Variation of intra-crown leaf plasticity of Fagus crenata across its geographical range in Japan

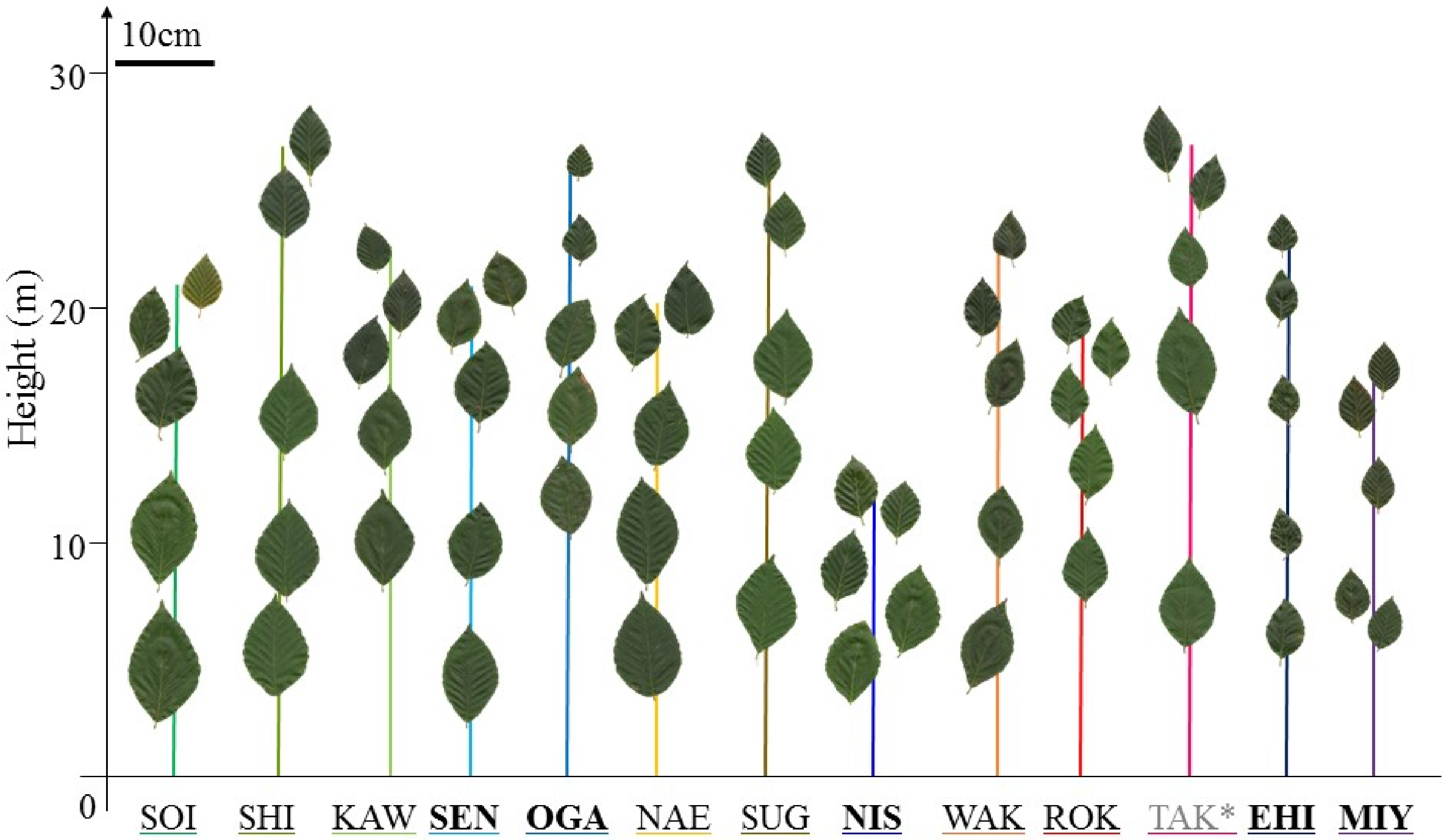
Ishii, H. Roaki
Horikawa, Shin-ichiro
Noguchi, Yuiko
Azuma, Wakana

(Citation)
Forest Ecology and Management,429:437-448

(Issue Date)
2018-12

(Resource Type)
journal article

(Version)
Accepted Manuscript



Intra-crown variation of leaf morphology among the 13 *F. crenata* populations in Japan. Scanned leaf images from single trees are shown in relation to height. Leaf morphological plasticity decreases with decreasing latitude (north to south from left to right), suggesting low phenotypic plasticity and acclimation potential to climate change of southern and Pacific populations.

Variation of intra-crown leaf plasticity of *Fagus crenata* across its geographical range in Japan

Running title: Intra-crown leaf plasticity of *Fagus crenata*

H. Roaki Ishii[1]*, Shin-ichiro Horikawa[1]*, Yuiko Noguchi[1], Wakana Azuma[1,2]

[1]Graduate School of Agricultural Science, Kobe University, Kobe 657-8501, JAPAN

[2]Present address: Graduate School of Agriculture, Kyoto University, Kyoto 608502, JAPAN

*These authors share first authorship.

Author for correspondence: H. Roaki Ishii

Email: hishii@alumni.washington.edu

Phone: +81-78-803-5933

Abstract

Because rates of migration and genetic adaptation are slow, individual trees must initially acclimate to climate change via individual-level plasticity. Therefore, when predicting distribution and persistence of tree species under future climate change scenarios, we must take into account geographical variation in intra-individual plasticity. Here, we investigated geographical variation of intra-individual plasticity of *Fagus crenata* Blume (Japanese beech), a dominant species in late-successional, cool-temperate forests of Japan. We compared within-crown variation of leaf morphology (intra-crown leaf plasticity, ILP) among 13 sites across the full distribution range of *F. crenata*. Generally, ILP was lower for trees in the Pacific than Japan-Sea genetic lineages, low for trees in southern sites, and high for trees in sites near the northern and altitudinal range edges. Among the 13 sites, ILP was correlated with environmental variables associated with temperature. Positive correlation between ILP and temperature variation suggested that environmental perturbation selects for high intra-individual plasticity near northern and altitudinal range edges where *F. crenata* is expanding its distribution range. On the other hand, low ILP of trees in Pacific and southern sites, comprising geographically isolated populations, may reflect low acclimation potential to environmental perturbation. This could lead to local extinction if climatic conditions exceed the range of tolerance resulting in retreat of the Pacific and southern range edges of *F. crenata* in Japan.

Keywords: acclimation; geographical variation; habitat fragmentation; leaf functional trait; local adaptation; distribution range

Introduction

Beech (*Fagus* spp.) occurs widely across cool-temperate forests of Asia, Europe, and North America (Fang and Lechowicz, 2006). Thermal conditions, such as growing season warmth determine geographical limits of the distribution of beech (Matsui *et al.*, 2004a; Fang and Lechowicz, 2006; Bolte *et al.*, 2007), which suggests that future climate change could impact beech distribution ranges (Matsui *et al.*, 2004b; Gessler *et al.*, 2007; Friedrichs *et al.*, 2009; Dulamsuren *et al.*, 2017). For example, recent growth decline observed in European beech (*Fagus sylvatica* L.) populations near its southern distribution limit could lead to consequent retreat of the southern range edge if warming and drying trends continue (Jump *et al.*, 2006; Piovesan *et al.*, 2008; Hacket-Pain *et al.*, 2016). However, there are also contradicting reports of growth increase of European beech in the late twentieth century (Tegel *et al.*, 2014), which has been attributed in part to the ability of trees to acclimate to climate variation and recover from stress-induced growth decline (Dulamsuren *et al.*, 2017).

Trees have evolved retaining high intra-individual plasticity, which allows them to acclimate to changing environmental conditions during their long lifespan (Petit and Hampe, 2006; Ishii *et al.*, 2013; Duptie *et al.*, 2015). Plasticity is highly adaptive for shade-tolerant trees such as beech, whose seedlings and saplings establish in the dark understory, and eventually grow to reach the bright canopy. European beech has high plasticity that allows it to acclimate to more severe drought conditions than previously assumed (Bolte *et al.*, 2007). For example, European beech exhibits high phenological plasticity (Vitasse *et al.*, 2010), which may enable it to acclimate to future climate conditions and persist in the trailing southern range edge (Duptie *et al.*, 2015). For trees, whose rates of migration and genetic adaptation are slow (Petit and Hampe, 2006; Aitken *et al.*, 2008; Shaw *et al.*, 2012), intra-individual plasticity may be an important trait contributing to greater acclimation potential and persistence through future climate change (Thuiller *et al.*, 2008; Chevin *et al.*, 2010; Matesanz, 2010; Richter *et al.*, 2012; Franks *et al.*, 2014).

Adaptation of tree species to regional environmental conditions involve both genetic and phenotypic adaptation (Tateishi et al. 2010). For European beech, phenotypic plasticity at the population level has been compared using common garden experiments and provenance trials (e.g., Garcia-Plazaola and Becerril, 2000; Balaguer *et al.*, 2001; Vitasse *et al.*, 2009; Kreyling *et al.*, 2014; e.g., Stojnic *et al.*, 2015). However, artificial growing conditions may affect the expression of phenotypic plasticity (Urbas and Zobel, 2000) and because trees are long-lived, it is difficult to measure the expression of phenotypic plasticity through ontogeny. On the other hand, trees express plasticity at the individual level, such as intra-canopy trait variation of sun- vs. shade-leaves (Masarovicova and Stefancik, 1990; Sack *et al.*, 2006). Because leaves of a single tree are genetically identical, within-tree trait variation represents intra-individual plasticity expressed in response to spatial (as opposed to temporal) variation in environmental conditions (Sultan, 2000; Sack *et al.*, 2006; Ishii *et al.*, 2007). Long-lived, sessile organisms like trees must cope with environmental perturbation through intra-individual plasticity and this could determine their acclimation potential to future climate change. Geographical variation in intra-individual plasticity will influence population dynamics through its effects on tree growth and survival. Such effects should be considered when predicting future geographical distribution of tree species in relation to climate change (Nicotra *et al.*, 2010; Vitasse *et al.*, 2010; Duptie *et al.*, 2015).

Leaf functional traits reflect the growth strategy, carbon economy, and resource use of plants worldwide (Wright *et al.*, 2004; Perez-Harguindeguy *et al.*, 2013). Functional-trait variation at the species level represents niche breadth (McGill *et al.*, 2006; Nicotra *et al.*, 2010), while that at the individual level represents acclimation potential to environmental perturbation (Valladares *et al.*, 2014). Leaf trait variation among species, as well as within species and individuals, is considered an important predictor of plant response to climate change (Soudzilovskaia *et al.*, 2013; Liancourt *et al.*, 2015). Here, we compared within-crown variation of leaf morphology among trees in 13 sites across the full distribution range of *F. crenata* to elucidate geographical variation of intra-individual plasticity. *F. crenata* is a dominant species in late-successional, cool-temperate forests of Japan (Matsui *et al.*, 2004a). It has a wide north-south distribution, ranging from Kuromatsunai Town in Hokkaido Prefecture (42.7°N, 140.3°E) to Mt. Takakuma in Kyushu Prefecture (31.3°N, 130.8°E) (Tomaru *et al.*, 1998). The present distribution of *F. crenata* is believed to have been established about 7000 years ago as a result of northward and upward migration after the last glacial maximum, followed by retreat from the lowlands to high altitudes (Tsukada, 1982; Okaura and Harada, 2002; Hiraoka and Tomaru, 2009). On Honshu Island, the center of its distribution range, the altitudinal limit of *F. crenata* is approximately 1400 m (Okaura and Harada, 2002). In southwestern Japan (southern Honshu, Shikoku, and Kyushu islands), upward migrating populations became isolated on high elevation mountains and could face high risk of local extinction if growing conditions change due to climate change (Tomaru *et al.*, 1998; Fujii *et al*. 2002; Matsui *et al.*, 2004a; Hanaoka *et al.*, 2007).

In adult trees of *F. crenata*, mean leaf size is larger for northern than southern populations (Hiura *et al.*, 1996). Among populations within a narrow longitudinal range (34.5−37.5°E) on Honshu Island, sun leaves are thicker for northern than southern populations, while shade leaves are thinner, resulting in higher intra-crown leaf plasticity (ILP) of northern populations (Shiraishi and Watanabe, 2002). Low ILP of southern populations may reflect low intra-individual plasticity, which could constrain their ability to acclimate to climate change. The objective of this study was to infer geographical variation of intra-individual plasticity and acclimation potential of *F. crenata* by comparing ILP across the full distribution rage. In addition, to predict possible effects of climate change on the future distribution of *F. crenata* in Japan, we investigated environmental variables influencing ILP.

Methods

Study sites

To sample *F. crenata* across its full geographical range, we selected 13 study sites ranging from Soibetsu Beech Forest in Hokkaido Prefecture to Kyushu University Miyazaki Research Forest in Kyushu Prefecture near the northern to southern range edges, respectively (Table 1, Fig. 1). Shinshu University Alpine Field Center Nishikoma Field Station (1600 m a.s.l) and Sugadaira Daido Beech Forest (1315 m) in Nagano Prefecture were selected to represent altitudinal range edges in the center of the distribution.

Genetic studies of *F. crenata* indicate low allozyme-based genetic variation among populations, suggesting limited seed dispersal distance (Takahashi *et al.*, 1994; Tomaru *et al.*, 1997), whereas mitochondrial DNA analyses indicate high genetic variation among populations suggesting extensive pollen dispersal and diversion into several regional groups (Koike *et al.*, 1998; Tomaru *et al.*, 1998; Fujii *et al.* 2002). Populations distributed in Hokkaido and northwestern, Japan Sea side of Honshu Island are genetically distinct from northeastern and southern populations on the Pacific side (Koike *et al.*, 1998; Hiraoka and Tomaru, 2009). The genetic lineages of the sites in this study are indicated in Table 1 and Fig. 1.

Field sampling

At each study site, we selected four to six mature trees of *F. crenata* for sampling. We avoided suppressed trees so that treetop leaves of all sample trees were fully exposed to the sky. Using modern arborist-style techniques, we climbed each tree using ropes and sampled branches comprising several shoots with mature leaves (ca. 50 cm long) from the treetop, approximately 1 m below treetop, and from the lowest branch. We also sampled branches from two to three equidistant locations between the treetop and lowest branch. The sampled branches were sealed in black plastic bags to prevent leaf dehydration, and transported to the laboratory for further measurement on the day of sampling. The height (*H*, m) of each sampling location was measured using a tape measure stretched from average ground level. Hemispherical photographs were taken at each sampling location and analyzed using Gap Light Analyzer ver. 3.0 (Simon Frazer University, Burnaby, BC, Canada) to quantify the light environment as canopy openness (%) and to estimate LAI.

Leaf morphological traits

From each branch, we randomly selected 15 fully developed, mature leaves with no evidence of damage or herbivory, for measurement of leaf morphological traits. The leaves were scanned using a portable flatbed scanner (LiDE 90, Canon, Tokyo, Japan). We measured leaf thickness at two locations on either side of the leaf using a digital thickness meter (PK-1-12UE, Mitsutoyo, Tokyo, Japan). Here, leaf thickness includes that of the secondary leaf vein. We decided to include vein thickness for all leaves, because for small leaves, the diameter of the thickness meter head was larger than the inter-vein distance such that the vein could not be avoided. The leaves were then oven-dried at 65°C to constant weight and weighted to determine dry mass. Using the scanned leaf images, we measured the area, length, width and number of veins of the sample leaves. Specific leaf area (SLA) was calculated as the ratio of leaf area to dry mass. Leaf shape index (LS) was calculated as leaf length/(distance from leaf base to widest part of leaf).

Environmental variables

To examine the effect of environmental conditions on leaf trait variation, we calculated a suite of environmental variables representing climate and geographical location of each site (latitude, longitude, elevation). Climate data over the past 50 years (1965−2015) were obtained from the nearest Japan Meteorological Society weather station for each site (Table 1) and used to calculate a suite of climate variables representing mean conditions (daily/monthly/annual mean temperature, precipitation, snowfall), variation (daily/monthly/annual ranges) and extremes (lowest/highest recorded). Data on relative humidity was only available for some of the sites. Therefore, water availability was assessed by the standardized precipitation evapotranspiration index (SPEI) downloaded from the Spanish National Research Council's global database (http://spei.csic.es/). We also investigated relationships between tree structural characteristics (tree height, DBH, crown depth, LAI, etc.) and leaf traits. See Table S1 for a list of all environmental and structural variables analyzed.

Statistical analyses

We used principle components analysis (PCA) to investigate variation in leaf traits among the 13 sites. To compare intra-crown leaf plasticity (ILP) between the two genetic lineages and among the 13 study sites, each trait was analyzed in relation to height and canopy openness using regression analysis. Because our main objective was to compare ILP among sites, data from individual trees were pooled for each site. We checked all data for normality and heteroscedasticity before analyses. Canopy openness was log-transformed to normalize the variance. The regression slope was considered a quantitative measure of ILP (Niinemets *et al.*, 2003; Ishii *et al.*, 2007). Because tree height varied among sites, we calculated relative height ($H_{\mathrm{rel}} = H$ / tree height) of each branch to compare sites using a common independent variable representing both height and light factors.

We compared regression slopes between Japan-Sea and Pacific genetic lineages in an analysis of covariance (ANCOVA) with height, canopy openness and relative height as covariates, where a significant interaction term indicates difference in slope (Niinemets *et al.*, 2003). To compare regression slopes among the 13 sites, paired ANCOVA comparisons were made in descending order of slope estimates. We also compared regressions parameters simultaneously among all sites, where dummy variables corresponding to each site were tested for significance in a multiple regression model. Both analyses yielded similar statistical results. To infer the effect of environmental conditions at each site on ILP, Spearman's rank correlation coefficients were calculated between plasticity of leaf traits (absolute value of the regression slope) and environmental variables.

For logistic reasons, our sampling had to be spread over three field seasons (2015~2017). To compare potential inter-annual variation, we conducted field sampling every year in Mt. Rokko, Hyogo Prefecture. Although 2015 was a mast year, 2016 and 2017 were non-mast years, inter-annual variation of ILP among sampling years was non-significant or inconsistent (Table S2). We, therefore, inferred that geographical variation of ILP is greater than inter-annual variation and that data from different years could be compared among the 13 sites.

Results

Scanned leaf images from representative trees at each site are shown in relation to height in Fig. 2. Although tree height and crown-base height varied among sites, there was no consistent trend with latitude or genetic lineage. Both sun and shade leaves tended to be larger for trees in northern than southern sites. The difference in leaf area was more marked for shade leaves. These trends were reflected in the results of PCA, where northern sites were distributed toward the upper right (greater leaf thickness, mass and area), while southern sites were distributed toward the lower left (Fig. 3). Axis 1 and 2 explained 44.1 and 25.1%, respectively, of the total variance in leaf traits among sites. Axis 1 was positively correlated with measures of leaf size (area, length, width). We chose leaf area to represent this variation. Axis 2 was positively correlated with measures of leaf volume (mass, thickness) and negatively correlated with measures of leaf dimensions (length/width ratio). We chose leaf thickness and mass to represent this variation. Reflecting these relationships, SLA was positively correlated with both Axis 1 and 2.

There was no difference between Japan-Sea and Pacific genetic lineages in plasticity of leaf area in response to height and relative height, as indicated by similar regression slopes (Table 2). Leaf-area plasticity in response to canopy openness was higher for trees in the Pacific genetic lineage. In contrast, plasticity of leaf thickness, mass and SLA were all lower for trees in the Pacific genetic lineage. Leaf-area plasticity in response to height was higher (steeper regression slopes) for trees in northern than southern sites (Fig. 4). Leaf-area plasticity was highest (steepest, most negative slope) for trees in Nishikoma followed by Soibetsu, representing the altitudinal and northern range edge, respectively. Leaf-area plasticity was high for trees in northern sites (Shirakami, Kawatabi, Naeba, Ogawa, and Sugadaira) and low for southern sites (Wakasugi, Rokko, Takanosu, Ehime, and Miyazaki). Similar latitudinal trends in leaf-area plasticity were observed in response to canopy openness and relative height (Table 3). Among the three independent variables, relative height showed the highest correlation with leaf area, as assessed by r-square values. The latitudinal trend in plasticity was not as apparent for leaf thickness and leaf mass. Plasticity of SLA in response to height and relative height was highest for trees in Kawatabi (third highest latitude) and Sugadaira (second highest altitude). SLA plasticity in response to canopy openness was high for trees in northern sites (Soibetsu, Kawatabi Naeba, and Sugadaira), while it was low for sites south of Wakasugi. Nishikoma (altitudinal range edge), however, was among the sites with low SLA plasticity (Fig. 5).

Among leaf traits, only leaf-area plasticity, which showed greatest variability among sites, yielded statistically significant relationships with environmental variables (Table 4). Reflecting the latitudinal and altitudinal trends, leaf-area plasticity (absolute value of the regression slope in relation to height, canopy openness and relative height) was correlated with environmental variables associated with temperature. Leaf-area plasticity in response to canopy openness was positively correlated with days of precipitation. Among the environmental variables, the highest R_S value (−0.936) was observed for the relationship between leaf-area plasticity in relation to relative height and lowest recorded daily minimum temperature. Leaf-area plasticity was correlated with several variables reflecting variation and extremes in environmental conditions (minimum/maximum, highest/lowest recorded, historical variation). For each independent variable, the relationship between the top three environmental variables and leaf-area plasticity are shown in Fig. 5. Other significant correlations are listed in Table S3. Structural characteristics, including crown depth and LAI, were not correlated with plasticity, suggesting that structural variation, such crown recession, nor variation of crown light environment among sites are not the cause of geographical variation in ILP.

Discussion

Our results show that intra-crown leaf plasticity (ILP) of *F. crenata* varies across its geographical distribution range. Of the leaf traits examined, leaf area showed the greatest geographical variation of ILP. While minimum leaf area of sun leaves was similar (ca. 10 cm^2) among the sites, maximum leaf area of shade leaves varied more than three-fold, ranging from ca 20 cm^2 near the southern range (Miyazaki) to ca 70 cm^2 near the northern range edge (Soibetsu). The high variability of shade-leaf area contributed to variation of leaf-area plasticity among sites. As illustrated in the relationship between SLA and canopy openness (Fig. 5), low ILP was not necessarily caused by variation in intra-canopy light environment among sites. Although, some sites with low ILP like EHI and MIY had higher minimum canopy openness, reflecting shallower, less shaded crowns, minimum canopy openness was also high for SOI and NAE, which had high ILP. This is also reflected in the lack of correlation between ILP and LAI. In many plants, low-light conditions of the lower canopy favor greater resource allocation to light-intercepting area (Tognetti *et al.*, 1998; Pearcy, 2007; Valladares and Niinemets, 2007). Our results indicate that *F. crenata* trees in northern sites are able to realize larger light-intercepting area of shade-leaves in response to the same gradient of within-crown light intensity than trees in southern sites. Leaf thickness is also an important morphological trait that varies vertically within the crown of many tree species (e.g., Eschrich *et al.*, 1989; Gratani *et al.*, 2006; Sack *et al.*, 2006; Hallik *et al.*, 2012). Thicker leaves with more developed palisade parenchyma are adaptive for exploiting the high-light environment of the upper canopy, as well as for decreasing surface-area to volume ratio in response to increasing evaporative demand (Pallardy, 2008; Coble and Cavaleri, 2015). While we observed intra-crown plasticity of leaf thickness in all 13 sites, there was less geographical variation among sites compared to leaf area. This may be due to our measurement method, which included leaf veins in leaf thickness. More detailed examinations of leaf anatomy (e.g., Sack *et al.*, 2006; Chin and Sillett, 2017; Coble and Cavaleri, 2017) may elucidate clearer differences among sites underlying geographical variation of leaf-thickness plasticity.

SLA is a leaf functional trait that reflects the resource exploitation/conservation trade-off (Perez-Harguindeguy *et al.*, 2013). Among the 13 sites, SLA converged to ca 0.1 cm^2 g^{-1} at treetop, suggesting this is the minimum attainable value for *F. crenata* representing the conservative leaf-trait syndrome of tolerance to drought stress in response to the high evaporative demand of the treetop. Differences among sites in SLA plasticity was, therefore determined by its maximum value (i.e., SLA of shade leaves) representing the exploitative leaf-trait syndrome where resource allocation to light-intercepting area is maximized under low-light conditions (Fajaro and Siefert, 2016; Liu *et al.*, 2016). When compared among species, high SLA plasticity is associated with low productivity (Liu *et al.*, 2016). In this study, however, because SLA converges among sites to a minimum value at treetop, where sun-leaves of all sample trees are receiving high irradiance, high SLA plasticity reflects greater acclimation potential to low irradiance, i.e., exploitation of the full gradient of light intensities from treetop to lower canopy. Our results indicate that in response to the same gradient of within-crown light intensity, trees in Japan-Sea and northern sites are able to allocate resources to light-capturing area of shade leaves more efficiently than trees in Pacific and southern sites. Japan-Sea and northern regions of Japan receive less solar radiation throughout the year than Pacific and southern regions (Iizumi et al. 2008). Greater SLA plasticity may reflect broader light-resource niche and contribute to increasing photosynthetic productivity of *F. crenata* giving them a competitive advantage over other tree species (Coble *et al.*, 2017). In these regions, *F. crenata* dominates over other species in mature late-successional forest, contributing more than 90% of stand basal area (Nakashizuka, 1988; Homma *et al.*, 1999; Yasaka *et al.*, 2003). Our results also expand the findings of Shiraishi (2002), who found higher ILP for northern populations within a limited longitudinal range in northern Honshu, to the full distribution range of *F. crenata*.

Variation among sites in ILP suggests intra-individual plasticity also varies among regions, which could affect acclimation potential of individual trees to future climate change. Sites near the northern and altitudinal range edges represent the leading edge of northward and upward migration of *F. crenata* after the last glacial maximum (Tsukada, 1982; Okaura and Harada, 2002; Hiraoka and Tomaru, 2009). Trees in these sites exhibited high ILP, which was associated with greater environmental variation, namely temperature. Intra-individual plasticity may be adaptive in novel sites after colonization or migration, because it enables individuals to acclimate quickly to new environmental conditions (Agrawal, 2001; Yeh and Price, 2004). Although genetic diversity tends to be low for populations near range edges (Vucetich and Waite, 2003; Chang *et al.*, 2004; Hampe and Petit, 2005; Bridle and Vines, 2007; Kawecki, 2008), intra-individual plasticity could compensate for slow genetic adaptation of long-lived organisms and contribute to their persistence in variable environments by increasing individual-level acclimation potential (Magi *et al.*, 2011; Reed *et al.*, 2011). Intra-individual plasticity is more adaptive in environments where individuals experience heterogeneous conditions, because it broadens the fundamental niche of a species (Valladares *et al.*, 2007). Because the annual range of climatic fluctuation is greater at higher latitudes, species adapted to such conditions should have broader thermal tolerance niche (climatic variability hypothesis, sensu Janzen, 1967), which could be realized by increasing physiological flexibility and intra-individual plasticity (Valladares *et al.*, 2014). Along with latitude, environmental variation also tends to be greater in sub-alpine environments (Billings and Mooney, 1968; Smithson *et al.*, 2008). Environmental fluctuation at high latitude and altitude, therefore, is likely to select for high intra-individual plasticity in plants (Bradshaw, 1965; Ghalambor *et al.*, 2007), especially long-lived trees (Sultan, 2000; Sultan and Spencer, 2002; Vasseur and McCann, 2007; Richter *et al.*, 2012). In Japan, winter temperatures are lower and snow fall is greater on the Japan Sea side resulting in highly variable climate, which could select for high intra-individual plasticity in *F. crenata*. Plasticity modulates species responses to changing environments and could buffer against immediate fitness declines due to rapid climate change (Reed *et al.*, 2011; Richter *et al.*, 2012; Jung *et al.*, 2014; Anderson and Gezdon, 2015). Acclimation via intra-individual plasticity may also explain growth increase of European beech in response to climate change at higher elevations in the center of its distribution range (Dulamsuren *et al.*, 2017). As with *F. crenata*, this growth increase may reflect advancement of the altitudinal distribution range of beech in response to global warming.

Because plasticity incurs costs such as maintaining sensory and regulatory mechanisms to detect environmental conditions, it may not be adaptive in stable environments (DeWitt *et al.*, 1998). Fixed traits, as opposed to plasticity, are favored in stressful environments (Van Kleunen and Fischer, 2005; Ghalambor *et al.*, 2007; Sambatti and Caylor, 2007; Sánchez-Gómez *et al.*, 2008; Auld *et al.*, 2010). In marginal populations, plasticity may not be adaptive because high levels of environmental stress render the relative cost of plasticity higher than for central populations (Magi *et al.*, 2011). In European beech, stronger adaptation to local climate of geographically marginal than central populations (Kreyling *et al.*, 2014) and high degree of drought resistance of populations near the southern range edge (Sánchez-Gómez *et al.*, 2013), are both associated with low plasticity. In this study, low intra-individual plasticity was associated with higher temperature and fewer days of precipitation, suggesting that hotter, dryer conditions may select for low plasticity in *F. crenata*. However, measures of aridity, such as SPEI, were not correlated with leaf-area plasticity in this study, suggesting that further investigation is needed to elucidate the effect of water availability on leaf trait plasticity of *F. crenata.*

The degree of plasticity and the rate of genetic evolution of a population, determine its acclimation and adaptation potentials, respectively, to environmental perturbation (Thuiller *et al.*, 2008). Initially, trees can respond to climate change through plasticity, i.e. individual-level acclimation in phenology, resource allocation, etc. (DeLucia *et al.*, 2000; Rehfeldt *et al.*, 2002; Vitasse *et al.*, 2010). However, if the rate of adaptive evolution lags behind environmental change and genetic adaptation is slow, then tree populations may not be able to persist in the long term (Aitken *et al.*, 2008; Lindner *et al.*, 2009; Kuparinen *et al.*, 2010; Shaw *et al.*, 2012). Studies of forest dynamics along altitudinal gradients suggest that changes in tree species composition due to climate change are already taking place (Lenoir *et al.*, 2009). Compared to other plants, trees tend to have low migration rates (Aitken *et al.*, 2008). In addition, dispersal may be limited by physical barriers such as geographical features (mountains and valleys) as well as anthropogenic habitat fragmentation (Honnay *et al.*, 2002; Jump and Penuelas, 2005; Jackson and Sax, 2010). Because of milder weather conditions, human population densities are higher on the Pacific side of Japan. As a result, many natural forests comprising *F. crenata* have been cleared and those remaining have become geographically isolated (Nagaike and Kamitani, 1999; Hiraoka and Tomaru, 2009). Our results suggest trees in isolated populations of *F. crenata* in Pacific and southern regions of Japan have limited acclimation potential to climate change and these populations may risk local extinction due to increased mortality if climatic conditions exceed their acclimation potential or the rate of change in environmental conditions exceeds that of genetic adaptation. This would lead to future retreat of the Pacific and southern range edges of *F. crenata*. On the other hand, increased mortality can accelerate evolutionary adaptation of trees to climate change by shortening generation turnover time (Kuparinen *et al.*, 2010).

Most models predicting future vegetation change in response to climate change assume species responses to environmental conditions are similar across distributional ranges (e.g., Matsui *et al.*, 2004b for *F. crenata*). Although some models incorporate intraspecific variation and local adaptation to predict species distribution (e.g., Oney *et al.*, 2013), these variations reflect genetic differences among populations and not plasticity within populations and individuals. Similarly, previous studies on trait variation of *F. crenata* compared only mean traits among a few sites (e.g., Tateishi et al. 2010) or in a common garden experiment (Yamasaki et al. 2007; Osada et al. 2015), which represent genetic variation among and phenotypic variation within populations, This study is a first attempt to compare intra-individual plasticity across the full geographic distribution range of *F. crenata.* Our results, therefore, contribute to understanding of the geographical variation in individual-level acclimation potential and help improve predictions of the future distribution of *F. crenata* in response to climate change.

Acknowledgements

We thank faculty and staff of all research sites, especially, Drs. T. Hiura, S. Ishida, Y. Suyama, H. Qingmin, T. Shirota, H. Kobayashi, H. Kurokawa, M. Shibata, T. Kenta, Y. Miyazaki, E. Nabeshima, M. Toda, M. Ishihara, T. Enoki, T. Hishi, S. Ugawa for facilitating our sampling. Members of the Laboratory of Forest Resources, Kobe University (especially A. Shiraki, N. Myokai, K. Nada) provided field assistance and helpful discussion. We thank Dr. H. Rockwell (California State University) for statistical advice and English correction. Part of this research was funded by JSPS Grants in Aid for Scientific Research (#16K14944).

References

Agrawal, A.A., 2001. Phenotypic plasticity in the interactions and evolution of species. Science 294, 321-326.

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T., Curtis-McLane, S., 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications 1, 95-111.

Anderson, J.T., Gezdon, Z.J., 2015. Plasticity in functional traits in the context of climate change: a case study of the subalpine forb *Boechera stricta* (Brassicaceae). Global Change Biology 21, 1689-1703.

Auld, J.R., Agrawal, A.A., Relyea, R.A., 2010. Re-evaluating the costs and limits of adaptive phenotypic plasticity. Proceedings of The Royal Society B Biological Science 277, 503-511.

Balaguer, L., Martínez-Ferri, E., Valladares, F., Pérez-Corona, M.E., Baquedano, F.J., Castillo, F.J., Manrique, E., 2001. Population divergence in the plasticity of the response of *Quercus coccifera* to the light environment. Functional Ecology 15, 124-135.

Billings, W.D., Mooney, H.A., 1968. The ecology of arctic and alpine plants. Biological Reviews 43, 481-529.

Bolte, A., Czajkowski, T., Kompa, T., 2007. The north-eastern distribution range of European beech - a review. Forestry 80, 413-429.

Bradshaw, A.D., 1965. Evolutionary significance of phenotypic plasticity in plants. Advances in Genetics 13, 115-155.

Bridle, J.R., Vines, T.H., 2007. Limits to evolution at range margins: when and why does adaptation fail? Trends in Ecology and Evolution 22, 140-147.

Chang, C.S., Kim, H., Park, T.Y., Maunder, M., 2004. Low levels of genetic variation among southern peripheral poulations of the threatened herb, *Leontice microrhyncha* (Berberidaceae) in Korea. Biological Conservation 119, 387-396.

Chevin, L.-M., Lande, R., Mace, G.M., 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. PLoS Biology 8, e1000357.

Chin, A.R.O., Sillett, S.C., 2017. Leaf acclimation to light availability supports rapid growth in tall *Picea sitchensis* trees. Tree Physiology 10, 1352-1366.

Coble, A.P., Cavaleri, M.A., 2015. Light acclimation optimizes leaf functional traits despite height-related constraints in a canopy shading experiment. Oecologia 177, 1131-1143.

Coble, A.P., Cavaleri, M.A., 2017. Vertical leaf mass per area gradient of mature sugar maple reflects both height-driven increases in vascular tissue and light-driven increases in palisade layer thickness. Tree Physiology 10, 1337-1351.

Coble, A.P., Fogel, M.L., Parker, G.G., 2017. Canopy gradients in leaf functional traits for species that differ in growth strategies and shade tolerance. Tree Physiology 10, 1415-1425.

DeLucia, E.H., Maherali, H., Carey, E.V., 2000. Climate-driven changes in biomass allocation in pines. Global Change Biology 6, 587-593.

DeWitt, T.J., Sih, A., Wilson, D.S., 1998. Costs and limits of phenotypic plasticity. Trends in Ecology and Evolution 13, 77-81.

Dulamsuren, C., Hauck, M., Kopp, G., Ruff, M., Leuschner, C., 2017. European beech responds to climate change with growth decline at lower, and growth increase at higher elevations in the center of its distribution range. Trees 31, 673-686.

Duptie, A., Rutschmann, A., Ronce, O., Chuine, I., 2015. Phenological plasticity will not help all species adapt to climate change. Global Change Biology 21, 3062-3073.

Eschrich, W., Buchardt, R., Essiamah, S., 1989. The induction of sun and shade leaves of the European beech (*Fagus sylvatica* L.): anatomical studies. Trees 3, 1-10.

Fajaro, A., Siefert, A., 2016. Temperate rain forest species partition fine-scale gradients in light availability based on their leaf mass per area (LMA). Annals of Botany 118, 1307-1315.

Fang, J., Lechowicz, M.J., 2006. Climatic limits for the present distribution of beech (*Fagus* L.) species in the world. Journal of Biogeography 33, 1804-1819.

Franks, S.J., Weber, J.J., Aitken, S.N., 2014. Evolutionary and plastic responses to climate change in terrestrial plant populations. Ecological Applications 7, 123-139.

Friedrichs, D.A., Trouet, V., Buntgen, U., Frank, D.C., Esper, J., Neuwirth, B., Loffler, J., 2009. Species-specific climate sensitivity of tree growth in Central-West Germany. Trees 23, 729-739.

Fujii, N., Tomaru, N., Okuyama, K., Koike, T., Mikami, T., Ueda, K. 2002 Chloroplast DNA phylogeography of *Fagus crenata* (Fagaceae) in Japan. Plant Systematics and Evolution 232:21-33.

Garcia-Plazaola, J.I., Becerril, J.M., 2000. Photoprotection mechanisms in European beech (*Fagus sylvatica* L.) seedlings from diverse climatic origins. Trees 14, 339-343.

Gessler, A., Keitel, C., Kreuzwieser, J., Matyssek, R., Seiler, W., Rennenberg, H., 2007. Potential risks for Eurpean beech (*Fagus sylvatica* L.) in a changing climate. Trees 21, 1-11.

Ghalambor, C.K., McKay, J.K., Carroll, S.P., Reznick, D.N., 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Functional Ecology 21, 394-407.

Gratani, L., Covone, F., Larcher, W., 2006. Leaf plasticity in response to light of three evergreen species of the Mediterranean maquis. Trees 20, 549-558.

Hacket-Pain, A.J., Cavin, L., Friend, A.D., Jump, A.S., 2016. Consistent limitation of growth by high temperature and low precipitation from range core to southern edge of European beech indicates widespread vulnerability to changing climate. European Journal of Forest Research 135, 897-909.

Hallik, L., Niinemets, U., Kull, O., 2012. Photosynthetic acclimation to light in woody and herbaceous species: a comparison of leaf structure, pigment content and chlorophyll fluorescence characteristics measured in the field. Plant Biology 14, 88-99.

Hampe, A., Petit, R.J., 2005. Conserving biodiversity under climate change: the rear edge matters. Ecology Letters 8, 461-467.

Hanaoka, S., Yuzurihara, J., Asuka, Y., Tomaru, N., Tsumura, Y., Kakubari, Y., Mukai, Y., 2007. Pollen-mediated gene flow in a small, fragmented natural population of *Fagus crenata*. Botany 85, 404-413.

Hiraoka, K., Tomaru, N., 2009. Genetic divergence in nuclear genomes between populations of *Fagus crenata* along the Japan Sea and Pacific sides of Japan. Journal of Plant Research 122, 269-282.

Hiura, T., Koyama, H., Igarashi, T., 1996. Negative trends between seed size and adult leaf size throughout the geographical range of *Fagus crenata*. Ecoscience 3, 226-228.

Homma, K., Akashi, N., Abe, T., Hasegawa, M., Harada, K., Hirabuki, Y., Irie, K., Kaji, M., Miguchi, H., Mizoguchi, N., Mizunaga, H., Nakashizuka, T., Natume, S., Niiyama, K., Ohkubo, T., Sawada, S.-i., Sugita, H., Takatsuki, S., Yamanaka, N., 1999. Geographical variation in the early regeneration process of Siebold's Beech (*Fagus crenata* BLUME) in Japan. Plant Ecology 140, 129-138.

Honnay, O., Verheyen, K., Butaye, J., Jacquemyn, H., Bossuyt, B., Hermy, M., 2002. Possible effects of habitat fragmentation and climate change on the range of forest plant species. Ecology Letters 5, 525-530.

Iizumi, T., Nishimori, M., Yokozawa, M. 2008. Combined equations for estimating global solar radiation: projection of radiation field over Japan under global warming conditions by statistical downscaling. Journal of Agricultural Meteorology 64: 9-23.

Ishii, H., Azuma, W., Nabeshima, E., 2013. The need for a canopy perspective to understand the importance of phenotypic plasticity for promoting species coexistence and light-use complementarity in forest ecosystems. Ecological Research 28, 191-198.

Ishii, H., Kitaoka, S., Fujisaki, T., Maruyama, Y., Koike, T., 2007. Plasticity of shoot and needle morphology and photosynthesis of two *Picea* species with different site preferences in northern Japan. Tree Physiology 27, 1595-1605.

Jackson, S.T., Sax, D.F., 2010. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. Trends in Ecology and Evolution 25, 153-160.

Janzen, D.H., 1967. Why mountain passes are higher in the tropics. American Naturalist 101, 233-249.

Jump, A.S., Hunt, J.M., Penuelas, J., 2006. Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. Global Change Biology 12, 2163-2174.

Jump, A.S., Penuelas, J., 2005. Running to stand still: adaptation and the response of plants to rapid climate change. Ecology Letters 8, 1010-1020.

Jung, V., Albert, C.H., Violle, C., Kunstler, G., Loucougaray, G., Spiegelberger, T., 2014. Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events. Journal of Ecology 102, 45-53.

Kira, T. (1991) Forest ecosystems of East and Southeast Asia in a global perspective. Ecological Research 6: 185-200.

Kawecki, T.J., 2008. Adaptation to marginal habitats. Annual Review of Ecology and Systematics 39, 321-343.

Koike, T., Kato, S., Shimamoto, Y., Kitamura, K., Kawano, S., Ueda, K., Mikami, T., 1998. Mitochondrial DNA variation follows a geographic pattern in Japanese beech species. Plant Biology 111, 87-92.

Kreyling, J., Buhk, C., Backhaus, S., Hallinger, M., Huber, G., Huber, L., Jentsch, A., Konnert, M., Thiel, D., Wilmking, M., Beierkuhnlein, C., 2014. Local adaptations to frost in marginal and central populations of the dominant forest tree *Fagus sylvatica* L. as affected by temperature and extreme drought in common garden experiments. Ecology and Evolution 4, 594-605.

Kuparinen, A., Savolainen, O., Schurr, F.M., 2010. Increased mortality can promote evolutionary adaptation of forest trees to climate change. Forest Ecology and Management 259, 1009-1008.

Lenoir, J., Gégout, J.C., Pierrat, J.C., Bontemps, J.D., Dhôte, J.F., 2009. Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986-2006). Ecography 32, 765-777.

Liancourt, P., Boldgiv, B., Song, D.S., Spence, L.A., Helliker, B.R., Petraitis, P.S., Casper, B.B., 2015. Leaf-trait plasticity and species vulnerability to climate change in a Mongolian steppe. Global Change Biology 21, 3489-3498.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolstrom, M., Lexer, M.J., Marchetti, M., 2009. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. Forest Ecology and Management 259, 698-709.

Liu, Y., Dawson, W., Pratti, D., Haeuser, E., Feng, Y., Van Kleunen, M., 2016. Does greater specific leaf area plasticity help plants to maintain a high performance when shaded? Annals of Botany 118, 1329-1336.

Magi, M., Semchenko, M., Kalamees, R., Zobel, K., 2011. Limited phenotypic plasticity in range-edge populations: a comparison of co-occurring populations of two *Agrimonia* species with different geographical distributions. Plant Biology 13, 177-184.

Masarovicova, E., Stefancik, L., 1990. Some ecophysiological features in sun and shade leaves of tall beech trees. Biologia Plantarium 32, 374-387.

Matesanz, S., Gianoli, E. & Valladares, F. (2010). Ann. N. Y. Acad. Sci., 2, 35–55., 2010. Global change and the evolution of phenotypic plasticity in plants. Annals of the New York Academy of Sciences 2, 35-55.

Matsui, T., Yagihashi, T., Nakaya, T., Tanaka, N., Taoda, H., 2004a. Climatic controls on distribution of *Fagus crenata* forests in Japan. Journal of Vegetation Science 15, 57-66.

Matsui, T., Yagihashi, T., Nakaya, T., Taoda, H., Yoshinaga, S., Daimaru, H., Tanaka, N., 2004b. Probability distributions, vulnerability and sensitivity in *Fagus crenata* forests following predicted climate changes in Japan. Journal of Vegetation Science 15, 605-614.

McGill, B.J., enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21, 178-185.

Nagaike, T., Kamitani, T., 1999. Factors affecting changes in landscape diversity in rural areas of the *Fagus crenata* forest region of central Japan. Landscape and Urban Planning 43, 209-216.

Nakashizuka, T., 1988. Regeneration of beech (*Fagus crenata*) after simultaneous death of undergrowing dwarf bamboo (Sasa kurilensis). Ecological Research 3, 21-35.

Nicotra, A.B., Atkin, O.K., Bonser, S.P., Davidson, A.M., Finnegan, E.J., Mathesius, U., Poot, P., Purugganan, M.D., Richards, C.L., Valladares, F., van Kleunen, M., 2010. Plant phenotypic plasticity in a changing climate. Trends in Plant Science 15, 684-692.

Niinemets, U., Valladares, F., Ceulemans, R., 2003. Leaf-level phenotypic variability and plasticity of invasive *Rhododendron ponticum* and non-invasive *Ilex aquifolium* co-occuring at two contrasting European sites. Plant, Cell and Environment 26, 941-956.

Okaura, T., Harada, K., 2002. Phylogeographical structure revealed by chloroplast DNA variation in Japanese Beech (*Fagus crenata* Blume). Heredity 88, 322-329.

Oney, B., Reineking, B., O'Neill, G., Kreyling, J., 2013. Intraspecific variation buffers projected climate change impacts on *Pinus contorta*. Ecology and Evolution 3, 437-449.

Osada, N., Nabeshima, E., Hiura, T. 2015. Geographic variation in shoot traits and branching intensity in relation to leaf size in *Fagus crenata*: A common garden experiment. American Journal of Botany 102: 878-887.

Pallardy, S.G., 2008. Physiology of woody plants, third edition. Academic Press, San Diego.

Pearcy, R.W., 2007. Responses of plants to heterogeneous light environments. In: Pugnaire, F., Valladares, F. (Eds.), Functional plant ecology. Taylor and Francis, New York, pp. 213-257.

Perez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., Funes, G., Quetier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New handbook for standardised measurement of plant functional traits worldwide. Australian Journal of Botany 61, 167-234.

Petit, R.J., Hampe, A., 2006. Some evolutionary consequences of being a tree. Annual Review of Ecology, Evolution, and Systematics 37, 187-214.

Piovesan, G., Biondi, F., Di Filipo, A., Maugeri, M., 2008. Drought-driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. Global Change Biology 14, 1265-1281.

Reed, T.E., Schindler, D.E., Waples, R.S., 2011. Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. Conservation Biology 25, 56-63.

Rehfeldt, G.R., Tchebakova, N.M., Parfenova, Y.I., Wykoff, W.R., Kuzmina, N.A., Milyutin, L.I., 2002. Intraspecific responses to climate change in *Pinus sylvestris*. Global Change Biology 8, 912-929.

Richter, S., Kipfer, T., Wohlgemuth, T., Calderón Guerrero, C., Ghazoul, J., Moser, B., 2012. Phenotypic plasticity facilitates resistance to climate change in a highly variable environment. Oecologia 169, 269-279.

Sack, L., Melcher, P.J., Liu, W.H., Middleton, E., Pardee, T., 2006. How strong is intracanopy leaf plasticity in temperate deciduous trees? American Journal of Botany 93, 829-839.

Sambatti, J.B.M., Caylor, K.K., 2007. When is breeding for drought tolerance optimal if drought is random? New Phytologist 175, 70-80.

Sánchez-Gómez, D., Robson, T.M., Gasco, A., Gil-Pelegrin, E., Aranda, I., 2013. Differences in the leaf functional traits of six beech (*Fagus sylvatica* L.) populations are reflected in their response to water limitation. Environmental and Experimental Botany 87, 110-119.

Sánchez-Gómez, D., Zavala, M.A., Valladares, F., 2008. Functional traits and plasticity linked to seedlings' performance under shade and drought in Mediterranean woody species. Annals of Forest Science 65, 311.

Shaw, R., Etterson, J.N., 195:752–765, P., 2012. Rapid climate change and the rate of adaptation: insight from experimental quantitative genetics. New Phytologist 195, 752-765.

Shiraishi, T., Watanabe, S., 2002. Research on morphological differences of *Fagus crenata* leaves in the Chubu mountains of Honshu, Japan. Geo-environmental Research 4, 23-38.

Smithson, P., Addison, K., Atkinson, K., 2008. Polar and alpine environments. In, Fundamentals of the physical environment. Routledge, Oxford, pp. 594-634.

Soudzilovskaia, N.A., Elumeeva, T.G., Onipchenko, V.G., Shidakov, I.I., Salpagarova, F.S., Khubiev, A.B., Tekeev, D.K., Cornelissen, J.H.C., 2013. Functional traits predict relationship between plant abundance dynamic and long-term climate warming. Proceedings of the National Academy of Sciences 110, 18180-18184.

Stojnic, S., Orlovic, S., Miljkovic, D., Galic, Z., Kebert, M., von Wuehlisch, G., 2015. Provenance plasticity of European beech leaf traits under differing environmental conditions at two Serbian common garden sites. European Journal of Forest Research 134, 1109-1125.

Sultan, S.E., 2000. Phenotypic plasticity for plant development, function and life history. Trends in Plant Science 5, 537-542.

Sultan, S.E., Spencer, H.G., 2002. Metapopulation structure favors plasticity over local adaptation. American Naturalist 160, 271-283.

Takahashi, M., Tsumura, Y., Nakamura, T., Uchida, K., Ohba, K., 1994. Allozyme variation in *Fagus crenata* in northeastern Japan. Canadian Journal of Forest Research 2, 1071-1074.

Tateishi, M., Kumagai, T., Suyama, Y., Hiura, T. 2010. Differences in transpiration characteristics of Japanese beech trees, *Fagus crenata*, in Japan. Tree Physiology 30: 748-760.

Tegel, W., Seim, A., Hakelberg, D., Hoffmann, S., 2014. A recent growth increase of European beech (*Fagus sylvatica* L.) at its Mediterranean distribution limit contradicts drought stress. European Journal of Forest Research 133, 61-71.

Thuiller, W., Albert, C.H., Araújo, M.B., Berry, P.M., Cabeza, M., Guisan, G., Hickler, T., Midgley, G.F., Paterson, J., Schurr, F.M., Sykes, M.T., Zimmermann, N.E., 2008. Predicting global change impacts on plant species distributions: future challenges. Perspectives in Plant Ecology, Evolution and Sytematics 9, 137-152.

Tognetti, R., Minotta, G., Pinzauti, S., Michelozzi, M., Borghetti, M., 1998. Acclimation to changing light conditions of long-term shade-grown beech (*Fagus sylvatica* L.) seedlings of different geographic origins. Trees 12, 326-333.

Tomaru, N., Mitsutsuji, T., Takahashi, M., Tsumura, Y., Uchida, K., Ohba, K., 1997. Genetic diversity in *Fagus crenata* (Japanese beech): influence of the distributional shift during the late-Quaternary. Heredity 78, 241-251.

Tomaru, N., Takahashi, M., Tsumura, Y., Takahashi, M., Ohba, K., 1998. Intraspecific variation and phylogeographic patterns of *Fagus crenata* (Fagaceae) mitochondrial DNA. American Journal of Botany 85, 636.

Tsukada, M., 1982. Late-Quaternary shift of *Fagus* distribution. Botanical Magazine Tokyo 95, 203-217.

Urbas, P., Zobel, K., 2000. Adaptive and inevitable morphological plasticity of three herbaceous species in a multi-species community: field experiment with manipulated nutrients and light. Acta Oecologia.

Valladares, F., Gianoli, E., Gómez, J.M., 2007. Ecological limits to plant phenotypic plasticity. New Phytologist 176, 749-763.

Valladares, F., Matesanz, S., Guihaumon, F., Araujo, M.B., Balaguer, L., Benito-Garzon, M., Corwell, W., Gianoli, E., Van Kleunen, M., Naya, D.E., Nicotra, A.B., Poorter, H., Zavala, M.A., 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. Ecology Letters 17, 1351-1364.

Valladares, F., Niinemets, U., 2007. The architecture of plant crowns: form design rules to light capture and performance. In: Pugnaire, F., Valladares, F. (Eds.), Functional plant ecology. Taylor and Francis, New York, pp. 101-149.

Van Kleunen, M., Fischer, M., 2005. Constraints on the evolution of adaptive phenotypic plasticity in plants. New Phytologist 166, 49-60.

Vasseur, D.A., McCann, K.S., 2007. The impact of environmental variability on ecological systems. Springer, Dordrecht.

Vitasse, Y., Bresson, C., Kremer, A., Michalet, R., Delzon, S., 2010. Quantifying phenological plasticity to temperature in two temperate tree species. Functional Ecology 24, 1211-1218.

Vitasse, Y., Delzon, S., Bresson, C.C., Michalet, R., Kremer, A., 2009. Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. Canadian Journal of Forest Research 39, 1259-1269.

Vucetich, J.A., Waite, T.A., 2003. Spatial patterns of demography and genetic processes across the species' range: null hypotheses for landscape conservation genetics. Conservation Genetics 4, 639-645.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, P.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428, 821-827.

Yamazaki, J., Yoda, E., Takahashi, A., Sonoike, K., Maruta, E. 2007. Pacific Ocean and Japan Sea ecotypes of Japanese beech (*Fagus crenata*) differ in photosystem responses to continuous high light. Tree Physiology 27: 961-968.

Yasaka, M., Terazawa, K., Koyama, H., Kon, H., 2003. Masting behavior of *Fagus crenata* in northern Japan: spatial synchrony and pre-dispersal seed predation. Forest Ecology and Management 184, 277-284.

Yeh, P.J., Price, T.D., 2004. Adaptive phenotypic plasticity and the successful colonization of a novel environment. American Naturalist 164, 531-542.

Table 1. Description of study sites and sample trees for the 13 sites of *F. crenata*. Sites are listed in order of decreasing latitude (north to south) with prefectures in ( ). Site names in normal and bold fonts indicate Japan-Sea and Pacific genetic lineages, respectively.

Site	Site Code	Location	Elevation (m a.s.l.)	Mean temperature (°C)	Precipitation (mm yr^{-1})	Meteorological station	Number of trees	DBH (cm)	Tree height (m)
Soibetsu Beech Forest (Hokkaido)	SOI	42°41’N, 140°16’E	45	7.9	1400	Kuromatsunai	4	25~38	17~24
Shirakami Range (Aomori)	SHI	40°34’N, 140°08’E	342	7.2	1550	Ikarigaseki	4	51~79	27~28
Kawatabi Field Center (Miyagi)	KAW	38°47’N, 140°47’E	560	8.3	1650	Kawatabi	4	18~42	20~23
Sendai Tohoku Univ. Botanical Garden (Miyagi)	**SEN**	38°15’N, 140°51’E	140	11.9	1250	Sendai	4	27~50	20~23
Mt. Naeba (Niigata)	NAE	36°47’N, 138°46’E	860	8.9	2230	Naeba	4	22~28	20~23
Ogawa Forest Reserve (Ibaragi)	**OGA**	36°56’N, 140°35’E	635	9.6	1450	Daigo	5	88~109	22~27
Sugadaira Daido Beech Forest (Nagano)	SUG	36°30’N, 138°20’E	1315	6.2	1200	Sugadaira	4	37~94	22~28
Nishikoma Field Station (Nagano)	**NIS**	35°49'N, 137°51’E	1600	3.0	2250	Ina	4	25~72	12~16
Wakasugi Natural Forest (Okayama)	WAK	35°15’N, 134°24’E	1045	9.1	2950	Imaoka	4	51~76	22~27
Mt. Rokko (Hyogo)	ROK	34°47’N, 135°16’E	800	10.1	1850	Kobe	6	18~64	19~23
Mt. Takanosu (Hiroshima)	TAK*	34°34’N, 132°45’E	864	10.3	1450	Higashihiroshima	4	46~87	24~27
Komenono Field Station (Ehime)	**EHI**	33°55’N, 132°55’E	880	10.5	1800	Matsuyama	4	30~73	16~22
Miyazaki Research Forest (Miyazaki)	**MIY**	32°23’N, 131°01’E	1190	9.9	3100	Kuraoka	4	17~43	13~17

*Genetic lineage of the Mt. Takanosu site is unknown.

Table 2. Results of linear regression analyses comparing leaf morphological traits between Japan-Sea and Pacific genetic lineages of *F. crenata* in relation to height (H), canopy openness (O_C) and relative height (H_{rel}). All regressions were significant ($P < 0.05$) except for the one with r-square value in grey. Regression slopes, representing plasticity, and intercepts were compared among sites (excluding Takanosu whose genetic lineage is unknown) by ANCOVA. Genetic lineages with significantly steeper slopes (higher plasticity) and greater intercepts are indicated in bold ($P < 0.05$).

Leaf trait	lineage	H (m)			O_c (%)			H_{rel}		
		Slope	Intercept	r^2	Slope	Intercept	r^2	Slope	Intercept	r^2
Area	Jpn Sea	-0.773	**38.6**	0.168	-14.1	45.6	0.145	-23.5	**42.0**	0.252
(cm^2)	Pacific	-0.682	30.2	0.147	**-22.4**	**53.1**	0.432	-20.1	34.5	0.239
Thickness	Jpn Sea	**0.008**	0.164	0.494	**0.162**	0.067	0.446	**0.210**	0.155	0.529
(mm)	Pacific	0.005	**0.225**	0.352	0.114	**0.141**	0.389	0.145	**0.198**	0.484
Leaf mass	Jpn Sea	**3.544**	90.3	0.123	**81.9**	33.7	0.149	**91.9**	83.4	0.134
(mg)	Pacific	1.933	**105.0**	0.044	-9.9	**140.1**	0.002	55.0	93.2	0.053
SLA	Jpn Sea	**-0.011**	**0.383**	0.627	**-0.207**	**0.485**	0.593	**-0.308**	**0.416**	0.766
(cm^2 mg^{-1})	Pacific	-0.007	0.259	0.517	-0.152	0.380	0.620	-0.198	0.300	0.716

Table 3. Results of linear regression analyses comparing leaf morphological traits of *F. crenata* among the 13 sites in relation to height (*H*), canopy openness (O_C) and relative height (H_{rel}). Regression significance is indicated by asterisks next to r-square values (** P < 0.01). Regression slopes, representing plasticity, and intercepts were compared among sites by ANCOVA. Sites with the same letter are not significantly different (P < 0.05). Site names in bold indicate Pacific genetic lineage.

Leaf trait	Site	*H* (m)			O_c (%)			H_{rel}		
		Slope	Inercept	r^2	Slope	Inercept	r^2	Slope	Inercept	r^2
Area (cm^2)	SOI	-2.13 .B....	68.8 A.......	0.454 **	-57.1 A......	124.9 A......	0.455 **	-53.9 A......	74.2 A......	0.578 **
	SHI	-1.20 ..C...	52.4 ..C.....	0.584 **	-22.6 ..CD...	59.2 ..C....	0.409 **	-32.6 ..C....	52.4 ..C....	0.588 **
	KAW	-1.02 ..CD..	41.0 ....E...	0.321 **	-24.6 ..C....	63.3 ..C....	0.368 **	-20.5 ....EF.	39.8 ...D...	0.276 **
	SEN	-0.69 ....E.	38.3 ....E...	0.312 **	-13.0 .....F.	46.3 ...D...	0.241 **	-14.9 .....F.	38.2 ...D...	0.304 **
	NAE	-1.12 ..CD..	40.6 ....E...	0.389 **	-29.7 .B.....	71.1 .B.....	0.463 **	-23.5 ....E..	39.8 ...D...	0.344 **
	OGA	-1.22 ..C...	43.1 ....E...	0.609 **	-21.1 ..CDE..	50.7 ...D...	0.565 **	-28.5 ...D...	40.3 ...D...	0.492 **
	SUG	-1.27 ..C...	48.8 ...D....	0.568 **	-20.0 ..CDE..	48.9 ...D...	0.597 **	-34.6 ..C....	49.7 ..C....	0.610 **
	NIS	-3.23 A.....	56.9 .B......	0.761 **	-16.9 ....E..	49.5 ...D...	0.284 **	-39.9 .B.....	57.4 .B.....	0.779 **
	WAK	-0.87 ...D..	42.0 ....E...	0.256 **	-9.4 .....FG	41.4 ....E..	0.075 **	-21.3 ....EF.	42.4 ...D...	0.247 **
	ROK	-0.30 .....F	18.9 ......G.	0.195 **	-5.5	22.0 ......G	0.275 **	-7.1 ......G	19.8 .....F.	0.248 **
	TAK	-0.67 ....E.	28.5 .....F..	0.504 **	-11.7 .....FG	32.3 .....F.	0.364 **	-17.0 ....EF.	28.5 ....E..	0.493 **
	EHI	-0.57 ....E.	21.5 ......G.	0.190 **	-18.4 ...DE..	41.8 ....E..	0.364 **	-18.1 ....EF.	26.5 ....E..	0.446 **
	MIY	-0.33 .....F	16.0 ....H	0.162 **	-7.8 ......G	25.1 ......G	0.195 **	-5.2 ......G	15.8 ......G	0.147 **
Thickness (mm)	SOI	0.011 ..CD...	0.136 ...D..	0.566 **	0.350 A......	-0.248 ....H	0.680 **	0.253 ...D...	0.129 .....F.	0.558 **
	SHI	0.004 ......G	0.234 A.....	0.346 **	0.151 ....E..	0.107 ..C.....	0.599 **	0.145 .....F.	0.218 .B.....	0.604 **
	KAW	0.015 A......	0.073 .....F	0.793 **	0.236 ..C....	-0.052 .....F..	0.757 **	0.326 .B.....	0.072 ......G	0.800 **
	SEN	0.009 ....E..	0.210 .B....	0.721 **	0.177 ...D...	0.072 ...D....	0.669 **	0.128 .....F.	0.247 A......	0.566 **
	NAE	0.006 .....F.	0.174 ..C...	0.578 **	0.141 ....E..	0.052 ...D....	0.760 **	0.131 .....F.	0.178 ...D...	0.529 **
	OGA	0.004 ......G	0.212 .B....	0.357 **	0.096 .....F.	0.168 .B......	0.499 **	0.127 .....F.	0.200 .BCD...	0.435 **
	SUG	0.011 ..C....	0.109 ....E.	0.607 **	0.215 ..C....	0.034 ...D....	0.702 **	0.350 A......	0.068 ......G	0.711 **
	NIS	0.006 .....F.	0.229 A.....	0.215 **	0.076 ......G	0.194 A.......	0.229 **	0.093 ......G	0.207 .BC....	0.557 **
	WAK	0.010 ...D...	0.145 ...D..	0.458 **	0.221 ..C....	-0.007 ....E...	0.566 **	0.287 ..C....	0.117 .....F.	0.572 **
	ROK	0.007 .....F.	0.207 .B....	0.382 **	0.102 .....F.	0.160 .B......	0.381 **	0.150 .....F.	0.189 ..CD...	0.508 **
	TAK	0.010 ..CD...	0.118 ....E.	0.684 **	0.184 ...D...	0.051 ...D....	0.718 **	0.253 ...D...	0.116 .....F.	0.690 **
	EHI	0.009 ....E..	0.184 ..C...	0.615 **	0.158 ....E..	0.053 ...D....	0.293 **	0.146 .....F.	0.193 .BCD...	0.446 **
	MIY	0.013 .B.....	0.149 ...D..	0.784 **	0.280 .B.....	-0.159 ......G.	0.734 **	0.223 ....E..	0.149 ....E..	0.783 **
Leaf mass (mg)	SOI	3.77 ..CD...	146.5 A....	0.084 **	49.9 .B.	127.2 A....	0.017 NS	71.9 .BC..	151.6 A....	0.061 **
	SHI	2.46 ....EF.	109.1 ..C..	0.155 **	73.4 .B.	66.9 .BC..	0.315 **	94.4 .B...	99.6 ..C..	0.307 **
	KAW	3.85 ..CD...	89.2 ..CD.	0.144 **	67.2 .B.	46.4 .BC..	0.117 **	83.0 .B...	89.0 ..C..	0.145 **
	SEN	6.72 A......	76.3 ...D.	0.336 **	157.4 A..	-48.2 ....E	0.404 **	154.6 A....	69.9 ...D.	0.369 **
	NAE	1.46 .....F.	104.5 ..C..	0.033 NS	13.3 ..C	92.7 .B...	0.017 NS	39.4 ..CDE	99.6 ..C..	0.049 *
	OGA	0.31 ......G	127.9 .B...	0.002 NS	4.0 ..C	128.1 A....	0.001 NS	13.3 ....E	123.9 .B...	0.005 NS
	SUG	2.62 ...DEF.	54.3 ....E	0.273 **	26.4 ..C	67.8 .BC..	0.107 **	59.6 .BCD.	59.7 ...DE	0.213 **
	NIS	3.33 ..CDE..	125.4 .B...	0.066 *	22.5 ..C	125.9 A....	0.009 NS	98.3 .B...	97.8 ..C..	0.236 **
	WAK	4.29 ..C....	98.7 ..CD.	0.154 **	142.9 A..	-11.8 ...D.	0.265 **	97.8 .B...	105.4 ..C..	0.120 **
	ROK	3.62 ..CD...	50.2 ....E	0.395 **	56.9 .B.	25.8 ..C..	0.378 **	81.6 .BC..	41.1 ....E	0.481 **
	TAK	2.21 ....EF.	58.9 ....E	0.155 **	52.9 .B.	27.0 ..C..	0.208 **	66.6 .BC..	51.7 ...DE	0.210 **
	EHI	0.24 ......G	82.2 ...D.	0.001 NS	-21.5 ..C	120.5 A....	0.016 NS	-27.7 ...DE	105.6 ..C..	0.040 *
	MIY	5.22 .B.....	42.3 ....E	0.555 **	84.2 .B.	-49.0 ....E	0.247 **	86.4 .B...	43.0 ...DE	0.542 **
SLA (cm^2 mg^{-1})	SOI	-0.013 ..C..	0.379 ...D....	0.814 **	-0.298 A......	0.649 A.....	0.522 **	-0.298 ...D....	0.393 ....E....	0.883 **
	SHI	-0.011 ...DE	0.410 ..C.....	0.812 **	-0.181 ....E..	0.427 ...D..	0.774 **	-0.295 ...D....	0.411 ...D.....	0.820 **
	KAW	-0.018 A....	0.461 .B......	0.977 **	-0.255 .B.....	0.575 .B....	0.791 **	-0.377 .B......	0.459 .B.......	0.967 **
	SEN	-0.011 ...DE	0.328 .....F..	0.903 **	-0.207 ...D...	0.473 ..C...	0.634 **	-0.228 .....F..	0.326 ....H.	0.882 **
	NAE	-0.011 ...DE	0.360 ....E...	0.739 **	-0.239 ..C....	0.559 .B....	0.880 **	-0.232 .....F..	0.357 ......G..	0.702 **
	OGA	-0.010 ...DE	0.347 ....EF..	0.813 **	-0.158 .....F.	0.377 ....E.	0.673 **	-0.261 ....E...	0.353 ......G..	0.806 **
	SUG	-0.016 .B...	0.520 A.......	0.804 **	-0.255 .B.....	0.568 .B....	0.690 **	-0.437 A.......	0.556 A........	0.873 **
	NIS	-0.009 ....E	0.266 ....H	0.409 **	-0.159 ....EF.	0.371 ....E.	0.710 **	-0.151 ....H	0.280 I	0.583 **
	WAK	-0.010 ....E	0.337 ....EF..	0.778 **	-0.177 ....E..	0.415 ...D..	0.584 **	-0.281 ...D....	0.373 .....F...	0.891 **
	ROK	-0.011 ...D.	0.308 ......G.	0.594 **	-0.139 ......G	0.350 .....F	0.446 **	-0.232 .....F..	0.329 ....H.	0.686 **
	TAK	-0.014 ..C..	0.423 ..C.....	0.878 **	-0.214 ...D...	0.478 ..C...	0.565 **	-0.350 ..C.....	0.429 ..C......	0.913 **
	EHI	-0.010 ....E	0.277 ....H	0.734 **	-0.173 ....EF.	0.414 ...D..	0.631 **	-0.183 ......G.	0.281 I	0.764 **
	MIY	-0.010 ....E	0.255 ....H	0.878 **	-0.183 ....E..	0.446 ...D..	0.748 **	-0.135 ....H	0.235	0.795 **

Table 4. Spearman's rank correlation coefficients (R_s) between plasticity (absolute value of the regression slope in relation to independent variable) of leaf area and environmental variables. Top ten environmental variables are listed in order of decreasing R_s.

Independent variable	Environmental variable	R_S	P
Height	Annual mean temperature	-0.857	<0.001
	Minimum daily mean temperature	-0.827	<0.001
	Lowest recorded daily minimum temperature	-0.822	<0.001
	Lowest recorded monthly mean temperature	-0.710	0.007
	Mean temperature during leafy season	-0.674	0.012
	Historical monthly variation (max – min recorded)	0.644	0.018
	Highest recorded monthly precipitation	-0.642	0.018
	Minimum monthly mean temperature	-0.640	0.019
	Mean temperature at bud formation	-0.620	0.024
	Maximum monthly mean temperature	-0.607	0.028
Canopy openness	Latitude	0.793	0.001
	Monthly days of precipitation (winter)	0.787	0.001
	Monthly days of precipitation (annual)	0.767	0.002
	Lowest recorded minimum daily temperature	-0.690	0.009
	Elevation	-0.688	0.009
	Daily minimum temperature	-0.638	0.019
	Highest recorded monthly days of precipitation	0.594	0.032
	Lowest recorded monthly mean temperature	-0.592	0.033
	Historical monthly variation (max – min recorded)	0.588	0.035
	Monthly precipitation (summer)	-0.579	0.038
Relative height	Lowest recorded daily minimum temperature	-0.937	<0.001
	Minimum daily temperature	-0.847	<0.001
	Mean temperature at leaf emergence	-0.796	0.001
	Historical monthly variation (max – min recorded)	0.719	0.006
	Latitude	0.718	0.006
	Lowest recorded monthly mean temperature	-0.716	0.006
	Highest recorded monthly precipitation	-0.715	0.006
	Mean temperature during leafy season	-0.692	0.009
	Mean annual temperature	-0.679	0.011
	Maximum temperature at leaf emergence	-0.677	0.011

Figure captions

Fig. 1. Location and elevation of 13 study sites spread across the full distribution range of *F. crenata* in Japan. See Table 1 for names of study sites. Site names in normal and bold fonts indicate Japan-Sea and Pacific genetic lineages, respectively. *The genetic lineage of the Mt. Takanosu site is unknown. Lines indicate northern and southern distribution limits. Dotted line indicates the geographic boundary between the two genetic lineages.

Fig. 2. Intra-crown variation of leaf morphology among 13 study sites of *F. crenata*. Scanned leaf images from single trees at each site are shown in relation to height. The center of each leaf is plotted at the height of its location in the crown. Sites are in order of descending latitude (north to south from left to right). Site names are as in Table 1 and Fig. 1.

Fig. 3. Ordination diagram of the results of principle component analysis (PCA) based on leaf traits of 13 study sites. Centroids of each site are plotted. Symbol shapes indicate genetic lineage (△: Japan Sea; O: Pacific; ◊: Unknown). Site names are as in Table 1 and Fig. 1. Leaf trait codes are as follows: LA: leaf area; LT: leaf thickness; LM: leaf mass; SLA: specific leaf area; LL: leaf length; LW: leaf width; LL/LW: leaf length to width ratio; LS: leaf shape index; LV: number of leaf veins. Table shows r^2 values of the relationship between axis scores and trait values. Asterisks indicate significant correlations (** $P < 0.01$).

Fig. 4. Relationship between leaf area and height of *F. crenata* at 13 study sites. Graphs are arranged in order of descending latitude (north to south) of the study sites (left to right, top to bottom). Symbols represent individual trees within each site. Comparison of regression lines for all sites shown in lower right (See Table 3 for statistical test results). Site names are as in Table 1 and Fig. 1.

Fig. 5. Relationship between specific leaf area (SLA) and canopy openness of *F. crenata* at 13 study sites. Graphs are arranged in order of descending latitude (north to south) of the study sites (left to right, top to bottom). Symbols represent individual trees within each site. Comparison of regression lines for all sites shown in lower right (See Table 3 for statistical test results). Site names are as in Table 1 and Fig. 1.

Fig. 6. Relationship between intra-crown leaf-area plasticity of *F. crenata* (absolute value of the regression slope in relation to independent variable) and environmental variables for the 13 study sites. For each independent variable, three environmental variables with highest correlations from Table 4 are shown. Symbols are as in Fig. 3.

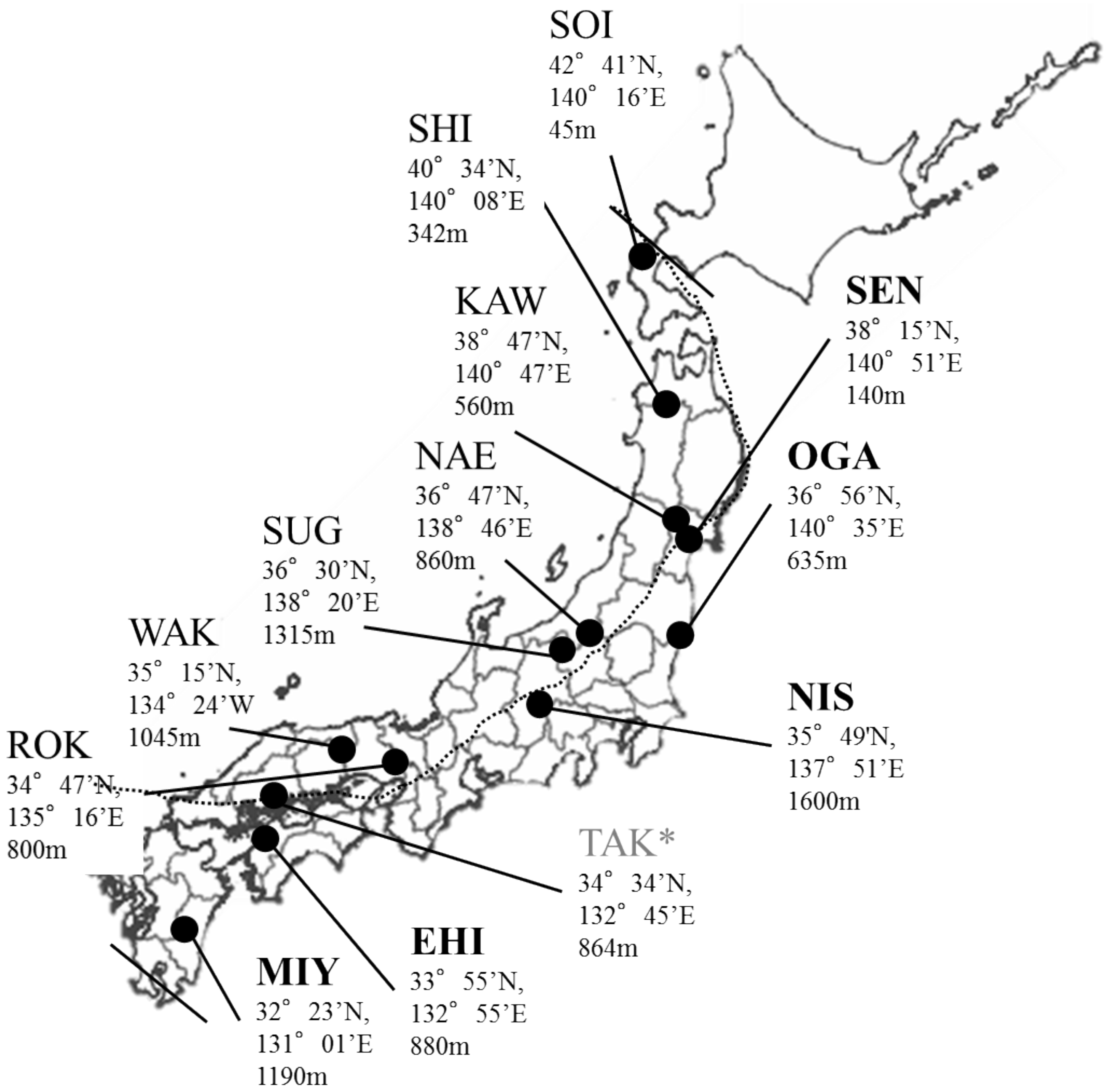

SOI
42° 41’N,
140° 16’E
45m
SHI
40° 34’N,
140° 08’E
342m
KAW
38° 47’N,
140° 47’E
560m
SEN
38° 15’N,
140° 51’E
140m
NAE
36° 47’N,
138° 46’E
860m
OGA
36° 56’N,
140° 35’E
635m
SUG
36° 30’N,
138° 20’E
1315m
WAK
35° 15’N,
134° 24’W
1045m
NIS
35° 49'N,
137° 51’E
1600m
ROK
34° 47’N,
135° 16’E
800m
TAK*
34° 34’N,
132° 45’E
864m
EHI
33° 55’N,
132° 55’E
880m
MIY
32° 23’N,
131° 01’E
1190m

Fig. 1

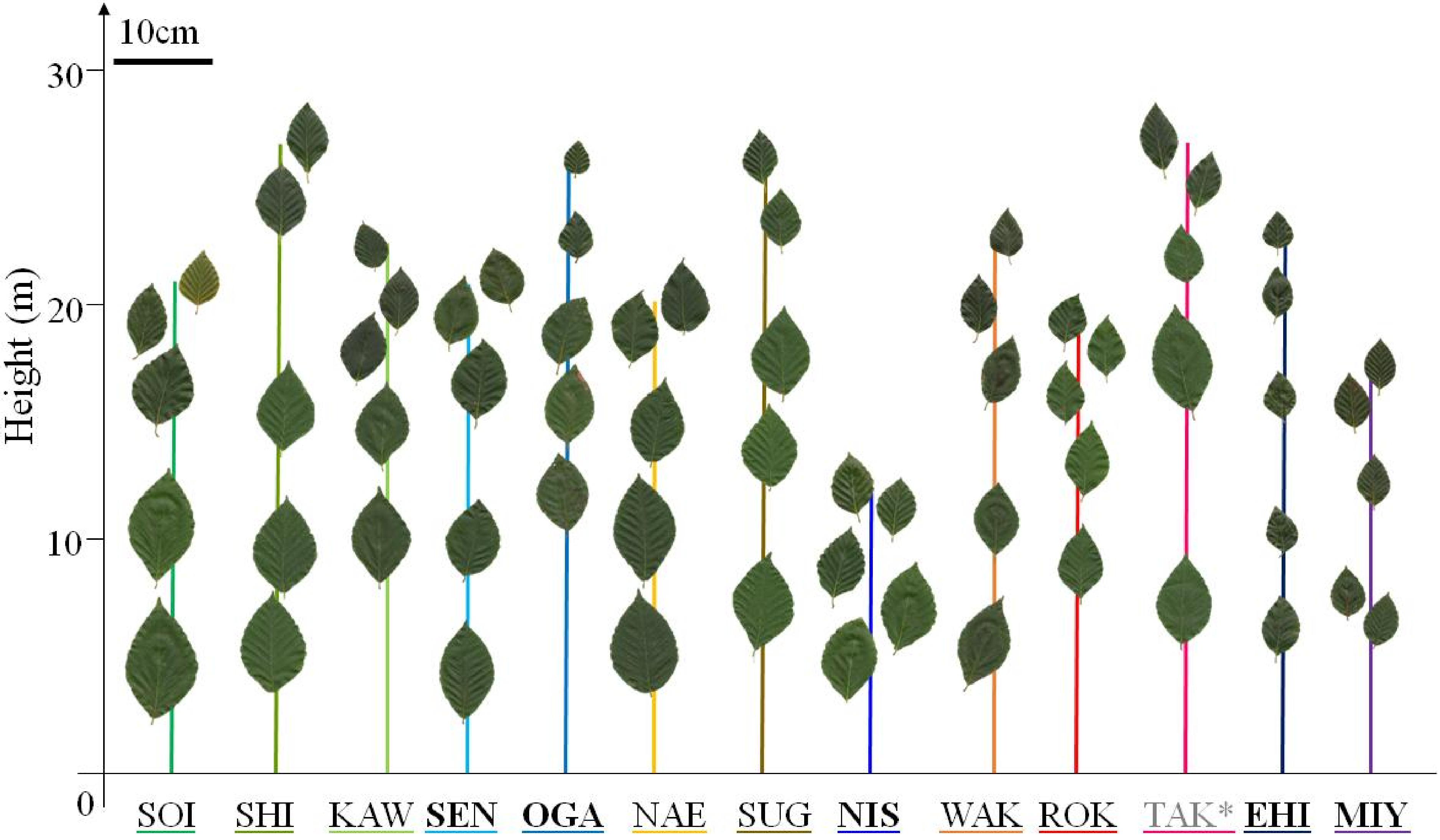

10cm
30
20
10
0
Height (m)
SOI
SHI
KAW
SEN
OGA
NAE
SUG
NIS
WAK
ROK
TAK*
EHI
MIY

Fig. 2

	LA	LT	LM	SLA	LL	LW	LL/LW	LS	LV
Axis 1	0.899 **	0.193 **	0.145 **	0.462 **	0.916 **	0.854 **	0.000 ns	0.042 **	0.454 **
Axis 2	0.057 **	0.632 **	0.775 **	0.396 **	0.025 **	0.100 **	0.169 **	0.106 **	0.042 **

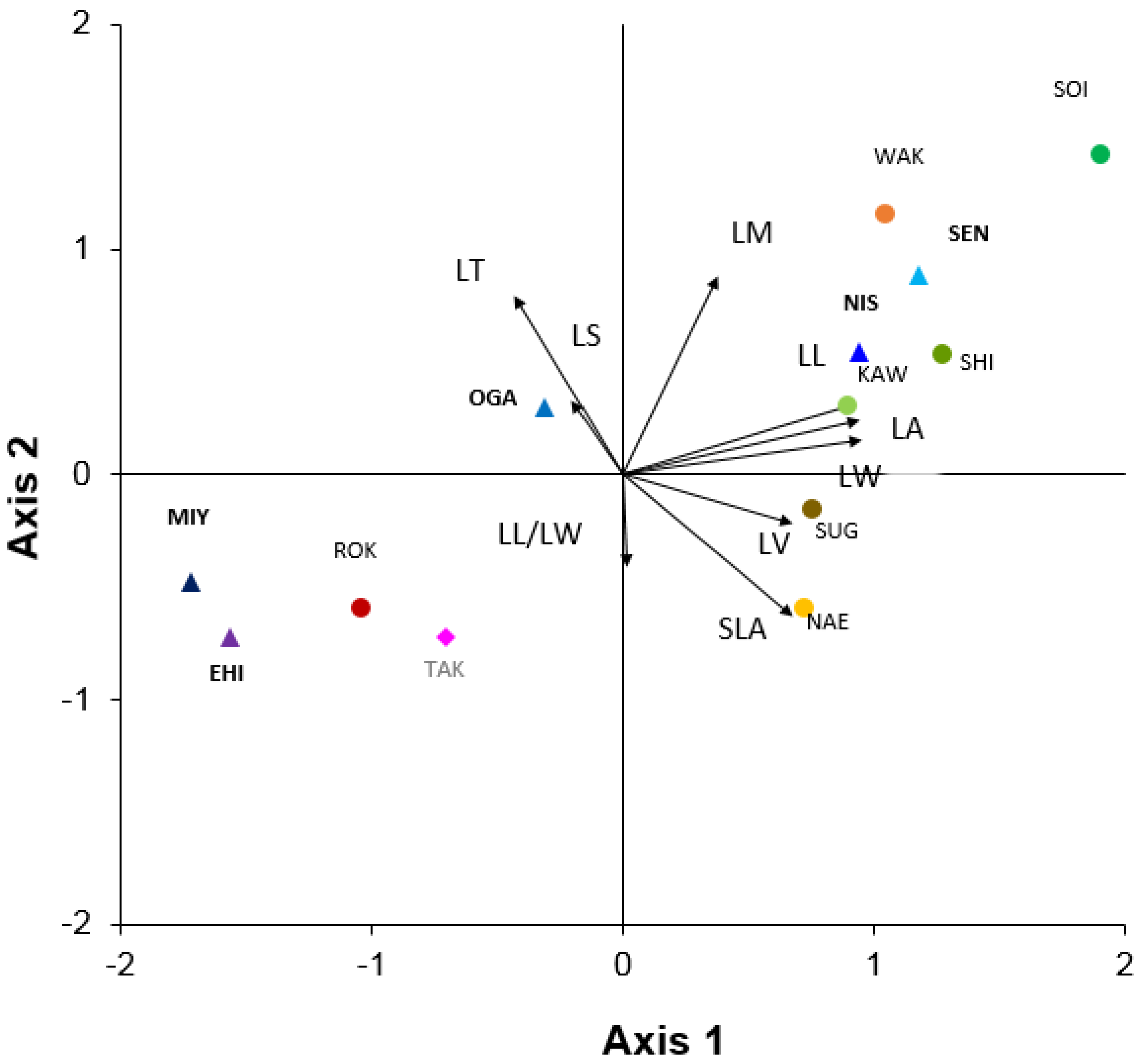


Fig. 3

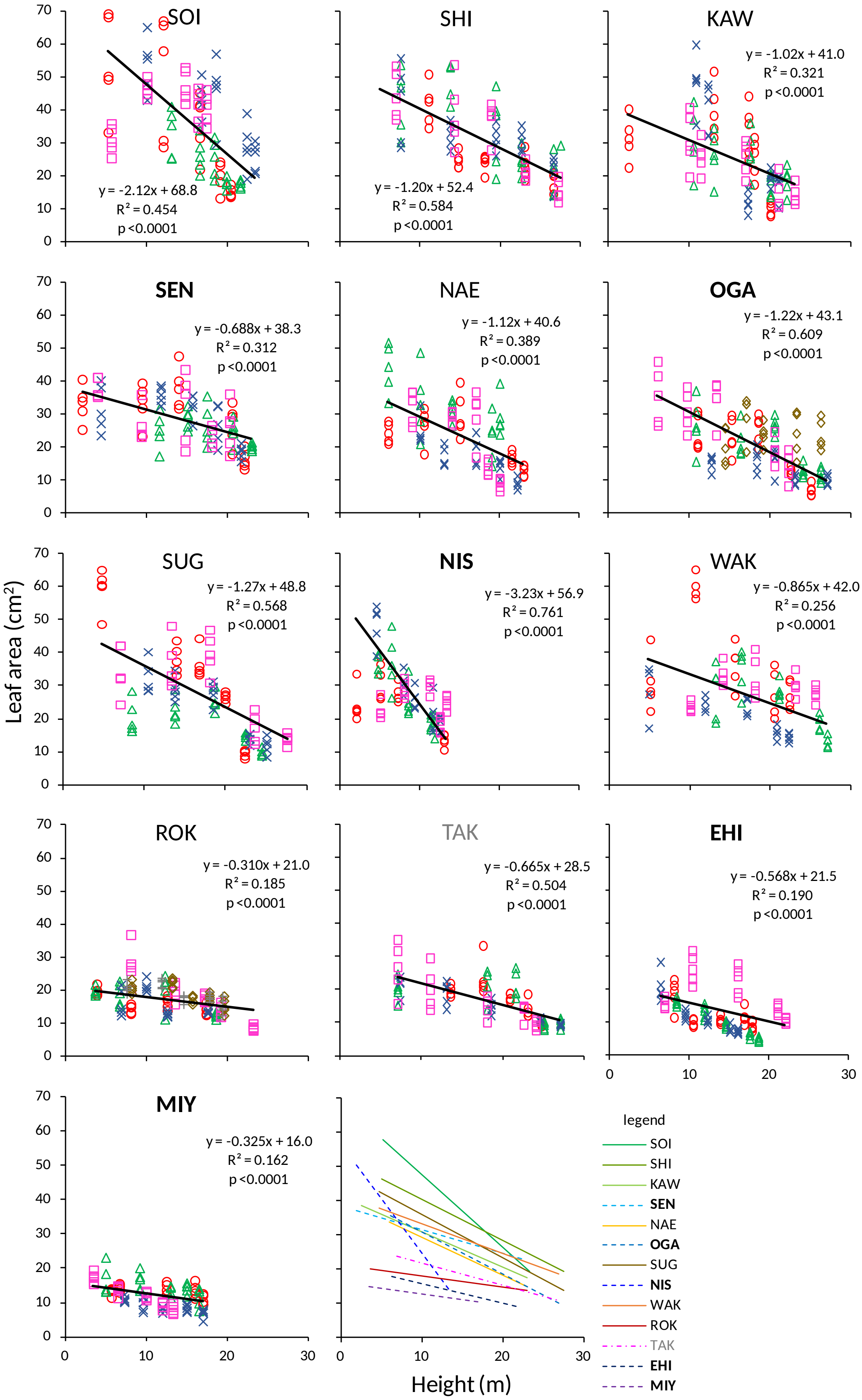

SOI
y = -2.12x + 68.8
R² = 0.454
p <0.0001
SHI
y = -1.20x + 52.4
R² = 0.584
p <0.0001
KAW
y = -1.02x + 41.0
R² = 0.321
p <0.0001
SEN
y = -0.688x + 38.3
R² = 0.312
p <0.0001
NAE
y = -1.12x + 40.6
R² = 0.389
p <0.0001
OGA
y = -1.22x + 43.1
R² = 0.609
p <0.0001
SUG
y = -1.27x + 48.8
R² = 0.568
p <0.0001
NIS
y = -3.23x + 56.9
R² = 0.761
p <0.0001
WAK
y = -0.865x + 42.0
R² = 0.256
p <0.0001
ROK
y = -0.310x + 21.0
R² = 0.185
p <0.0001
TAK
y = -0.665x + 28.5
R² = 0.504
p <0.0001
EHI
y = -0.568x + 21.5
R² = 0.190
p <0.0001
MIY
y = -0.325x + 16.0
R² = 0.162
p <0.0001
Leaf area (cm²)
Height (m)
0
10
20
30
40
50
60
70
0
10
20
30
legend
SOI
SHI
KAW
SEN
NAE
OGA
SUG
NIS
WAK
ROK
TAK
EHI
MIY

Fig. 4

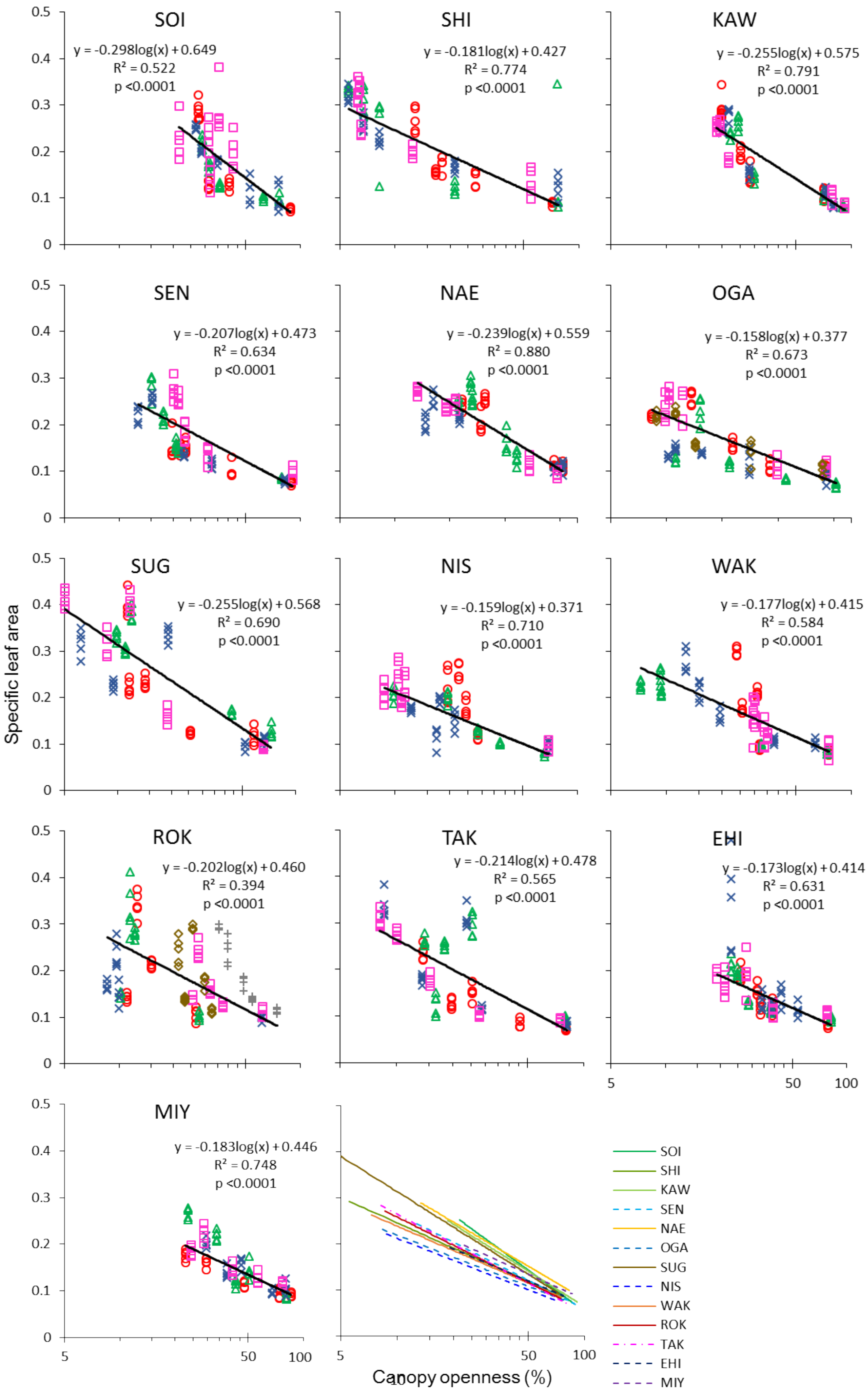

SOI
y = -0.298log(x) + 0.649
R² = 0.522
p <0.0001
SHI
y = -0.181log(x) + 0.427
R² = 0.774
p <0.0001
KAW
y = -0.255log(x) + 0.575
R² = 0.791
p <0.0001
SEN
y = -0.207log(x) + 0.473
R² = 0.634
p <0.0001
NAE
y = -0.239log(x) + 0.559
R² = 0.880
p <0.0001
OGA
y = -0.158log(x) + 0.377
R² = 0.673
p <0.0001
SUG
y = -0.255log(x) + 0.568
R² = 0.690
p <0.0001
NIS
y = -0.159log(x) + 0.371
R² = 0.710
p <0.0001
WAK
y = -0.177log(x) + 0.415
R² = 0.584
p <0.0001
ROK
y = -0.202log(x) + 0.460
R² = 0.394
p <0.0001
TAK
y = -0.214log(x) + 0.478
R² = 0.565
p <0.0001
EHI
y = -0.173log(x) + 0.414
R² = 0.631
p <0.0001
MIY
y = -0.183log(x) + 0.446
R² = 0.748
p <0.0001
Specific leaf area
0
0.1
0.2
0.3
0.4
0.5
5
50
100
Canopy openness (%)
SOI
SHI
KAW
SEN
NAE
OGA
SUG
NIS
WAK
ROK
TAK
EHI
MIY

Fig. 5

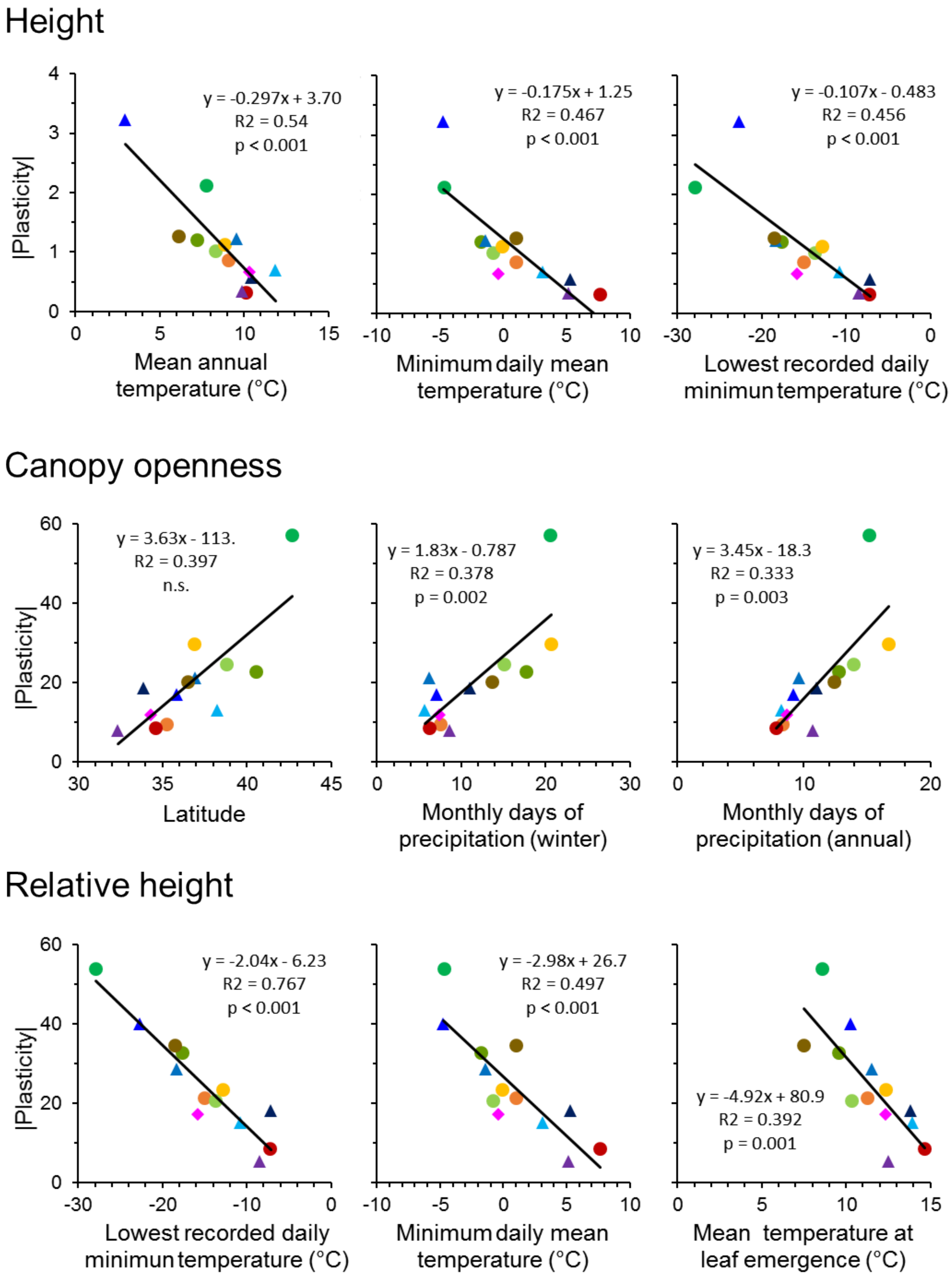

Height
|Plasticity|
y = -0.297x + 3.70
R2 = 0.54
p < 0.001
Mean annual temperature (°C)
y = -0.175x + 1.25
R2 = 0.467
p < 0.001
Minimum daily mean temperature (°C)
y = -0.107x - 0.483
R2 = 0.456
p < 0.001
Lowest recorded daily minimun temperature (°C)
Canopy openness
|Plasticity|
y = 3.63x - 113.
R2 = 0.397
n.s.
Latitude
y = 1.83x - 0.787
R2 = 0.378
p = 0.002
Monthly days of precipitation (winter)
y = 3.45x - 18.3
R2 = 0.333
p = 0.003
Monthly days of precipitation (annual)
Relative height
|Plasticity|
y = -2.04x - 6.23
R2 = 0.767
p < 0.001
Lowest recorded daily minimun temperature (°C)
y = -2.98x + 26.7
R2 = 0.497
p < 0.001
Minimum daily mean temperature (°C)
y = -4.92x + 80.9
R2 = 0.392
p = 0.001
Mean temperature at leaf emergence (°C)

Fig 6.

Table S1. List of environmental/structural variables investigated in relation to intra-individual plasticity.

Variable type	Variable name
Temperature/precipitation	Annual mean
	Maximum annual mean
	Minimum annual mean
	Year to year variation (maximum – minimum annual mean)
	Monthly mean (annual/summer/winter)
	Maximum monthly mean
	Minimum monthly mean
	Highest recorded monthly mean
	Lowest recorded monthly mean
	Historical monthly variation (highest –lowest recorded monthly mean)
	Daily mean temperature
	Daily maximum temperature
	Daily minimum temperature
	Highest recorded daily maximum temperature
	Lowest recorded daily minimum temperature
	Historical daily temperature variation (highest daily max – lowest daily min)
	Monthly days of precipitation (annual/summer/winter)
	Highest recorded monthly days of precipitation
	Lowest recorded monthly days of precipitation
	Historical monthly precipitation variation (highest – lowest recorded days/mo)
Aridity	Annual mean SPEI*
	Maximum annual SPEI
	Minimum annual SPEI
	Historical variation (maximum – minimum annual SPEI)
Growing season	Days of growing season**
	Mean/max/min temperature at bud formation
	Mean/max/min temperature at leaf emergence
	Mean/max/min temperature during growing season
	Monthly precipitation during growing season
	Monthly days of precipitation during growing season
Location	Latitude
	Longitude
	Elevation
Tree structure	Diameter at breast height
	Tree height
	Crown-base height
	Crown depth
	Crown width
	Leaf area index

* Standardized Precipitation-Evaporation Index

** Monthly mean temperature > 5°C (Kira 1991)

TableS2. Results of linear regression analyses comparing leaf morphological traits among observation years for *F. crenata* in Mt. Rokko in relation to height (H), canopy openness (O_C) and relative height (H_{rel}). Regression slopes, representing plasticity, and intercepts were compared among sites by ANCOVA. All All regressions were significant ($P < 0.01$). Estimates of slopes and intercepts labeled with the same letter are not significantly different ($P < 0.05$).

Leaf trait	Year	H (m)			O_c (%)			H_{rel}		
		Slope	Intercept	r^2	Slope	Intercept	r^2	Slope	Intercept	r^2
Area (cm^2)	2015	-0.31 A	21.0 A	0.185	-8.4 A	27.4 A	0.301	-8.6 A	21.9 A	0.266
	2016	-0.29 A	17.6 B	0.263	-5.9 B	22.2 B	0.319	-6.9 A	18.5 B	0.344
	2017	-0.24 A	18.4 B	0.160	-5.0 B	20.9 B	0.358	-5.4 A	18.9 B	0.182
Thickness (mm)	2015	0.007 A	0.200 A	0.495	0.078 B	0.182 A	0.174	0.159 A	0.182 B	0.629
	2016	0.006 A	0.218 A	0.342	0.180 A	0.055 B	0.651	0.176 A	0.181 B	0.556
	2017	0.006 A	0.205 A	0.330	0.091 B	0.182 A	0.533	0.103 B	0.211 A	0.306
Leaf mass (mg)	2015	4.77 A	43.3 A	0.597	48.9 B	39.2 A	0.135	91.0 A	41.1 A	0.613
	2016	3.04 B	55.6 A	0.316	71.9 A	-3.4 C	0.470	78.0 A	41.7 A	0.450
	2017	3.53 B	48.4 A	0.395	63.6 A	21.2 B	0.650	79.3 A	40.5 A	0.458
SLA ($cm^2\,mg^{-1}$)	2015	-0.014 A	0.375 A	0.806	-0.202 A	0.460 A	0.394	-0.28 A	0.384 A	0.856
	2016	-0.011 B	0.281 B	0.691	-0.169 B	0.396 B	0.601	-0.203 B	0.298 B	0.669
	2017	-0.009 B	0.290 B	0.528	-0.141 C	0.340 C	0.610	-0.210 B	0.311 B	0.615

Table S3. Spearman's rank correlation coefficients (R_s) between plasticity (absolute value of the regression slope in relation to independent variable) of leaf traits and climatic variables. Statistically significant ($P < 0.05$) environmental variables are listed in order of decreasing R_s.

Leaf trait	Independent variable	Climatic variable	R_S	*P*
Thickness	Relative height	Maximum temperature (leaf emergence)	-0.562	0.046
SLA	Relative height	Mean monthly precipitation (summer)	-0.622	0.023
		Mean tree height	0.598	0.031
		Maximum temperature (leaf emergence)	-0.578	0.039
SLA	Canopy openness	Mean monthly days of precipitation (winter)	0.667	0.013
		Mean monthly days of precipitation (annual)	0.656	0.015
		Lowest recorded monthly days of precipitation	0.623	0.023
		Maximum temperature (leaf emergence)	-0.605	0.028
		Distance from Sea of Japan	-0.554	0.050