \pm 180$) and a minor trough (local minimum at $\theta = 0$) as in Fig. 4b; the two troughs occur at the two equilibrium points, i.e., at the two null-positions for gravitational curvature.

Table 1 summarises the process of fruit-body development using angle θ as the variable. Since θ is θ_i initially, θ_p at the end of the phototropic stage and θ_g at the end of the gravitropic stage, θ_g is determined by θ_i and θ_p as discussed below.

Gravitropic bending corresponds to 'transition' When a fruit-body which has grown downward bends upward gravitropically, the ball in Fig. 6 moves from the unstable equilibrium to the stable one. This movement may be regarded as a 'transition', a movement from one 'stationary' state to another. ('Equilibrium' is one of the 'stationary' state.) Namely, the gravitropic bending mentioned above may correspond to a transition which may be caused by a deviation of the ball from θ_r, the critical range of θ in which downward growth occurs (see Figs. 7–10).

Discussion

Causes of gravitropic bending (transition) Cause 1: Exposure to light from obliquely below. A fruit-body exposed to light from obliquely below eventually grows upward by gravitropic bending (Figs. 8, 9, 12 in KS2001). Its obliquely downward growth toward the light represents a deviation of the ball from the range θ_r to the point θ_p in the present model (Fig. 7); the deviation causes a transition from the unstable *equilibrium to the* stable one; the transition represents gravitropic bending in actuality. Figure 7 can be modified as Fig. 8, which shows that all fruit-bodies eventually grow upward, except those exposed to the vertically-directed light from below and growing straight downward (Figs. 3–7 in KS2001).

Cause 2: Oblique emergence of the fruit-bodies. Oblique emergence of the fruit-body represents a deviation of the ball from the range θ_r to the point θ_i (Fig. 9); the deviation may cause a transition; the transition

Table 1. Fruit-body development represented by angle θ (the growth direction; see Fig. 5) and parameter t.

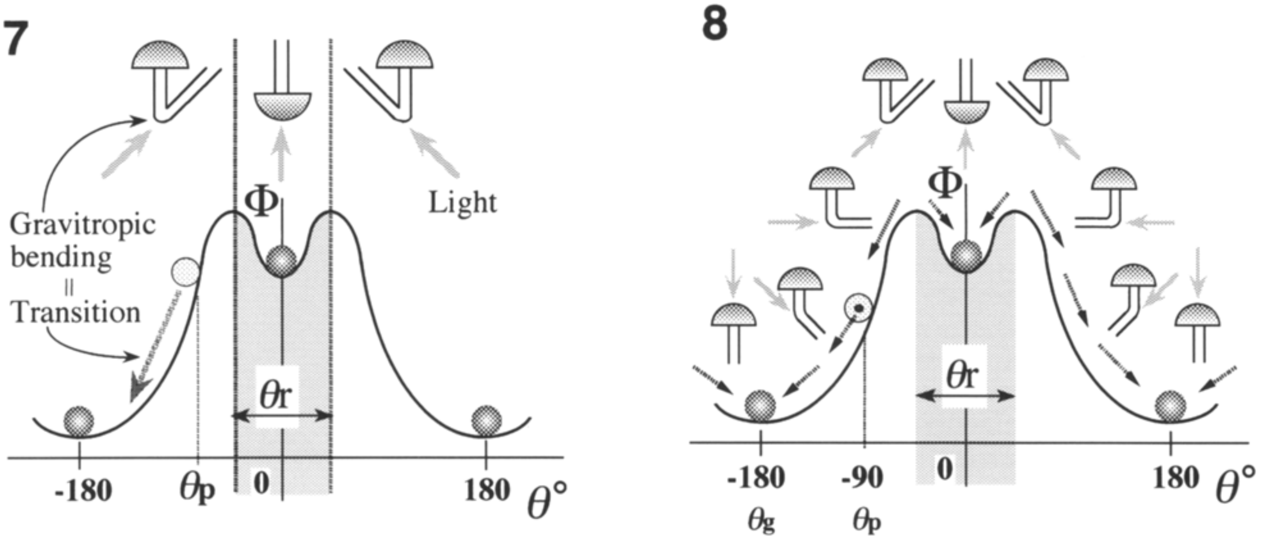
	Time elapsed				
	$t=0$	$0<t<Tg$	$t=Tg$	$Tg<t<\infty$	$t=\infty$
Growth direction θ	θ_i	—	θ_p	—	$\theta_g = \pm 180$ (0)
Developmental stage	—[a]	phototropic	—	gravitropic	—
Target direction[b]	—[a]	toward light	—	upward (downward)	—

The case in which a fruit-body grows straight downward in response to light from below is shown in parentheses.

t: the time elapsed from the primordium emergence; Tg: the time when gravitropic growth begins; ∞: the time when the fruit-body development ceases; —: no corresponding terms or variables.

[a] Primordia are known to emerge perpendicularly away from the substratum (Buller, 1909).

[b] A fruit-body may grow in the target direction from the beginning, or it may not attain the target direction at all (see Case III in Fig. 9 and also Fig. 13).



Figs. 7, 8. Diagrams illustrating responses of agaric fruit-bodies to light from different directions, using the potential graph shown in Fig. 6. For simplicity, the fruit-body is assumed to grow toward light from the beginning of its development ($\theta_i = \theta_p$ in Table 1).
7. Diagram for the fruit-bodies exposed to light from directly or obliquely below. 8. Diagram for the fruit-bodies exposed to light from all possible directions. Balls in Figs. 7 and 8 remain at $\theta = \theta_p$ during the phototropic stage, then move (in the directions of the arrows) during the gravitropic stage and finally reach $\theta_g = \pm 180$ or 0. The ball at $\theta_p = -90$ in Fig. 8 represents the fruit-body exposed to light from side; it will finally reach $\theta_g = -180$.

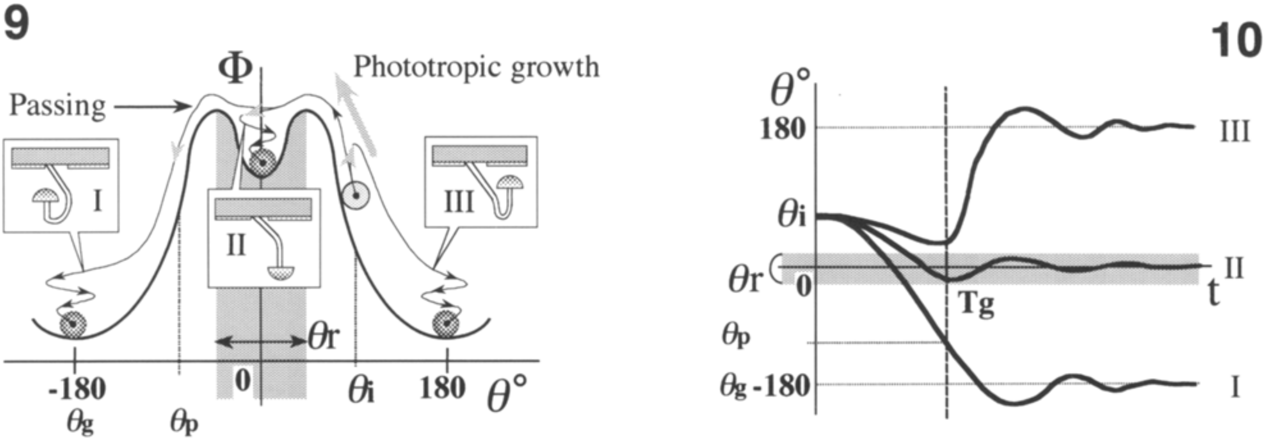
represents gravitropic bending (Figs. 13–15 in KS2001). Fruit-bodies grow first obliquely downward due to their obliquely downward emergence, and then downward by phototropism (see the windows in Fig. 9); here, θ is first θ_i, and then approaches 0 (Fig. 10). After gravitropic growth has begun at t=Tg, when $\theta = \theta_p$, three cases may occur depending on θ_p (Figs. 9, 10):

Case I, the fruit-body grows upward (Fig. 11); when $\theta_p < -\theta_r/2$, $\theta_g = -180$.

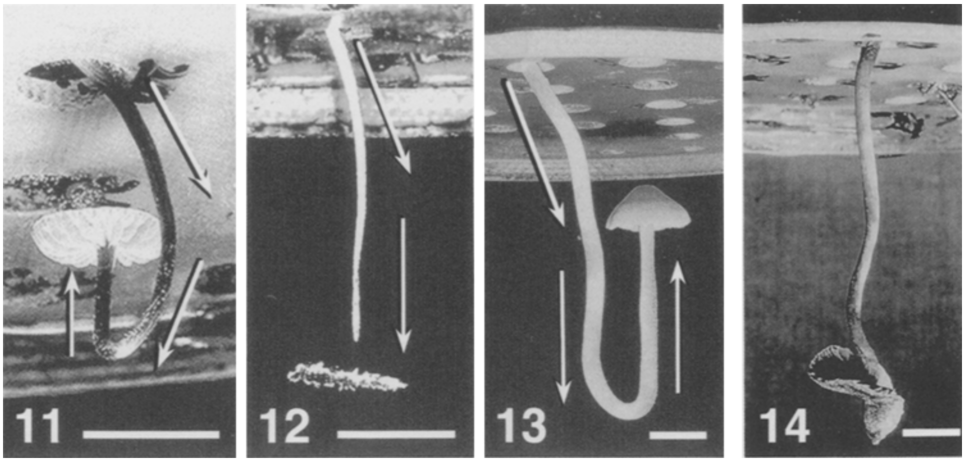
Case II, the fruit-body grows downward (Fig. 12); when $-\theta_r/2 < \theta_p < \theta r/2$, $\theta_g = 0$.

Case III, the fruit-body grows upward (Fig. 13); when $\theta_p > \theta_r/2$, $\theta_g = 180$.

Damped oscillation of the growth direction around $\theta = 0$ or ± 180 (Figs. 9, 10), or passing the vertical position (as in Case I) and returning to it, has been variously



Figs. 9, 10. Diagrams illustrating responses of agaric fruit-bodies that have emerged obliquely downward in light from below, using the potential graph. 9. The fruit-body grows first obliquely downward (at θ_i), and then downward by phototropism (at θ_p as indicated by larger arrowheads). Three cases follow: Case I, passing the vertical position, the fruit-body finally bends inside and then upward (see Fig. 11; $\theta_p < -\theta_r/2$, $\theta_g = -180$); Case II, the fruit-body continues growing downward, even during the presumed gravitropic stage (see Fig. 12; $-\theta_r/2 < \theta_p < \theta_r/2$, $\theta_g = 0$); Case III, the fruit-body bends outside and then upward (see Fig. 13; $\theta_p > \theta_r/2$, $\theta_g = 180$). Curved lines with arrowheads indicate the movement of the ball, their zigzag parts showing fluctuation in the movement. Larger arrowheads indicate the position of the ball at $\theta = \theta_p$ (t=Tg). 10. Changes of growth direction θ as a function of time t. In all cases (I–III) the growth direction will eventually reach an equilibrium point after 'geotropic swinging'. For I–III, see cases in Fig. 9. For t, Tg, θ_i, θ_p and θ_g, see Table 1. θ_p and θ_g for Case I are shown in Figs. 9 and 10.



Figs. 11–14. Fruit-body developments discussed in Figs. 9 and 10. 11. *Tephrocybe tesquorum* fruit-body corresponding to Case I in Fig. 9. 12. *Coprinus neolagopus* fruit-body corresponding to Case II in Fig. 9. 13. *Tephrocybe tesquorum* fruit-body under low-intensity light (800 lx), corresponding to Case III in Fig. 9. 14. *Tephrocybe tesquorum* fruit-body exposed to light from below, with its stipe swinging around the vertical, which represents fluctuation of the growth direction θ (see Figs. 9, 10). Scale bar=1 cm.

termed, e.g., 'geotropic swinging' in agaric fruit-bodies (Buller, 1909), 'tropic reversal' in *Phycomyces* sporangiophores (Galland and Russo, 1985), 'oscillatory movement' in wheat coleoptiles (Tarui and Iino, 1997), 'spatial memory' in maize coleoptiles (Nick et al., 1990) and 'autotropism' in seedlings (Heathcote, 1987).

Cause 3: Fluctuation of the growth direction. Twisting or swinging of the stipe (Fig. 14) may represent fluctuation of the growth direction θ. When fluctuation of θ is large, the ball may deviate from the range θ_r, and therefore a transition may occur (Fig. 16 *in* KS2001). In general, the more unstable the system becomes, the larger the fluctuation may grow. In this case, instability of the straight downward growth may cause fluctuation (or FA: fluctuating asymmetry) large enough to cause gravitropic bending. Here, gravitropic bending may be caused only by internal, developmental factors, but not by external, physical ones like the above causes 1 and 2.

Necessary conditions for the straight downward growth For a fruit-body to grow downward throughout its development, it must first emerge downward and be exposed to (vertically-directed) light from below; for θ_g to be 0, both θ_i and θ_p should be 0 (see Table 1). In addition, the fruit-body must grow straight without fluctuation of the growth direction θ; the value θ must not fluctuate. These conditions correspond to the previously mentioned conditions necessary for a system to remain in an unstable equilibrium.

Frequency of gravitropic bending (probability of transition) Table 1 in KS2001 showed that the lower the light intensity was, the more frequently the gravitropic bending occurred. This suggests that θ_r, the range of θ in which downward growth occurs, is affected by the intensity of light: θ_r is small under low-intensity light (Fig. 15a). The probability that gravitropic bending occurs may correspond to the probability of transition (Pt). All fruit-bodies exposed to light of 800 lx or lower intensities bent upward (Figs. 13, 14 in KS2001). In those fruit-bodies, Pt is 100%, θ_r is 0 and the curve of potential is simple as in Fig. 4a.

In our experiments (KS2001), *Coprinus* spp. grew faster than *T. tesquorum*. This means that, in my model, the velocity (V) and the deviation of the ball for *Coprinus* are larger than those for *T. tesquorum*. Their stipes were thin and soft, and, probably for that reason, easily bent, which makes θ_r smaller. These experimental results lead to the conclusion that Pt for *Coprinus* should theoretically be higher, as in Fig. 15a; conversely,

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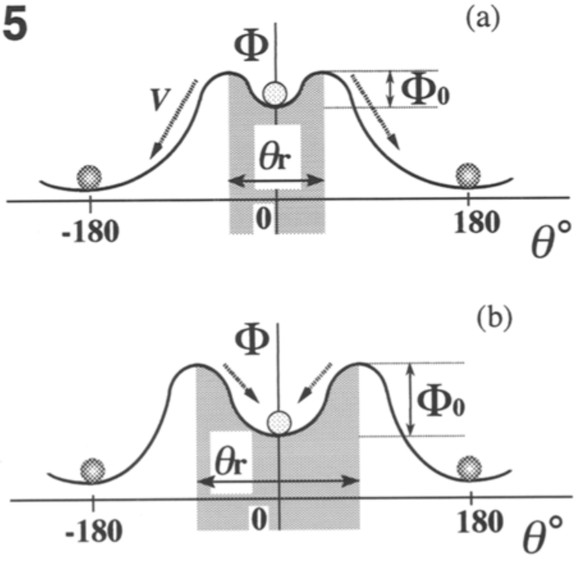

Fig. 15. Potential graphs for two cases with different transition probabilities. Φ_0: the height of the barrier; V: velocity of the ball. The transition probability in (a) is higher than in (b), owing to smaller θ_r, smaller Φ_0 or larger V. θ_r is small when light intensity is low, and V is large when a fruit-body grows fast, like those of *Coprinus* spp.

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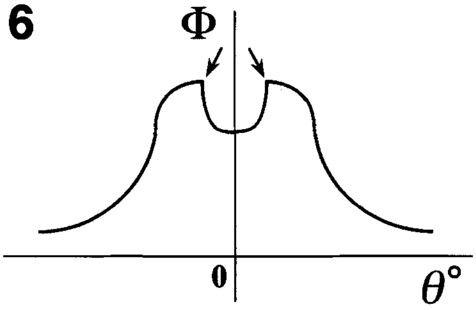

Fig. 16. Modification of the potential graph to include other observations, e.g., slightly obliquely downward growth. Arrows indicate the points where there exist catastrophes (discontinuities) bounding (obliquely) downward growth and upward growth.

this conclusion is in agreement with the experimental finding that *Coprinus* fruit-bodies bent more frequently (Table 1 in KS2001).

The potential with smaller θ_r and smaller Φ_0 (the height of the barrier, analogous to 'activation energy' in a chemical reaction) has a higher Pt than that with larger θ_r and larger Φ_0 (Fig. 15). In Fig. 15a, the ball can fluctuate only slightly around $\theta=0$. This is in agreement with the characteristic of homeostasis: if only a slight fluctuation is allowed around the set point (equilibrium), a system in homeostasis may become unstable and destroyed by the fluctuation.

Modification of the potential graph The finding that some fruit-bodies grow asymmetrically (Figs. 16, 19 in KS2001) shows that the curve of potential, which was assumed to be symmetrical, might actually be asymmetric.

Further, the finding that some fruit-bodies grew slightly obliquely downward with the caps tilting (Figs. 12, 14) shows that the curve of potential, which was assumed to be smooth, might actually be not smooth owing to a 'catastrophe' (Fig. 16). (A catastrophe is a sudden, discontinuous and qualitative change, as is known for phase transition and biological processes.) In Fig. 16, the potential decreases abruptly near $\theta=0$, and hence shows a higher stability and lower Pt in the downward growth. Fruit-bodies in Figs. 12 and 14 seem to have almost the same potential as those growing vertically downward, and hence potential around $\theta=0$ is almost constant, as in 'neutral equilibrium'. (This area around $\theta=0$ is bounded by the potential walls, whereby stability of the system is assured.)

Application of the equilibrium concept to Aphyllophorales, *Phycomyces* and plants Plunkett (1961) exposed the fruit-bodies of *Polyporus brumalis* to light first from above, then from the side and finally from below. As a result, the fruit-bodies grew toward the light source throughout development, and eventually formed an inverted 'U' shape; their growth direction changed from upward to downward. This can be explained by the present model as follows: the shift of light source caused a transition from the stable equilibrium to the unstable one, a transition in the opposite direction to that treated above. In this way, the present model can also explain the development of pedunculate Aphyllophorales, and thus seems to be applicable to all hymenomycete fungi.

In plant shoots and *Phycomyces* sporangiophores, unlike in hymenomycete fruit-bodies which are first phototropic and then gravitropic, there may occur competition between phototropism and gravitropism (Hangarter, 1997), and vectoral balance between them is called 'photogravitropic equilibrium' (for plants: Neumann and Iino, 1997; for *Phycomyces*: Galland, 1983). In such cases, the potential for phototropism and the potential for gravitropism must be superimposed or overlapped, resulting in one potential with one minimum point. This minimum corresponds to the *equilibrium in* the present model (Fig. 2b), and may be equivalent to the 'photogravitropic equilibrium' in actuality. In *Phycomyces* sporangiophores, in addition to photo- and gravitropisms, the optical properties which suppress phototropism should also be involved in the equilibrium bending angle (Ootaki et al., 1991). In this case, potentials for these three factors should be superimposed. Thus, even if plural tropisms act at the same time, superimposing of plural potentials will result in one potential with one (or more) equilibrium point(s). In any case, axial organs will finally reach an equilibrium point where the potential has a (local) minimum, and therefore the present model seems to be applicable to all axial organs.

Acknowledgements——I thank Prof. Naohiko Sagara for suggesting me to theorize the development of agaric fruit-bodies and for reading the manuscript.

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