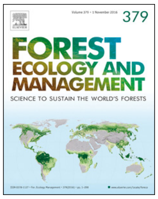
Forest Ecology and Management 429 (2018) 437–448

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



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

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

Graduate School of Agricultural Science, Kobe University, Kobe 657-8501, Japan

ARTICLE INFO

Keywords:
Acclimation
Geographical variation
Habitat fragmentation
Leaf functional trait
Local adaptation
Distribution range

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.

1. 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 et al., 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

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* Corresponding author.
E-mail address: hishii@alumni.washington.edu (H.R. Ishii).

[1] These authors share first authorship.

[2] Present address: Graduate School of Agriculture, Kyoto University, Kyoto 606-8502, Japan.

https://doi.org/10.1016/j.foreco.2018.07.016
Received 8 February 2018; Received in revised form 16 April 2018; Accepted 5 July 2018

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

[a] Genetic lineage of the Mt. Takanosu site is unknown.

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; 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 (Kira, 1991; 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.