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博士論文

Effects of topography on the community dynamics in a warm–temperate mixed forest

（暖温帯針広混交林の群集動態に影響する地形要因）

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1. Introduction

It has been recognized that a mature forest stand shows spatio-temporal heterogeneity and it is maintained by gap formation and repair of the canopy layer by natural disturbance (e.g. Runkle 1985, Pickett and White 1985). It has been found that the forest structure constructed by trees which have a long life span is affected and defined by a rare big event such as strong typhoon (e.g. Suzuki 1979, Sakai et al. 1999), so analysis of 10-20 years or so on plot scale is insufficient to explain the forest dynamics. It is considered necessary both the investigation of catchment scale to reveal canopy dynamics of the long-term and plot scale survey to examine the effect of site environment on the mortality and growth of the individual level.

How does topographic factors effect to tree species distribution and determine it in many species mixed forest? The fine-scale distributions of tree species often vary with factors such as elevation, inclination and moisture regime, and differential performance across such gradients contributes to species diversity and co-existence (e.g. Ashton 1976; Gunatellike et al. 2003; Davies et al. 2005). In contrast, other models hypothesise that the distribution of tree species is neutral, with no significant relationship between the environment and tree location (e.g. Wong and Whitmore 1970; Hubbell 2001). When habitat conditions are similar, other factors such as dispersal may maintain species diversity (Harms et al. 2001; Valencia et al. 2004). In order to quantify how habitat conditions contribute to the maintenance of species diversity, it is necessary to test for a relationship between the dynamics and habitat of the target population (Russo et al. 2005; Ito 2006). Because the distribution of trees reflects dynamic processes such as seed dispersal, germination, seedling establishment, growth and mortality, tree distribution patterns should help to clarify how differences between habitat location and disturbance regime affect these processes. In other words, patterns of mortality, recruitment and growth of some species may shift along environmental gradients. For example, topography provides a diversity of habitats for trees in forest ecosystems. The relationship between vegetation and topographic position has often been attributed to soil moisture and soil fertility gradients along slopes (e.g. Day and Monk 1974; Basnet 1992; Chen et al. 1997; Chase et al. 2012).

Several studies have demonstrated that instability of the ground surface is also an important factor generating differences in species distribution along micro-topographical gradients (e.g. Sakai and Ohsawa 1994; Hara et al. 1996; Nagamatsu and Miura 1997; Ohnuki et al. 1998; Hirayama and Sakimoto 2003). In addition, previous research has also examined species differences in demographic parameters (mortality, recruitment and growth) among habitats and their relationship to population structure (Nagamatsu et al. 2003; Tsujino et al. 2006; Nakamori et al. 2009; Suzuki 2011). However, the degree of instability of the ground surface was not measured in these studies, and the relationships between the distribution of species and habitat gradients are not clear. Ohnuki et al. (1998) and Nagamatsu and Miura (1997) demonstrated that movement of the ground surface of a lower valley-side slope was greater than movement of the upper valley-side slope, whereas other studies have not detected differences in instability of the ground surface along crest slopes to lower valley-side slopes (Nagamatsu et al. 2002; Kubota et al. 2007).

Coexistence of trees species is maintained by various regeneration processes in heterogeneous environmental conditions those are caused by natural disturbances. In forest stands various types and magnitudes disturbances occur, and the canopy gaps created a spatio-temporal heterogeneity of nutrient resources and light condition and then alter stand structure and dynamics (e.g. Pickett and White 1985; Takafumi et al. 2010). The importance of disturbance for regeneration was pointed out many studies (e.g. Pickett and White 1985).

To explain the spatial distribution of tree species, and the species coexistence, it is important to reveal how canopy gaps occur whether randomly or non-randomly in space and time, depending on the stand structure and/or topography. Scale and magnitude of gap formation are diverse, e.g. from a branch fall, to catastrophic blow down due to strong winds such as typhoons, ground surface movement such as landslides (Mooney and Godron 1983). Permanent plots study was the major method for gap formation and stand dynamics (Nakashizuka et al.1995; Hubbell et al. 1999), however recently time series of aerial photographs are used to analyze the dynamics in deciduous broad-leaved forest (Tanaka and Nakashizuka 1997; Henbo et al. 2004) and in the evergreen broad-leaved forest (Fujita et al.2003ab; Itaya et al.2004; Yamamoto et al. 2011). Furthermore analysis by airborne LiDAR data and satellites for canopy dynamics in long-term and wider area performed (e.g Asner et al. 2002, 2013; Kellner et al. 2009; Vega and St-Onge2009). The long-term and large scale study clarified that there was a tendency to spread gap around the former gap (e.g. Runkle 1985; Kubo et al. 1996), and the phenomenon was explained by the lattice-structured forest model (Kubo et al. 1996; Schlicht and Iwasa 2004, 2006). However, previous researches were done in a relatively flat topography such as plain and hills (Kubo et al. 1996; Asner et al. 2013). There is little study to clarify the relationship between canopy dynamics and topography in steep slope mountains in a watershed scale. In addition, the difference of canopy dynamics depending on the life-form such as conifer and evergreen broad-leaved tree by aerial photographs has never been done mostly in warm temperate forests (but in a northern mixed forest, see Vepakomma et al. 2012). Before the land use by humans about 1000 years ago, there were old growth temperate mixed forests composed by conifers *Chamaecyparis, Cryptomeria, Tsuga, Sciadopitys* with evergreen or deciduous broad-leaved trees, but the most part of forest in Japan has been lost after human activities (Takahara et al. 2000). It is not well understood the structure and dynamics of community of the mixed temperate conifer and broad leaved mixed forest.

Therefore, firstly in 1ha plot scale, I directly measured movement of the ground surface within several topographic units and investigated the relative contribution of environmental factors, including the degree of instability of the ground surface, to mortality and recruitment rate of tree species. In a warm–temperate forest composed of evergreen conifers and evergreen broad-leaved trees along a steep mountain slope I focused on the following questions: Does the degree of instability of the ground surface affect tree distribution? Does an advantage exist in terms of lower mortality, higher recruitment and enhanced growth of particular habitats for major species that have habitat specificity?

Then, secondarily I analyzed canopy dynamics of the stand in a catchment scale by using aerial photography for several decades. I addressed the following subjects to clarify the relationship between gap formation process and topography and/or stand structure, and how does the topography affect the distribution of conifer trees and coexistence mechanism of mixed forest community?

2. Study site

The study site was located at Ichinomata Conservation Forest in the Shimanto River watershed in southwest Shikoku, Japan (33.14°N, 132.91°E, see Fig.1). The study forest area was covered by a 52-ha old-growth forest surrounded by plantations. The elevation of the forest was 450–780 m and mean elevation was ca. 580m (see Fig.2). Annual mean temperature at 500-m elevation was 12.7°C, as estimated from the nearest meteorological station. Average annual precipitation was about 3000 mm (Japan

Meteorological Agency http://www.jma.go.jp/jma/indexe.html). The study forest is composed of conifers and evergreen broad-leaved tree species in the upper region of the warm–temperate zone. Dominant species are *Chamecyparis obtusa*, *Tsuga sieboldii* as conifers and some *Quercus species* as broad-leaved trees (see table 2). The topography is extremely steep; the average inclination is about 40–45° on slopes and approximately 25–35° on the ridge. Based on aerial photos, conifer and evergreen broad-leaved trees are mainly distributed on the ridge and on the slope, respectively. Surface geology at the site consists of Mesozoic sandstones and shales of the Shimanto group (http://riodb02.ibase.aist.go.jp/db084/index.html). Soil types in study site are BD on lower slope, BD(d), BC on middle and upper slope, PD on ridge (Hirai et al. 2007). Temperate coniferous forests containing extremely high biomass have been observed in regions of the Northern Hemisphere that experience high precipitation and relatively warm winters (Franklin and Dyrness 1973; Sillett and van Pelt 2000; Takyu et al. 2005). The combined aboveground and belowground biomass of the study forest is about 800 t/ha (Ando et al. 1977; Ishihara et al. 2011). Most old-growth forests of the warm–temperate zone in Japan have disappeared due to logging; thus, remnant stands and relevant information are extremely limited.

3. Methods

3-1. Plot scale

Field survey

In 1994, I established a permanent 100 × 100-m plot that included a ridge between two small valleys across an elevation gradient of 480–550 m on a north-facing slope (see Fig. 2 and Fig. 3). The plot was divided into 100 subplots (10 × 10 m). All trees [diameter at breast height (DBH) ≥ 5 cm] were tagged, identified and their DBH were measured at 1.3 m to the nearest millimetre. The locations of trunk bases were mapped using a transit compass. Forty-six species appeared in the study plot in 1994. Nomenclature followed Satake et al. (1989)

A 10 × 50-m escarpment (inclination > 50°) along one side of the plot was excluded from monitoring and analysis. I censused the plot six times between 1994 and 2007. The types of injuries incurred by dead trees were classified into three types: standing dead, uprooted and broken main stem.

Airborne LiDAR data were collected around the study site to develop 1-m grid digital elevation models (DEMs; Onda et al. 2010). A contour map of the study site was generated based on these data. A differential GPS (using a Trimble Geo XH) survey was conducted at four points within the study site, which was then positioned upon the contour map. I determined the micro-topography within the subplots using Tamura's classification (Tamura 1980, 1981). This classification is clearly explained below and was previously used by Nagamatsu et al. (2002). A crest slope (CS) has a gentle gradient and occupies the uppermost area of a slope, including the drainage divide. The upper side-slope (US) is a downward slope adjacent to the CS. Both the upper and lower borders of this unit are convex break-in slopes. The head hollow (HH) is a concave slope draining overland flow that is located at the top of a watershed. The lower side-slope (LS), which is the steepest slope of the six micro-landform units, is adjacent to the US. The upper border is often delimited by a sharp, convex break-in slope, and the lower border is concave. A foot slope (FS) is a gentle slope in which debris from the upper units (mostly from LS) accumulates. Riverbed (RB) is a flat floor along a stream. A clear border divides these six micro-landform units into two groups: the stable upper hillslope area (CS, US and HH) and the disturbed lower hillslope area (LS, FS and RB).

The amount of sediment and litter movement was measured as an index of the stability of the ground surface. I used small sediment traps (15 × 25 × 20 cm) to measure transported materials (Tsukamoto 1991; Miura et al. 2002). A 0.5mm-thick aluminium sheet was attached horizontally to the front opening to prevent materials from passing beneath the trap, and the rear opening was covered with mesh and plastic sheeting. In August 1993 and December 2007, I set up 40 and 44 traps, respectively, to measure the amount of sediment and litter movement for about 1 year. These traps were placed within a variety of micro-topographies from the ridge to the valley. Different subplots were selected in two periods. There were 36 traps in upper area and 48 in lower area as a result (A: 18, B: 4, C: 15, D: 6, E: 16, F: 15; see Results). Samples were collected at intervals of about 1–2 months. Samples were dried at 80°C for 48 h and weighed. The samples were separated into two size classes using standard sieves with mesh sizes of 2.0 mm; size classes were defined as fine earth (<2.0 mm) and gravel or litter (≥2.0 mm). Gravel and litter were carefully separated by hand. The dry mass (g) of each separated size class was determined. If there were traps in the same subplots, the amount of movement was calculated as the average values.

To determine the light environment at the forest floor, I measured canopy openness using hemispherical photographs analysed using computer software Hemiphot (ter Steege 1993). Hemispherical photographs were taken at 1.3 m height in 22 subplots during September 1998. Among the 22 subplots, 18 were located in the upper area and four were located in the lower area.

Statistical analysis

The topographic wetness index (TWI; Beven and Kirkby 1979) of each subplot was calculated. TWI reflects the catchment area per unit area and is a useful indicator of moisture conditions (Yagihashi et al. 2010). I used the open-source GIS software GRASS (Grass ver.6.3) to calculate TWI using DEM data (at 10-m intervals) in a 120 × 160-m quadrat that included the study plot. The aspect and average inclination of each subplot were calculated from the DEM data using ArcGIS9.3. To analyse the species composition of each subplot, the dominance of tree species was evaluated using the proportional density of each tree species in 2007. Subplots were ordinated by using non-metric dimensional scaling (NMDS biplot see Fig.4). I use the package “vegan” in R (R Development Core Team 2008) for this analysis. The value of the first NMDS axis was assumed to reflect some environment conditions of subplots such as micro-topographic division, TWI, slope inclination and aspect. The factors affecting the distribution of species were analysed using regression tree analysis (De’ath and Fabricius 2000). The regression tree analysis is well suited for modelling complex interactive relationships among explanatory variables (Clark and Pregibon 1992). The best division frequency for the regression tree was determined by 200- hold cross-validation (see Fig. 5). Analyses were conducted using R (R Development Core Team 2008).

To determine the environmental preference identified by the regression tree analysis for major species (N > 30), I analysed the difference between an actual distribution and a random distribution using Monte Carlo simulations based on the methods by Ito et al. (2007). The simulation frequency was set at 10 000 permutations. I categorized the major tree species into three groups according to whether the species occurrence was biased to upper or lower area based on the significant level by the Monte Carlo simulations $\alpha = 0.001$ (Table 3).

To quantify the frequency distribution of species’ sizes in the upper and lower areas, I calculated the third moment around the midpoint of the diameter at breast height (DBH) range as the size distribution index (SDI; Hubbell 1979; Masaki et al. 1992, 1999, Shibata et al. 2013). SDI was calculated using the following expression:

$$SDI_i = \frac{1}{n_i}\sum_{j=1}^{n_i}\left(x_{ij} - 0.5\right)^3 \qquad \text{eq.1}$$

where x_{ij} is the standardised DBH (ranging from 0 to 1) of the jth stem of the ith species, and n_i is the number of stems of the ith species. x_{ij} was calculated using the equation $x_{ij} = (d_{ij} - 5)/(D_i - 5)$, where d_{ij} is the DBH of the jth stem of the ith species, and D_i is the maximum DBH of the ith species. Plots of SDI against the maximum DBH for each forest had been suggested population structure (Masaki et al. 1992, 1999). When the SDI is small, the population includes many small trees; i.e. the size distribution often shows a reversed J-shape. When the SDI is large, however, the population includes fewer small trees and is often bell-shaped. Plots of SDI against the logarithm of maximum DBH for each forest, which had been suggested as an indicator of population structure (Masaki et al. 1992, 1999).

Mortality, recruitment and the relative growth rate of diameter (RGRD) were estimated by the following equations:

Mortality: $\ln(N1994/N(1994–2007))/13$ eq.2

Recruitment rate: $(\ln(N2007/N(1994–2007))/13$ eq.3

where N1994 is the number of trees in 1994, N (1994–2007) is the number of trees surviving from 1994 to 2007 and N2007 is the number of living trees in 2007 (Sheil and May 1996).

$$\mathrm{RGRD} = 1/\mathrm{DBH} \cdot d\mathrm{DBH}/dt = (\ln \mathrm{DBH}2007 - \ln \mathrm{DBH}1994)/13$$

$$= a - b \ln \mathrm{DBH}1994 \qquad \text{eq.4}$$

I was interested in not only relative diameter growth rate but also the maximum diameter of species at each habitat because the maximum value indicates the potential life span. Frequently, however, I could not determine longevity by the actual maximum diameter due to small sample size. I assumed that the maximum diameter (DBHmax) was reached when the approximation of RGRD became 0 in eq.4 (Aiba and Kohyama 1996).

3-2 Catchment scale

Analysis of aerial photography to identify canopy gaps and conifer trees

Airborne LiDAR data were collected around the study site to develop 1-m grid Digital Terrain Model (DTM; Onda et al. 2010). I created the digital surface model (DSM) from aerial photographs of 1969, 1985, 2005 (Shooting date: 1969/5/21 camera:RC-8 F = 210.63 mm, photographic magnification 1:20000, Shooting date:1985 / 10/ 2 camera: RMK-A(21/23), F = 208.26 mm, magnification 1:16000, Shooting date: 2005 / 4 /28, camera : RC-30 21/23, F = 213.73 mm, photographic magnification 1:16000). I estimated a digital canopy height model (DCHM) of each year from the difference between the DTM. DSM, DTM and DCHM obtained at 1m mesh unit (Fig.11).

I extracted the canopy gaps from DSM defining gaps as areas with a canopy lower than 15 m and the area ≧10 m^2. In addition, I extracted the new created gaps during 1969 to 1985, and 1985 to 2005. I defined as part of the area more than 10m^2 and 10m less than the difference between the DSM a new created gap. I identified the conifer trees in each year by the stereoscopic aerial photographs. I used PC software “imagine stereo analysis” in stereoscopic vision.

I verified the certainty of extraction of conifer canopy by matching the ground tree data of 1ha, I recognized 68 conifer trees by aerial photography for real 85 conifer trees, and then the correct probability was 80%.

Statistical analysis

I set a target area of 39ha in a watershed, 50m inside of the forest edge from the remaining stands (52ha) to remove an edge effect.

I analyzed for gap formation by a logistic regression the factors as eq.1. Each variable was required by 5m mesh grid divided in the study area.

$$\text{logit (gap)} = \alpha + \beta 1\ (\text{slope}) + \beta 2\ (\text{TWI}) + \beta 3\ (\text{RVR}) + \beta 4\ (\text{NS}) + \beta 5\ (\text{EW}) + \beta 6\ (\text{DCHM}) + \beta 7\ (\text{conifer}) + \beta 8\ (\text{neighbor}) \qquad \text{eq.5}$$

where, α = intercept , β = coefficients, explained variable: inclination (slope), topographic wetness index (TWI) (Beven and Kirkby 1979), spatial index shown relatively from valley to ridge of each mesh (RVR: which value range -1(thalweg) $\leq$ RVR $\leq$1(ridge)), slope direction from north to south (NS), slope direction from east to west (EW), average canopy height (DCHM), life form (conifers), adjacent to the former gap (neighbor). RVR were calculated proportion from -1 (valley) to 1(ridge) location There was a loss of 17 trees and then nine gaps created gap by selective cutting in a part of stand (ca. 2.5 ha) in 1985 -1986. The gaps caused by selective cutting were excluded from the new gap analysis. I analyzed factors which affected the gap area by GLM as eq. 6. Response variable is assumed to be an exponential distribution, the link function using logarithm)

$$\text{Gap area} = \alpha + \beta1\ (\text{slope}) + \beta2\ (\text{TWI}) + \beta3\ (\text{RVR}) + \beta4\ (\text{NS}) + \beta5\ (\text{EW}) + \beta6\ (\text{DCHM}) + \beta7\ (\text{conifer}) + \beta8\ (\text{neighbor}) \qquad \text{eq.6}$$

In order to clarify the determinants of the distribution of conifer, I performed logistic regression as eq.7.

$$\text{logit (conifer)} = \alpha + \beta1\ (\text{slope}) + \beta2\ (\text{TWI}) + \beta3\ (\text{RVR}) + \beta4\ (\text{NS}) + \beta5\ (\text{EW}) \qquad \text{eq. 7}$$

I checked the VIF to void multicollinearity between 8 explanatory variables by VIF.

I analyzed in order to reveal factors which affected the DCHM change by GLM as eq. 8 Response variable is assumed to be normally distributed distribution, the link function is the identity. For analysis, I divided into the two cases in accordance with the definition of the foresy canopy and gaps. ($DCHM \geq 15m$ and $DCHM < 15m$)

$$\text{Amount of DCHM change} = \alpha + \beta1\ (\text{slope}) + \beta2\ (\text{TWI}) + \beta3\ (\text{RVR}) + \beta4\ (\text{NS}) + \beta5\ (\text{EW}) + \beta6\ (\text{DCHM}) + \beta7\ (\text{conifer}) + \beta8\ (\text{neighbor}) \qquad \text{eq.8}$$

α = intercept, β = coefficient

I calculated the mortality as eq.9.

$$\text{Mortality} = \ln(\text{Nbeginning}/\text{Nsurvive})/t\ (\text{year}) \qquad \text{eq.9}$$

where Nbeginning is the number of trees in beginning observation, Nsurvive is the number of trees surviving between observation period (t). (Sheil and May 1996).

4. Results

4-1 Plot scale

Environmental variability and vegetation categorisation

The subplots were classified into four landform-unit categories: crest slope (CS), upper side-slope (US), lower side-slope (LS) and foot slope (FS). No subplots were classified as head hollow (HH) or riverbed (RB). Foot slope was categorised within upper side-slope. The inclinations of CS, US and LS were ca. 25–40°, 30-50° and 30-50°, respectively. The value of TWI increased from the ridge toward the LS (Fig. 3, Table 1).

Cross-validation revealed that the optimum number of terminal nodes was 6-8. Thus, I decided to the model with the terminal node of 6 to make the model simple (Fig. 5). The regression tree analysis revealed that landform unit including some environmental conditions such as the instability of the land surface was a primary factor affecting the vegetation structure of the study plot (Fig. 6). The subplots were primarily divided into two groups: the upper area consisted of CS and US, and the lower area comprised LS and FS. TWI was the second-most important factor affecting species composition in the upper area, which was then further divided into four categories. The lower area was divided into two categories based on inclination. Thus, landform unit, TWI and inclination were the likely factors affecting the vegetation distribution.

The amount of sediment and litter movement drastically differed between the upper area (sediment: 1329g/m/yr. (±335.9 SE) $P < 0.0001$ litter: 308g/m/yr. (±39.3 SE) $P = 0.0005$, ANOVA) and lower area (sediment: 3956g/m/yr. (±392.8 SE) $P < 0.0001$, litter: 554.7g/m/yr. (±39.1 SE) $P = 0.0005$, ANOVA). Sediment and litter movement in the lower area were 10–100 times and 10 times higher, respectively, than in the upper area. The amount of litter movement was significantly positively associated with inclination in the upper and marginally in so lower areas (upper area: litter = 20.6 × (subplot inclination) –492.2, $P = 0.0023$, $R^2 = 0.196$; lower area: litter = 16.2 × (subplot inclination) – 119.5, $P = 0.058$, $R^2 = 0.094$). The amount of sediment movement was not significantly correlated with inclination in the upper or lower area.

Average canopy openness was 5.6% (±0.46 SE) in the upper area and 5.0% (± 0.26 SE) in the lower area, and openness did not significantly differ among landform units ($P = 0.74$). Moreover, openness and inclination were not related ($P = 0.379$).

Distribution and dynamics of dominant species

Castanopsis sieboldii, *Symplocos myrtacea*, *Symplocos prunifolia*, *Pieris japonica* and the conifers *Chamaecyparis obtusa* and *Tsuga sieboldii* tended to be distributed within habitats A and B (Table 3, Fig. 6) in the upper area; these species are called the “upper species”. *Machilus japonica* and *Neolitsea aciculata* were distributed within the lower area (habitats E, F); these two species are the “lower species”. *Camellia japonica*, *Quercus salicina*, *Cleyera japonica*, *Illicium anisatum* and *Eurya japonica* did not exhibit notable preferences; these species are the “common species”.

The maximum diameter and SDI value were high for *C. obtusa* and *T. sieboldii* (Fig. 7). The SDI of evergreen broad-leaved species was low. The SDIs of the upper species were lower in the upper area than in the lower area. In contrast, the SDIs of the lower species were lower in the lower area than in the upper area. The SDIs of the common species were similar in both the upper and lower areas, with the exception of *E. japonica* that showed lower SDI value in the upper area.

The maximum sizes of species in the upper and lower areas did not differ across locations (Fig. 8). *Illicium anisatum* and most species found primarily in the upper area could not be compared across locations due to their rarity in the lower region.

The mortalities of most species were higher in the lower area than in the upper area (Table 2), with the exception of the two lower species (1.97%/year and 1.72%/year for *N. aciculata*, 2.13%/year and 4.30%/year for *M. japonica* in the lower and upper area, respectively). The recruitment rates of almost all species were higher in the upper area than in the lower area. Year-to-year variation in the recruitment rate and mortality during the measurement period was small.

The proportion of dead trees that had been uprooted was three times higher in the lower area (19/107) than in the upper area (9/139; Table 4).

Relationship between the environment and population dynamics

For nearly all tree species, the number of trees that died increased in proportion to the amount of sediment movement [generalized linear model (GLM), binomial distribution; $P < 0.001$; Fig. 9]. This pattern was particularly strong for smaller trees (5 cm ≤ DBH < 10 cm; $P < 0.001$) but only marginal for larger trees (DBH > 10 cm; $P = 0.073$). Tree mortality was significantly positively correlated with sediment movement for upper species including *S.prunifolia* ($P = 0.0005$ for all upper species, $P = 0.006$ for *S. prunifolia*) as well as for common species ($P = 0.019$ for all common species). However, this relationship did not hold for any of the lower species, including *M. japonica* ($P = 0.321$ for all lower species, $P = 0.479$ for *M. japonica*).

Recruitment rate was lower at sites experiencing a large amount of sediment movement for all upper species, including *S. prunifolia* ($P = 0.0050$ for all upper species, $P = 0.007$ for *S. prunifolia)* and for the common species, including *Camellia japonica* ($P = 0.015$ for all common species, $P = 0.025$) (fig. 9). However, this relationship was not significant for the lower species ($P = 0.340$); in fact, the opposite pattern (more recruitment stems at sites with more sediment movement) was significant for the lower species *M. japonica* ($P = 0.002$).

The number of dead stems and TWI were significantly related for all upper species, including *S. prunifolia* and *P. japonica* (*P* = 0.006 for all upper species, *P* = 0.027 for *S. prunifolia*, *P* = 0.015 for *P. japonica*) (Fig. 10). However, these variables were not correlated for the lower species, including *M. japonica* (*P* = 0.995 for all lower species, *P* = 0.932 for *M. japonica*). However, recruitment rate and TWI in the upper area were significantly related for the lower species, including *M. japonica* (*P* = 0.046 for all lower species, *P* = 0.049 for *M. japonica*).

4-2 Catcment scale

*Gap creation process depending on the topography and stand structur*e

The average canopy height and maximum tree height were ca. 23.8m and 50m respectively in 1969 (Fig.11). There were 380 gaps and its total area was 2.28hain 1969. There were 318 and 237 gaps and its total areas were 1.86ha and 1.19ha in 1985 and 2005, respectively, then the gap area decreased year by year (Fig. 12). Frequency distribution of gap size did not follow both power and log-normal.

The numbers of new created gaps were 201 and 156 for 1969-1985 (a total area of 1.38ha) and 1985-2005 (a total area of 0.64 ha), respectively. Gap formation rate during 1969-1985 was 3 times higher than during 1985-2005 (Fig.13).

There was no significant relationship between gap formations and life form, but significant positive relationship with neighbor and DCHM of both durations and negative relationship with TWI and RVR (Table 5). There was a significant positive relationship between the gap formation and slope during 1969-1985. DCHM was the largest factor in both durations by standardized partial regression coefficient. There were significant relationship between gap formation and direction and effects of direction were different in both durations. There was no significant relationship between gap area and topographic factors (Table 6). Gap area shows the significant positive relationship between neighbor and DCHM during 1969-1985 and 1985-2005, gap area shows significant positive relationship between life form in 1969-1985.

Gap formation process due to the difference in life form

Distribution of conifer tree was concentrated in the ridge area in the watershed (Table 7, Fig. 14). There were significant relationships between the distributions of conifer trees and topographic factors (slope, TWI, RVR) corresponded to gentle dry ridge. Average canopy height of 5m mesh in which there was conifer tree is 28.5m±0.20m (SE) in 1969. Average canopy height of 5m mesh without conifer is23.5m±0.04m (SE), then conifer canopy height was higher than broad leaved tree.

Frequency distributions of new created gaps by each life form did not follow both the power and log-normal distributions (Fig. 15). Large gaps were created by conifers especially in 1969-1985.

Factors affecting on the changes of height were different between height categories and durations (Fig. 16, Table 8). Almost factors had significant effects on the height change in the canopy. In the place where is steep, wet, near valley, not neighbor of former gap, low canopy height and with conifer species, canopy height increased (Table 8). Direction showed significant effects and the effects were varied both durations. There were significant effects of slope, TWI and DCHM in both periods, however, factors of RVR, neighbor and life form showed various effects in both periods for DCHM < 15m.

5. Discussion

Instability on steep slopes mediates tree species co-existence

Landform unit was selected as the most important factor determining vegetation patterns (Fig. 6). In the present study, the movement of sediment and litter on the ground surface was measured directly. Thus, I were able to demonstrate that movement of these materials was much higher on the lower side-slope and the foot slope below clear borderline that divide the landform than on the crest slope and upper side-slope. These results indicate that instability on the ground surface is a likely factor affecting the distribution of tree species in this forest. Previous studies on the relationship between landform unit and vegetation distribution have assumed that instability on the ground surface directly affects vegetation structure (Sakai and Ohsawa 1994; Hara et al. 1996; Nagamatsu and Miura 1997; Hirayama and Sakimoto 2003). The amount of sediment movement in the lower area at the study site was 10–100 times higher than that observed along upper side-slopes in artificial stands and in a deciduous secondary forest at inclinations of 30–35° (Tsukamoto 1991; Miura et al. 2002). The amount of movement found here was similar to that observed on a steep slope in a cool–temperate forest (Nagamatsu et al. 2002).

Litter and sediment movement is also expected to affect seedling survival (Nagamatsu et al. 2002; Kubota et al. 2007). In the present study, the mortalities of upper and common species were higher at sites with a great deal of sediment movement, and dead uprooted trees were more frequent in the lower area (Fig. 9). These results suggest that physical instability of the habitat caused mortality and uprooting in the lower area. Recruitment and the annual amount of transported sediments were significantly negatively related for all upper species, including *S. prunifolia*, and all common species, including *C. japonica*. In contrast, the lower species, including *M. japonica*, did not exhibit a clear relationship between mortality and the amount of sediment movement, and for some species, recruitment rates were significantly positively related to the amount of sediment movement. These patterns are likely driven by different dynamic processes occurring under different topographic conditions, resulting in, e.g. the biased distribution of *M. japonica* within the lower area and of *S. prunifolia* within the upper area. The significant relationships between demographic parameters and sediment movement highlight the advantages that both upper and lower species gain by their respective habitat distributions

For nearly all tree species examined, mortality was higher and recruitment rate was lower in the lower area compared to the upper area (Table 2). In addition, almost all species whose maximum DBH was less than 30 cm tended to continuously regenerate in the upper area, based on SDI values. The lower area presumably experiences more severe conditions for regeneration compared to the upper area for almost all species, although growth rates did not significantly differ between the upper and lower areas. Based on the SDI, the size distribution of lower species such as *M. japonica* and *N. aciculata* was reverse-J shaped, and these species exhibited high recruitment rates in the lower area. *Machilus japonica* and *N. aciculata* may be able to maintain their populations by forming a bank of small trees in the lower area. *Machilus japonica* sprouts stems by root suckers as well as from main stems; such sprouting ability would strongly contribute to population maintenance (Sakai and Osawa 1994, Bellingham & Sparrow 2009, Clarke et al. 2013). Kohyama and Grubb (1994) pointed out that the large seeds of *N. aciculata* grow a vertical tap root immediately after germination, conferring a potential advantage in establishment on unstable sites with deep soil, such as foot slopes.

TWI was identified as the second-most important factor affecting species distribution in the upper area (Fig. 6), suggesting that the soil moisture regime in the upper area helps to structure vegetation patterns. In addition, TWI and mortality were significantly positively related for upper species such as *S. prunifolia* and *P. japonica*, whereas TWI and recruitment were positively related for lower species, such as *M. japonica* (Fig. 10). These results suggest that TWI affected the population dynamics of both upper and lower species.

However, by 1 ha plot data the distributions of the conifers *C. obtusa* and *T. sieboldii*, which together accounted for the high biomass in the upper area, could not be clearly explained. These two species exhibited bell-shaped size structures, low mortality and no recruitment. Furthermore, instability of the ground surface and demographic parameters were not significantly related for many species. For these species, other environmental factors may drive their distributions, or instability may more strongly affect another life stage, such as juveniles and seedlings, neither of which were examined in this study. Soil fertility and canopy openness may be the other factors affecting distribution of the species. However, canopy openness was not significantly different among subplots. In addition, nitrogen mineralization rates were also not significantly different among the landform-unit categories in this site (Hirai et al.2007), and the potential life spans for each species estimated by relative growth rate were not different between upper and lower area (Fig. 8). Therefore it was suggested that these factors did not contribute the species distribution. Alternatively, the distribution of these species may be determined by seed dispersal, regardless of the environmental conditions of the habitat. In conclusion, for some major tree species, instability of the ground surface contributed to species co-existence through among-species variation in sensitivity to stability due to topography.

Relationship between gap formation process and factors of topography and stand structure

Gap formation process varied temporally and spatially depending on factors of topography and stand structure. Factors of stand structure strongly affected to gap formation than those of topography. Neighboring to the former gap and higher canopy tended to create a gap. Domino effect has been demonstrated from past studies. The present study showed a domino effect of gap formation in a warm temperate forest similar to previous studies (e.g. Runkle 1985, Kubo et al. 1996). Furthermore, there was a tendency to reduce the height increment at DCHM>15m and neighbors to the gap. Physical stressed such as wind (Gray et al. 2012) is the reason of reduction in the neighbor of the gap and higher canopy. And an increase of sensitivity to disturbance as the individual height increases, and an increase of mortality to attain would be the reason why the gap formation easily occurred at higher canopy. In mature natural forests, higher mortalities were observed for large conifer trees in boreal forest (Hiura and Fujiwara 1999; Kubota et al 2000, 2007) and in warm temperate forest (Nakamori et al. 2009), and higher canopy trees in in the tropical forests (Kellner et al. 2009).

Gap formation often occurred significantly in the space where the slope was steep in

1969-1985, but such trend was not observed in 1985- 2005. Mortality of the canopy trees depended on topography, but it not always seemed robust. In 1969-1985, the gap formation rate was higher and the gap size was larger at steep slopes, then the severity of disturbances on the steep slope might be higher when a strong disturbance occurred. According to the weather records near the study area, six typhoons (> 40m/s) came to the area, and the maximum wind speed was 52.1m / s during 1969-1985. Three typhoons (>40 m/s) came to the area and the maximum wind speed was 44.5m/s during 1985-2005 (Japan Meteorological Agency, http://www.jma.go.jp/jma/indexe.html). The magnitude of disturbance by wind would be more severe in 1969-1985 than in 1985-2005, and the sever events influenced the gap formation.

How does topography affect coexistence mechanism and dynamics of mixed forest?

Conifer trees were distributed around ridge in the catchment (Table 7). The gaps caused by conifer tended to be larger (Table6, Fig.14) although there was no difference in gap formation rate among the life-form (Table 5). Frequency distribution of the gap size of the study area deviated from both the power and log-normal distribution, then it was suggested that gaps did not generate randomly and this tendency would be derived due to gaps by conifer in this forest. Conifer trees would create larger gaps than broad-leaved trees because the ever green conifer has emergent crown (Aiba et al. 2013) and tend to make up-rootings by its shallow-root system of *C. obtuse* and *T. sieboldii*

(Karizumi 1979), although in Canadian mixed forest gap size created by conifer is not so larger than gaps created by deciduous broad-leaved tree (Vepakomma et al. 2012). The mortality of emergent canopy trees in tropical forest is lower than the other canopy trees (Thomas et al. 2013), but there was no difference between gap formation rate by evergreen broad-leaved and by conifers in this study.

There was no gap which was repaired by new conifer in the aerial photo analysis. Regenerated conifer has not been seen in the plot data and the number of conifer tree decreased (Table 2). There was no difference in gap creation between by conifer and by broad-leaved tree and gaps were repaired by broad-leaved trees in this stand. As a result, the proportion of evergreen broad-leaved tree was increasing gradually in the canopy layer. Regeneration of *T. sieboldii* (warm-temperate conifer) would be started after a large disturbance such as a big typhoon (Suzuki 1979, 1981), and regeneration of *C. obtusa* needs disturbance with exposure of the mineral soil (Akashi 1996). Then large disturbances might be required for the regeneration of *C. obtuse* and *T. sieboldii* which dominated in this stand.

If conifer species could regenerate in the gap created on the ridge, a maintenance mechanism of the distribution of conifers can be explained. In the cool-temperate mixed forests reciplocal replacements of conifer and broad-leaved trees were found; conifers regenerate in gaps created by deciduous tree or under the canopy, and deciduous tree regenerates in gaps created by conifer (Nakashizuka and Kohyama 1995; Hiura and

Fujiwara 1999; Kubota 2000). But in Yakushima Island, *Cryptomeria japonica* has an emergent canopy, and *C. japonica* could not regenerate under the canopy of evergreen broad-leaved trees which foliage concentrated to canopy top in the warm temperate forest (Suzuki and Tsukahara 1987; Aiba et al. 2013). However, very long life span of *C. japonica* enables to maintain their population and to add large biomass to the forest ecosystem (Aiba et al.2007). *C. obtuse* and *T. sieboldii* on the ridge in our study site might contribute to the additive large biomass and to create large gaps. I consider that these temperate conifer trees are long-lived pioneer (e.g. Lusk 1999; Sakai et al. 1999).

I showed that the stand structure itself would contribute to the maintenance mechanism of species coexistence by gap formation process depending on the topography. Topography has an important role for establishment of seedling and juvenile stage (Tsujino and Yumoto 2007), but topography would affect partially to the gap formation, and it might increase spatio-temporal variations of the regeneration process in the forest community.

Conclusion

The following were conclusions in relation to the effects of topography on the community dynamics of warm temperate mixed forest with ever green conifers and broad-leaved trees.

(1) Instability of the ground surface in the steep slopes effects mortality and recruit rate of component tree species. It is a factor that defines the distribution of tree species.

(2) Warm temperate conifers *C. obtuse* and *T. sieboldii* developed high canopy stand around ridge in the watershed and tend to make a large gap. There is a mechanism to maintain distribution of these conifers if these conifers regenerate on the large gap.

(3) It was observed that gap formation is likely to occur in the steep slope when more gaps were created in particular. A possibility is suggested that the disturbance of high frequency in the steep slope facilitate distribution of broad-leaved tree species.

(4) It is considered that correlations in three factors as stand structure, disturbance regime and topography constructs maintenance mechanism of mixed forest with coniferous and broad-leaved trees in the warm-temperate zone.

(5) A further study of regeneration in the variety gap should be conducted in warm temperate mixed forest in order to understand community maintain mechanism.

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Figures & Tables

Fig. 1 Location of study site

Fig. 2 Permanent plot location and topography in study area

Fig. 3 Landform units, TWI and categories from the regression tree analyses plotted on the contour map by subplots; Landform units, CS: crest slope, US: upper side-slope, LS: lower side-slope, FS: foot slope

Fig. 4 NMDS biplot: Ordination of subplots (10mx10mx95) by non-metric dimensional scaling and significant vector of TWI and factor of landform units ($p < 0.001$). A-F are vegetation-type categories divided by regression tree analysis

Fig. 5 Cross-validation for the optimum number of terminal nodes of tree regression model

Fig. 6 Results of regression tree model analyses. A–F: vegetation type categories, Landform units, CS: crest slope, US: upper side-slope, LS: lower side-slope, FS: foot slope

Fig. 7 The size distribution index (SDI) and observed maximum DBH of dominant species in upper and lower areas. Open and solid circles show values in upper and lower areas, respectively. We added an asterisk after the abbreviation of the upper species and two asterisks of the lower species. Species abbreviations are the same as in Table 3

Fig. 8 Estimated maximum DBH of dominant species in the upper and lower areas. Values for TS, CO, PJ and SM could not be estimated in the lower area because of low population numbers; the DBH values for these species are plotted as 1 cm along the y-axis. The values for TS in the upper area and IA in the lower area did not converge and appeared to be outliers. Species abbreviations are as in Table 3

Fig. 9 Relationships between the amount of sediment transported and rates of tree mortality (upper panels) and recruitment (lower panels) of upper, common and lower species. Open circles with solid lines represent upper, common and lower species; solid circles with dotted lines represent SP, CAJ and MJ. Species abbreviations are as in Table 3

Fig. 10 Relationships between TWI and rates of tree mortality (upper panels) and recruitment (lower panels) for upper, common and lower species. Open circles with solid lines represent upper, common and lower species; solid circles with dotted lines represent SP, CAJ and MJ. Species abbreviations are as in Table 3

Fig. 11-1, 2, 3 Permanent plot location, topography and DCHM in 1969, 1985, 2005 map of in study area

Fig. 12 Number and size of gaps (under 15m canopy height area) in 1969, 1985 and 2005

Fig. 13 Distribution of new created gaps in 1969-1985 and 1985-2005

Fig. 14 Distribution of conifer trees and gap makers in 1969-2005

Fig. 15 Number and size of gaps created in 1969-1985 and 1985-2005 by gap makers with conifer and by only broad leaved tree species.

Fig. 16-1, 2 DCHM change of study site in 1969-1985, 1985-2005.

Table 1 Number and steepness of the 95 subplots in the study site. CS: crest slope; UL: upper side-slope; LS: lower side-slope; FS: foot slope

Table 2 Species composition and population dynamics parameters in the upper and lower areas. Species groups, U: upper species; C: common species; L: lower species; INF: infrequent species, Life-forms, C: conifers; E: evergreen broad-leaved species; D: deciduous broad-leaved species

Table 3 Habitat preferences of dominant species determined using randomisation tests. Species groups, U: upper species; L: lower species; C: common species. Life form, C: conifer; E: evergreen broad leaved

+++/–––, $P < 0.001$; ++/––, $P < 0.01$; +/–, $P < 0.05$

Table 4 Number and state of injuries from 1994 to 2007.

Table 5 The coefficient of Logistic regression model for gap formation by spatial environment and stand structure. TWI: topographic wetness index, RVR: relative distance from valley to ridge, DCHM: digital canopy height model, Neighbor: beside former gap or not, Life form: Conifer or not

Table 6 The coefficient of GLM regression model for gap area by spatial environment and stand structure. TWI: topographic wetness index, RVR: relative distance from valley to ridge, DCHM: digital canopy height model, Neighbor: beside former gap or not, Life form: Conifer or not

Table 7 The coefficient of logistic regression model for conifer grid and spatial environment

Table 8 The results of GLM analysis for DCHM change with spatial environment stand structure

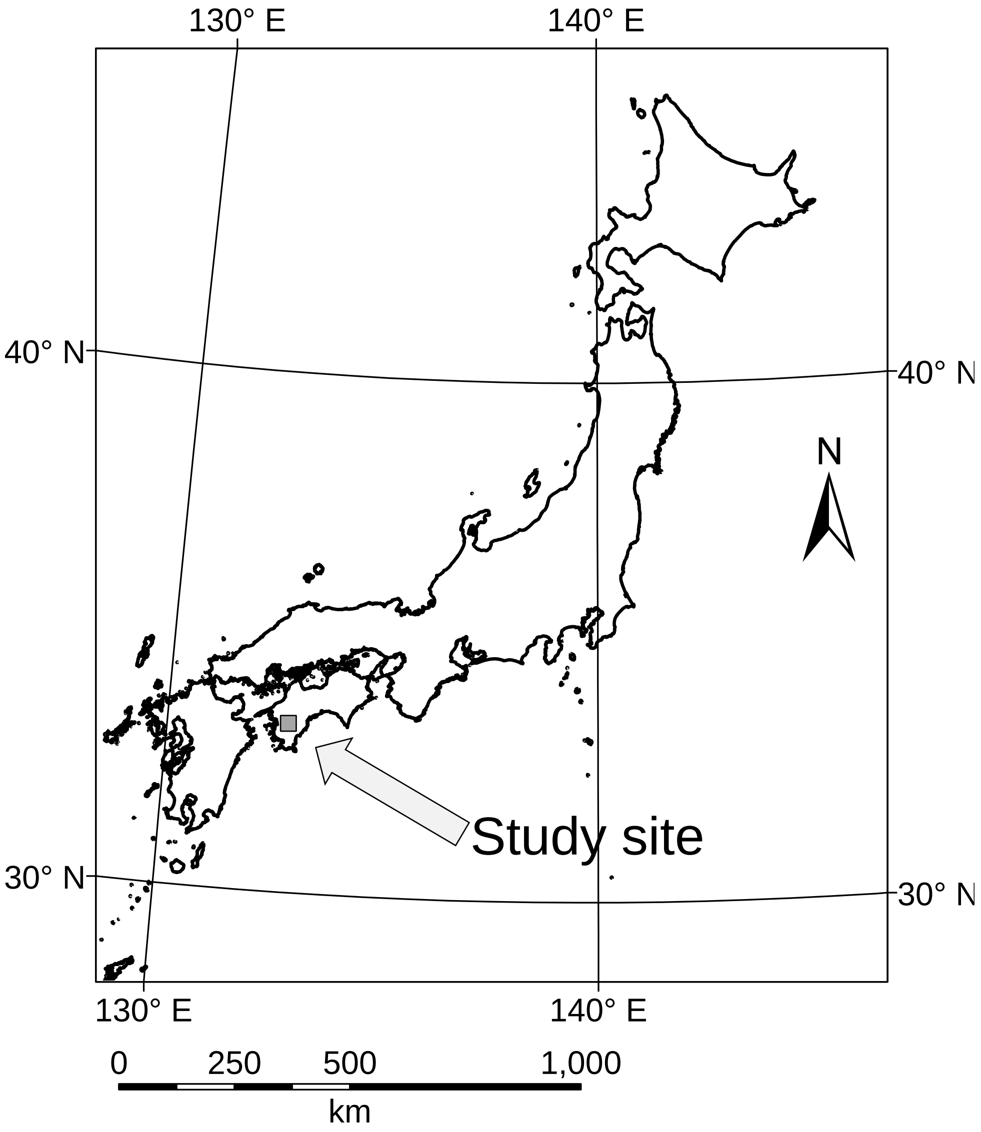

Fig. 1 Location of study site

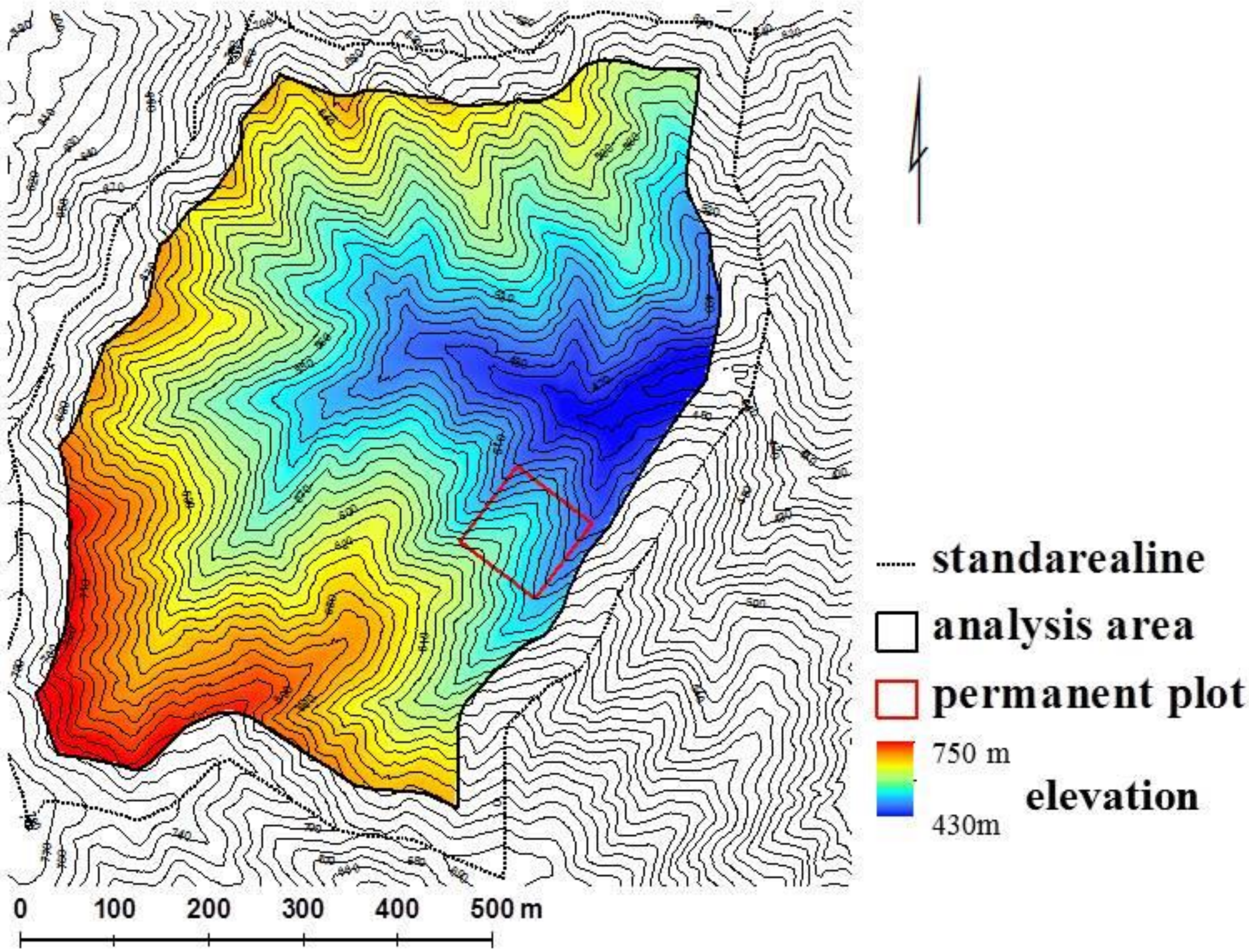

Fig. 2 Permanent plot location and topography in study area

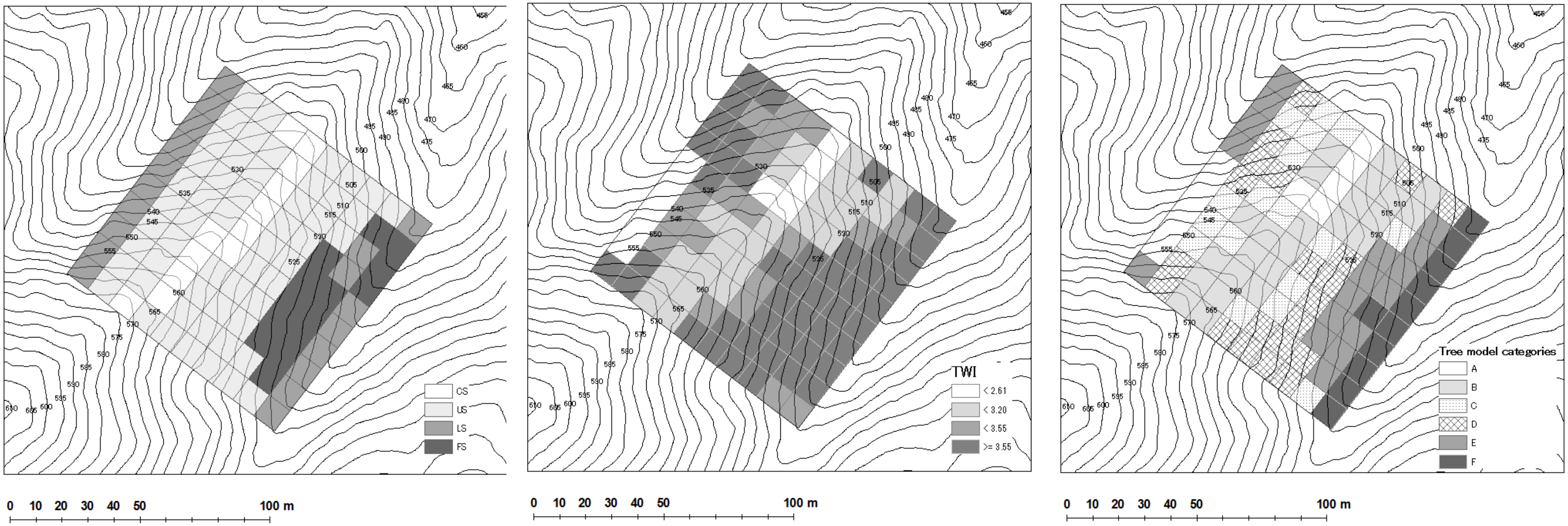

Fig. 3 Landform units, TWI and categories from the regression tree analyses plotted on the contour map by subplots; Landform units, CS: crest slope, US: upper side-slope, LS: lower side-slope, FS: foot slope

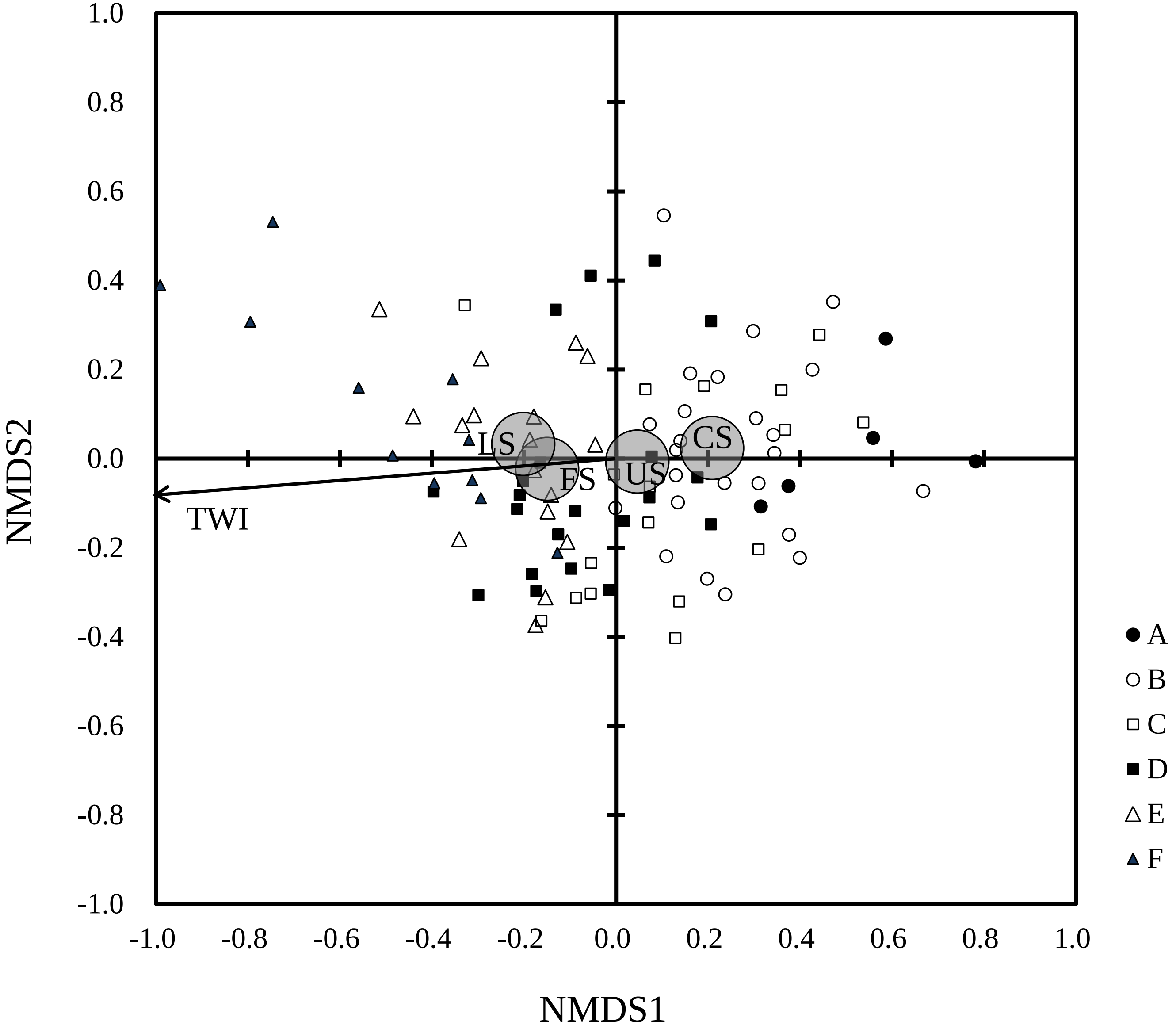

Fig. 4 NMDS biplot: Ordination of subplots (10mx10mx95) by non-metric dimensional scaling and significant vector of TWI and factor of landform units ($p < 0.001$). A-F are vegetation-type categories divided by regression tree analysis.

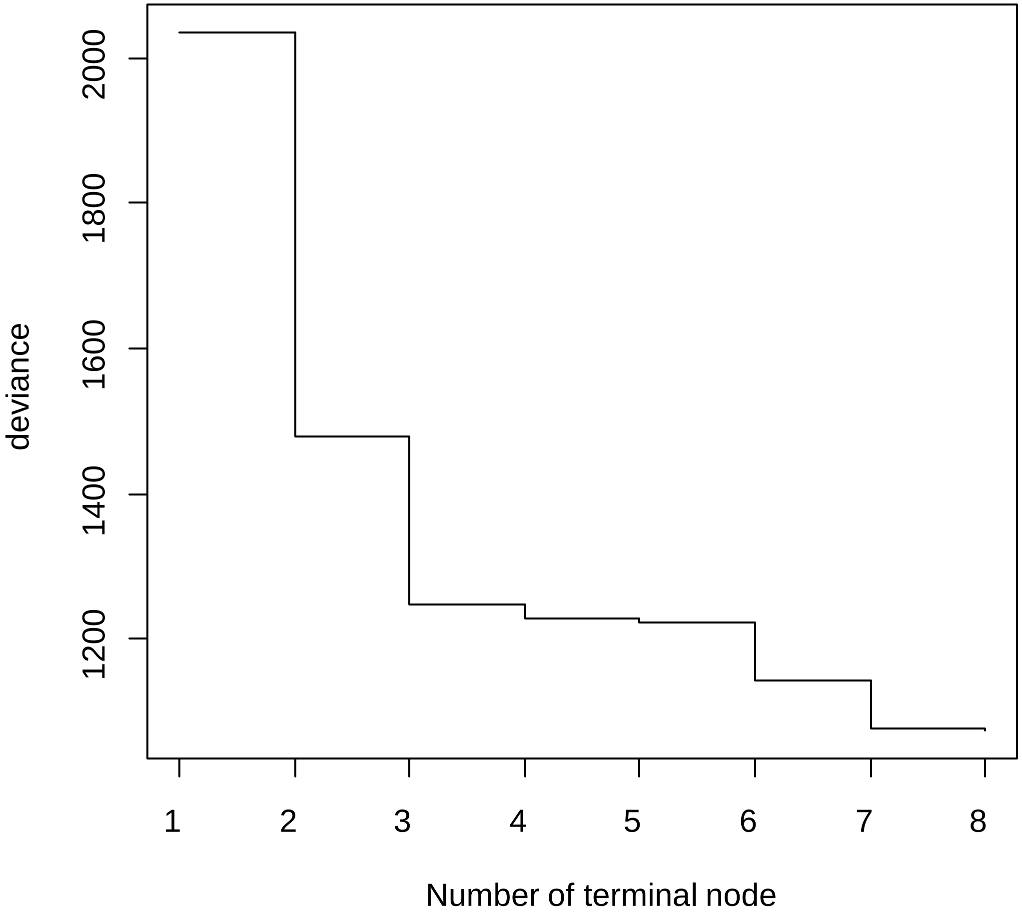

Fig. 5 Cross-validation for the optimum number of terminal nodes of tree regression model.

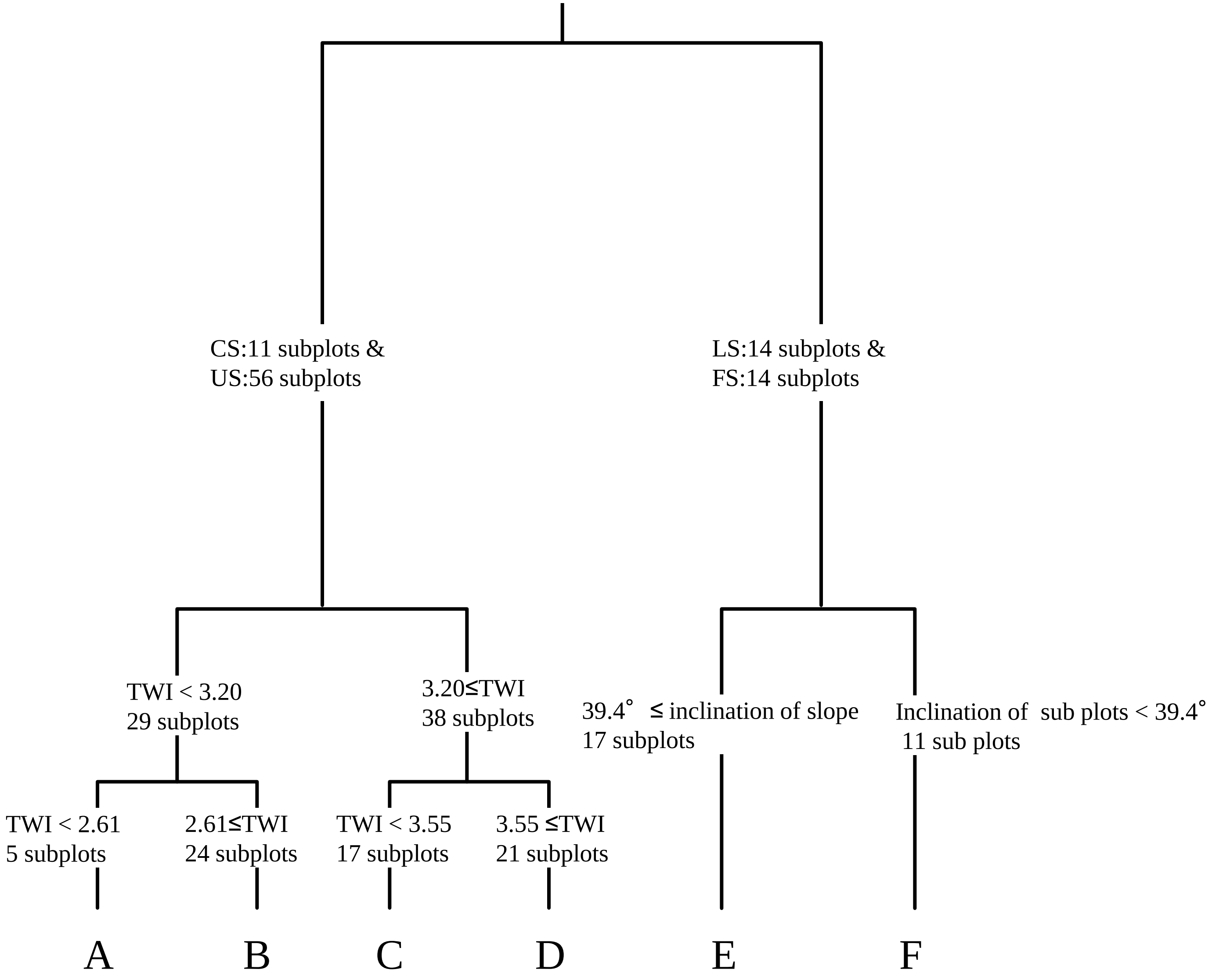

Fig. 6 Results of regression tree model analyses. A–F: vegetation type categories, Landform units, CS: crest slope, US: upper side-slope, LS: lower side-slope, FS: foot slope

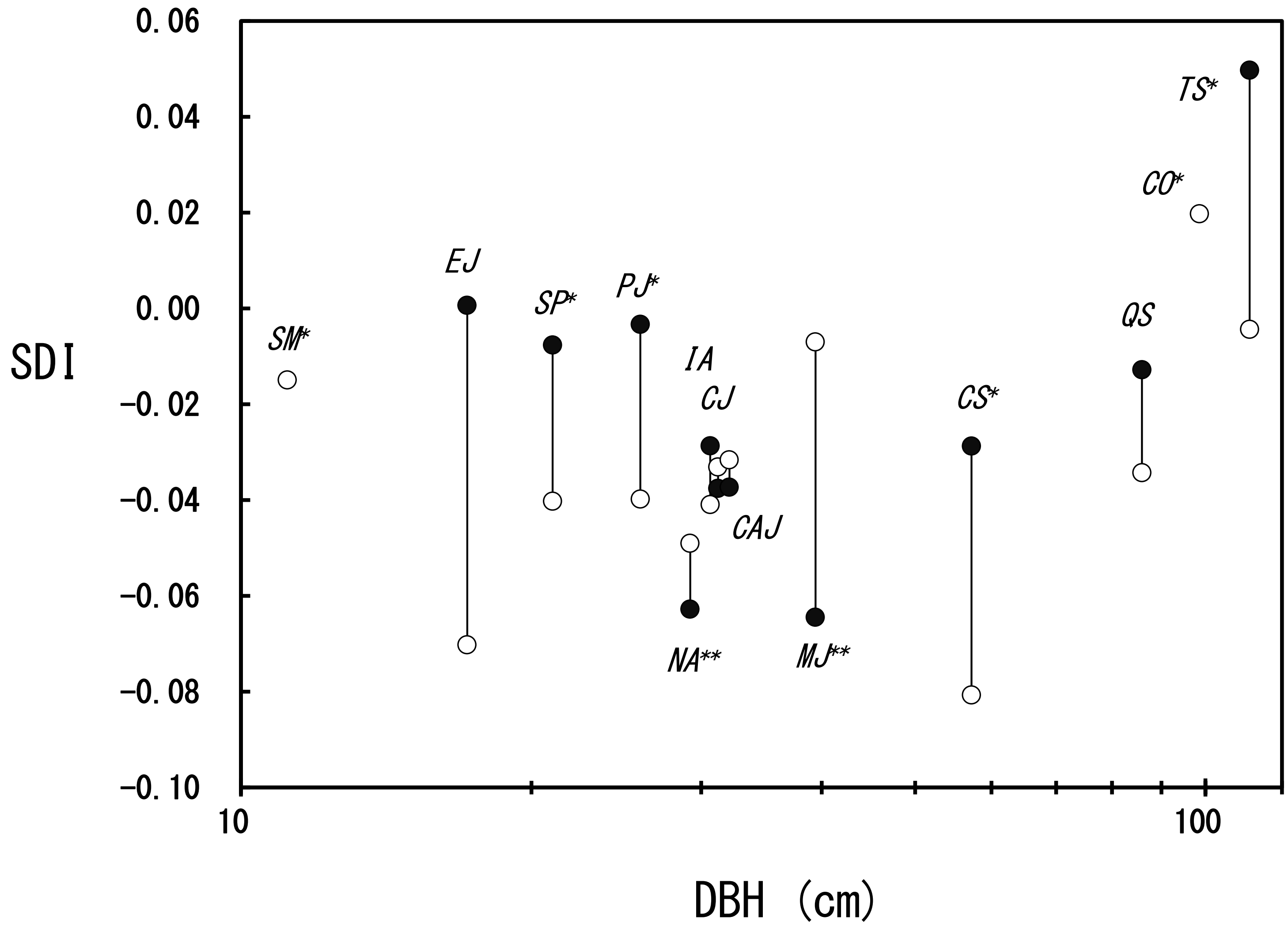

Fig. 7 The size distribution index (SDI) and observed maximum DBH of dominant species in upper and lower areas. Open and solid circles show values in upper and lower areas, respectively. We added an asterisk after the abbreviation of the upper species and two asterisks of the lower species. Species abbreviations are the same as in Table 3

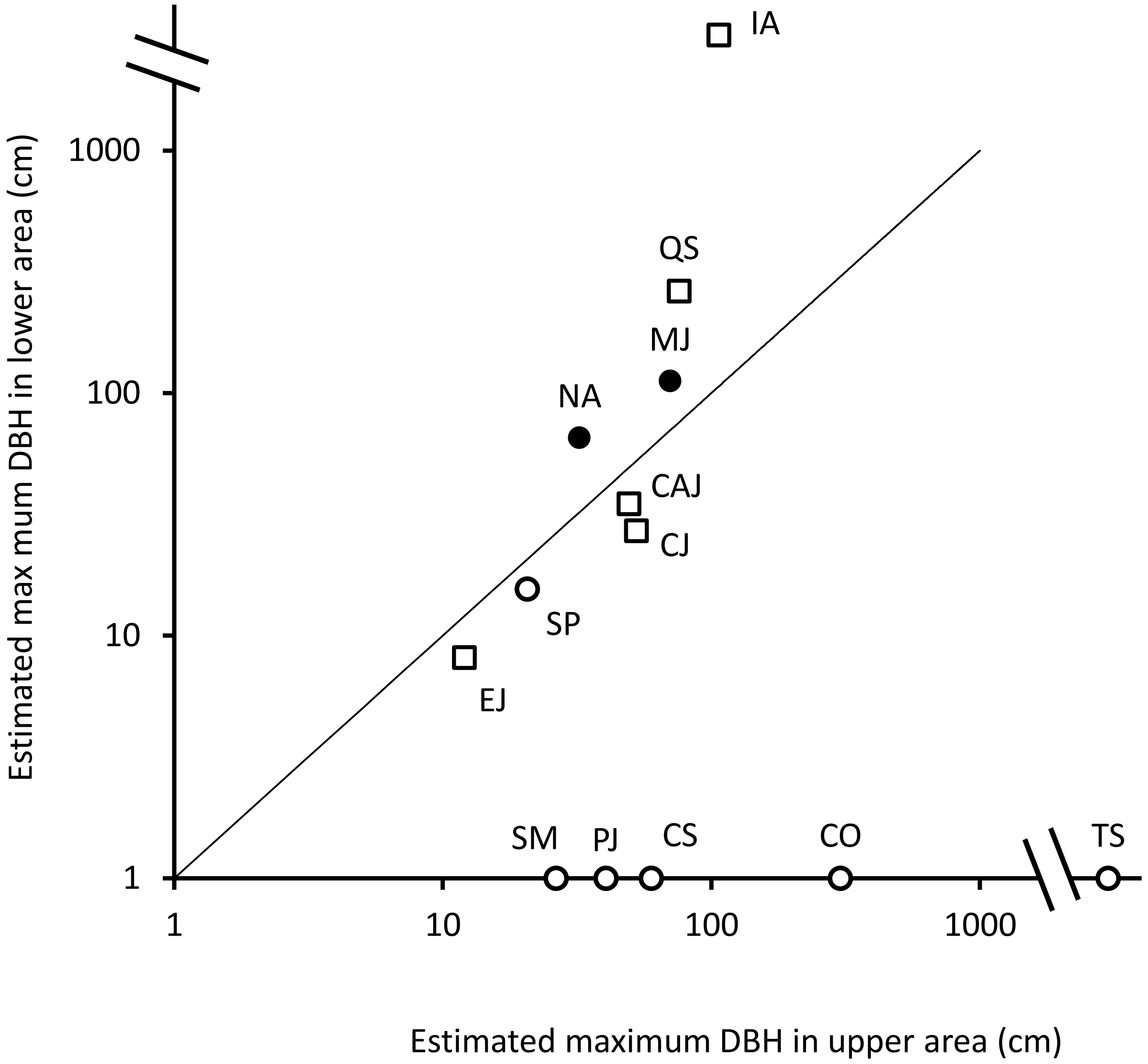

Fig. 8 Estimated maximum DBH of dominant species in the upper and lower areas.
Values for TS, CO, PJ and SM could not be estimated in the lower area because of low population numbers; the DBH values for these species are plotted as 1 cm along the y-axis. The values for TS in the upper area and IA in the lower area did not converge and appeared to be outliers.
Species abbreviations are as in Table 3

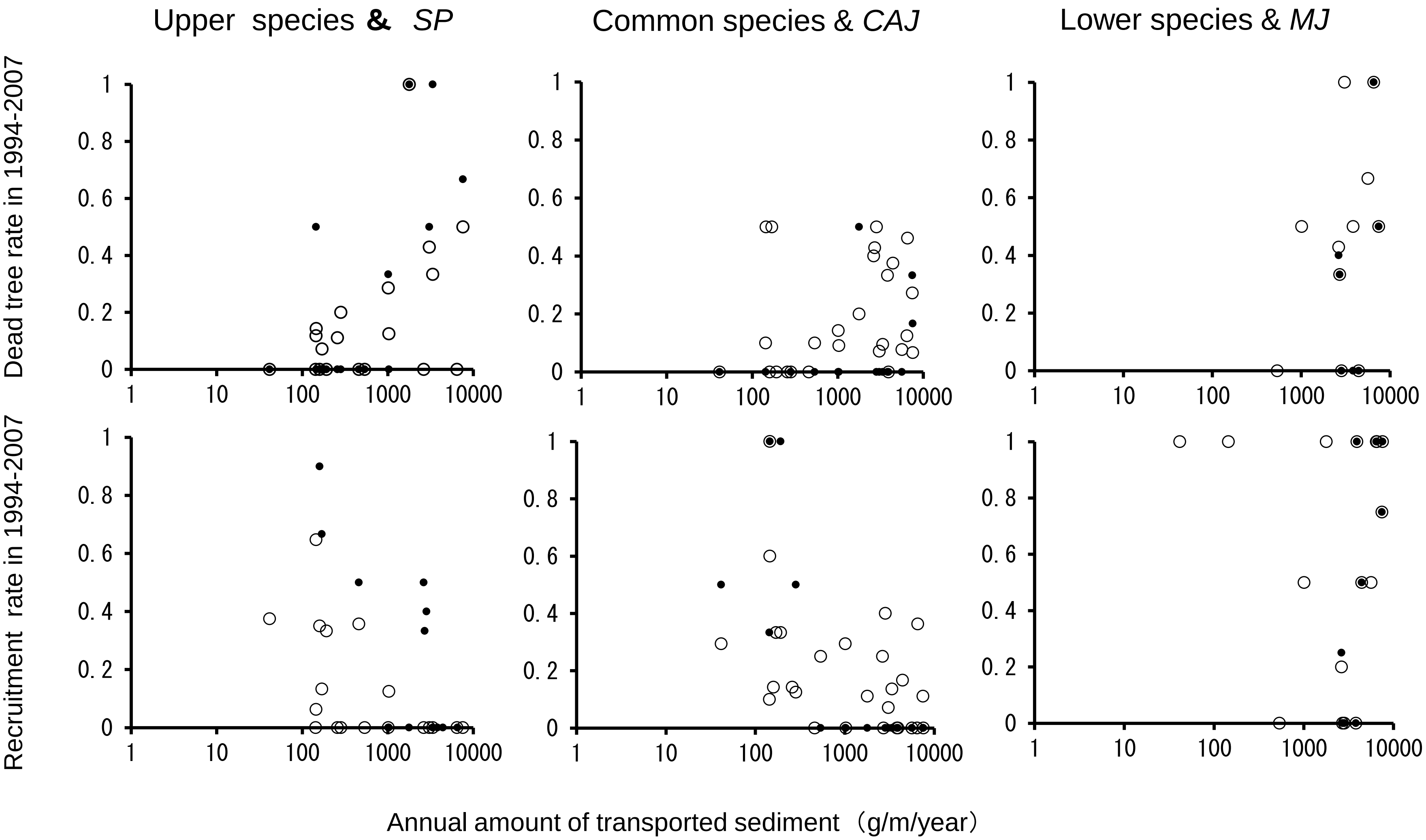

Fig. 9 Relationships between the amount of sediment transported and rates of tree mortality (upper panels) and recruitment (lower panels) of upper, common and lower species. Open circles with solid lines represent upper, common and lower species; solid circles with dotted lines represent SP, CAJ and MJ. Species abbreviations are as in Table 3

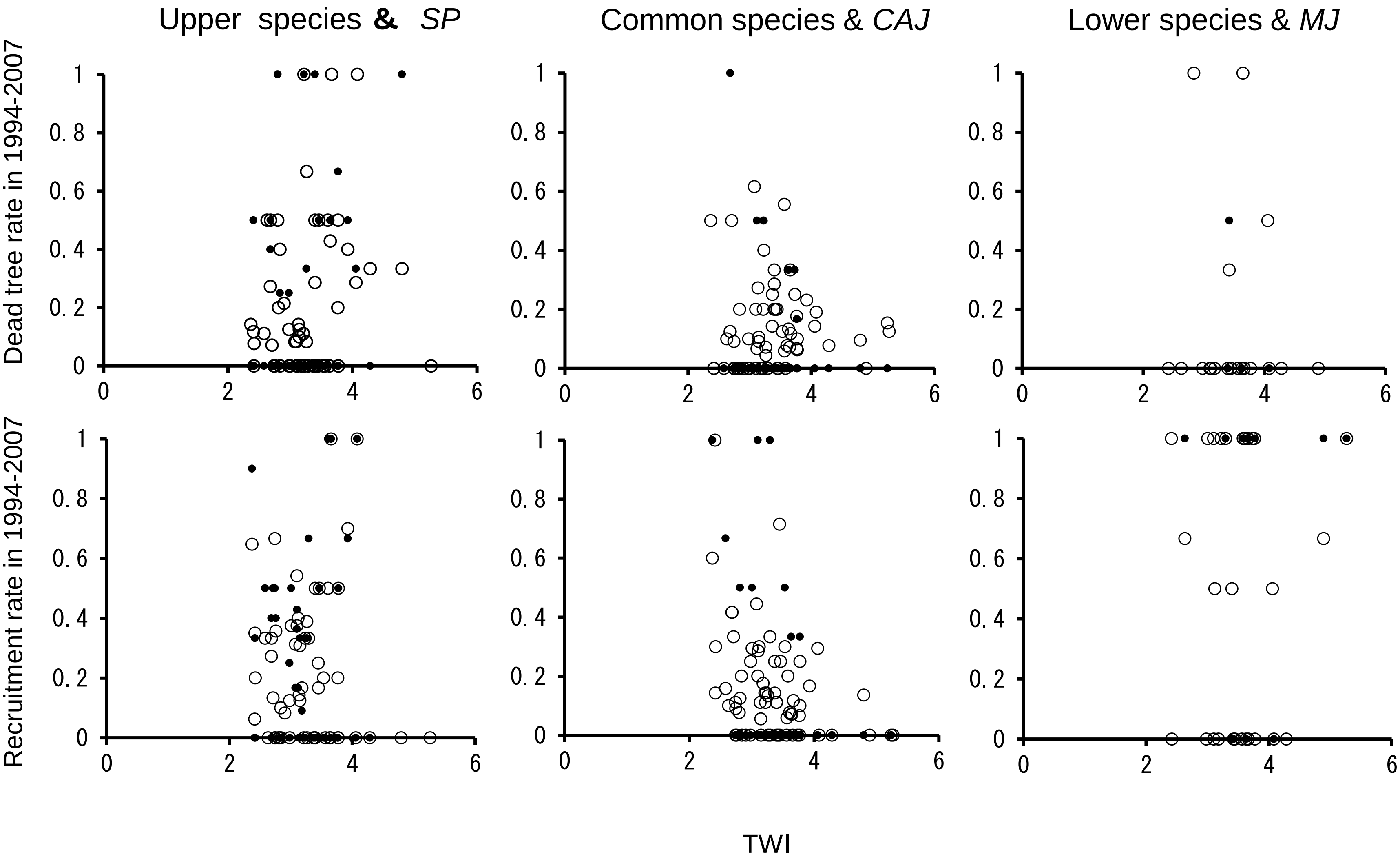

Fig. 10 Relationships between TWI and rates of tree mortality (upper panels) and recruitment (lower panels) for upper, common and lower species. Open circles with solid lines represent upper, common and lower species; solid circles with dotted lines represent SP, CAJ and MJ. Species abbreviations are as in Table 3

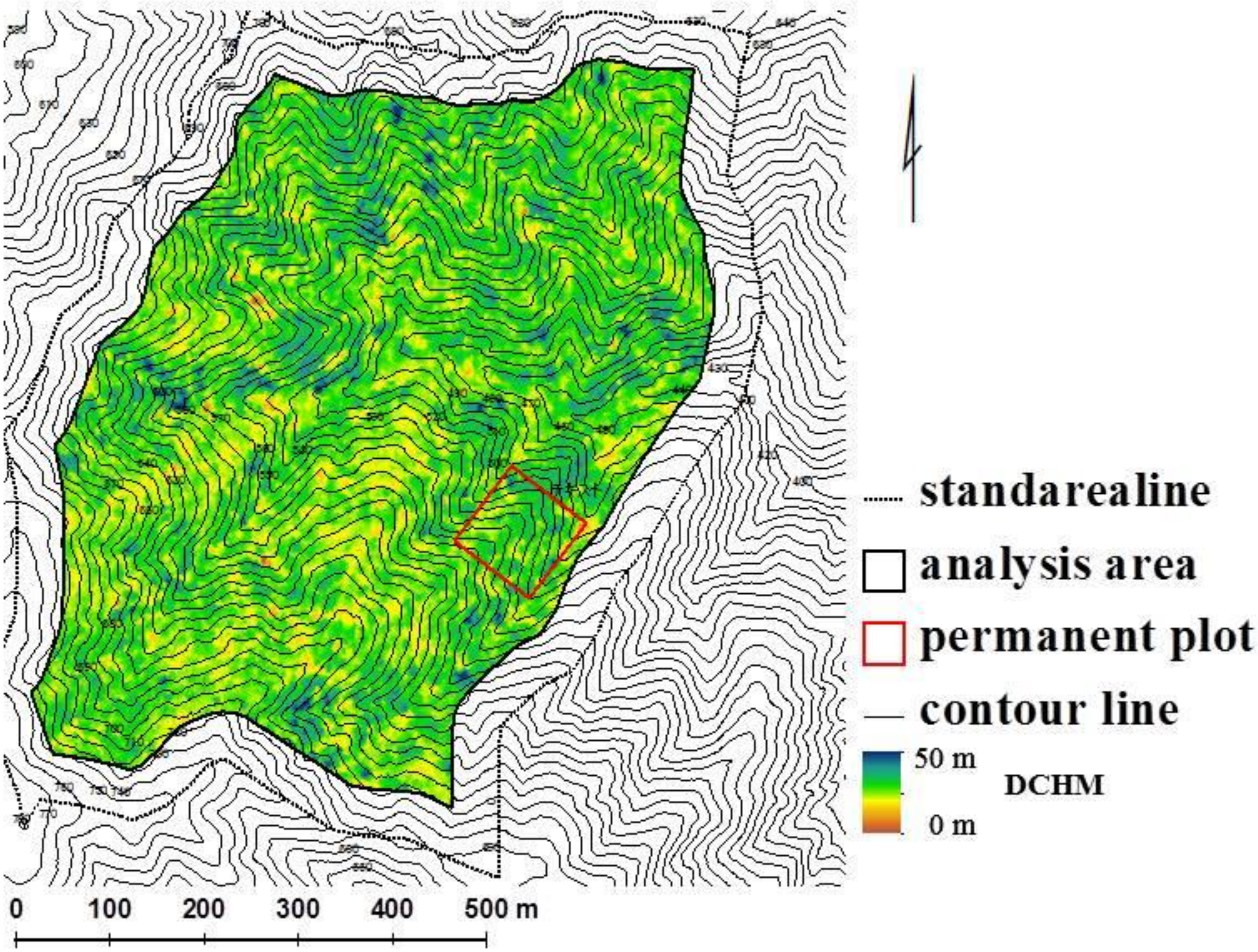

Fig. 11-1 Permanent plot location, topography and DCHM in 1969 map of in study area

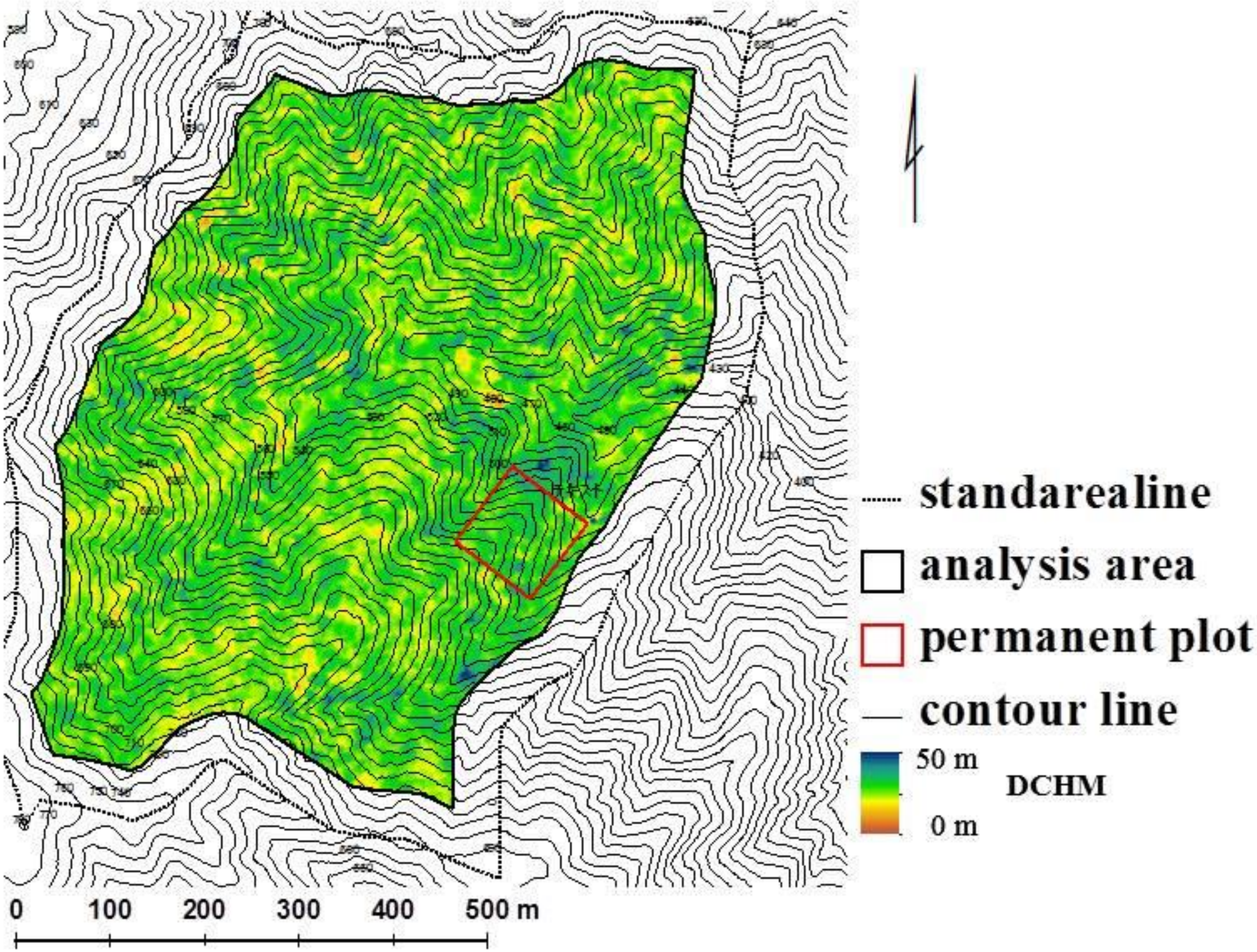

Fig. 11-2 Permanent plot location, topography and DCHM in 1985 map of in study area

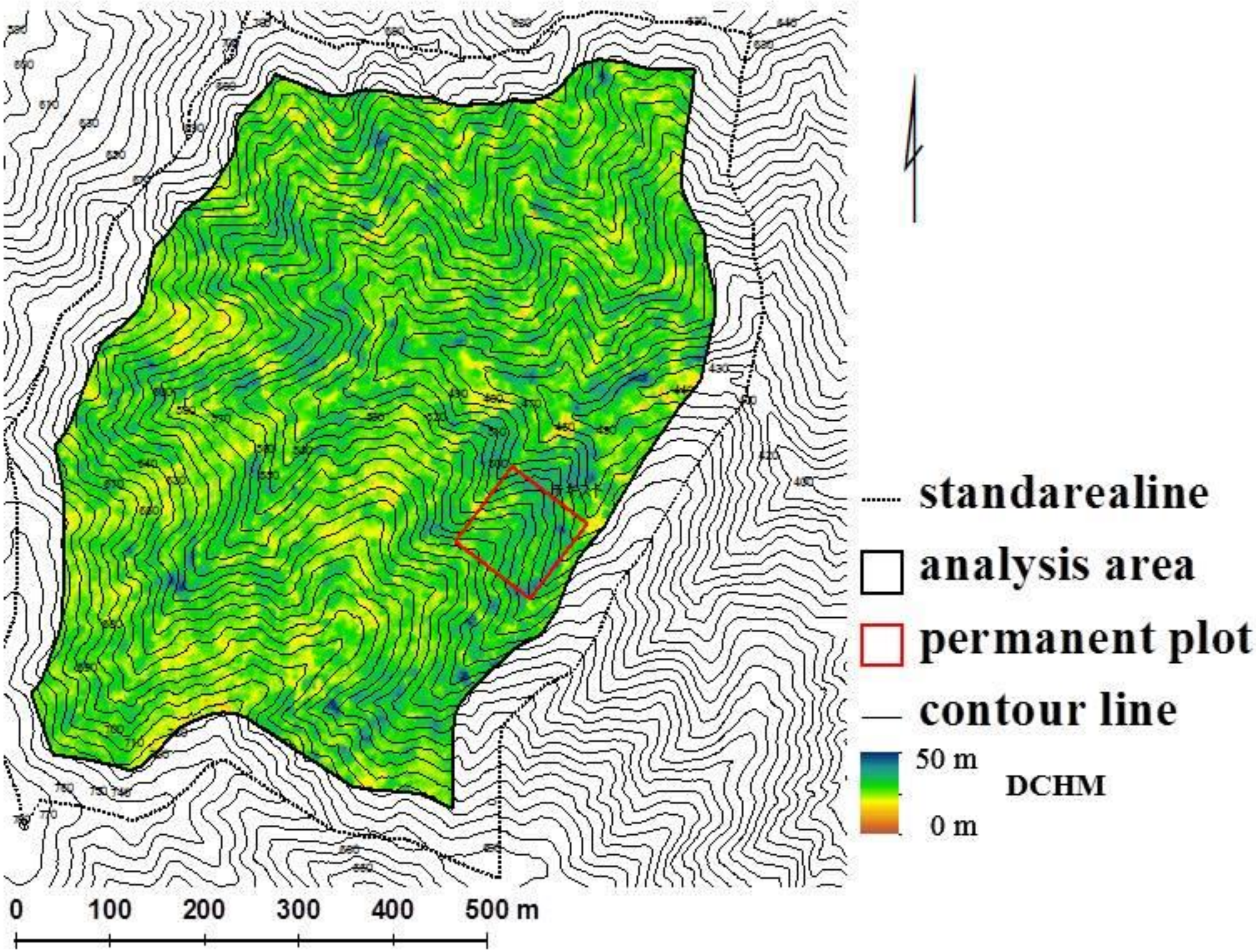

Fig. 11-3 Permanent plot location, topography and DCHM in 2005 map of in study area

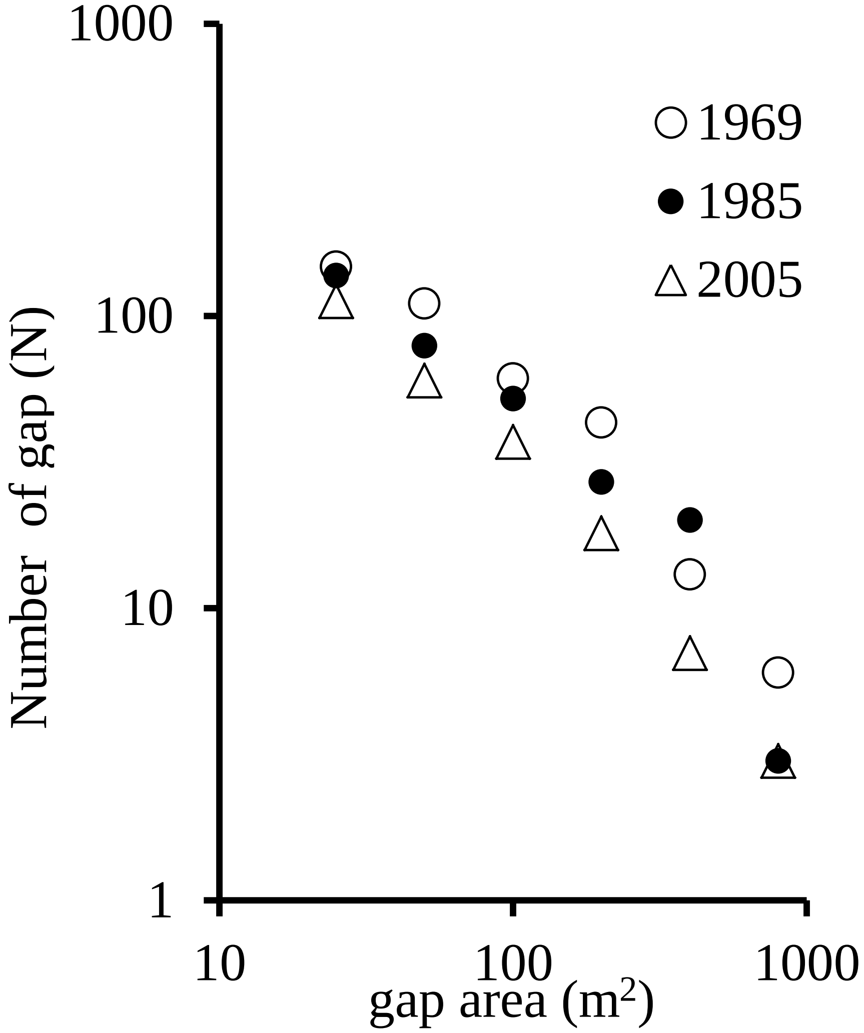

Fig. 12 Number and size of gaps (under 15m canopy height area) in 1969, 1985 and 2005

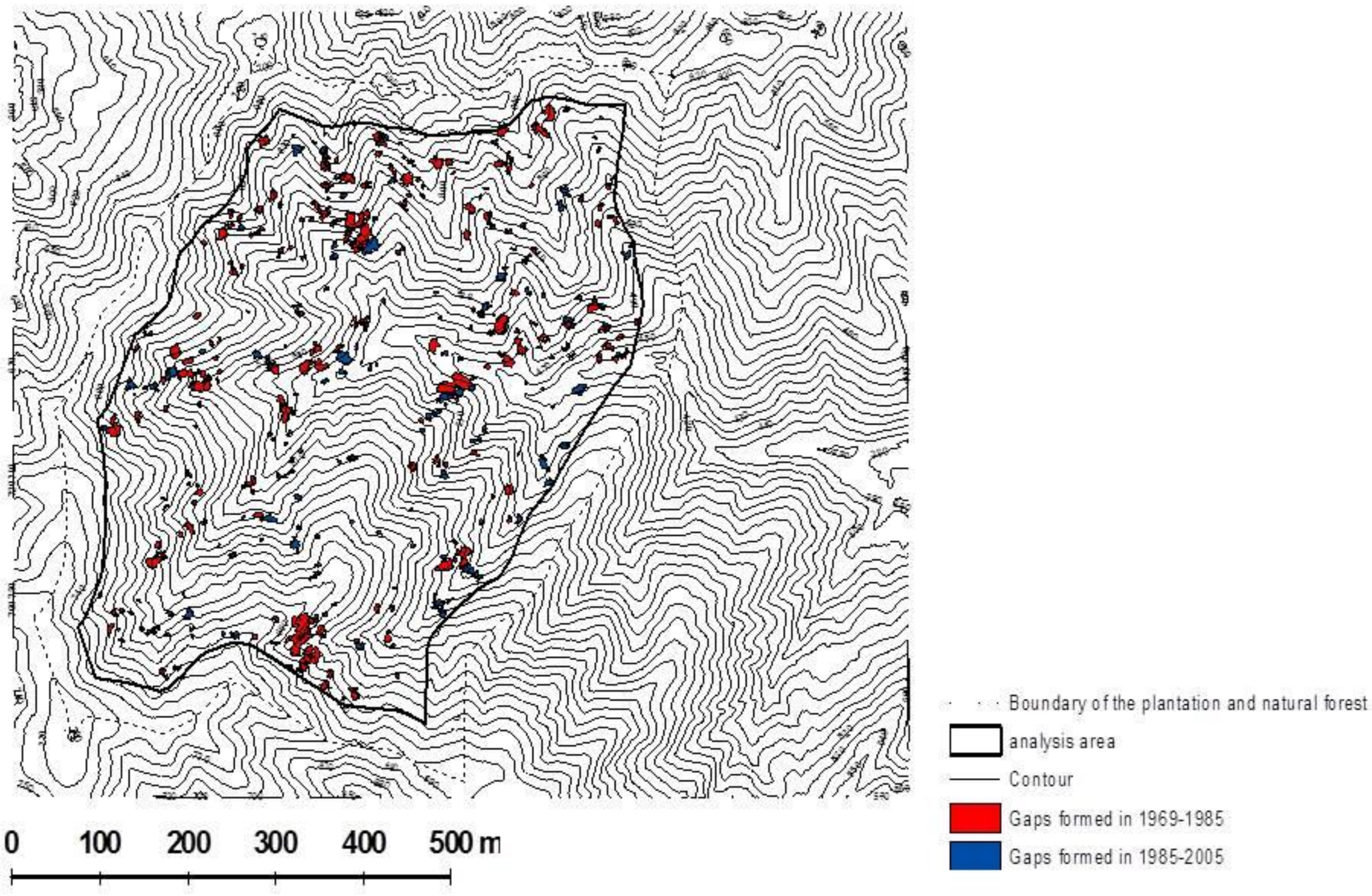

Fig 13 Distribution of new created gaps in 1969-1985 and 1985-2005

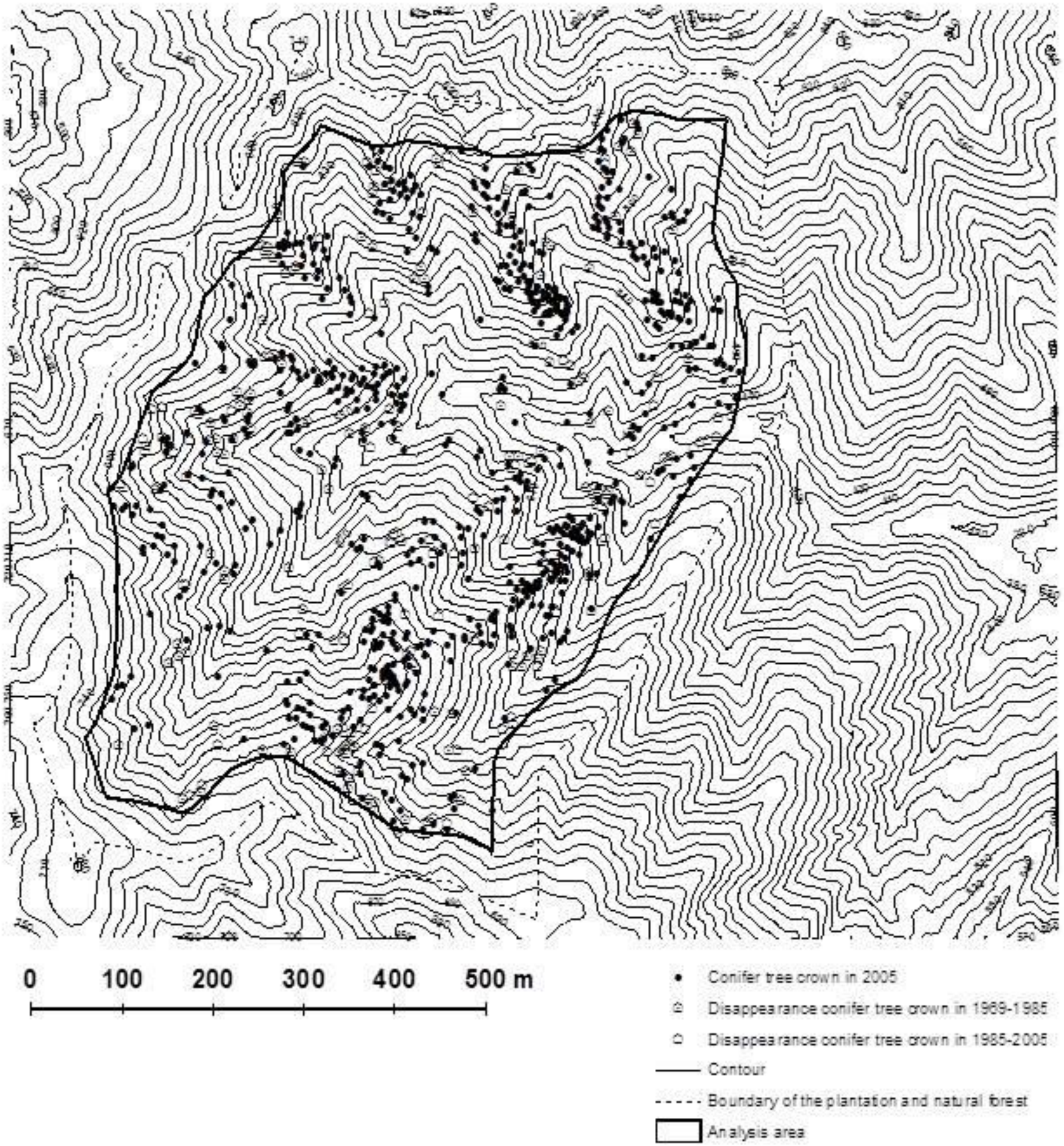

Fig. 14 Distribution of conifer trees and gap makers in 1969-2005

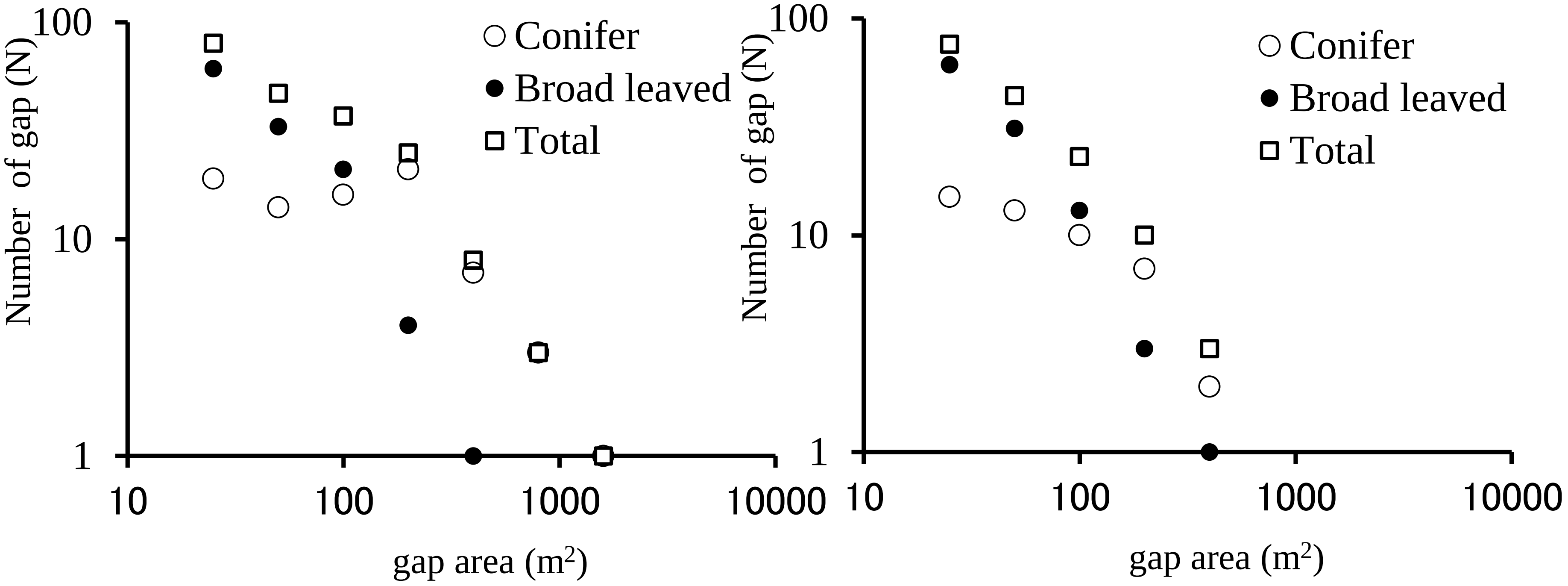

Fig. 15 Number and size of gaps created in 1969-1985 and 1985-2005 by gap makers with conifer and by only broad leaved tree species.

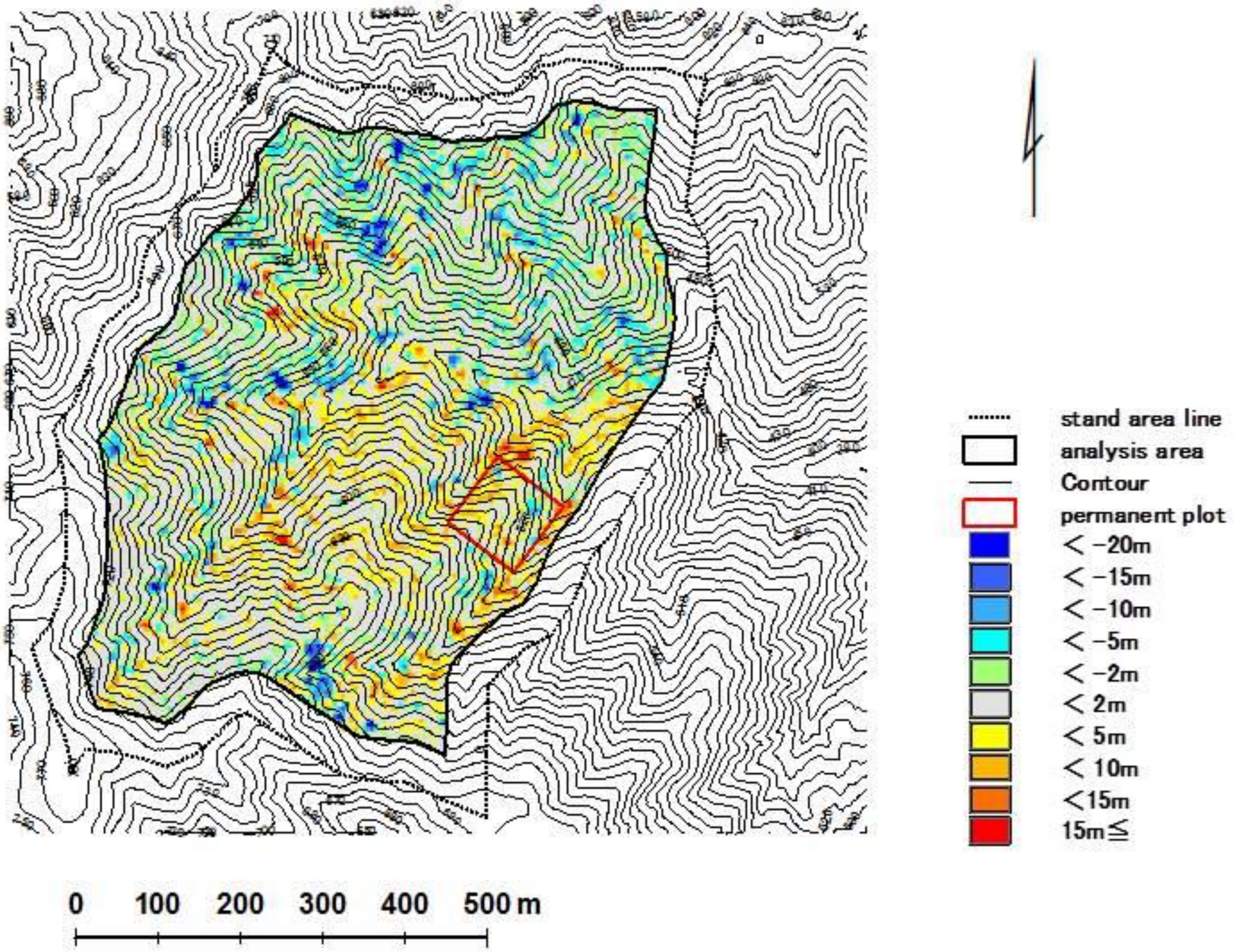

Fig. 16-1 DCHM change of study site in 1969-1985.

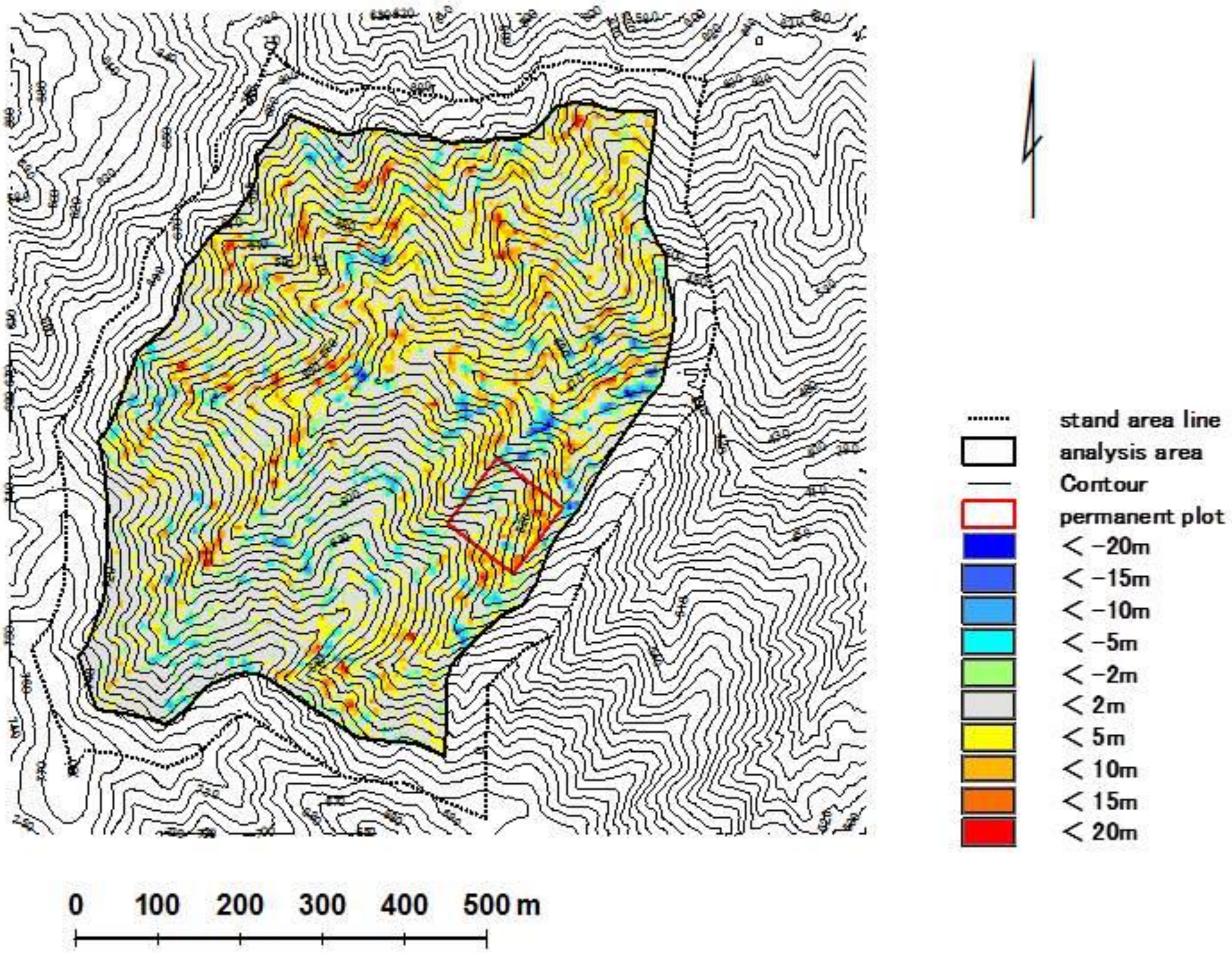

Fig. 16-2 DCHM change of study site in 1985-2005.

Table 1 Number and steepness of the 95 subplots in the study site. CS: crest slope; UL: upper side-slope; LS: lower side-slope; FS: foot slope

		slope (°)		
	n	mean	max	min
CS	11	35.3	42.2	24.8
US	56	42.0	50.7	32.2
LS	14	42.4	50.8	28.4
FS	14	40.1	46.5	27.5

Table 2 Species composition and population dynamics parameter in the upper and lower area. Species groups: U: upper species, C: common species , L: lower species, INF: infrequent species Life forms: C: Conifer, E: Evergreen broad-leaved species, D: Deciduous broad-leaved tree

			Density			Basal area			Mortality			Recruitment rate		
			1994 (No./ha)	1994 (No./ha)	1994 (No./ha)	1994 (m^2/ha)	1994 (m^2/ha)	1994 (m^2/ha)	1994-2007 (%/yr)	1994-2007 (%/yr)	1994-2007 (%/yr)	1994-2007 (%/yr)	1994-2007 (%/yr)	1994-2007 (%/yr)
Species	Species group	Life form	all	upper area	lower area	all	upper area	lower area	all	upper area	lower area	all	upper area	lower area
Chamaecyparis obtusa	U	C	42	63	0	16.37	24.50	0.00	0.19	0.19	-	0.00	0.00	-
Tsuga sieboldii	U	C	51	71	10	12.25	17.28	2.12	0.85	0.72	3.12	0.00	0.00	0.00
Symplocos prunifolia	U	E	133	184	29	1.00	1.42	0.16	1.70	1.67	2.21	3.19	3.36	0.00
Castanopsis sieboldii	U	E	64	91	10	0.90	1.13	0.45	0.39	0.41	0.00	3.71	3.79	2.21
Pieris japonica	U	E	68	96	13	0.65	0.95	0.06	1.29	1.25	1.72	1.17	1.25	0.00
Symplocos myrtacea	U	E	35	52	0	0.15	0.23	0.00	6.07	5.58	-	6.73	6.29	-
Cleyara japonica	C	E	495	529	425	5.36	5.15	5.80	1.26	0.89	2.13	0.61	0.69	0.40
Quercus salicina	C	E	74	83	54	4.27	3.13	6.56	0.34	0.49	0.00	0.76	1.09	0.00
Camellia japonica	C	E	133	139	121	1.56	1.49	1.69	0.70	0.58	0.95	0.76	0.94	0.39
Illicium anisatum	C	E	95	98	89	1.11	1.19	0.96	3.08	2.43	4.43	0.49	0.52	0.42
Eurya japonica	C	E	72	80	54	0.25	0.29	0.18	1.22	1.00	1.82	3.96	4.18	3.29
Machilus japonica	L	E	73	17	184	0.83	0.14	2.20	2.33	4.30	2.13	4.11	14.10	2.13
Neolitsea aciculata	L	E	48	27	92	0.48	0.19	1.07	1.89	1.72	1.97	3.53	5.33	2.45
Abies firma	INF	C	13	16	6	6.57	8.08	3.51	0.67	1.03	0.00	0.00	0.00	0.00
Quercus sessilifolia	INF	E	21	27	10	2.47	2.57	2.28	0.81	0.50	2.21	0.81	0.96	0.00
Quercus acuta	INF	E	16	20	6	1.63	2.35	0.18	1.10	0.00	-	0.57	0.57	-
Ternstroemia gymnanthe	INF	E	18	25	3	0.39	0.57	0.03	0.47	0.47	-	0.91	0.91	-
Betula grossa	INF	D	3	3	3	0.35	0.27	0.50	0.00	0.00	0.00	0.00	0.00	0.00
Distyliam racemosum	INF	E	16	19	10	0.33	0.48	0.05	1.10	0.73	2.21	2.06	2.02	2.21
Carpinus laxiflora	INF	D	6	5	10	0.27	0.19	0.42	1.40	5.33	0.00	0.00	0.00	0.00
Litsea coreana	INF	E	5	3	10	0.25	0.10	0.56	0.00	0.00	0.00	3.62	8.45	1.72
Quercus glauca	INF	E	8	6	13	0.16	0.10	0.29	2.21	0.00	3.12	1.19	0.00	1.72
Acer amoenum	INF	D	1	2	0	0.16	0.24	0.00	0.00	0.00	-	0.00	0.00	-
Stewartia monadelpha	INF	D	1	2	0	0.15	0.22	0.00	0.00	0.00	-	0.00	0.00	-
Rhododendron weyrichii	INF	D	21	30	3	0.15	0.21	0.01	0.81	0.86	0.00	0.81	0.86	0.00
Ilex macropoda	INF	D	6	8	3	0.12	0.18	0.01	1.40	0.00	-	0.00	0.00	-
Magnolia obovata	INF	D	2	3	0	0.08	0.11	0.00	0.00	0.00	-	0.00	0.00	-
Lyonia ovalifolia var. elliptica	INF	D	5	8	0	0.07	0.11	0.00	3.93	3.93	-	0.00	0.00	-
Diospyros japonica	INF	D	1	0	3	0.07	0.00	0.20	0.00	-	0.00	0.00	-	0.00
Cinnamomum japonicum	INF	E	4	5	3	0.06	0.09	0.01	0.00	0.00	0.00	5.33	6.52	0.00
Cornus controversa	INF	D	1	0	3	0.05	0.00	0.16	0.00	-	0.00	0.00	-	0.00
Ilex pedunculosa	INF	E	2	3	0	0.05	0.08	0.00	5.33	5.33	-	0.00	0.00	-
Mallotus japonicus	INF	D	3	0	10	0.05	0.00	0.16	3.12	-	3.12	0.00	-	0.00
Machilus thunbergii	INF	E	8	9	6	0.05	0.06	0.02	2.21	0.00	8.45	3.93	2.59	8.45
Sapium japonicum	INF	D	9	2	25	0.04	0.01	0.10	1.93	0.00	2.21	4.76	12.38	2.21
Daphniphyllum macropoum	INF	E	4	3	6	0.03	0.04	0.02	-	-	-	-	-	-
Zanthoxylum ailanthoides	INF	D	1	0	3	0.02	0.00	0.07	-	-	-	-	-	-
Ilex integra	INF	E	1	2	0	0.02	0.03	0.00	0.00	0.00	-	5.33	5.33	-
Vaccinium bracteatum	INF	E	2	3	0	0.02	0.02	0.00	0.00	0.00	-	0.00	0.00	-
Ilex goshiensis	INF	E	2	3	0	0.02	0.02	0.00	0.00	0.00	-	0.00	0.00	-
Premna microphylla	INF	D	2	0	6	0.02	0.00	0.05	0.00	-	0.00	0.00	-	0.00
Callicarpa mollis	INF	D	2	0	6	0.01	0.00	0.03	-	-	-	-	-	-
Lindera erythrocarpa	INF	D	1	0	3	0.01	0.00	0.02	-	-	-	-	-	-
Prunus jamasakura	INF	D	1	0	3	0.00	0.00	0.01	-	-	-	-	-	-
Dendropanax trifidus	INF	E	0	0	0	0.00	0.00	0.00	-	-	-	-	-	-
Total			1571	1737	1235	58.86	73.22	29.92	1.38	1.08	2.17	1.68	1.87	1.15

Table 3 Habitat preferences of dominant species examined by randomization test.

Species group	**Life-form**	**Species**	**Abbreviation**	**Number of trees in 1994**	**Vegetation-type categories**					
					A	**B**	**C**	**D**	**E**	**F**
U	**C**	*Chamaecyparis obtusa*	*CO*	**40**	+++	++	++	---	---	---
U	**C**	*Tsuga sieboldii*	*TS*	**48**	+++	+++	-	n.s.	---	---
U	**E**	*Castanopsis sieboldii*	*CS*	**61**	+++	+++	n.s.	---	---	---
U	**E**	*Pieris japonica*	*PJ*	**65**	+++	+++	n.s.	---	---	---
U	**E**	*Symplocos myrtacea*	*SM*	**33**	+++	++	n.s.	-	---	---
U	**E**	*Symplocos prunifolia*	*SP*	**126**	+++	+++	-	---	---	---
C	**E**	*Camellia japonica*	*CAJ*	**126**	--	n.s.	n.s.	+	n.s.	-
C	**E**	*Cleyara japonica*	*CJ*	**470**	n.s.	+	n.s.	n.s.	n.s.	---
C	**E**	*Eurya japonica*	*EJ*	**68**	n.s.	n.s.	n.s.	n.s.	n.s.	-
C	**E**	*Illicium anisatum*	*IA*	**90**	---	++	n.s.	n.s.	n.s.	n.s.
C	**E**	*Quercus salicina*	*QS*	**70**	n.s.	n.s.	n.s.	n.s.	n.s.	-
L	**E**	*Machilus japonica*	*MJ*	**69**	---	---	--	n.s.	+++	+++
L	**E**	*Neolitsea aciculata*	*NA*	**46**	n.s.	-	n.s.	n.s.	+++	n.s.
		Total		**1492**	+++	+++	n.s.	--	---	---

Species groups: U: uppe species, L: lower species , C: common species

Life form: C: conifer, E: evergreen broad leaved

+++/---: P<0.001 ++/--: P<0.01 +/-: P<0.05

Table 4. Number and state of injuries from 1994 to 2007.

Micro-topography	Number of dead trees	Dead trees/ha	SD		UR		BT		CD		unknown	
			N	(%)	N	(%)	N	(%)	N	(%)	N	%
CS	13	121	12	92.3	0	0.0	1	7.7	0	0.0	0	0.0
US	126	239	71	56.3	9	7.1	34	27.0	5	4.0	7	5.6
Total of upper area	139	219	83	59.7	9	6.5	35	25.2	5	3.6	7	5.0
LS	53	385	23	43.4	15	28.3	15	28.3	0	0.0	0	0.0
FS	54	304	34	63.0	4	7.4	12	22.2	2	3.7	2	3.7
Total of lower area	107	340	57	53.3	19	17.8	27	25.2	2	1.9	2	1.9

CS: crest slope; UL: upper sideslope; LS: lower sideslope; FS: footslope

SD: standing dead, UR: uprooted, BT: broken trunk, CD: collateral damage

Table. 5 The coefficient of logistic regression model for gap formation by spatial environment and stand structure. TWI: topographic wetness index, RVR: relative distance from valley to ridge, Direction(NS): north-south (0-180°), Direction(EW): east-west (0-180°), DCHM: digital canopy height model, Neighbor: beside former gap or not, Life form: Conifer or not

Year	Variables	Coefficient	Standard Error	P Value
1969-1985	Slope	0.021	0.004	<0.0001
	TWI	-0.118	0.025	<0.0001
	RVR	-0.157	0.050	0.0016
	Direction(NS)	0.007	0.001	<0.0001
	Direction(EW)	-0.003	0.001	<0.0001
	DCHM	0.180	0.006	<0.0001
	Neighbour	0.176	0.047	<0.0002
	Life form	-0.058	0.050	0.2458
	Intercept	-6.560	0.356	<0.0001
1985-2005	Slope	-0.002	0.004	0.6472
	TWI	-0.182	0.030	<0.0001
	RVR	-0.232	0.060	<0.0001
	Direction(NS)	0.001	0.001	0.2807
	Direction(EW)	0.008	0.001	<0.0001
	DCHM	0.165	0.007	<0.0001
	Neighbor	0.633	0.083	<0.0001
	Life form	0.003	0.061	0.958
	Intercept	-5.088	0.419	<0.0001

Table 6 The coefficient of GLM regression model for gap area by spatial environment and stand structure. TWI: topographic wetness index, RVR: relative distance from valley to ridge, Direction(NS): north-south (0-180°), Direction(EW): east-west (0-180°), DCHM: digital canopy height model, Neighbor: beside former gap or not, Life form: Conifer or not

Year	Variables	Coefficient	Standard Error	P Value
1969-1985	Slope	0.014	0.010	0.1704
	TWI	0.034	0.035	0.3323
	RVR	0.101	0.121	0.4042
	Direction(NS)	0.000	0.002	0.9829
	Direction(EW)	0.001	0.002	0.6703
	DCHM	0.037	0.014	0.0110
	Neighbor	0.214	0.097	0.0231
	Life form	0.458	0.081	<0.0001
	Intercept	2.065	0.715	0.0032
1985-2005	Slope	-0.009	0.010	0.3470
	TWI	-0.069	0.037	0.0626
	RVR	-0.190	0.136	0.1561
	Direction(NS)	-0.001	0.001	0.3657
	Direction(EW)	-0.001	0.002	0.4518
	DCHM	0.037	0.048	0.0151
	Neighbor	0.330	0.101	0.0009
	Life form	0.119	1.507	0.2196
	Intercept	4.200	33.366	<0.0001

Table 7 The coefficient of logistic regression model for conifer grid and spatial environment

Variables	Coefficient	Standard Error	P Value
Slope	-1.222	0.392	0.0163
TWI	-0.270	0.036	0.0016
RVR	0.697	0.071	<0.0001
Direction(NS)	0.001	0.001	0.3055
Direction(EW)	-0.003	0.001	0.0008
Intercept	-1.222	0.392	<0.0001

Table 8 The results of GLM analysis for DCHM change with spatial environment, stand structure

DCHM < 15m					DCHM > 15m				
Year	Variables	Coefficient	Standard Error	P Value	Year	Variables	Coefficient	Standard Error	P Value
1969-1985	Slope	0.084	0.018	<0.0001	1969-1985	Slope	0.034	0.004	<0.0001
	TWI	0.188	0.118	0.1109		TWI	0.196	0.027	<0.0001
	RVR	-1.911	0.227	<0.0001		RVR	-0.342	0.054	<0.0001
	Direction (NS)	-0.022	0.003	<0.0001		Direction (NS)	-0.017	0.001	<0.0001
	Direction (EW)	-0.002	0.018	0.5575		Direction (EW)	0.001	0.001	0.0651
	DCHM	-0.763	0.071	<0.0001		DCHM	-0.483	0.007	<0.0001
	Neighbor	1.288	0.289	<0.0001		Neighbor	-0.431	0.044	<0.0001
	Life form	2.117	0.708	0.0029		Life form	0.467	0.065	<0.0001
	Intercept	12.055	1.849	<0.0001		Intercept	8.698	0.384	<0.0001
1985-2005	Slope	0.088	0.019	<0.0001	1985-2005	Slope	0.554	0.004	<0.0001
	TWI	0.617	0.137	<0.0001		TWI	0.356	0.026	<0.0001
	RVR	-0.326	0.292	0.2638		RVR	-0.066	0.051	0.193
	Direction (NS)	0.019	0.003	<0.0001		Direction (NS)	0.008	0.001	<0.0001
	Direction (EW)	-0.011	0.004	0.0041		Direction (EW)	-0.014	0.001	<0.0001
	DCHM	-0.823	0.079	<0.0001		DCHM	-0.330	0.007	<0.0001
	Neighbor	-0.315	0.279	0.2585		Neighbor	-0.209	0.037	0.0017
	Life form	0.509	0.396	0.1995		Life form	0.722	0.061	<0.0001
	Intercept	4.265	2.021	<0.0001		Intercept	2.558	0.362	<0.0001