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ORIGINAL ARTICLE

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Pattern of changes in species diversity, structure and dynamics of forest ecosystems along latitudinal gradients in East Asia

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Abstract We examined effects of seasonality of climate and dominant life form (evergreen/deciduous, broadleaf/coniferous) together with energy condition on species diversity, forest structure, forest dynamics, and productivity of forest ecosystems by comparing the patterns of changes in these ecosystem attributes along altitudinal gradients in tropical regions without seasonality and along a latitudinal gradient from tropical to temperate regions in humid East Asia. We used warmth index (temperature sum during growing season, WI) as an index of energy condition common to both altitudinal and latitudinal gradients. There were apparent differences in patterns of changes in the ecosystem attributes in relation to WI among four forest formations that were classified according to dominant life form and climatic zone (tropical/temperate). Many of the ecosystem attributes—Fisher's alpha of species-diversity indices, maximum tree height and stem density, productivity [increment rate of aboveground biomass (AGB)], and population and biomass turnover rates—changed sharply with WI in tropical and temperate evergreen broad-leaved forests, but did not change linearly or changed only loosely with WI in temperate deciduous broad-leaved and evergreen coniferous forests. Values of these ecosystem attributes in temperate deciduous broad-leaved and evergreen coniferous forests were higher (stem density was lower) than those in tropical and temperate evergreen broad-leaved forests under colder conditions (WI below 100°C). Present results indicate that seasonality of climate and resultant change in dominant life form work to buffer the effects of energy reduction on ecosystem attributes along latitudinal gradients.

Keywords Species diversity · Aboveground net primary productivity · Forest dynamics · Forest structure · Latitude

Introduction

A latitudinal gradient from tropical to boreal regions is not only an energy gradient but also a gradient of duration of growing season. As the growing season shortens and latitude increases, dominant life forms of forest ecosystems change from evergreen broad-leaved trees through deciduous broad-leaved trees to coniferous trees (Holdridge 1947; Kira 1976; Ohsawa 1995). In tropical regions, evergreen broad-leaved trees dominated across the altitudinal gradients despite the decline in air temperature because there was no seasonality in climate (Whitmore 1990; Kitayama 1992).

Many previous studies on changes in forest ecosystem attributes along latitudinal gradients have focused on the relationships with energy rather than on the relationships with seasonality of climate and/or dominant life forms. Net primary productivity has been estimated using actual evapotranspiration (e.g., Miami model of Lieth 1975; Chikugo model of Uchijima and Seino 1985). The species–energy hypothesis explains that energy availability may

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constrain the number of species that can coexist in a community (Hutchinson 1959; Adams and Woodward 1989; Currie 1991). However, since life form is an adaptation to seasonality of climate, the pattern of changes in ecosystem attributes along latitudinal gradients may be affected by dominant life forms of forest ecosystems. Deciduousness is an adaptive leafing phenology to achieve sufficient productivity during the hot summer in temperate regions (Kikuzawa 1991). It is well known that conifers have greater maximum tree size and lifespan than broad-leaved trees (Waring and Franklin 1979; Suzuki and Tsukahara 1987). These differential functions among life forms may work as a buffer to the effects of energy reduction on productivity and biomass along a latitudinal gradient, and ecosystem attributes may be different depending on forest formations with different dominant life forms. Accordingly, we have to consider the effects of seasonality of climate and resultant change in dominant life form on ecosystem attributes to understand latitudinal changes in forest ecosystems.

Recently, many studies have examined patterns in ecosystem attributes at global scales using databases of plot-level forest inventory data (Adams and Woodward 1989; Currie 1991; Phillips et al. 1994; Cornelissen 1996; Reich and Bolstad 2001). However, there are few studies that have focused on the geographical patterns in East Asia (Ohsawa 1995; Kohyama 1999). In East Asia, the humid climate extends continuously from tropical to boreal regions without deserts at middle latitudes. This condition provides us good opportunities to examine the effects of air temperature on ecosystem attributes without considering the effects of seasonality of precipitation. The objectives of this study were to examine the effects of seasonality of climate and the resultant differences in dominant life form on species diversity, structure, dynamics, and productivity of forest ecosystems along a latitudinal gradient in humid East Asia.

In the present study, in order to distinguish the effects of seasonality and dominant life forms from the effects of energy condition, we compared the patterns of changes in ecosystem attributes along a latitudinal gradient from tropical to boreal regions with the patterns of changes along altitudinal gradients in tropical regions.

Methods

We collected tree census data by using the database PlotNet, which includes plot-level forest inventory data from equatorial regions in Southeast Asia to boreal regions in East Asia (http://eco1.ees.hokudai.ac.jp/~plotnet/db/). From the study plots collected, we chose 48 plots that met the following conditions: more than 1,000 mm of annual precipitation, primary forest with no record of logging, more than 1,000 m^2 in plot area (Appendix 1). We used plots with large areas because some ecosystem attributes vary depending on plot area, especially species diversity and forest dynamics. However, the effects of plot area may not be excluded completely because half of the plots were less than 1 ha in area. We used census data collected from 1990–2001 for trees≥10 cm in diameter at breast height (DBH). Since seven plots lacked recensus data and 27 plots lacked litterfall data, sample sizes were different among analyses (Table 1).

For forest structural attributes, maximum DBH and tree height (*H*), stem density, and aboveground biomass (AGB) were calculated. AGB was estimated from allometric regressions between aboveground tree mass and DBH^2×*H* reported for each forest formation in previous studies (Appendix 2). For some plots without tree height data, allometric regressions between aboveground tree mass and DBH were adopted for the estimation of AGB. Aboveground net primary production (ANPP) was calculated as annual increment in AGB of surviving trees between two censuses (AGB increment rate) plus mean annual fine litterfall. Fine litterfall included all organs greater than 2 mm in diameter (leaves and branches less than about 2 cm in diameter and flowers, fruits, and dust); it was collected by litter traps that were made of 1- or 2-mm mesh and were cone- or rectangular-shaped with a 0.5-m^2 opening. Fisher's alpha and Shannon-Wiener's *H*′ were calculated as species diversity indices.

Mortality (*mt*), recruitment (*rc*), population turnover (*pt*), and biomass turnover (*bt*) rates were calculated as attributes of forest dynamics from the following equations:

Table 1 Number of sampled plots for species diversity and attributes of forest structure and dynamics

Formation type	Species diversity	Maximum tree size	AGB	Population dynamics	AGB increment	ANPP
Temperate deciduous broad-leaved forests	11	12	12	8	8	4
Temperate evergreen coniferous forests	14	15	15	13	14	2
Temperate evergreen broad-leaved forests	8	9	9	8	8	4
Tropical evergreen broad-leaved forests	11	12	12	11	11	11
Total	44	48	48	40	41	21

$$mt = 100[\ln(N\mathrm{o}) - \ln(N\mathrm{s})]/t$$

$$rc = 100[\ln(N\mathrm{f}) - \ln(N\mathrm{s})]/t$$

$$pt = (mt + rc)/2$$

$$bt = \text{annual AGB increment/AGB}$$

where $N\mathrm{o}$ = number of stems at start, $N\mathrm{s}$ = survived stems, $N\mathrm{f}$ = final stems (survived stems + recruits), and t = census span (year).

As an index of energy condition, we used warmth index (WI, Kira 1948):

$$\mathrm{WI} = \sum(\mathrm{MMAT} - 5)$$

where MMAT is monthly mean air temperature for months with a mean above 5°C. We did not use actual evapotranspiration (AET) as an index of energy condition, though many previous studies have. AET explained well the changes in ANPP along both temperature and humidity gradients (Lieth 1975), since it is a function of net radiation and saturation deficit. However, AET is independent of altitude, and it cannot explain changes in ecosystem attributes along an altitude gradient, since solar radiation is generally independent of altitude. Therefore, we used WI as an index of energy condition common to both latitudinal and altitudinal gradients. Since study plots used in this study were located in humid regions, we did not need to consider the effects of deficiency of precipitation. For 26 plots below 1,000 m in altitude, WI significantly correlated with AET when we estimated AET from monthly mean air temperature and precipitation following Takahashi (1979) ($r^2 = 0.78$). Annual temperature range (mean temperature of the warmest month minus the coldest month) was used as an index of seasonality of climate. Although day length during the growing season may change in relation to annual temperature range along a latitudinal gradient, effects of day length could not be distinguished from effects of annual temperature range in this study.

Figure 1 shows latitudinal changes in WI, annual temperature range, and relative basal area of evergreen broad-leaved trees (RBA-EB) for the 48 plots. WI ranged from 20.3°C month in boreal coniferous forests to 261.1°C month in tropical lowland rain forests. As annual temperature range increased above 20°C and WI fell below 80°C month in temperate regions, RBA-EB decreased from 100 to 0% abruptly, and deciduous broad-leaved and evergreen coniferous trees predominated. In tropical regions, evergreen conifers increased as WI decreased below 100°C month, but evergreen, broad-leaved trees predominated in all plots but one. Therefore, we divided vegetation types into four formations based on the climatic zone and dominant life form: tropical evergreen broad-leaved forests, temperate (warm-temperate) evergreen broad-leaved forests, temperate (cool-temperate) deciduous broad-leaved forests, and temperate (cool-temperate and boreal) evergreen coniferous forests, and we compared the pattern of changes for ecosystem attributes along WI among the four formations in this study.

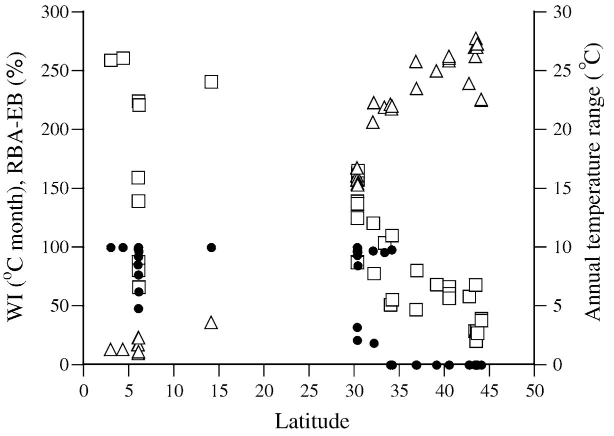


Fig. 1 Latitudinal changes in warmth index (WI, *open squares*), annual temperature range (*open triangles*), and relative basal area of evergreen broad-leaved trees (RBA-EB, *closed circles*) for the 48 study plots

To compare ecosystem attributes among the four formations, correlation between ecosystem attributes and WI in each formation was tested by ANOVA, and slopes and intercepts of regression lines against WI were compared by Bonferroni test after ANCOVA. To test the effects of energy condition, seasonality of climate, and dominant life forms on ecosystem attributes, multiple regression analysis was adopted. In this analysis, three explanatory variables were used: WI as an index of energy condition, annual temperature range as an index of seasonality of climate, and RBA-EB as an index of dominant life form.

Results

The species diversity indices, Fisher's alpha and Shannon-Wiener's H' (data not shown), increased with increasing WI in each formation (ANOVA, $P < 0.01$; Fig. 2). For Fisher's alpha, the slope of the regression line against WI for temperate deciduous broad-leaved and evergreen coniferous forests was significantly looser than for tropical and temperate evergreen broad-leaved forests (ANCOVA, $P < 0.01$). The slope of the regression for the temperate deciduous broad-leaved and evergreen coniferous forests was greater than for the tropical and temperate evergreen broad-leaved forests at a comparable WI under colder conditions (WI < 100°C month). For Shannon-Wiener's H', neither the slopes nor the intercepts of the regression lines against WI were significantly different among the four formations.

For forest structural attributes, there were apparent differences among the four formations. Maximum DBH increased with increasing WI in each formation (ANOVA, $P < 0.01$; Fig. 3a), but the slope of the regression line against WI was greater for the temperate deciduous broad-leaved and evergreen coniferous forests

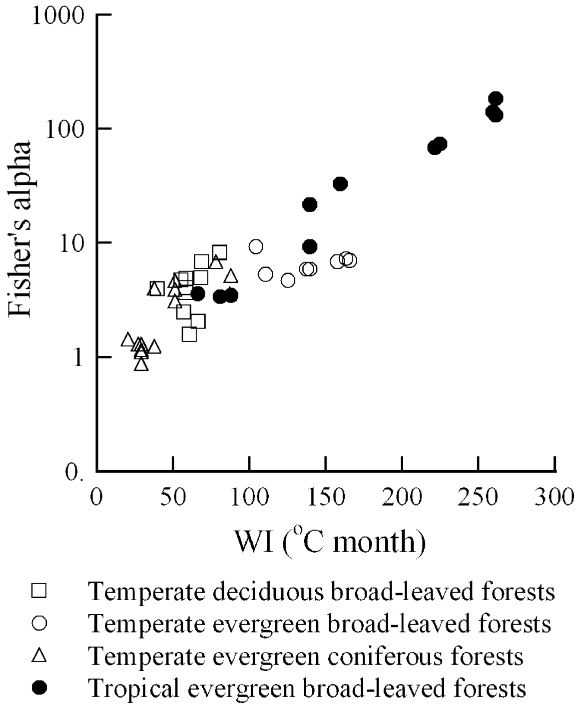
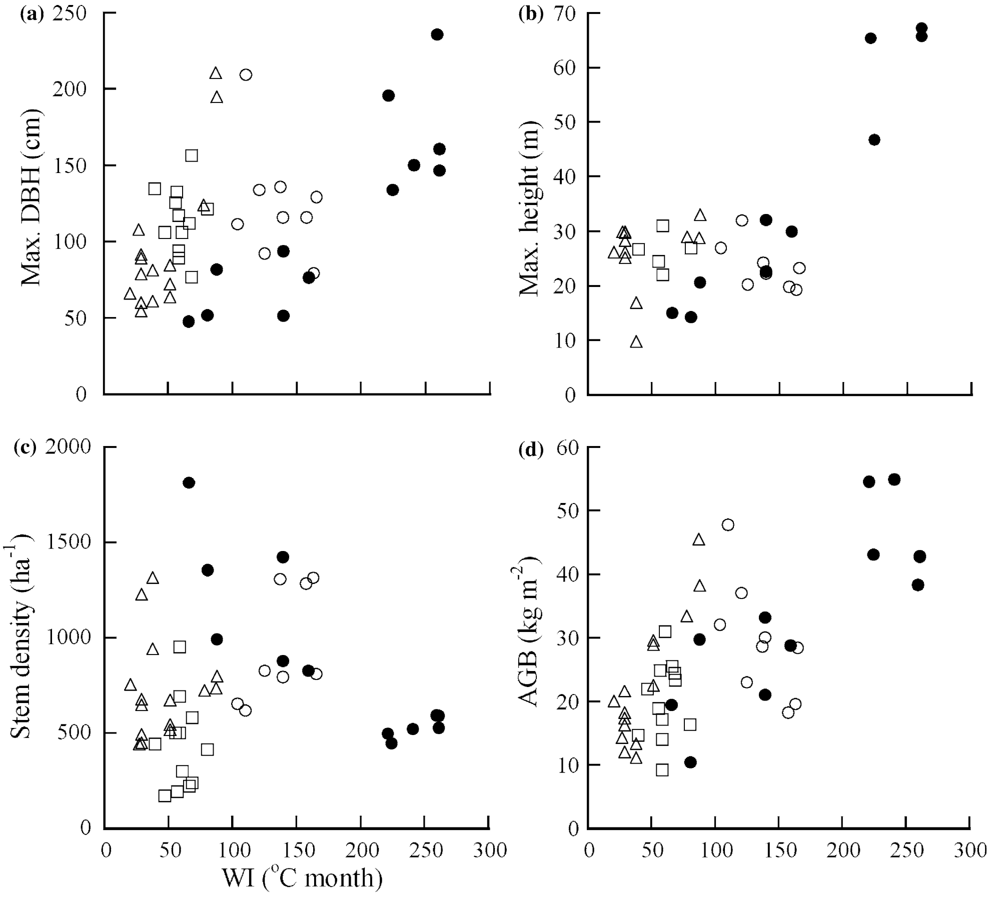


Fig. 2 Changes in species diversity (Fisher's alpha) of four forest formations in relation to WI

than for the tropical and temperate evergreen broad-leaved forests (ANCOVA, $P < 0.05$). Maximum tree height increased with increasing WI in tropical and temperate evergreen broad-leaved forests (ANOVA, $P < 0.01$), but showed similar values and no significant relationships with WI in temperate deciduous broad-leaved and evergreen coniferous forests (ANOVA, $P > 0.05$; Fig. 3b). Thus, maximum tree height was higher in temperate deciduous broad-leaved and evergreen coniferous forests than in tropical and temperate evergreen broad-leaved forests under colder conditions (WI < 100°C month).

Stem density decreased with increasing WI in tropical and temperate evergreen broad-leaved forests (ANOVA, $P < 0.01$) while it varied independently of WI in temperate deciduous broad-leaved and evergreen coniferous forests (ANOVA, $P > 0.05$; Fig. 3c). For stem density, the intercept of the regression line against WI for the tropical and temperate evergreen broad-leaved forests was significantly greater than that for the temperate deciduous broad-leaved and evergreen coniferous forests (ANCOVA, $P < 0.01$). The low stem density under colder conditions in temperate deciduous broad-leaved and evergreen coniferous forests was explained by the decrease in stem density of small trees (10 cm ≤ DBH < 15 cm) at low WI (Fig. 4).

Fig. 3 Changes in forest structural attributes in four forest formations in relation to WI. **a** Maximum DBH. **b** Maximum tree height. **c** Stem density of trees≥10 cm in DBH. **d** Aboveground biomass (AGB). *Symbols* are the same as Fig. 2



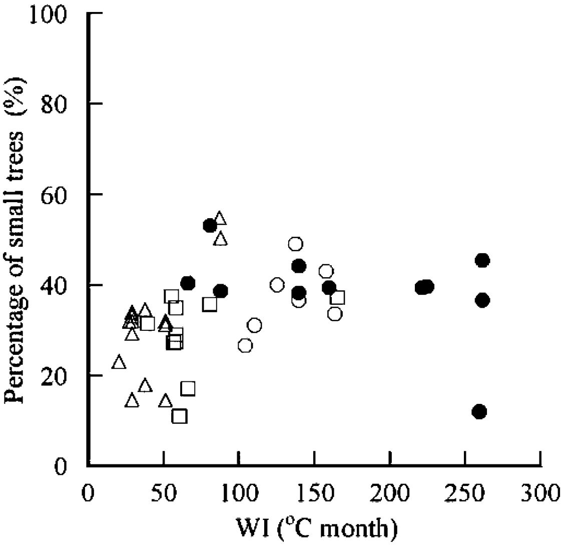


Fig. 4 Changes in percentage of small trees (10 cm ≤ DBH Symbols are the same as Fig. 2

AGB increased with increasing WI in each formation (ANOVA, $P<0.01$; Fig. 3d), and there were no significant differences in slopes and intercepts of the regression lines among the four formations. Accordingly, the distribution of carbon in biomass differed among the four formations. Under colder conditions (WI < 100°C month) in temperate deciduous broad-leaved and coniferous forests, a greater part of the assimilated carbon was concentrated in a few large canopy trees rather than small trees. In contrast, under colder conditions in tropical and temperate evergreen broad-leaved forests, canopy trees were smaller but had greater stem density, with assimilated carbon shared among a greater number of trees.

ANPP was positively correlated with WI for the 21 plots for which ANPP data was available (ANOVA, $P<0.01$; Fig. 5a). However, we could not compare among the four formations due to the small sample size. Therefore among the four formations, we compared AGB increment rate, which is recognized to be a good estimate for ANPP (Clark et al. 2001). AGB increment rates in temperate deciduous broad-leaved and evergreen coniferous forests were similar and had no significant relationship with WI (ANOVA, $P>0.05$), while increment rates in tropical and temperate evergreen broad-leaved forests increased with WI (ANOVA, $P<0.01$; Fig. 5b). AGB increment rates in temperate deciduous broad-leaved and evergreen coniferous forests were greater than those in tropical and temperate evergreen broad-leaved forests at WI below 100°C month.

In tropical and temperate evergreen broad-leaved forests, mortality, recruitment rate, and population turnover rates increased with increasing WI, but one plot showed a high rate below 80°C month of WI (Fig. 6). In contrast, these attributes of forest dynamics varied independently of WI in temperate deciduous broad-leaved and evergreen coniferous forests (ANOVA, $P>0.05$). Biomass turnover rate, which was independent of population turnover rate, showed a pattern similar to population turnover rates. Values for these four attributes of forest dynamics tended to be higher in temperate deciduous broad-leaved and evergreen coniferous forests than in tropical and temperate evergreen broad-leaved forests under colder conditions (WI < 100°C month).

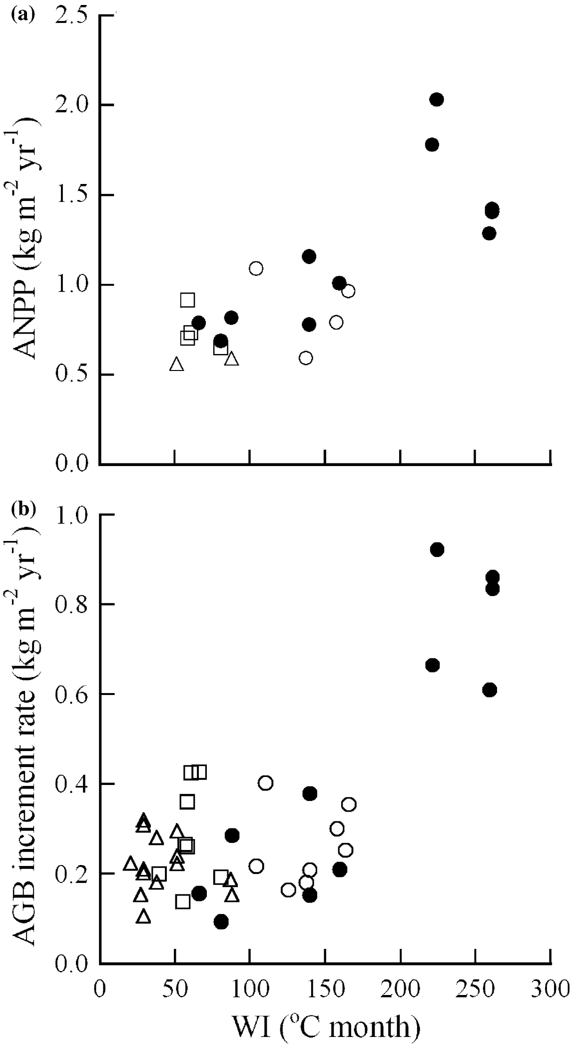


Fig. 5 Changes in **a** aboveground net primary productivity and **b** aboveground biomass increment rate (AGB increment rate) in four forest formations in relation to WI. *Symbols* are the same as Fig. 2

Multiple regression analysis was significant in clarifying the variance in 10 of 12 ecosystem attributes. For 6 of the 10 attributes—Fisher's alpha, maximum tree height, stem density, AGB increment rate, population turnover rate, and biomass turnover rate—multiple regression analysis demonstrated that RBA-EB together with WI explained a significant amount of the variance (Table 2). For these six attributes, regression against WI was not significant or the slopes of the regression lines were significantly looser for the temperate deciduous broad-leaved and evergreen coniferous forests compared to those for the tropical and temperate evergreen

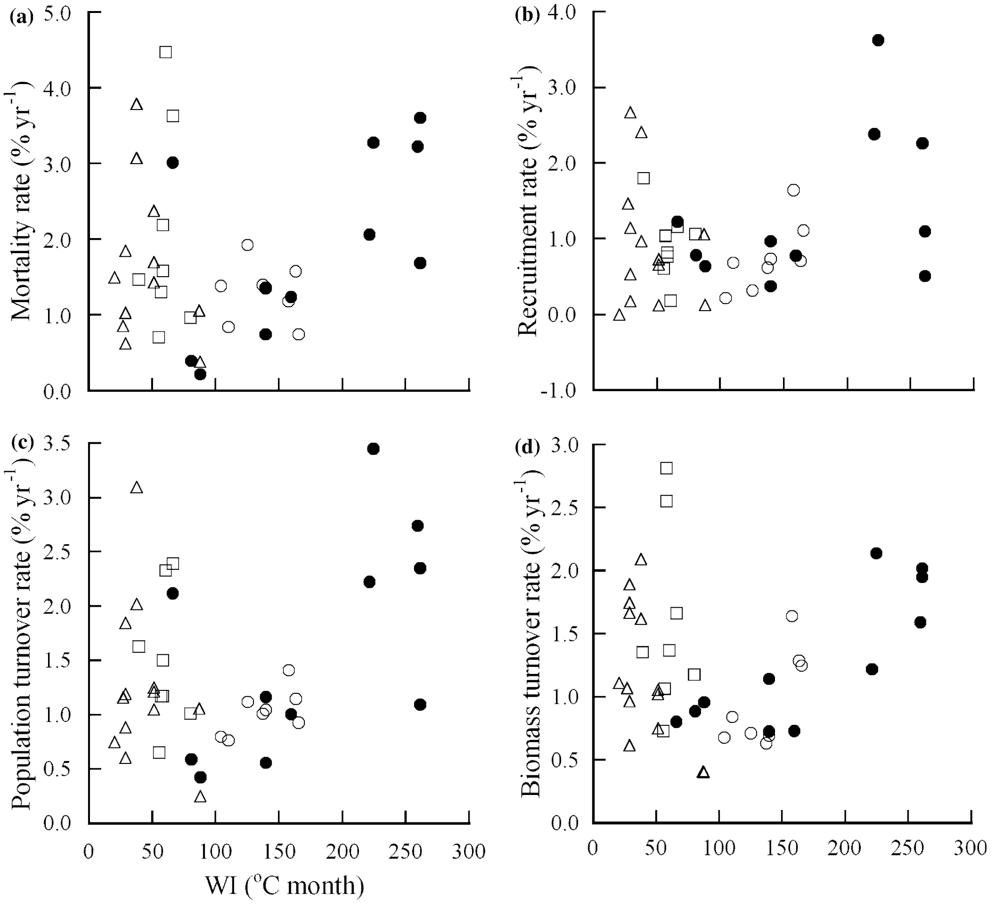


Fig. 6 Changes in forest dynamics in four forest formations in relation to WI. **a** Mortality rate. **b** Recruitment rate. **c** Population turnover rate = (mortality + recruitment rate)/2. **d** Biomass turnover rate = AGB increment rate/AGB. *Symbols* are the same as Fig. 2

broad-leaved forests. Annual temperature range played a significant role in only three attributes—Shannon-Wiener's H', maximum DBH, and stem density.

Discussion

The pattern of changes in ecosystem attributes in relation to WI was distinctively different for two groups of formations. One group included tropical and temperate evergreen broad-leaved forests, and the other included temperate deciduous broad-leaved and evergreen coniferous forests. Multiple regression analysis demonstrated that not only energy condition but also seasonality of climate and dominant life form significantly contributed to explaining the variance in many ecosystem attributes in humid East Asia. Dominant life form, especially, affected ecosystem attributes much more than seasonality

Table 2 Results of multiple regression analysis between forest ecosystem attributes as criterion variables and three explanatory variables: warmth index (*WI*), annual temperature range (*Temp range*), and relative basal area of evergreen broad-leaved trees (*RBA-EB*). Coefficient of determination (r^2) and probability of significance (P) for the multiple regression and number of samples (n) are shown for each attribute. Standard regression coefficient and probability of significance for the three explanatory variables are also shown

Attribute	n	r^2	P	Standard regression coefficient			Probability		
				WI	Temp range	RBA-EB	WI	Temp range	RBA-EB
Fisher's alpha	44	0.79	0.00	1.29	−0.17	−0.72	0.00	0.18	0.00
Shannon-Wiener's H'	43	0.82	0.00	0.74	−0.40	−0.19	0.00	0.00	0.18
Max. DBH	48	0.39	0.00	1.04	0.50	−0.17	0.00	0.02	0.48
Max. tree height	35	0.64	0.00	1.40	0.07	−0.82	0.00	0.69	0.00
Stem density	47	0.44	0.00	−1.09	−0.63	0.76	0.00	0.00	0.00
AGB	48	0.50	0.00	0.77	0.17	0.08	0.00	0.34	0.70
ANPP	21	0.62	0.00	0.78	−0.09	−0.07	0.00	0.68	0.81
AGB increment rate	41	0.65	0.00	1.33	0.10	−0.62	0.00	0.53	0.00
Mortality rate	40	0.17	0.09	0.76	0.04	−0.66	0.02	0.87	0.04
Recruitment rate	40	0.13	0.15	0.57	−0.14	−0.47	0.07	0.58	0.13
Population turnover rate	40	0.21	0.03	0.84	−0.04	−0.71	0.01	0.86	0.02
Biomass turnover rate	41	0.23	0.02	0.90	0.16	−0.79	0.00	0.51	0.01

of climate. These results indicate that seasonality of climate and resultant changes in dominant life form work to buffer the effects of energy reduction on ecosystem attributes along a latitudinal gradient. As well, the effects of dominant life form are more important than the direct effects of seasonality of climate in many cases.

AGB increment rates of temperate deciduous broad-leaved and evergreen coniferous forests did not decrease with decreasing WI, while those of tropical and temperate evergreen broad-leaved forests did. Reich (1993) compared net photosynthetic capacity, leaf N concentration, and specific leaf area in relation to leaf lifespan among some formations, and showed that values for these three leaf traits were higher in deciduous broad-leaved trees than in evergreen broad-leaved trees. Accordingly, deciduous broad-leaved trees achieve high photosynthetic capacity per unit time by allocating much N to leaves, which may contribute to the greater annual productivity of temperate deciduous broad-leaved forests than tropical and temperate evergreen broad-leaved forests under colder conditions ($\mathrm{WI} < 100°\mathrm{C}$ month) despite the shorter growing season. Although day length during growing season increased with increasing latitude and may contribute to the high productivity in forests at high latitudes, we could not examine the effects of day length on productivity in this study. The higher concentration of leaf N leads to higher litter decomposition rates in temperate deciduous broad-leaved forests compared to tropical and temperate evergreen broad-leaved forests (Cornelissen 1996). The high productivity and decomposition rate may provide the basis for the high biomass turnover rate in temperate deciduous broad-leaved forests.

Stem density in temperate deciduous broad-leaved and evergreen coniferous forests was lower than in tropical and temperate evergreen broad-leaved forests at a comparable WI due to the low density of small trees, though stem density varied independently of WI in temperate deciduous broad-leaved and evergreen coniferous forests. This suggests that large canopy trees may share a greater part of the resources and suppress small trees in temperate deciduous broad-leaved and evergreen coniferous forests. Takyu et al. (1994) showed that shrub species had much higher mortality and recruitment rates than canopy species in a temperate coniferous forest. Temperate evergreen conifers generally have a longer lifespan and greater maximum tree size than deciduous and evergreen broad-leaved trees (Waring and Franklin 1979; Suzuki and Tsukahara 1987). The high population turnover rate of temperate evergreen coniferous forests may result from the high population turnover rate of shrub species due to severe suppression by large canopy trees, although we could not compare the differences in population turnover rates between canopy and shrub species in our data set. However, we could not deny the effect of variation in gap formation among study plots on the forest dynamics in temperate evergreen coniferous forests, since attributes of forest dynamics varied independently of WI in this forest formation. Since the death of large canopy trees in coniferous forests may create large gaps, attributes of forest dynamics may vary if a study plot includes large gaps. On the other hand, high productivity due to the exclusive use of resources and the long lifespan of large canopy trees may result in the high AGB increment rate of temperate evergreen coniferous forests under colder conditions.

This study is a preliminary step in examining the effects of seasonality of climate and resultant changes in dominant life form using a database of forest inventory data; however, the database is not yet adequate for data from East Asia. The development of networks among forest ecologists and the accumulation of forest inventory data are necessary for understanding patterns and mechanisms of changes in ecosystem attributes along a latitudinal gradient and for monitoring changes in ecosystems in East Asia due to global climatic changes.

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Appendix 1

Table 3 List of study plots

Plot name	Region/country	Latitude	Longitude	Altitude (m)	Plot area (m^2)	Reference
Pasoh	Peninsular Malaysia/Malaysia	2°59′N	102°19′E	100	60,000	Niiyama et al. (2003)
Lambir CBP	Sarawak/Malaysia	4°2′N	113°5′E	200	80,000	Nakagawa et al. (2000)
Lambir Crane	Sarawak/Malaysia	4°2′N	113°5′E	200	40,000	Nakagawa et al. (2000)
Kinabalu 07T	Sabah/Malaysia	6°03′N	116°42′E	650	10,000	Aiba and Kitayama (1999)
Kinabalu 07U	Sabah/Malaysia	6°06′N	116°42′E	700	10,000	Aiba and Kitayama (1999)
Kinabalu 17T	Sabah/Malaysia	6°N	116°32′E	1,560	10,000	Takyu et al. (2002)
Kinabalu 17Q	Sabah/Malaysia	6°01′N	116°32′E	1,860	10,000	Takyuet al. (2002)
Kinabalu 17U	Sabah/Malaysia	6°03′N	116°36′E	1,860	2,000	Aiba and Kitayama (1999)
Kinabalu 27T	Sabah/Malaysia	6°03′N	116°32′E	2,590	2,500	Aiba and Kitayama (1999)
Kinabalu 27U	Sabah/Malaysia	6°03′N	116°32′E	2,700	2,000	Aiba and Kitayama (1999)
Kinabalu 31T	Sabah/Malaysia	6°05′N	116°33′E	3,080	2,000	Aiba and Kitayama (1999)
Mt.Makiling long-term monitoring plot	Luzon Island/Philippines	14°08′N	121°11′E	400	40,000	Luna et al. (1999)
Yakushima AIK	Kagoshima/Japan	30°23′N	130°38′E	170	5,000	Aiba (unpublished)
Yakushima KAW	Kagoshima/Japan	30°21′N	130°24′E	200	2,500	Aiba et al. (unpublished)
Yakushima HAN	Kagoshima/Japan	30°22′N	130°23′E	280	5,000	Aiba (unpublished)
Yakushima KOY1	Kagoshima/Japan	30°18′N	130°27′E	700	2,500	Aiba and Kohyama (1997)
Yakushima KOY2	Kagoshima/Japan	30°18′N	130°27′E	540	2,500	Aiba and Kohyama (1997)
Yakushima ANB	Kagoshima/Japan	30°19′N	130°36′E	570	5,000	Aiba (unpublished)
Yakushima ARA	Kagoshima/Japan	30°18′N	130°34′E	1,180	5,000	Aiba (unpublished)
Yakushima MIG	Kagoshima/Japan	30°19′N	130°29′E	1,200	10,000	Akashi et al. (unpublished)
Kirishima	Kagoshima/Japan	31°7′N	130°27′E	1,140	10,000	Kubota (unpublished)
Aya	Miyazaki/Japan	32°04′N	131°09′E	400	40,000	Tanouchi and Yamamoto (1995)
Ohkuchi	Kagoshima/Japan	32°8′N	130°32′E	490	4,700	Tanouchi et al. (1994)
Mt. Tatera	Nagasaki/Japan	34°08′N	129°13′E	170	40,000	Miura et al. (2001)
Ohdaigahara	Nara/Japan	34°11′N	136°04′E	1,450	10,000	Akashi and Nakashizuka (1999)
Ohdaigahara Belt 1	Nara/Japan	34°N	136°E	1,550	4,000	Nakashizuka (1991)
Ohdaigahara Belt 2	Nara/Japan	34°N	136°E	1,550	2,000	Nakashizuka (1991)
Ohdaigahara Belt 3	Nara/Japan	34°N	136°E	1,550	2,000	Nakashizuka (1991)
Ogawa	Ibaraki/Japan	36°54′N	140°35′E	555	60,000	Nakashizuka and Matsumoto (2002)
Kayanodaira	Nagano/Japan	36°5′N	138°3′E	1,500	10,000	Ida (unpublished)
Kanumazawa Riparian Research Forest	Iwate/Japan	39°06′N	141°52′E	430	47,100	Suzuki et al. (2002)
Shirakami Akaishizawa	Aomori/Japan	40°3′N	140°7′E	380	10,000	Nakashizuka (unpublished)
Shirakami Kumagera	Aomori/Japan	40°3′N	140°7′E	520	10,000	Nakashizuka (unpublished)
Shirakami Kushiishione	Aomori/Japan	40°3′N	140°7′E	624	10,000	Nakashizuka (unpublished)
Tomakomai Horonai	Hokkaido/Japan	42°43′N	141°34′E	90	12,000	Wada and Ribbens (1997)
Tomakomai Horonai hills	Hokkaido/Japan	42°43′N	141°34′E	90	6,800	Seino (unpublished)
Tomakomai Midori-no-tunnnel	Hokkaido/Japan	42°43′N	141°34′E	90	10,000	Kohyama et al. (1999)
Nukabira	Hokkaido/Japan	43°21′N	143°09′E	1,000	22,500	Takahashi (1994)
Taisetsu onsen	Hokkaido/Japan	43°21′N	143°1′E	1,000	18,000	Kubota et al. (1994)
Nopporo	Hokkaido/Japan	43°25′N	141°32′E	100	1,200	Seino (unpublished)
Taisetsu nipesotu	Hokkaido/Japan	43°29′N	143°04′E	1,400	1,200	Kubota (1995)
Taisetsu 13–1	Hokkaido/Japan	43°31′N	143°12′E	1,000	2,000	Kubota (1995)
Taisetsu 13–2	Hokkaido/Japan	43°31′N	143°12′E	1,000	1,600	Kubota (1995)
Taisetsu mikuni	Hokkaido/Japan	43°34′N	143°08′E	1,000	2,000	Kubota (1995)
Tokachigawa	Hokkaido/Japan	43°39′N	142°57′E	1,100	65,000	Kubota and Nagaike (unpublished)
Shiretoko 1	Hokkaido/Japan	44°04′N	145°02′E	200	22,500	Kubota (2000)
Shiretoko 2	Hokkaido/Japan	44°04′N	145°02′E	250	1,600	Kubota (unpublished)
Shiretoko 3	Hokkaido/Japan	44°04′N	145°02′E	250	1,600	Kubota (unpublished)

Appendix 2

Table 4 Allometric regressions among aboveground tree mass $W\mathrm{t}$ (kg), stem diameter DBH (cm), and tree height H (m) in each forest formation. $W\mathrm{t}$ is total of stem ($W\mathrm{s}$), branch ($W\mathrm{b}$), and leaf weights ($W\mathrm{l}$)

$W\mathrm{s}$	$W\mathrm{b}$	$W\mathrm{l}$	Reference
Cool-temperate/boreal mixed coniferous and deciduous broad-leaved forests			
$\ln W\mathrm{s}=0.884\ln(\mathrm{DBH}^2H)-3.089$	$\ln W\mathrm{b}=0.917\ln(\mathrm{DBH}^2H)-4.939$	$\ln W\mathrm{l}=0.904\ln(\mathrm{DBH}^2H)-6.846$	Takahashi et al. (1999)
$\ln W\mathrm{s}=2.424\ln\mathrm{DBH}-2.505$	$\ln W\mathrm{b}=2.572\ln\mathrm{DBH}-4.453$	$\ln W\mathrm{l}=2.500\ln\mathrm{DBH}-6.288$	Takahashi et al. (1999)
Boreal/subalpine coniferous forests			
$W\mathrm{s}=0.02847(\mathrm{DBH}^2H)^{0.919}$	$W\mathrm{b}=0.003938(\mathrm{DBH}^2H)^{0.928}$	$W\mathrm{l}=0.006117(\mathrm{DBH}^2H)^{0.8506}$	Research group on forest productivity of the four universities (1960)
$W\mathrm{s}=0.04653\mathrm{DBH}^{2.550}$	$W\mathrm{b}=0.006468\mathrm{DBH}^{2.570}$	$W\mathrm{l}=0.009640\mathrm{DBH}^{2.356}$	
Cool-temperate deciduous forests			
$W\mathrm{t}=0.00158(\mathrm{DBH}^2H)^{0.865}$, H (cm)			Nakashizuka (1984)
$W\mathrm{s}+b=0.122\mathrm{DBH}^{2.380}$		$W\mathrm{l}=0.0303\mathrm{DBH}^{1.72}$	Ikushima (1964)
Warm-temperate mixed coniferous and broad-leaved forests			
For *Abies firma*			
$W\mathrm{s}=0.0871(\mathrm{DBH}^2H)^{0.8269}$	$W\mathrm{b}=0.0088(\mathrm{DBH}^2H)^{0.9216}$	$W\mathrm{l}=0.0160(\mathrm{DBH}^2H)^{0.7466}$	Nakao (1985)
For *Tsuga sieboldii*			
$W\mathrm{s}=0.0361(\mathrm{DBH}^2H)^{0.9184}$	$W\mathrm{b}=0.0155(\mathrm{DBH}^2H)^{0.8979}$	$W\mathrm{l}=0.0790(\mathrm{DBH}^2H)^{0.8196}$	Nakao (1985)
For deciduous broad-leaved trees			
$W\mathrm{s}=0.0875(\mathrm{DBH}^2H)^{0.8581}$	$W\mathrm{b}=0.0134(\mathrm{DBH}^2H)^{0.9917}$	$W\mathrm{l}=0.0080(\mathrm{DBH}^2H)^{1.0383}$	Nakao (1985)
For evergreen broad-leaved trees			
$W\mathrm{s}=0.0495(\mathrm{DBH}^2H)^{0.9274}$	$W\mathrm{b}=0.0134(\mathrm{DBH}^2H)^{0.9917}$	$W\mathrm{l}=0.0190(\mathrm{DBH}^2H)^{0.6785}$	Nakao (1985)
For *Abies firma* with DBH ≥30 cm without tree height data			
$\log W\mathrm{s}=1.8071\log\mathrm{DBH}-0.0515$	$\mathrm{Log}\ W\mathrm{b}=2.4586\log\mathrm{DBH}-1.9471$	$\log W\mathrm{l}=1.7083\log\mathrm{DBH}-1.1837$	Ando et al. (1977)
For *Abies firma* with DBH			
$\log W\mathrm{s}=2.4748\log\mathrm{DBH}-1.1222$	$\log W\mathrm{b}=2.5308\log\mathrm{DBH}-2.0537$	$\log W\mathrm{l}=2.7036\log\mathrm{DBH}-2.6844$	Ando et al. (1977)
For *Tsuga sieboldii* without tree height data			
$\log W\mathrm{s}=2.1845\log\mathrm{DBH}-0.7232$	$\log W\mathrm{b}=3.0895\log\mathrm{DBH}-2.8608$	$\log W\mathrm{l}=2.4057\log\mathrm{DBH}-2.7498$	Ando et al. (1977)
For broad-leaved trees without tree height data			
$\log\mathrm{Ws}=2.5857\log\mathrm{DBH}-1.2268$	$\log W\mathrm{b}=2.6560\log\mathrm{DBH}-1.8546$	$\log W\mathrm{l}=1.7433\log\mathrm{DBH}-1.6735$	Ando et al. (1977)
Warm temperate evergreen broad-leaved forests			
$W\mathrm{t}=0.0303D_{0.1}^2H$, $D_{0.1}=0.941\mathrm{DBH}+0.734$		Nagano (1978)	
$W\mathrm{s}+b=0.119\ \mathrm{DBH}^{2.390}$		$W\mathrm{l}=0.0236\mathrm{DBH}^{1.93}$	Kimura (1960)
Tropical evergreen broad-leaved forests			
$W\mathrm{s}=0.02903(\mathrm{DBH}^2H)^{0.9813}$	$W\mathrm{b}=0.1192W\mathrm{s}^{1.059}$	$W\mathrm{l}=0.09146(W\mathrm{s}+W\mathrm{b})^{0.7266}$	Yamakura et al. (1986)
$W\mathrm{t}=\exp(-2.134+2.530\ln\mathrm{DBH})$			Brown (1997)

References

Adams JM, Woodward FI (1989) Patterns in tree species richness as a test of the glacial extinction hypothesis. Nature 339:699–701

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

Aiba S, Kohyama T (1997) Crown architecture and life-history traits of 14 tree species in a warm-temperate rain forest: significance of spatial heterogeneity. J Ecol 85:611–624

Akashi N, Nakashizuka T (1999) Effects of bark-stripping by Sika deer (*Cervus nippon*) on population dynamics of a mixed forest in Japan. For Ecol Manage 113:75–82

Ando T, Chiba K, Nishimura T, Tanimoto T (1977) Temperate fir and hemlock forests in Shikoku. In: Shidei T, Kira T (eds) Primary productivity of Japanese forests (JIBP synthesis 16). University of Tokyo Press, Tokyo, pp 213–244

Brown S (1997) Estimating biomass and biomass change of tropical forests. A primer. FAO Forestry Paper 134. A Forest Resource Assessment Publication

Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J, Holland EA (2001) Net primary production in tropical forests: an evaluation and synthesis of existing field data. Ecol Appl 11:371–384

Cornelissen JHC (1996) An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. J Ecol 84:573–582

Currie DJ (1991) Energy and large-scale patterns of animal- and plant-species richness. Am Nat 137:27–49

Holdridge LR (1947) Determination of world plant formations from simple climatic data. Science 105:367–368

Hutchinson GE (1959) Homage to Santa Rosalia, or why are there so many kind of animals? Am Nat 93:145–159

Ikushima I (1964) Productive structure of tree communities. In: National Park Agency of Japan (ed) Report on scientific research of Mount Ohyama in Tanzawa Mountains. Kanagawa Prefecture, Yokohama, pp 106–125

Iwasa Y, Sato K, Kakita M, Kubo T (1993) Modeling biodiversity: latitudinal gradient of forest species diversity. In: Schulze ED, Mooney HA (eds) Biodiversity and ecosystem function. Springer, Berlin Heidelberg New York, pp 433–451

Kikuzawa K (1991) A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. Am Nat 138:1250–1263

Kimura M (1960) Primary production of the warm-temperate laurel forest in the southern part of Oosumi Peninsula, Kyushu, Japan. Misc Rep Res Inst Nat Res 52–53:36–47

Kira T (1948) On the altitudinal arrangement of climatic zones in Japan (in Japanese). Kanti-Nogaku 2:142–173

Kira T (1976) Terrestrial ecosystems, ecological studies 2 (in Japanese). Kyoritu Shuppan, Tokyo

Kitayama K (1992) An altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. Vegetatio 102:149–171

Kohyama T, Suzuki E, Aiba S, Seino T (1999) Functional differentiation and positive feedback enhancing plant biodiversity. In: Kato M (ed) The biology of biodiversity. Springer, Berlin Heidelberg New York Tokyo, pp 179–191

Kubota Y (1995) Effects of disturbance and size structure on the regeneration process in a sub-boreal coniferous forest, northern Japan. Ecol Res 10:135–142

Kubota Y (2000) The spatial dynamics of regeneration in a conifer/broadleaf mixed forest in northern Japan. J Veg Sci 11:633–640

Kubota Y, Hiura T, Konno Y (1994) Stand structure and growth patterns of understory trees in a coniferous forest, Taisetsuzan National Park, Japan. Ecol Res 9:333–341

Lieth H (1975) Modeling the primary productivity of the world. In: Lieth H, Whittaker RH (eds) Primary productivity of the biosphere. Springer, Berlin Heidelberg New York Tokyo, pp 237–263

Luna AC, Osumi K, Gascon AF, Lasco RD, Palijon AM, Castillio ML (1999) The community structure of a logged-over tropical rain forest in Mt. Makiling Forest Reserve, Philippines. J Trop For Sci 11:446–458

Miura M, Manabe T, Nishimura N, Yamamoto S (2001) Forest canopy and community dynamics in a temperate old-growth evergreen broad-leaved forest, south-western Japan: a 7-year study of a 4-ha plot. J Ecol 89:841–849

Nagano M (1978) Dynamics of stand development. In: Kira T, Ono Y, Hosokawa T (eds) Biological production in a warm-temperate evergreen oak forest of Japan (JIBP synthesis 18). University of Tokyo Press, Tokyo, pp 21–32

Nakagawa M, Tanaka K, Nakashizuka T, Ohkubo T, Kato T, Maeda T, Sato K, Miguchi H, Nagamasu H, Ogino K, Teo S, Hamid AA, Seng LH (2000) Impact of severe drought associated with the 1997–1998 El Nino in a tropical forest in Sarawak. J Trop Ecol 16:355–367

Nakao T (1985) Ecological studies of *Abies* and *Tsuga* forests in Kyushu, Japan. Bull Miyazaki Univ For 25:1–156

Nakashizuka T (1984) Regeneration process of climax beech (*Fagus crenata*) forests V. Population dynamics of beech in a regeneration process. Jpn J Ecol 34:411–420

Nakashizuka T (1991) Population dynamics of coniferous and broad-leaved trees in a Japanese temperate mixed forest. J Veg Sci 2:413–418

Nakashizuka T, Matsumoto Y (2002) Diversity and interaction in a temperate forest community. Springer, Berlin Heidelberg New York Tokyo

Niiyama K, Kassim AR, Iida S, Kimura K, Ripin A, Appanah S (2003) Regeneration of a clear-cut plot in a lowland dipterocarp forest in Pasoh Forest Reserve, Peninsular Malaysia. In: Okuda T, Manokaran N, Matsumoto Y, Niiyama K, Thomas SC, Ashton PS (eds) Pasoh: ecology of a lowland rain forest in Southeast Asia. Springer, Berlin Heidelberg New York Tokyo, pp 559–568

Ohsawa M (1995) Latitudinal comparison of altitudinal changes in forest structure, leaf-type, and species richness in humid monsoon Asia. Vegetatio 121:3–10

Phillips OL, Hall P, Gentry AH, Sawyer SA, Váquez R (1994) Dynamics and species richness of tropical rain forests. Proc Natl Acad Sci USA 91:2805–2809

Reich PB (1993) Reconciling apparent discrepancies among studies relating life span, structure and function of leaves in contrasting plant life forms and climates: ‘the blind men and the elephant retold’. Funct Ecol 7:721–725

Reich PB, Bolstad P (2001) Productivity of evergreen and deciduous temperate forests. In: Roy J, Saugier B, Mooney HA (eds) Terrestrial global productivity. Academic, San Diego, pp 245–283

Research group on forest productivity of the four universities (1960) Studies on the productivity of the forest. Part I. Essential needle-leaved forests of Hokkaido. Kokusaku Pulp, Tokyo

Runkle JR (1989) Synchrony of regeneration, gaps, and latitudinal differences in tree species diversity. Ecology 70:546–547

Suzuki E, Tsukahara J (1987) Age structure and regeneration of old growth *Cryptomeria japonica* forests on Yakushima Island. Bot Mag Tokyo 100:223–241

Suzuki W, Osumi K, Masaki T, Takahashi K, Daimaru H, Hoshizaki K (2002) Disturbance regimes and community structure of a riparian and an adjacent terrace stand in the Kanumazawa Riparian Research Forest, northern Japan. For Ecol Manage 157:285–301

Takahashi K (1979) Estimate of evapotranspiration based on monthly temperature and precipitation (in Japanese). Tenki 26:759–762

Takahashi K (1994) Effect of size structure, forest floor type and disturbance regime on tree species composition in a coniferous forest in Japan. J Ecol 82:769–773

Takahashi K, Yoshida K, Suzuki M, Seino T, Tani T, Tashiro N, Ishii T, Sugata S, Fujito E, Naniwa A, Kudo G, Hiura T, Kohyama T (1999) Stand biomass, net production and canopy structure in a secondary deciduous broad-leaved forest, northern Japan. Res Bull Hokkaido Univ For 56:70–85

Takyu M, Ohsawa M, Ozaki K, Ohtsuka Y, Yoshida N, Honma K, Ono M, Egusa K (1994) Community dynamics of a *Cryptomeria japonica* forest during 10 years in the Yakushima wilderness area, Yakushima island, southern Japan. In: Environment Agency, Nature Conservation Bureau (ed) Long term ecological studies in the Yakushima wilderness area and its surrounding areas, 1994 reports (in Japanese with English summary). Nature Conservation Society of Japan, Tokyo, pp 3–19

Takyu M, Aiba S, Kitayama K (2002) Effects of topography on tropical lower montane forests under different geological conditions on Mount Kinabalu, Borneo. Plant Ecol 159:35–49

Tanouchi H, Yamamoto S (1995) Structure and regeneration of canopy species in an old-growth evergreen broad-leaved forest in Aya district, southwestern Japan. Vegetatio 117:51–60

Tanouchi H, Sato T, Takeshita K (1994) Comparative studies on acorn and seedling dynamics of four Quercus species in an evergreen broad-leaved forest. J Plant Res 107:153–159

Thornthwaite CW (1948) An approach toward a rational classification of climate. Geogr Rev 21:633–651

Uchijima Z, Seino H (1985) Agroclimatic evaluation of net primary productivity of natural vegetations. I. Chikugo model evaluating net primary productivity. J Agr Meteorol 40:343–352

Wada N, Ribbens E (1997) Japanese maple (*Acer palmatum* var. *matsumurae*, Aceraceae) recruitment patterns:seeds, seedlings, and saplings in relation to conspecific adult neighbors. Am J Bot 84:1294–1300

Waring RH, Franklin JF (1979) Evergreen coniferous forests of the Pacific Northwest. Science 204:1380–1386

Whitmore TC (1990) An introduction to tropical rain forests. Clarendon Press, Oxford

Yamakura T, Hagiwara T, Sukardjo S, Ogawa H (1986) Aboveground biomass of tropical rain forest stands in Indonesian Borneo. Vegetatio 68:71–82