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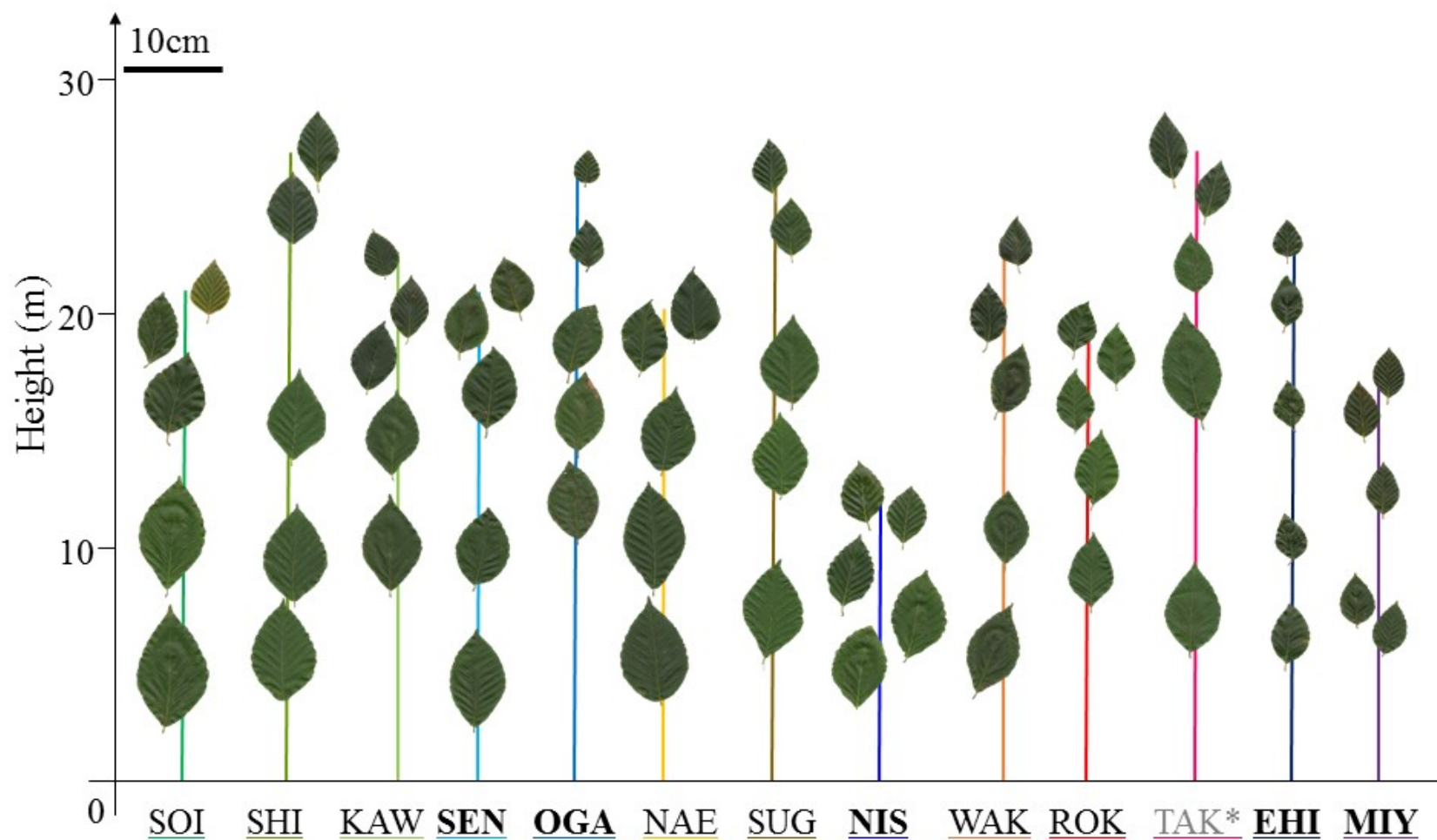
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Intra-crown variation of leaf morphology among the 13 *F. crenata* populations in Japan. Scanned leaf images from single trees are shown in relation to height. Leaf morphological plasticity decreases with decreasing latitude (north to south from left 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*

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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 range](#). [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 Fraser 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 ($H_{rel} = H / \text{tree height}$) 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 cm²) among the [sites](#), maximum leaf area of shade leaves varied more than three-fold, ranging

from ca 20 cm² near the southern range (Miyazaki) to ca 70 cm² 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 cm² 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 Gezdou, 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.

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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 (cm ²)	Jpn Sea	-0.773	38.6	0.168	-14.1	45.6	0.145	-23.5	42.0	0.252
	Pacific	-0.682	30.2	0.147	-22.4	53.1	0.432	-20.1	34.5	0.239
Thickness (mm)	Jpn Sea	0.008	0.164	0.494	0.162	0.067	0.446	0.210	0.155	0.529
	Pacific	0.005	0.225	0.352	0.114	0.141	0.389	0.145	0.198	0.484
Leaf mass (mg)	Jpn Sea	3.544	90.3	0.123	81.9	33.7	0.149	91.9	83.4	0.134
	Pacific	1.933	105.0	0.044	-9.9	140.1	0.002	55.0	93.2	0.053
SLA (cm ² mg ⁻¹)	Jpn Sea	-0.011	0.383	0.627	-0.207	0.485	0.593	-0.308	0.416	0.766
	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	Intercept	r^2	Slope	Intercept	r^2	Slope	Intercept	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 FC. .	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 FC. .	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	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	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 F. .	0.734 **	-0.173 EF. .	0.414 D. .	0.631 **	-0.183 G. .	0.281 I. .	0.764 **
	MIY	-0.010 E. .	0.255	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 (Δ : Japan Sea; O: Pacific; \diamond : 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.

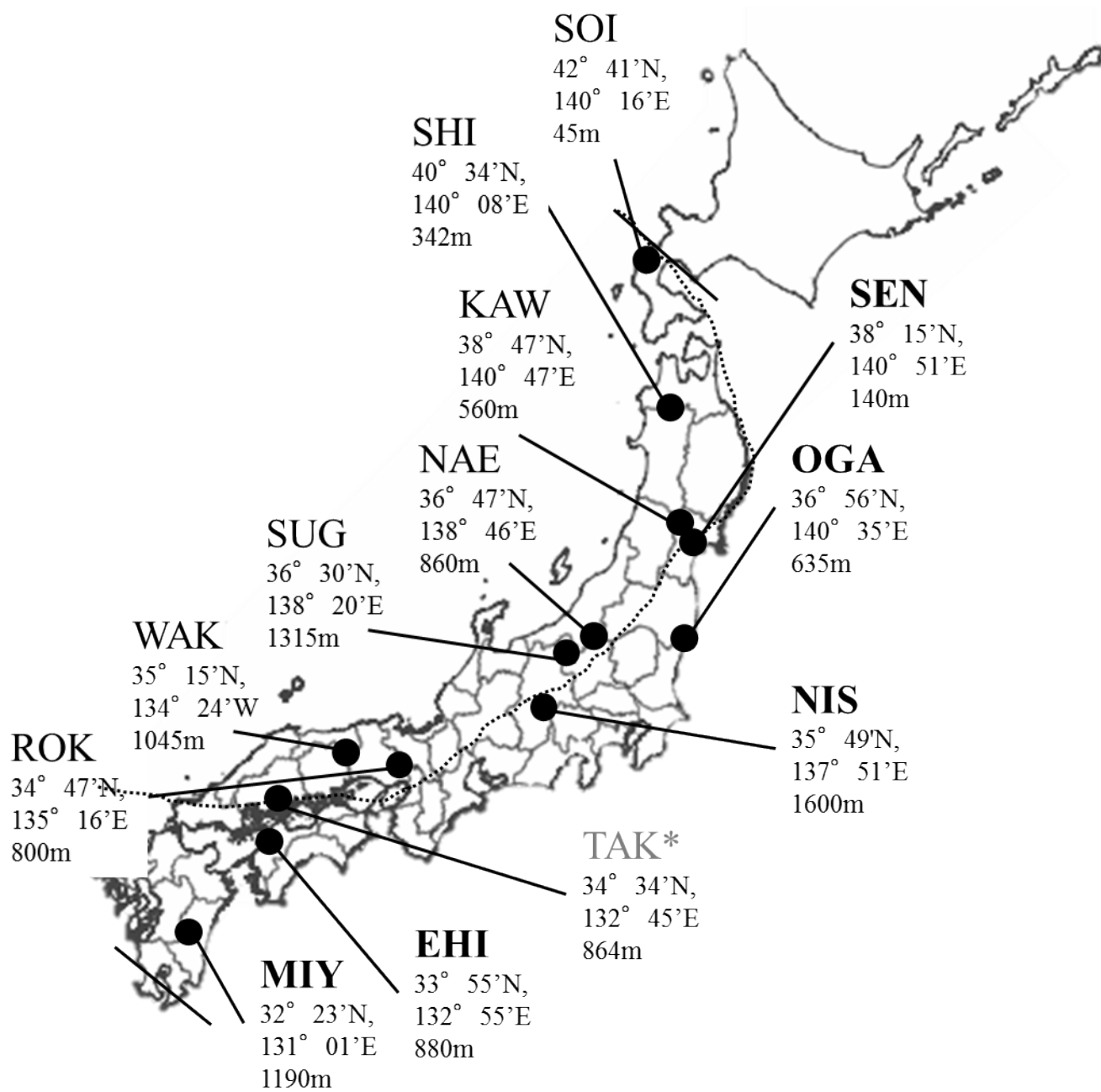


Fig. 1

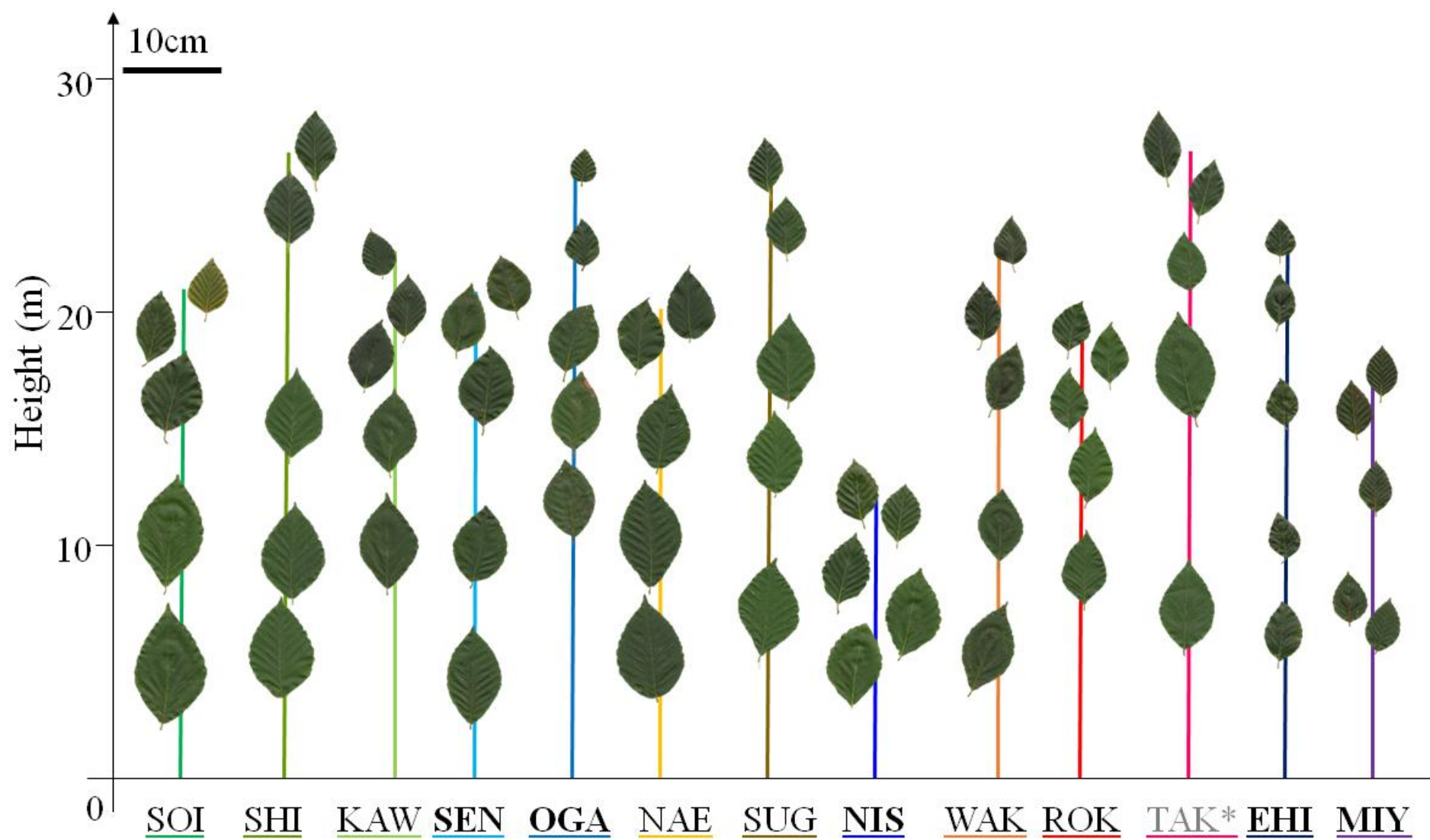


Fig. 2

	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 **

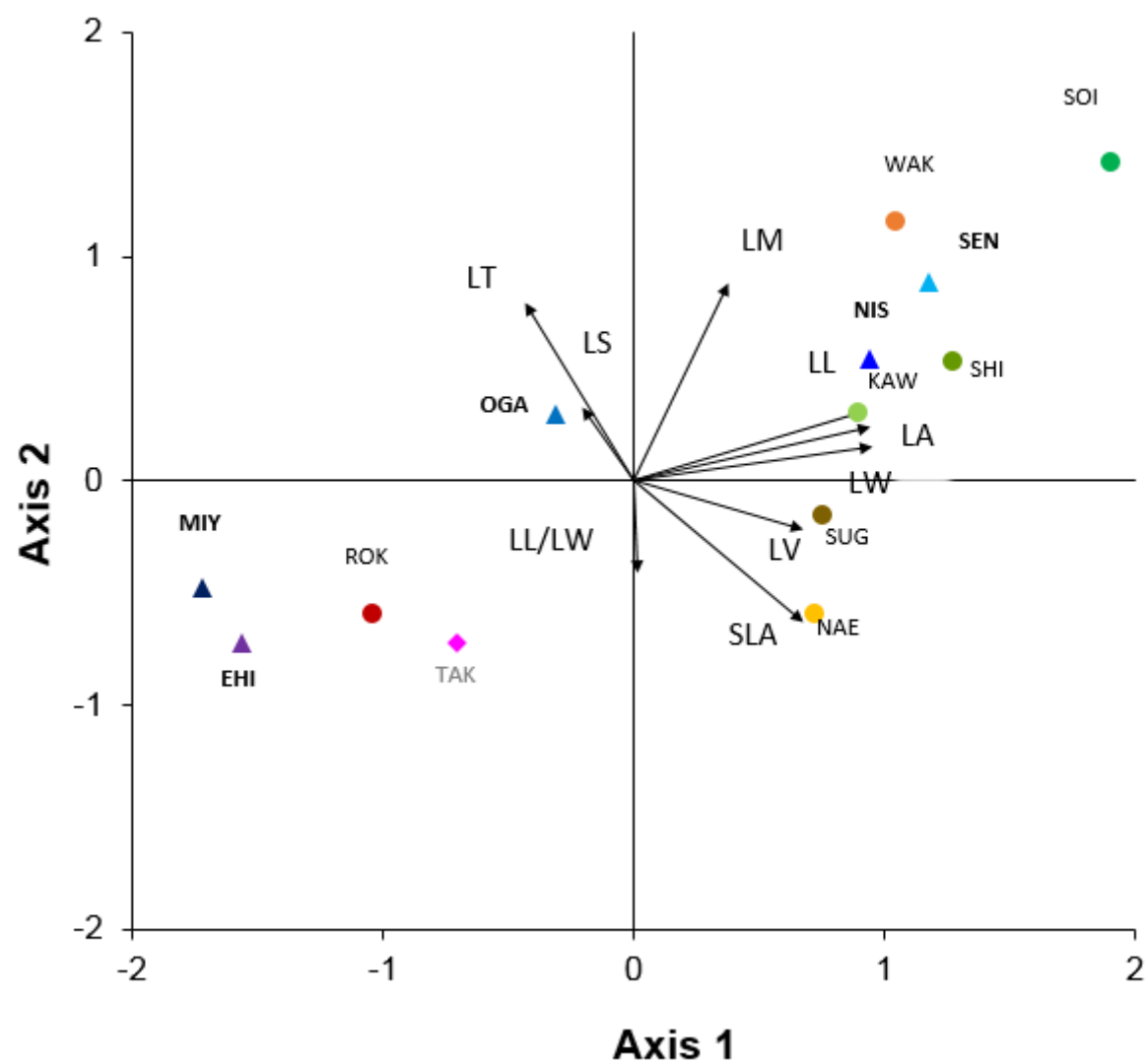


Fig. 3

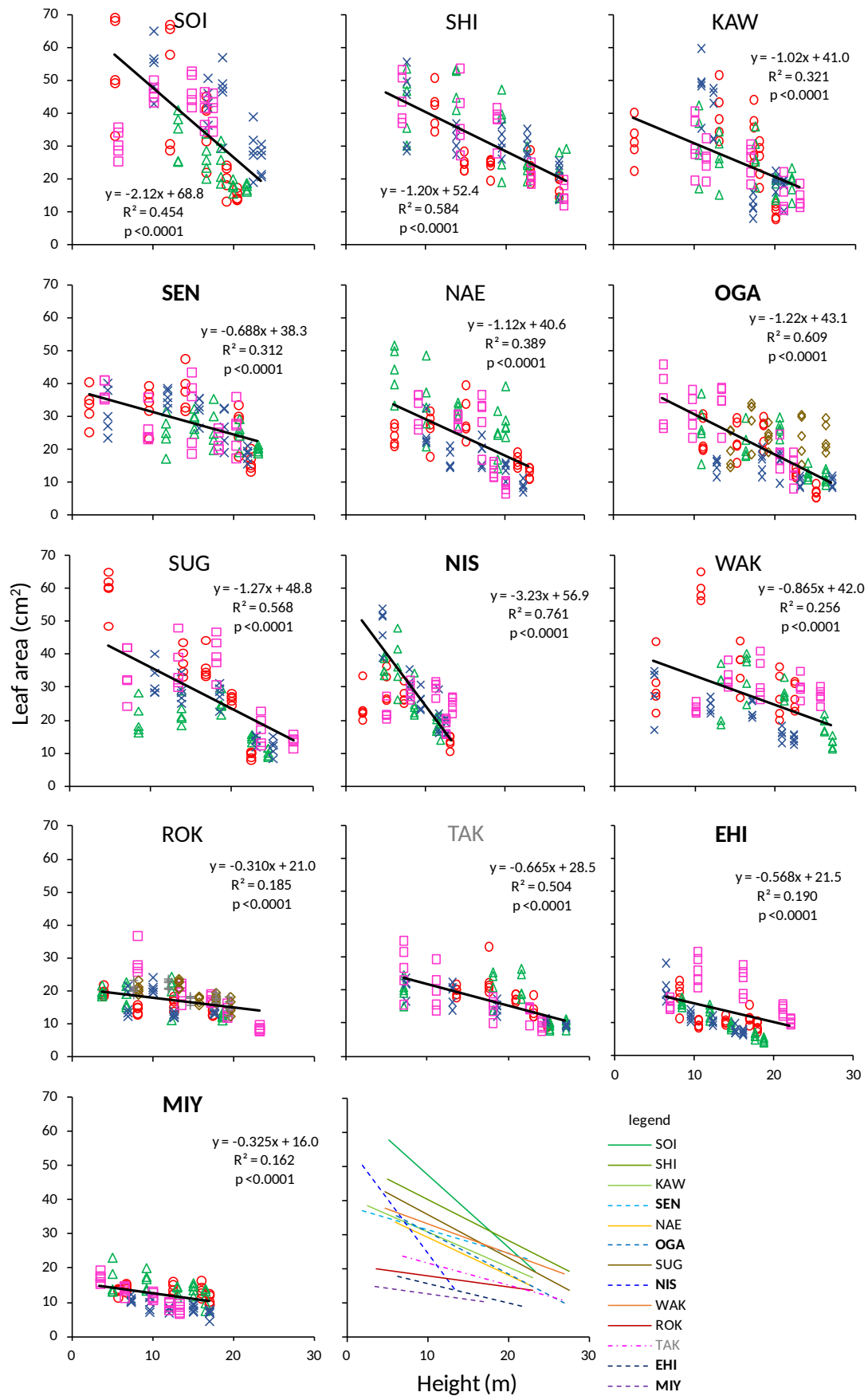


Fig. 4

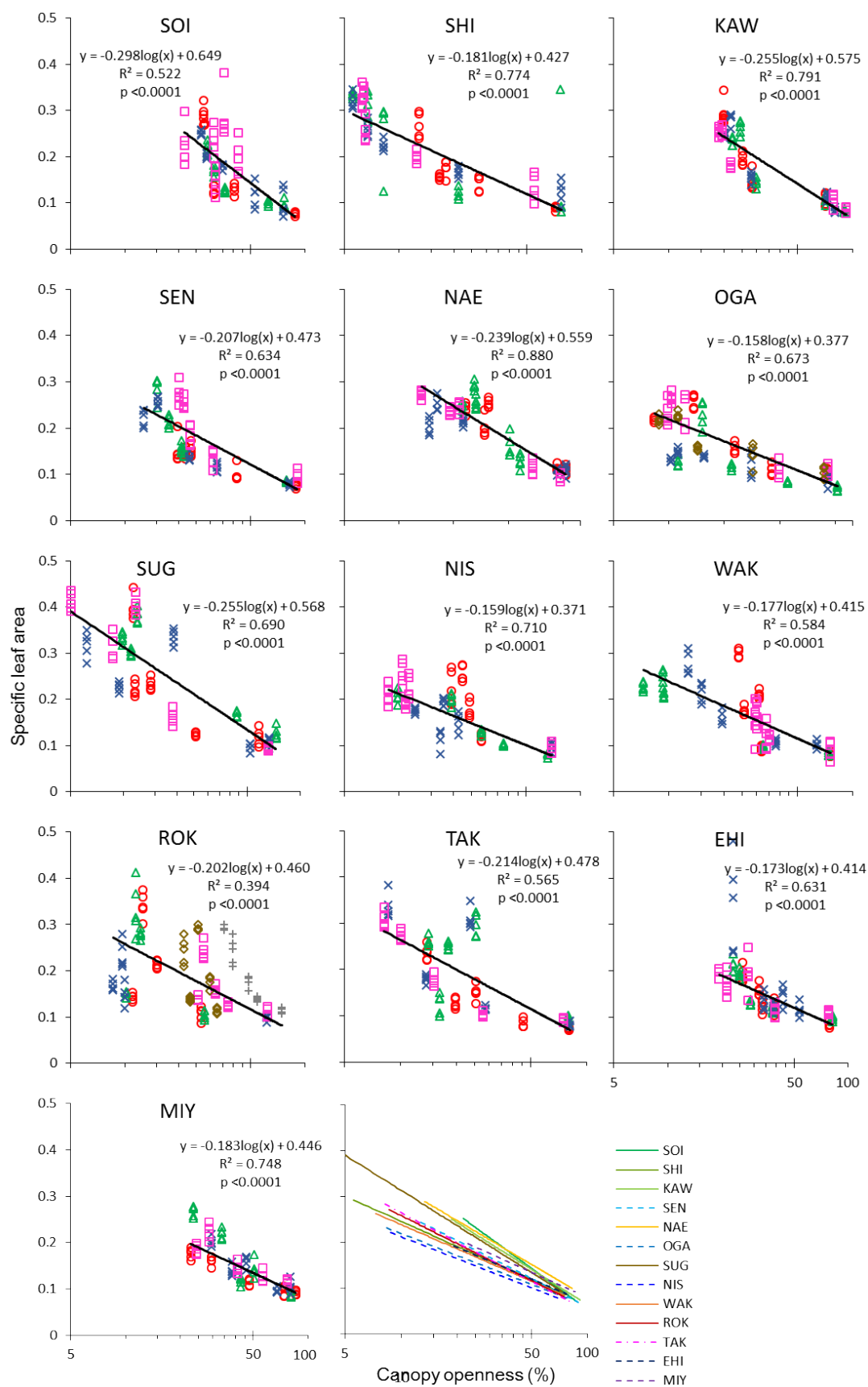
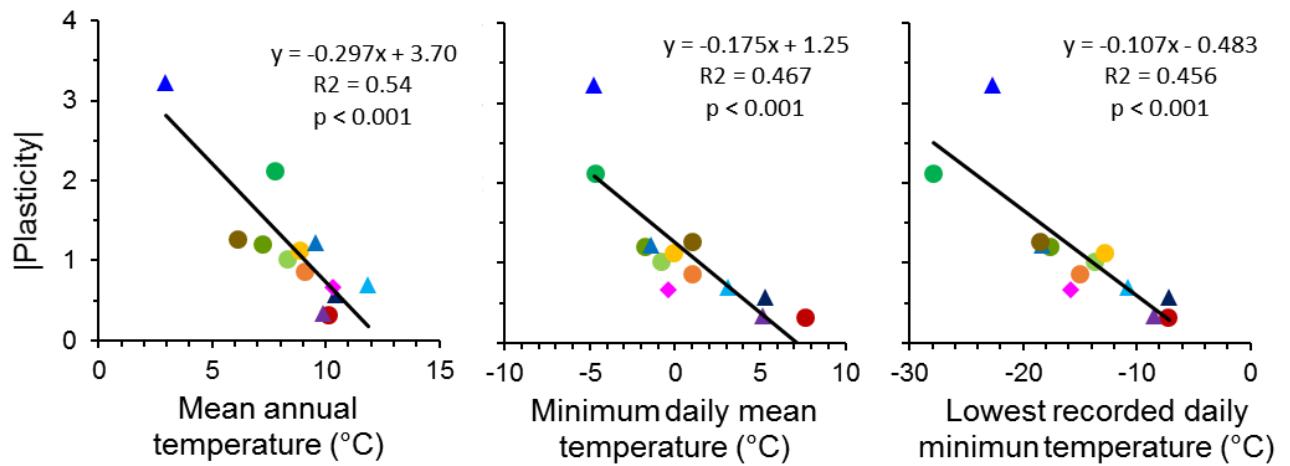
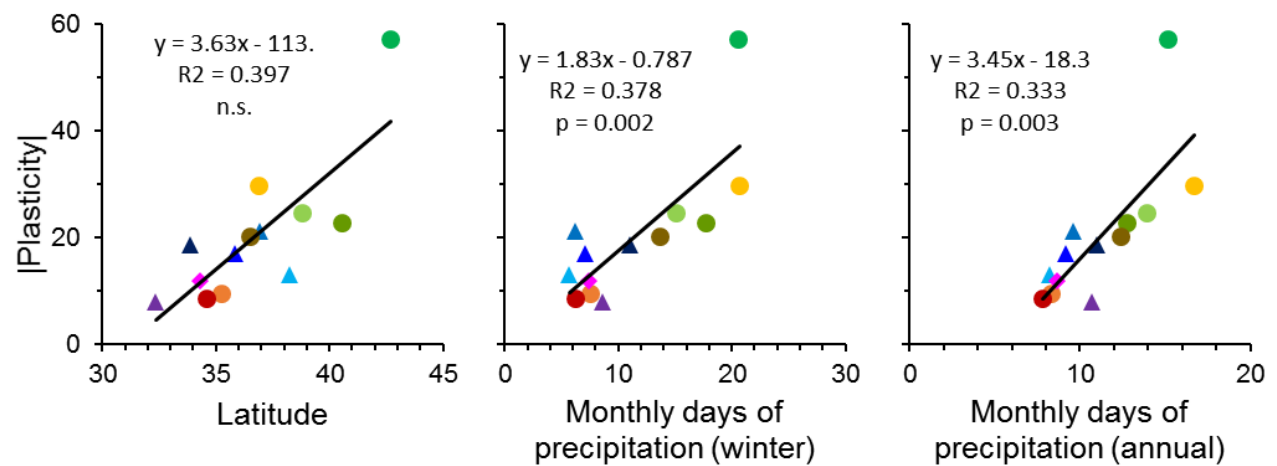


Fig. 5

Height



Canopy openness



Relative height

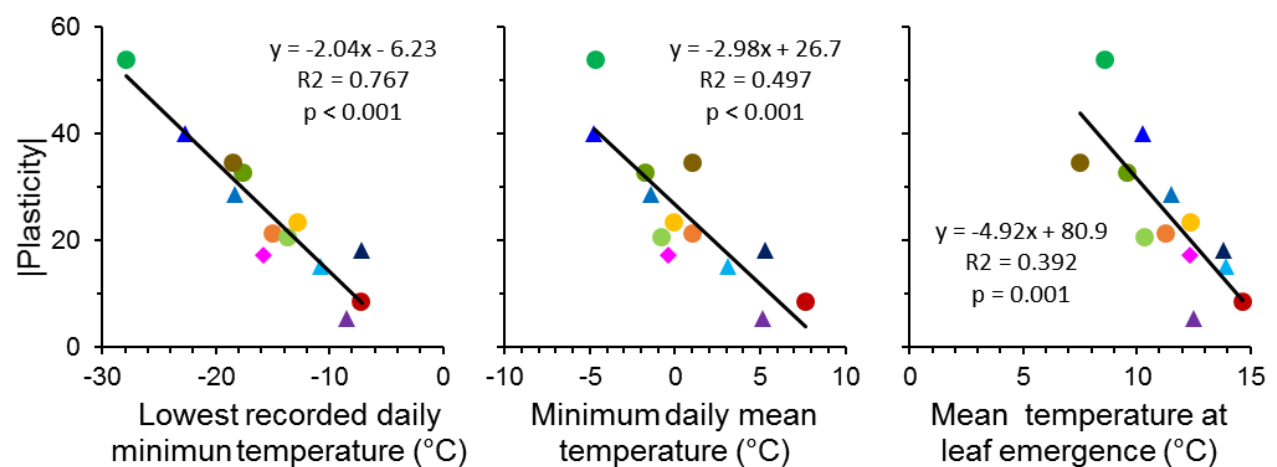


Fig 6.

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 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