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THE CONCEPT OF " LIFE TYPES " IN TETRANYCHINAE *.
AN ATTEMPT TO CLASSIFY THE SPINNING BEHAVIOUR
OF TETRANYCHINAE

BY Yutaka SAITÔ **

LIFE PATTERNS
TETRANYCHIDAE
SPINNING
BEHAVIOUR
LITTLE WEB
COMPLICATED
WEB
WEB NEST
RELATIONSHIPS
WITH
PHYLOGENY
AND
LIFE CYCLES

ABSTRACT : Life patterns of thirty-one spider mite species in Japan were observed and categorized in three basic ' life types ', including several subtypes, using characteristics of spinning behaviour, structure of web as well as other habits.

A ' little web (LW) ' life type, which includes four subtypes was recognized in four genera, namely *Aponychus*, *Eurytetranychus*, *Panonychus* and *Yezonychus*. Many species of *Tetranychus* and *Eotetranychus*, and a few of *Oligonychus*, *Panonychus* and *Schizotetranychus* are accommodated in a category of ' complicated web type (CW) ', which includes five subtypes. The third life type is characterized by a web nest (WN) ; it has five subtypes, and is found in the genera *Eotetranychus*, *Schizotetranychus* and *Oligonychus*.

It is postulated that the relationship between mite genus and level of life type complexity agrees with Tetranychinae phylogeny as proposed by GUTIERREZ *et al.* (1971). Relationships between host plants and spider mite life types operating on them indicated that polyphagous mites which live on unstable, annual host plants have only a single life type. This may be related to their mode of life as *r*-strategists. The life types of mites living on stable host plants, on the other hand, were quite diverse.

Significance and problems of classification of life types in Tetranychinae, and relationships between the life types and life histories are also discussed.

MODE
DE VIE
TETRANYCHIDAE
COMPORTEMENT
DE
TISSAGE
TOILE
PAUVRE
TOILE
COMPLEXE
NID DE
TOILE
RAPPORTS

RÉSUMÉ : À partir de l'observation du mode de vie de trente et une espèces d'araignées rouges du Japon et en se basant sur les caractéristiques du comportement de tissage, sur celles de la structure de la toile, ainsi que sur celles d'autres habitudes, on a pu distinguer trois types de vie, comprenant eux-mêmes plusieurs sous-types.

Le premier type de vie « avec de la toile pauvre » (« little web » = LW), avec quatre sous-types, a été observé chez quatre genres : *Aponychus*, *Eurytetranychus*, *Panonychus* et *Yezonychus*. Plusieurs espèces de *Tetranychus* et d'*Eotetranychus* ainsi que quelques représentants des genres *Oligonychus*, *Panonychus* et *Schizotetranychus*, appartiennent à une seconde catégorie du type « toile complexe » (« complicated web » = CW), qui comporte cinq sous-types. Le troisième type caractérisé par un « nid de toile » (« web nest » = WN), avec également cinq sous-types, a été reconnu dans les genres *Eotetranychus*, *Schizotetranychus* et *Oligonychus*.

* Study on spinning behaviour of spider mites IV. This work was presented in 16th International Congress of Entomology, 1980 in Kyoto, Japan.

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AVEC
PHYLOGENÈSE
ET
CYCLES
BIOLOGIQUES

La relation entre le genre et le niveau de complexité du type de vie semble rejoindre les propositions phylogénétiques de GUTIERREZ *et al.* (1971). La parenté entre la plante hôte et le type de vie, qui y est mené, indique que les acariens à régime polyphage et vivant sur des plantes non stables, telles que des annuelles, ont un seul type de vie, qui peut être lié à la valeur élevée du taux d'accroissement naturel de leurs populations, tandis que ceux qui vivent sur des plantes hôtes stables ont des comportements assez diversifiés.

La discussion porte sur la signification et les problèmes de classification des types de vie chez les Tetranychinae, et sur les relations entre le type de vie et le cycle biologiques.

INTRODUCTION

The life and web patterns of various spider mite species were described by GUTIERREZ *et al.* (1971), in their cytogenetic and phylogenetic study of tetranychids. In Japan, the life pattern of a spider mite was first described by YOKOYAMA (1932), working with *Eotetranychus suginamensis* (Yokoyama). After that, however, only fragmentary data were published on life patterns as related to spider mites' webbing and/or their behavioural characteristics.

SAITÔ (1979 *a*) and SAITÔ and UENO (1979), who studied the relationship between life history parameters and host plant stability, pointed out that characteristics of life type (this term will be defined below) of certain mite species also correspond to their life history and habitats. However, mite life types were not defined in those reports.

On the other hand, the spider mite webbing which characterizes Tetranychini life type has drawn the attention of many workers (eg. HAZAN *et al.*, 1974 and 1975, SAITÔ, 1977 *a*, 1977 *b* and 1979 *b*); GERSON (1979) reviewed the functions of spider mites' webs, and pointed out that webbing behaviour is one of the important criteria for interpreting the adaptation of this group of mites.

Various life patterns related to web structures, spinning behaviour and so on will be described in this report and they will be divided into categories being called as 'life type'.

MATERIALS AND METHODS

Collection records of the thirty-one spider mite species used in this study are shown in Table 1.

TABLE 1. Collection records of tetranychid species used in the present study.

Mite	Date	Locality (Prefecture)	Host plant	Type
<i>Aponychus</i>				
<i>firmiana</i>	Jun. 18, 1980	Tokyo	<i>Firmiana simplex</i>	A
<i>corpuzae</i>	Sep. 26, 1977	Hokkaido	<i>Sasa senanensis</i>	B
<i>Eotetranychus</i>				
<i>celtis</i>	Jul. 25, 1978	Kyoto	<i>Celtis sinensis</i>	A
<i>querci</i>	Jul. 4, 1981	Hokkaido	<i>Tilia japonica</i>	A
<i>shii</i>	Jul. 30, 1978	Tochigi	<i>Castanopsis sieboldii</i>	C
<i>smithi</i>	Jul. 30, 1978	Ibaraki	<i>Milletia japonica</i>	A
<i>suginamensis</i>	Jun. 6, 1978	Hokkaido	<i>Morus bombycis</i>	A
<i>tiliarium</i>	Aug. 19, 1978	Hokkaido	<i>Alnus hirsuta</i>	A
			<i>Alnus japonica</i>	A
<i>uncatus</i>	Aug. 19, 1978	Hokkaido	<i>Betula platyphylla</i>	A
sp. 1	Jun. 26, 1978	Hokkaido	<i>Quercus dentata</i>	A
sp. 2	Jul. 13, 1980	Hokkaido	<i>Tilia maximowicziana</i>	A
sp. 3	Jul. 29, 1981	Hokkaido	<i>Ulmus laciniata</i>	A
<i>Eurytetranychus</i>				
<i>japonychus</i>	Jul. 30, 1978	Tochigi	<i>Quercus glauca</i>	C
<i>Oligonychus</i>				
<i>rubicundus</i>	Aug. 1, 1978	Aomori	<i>Miscanthus sinensis</i>	D
<i>ununguis</i>	Mar. 7, 1979	Hokkaido	<i>Castanea crenata</i>	A
<i>Panonychus</i>				
<i>akitonus</i>	Aug. 18, 1979	Hokkaido	<i>Sasa senanensis</i>	B
<i>citri</i>	Apr. 5, 1975	Tochigi	<i>Citrus</i> sp.	C
<i>ulmi</i>	Jun. 6, 1976	Hokkaido	<i>Malus pulima</i>	A
<i>Schizotetranychus</i>				
<i>bambusae</i>	Dec. 3, 1979	Aichi	<i>Phyllostachys nigra</i>	B
<i>celarius</i>	Oct. 2, 1976	Hokkaido	<i>Sasa senanensis</i>	B
<i>cercidiphylli</i>	Aug. 2, 1979	Hokkaido	<i>Cercidiphyllum japonicum</i>	A
<i>leguminosus</i>	Jul. 25, 1978	Aichi	<i>Wisteria sinensis</i>	A
<i>recki</i>	Aug. 3, 1979	Hokkaido	<i>Sasa senanensis</i>	B
<i>schizopopus</i>	Jul. 4, 1978	Hokkaido	<i>Salix subfragilis</i>	A
sp. 1	Jul. 24, 1978	Kyoto	<i>Quercus glauca</i>	C
<i>Tetranychus</i>				
<i>cinnabarinus</i>	Jul. 30, 1978	Tochigi	<i>Rubus</i> sp.	E
<i>desertorum</i>	Jul. 28, 1978	Chiba	<i>Solidago altissima</i>	E
<i>kanzawai</i>	Mar. 7, 1977	Hokkaido	<i>Althaea rosea</i>	E
<i>urticae</i>	Jul. 10, 1975	Hokkaido	<i>Sambucus sieboldiana</i>	A
<i>viennensis</i>	Jul. 13, 1980	Hokkaido	<i>Quercus mongolica</i>	A
<i>Yezonychus</i>				
<i>sapporensis</i>	Sep. 28, 1979	Hokkaido	<i>Sasa senanensis</i>	B

A, broad-leaved deciduous tree; B, bamboo plant; C, broad-leaved evergreen tree; D, perennial herbaceous plant; E, annual plant.

Mite-infested leaves were collected in the field and brought to the laboratory packed in plastic bags. The leaves were carefully observed under a dissecting microscope to check the life pattern of the mite species on them. Some mites were thereafter kept on detached leaf cultures, to complement data obtained from field samples, while others were mounted in Hoyer's medium for identification. These cultures were placed in a temperature-controlled chamber kept at $25 \pm 1^\circ\text{C}$, with humidity varying between 50 to 70 % RH and the light period (15 : 9 = L : D) controlled with two 40-watt fluorescent tubes. Leaf surface condition

in the cultures (the surface positioned upward) was generally different from the natural situations, because most species inhabited the lower surface of the leaves in nature. This may explain some discrepancies between data from the field and laboratory observations on detached leaf cultures. Whenever this occurred, the former data were used. Most species were identified according to EHARA and SHINKAJI (1975). Each record of the first description in Japan (EHARA, 1978 and 1980, and also cf. EHARA and SCHINKAJI, 1975) was then referred to for final identification.

RESULTS AND DISCUSSION

1. Description of life types.

Ten items were selected to describe the characteristics of the life of spider mites (cf. Table 2, 3 and 4), i.e. 1. Kind of host plant (annual, perennial, etc.); 2. Leaf side inhabited; 3. Structure of web constructed by mites; 4. Density of web; 5. Site for placing eggs; 6. Egg cover produced by females; 7. Site where mites enter quiescent stages; 8. Preferred site for feeding and walking; 9. Spinning behaviour during walking; 10. site for defecation.

Several terms are available to express the peculiarities of spider mite life, i.e. life pattern, life style, life form and life type. These terms were often used without clear definitions, so that there seems to be some confusion. Items 3 to 10, as mentioned above, are used to characterize the term 'life type' in this study.

Based on these items, it appears that the lives of many tetranychids may be divided into three main types, which will be symbolically written as LW (little-web type), CW (complicated-web type) and WN (web-nest type). Each life type includes several subtypes. The life types and subtypes recognized in this study are discussed below.

Life type, LW

The first life type, LW, included four subtypes (Fig. 1, Table 2).

TABLE 2. Characteristics of subsidiary types categorized in the LW life type.

Subtype Item	LW-f	LW-j	LW-c	LW-s
1. Host plant type ¹	A	B	A & C	B
2. Leaf side inhabited	Both	Under-Both	Both	Under
3. Structure of web ²	—	—	Threads on LS	Threads on LS
4. Density of web ³	—	—	±	±
5. Place for placing eggs	LS along ribs	Shallow gutter of LS	LS along ribs	Tip of leaf hair
6. Egg cover	—	Dense web	Guy ropes	—
7. Site for quiescence	LS along ribs	Overall LS	Overall LS	Tip of Leaf hair
8. Preferred site for Feeding & walking	Overall LS	Overall LS	Overall LS	Overall LS
9. Spinning during walking ⁴	—	—	+	+
10. Site for defecation	Overall LS	Overall LS	Overall LS	Overall LS

LS : leaf surface.

1. See Table 1.

2. —, No web or threads is observed.

3. —, nothing; ±, low; +, medium; ++, high; +++, extremely high.

4. —, without; +, with.

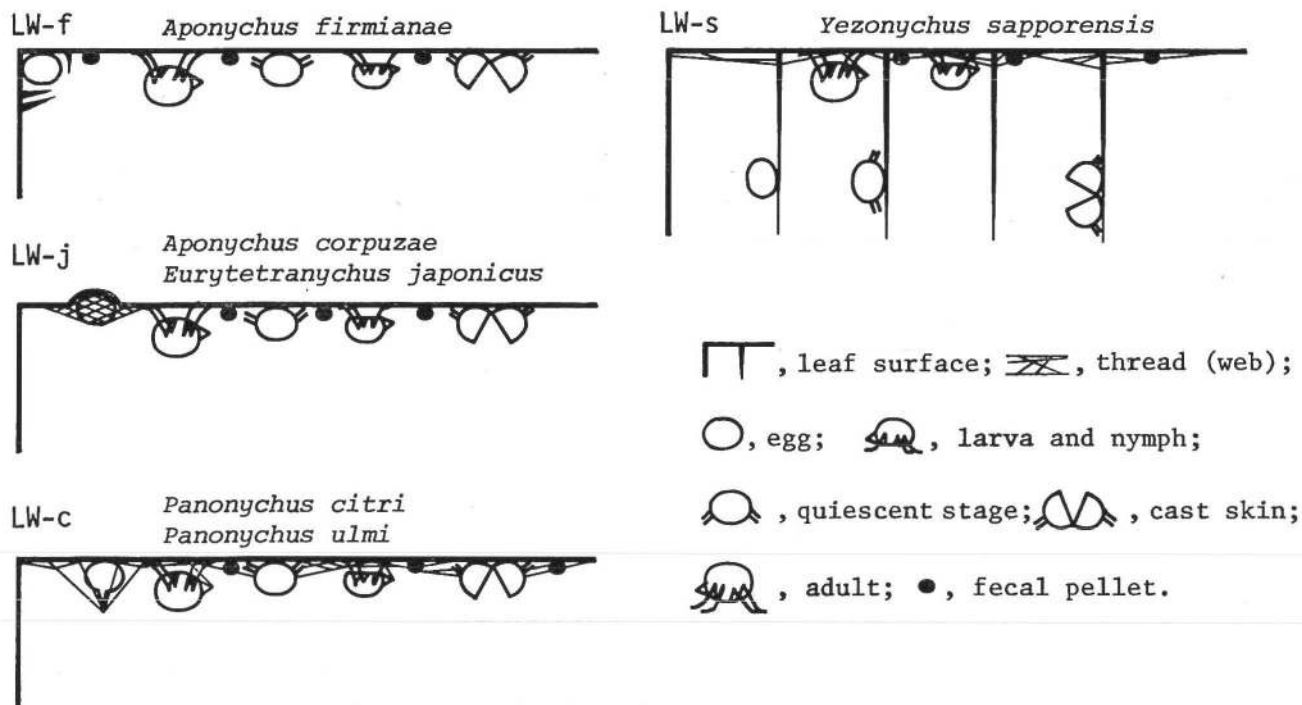


FIG. 1. Schematic expression of subsidiary types categorized in the LW life type.

1) Mites of the LW-f type spin no threads and webs. In Japan, a single species of this type, *Aponychus firmianae* Ma et Yuan, has been found on a deciduous tree, chinese parasol (*Firmiana simplex* (Linn.)) (Fig. 1, Table 2). Eggs of this species are deposited under dense leaf hairs along the veins. LW-f subtype is the simplest life type known from Japan.

2) Species of LW-j subtype have only webbed egg covers, spinning no threads while walking (Table 2, Fig. 1). *Aponychus corpuzae* Rimando on sasa bamboo, *Sasa senanensis* (Franch. et Sav.), and *Eurytetranychus japonicus* Ehara on evergreen oak, *Quercus glauca* Thunb., fall into this subtype. This type is probably more complex than LW-f because of the egg covering. GERSON (1979) believed that web production by Tetranychidae apparently first served to cover and thus protect the eggs. Although his statement is important regarding the function of the egg cover, it is not actually known against which factors the eggs are protected.

3) The LW-c type appears in two common spider mites, *Panonychus citri* (McGregor) and *Panonychus ulmi* (Koch), infesting citrus and apple, respectively. These two species spin silk threads while walking on the leaf and weave egg guy ropes, but make no other complex web structures (Table 2, Fig. 1). LW-c is considered to be more advanced than LW-f and LW-j, because the spinning behaviour continues during the entire life cycle¹. The function of guy ropes is to maintain the egg in an upright position for a brief period, in order to waterproof it (BEAMENT, 1951). The spinning threads produced while walking serve as 'life lines' (SAITÔ, 1979 b) throughout the mite's life on trees. This is apparently similar to facilitating mite locomotion over the leaf surface, preventing their dropping off their hosts. When mite population density becomes high and the plant deteriorates, the life lines serve as ballooning threads for migration of adult females, as described by FLESHNER *et al.* (1956).

4) Mites of the LW-s type spin life lines while

1. Adults males of *P. citri* produced no threads while walking (SAITÔ, unpublished data).

walking, but no other use of threads was observed (Table 2, Fig. 1). *Yezonychus sapporensis* Ehara on sasa bamboo belongs to this subtype. It is characterized by various habits : mites attach their eggs on the tip of a leaf hair, and quiescent stages rest in a similar position (Fig. 1, Table 2). Because of these special habits, it is thought that LW-s is the most complex subtype among the LW life types. The egg laying and quiescence habits seem to protect immobile mites from predators.

The genus *Yezonychus* may be closely related to the genus *Schizotetranychus* (which includes many web spinning species as mentioned below), because it is also characterized by having laterally-divided empodial claws. According to the phylogeny proposed by GUTIERREZ *et al.* (1971), this species is distantly related to the other species of the LW type. Therefore it may be speculated that it originated from a group which produces highly-complex web structures, but its weaving habits have been secondarily suppressed possibly as a result of its special habits, as mentioned above.

Thus the LW life type consists of a series of three subtypes (LW-f, LW-j and LW-c), and a fourth (LW-s) which may be qualitatively different from the first three. The LW life type is the simplest of three proposed in the present study, and it may be the basic life type of Tetranychini.

Life type CW

The second life type, CW, is characterized by complicated webs (thus CW) which are quite different from LW (Fig. 2, Table 3). The fundamental feature of this life type lies in the web which is a three-dimensional and irregularly-complicated structure. Five subtypes were recognized in this life type.

1) The simplest one (CW-p) appears in *Eotetranychus* sp. 1 on deciduous oak, *Quercus mongolica* Fischer. This species produces silk threads while walking, and the threads accumulate on the inhabited leaf surface. The mites tend to walk on the web and they lay their eggs and pass their quiescent stages on the leaf surface under the web. In this subtype, the web appears to serve

as footing when mites traverse the leaf surface. The web and threads produced while walking facilitate mite locomotion over the leaf.

TABLE 3. Characteristics of subsidiary types categorized in the CW life type.

Subtype Item	CW-p	CW-r	CW-u	CW-b	CW-a
1. Host plant type ¹	A	A & D	C, D & E	B	B
2. Leaf side inhabited	Under	Under	Under	Under	Under
3. Structure of web ²	IC	IC	IC	CS	CS
4. Density of web ³	+	+	+	++	++
5. Place for placing eggs	LS along ribs under IC	LS under IC	On threads of IC ⁵	On threads of CS ⁵	Always on threads of CS
6. Egg cover	—	—	— ⁶	—	—
7. Site for quiescence	LS along ribs under IC	LS under IC	On threads of IC ⁵	LS under CS	Always on threads of CS
8. Preferred site for feeding & walking	On, in & under IC	On, in & under IC	On, in & under IC	On, in & under CS	On, in & under CS
9. Spinning during walking ⁴	+	+	+	+	+
10. Site for defecation	LS under IC	On threads of IC ⁵	On threads of IC ⁵	LS under CS	LS under CS

Italicized words are as follows ; LS, leaf surface ; IC, irregularly complicated web ; CS, complicated stratified web.

1. See Table 1.
- 2, 3 and 4. The same as Table 2 respectively.
5. This tendency especially appears under high population density.
6. In *Tetranychus viennensis*, high dense egg cover is sometimes observed.

2) Subtype CW-r may be directly derived from CW-p. Though the complicated web in CW-p only serves as footing for active mites, that in CW-r is used for sites on which to deposit their feces (Fig. 2, Table 3). Four species, *Eotetranychus celtis* Ehara on *Celtis sinensis* Pers., *Eotetranychus smithi* Pritchard et Baker on *Millettia japonica* (Sieb. et Zucc.), *Eotetranychus tiliarium* (Hermann) on hairy leaves of *Alnus hirsuta* Turcz. and *Oligonychus rubicundus* Ehara on perennial grasses, *Miscanthus sinensis* Anderss belong to this subtype. The placement of feces on the threads may be related to a possible func-

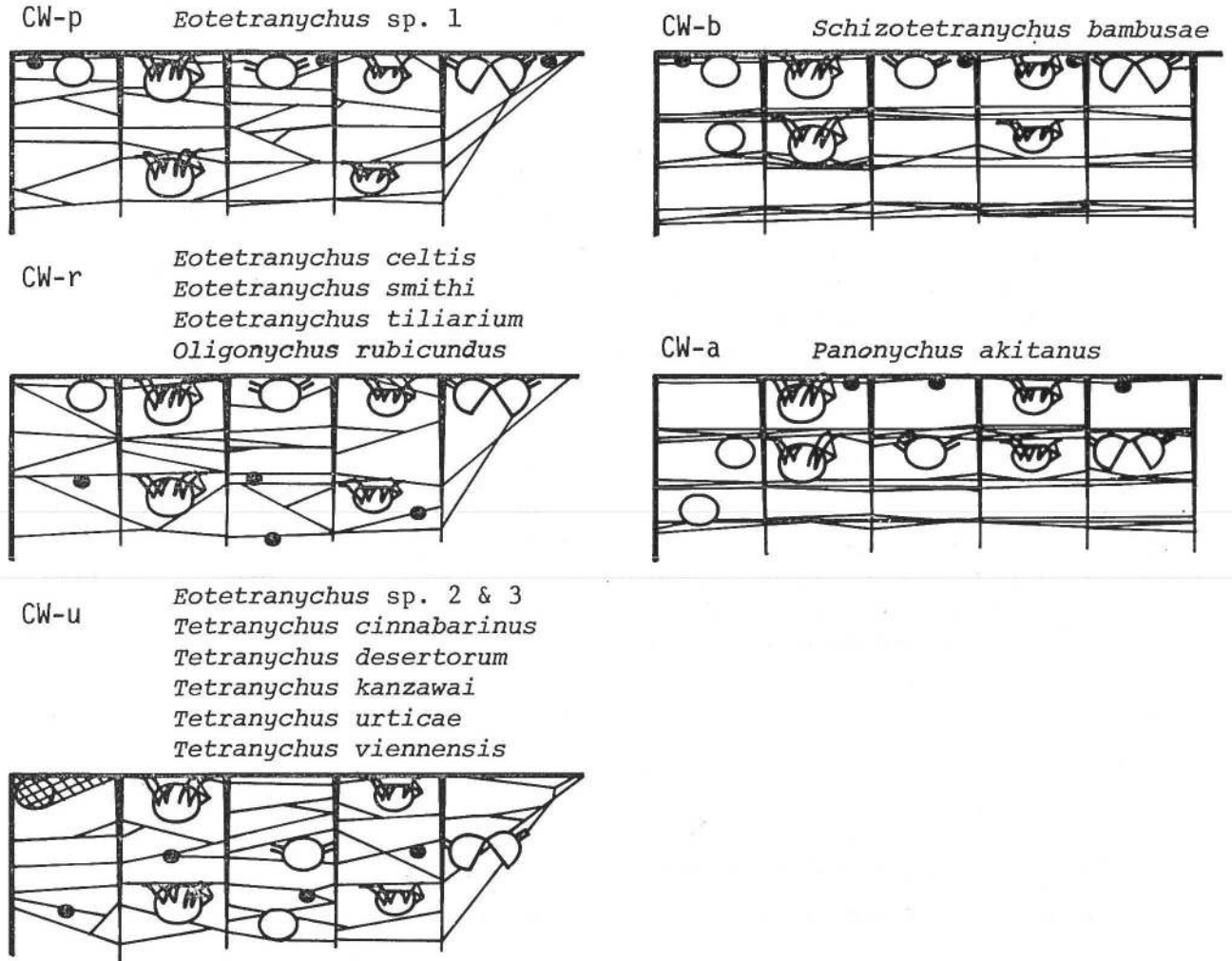


FIG. 2. Schematic expression of subsidiary types categorized in the CW life type. Symbols in this figure as in Fig. 1.

tion of the web, i.e. to prevent the surface inhabited from biological conditioning through the accumulation of feces. The other functions of the web and threads are the same as in CW-p. CW-r seems to be more complicated than CW-p, because of the additional function concerning the web.

3) In the CW-u subtype, the mites construct a highly complicated and irregular web on the leaf surface. In addition to this, a few species, such as *Tetranychus viennensis* Zacher, sometimes weave an egg cover. When the population density becomes high, numerous fecal pellets, egg and

cast skins accumulate on the complicated web threads. These habits, especially depositing feces on the threads, have drawn some workers' attention. HAZAN *et al.* (1973) developed a method for quantitative evaluation of the web through these habits. This subtype appeared in the two-spotted spider mite which is known as the most destructive pest of many crops, and it is common in the genus *Tetranychus* (Fig. 2). Two species (*Eotetranychus* sp. 2 and sp. 3) other than *Tetranychus* also belong to this subtype. Here it is obvious that the web serves to prevent the habitat and food from being dirtied or biologically

conditioned, because these habits conspicuously appear under conditions of high population density. And CW-u subtype is also thought to have several functions which were noted in regard to CW-r.

4) The subtype CW-b as well as CW-a are believed to be somewhat different from CW-p and CW-u. For the time being they were categorized within the CW life type. The mites of CW-b construct a dense web which appears stratiform rather than complicated. *Schizotetranychus bambusae* Reck on bamboo, *Phyllostachys nigra* (Lodiges), falls into this subtype. The eggs are usually oviposited on the leaf surface under the web (Fig. 2, Table 3), although some are laid on the web when the population increases. The threads are extremely thin, and the mites usually translocate between the web layers. EHARA (1973) stated that this species lives selectively on bamboo leaf surfaces, near the stem. This habitat preference may relate to the condition of the surface on which many short hairs grow, as these possibly facilitate web construction by the mites. The web of CW-p seems to serve as footing for translocation, and as a defence mechanism against predators.

5) *Panonychus akitanus* Ehara, living on sasa bamboo, represents the CW-a subtype. The web structure of CW-a is approximately the same as that of CW-b. The mites lay all their eggs on the web, and quiescent stages are found attached there (Fig. 2, Table 3). These habits remind us of LW-s, in which the mites lay all their eggs on the tip of leaf hairs and the quiescent stages are also found there. These habits were always observed under low population density. Hence it is thought that they may be related to protection from predators. The mites of this subtype can easily walk between web layers. It is apparent that the web functions to facilitate locomotion, also serving as footing. CW-a is considered to be more advanced than CW-b.

The complicated web is believed to be a consequence of thread accumulation produced by the mites while walking. Therefore, it is reasonable to regard the CW life type as more complex than LW. In the CW, the weaving behaviour which

results in a particular web structure was rarely observed.

Life type WN

Weaving behaviour predominates in this life type. Though many of the species of this type retain the habit of spinning while walking (dragging behaviour), in highly specialized species it is completely suppressed.

1) The simplest one is WN-u (Fig. 3, Table 4). Superficially this subtype resembles subtype CW-p, but it differs from it in that the mites of this subtype always feed and walk under the webs. WN-u is common in *Oligonychus ununguis* (Jacobi) on chestnut, *Eotetranychus uncatus* Garman on *Betula platyphylla* Sukatchev, *Eotetranychus querci* Reeves on *Tilia japonica* (Miq.)

TABLE 4. Characteristics of subsidiary types categorized in the WN life type.

Subtype Item	WN-u	WN-t	WN-s	WN-c	WN-r
1. Host plant type ¹	A (& coniferous)	A & C	A & C	B	B
2. Leaf side inhabited	Under-Upper	Under	Under	Under	Under
3. Structure of web ²	Irregular NW	One layer NW	One layer NW	One layer NW	Individual NW
4. Density of web ³	+	++	++	+++	+
5. Place for placing eggs	LS under NW	LS inner edge of NW ⁵	LS under NW	LS under NW	LS among leaf hairs (in NW)
6. Egg cover	Dense web, guy ropes	Dense web	Dense web	Sparse web ⁵	Dense web ⁵
7. Site for quiescence	LS under NW	LS under NW	LS under NW	LS under NW	LS among leaf hairs ⁵
8. Preferred site for feeding & walking	Only under NW	Only under NW	Only under NW	Only under NW	Feeding in WN, walking overall LS
9. Spinning during walking ⁴	+	+	±	—	+
10. Site for defecation	LS under NW	Only inner edge of NW ⁵	On threads of NW outside of nest	LS outside of NW ⁵	Overall LS

Italicized words are as follows; LS, leaf surface; NW, nest web.

1. See Table 1.

2, 3 and 4. The same as Table 2 respectively.

5. See text and Fig. 3.

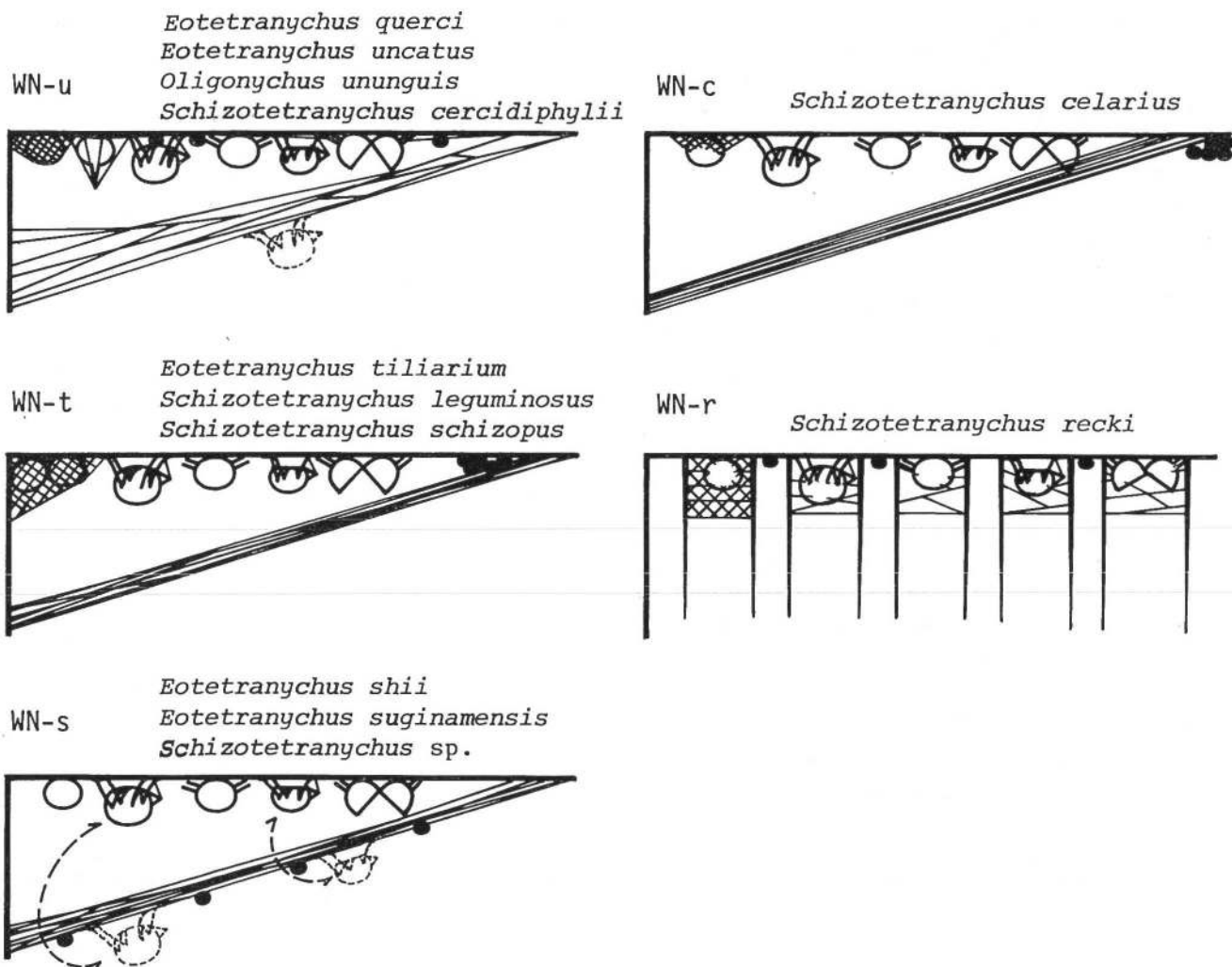


FIG. 3. Schematic expression of subsidiary types categorized in the WN life type. Symbols in this figure as in Fig. 1.

and *Schizotetranychus cercidiphyllii* Ehara on *Cercidiphyllum japonicum* Sieb. et Zucc. SAITÔ (1979 b) reported how *O. ununguis* comes to live under its webs. The report said ; " The females of *O. ununguis* initially walked over all the leaf surface after immigration. The mites spun threads while walking, and then the threads accumulated on the leaf surface. After a while the threads, which were produced over the leaf depression, accumulated and become a feature of woven roof. Once the web above the leaf depression was constructed, the mites entered the nest-like web and began feeding and resting. " This process of web construction appears to be similar

to the CW life type. It differs from the latter because mite behaviour in WN-u on the webless leaf and under the webs is quite different. This suggests that the WN-u subtype is actually in the process of changing from CW to WN. In *E. uncatus*, *E. querci* and *S. cercidiphyllii*, the webs may be recognized better as distinct nest webs. Egg guy ropes sometimes appear in *O. ununguis*, while egg cover webs appear in the other three species. The web of WN-u serves to shelter the mites from adverse climatic factors and from predators. The functions of threads spun while walking are the same as in the CW life type. In *O. ununguis* these threads, which usually serve as

life lines, change their function when the population density becomes high and resource deteriorates, at which time they become ballooning threads for adult females (WANIBUCHI and SAITÔ, 1983).

2) Mites of WN-t subtype are characterized by their habit of depositing feces near the margin of their web nest. There are three species of this subtype, *Eotetranychus tiliarium* on *Alnus japonica* Steud., *Schizotetranychus leguminosus* Ehara on *Wisteria sinensis* Sweet, and *Schizotetranychus schizopus* (Zacher) on willow, *Salix subfragilis* Anders. In this subtype, the mites seldom move out of the nest web, feeding and ovipositing only under this nest. Consequently the injury caused by these mites is seen as large spots along the leaves' midribs, where the mites prefer to construct webs. Egg covers were commonly observed in these species. The web of WN-t is comparatively dense and is believed to serve as shelter against bad weather conditions, predation and dust. The role of the egg cover is not known. The habit of depositing feces near the margin of the nest web seems an adaptation to prevent fouling of the infestation site.

3) The subtype WN-s is characterized by the mites' habit of depositing feces on their nest web threads (Table 4, Fig. 3). The mites usually live under a very densely woven roof, but they come out of their nest for the purpose of defecating on the roof. Three species, namely *Eotetranychus shii* Ehara on *Castanopsis sieboldii* (Makino), *Schizotetranychus* sp. on *Quercus glauca* Thunb., and *E. suginamensis* on mulberry, *Morus bombycis* Koidz. belong to this subtype. The web has the same functions as in WN-t, and in addition, the threads serve as the surface on which to deposit feces. This habit probably relates to preventing the rather limited resource from becoming dirtied, and possibly also repels predators. Furthermore there is the possibility that fecal pellets may function as « anchors » in stabilizing webbing (GERSON, 1979). The mites in WN-s

have somewhat flattened bodies as an apparent adaptation to their life type.

4) The most specialized life subtype of the Tetranychinae can be seen in WN-c (Fig. 3, Table 4). Here, an extremely densely woven roof (nest) is constructed by the mites over the depression on the leaf lower surface. Spinning while walking is completely suppressed in this subtype and weaving is restricted to construction of nest and egg covers. One or two sites (along the " gutter " over which the woven roof is constructed) outside and near the woven nest are used for defecation. All individuals living together in the same nest always deposit their feces in these sites. At present *Schizotetranychus celarius* (Banks) on sasa bamboo and bamboo is the sole representative of this subtype known from Japan. We have found some variation in nest size, presumably in connection with natural enemies² (SAITÔ and TAKAHASHI, 1980). The woven roof (web nest) appears to protect the mites against their predators. The peculiar excretion habit may be related to preserving the resource from fecal foulness and/or to repelling predators (GERSON, personal communication). WN-c is undoubtedly more complex than WN-s, t and u.

5) *Schizotetranychus recki* Ehara on sasa bamboo is of another curious life type, WN-r (Fig. 3, Table 4). It is characterized by constructing cells by and for individual mites. A larva, a nymph or an adult constructs a small nest web around three or four leaf hairs when it feeds or rests. The egg is invariably covered with a highly dense web like a curtain, woven by its mother. The webs of the other stages are loosely constructed in comparison with this egg cover. The webs constructed by this species are qualitatively different from those spun by the other subtypes. For the present, this subtype is categorized within the WN life type, but its position there is not certain. WN-r mites were not able to infest hairless leaf surfaces because of their special webbing habits (Table 4). The injury spot of this species is

2. In *S. celarius* there are, at least, three different populations in nest size which correlates with the length of dorsal setae (SAITÔ and TAKAHASHI, 1980). Small nest constructed by short dorsal seta form was invaded by *Agistemus* sp. but not by *Typhlodromus bambusae* Ehara, while large nest by long seta form was invaded by *T. bambusae* (TAKAHASHI, unpublished data).

rather small as compared with those caused by mites of the other WN subtypes, but larger than those by mites belonging to the LW or CW life types. Mites of WN-r spun threads while walking. Their individual webs may serve to protect them, while inside, against predators, as well as against adverse climatic conditions. The spinning threads function as life lines when the mite walks over the leaf.

Life type WN appears to be qualitatively different from CW, but it is uncertain whether it is more derivative than CW. Both WN and CW life types appear to be derived from the LW life type, and seem to have developed in a parallel way in the Tetranychinae.

We have classified spider mite life types into three main types, and these into fourteen subtypes. All subtypes and patterns of spinning behaviour related to them are summarized in

Fig. 4. In this figure, spinning behaviour of tetranychids may be divided into two basic categories, weaving and dragging. Weaving results generally in three forms of web structures. Dragging is basically different from weaving, because the threads of the former behaviour function themselves as life lines or ballooning threads, while the threads of the latter are only material to construct certain web structures. The latter behaviour links up certain functions when the web structure is completed (Fig. 4). Sometimes the dragging behaviour also results in webs which appear in CW life type. The relationships between spinning behaviour, web structures, use and supposed functions are also shown in this schema. Four forms are thus distinguishable in the web structures, namely, nest web, complicated web (including both irregularly complicated web and complicatedly stratified web), egg cover and guy

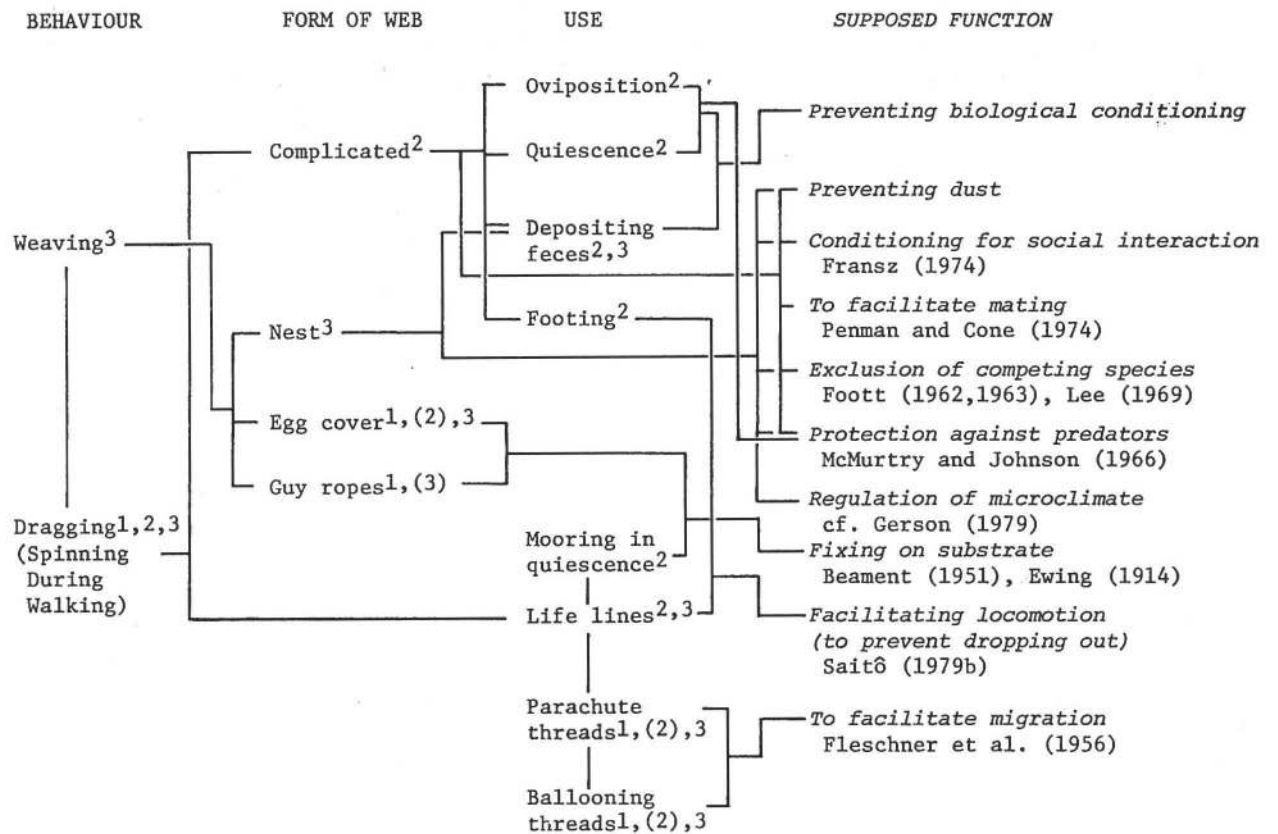


FIG. 4. Spinning behaviour and web structures occurring in the Tetranychinae, and their supposed functions. 1, Mainly appears in LW life type; 2, in CW; 3, in WN.

ropes. How tetranychid mites use these threads and webs is shown in the third column of Fig. 4. Nest web and complicated web threads occasionally serve for placing feces. Complicated web threads serve for oviposition (HAZAN *et al.*, 1974) as well as for quiescence. Spun threads are often useful for mooring of quiescent stages (EWING, 1914), and also life lines when the mites walk on the leaf lower surface (SAITÔ, 1977 *b*). When overpopulation and consequent leaf deterioration cause the mites to migrate, the life line threads are used by adult females as ballooning threads in some species having the LW and WN life types (FLESCNER *et al.*, 1956).

The functions of various threads and webs as postulated by the respective authors are shown in the last column of Fig. 4. Specific functions may be different in their importance. Three functions are thought to be the most important in the lives of tetranychids belonging to three life types: protection against predators in WN, prevention of biological conditioning due to the accumulation of fecal pellets and cast skins in CW, and facilitation of locomotion (prevention of dropping off leaves) in LW, respectively. Somewhat less important functions, such as regulation of microclimate, attaching bodies to the leaf substrate and facilitation of migration should also be taken into consideration.

2. Significance and problems in the classification of life type.

As noted, it is easy to postulate many functions concerning the respective life types classified in the present study, but good evidence that these functions are actually related to the evolution of individual species is rather scarce. Thus it was to be expected that there are many discrepancies in the interpretation of life type significance among various authors (cf. GERSON, 1979). Although many observations concerning life types were mentioned here, actually they are only rather fragmentarily described in many reports on spider mite biology. The reason for the present study was the lack, and therefore the necessity, of describing the life pattern in various spider mite spe-

cies in a uniform way. If we want to understand the characteristics of spider mite life, knowledge of their life patterns and interspecific comparisons are necessary. The life type is useful as a criterion for identifying spider mite species, as mentioned by REEVES (1963). In addition, the meaning of morphological characters used as important criteria in tetranychid systematics may become more clear through studies on life type peculiarities (SAITÔ and TAKAHASHI, 1980). These reinforce the usefulness of recognizing life types.

Observing and ascertaining life type includes some difficulties. For instance, the subtype of *E. tiliarium* on the glabrous leaves of *Alnus japonica* was categorized in WN-t, while that on the hirsute leaves of *A. hirsuta* in CW-r. The fact that mites of the same species infesting leaves of different plant species show different life types probably indicates that the life type (and also the subtype) of certain species is not always fixed, but may depend on microhabitat features. This phenomenon, while important for studying the real function of the mite's life type, simultaneously suggests the need of comparative investigations on various host plants.

3. Life type and phylogenesis.

HELLE *et al.* (1970) stated that the production of web structure was an important evolutionary step within the Tetranychidae. GUTIERREZ *et al.* (1971) used web structure as a subsidiary criterion to arrange the phylogeny of Tetranychidae, while they based most of their conclusions on cytogenetical evidence. It is thought that adaptive radiation in Tetranychinae closely relates to evolution of webbing habit apart from another subfamily Briobiinae which has no silk production. Therefore the life type appears to be useful to arrange the phylogeny of Tetranychinae.

In the present study, though the life type was characterized through various behavioural characteristics including the spinning behaviour, most of the life type classification is based on web patterns and use of silk threads. Life type may thus also reflect the phylogeny of tetranychid mites.

TABLE 5. Life types appeared in various genera of Tetranychinae.

Genus ¹	Life type	LW					CW					WN				
	Subtype	f	j	c	s	r	u	b	a	u	t	s	c	r		
<i>Eurytetranychus</i>				*												
<i>Panonychus</i>				*							*					
<i>Eotetranychus</i>							*	*	*	*	*	*	*	*		
<i>Schizotetranychus</i>							*			*	*	*	*	*		
<i>Yezonychus</i>				*												
<i>Aponychus</i>			*	*												
<i>Oligonychus</i>							*						*			
<i>Tetranychus</i>							*									

1. Genera are arranged according to the phylogeny in GUTIERREZ *et al.* (1971). The tops respective columns appear to be most ancestral genera of all.

2. With two pairs of para-anal setae.

3. With one pair of para-anal setae.

Table 5 shows life types which were recognized in each genus, the arrangement of genera in the two columns basically being according to GUTIERREZ *et al.* (1971). In the more ancestral forms, like *Eurytetranychus*, *Aponychus* and *Panonychus* (excepting the subgenus *Sasanychus*), only one or two simple subtypes were recognized. On the other hand, there was only a single subtype (CW-u) in *Tetranychus* which appears to be the most advanced genus according to GUTIERREZ *et al.* (1971). Much variation in subtypes was seen in *Eotetranychus* and *Schizotetranychus*. The trend that the more primitive genus has simpler types and the more advanced one more complex types, as shown in Table 5, seems to agree with the proposition of GUTIERREZ *et al.* (1971). But we should try to understand why there are many diversities in the life types of *Eotetranychus* and *Schizotetranychus*, and only a single one in *Tetranychus*. As mentioned, species of *Eotetranychus* and *Schizotetranychus* infest many kinds of deciduous and evergreen trees, each species of these two genera appearing to be monophagous. Therefore, it is postulated that these diversities in life types correspond to the specialization (or adaptation) of the various mite species to their specific host plants.

On the other hand, the most advanced genus, *Tetranychus*, does not shown any diversities in its

life type. The host plants of mite in this genus appear to be mainly herbacious (SAITÔ, 1979 *a*) in Japan (except *T. viennensis*). They have an extremely wide range of host plants and are very polyphagous. This food habit does not lead the species to specialize their life pattern on certain host plants. Their CW-u life type is probably related to their effective use of time-limited food resources (such as annual plants). It is postulated that the life type CW-u, which prevents biological host conditioning, also constitutes a case of successful adaptation to unstable habitats, i.e. annual plants. MITCHELL (1973) observed the same situation in regard to *T. cinnabarinus*, without, however, any comparative data. Life type uniformity in *Tetranychus* probably corresponds to its *r*-selected mode of life (SAITÔ, 1979 *a*).

It is quite difficult to decide whether *Eotetranychus* or *Schizotetranychus* is more advanced in an evolutionary sense upon comparing the life types of these two genera. From Table 5, it may be noted that the CW type tends to be common in *Eotetranychus*, the WN type in *Schizotetranychus*, but much overlap in subtype is seen in species belonging to these genera. Therefore it can only be stated that differences in the subtypes of the respective genera exist, possibly in response to different processes of evolution.

It goes without saying that the species discussed in the present study are only a small part of all Tetranychidae, and that many further detailed studies are necessary in order to understand these relationships.

4. Life type and host plant.

As noted in the previous section, the relationships between life type and host plant (Fig. 5) are of importance. To some extent, it is possible to rank the various subtypes according to their complexity, notwithstanding the qualitative and arbitrary nature of the criteria. The abscissa in Fig. 5 shows the host plants arranged to reflect the level of stability (as habitats of spider mites), and the ordinate axis indicates the level of subtype complexity. Although the LW life type is

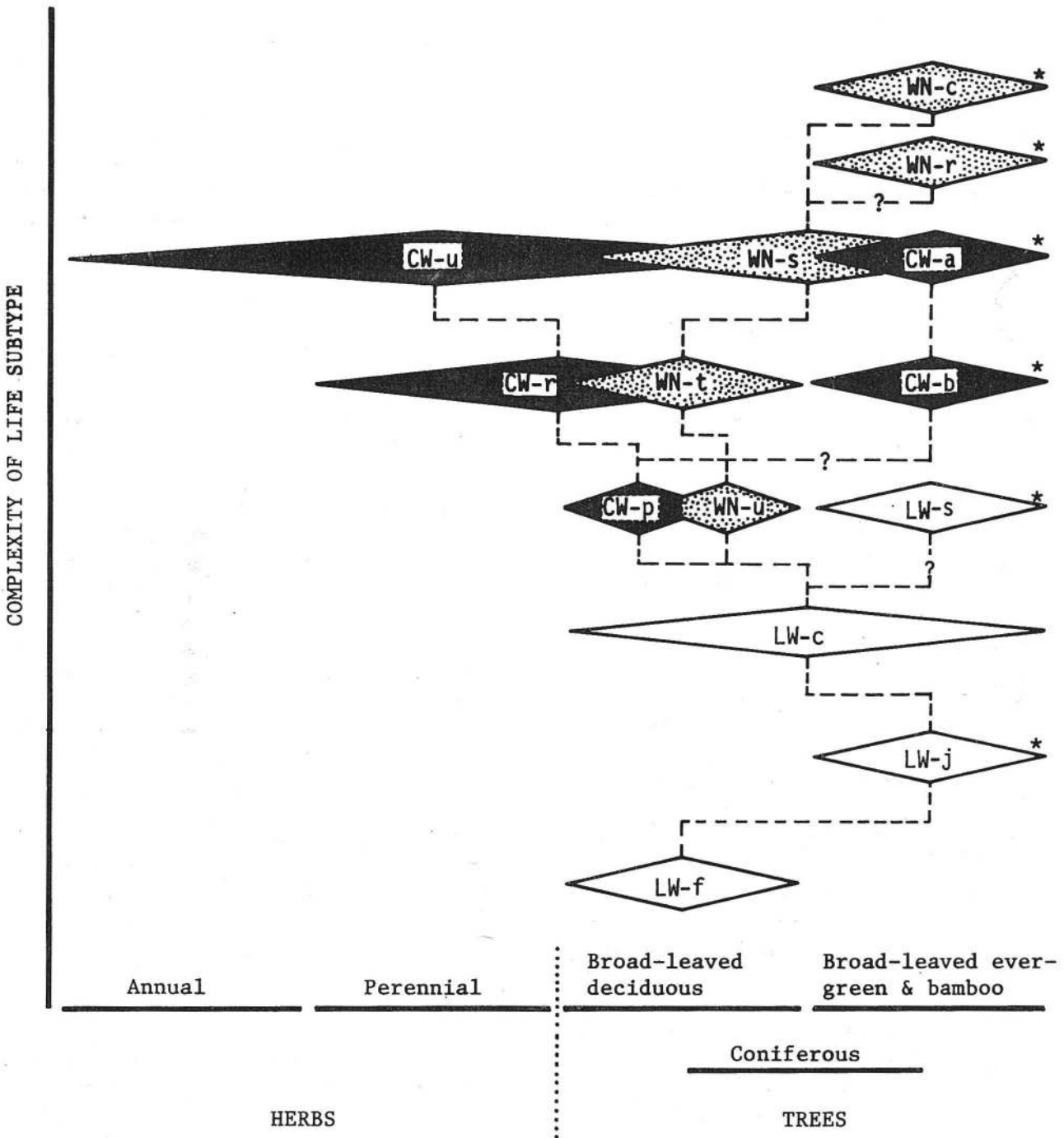


FIG. 5. Relationship between category of host plant and life subtype (web) complexity. Broken line indicates supposed connection. *, common on bamboo plant.

undoubtedly simpler than CW and WN, it is impossible to rank the latter types according to their level of complexity. Therefore it is assumed that they developed in a parallel manner from the LW type. Distance in ordinate between two subtypes is assumed to be uniform throughout. Broken lines show the postulated connections between various development degrees of these subtypes.

Mites of LW type commonly live on deciduous and evergreen trees including bamboo (Fig. 5). The most ancestral subtype in Japan, LW-f, is found on broad-leaved deciduous trees. The subtypes CW-p and WN-u are also found on such plants. As a close resemblance between these two subtypes exists, it is not unreasonable to assume that CW-p and WN-u are the basic types among the CW and WN subtypes, respectively, and that they are derived from the LW life type. The progress from CW-p to CW-u seems to correspond to the change of host plant from woody deciduous to herbaceous perennials and to annuals. On the other hand, so far as the WN type is concerned, it only develops on stable hosts such as evergreens and bamboos.

On perennial herbs, mites of the CW-r as well as the CW-u subtypes are found. There are various life types on evergreen trees, where mites of the CW-p, WN-u and WN-t types, which weave moderately complex web structures can be found. The life types of mites inhabiting both deciduous and evergreen trees are apparently diverse. The spider mites inhabiting bamboo show a highly diverse degree of life type development. Species of different life types live syntopically on one and the same leaf of the bamboo plant. On the other hand, only mites of the CW-u subtype inhabit annual plants. Could it be that only unstable habitats permit the survival of the CW-u types, while stable habitats allow the survival of other mites having much diversity of subtypes? More data are needed to decide whether the division of the host plant characteristics, as applied in the present study, is sufficient to interpret the relationships between life type and host plant.

SAITÔ (1979 *a*) and SAITÔ and UENO (1979) pointed out that the life history characteristics of

spider mites are also correlated with their life types. The comparative studies of life histories and life types of many species are thus believed to be of importance so as to clarify the process of adaptation in spider mites.

No theory is yet available for understanding the process of adaptation in the Tetranychinae. In this study I tried to summarize information hitherto obtained concerning life types of this subfamily. The data are still incomplete, and further investigations concerning life types are therefore necessary.

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