Changes with altitude of stand structure of temperate forests on Mount Norikura, central Japan

Yutaka Miyajima · Koichi Takahashi*

Department of Biology, Faculty of Science, Shinshu University, Matsumoto 390-8621,

Japan

*: corresponding author:

e-mail: koichit@gipac.shinshu-u.ac.jp, tel: 0263.37.2533, fax: 0263.37.2560

Abstract Altitudinal changes in stand structure were studied at 10 sites between 800 m and 2500 m a.s.l. in temperate forests on Mount Norikura (36˚06'N, 137˚33'E, 3026 m a.s.l.) in central Japan. Vegetation of this altitudinal range was roughly classified asa subalpine coniferous forest zone between 1600 m and 2500 m a.s.l.   the timberline. The frequency distribution of trunk height was a L-shaped pattern at 800 m a.s.l. and changed to   flat pattern with increasing altitude up to 2000 m a.s.l. it changed to L-shaped pattern again from 2000 m to 2500 m a.s.l. This altitudinal change frequency distribution of trunk height warelated to the altitudinal change   maximum trunk height. The maximum trunk height did not change with altitude between 800 m and 2000 m a.s.l., but it decreased from 2000 m to 2500 m a.s.l. Mechanical damage of conifer trunks and branches was not observed between 800 m and 2000 m a.s.l. However, the proportion of damaged trees increased from 2000 m to 2500 m a.s.l., suggesting thatsubalpine conifers cannot grow in height near the timberline due to mechanical damage. Therefore, the increase number of small trees from 2000 m a.s.l. to the timberline was to less developed canopy structure, i.e., small trees can grow without shading by canopy trees. This study suggests that the timberline formation.

Keywords mechanical damage · stand structure · timberline · trunk height

Introduction

vailable energy for plant growth, influences forest vegetation. Many researchers have

examined the altitudinal changes in forest vegetation in various forest ecosystems such

as tropical forests, subtropical forests, warm-temperate forests, temperate forests and

boreal forests (Takahashi 1962; Yamada 1977; Ohsawa 1984; Kirkpatrick and Hassall

1985; Kojima 1994; Lieberman et al. 1996; Tang and Ohsawa 1997; Kamijo et al. 2001).

For example, in central Japan,, forest vegetation changes from evergreen broad-leaved

forests at low altitude to deciduous broad-leaved forests at middle altitude, and to

evergreen coniferous forests at high altitude (Yoshino 1978). Takahashi et al. (2003,

2005) showed that theTakahashi et al. (2003, 2005) showed that   growth of *Betula*

ermanii differently respondeded to climatic conditions at its upper and lower

distribution limits in a subalpine forest on Mount Norikura, central Japan. High summer

temperature coupled with less precipitation increases the growth of *Betula ermanii* at its

upper distribution limit (i.e., the timberline) because of cool climate in this high altitude,

while the high temperature coupled with less precipitation decreases the growth at its

lower distribution limit probably because of the increase of drought stress (Takahashi et

al. 2003, 2005). Thus, tree regeneration may be different along altitudinal gradients

even within a same vegetation zone such as subalpine forest zone. However, little

information is available for altitudinal changes in forest regeneration.

The stand structure of forests is thought to reflect regeneration processes. From

the shape of size frequency distribution, we can suggest regeneration patterns.

Unimodal and bimodal distributions suggest a discontinuous regeneration pattern, while

L-shaped distributions suggest a continuous regeneration pattern (Veblen 1986;

Kohyama and Hotta 1990; Masaki et al. 1992). At the individual-tree level, the growth

in trunk height more decreases with increasing altitude, as compared with trunk

diameter (Aiba and Kitayama 1999), partly because strong wind inhibits the growth in height. Thus, a comparison of trunk height-diameter allometry among different altitudes shows the altitudinal changes in the growth traits (e.g., Wang et al. 2006). In addition, recently, some researchers showed that many trees in timberlines suffered severe mechanical damage due to strong wind and heavy snow (Kajimoto et al. 2002, 2004; Seki et al. 2005). Therefore, stand structural characteristics provide useful information to elucidate the altitudinal changes in regeneration. Although a few studies have been made on the altitudinal change in stand structure in tropical forests (e.g., Aiba and Kitayama 1999), little is known in temperate forests. Therefore, this studyinvestigateded the changes in stand structure including the proportion of damaged trees along an altitudinal gradient on Mount Norikura in central Japan.

Materials and methods

Study site

This study was carried out on the east slope of Mount Norikura (36˚06'N, 137˚33'E, 3026 m above sea level) in central Japan. Mean annual temperature recorded at Nagawa Weather Station (1068 m a.s.l., approximately 12 km in horizontal distance from the summit) was 8.4˚C in 2003. Mean monthly temperatures in the coldest month of January and the hottest month of August were –4.2 and 20.3˚C, respectively. Annual sum of precipitation was 2206 mm.

Three major vegetation zones of tree species were recognized between 800 m

and 3000 m a.s.l. on Mount Norikura, i.e.,   the montane deciduous broad-leaved forest

zone between 800 m and 1600 m a.s.l., the subalpine coniferous forest zone between

1600 m and 2500 m a.s.l. and the alpine dwarf pine *Pinus pumila* scrub zone between

2500 m and 3000 m a.s.l. The timberline was located at about 2500 m a.s.l. on the

examined east slope of Mount Norikura (Takahashi 2003). Kira's warmth index (WI)

also often used to express relationships between thermal conditions and vegetation (Kira

1948). WI expresses the approximate effective heat for plant growth. WI is calculated as

$\sum(m_t - 5)$, where m_t is mean monthly temperature above 5˚C. The WI was estimated as

48.5˚C months at 1600 m a.s.l. (the upper distribution limit of the montane broad-leaved

forest zone) and 21.9˚C months at 2500 m a.s.l. (the timberline) on Mount Norikura by

using decadal temperature data (1994 to 2003) in Nagawa Weather Station with a lapse

rate of –0.55˚C for each +100 m in altitude.

Vegetation between 800 m and 1600 m a.s.l. was partly subjected to

anthropogenic effects, but this study was done at the sites without the anthropogenic

effects. Anthropogenic effects on vegetation were negligible from 1600 m a.s.l. to the

summit. Dominant species were deciduous broad-leaved *Zeikova serrata*, *Juglans*

mandshurica var. *sachalinensis*, *Lindera praecox* at 800 m a.s.l., deciduous

broad-leaved *Quercus crispula*, *Castanea crenata*, *Betula platyphylla* var. *japonica* at

1400 m a.s.l., evergreen conifer *Abies veitchii*, *Tsuga diversifolia* at 1600 m – 2000 m

a.s.l., evergreen conifer *Abies mariesii*, deciduous broad-leaved *Betula ermanii*, *Sorbus*

matsumurana at 2200 m – 2500 m a.s.l.

Plant nomenclature was followed by Shimizu (1997).

Field measurements

Stand strucuture was surveyed at total 10 sites at 100 ~ 300 m altitudinal intervals between 800 m and 2500 m a.s.l. in 2003 and 2004. Two belt transects (5 × 50 m) were established at a representative vegetation site of each altitude. Species was identified, trunk height and diameter at breast height (DBH) were investigated for all trees taller than 1.3 m. Mechanical damage of trunks and branches was checked for conifers, according to Kajimoto et al. (2002). The mechanical damage includes flagged shape of crowns, tip dieback, broken stem and canopy anomaly with branch-lacking layers (cf. Kajimoto et al. 2002),. The mechanical damage is caused by strong wind and heavy snow in winter. In terms of , windblown snow and ice abrade leaves near timberlines, and then cause winter desiccation (Wardle 1968, 1985; Hadley and Smith 1983, 1986; Maruta 1996). As a result, wind-exposed trunks and branches are damaged or die (Arseneault and Payette 1992; Pereg and Payette 1998). Mechanical damage was not investigated for broad-leaved tree species because of the difficulty of identification of the its character.

The following expanded allometry was employed to describe the relationship between trunk height (H, m) and DBH (D, cm),

$$\frac{1}{H} = \frac{1}{A \cdot D^h} + \frac{1}{H^*}$$

where A (m/cm), h (dimensionless) and H^* (m) are constants. H^* is the expected maximum trunk height. These three constants were estimated by an iterative nonlinear regression that minimizes the sum of squires of residuals (RSS).

Results

The total basal area of trees taller than 1.3 m and the observed observed maximum DBH

did not decrease with increasing altitude (Fig. 1a, c). Although the observed observed

maximum trunk height did not change with increasing altitude between 800 m and 2000

m a.s.l., it largely decreased from 2000 m to 2500 m a.s.l. (Fig. 1d). The tree density

consistently decreased from 800 m to 2000 m a.s.l. (Fig. 1b). However, the tree density

increased from 2000 m to 2500 m a.s.l. (Fig. 1b). This increase of the tree density

corresponded with the reduction of the maximum trunk height (Fig. 1d).

The frequency distribution of trunk height was a L-shaped pattern at 800 m

a.s.l. (Fig. 2a). In this altitude, many small understory tree species present   in the

deciduous broad-leaved forestexisted. Of these species, a deciduous broad-leaved

Lindera praecox was the most dominanton the understory. The frequency distribution of

trunk height changed to the flat-shaped pattern with increasing altitude up to 2000 m

a.s.l. (Fig. 2a – g). This reduction at small size classes was mainly due to reduction of

small understory tree species. Small trees of trees of canopy and subcanopy tree species

were not frequent in the upper zone of the montane forest (1100 m and 1400 m a.s.l.)

and in the subalpine forest up to 2000 m a.s.l. (Fig. 2c – g). Especially at the lower

distribution limit (1600 m a.s.l.) of subalpine coniferous forest, there were few small

understory tree species and the frequency distribution of canopy and subcanopy tree

species was a flat pattern (Fig. 2e). However, the number of trees shorter than 5 m

increased from 2200 m to 2500 m a.s.l., and the size structure became to the an

L-shaped pattern again (Fig. 2h – i). A deciduous broad-leaved *Sorbus matsumurana*

and a dwarf pine *Pinus pumila* were dominant small tree species at the upper zone of

the subalpine forest (2400 m and 2500 m a.s.l.).

were shown in Figure 3. Expanded allometry fitted well to the relationship

between DBH and trunk height at the 10 altitudes between 800 m and 2500 m a.s.l.

(data not shown). Trunk heights at DBH 10, 20, 30 and 40 cm were estimated by the

expanded allometric regression of each altitude. Although trunk height at a given DBH

increased from 800 m to 1400 m a.s.l., it decreased from 1400 m to 2500 m a.s.l. (Fig.

3). The difference in of the estimated trunk height between DBH 10 cm and 40 cm was

about 14 m at 1600 m a.s.l. that was the lower distribution limit of the subalpine

coniferous forest dominated by *Abies mariesii* and *A. veitchii* (Fig. 3). However, this

difference was only 5 m at 2500 m a.s.l. that was the upper distribution limit of the

subalpine coniferous forest (i.e., timberline) (Fig. 3). Therefore, the growth in trunk

height near the timberline was considerably inhibited, compared with the growth in

trunk diameter.

Mechanical damage of conifer trunks and branches was not observed between

800 m and 2000 m a.s.l. (Fig. 1d). However, the proportion of damaged trees increased

from 2000 m to 2500 m a.s.l. (Fig. 1d). This increase was consistent with the reduction

of the maximum trunk height in these altitudes (Fig. 1d). Fig. 4 shows relationships

between trunk height and DBH of conifers at 2200 m, 2400 m and 2500 m a.s.l. Taller

trees tended to be damaged at higher altitudes. Thus,trees could not grow in height in

height near the timberline.

Discussion

In this temperate forest, the maximum DBH did not decrease with increasing altitude throughout the examined altitudinal range from 800 m to 2500 m a.s.l. of the timberline. The maximum trunk height also did not change between 800 m and 2000 m a.s.l., but decreased markedly from 2000 m a.s.l. to 2500 m a.s.l. at the timberline. In contrast, the maximum trunk height and DBH decrease continuously with increasing altitude in tropical forests (Yamada 1977; Ohsawa 1995; Aiba and Kitayama 1999). Reduction of air temperature with increasing altitude means the reduction of available energy for trees in tropical forests in non-seasonal environments, which reduces the maximum tree size in higher altitudes. On the contrary, Ohsawa (1995) showed that Ohsawa (1995) showed that the maximum trunk height did not change with increasing altitude, except for near the timberline, in temperate forests, like as shown in this study. Available energy for tree growth undoubtedly decreases with increasing altitude not only in tropical forests but also in temperate forests. However, the rate of decrease of rate of available energy for plants is lower in temperate forests than in tropical forests (Ohsawa 1995). Therefore, forest biomass and the maximum tree height do not decrease with increasing altitude, except for timberlines, in temperate forests.

Generally, the thermal conditions of many timberlines in the world correspond to WI 15°C months (Ohsawa 1990). However, timberlines in Japan often locates in the altitudes of WI greater than 15°C months (Okitsu and Ito 1984a). Actually, WI is 21.9°C months at the timberline on Mount Norikura, and therefore, Miyajima et al. (unpublished manuscript) it is suggested thatt altitudinal position of the timberline on

Mount Norikura is not regulated by thermal condition alone. In this study, the maximum tree height decreased sharply near the timberline, and this decrease corresponded with the occurrence of mechanical damage of trunks and branches. Okitsu and Ito (1989) reported that Wind velocity is considerably high in high altitudes, which causes the mechanical damages   trees by winter desiccation (Warren Wilson 1959; Hadley and Smith 1983, 1986). alpine dwarf pine *Pinus pumila* dominates above the timberline. was However, *Pinus pumila* is hardly damaged by winter winter desiccation (Maruta et al. 1996), because it is completely covered with snow in winter (Okitsu and Ito 1984b). Accordingly, not onlyit is suggested that thermal conditions during the growing season but also strong wind in winter largely affect the altitudinal position of timberline on Mount Norikura.

The frequency distribution of trunk height changed from the L-shaped pattern at 800 m a.s.l. to the a flat-shaped pattern at 2000 m a.s.l. However, the number of small trees increased from 2000 m to 2500 m a.s.l. of the timberline, and the size structure shifted to the L-shaped pattern again. The increase of small trees corresponded with the reduction of the maximum trunk height. The reduction of small trees from 800 m to 2000 m a.s.l. is probably ascribed to the reduction of available energy for the photosynthetic production of small understory trees. Photosynthetic production of understory trees is mainly limited by shortage of light resource, irrespective of altitudes. In addition, the growth period is shorter and air temperature during the growth period is lower with increasing altitude. Photosynthetic rate of plants is generally temperature dependent, and low temperatures reduce the photosynthetic production of alpine and subalpine plants (DeLucia and Smith 1987; Körner 1999). Therefore, the combined

stress (dark and cool conditions, and short growth period) is disproportionately more harmful for the photosynthetic production of understory trees at higher altitudes compared with canopy trees in sunlit conditions, which probably reduces the growth and survival of understory trees at higher altitudes. On the contrary, the increase of small trees from 2000 m to 2500 m a.s.l. of the timberline corresponded with the increase of the mechanical damage of trunks and branches. Reduced development of the canopy layer, due to the increas of trunk broken, brought about much light for small trees, which enabled small trees to grow and survive, which in turn brought about the L-shaped pattern near the timberline. Therefore, it is suggested that the stand structural change with increasing altitude was caused by the combined stress for understory trees and by the increase of the mechanical damage of trunks.

This study concluded that (1) the size structural changes along the altitudinal gradient were caused by the combined stress (dark and cool conditions, and short growth period) for understory trees and by the increase of the mechanical damage, which influenced the altitudinal change in the regeneration pattern, (2) not only thermal conditions during the growing season but also the mechanical damage in winter possibly determine the altitudinal position of the timberline. Therefore, this study suggests that the mechanical damage is the causal factor affecting the altitudinal changes in the regeneration pattern and determining the altitudinal position of the timberline.

Literature cited

Aiba S, Kitayama K (1999) Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. Plant Ecol 140:139–157

Arseneault D, Payette S (1992) A postfire shift from lichen-spruce to lichen-tundra vegetation at tree line. Ecology 73:1067–1081

DeLucia EH, Smith WK (1987) Air and soil temperature limitations on photosynthesis in Engelmann spruce during summer. Can J For Res 17:527–533

Hadley JL, Smith WK (1983) Influence of wind exposure on needle desiccation and mortality for timberline conifers in Wyoming, U.S.A. Arc Alp Res 15:127–135

Hadley JL, Smith WK (1986) Wind effects on needles of timberline conifers: seasonal influence on mortality. Ecology 67:12–19

Kajimoto T, Daimaru H, Okamoto T, Otani T, Onodera H (2004) Effects of snow avalanche disturbance on regeneration of subalpine *Abies mariesii* forest, northern Japan. Arc Antarc Alp Res 36:436–445

Kajimoto T, Seki T, Ikeda S, Daimaru H, Okamoto T, Onodera H (2002) Effects of snowfall fluctuation on tree growth and establishment of subalpine *Abies mariesii* near upper forest-limit of Mt. Yumori, northern Japan. Arc Antarc Alp Res 34:191–200

Kamijo T, Isogai T, Hoshino Y, Hakamada H (2001) Altitudinal zonation and structure of warm-temperate forests on Mikura-jima Island, Izu Islands, Japan. Veg Sci 18:13–22

Kira T (1948) On the altitudinal arrangement of climatic zones in Japan (in Japanese). Kanti-Nogaku 2:143–173

Kirkpatrick JB, Hassall DC (1985) The vegetation and flora along an altitudinal transect through tropical forest at Mount Korobaba, Fiji. NZ J Bot 23:33–46

Kohyama T, Hotta M (1990) Significance of allometry in tropical saplings. Funct Ecol 4:515–521

Kojima S (1994) Vegetation and environment of *Betula ermanii* forest on the Kamchatka Peninsula (in Japanese). Jpn J Ecol 44:49–59

Körner C (1999) Alpine Plant Life. Springer, Berlin

Lieberman D, Lieberman M, Peralata R, Hartshorn GS (1996) Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. J Ecol 84:137–152

Maruta E (1996) Winter water relations of timberline larch (*Larix leptolepis* Gord.) on Mt. Fuji. Trees 11:119–126

Maruta E, Nakano T, Ishida A, Iida H, Masuzawa T (1996) Water relations of *Pinus pumila* in the snow melting season at the alpine region of Mt. Tateyama. Proc. Nat. Inst. Polar Res. Symp. Polar Biol. 9:335–342

Masaki T, Suzuki W, Niiyama K, Iida S, Tanaka H, Nakashizuka T (1992) Community structure of a species-rich temperate forest, Ogawa Forest Reserve, central Japan. Vegetatio 98:97–111

Ohsawa M (1984) Differentiation of vegetation zones and species strategies in the

     subalpine region of Mt. Fuji. Vegetatio 57:15–52

Ohsawa M (1990) An interpretation of latitudinal patterns of forest limits in south and

     east Asian mountains. J Ecol 78:326–339

Ohsawa M (1995) Latitudinal comparison of altitudinal changes in forest structure,

     leaf-type, and species richness in humid monsoon Asia. Vegetatio 121:3–10

Okitsu S, Ito K (1984a) The relation of forest limit to the WI 15 in mountains of

     Hokkaido (in Japanese). Jpn J Ecol 34:341–346

Okitsu S, Ito K (1984b) Vegetation dynamics of the Siberian dwarf pine (*Pinus pumila*

     Regel) in the Taisetsu mountain range, Hokkaido, Japan. Vegetatio 58:105–113

Pereg D, Payette S (1998) Development of black spruce growth forms at treeline. Plant

     Ecol 138:137–147

Seki T, Kajimoto T, Sugita H, Daimaru H, Ikeda S, Okamoto T (2005) Mechanical

     damage on *Abies mariesii* trees buried below the snowpack. Arc Antarc Alp Res

     37:34–40

Shimizu T (1997) Flora of Nagano Prefecture (in Japanese). Shinano Mainichi

     Shinbunsha, Nagano

Takahashi K (1962) Studies on vertical distribution of the forest in middle Honshu (in

     Japanese). Bull Gov For Exp St 142:1–171

Takahashi K (2003) Effects of climatic conditions on shoot elongation of alpine dwarf

     pine (*Pinus pumila*) at its upper and lower altitudinal limits in central Japan. Arc

     Antarc Alp Res 35:1–7

Takahashi K, Azuma H, Yasue K (2003) Effects of climate on the radial growth of tree

species in the upper and lower distribution limits of an altitudinal ecotone on Mount Norikura, central Japan. Ecol Res 18:549–558

Takahashi K, Tokumitsu Y, Yasue K (2005) Climatic factors affecting the tree-ring width of *Betula ermanii* at the timberline on Mount Norikura, central Japan. Ecol Res 20:445–451

Tang CQ, Ohsawa M (1997) Zonal transition of evergreen, deciduous, and coniferous forests along the altitudinal gradient on a humid subtropical mountain, Mt. Emei, Sichuan, China. Plant Ecol 133:63–78

Veblen TT (1986) Age and size structure of subalpine forests in the Colorado Front Range. Bull Torrey Bot Club 113:225–240

Wang X, Fang J, Tang Z, Zhu B (2006) Climatic control of primary forest structure and DBH-height allometry in Northeast China. For Ecol Manage 234:264–274

Wardle P (1968) Engelmann spruce (*Picea engelmannii* Engel.) at its upper limits on the Front Range, Colorado. Ecology 49:483–495

Wardle P (1985) New Zealand timberlines. 1. Growth and survival of native and introduced tree species in the Craigiebun Range, Canterbury. NZ J Bot 23:219–234

Warren Wilson J (1959) Notes on wind and its effects in arctic-alpine vegetation. J Ecol 47:415–427

Yamada I (1977) Forest ecological studies of the montane forest of Mt. Pangrango, West Java. IV. Floristic composition along the altitude. South East Studies 15:226–254

Yoshino MM (1978) Altitudinal vegetation belts of Japan with special reference to

climatic conditions. Arc Alp Res 10:449–456

Figure legends

Fig. 1. Altitudinal changes in (a) the total basal area, (b) tree density (> 1.3 m tall), (c) the observed observed maximum DBH, (d) the observed observed maximum trunk height (solid circle) and proportion of trees with mechanical damage of trunks and branches (open circle) at 10 sites between 800 m and 2500 m a.s.l. on Mount Norikura in central Japan.

Fig. 2. Altitudinal changes in the frequency distribution of trunk height at 10 sites between 800 m and 2500 m a.s.l. on Mount Norikura in central Japan. Dark and light shaded bars indicate canopy and subcanopy tree species and small understory tree species, respectively. Note that ordinate scales of (i) and (j) are different from those of (a) ~ (h).

Fig. 3. Altitudinal changes in tree heights of DBH 10 cm (solid circle), 20 cm (open circle), 30 cm (solid triangle) and 40 cm (open triangle) between 800 m and 2500 m a.s.l. on Mount Norikura in central Japan. Tree height of each DBH at each altitude was

estimated from the expanded allometric regression.

Fig. 4. Relationships between trunk height and diameter at breast height of conifers at (a) 2200 m, (b) 2400 m and (c) 2500 m a.s.l. on Mount Norikura in central Japan. Solid and open circles represent trees with and without mechanical damages, respectively.
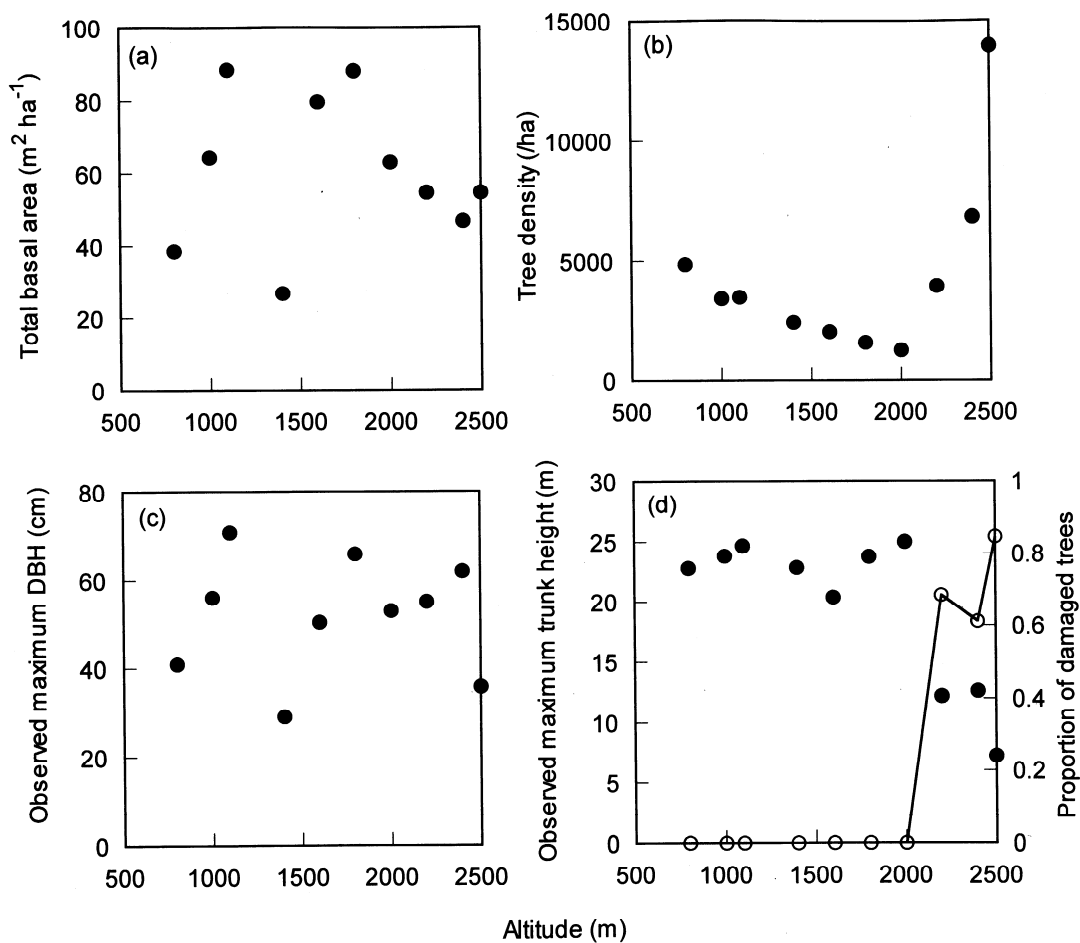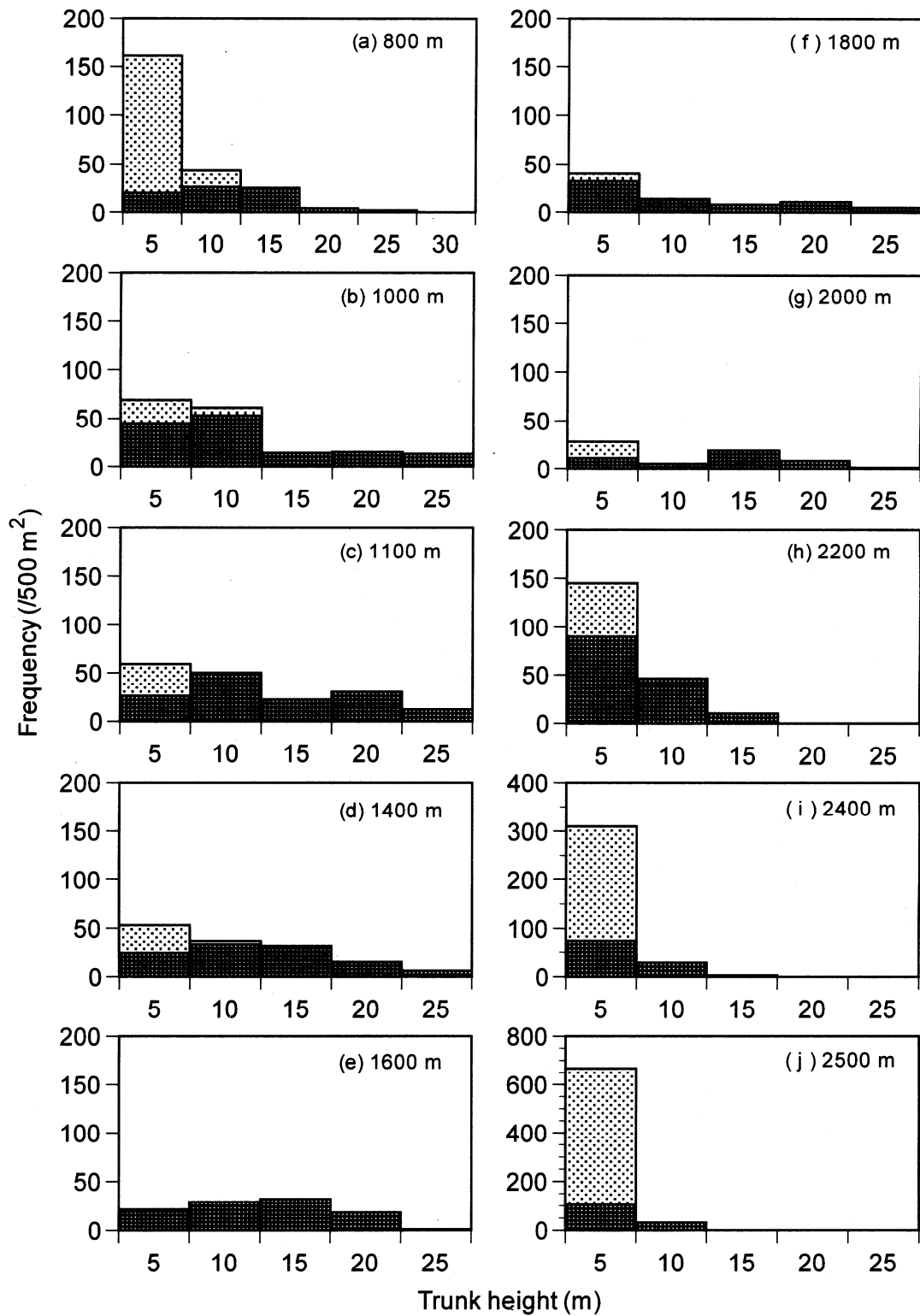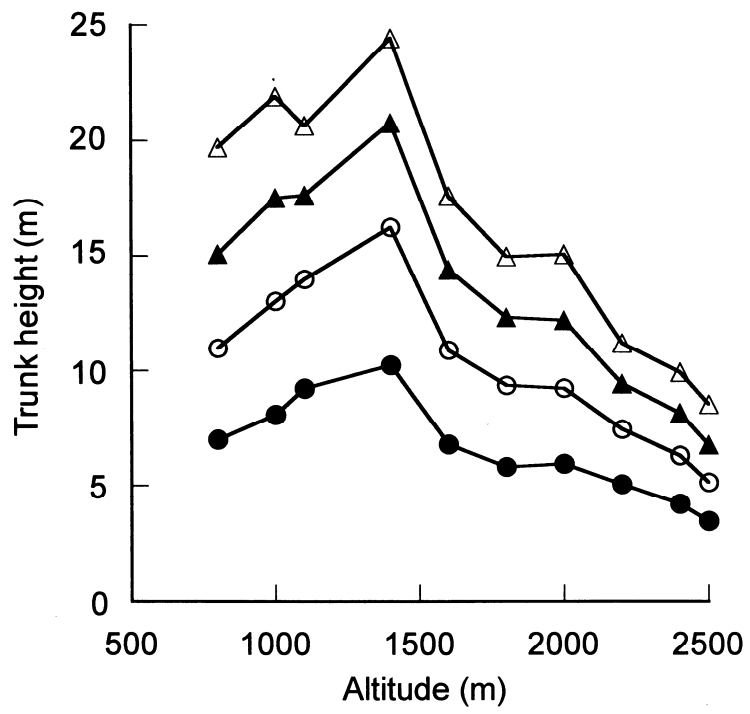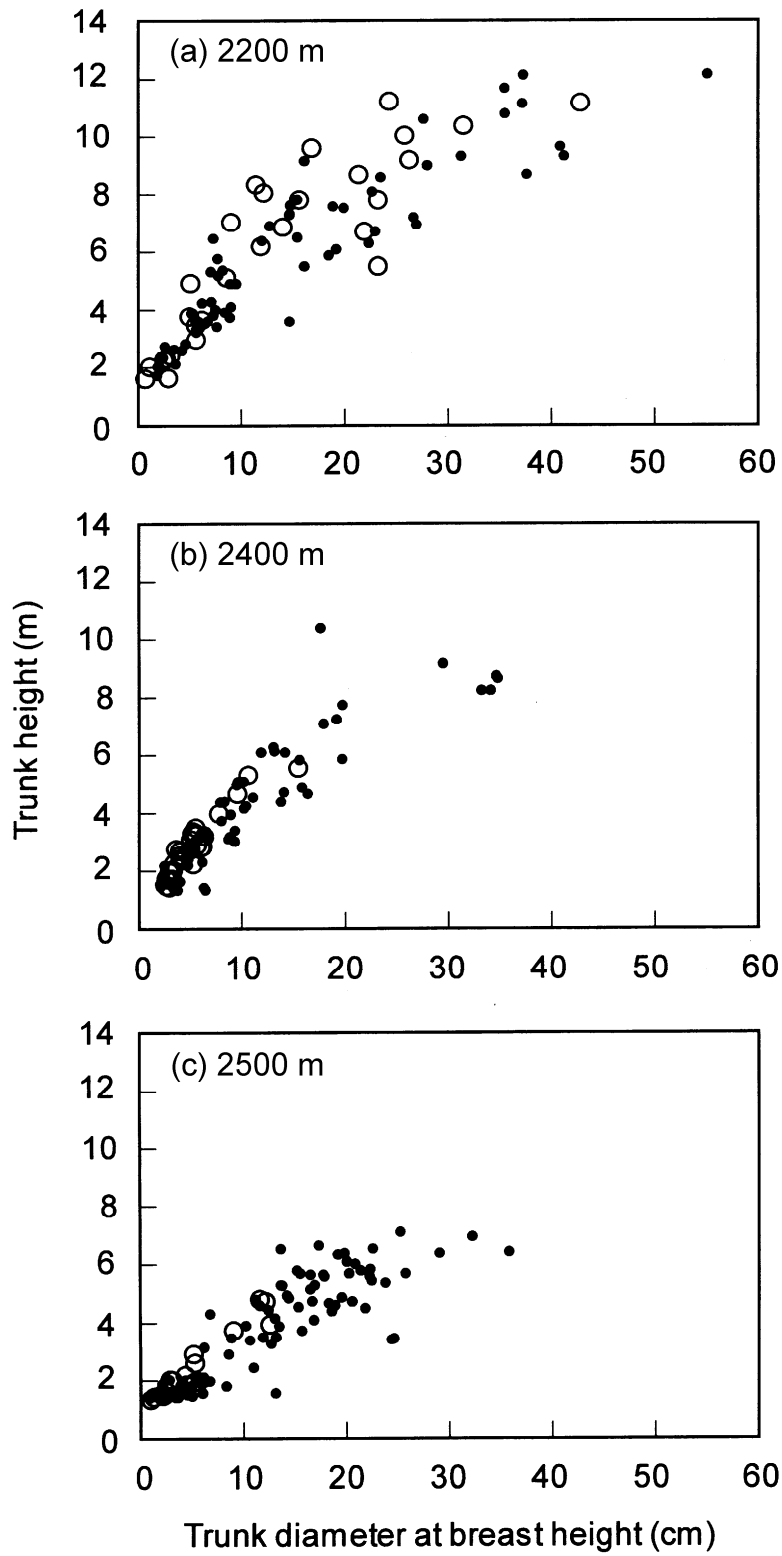
Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.