Structural comparison of tropical montane rain forests along latitudinal and altitudinal gradients in south and east Asia

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Abstract

Geographical patterns of altitudinal zonation, floristic composition, and structural features of tropical montane rain forests were examined along latitudinal gradients in south and east Asia. On equatorial mountains, the tropical montane rain forests occur above 1000 m. Toward middle latitudes, they come farther down and reach sea level at c. 35° N. Thus, the forests are equivalent to the subtropical rain forests of the latitudinal, horizontal zonation series. They exhibit gradual changes in floristic composition and structure along both altitudinal and latitudinal gradients. On equatorial mountains, they are divided into three types, i.e. tropical lower montane, upper montane, and subalpine forests. The three tree regeneration types, having emergent, sporadic and inverse-J type stem-diameter class frequency distributions, coexist in the lower montane forests, but the upper and subalpine forests display only the inverse-J type species with a few species of the sporadic type. Toward the northern latitudinal limit, the distinction between the three tropical montane forest zones in equatorial mountains becomes less clear. This can be explained by temperature conditions: on equatorial mountains, a temperature sum of 85 °C · months which controls the upper limit of the lower montane forests, and a coldest month mean temperature of −1 °C which controls the evergreen broad-leaved trees, appear at c. 2500 and c. 4000 m respectively. The altitudinal range between 2500 m and 3800 m, which is the upper forest limit, is covered by upper montane and subalpine forests. On the other hand, at the latitudinal northern limit, the tropical upper montane and subalpine forests cannot exist because the above mentioned two temperature conditions occur at nearly the same point. Thus, at the northern latitudinal limit of the tropical montane forests, the three zones of equatorial mountains amalgamate into a single subtropical lowland forest community. This is due to the seasonal temperature climate in middle latitudes in, e.g., central Japan and central China.

Introduction

The classical scheme of the latitudinal pattern of mountain vegetation zonation in humid east Asia by von Wissman (1938) and Troll (1948) has been

revised recently (Ohsawa 1990; Ohsawa in press). According to the revision, the mountain vegetation zonation has been divided into two types, a tropical and a temperate zonation type, below and above 20–30° N.

The classification and nomenclature of tropical mountain forests have been applied on an ad hoc basis for a long time (Robbins 1968). However, the equatorial mountain zonation can generally be divided into three types: tropical lowland, tropical lower montane, and tropical upper montane (Whitmore 1975; Grubb 1977; Ohsawa in press). Although van Steenis (1972) adopted a different system to divide tropical mountain vegetation into three zones, i.e. the tropical zone, the montane zone, and the subalpine zone, this system can be correlated with the above-mentioned system; it is a matter of nomenclature except for van Steenis's subalpine zone, which might better be divided into an upper montane and a subalpine zone.

The tropical zonation below 20° N is characterized by the prevalence of evergreen broad-leaved forests throughout the ranges. The tropical lower montane forests occupy the southernmost part of an extensive evergreen broad-leaved (notophyllous) forest formation mostly dominated by Fagaceae, Theaceae, Lauraceae, etc. The formation is specific to the humid mountainous terrain of south and east Asia. In horizontal, latitudinal series, this is the next formation north of the tropical lowland rain forest zone, and it occupies the northern margin of tropical evergreen forest (von Wissman 1948; Richards 1952; Wang 1961; Hou 1983; Song 1988; Ohsawa 1990). On temperate mountains, tropical montane forests are replaced by deciduous forests at their upper or northern limit instead of alpine grasslands as in the case of tropical mountains.

It appears, then, that tropical montane evergreen forests exhibit gradual changes in two ways. On the one hand, from lower montane, upper montane to subalpine forests along altitudinal gradients on equatorial mountains, on the other, from tropical montane forests to subtropical lowland forests at sea level along latitudinal and altitudinal gradients.

The object of the present study is to compare the two differentiation patterns of the tropical montane evergreen forests along altitudinal and latitudinal gradients in relation to climatic conditions.

Materials and methods

Quantitative vegetational data for south and east Asian mountain forests are based on Yamada (1977) for Mt. Pangrango, Java (3019 m; 6° 46′ S; 106° 56′ E), Ohsawa et al. (1985) for Mt. Kerinci, Sumatra (3800 m; 1° 43′ S, 101° 15′ E), Corner (1978) for Mt. Kinabalu, Borneo (4101 m; 6° 05′ N, 116° 30′ E), Ohsawa (1987) for the Bhutan Himalaya (c. 27–28° N), and Yoshioka (1963) for central Japan (c. 35–37° N).

Temperature conditions which control the distribution of various forest types are based on the same regional climatic data as used by Ohsawa (1990) with some additional data from the literature mentioned above. In addition to the monthly mean temperatures, the temperature sum (the sum of monthly mean temperatures above 5 °C) was used (Kira 1948, 1977; Tuhkanen 1980, Ohsawa 1990). The temperature sum indicates the available heat energy during summer.

Results and discussion

Altitudinal zonation in equatorial mountains

Figure 1 shows the floristic composition of the tropical montane rain forests above 1750 m of Mt. Kerinci, Sumatra, and above 1600 m of Mt. Pangrango, Java, in the form of abundance grid diagrams. Three floristic groups can be distinguished along altitudinal gradients. On Mt. Kerinci, the forests from 1700 to 2500 m, corresponding to the lower montane zone, are mainly composed of Myrtaceae, Fagaceae, Theaceae, Moraceae, and some other dominants having narrower distribution ranges such as Elaeocarpaceae, Hamamelidaceae, Flacourtiaceae, and
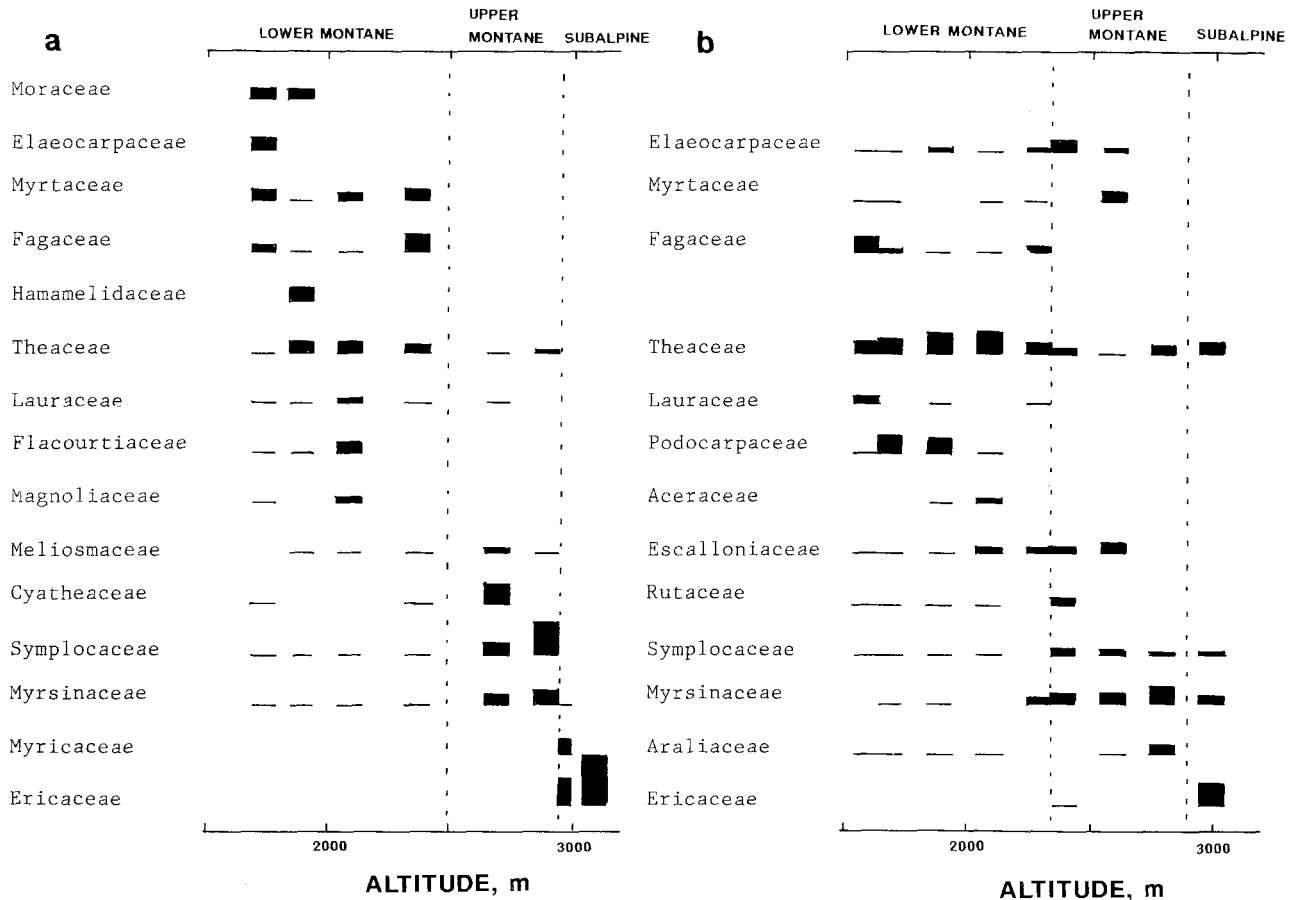
Mt. Kerinci, Sumatra Mt. Pangrango, Java

Fig. 1. Abundance grid diagrams showing altitudinal distributions of family composition on Mt. Kerinci, Sumatra (a, redrawn based on Ohsawa *et al.* 1985) and Mt. Pangrango (b, redrawn based on Yamada 1977).

Magnoliaceae. The forests from 2500 to 2900 m, corresponding to the upper montane zone, are dominated exclusively by trees of Symplocaceae and Myrsinaceae (Cyatheaceae, a tree fern, is also abundant in basal area value, however it is not comparable to that of other woody trees). Above this follows a narrow belt composed of Ericaceae and Myricaceae. This corresponds to the tropical subalpine forest zone. Often these forests are distinguished by the supreme dominance of Ericaceous shrub in the forest limit area (Sleumer 1965). On Mt. Pangrango, the principal pattern is similar to that of Mt. Kerinci, except for minor differences, e.g., Podocarpaceae are more prominent in the lower montane forests and Theaceae and Myrsinaceae in the upper and subalpine forests (Yamada 1977).

The floristic similarity among the altitudinal plots on both Mt. Kerinci and Mt. Pangrango can be examined by cluster analysis (Fig. 2). The percentage of similarity (SI) is calculated as $SI(\%) = 200 \, w/(a + b)$, where w is the common families at plots of comparable altitude and a and b are the families exclusive to either plots. The dendrograms of family composition indicate a clear division between subalpine and montane forests and a further subdivision of the latter into upper and lower montane forests at altitudes between 2370 and 2700 m plots on Mt. Kerinci, and between 2300 and 2400 m plots on Mt. Pangrango
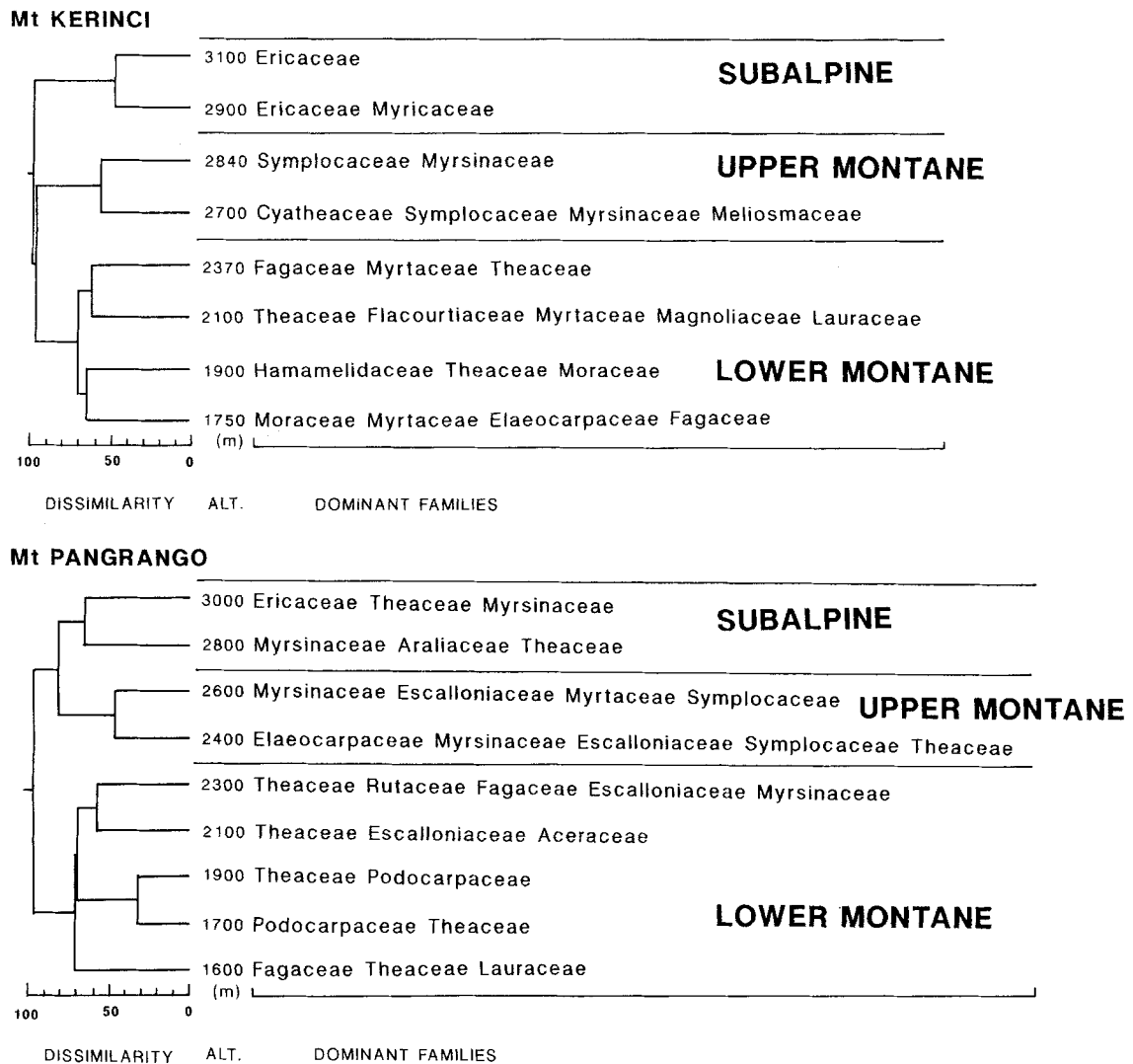
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Mt KERINCI

ALT.	DOMINANT FAMILIES	
3100	Ericaceae	**SUBALPINE**
2900	Ericaceae Myricaceae	
2840	Symplocaceae Myrsinaceae	**UPPER MONTANE**
2700	Cyatheaceae Symplocaceae Myrsinaceae Meliosmaceae	
2370	Fagaceae Myrtaceae Theaceae	
2100	Theaceae Flacourtiaceae Myrtaceae Magnoliaceae Lauraceae	
1900	Hamamelidaceae Theaceae Moraceae	**LOWER MONTANE**
1750	Moraceae Myrtaceae Elaeocarpaceae Fagaceae	

100   50   0

DISSIMILARITY   ALT.   DOMINANT FAMILIES

Mt PANGRANGO

ALT.	DOMINANT FAMILIES	
3000	Ericaceae Theaceae Myrsinaceae	**SUBALPINE**
2800	Myrsinaceae Araliaceae Theaceae	
2600	Myrsinaceae Escalloniaceae Myrtaceae Symplocaceae	**UPPER MONTANE**
2400	Elaeocarpaceae Myrsinaceae Escalloniaceae Symplocaceae Theaceae	
2300	Theaceae Rutaceae Fagaceae Escalloniaceae Myrsinaceae	
2100	Theaceae Escalloniaceae Aceraceae	
1900	Theaceae Podocarpaceae	
1700	Podocarpaceae Theaceae	**LOWER MONTANE**
1600	Fagaceae Theaceae Lauraceae	

100   50   0

DISSIMILARITY   ALT.   DOMINANT FAMILIES

Fig. 2. Dendrograms expressing the floristic similarity of altitudinal plots on Mt. Kerinci and Mt. Pangrango (redrawn from Ohsawa *et al.* 1985 and Yamada 1977) (altitude and dominant families are indicated).

(Fig. 2). In the latter case, upper montane forests are floristically much closer to subalpine forests than are lower montane forests. This leads to the conclusion that the dividing line between the lower and upper montane forests of the two equatorial mountains can be drawn at around 2500 m and that, floristically, the former is represented by Fagaceae and Theaceae and the latter by Symplocaceae and Myrsinaceae.

In tropical mountain zonation, a vicarious distribution was observed for closely related taxa in several zones. For example, many species of the genera *Leptospermum, Eugenia* and *Tristania* of the Myrtaceae are widely distributed from low to high altitudes on Mt. Kinabalu, Borneo (Corner 1978). A similar behavior is exhibited by the Theaceae. On Mt. Kerinci, for example, the lower montane, upper montane and subalpine zones are represented by *Schima, Haemochaeris* (*Gordonia*), and *Eurya*, respectively (Ohsawa *et al.* 1985). Bimodal distribution of Theaceae on both Mt. Kerinci and Mt. Pangrango (Fig. 1) is represented by *Schima wallichii* var. *noronhae* for the lower montane and by *Eurya obovata* var. *leticulata* for the

subalpine forests. On Mt. Kinabalu, *Schima wallichii* is an important component of the lower montane forests, *Ternstroemia lowii* is a component of the upper montane forests (2400–3080 m), and the *Eurya* species show a chain distribution ranging from low to high altitudes, *E. acuminata* at low altitudes, *E. trichocarpa* from 2240 to 2800 m, and *E. obovata* var. *reticulata* from 3080 to 3640 m (Corner 1978). It is worth mentioning that there are two closely related species of *Schima* on Mt. Kinabalu, one being *S. wallichii*, a lower montane zone species, and the other *S. brevifolia* which grows between 1700 and 3080 m (in some literature it is included in *S. wallichii*). These phenomena indicate that the zonation of tropical mountain vegetation here results from replacement of related taxa with changing altitude. This pattern is in tandem with a tendency of impoverishment of floristic diversity through elimination of accessory taxa in the forests at increasingly higher altitudes. This zonation pattern is in strong contrast to that in the temperate mountains in which each zone is composed of different floristic elements having contrasting life-forms (cf. Ohsawa 1990).

Structural comparison of lower montane, upper montane and subalpine forests in equatorial mountains

Figure 3 compares the structural make-up of the tropical lower montane, upper montane, and subalpine forests using the stem-diameter class frequency distributions which reflect regeneration types of trees for all dominant species. There are three tree regeneration types having characteristic stem-diameter class frequency distributions for the dominant species of lower montane forests, namely the emergent type, the sporadic type, and the inverse-J type. The emergent type, represented by *Exbucklandia populnea*, is a species represented by only a few giant specimens in the forest which constitute the emergent layer. A small number of specimens belonging to large diameter classes reflects sporadic and intermittent regeneration within a site, most probably after heavy disturb-

ances. They often act as pioneers at disturbed sites, such as roadsides and landslide areas as well as canopy gaps. *Exbucklandia populnea* is a well-known roadside pioneer in Malaya (Whitmore 1973) and in Bhutan (Ohsawa 1987, 1991). The sporadic type is represented by *Schima wallichii* var. *noronhae*, which is a main canopy component. The trees experience intermittent recruitment as shown by the random stem-diameter class frequency distribution and often become pioneer species of secondary succession after moderate disturbances, such as canopy gaps of a limited size. Pijl (1982) describes the characteristics of the species as somewhere between a nomadic pioneer and a climax species. Most of the sporadic type species can be regarded as a kind of pioneers in the climax forests called 'undifferentiated canopy components' (Ohsawa et al. 1986); they are fugitive members of the climax microsuccession in the sense of Forcier (1975). The inverse-J type species, represented by *Syzygium lineata* and *Eugenia* spp., display two peaks in their stem diameter class frequency distribution, i.e., a small peak in large diameter classes and a large peak in small diameter classes. They are shade tolerant climax trees often making up the canopy layer together with tree species of the sporadic type, the main difference between the two being that the former species have many young individuals in the understory, while the latter do not. These three groups are the principal structural components of the three-storied lower montane forests, and reflect the wide range of regeneration processes of the species maintaining the forests.

Contrastingly, the upper montane and the subalpine forests display only two types of stem-diameter class frequency distributions, i.e., the inverse-J type species such as the *Symplocos robinsonii* var. *latifolia* and *Rapanea papuana*, and the sporadic type species such as *Myrica javanica* and *Cyathea* sp. (Fig. 3). The forest is a two-storied community with regenerating trees and shrubs underneath. The inverse-J type species, *Symplocos* and *Rapanea*, of the upper montane forests are, as far as regeneration is concerned, ecological equivalents of *Syzygium* in the lower
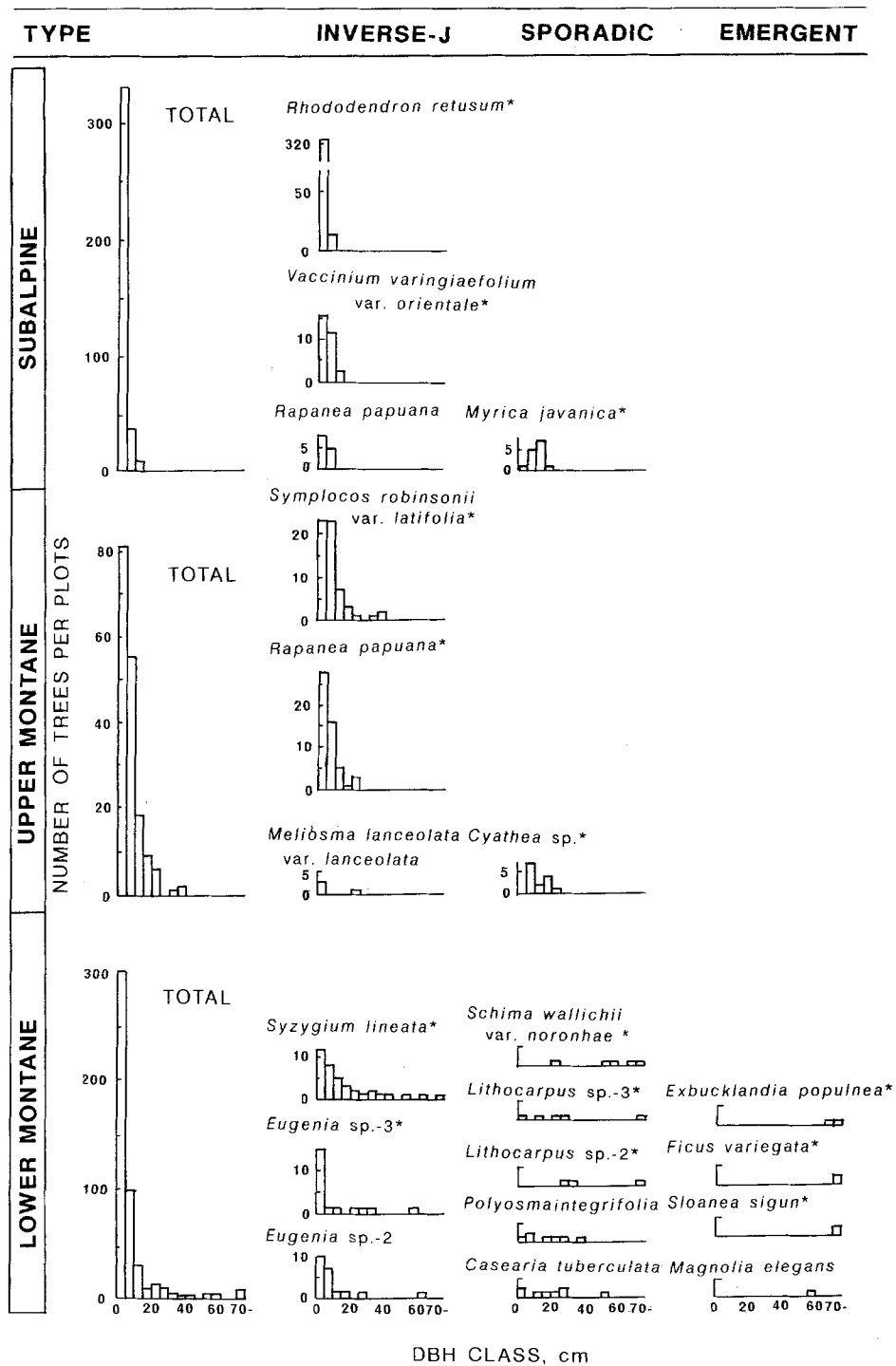
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TYPE INVERSE-J SPORADIC EMERGENT

Fig. 3. Three tree regeneration types as expressed by stem-diameter class frequency distributions for the dominant species in lower montane (1750, 1900, 2100, & 2370 m plots), upper montane (2700 & 2840 m plots), and subalpine (2900 & 3100 m plots) forests on Mt. Kerinci. All the plot data for each zone were recalculated from the dumped data. Dominant species are indicated with an asterisk, and are grouped by column into three tree regeneration types, i.e. the inverse-J type, the sporadic type, and the emergent type (data are based on Ohsawa *et al.* 1985).

montane forests. They have a similar population structure and are highly shade tolerant species. The emergent type is not prominent in the upper montane and subalpine forests.

The sporadic type trees of the upper montane and subalpine forests are composed of pioneer trees, such as *Cyathea* sp. and *Myrica javanica*, which lack younger individuals. In the relatively young subalpine forests on Mt. Kerinci, a young volcano, the sporadic type species are represented by only a single generation.

Thus in the tropical zonation, impoverishment of the floristic and structural features of forests from low to high altitudes corresponds to a gradual process of elimination of the tall tree layers from a community. To begin with, the emergent type species and then most of the sporadic type species are eliminated. Finally only some of the inverse-J type and sporadic type species remain in the upper montane zone.

Brown (1919) has clearly stated that the main difference between the dipterocarp forest below 1000 m and the *Quercus-Neolitsea* forest above on Mt. Maquiling, Philippines, is that the latter lacks the first story of the former, such as *Parashorea* and *Diplodiscus*. A similar phenomenon, namely that the overstory component of the lower zone is eliminated in the higher one, has also been reported for the lower montane and upper montane forest zones on both Mt. Pangrango, Java (Yamada 1976) and Mt. Kerinci, Sumatra (Ohsawa *et al.* 1985). Such features as well as the present results strongly support the notion that the zonation of tropical mountain vegetation is the result of a series of impoverishment processes of the floristic pool from low to higher altitudes.

Latitudinal pattern of subtropical lowland rain forests

The tropical montane forests on equatorial mountains are replaced by subtropical type forests toward the middle latitudes as for instance in the Himalaya and southwestern China. Further north they come down to sea level where tropical lowland rain forests do no longer occur. This hap-

pens around 20–30° N in east Asia. They reach their northern limit at sea level around 35° N in central Japan.

There are two gradual changes in tropical montane forests toward the higher latitudes. One is the disappearance of the upper montane forests where subtropical lowland forests emerge in middle latitudes; the other is the occurrence of sclerophyllous forests of *Quercus semecarpifolia* (Ohsawa 1987, 1991) and *Q. aquifolioides* (Yang 1990) and temperate conifers such as *Abies, Tsuga, Chamaecyparis*, etc. at the upper margin of the tropical montane forests around 2500–3000 m in the mountains of the marginal tropics such as the Himalaya, Taiwan, and Sichuan, China. These two phenomena may each require a separate explanation.

In the present paper the first question regarding the disappearance of the upper montane forests toward middle latitudes will be examined. Figure 4 shows the latitudinal pattern of tropical montane forests and provides possible explanations. Figure 4a indicates the distribution of the temperature sum conditions of 15 °C · months which control the upper forest limit. The figure also shows two temperature factors which control the northern limit of tropical evergreen broad-leaved forests in Japan and its surrounding areas, i.e., the temperature sum of 85 °C · months (Kira 1948, 1977), and the coldest month mean temperature of −1 °C (Ohsawa 1990). In equatorial mountains, these two temperature conditions occur at different altitudes. The 85 °C · months limit occurs at c. 2500 m and this is also the altitude of the upper limit of the lower montane rain forests or the lauro-fagaceous forest (Fig. 4). The −1 °C limit occurs above 4000 m. It has no effect on the forest distribution on equatorial mountains because it occurs far above the altitudinal forest limit (Ohsawa 1990). Accordingly, the mountain slopes between the upper limit of the lower montane forests at 2500 m and the upper forest limit at c. 3600–3800 m on equatorial mountains are covered by upper montane and subalpine evergreen forests. On the other hand, at the northern limit of the subtropical rain forests at middle latitudes, such as in Japan and in cen-
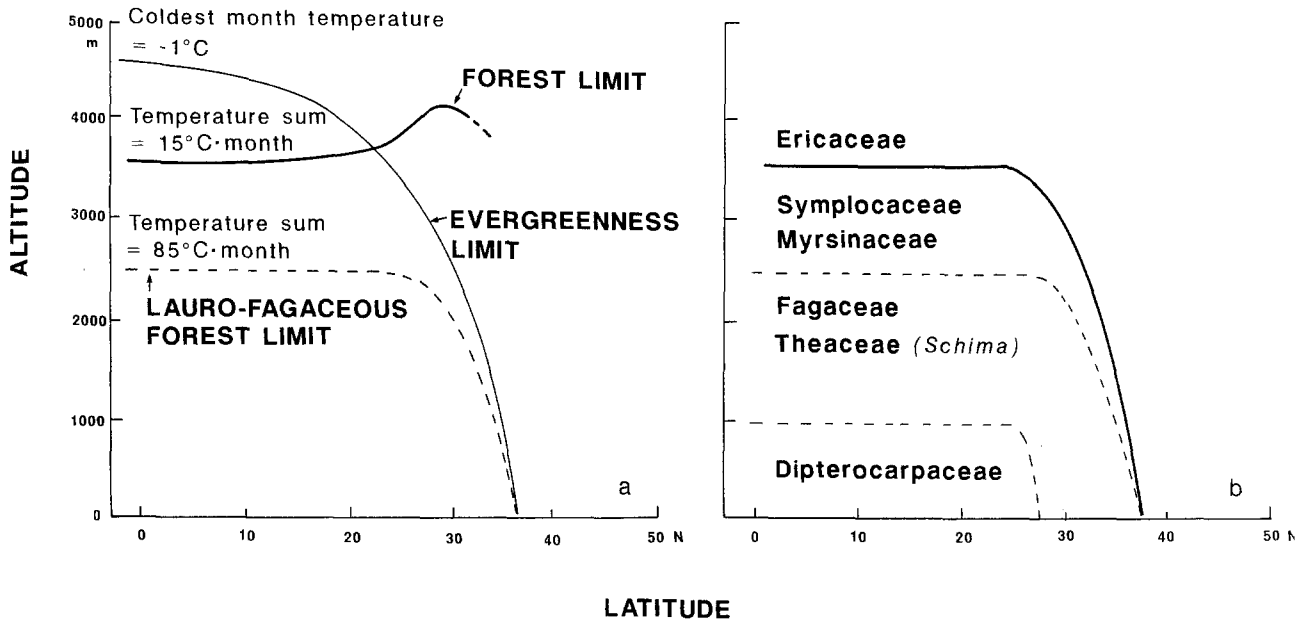
Fig. 4. Zonation pattern of tropical montane rain forests along latitudes. Tropical lowland, tropical lower montane, tropical upper montane, and tropical subalpine zones are indicated (a) together with two temperature parameters, the temperature sum of 85 °C·months, and the coldest month temperature of –1 °C. Both affect the pattern; – (b). The curve of the temperature sum of 15 °C·months is the condition which controls the upper forest limit.

tral China, the temperature sum condition of 85 °C·months and the low temperature conditions of the coldest month mean temperature of –1 °C occur at nearly the same altitudes (Fig. 4). This means that there are no locations within the subtropical lowlands where the temperature conditions are similar to the equatorial upper montane zone, that is, locations where the temperature sum is below 85 °C·months and the coldest month mean temperature is above –1 °C. Accordingly, the conditions for the existence of tropical upper montane forests are not found at the middle latitudes.

This discrepancy is brought about by the seasonality of the temperature regime at middle latitudes. The mean temperature of the coldest month at the point where the temperature sum is 85 °C·months for 226 climatic stations in south and east Asia, based on the same data used in Ohsawa (1990), is shown in Figure 5. In equatorial mountains, this condition of 85 °C·months coincides with a monthly and annual mean temperature of c. 12 °C. This means that it is warm enough for the growth of other evergreen broad-

leaved trees which are limited, however, by a coldest month mean temperature of –1 °C. The coldest month temperature drops toward the northern latitudes and approaches 0 to –1 °C at c. 35–37° N (Fig. 5). This represents the northern limit of subtropical rain forests composed of evergreen broad-leaved trees including lauro-fagaceous trees.

Thus two different temperature limits, i.e., the summer temperature sum and the low winter temperature, occur at different altitudes in tropical mountains due to the non-seasonal climate. At high latitudes, however, the seasonal climate often causes them to coincide. For this reason the tropical upper montane and subalpine forests cannot extend their range further north towards the subtropical latitudinal limit in central Japan. The northern-most lauro-fagaceous forests in east Asia are located near the sea coast in central Japan at 37° N. They are composed of evergreen genera with both tropical lower montane and upper montane elements such as *Castanopsis* and *Quercus* for the former and *Ilex, Eurya*, and *Ardisia* for the latter (Yoshioka 1963). Thus, the
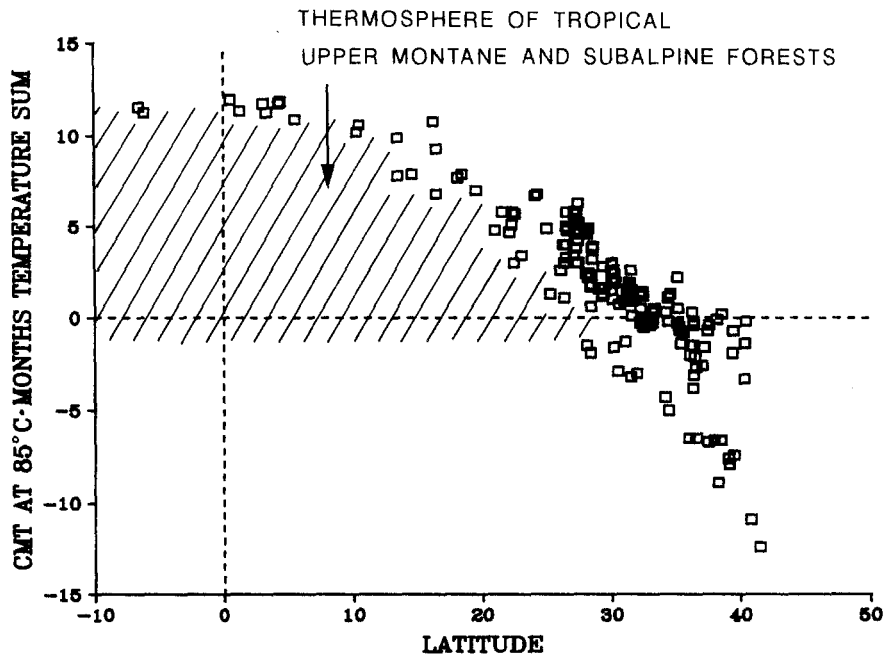
Fig. 5. Thermosphere of tropical upper montane and subalpine forests in south and east Asia, illustrated on a latitudinal pattern of the coldest month mean temperature at locations where the temperature sum is 85 °C·months.

latitudinal subtropical rain forests are floristically equivalent to the tropical lower montane forests with some mixture of tropical upper montane elements.

Conclusion

The tropical montane forests exhibit two differentiation patterns along altitudinal and latitudinal gradients. The altitudinal differentiation is from tropical lower montane, upper montane to subalpine. Each of the three zones has characteristic taxa. This differentiation, however, is a process of impoverishment of the forest structure by elimination of the upper story elements, with elements of the understory becoming dominants in the zone above. This pattern can occur in equatorial mountains because the temperature conditions which determine the upper limit of the lower montane lauro-fagaceous forests (temperature sum of 85 °C·months) and the temperature conditions which limit the evergreen trees of the upper montane forests (a coldest month mean temper-

ature of −1 °C) occur at different altitudes. However, the latitudinal pattern is not the same, because the two temperature conditions occur at nearly the same point at middle latitude lowlands due to seasonality in the climate. Accordingly, the two differentiation patterns of tropical montane forests are due to the different seasonality patterns in temperature, especially the lowering of the coldest month temperature toward high northern latitudes.

Acknowledgement

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