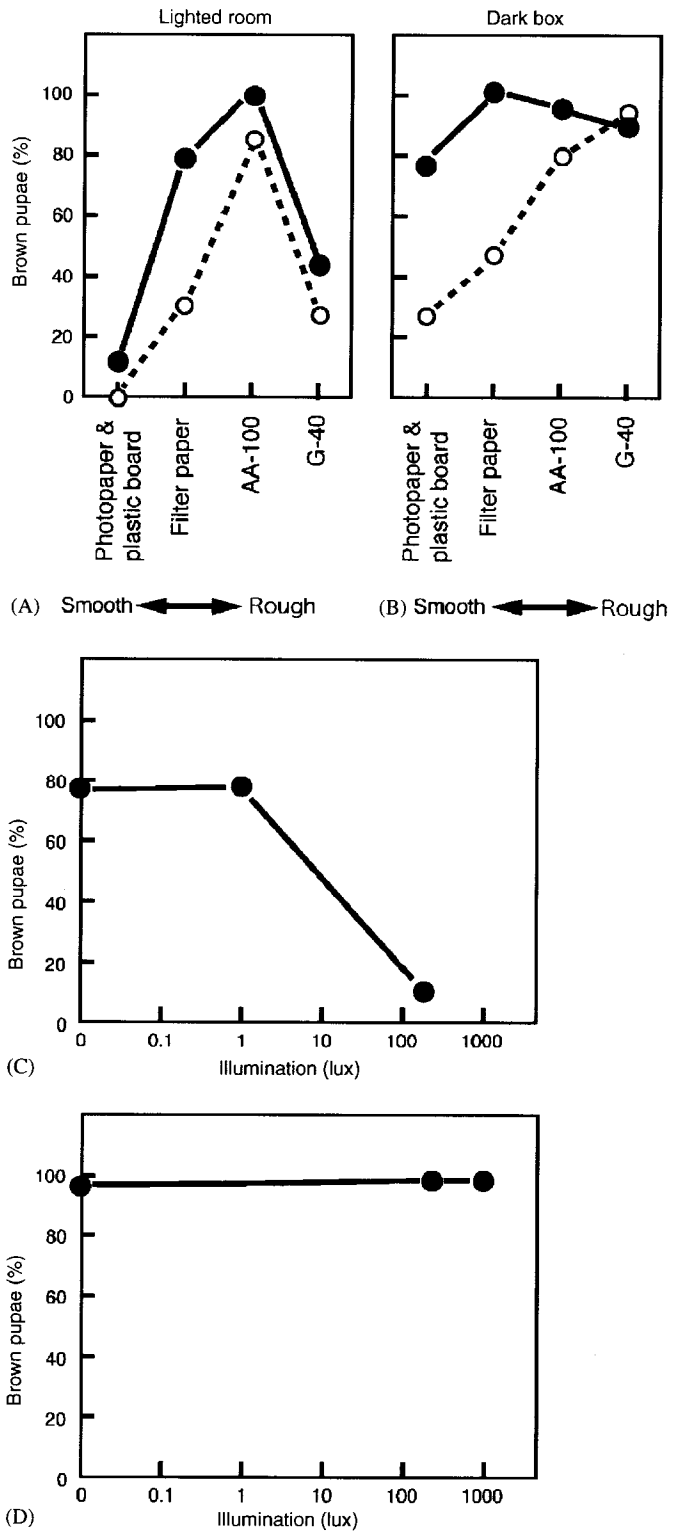

Fig. 3. Effects of surface roughness of the pupation site, sufficient light, darkness, and the presence of living leaves of a food plant (*Poncirus trifoliata*) on the number of brown pupae. (A) In a lighted room. (B) In completely dark boxes. Solid circles represent the number of brown pupae in the absence of living plant leaves. Open circles represent the number of brown pupae in the presence of living plant leaves. (C) Effects of different intensities of illumination on the pupal coloration on pupation boards of black photopaper. (D) Effects of different intensities of illumination on the pupal coloration on pupation boards of AA-100.

Table 4
Effect of living plant leaves, 100% humidity and 5% carbon dioxide gas on pupal coloration in complete darkness

Addition	Sample size	Brown pupae	2×2 (p-value)[a]		
			2	3	4
1. None	30	23 (77%)	.0010	.0962	.2750
2. Living leaves	15	3 (20%)			
3. 100% humidity	7	3 (43%)			
4. 5% carbon dioxide	22	16 (73%)			

Larvae were placed on photopaper boards and kept in a dark box or a carbon dioxide incubator (dark).
[a] χ^2test for independence.

3.7. *Effects of changing textures at the pupation site after girdle formation*

As described above, most pupating larvae became brown pupae on AA-100 in an lighted room (Table 2 Experiment 3 and Fig. 3A). On the other hand, most larvae pupating on photopaper produced green pupae in the same room (Table 2 Experiment 1 and Fig. 3A). To investigate the critical period that is required for determining pupal coloration, larvae (prepupae) that had just formed a girdle on AA-100 boards under sufficient light were transferred into conical bags of photopaper (Fig. 1D). Four larvae out of the five that were tested became brown pupae and one became a green pupa (Table 5 Experiment 1). Additionally, when a T-shaped sheet of black photopaper was inserted between the head–thorax region and the AA-100 board after formation of the girdle, eight larvae out of nine produced brown pupae (Table 5 Experiment 1). These results indicate that tactile signals received from the AA-100 board in the period prior to girdle formation are sufficient for determining the brown pupal coloration in most of the larvae under these conditions.

In reverse experiments, when the larvae had formed girdles on black photopaper and had released their abdominal prolegs from the pupation board, a T-shaped sheet of AA-100 (black) was inserted between the head–thorax region and the board. All of the larvae that were tested in this way formed brown pupae (Table 5 Experiment 2). This indicates that tactile signals received from the T-shaped AA-100 sheet after the release of the abdominal prolegs were also effective in determining the brown pupal coloration.

Similar experiments were performed on boards of white photopaper, as follows. When larvae had formed a girdle on white photopaper and had released their abdominal prolegs from the pupation board, a T-shaped sheet of AA-100 (black) was inserted between the head–thorax region and the white pupation board. Most of the larvae that were tested (eight out of nine) produced green pupae (Table 5 Experiment 2). The significant difference in pupal coloration between pupations on black and white photopaper before the release of prolegs will be discussed later.

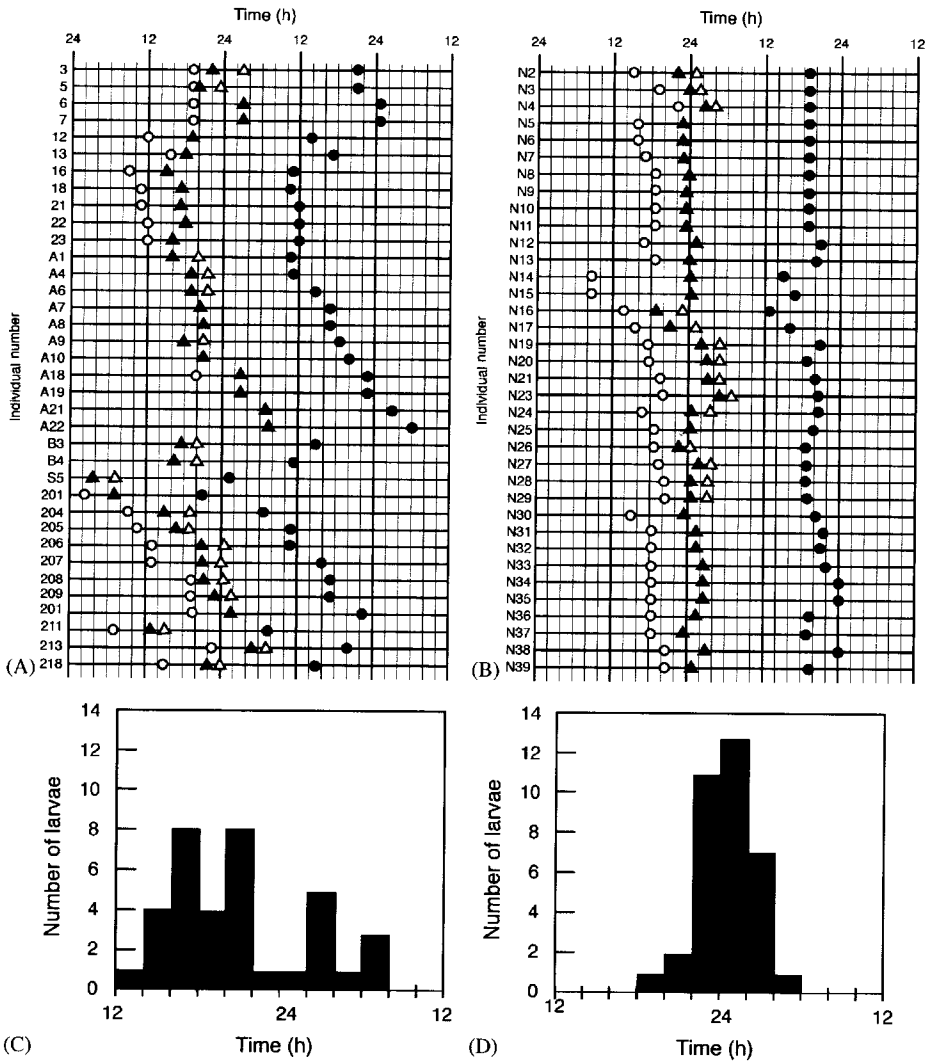

Fig. 4. Time course of events during the pupation period. (A) Thirty-six larvae reared under continuous lighting (200 lux) from fluorescent lamps during May and June are shown. (B) Thirty-six larvae reared under natural light in July are shown. The larvae were observed for pupation under continuous lighting (200 lux) throughout the pupation period. N2–N11 of the larvae had undergone larva–pupal ecdysis prior to 19:00 h, but the accurate time was not clear. The horizontal axis shows a duration of 2.5 days. Open circles show the time of final evacuation and rapid wandering. Solid triangles show the time of girdle formation. Open triangles show the time of releasing the abdominal prolegs from the pupation board. Solid circles showthe time of larva–pupal ecdysis. (C) Time of girdle formation in larvae reared under continuous lighting. (D) Time of girdle formation in larvae reared under natural light.

Table 5
Changing materials of the pupation site after girdling or releasing of prolegs in a lit room

Experiment	Timing of change	Material of pupation site	Sample size	Number of pupae	
				Green	Brown
Exp. 1	No change	AA-100	23	0 (0%)	23 (100%)
	After girdling	AA-100→photopaper (black, T-shaped)	9	1 (11%)	8 (89%)
	After girdling	AA-100→photopaper (white, conical bag)	5	1 (20%)	4 (80%)
Exp. 2	No change	Photopaper (black)	13	13 (100%)	0 (0%)
	After release of AP[a]	Photopaper (black)→AA-100 (T-shaped)	10	0 (0%)	10 (100%)
	No change	Photopaper (white)	10	9 (90%)	1 (10%)
	After release of AP[a]	Photopaper (white)→AA-100 (T-shaped)	9	8 (89%)	1 (11%)

[a]AP = abdominal prolegs.

3.8. Effects of changing the illumination intensity after girdle formation

To examine the effect of changing the intensity of the illumination during pupation, larvae were placed on boards of black photopaper under 200-lux illumination and then the apparatus containing the larvae was transferred into a dark box after girdle formation. Eight larvae out of the 11 under test (73%) became brown pupae under these conditions (Table 6 Experiment 1). On the other hand, in the case of continuous lighting throughout the pupation period, most larvae became green pupae (Experiment 1). This indicated that the transfer to darkness resulted in the frequent appearance of brown pupae. In the reverse experiment, when larvae that had formed a girdle on black photopaper in darkness were transferred to a lighted room, 60% of the larvae tested became green pupae (Table 6 Experiment 2). As a control (kept in darkness throughout the pupation period) most larvae (91%) became brown pupae. Thus, the intensity of the illumination was influential on the pupal coloration both before and after girdle formation.

3.9. Effects of pupation textures under natural light

As shown in Fig. 4B and D, larvae that were reared under a daily periodicity of the natural light formed a girdle around midnight. The resulting prepupae released their prolegs from the pupation board 2–4 h after girdle formation and passed throughout the daytime of the next day in that state. The prepupae then underwent larva–pupal ecdysis in the early nighttime of that day. Thus, these larvae passed both the nighttime and the daytime during pupation (see Fig. 5A). Therefore, the effects of the textures of the pupation sites on pupal coloration were actually examined under natural light in the absence of both leaves and 100% humidity. When the prepupae were placed in direct strong sunlight (110,000 lux) of a fine summer day, they frequently failed to undergo ecdysis and died, presumably due to overheating of their body by the strong sunshine. Therefore, prepupae were kept in indirect sunlight. Illumination was approximately 10,000 lux (cloudy 5000 lux, fair 20,000 lux) at noon. The majority of tested larvae became green pupae (77% green pupae) on black photopaper and brown pupae (63% brown pupae) on AA-100 from the window under natural light (Fig. 5B). Thus, significant differences in responses between photopaper and AA-100 were clearly observed even under natural light ($p = 0.0239$, Welch's test).

Table 6
Changing the illumination intensity on boards of black photopaper after girdling

Experiment	Timing of change	Intensity of llumination (lux)	Sample size	Number of pupae	
				Green	Brown
Exp. 1	No change	200	18	16 (89%)	2 (11%)
	After girdling	200→0	11	3 (27%)	8 (73%)
Exp. 2	No change	0	22	2 (9%)	20 (91%)
	After girdling	0→200	10	6 (60%)	4 (40%)

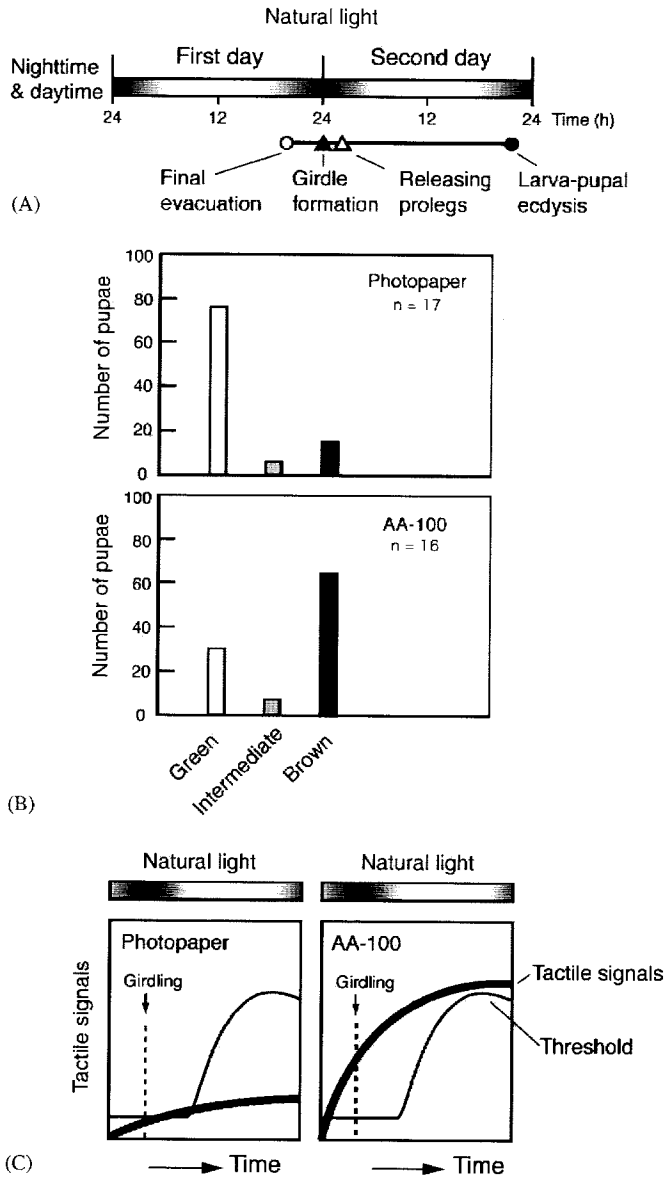

Fig. 5. Effect of textures of the pupation site on pupal coloration under natural light. (A) Events in pupation period under natural light. (B) Larvae that had been reared under natural light were tested for pupal coloration on black photopaper and on AA-100 boards under natural light. Open, solid, and gray bars represent green, brown and intermediate color pupae, respectively. n is the number of pupae tested. (C) Prediction of accumulated tactile signals (thick lines) and the threshold of tactile signals (thin lines) required for determination of brown pupal coloration in natural light. Upper bars with black and white areas represent nighttime and daytime zones. Vertical dotted line represents the time of girdle formation.

4. Discussion

The results of the present work indicate that the tactile signals received from the pupation site during pupation are

the environmental factors promoting induction of brown pupal coloration. In darkness, brown pupae were formed even on smooth surfaces (Fig. 3B). This indicates that light suppresses induction of brown pupal coloration. Other environmental factors, such as living plant leaves or 100% humidity, also appear to suppress the induction of brown pupal coloration (Fig. 6G). The suppression effect of living leaves on brown pupae formation was observed even in a dark box as shown in Fig. 3B. This result eliminates the possibility of a spectral effect of green reflection light from leaves. The suppression effect caused by plant leaves appears to be mainly due to the 100% humidity evaporated from the leaves as previously suggested by Ishizaki and Kato (1956) and Honda (1979). On the other hand, carbon dioxide, which may be emitted from living leaves in darkness, did not have the suppression effect. Smith (1978) also described previously that there is no effect of carbon dioxide on pupal coloration. The suppression effects of light and leaves were additive in terms of pupal coloration (Fig. 3A and B). The physiological conditions of pupating larvae appear to be affected by these environmental factors during the pupation period. The present

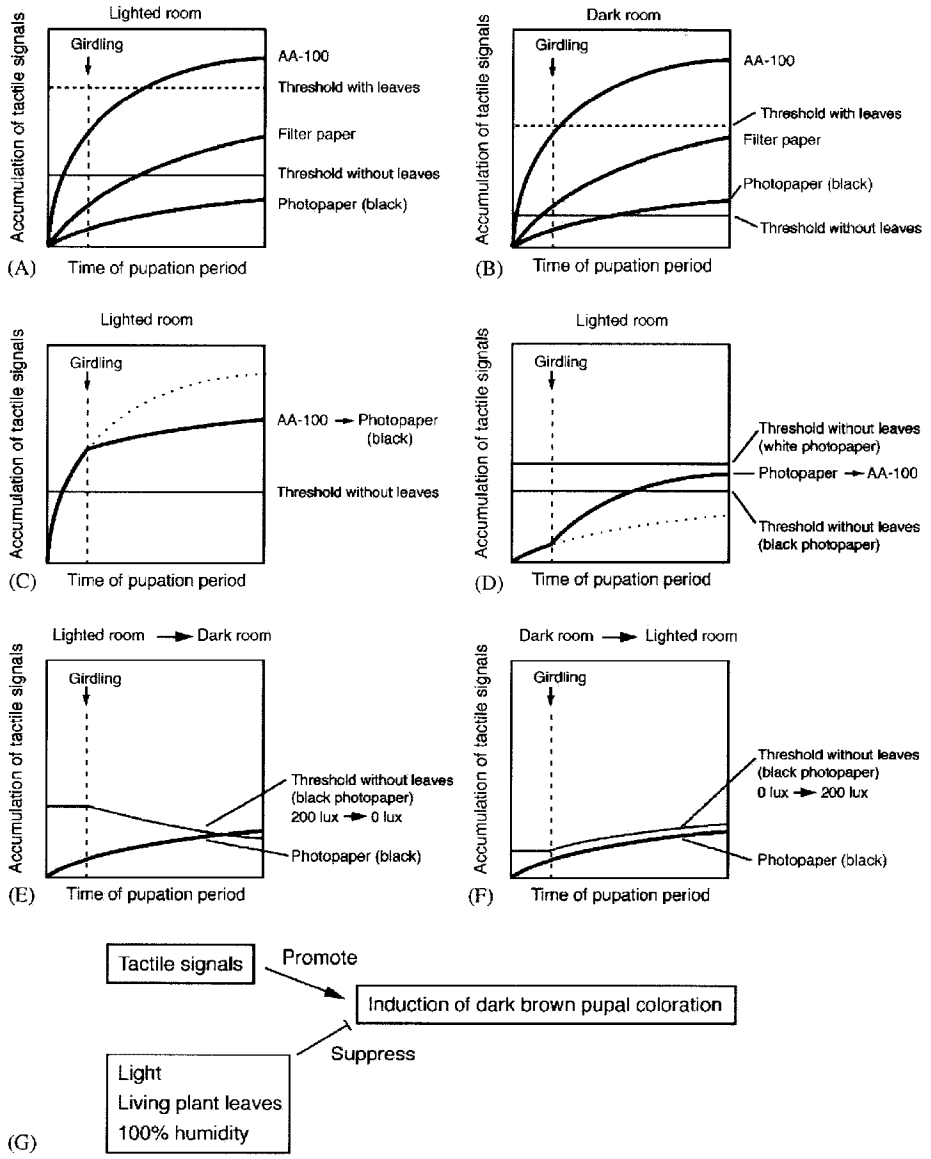

Fig. 6. The 'tactile signal accumulation hypothesis': schemata of the accumulation of the tactile signals received from various pupation boards and the threshold of the tactile signals required for determining the brown pupal coloration. (A) In a lighted room. (B) In a completely dark box. (C) Change of pupation materials from AA-100 to black photopaper after girdle formation in a lighted room. (D) Change of pupation materials from white or black photopaper to AA-100 after girdle formation in a lighted room. (E) Change of intensity of illumination (200–0 lux) after girdle formation on black photopaper. (F) Change of intensity of illumination (0 –200 lux) after girdle formation on black photopaper. Horizontal axis shows the time of pupation from determination of the pupation site to the larva–pupal ecdysis. Vertical dotted line represents the time of girdle formation. Thick black lines represent accumulated tactile signals received from indicated pupation boards. Thin red solid lines represent the threshold in the absence of living plant leaves. Thin green broken lines represent the threshold in the presence of living plant leaves. (G) Conclusion: environmental factors influencing the pupal coloration in *Papilio xuthus* (see text).

results revealed that tactile signals and light received both before and after girdle formation affected pupal coloration (Tables 5 and 6). Many researchers have reported previously that textures of pupation sites affect pupal coloration in *Papilio* butterflies (Hazel, 1977; Hazel and West, 1982; Hiraga, 2005; Honda, 1979, 1981; Smith, 1978).

Based on the present results, the tactile signal accumulation hypothesis is shown as follows. Fig. 6A and B show schemata of the accumulation of successive tactile signals and the threshold levels of tactile signals required for the induction of the brown pupal coloration in various environmental conditions. One possibility is that the tactile signals are strongest on the rough surface of AA-100, and weakest on smooth photopaper and plastic boards under sufficient light (Fig. 6A). The number of brown pupae was smaller on G-40 than on AA-100 under sufficient light (Table 2 and Fig. 3A). This is presumably due to the smaller number of particles per 100 mm^2 of G-40 than that of AA-100, although the mean particle size of G-40 is larger than that of AA-100 (Fig. 2B). An alternative possibility is that the lower frequency of brown pupation on G-40 is due to the suppression effect of reflection rays containing yellow rays from brown G-40 on brown pupal coloration. In complete darkness, almost all pupae were brown in both AA-100 and G-40 (Fig. 3B).

In complete darkness, the threshold level might be significantly lower than that under sufficient light by an unknown physiological mechanism (cf. Fig. 6A and B). Therefore, brown pupae frequently appeared even on the smooth surfaces of photopaper and plastic boards in completely dark boxes. The pupal coloration is thus significantly affected by the intensity of ambient light.

Living plant leaves might significantly increase the threshold level of the tactile signals required for the induction of brown coloration under both light and dark conditions, resulting in a reduced number of brown pupae (Fig. 6A and B). However, a significant reduction in brown pupae caused by leaves was not observed on AA-100 under light (Table 2 and Fig. 3A). Thus, the promotion function caused by strong tactile signals from AA-100 causing the brown pupal coloration dominated the suppression function induced by the presence of both light (200 lux) and leaves and also that caused by 200–1000-lux illumination (Fig. 3C). In darkness, the significant reduction in the number of brown pupae induced by the presence of leaves was observed on plastic, photopaper, and filter paper boards, but not on AA-100 and G-40 (Table 3 and Fig. 3B). The tactile signals might be in excess for the induction of brown pupal coloration on AA-100 and G-40, and therefore the suppressive effect caused by leaves might not be observed in darkness. These results all support the tactile signal accumulation hypothesis.

Hidaka (1961, 1975) described the result that the living leaves of a food plant (*Poncirus trifoliata*) and a non-food plant (*Ambrosia artemisiaefolier*) caused an increase in green pupae in a dark box in *Papilio xuthus*, suggesting an effect of odor from living leaves. Although a suppressive effect of living plant leaves on the induction of brown coloration was confirmed in the present work (Fig. 3B), 100% humidity also suppressed brown coloration (Table 4). There has been no description on a chemical compound of odor that suppresses the brown pupal coloration in *Papilio xuthus*. Honda (1979) reported that no suppressive effects on the brown coloration due to the leaves of a live food plant (*Zanthoxylum ailanthoides, Citrus unshiu* or *Citrus natsudaidai*) observed in conditions involving a rough-surfaced pupation site under light in the case of *Papilio protenor demetrius*. Similar results were obtained using AA-100 boards under light for *Papilio xuthus*, as shown in Fig. 3A.

As shown in Table 5 Experiment 2, all of the prepupae on black photopaper became brown pupae when a T-shaped AA-100 sheet was inserted after releasing the abdominal prolegs. In contrast, most prepupae became green pupae on white photopaper when a T-shaped AA-100 sheet was inserted. These different results may be due to the different intensities of light refracted from these boards; the light reflected from white photopaper may slightly increase the threshold level for the tactile signals, resulting in the production of green pupae (see Fig. 6D). Thus, the light reflected from the pupation board was able to significantly influence the threshold level of the tactile signals under these particular conditions.

The intensity of illumination also is effective in determining pupal coloration, even after girdle formation. In the case where a specimen was transferred from 200 to 0 lux after girdle formation, the physiological threshold level appears to decrease gradually after the transfer and finally became slightly lower than the level of the accumulated tactile signals, resulting in the frequent appearance (73%) of brown pupae (Fig. 6E). On the other hand, when pupating larvae were transferred from a 0 to a 200 lux environment after girdle formation, the threshold level might increase to slightly higher than the level of the accumulated tactile signals, resulting in the frequent appearance (60%) of green pupae (Fig. 6F). The above results indicate that prepupae are able to receive environment signals, which affect pupal coloration even after girdling.

The antennae and mechanoreceptor bristles that are located near the spinnerit might receive tactile signals from the pupation board, mainly during the process of spinning thread onto the board before girdle formation. However, after the release of the abdominal prolegs from the board, only the anal prolegs, thorax legs, and the front of the head (but not the antennae) were able to touch the pupation board (Fig. 1C and F). The mechanoreceptor bristles at the front of the head (vertex, fronts, clypeus, etc.) and/or thorax legs presumably received tactile signals from the inserted T-shaped sheet of AA-100 after the release of the abdominal prolegs. The front of the head also frequently touched the pupation board before girdle formation. Therefore the bristles of the front of the head appear to

receive tactile signals before and after girdle formation. Honda (1979) reported that most of the larvae of *Papilio protenor demetrius* molted into green pupae on thin wires (1.5-mm diameter). This suggests that the antennae and mechanoreceptor bristles at the front of the head might receive tactile signals at low frequency from the thin wires, because the wires were far narrower than the width (ca. 5 mm) of the head of the larvae. Signals through the nervous system might induce brown pupal coloration via the internal secretion system (Hidaka, 1956, 1961; Awiti and Hidaka, 1982; Yamanaka et al., 1999, 2005). If the internal secretion hormone is not sufficient, the pupae are intermediate in color.

When larvae were reared under natural light, they formed their girdles around midnight (Fig. 4B and D). In these larvae, the timing of girdle formation is likely determined by photoperiodic induction regulated by a biological clock that had been set during the larval period prior to gut purge. Although these larvae tend to form a girdle during the night, they might successively receive tactile signals in both darkness and daylight during pupation, because the pupation period is approximately 20–24 h, far longer than the darkness period of one night (see Figs. 4B and 5A). Therefore, the larvae received both tactile signals and optical signals of strong natural light even after girdle formation during pupation. These signals have an affect on pupal coloration in nature. Actually, most larvae became green pupae on photopaper and brown pupae on AA-100 under natural light in the absence of both living leaves and 100% humidity (Fig. 5B), as expected. Even a strong light of 5000–20,000 lux at noon on the second day was unable to suppress the induction of brown pupal coloration caused by the strong tactile signals received from AA-100 boards in a large number of pupae. This indicates that the texture of the pupation site is a key for determining pupal coloration besides light in natural environments. No other environment factor except tactile signals is known to induce the brown pupal coloration under natural light. This defends strongly the tactile signal accumulation hypothesis. Conversely, experimental conditions of complete darkness throughout the pupation period, such as those shown in Fig. 3B and Hidaka (1961, 1975), are artificial conditions and are unlikely to occur in the field. All pupating prepupae would normally receive strong natural light throughout the daytime in natural environments.

Wiklund (1972) described how larvae of *Papilio machaon* L. pupating on white-painted sticks produced significantly higher frequencies of green pupae when illuminated with green, yellow, or orange rays (550–620 nm wavelength, incident rays was 2×10^{-4} cal/cm^2/min) than when illuminated with red, blue or infrared rays, or in darkness. This result appears to show the biologically effective intensity of each wavelength in suppression of the brown pupal coloration. It is known that the stemmata of *Papilio xuthus* larvae have three types of optical receptor cells that receive respectively to ultraviolet, blue, and green rays, but they do not have receptor cells receiving red rays (Ichikawa, 1986; Ichikawa and Tateda, 1980). West and Hazel (1985) reported that *Eurytides marcellus* (Cramer) and *Papilio troilus* L., belonging to the family Papilionidae use chiefly the color of the pupation substrate to determine pupal coloration; *Papilio troilus* is hardly and *E. marcellus* is not at all affected by substrate texture. Yellow papers have been shown to be the strong cues in the production of green pupae. Hazel and West (1979) described that major environmental cues influencing pupal coloration in *Papilio polyxenes* and *B. philenor* were textural and optical. These results on colored substrates might reflect the biologically effective intensity of different wavelengths in suppression of brown coloration. Two remaining possibilities are as follows: (i) larvae of their butterfly species were more sensitive to ventral direction rays than dorsal direction rays, alternatively and (ii) these experiments were done under insufficient illumination, resulting in a requirement for dorsal plus ventral rays to suppress the brown coloration. No description of illumination intensity and roughness of the rough substrate was reported. Colors of pupation sites are known to affect pupal coloration in *Pieris* white butterflies belonging to the family Pieridae (Ohtaki, 1969; Kusano and Kawai, 1971; Kayser and Angersbach, 1974; Hidaka, 1975; Smith, 1980). In these white butterfly species, refection rays from yellow papers also suppress strongly induction of brown coloration.

In *Papilio xuthus*, different effects of reflection rays from different colors of pupation boards were not observed under 200 lux of sufficient white illumination (Table 1). I observed that different intensities of reflection rays from black and white boards affected differently pupal coloration under particular experimental conditions as shown in Exp. 2 of Table 5. Therefore, reflection rays from pupation sites could affect pupal coloration under paticular experimental conditions. The result of Table 1 does not eliminate the possibility that reflection rays from yellow papers could suppress induction of brown pupal coloration under experimental conditions of lower illumination intensities. To observe strong suppression effect of reflection rays from yellow papers on brown coloration, lower intensities of illumination (200 lux > incident rays > 1 lux; see Fig. 3C) should be used in *Papilio xuthus*. Presumably, although larvae of butterfly species having pupal color polyphenism may widely use optical sensory systems, which relate to pupal coloration, there may be differences in relative sensitivity to dorsal and ventral directions of light between species.

An important point in the present work is the precise analyses integrating various effects of environmental factors: especially, the interactions of these factors in the field to determine pupal coloration. Although larvae form girdles at midnight, the prepupae always receive strong daylight during the following day, and accumulated tactile signals received from the rough texture of the pupation site are able to induce brown pupal coloration even under strong light conditions. I consider this to be the most important original point in the present work.

If larvae get wet with rain during pupation in natural environments, the threshold level of brown color induction may be increased physiologically by the humidity, resulting in an increase of the number of green or intermediate color pupae in some circumstances. As regards to the main pupation sites in the field, living leaves and new twigs of plants are green and have smooth surfaces; on the other hand, large trunks and dead branches are dark grayish brown and have rough surfaces. Therefore, the sensory mechanism of pupal coloration via mechanoreceptors in *Papilio xuthus* might effectively act as a protective coloration system to mimic closely the colors of different pupation sites in nature, with the result that this mechanism avoids predation from insectivorous birds in their natural environments.

In the phylogenic tree of Papilionidae butterflies, the phylogenic branch that consists of *Graphium*, *Eurytides* and *Iphiclides* diverged as a clade from the other branch that consists of the following two phylogenic subgroups: the first subgroup consists of the genus *Papilio*, and the second subgroup includes the genus *Battus*, *Parides*, *Troides*, *Pachliopta*, and *Atrophaneura* (Zakharov et al., 2004). As previously described, larvae of *Graphium sarpedon nipponum* respond strongly to optical cues and are capable of differentially receiving dorsal and ventral directions of rays; however, they do not respond to textures to determine pupal coloration (Hiraga, 2005). West and Hazel (1985) reported that pupal coloration in *E. marcellus* (Cramer) was unaffected by pupation site texture, although a suppression effect of reflection rays from yellow papers was observed on brown pupal coloration. Larvae of *Eurytides* and *Graphium* may have sensory mechanoreceptor systems, in which tactile signals do not relate to determination of pupal coloration. On the other hand, *B. philenor* responds strongly to textural cues in addition to optical cues for determining pupal coloration (Hazel and West, 1979). These results suggest the possibility that a common ancestral species of *Papilio* and *Battus* butterflies acquired a sensory system of mechanoreceptors in which tactile signals were able to affect the determination of pupal coloration.

The oldest ancestral pupal color of the Papilionidae family was presumably monomorphic brown and the ancestral pupation site preference was a brown site on the ground, as usually *Luehdorfia japonica* Leech. During evolution, a polyphenic pupal coloration system in which light (particularly yellow rays) inhibits brown coloration might be first acquired, resulting in the capacity to produce green pupae on green plants. Secondarily, another polymorphic pupal coloration system in which both the light and texture of the pupation site affected pupal coloration might be acquired, resulting in the capacity to produce brown pupae on brown rough trunks, even under strong natural light.

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