

Intraspecific variations in leaf traits, productivity and resource use efficiencies in the dominant species of subalpine evergreen coniferous and deciduous broad-leaved forests along the altitudinal gradient

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Abstract

1. Many studies have reported intraspecific variations in leaf functional traits, but their contribution to plant performance and ecosystem function are poorly understood. We studied altitudinal gradients of intraspecific variations in leaf traits, productivity and resource use efficiency in the dominant species of subalpine evergreen coniferous and deciduous broad-leaved forests in Japan.
2. We addressed three hypotheses, which are exclusive to each other. (1) Leaf traits vary along the leaf economics spectrum (LES). Plants that grow at lower and higher altitudes have fast- and slow-return strategies, respectively, which improve productivity or resource use efficiency in the respective habitat. (2) Leaf trait variations are not consistent with the LES, but they contribute to improving productivity or resource use efficiency in the respective habitat. (3) Leaf trait variations do not contribute to improving productivity or resource use efficiency at higher altitudes.
3. On the studied mountain range, *Fagus crenata*, a deciduous broad-leaved tree, and *Abies mariesii*, an evergreen conifer, are the dominant species at lower and higher altitudes respectively. In *F. crenata*, leaf mass per area (LMA) and nitrogen concentrations were higher at higher altitudes. The net assimilation rate and light use efficiency during the growing season were greater at higher altitudes, which compensated for the shorter growing season in terms of annual productivity. In *A. mariesii*, the LMA was lower and the leaf life span was unchanged at higher altitudes. Productivity and resource use efficiency decreased with altitude.
4. *Synthesis*. We conclude that *F. crenata* improves its productivity and resource use efficiency at higher altitudes by altering its leaf functional traits (Hypothesis 2), whereas alterations to leaf traits in *A. mariesii* are not associated with any improvement

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at higher altitudes (Hypothesis 3), which may result from the negative impact of environmental stress. Hence, the ecological significance of altitudinal variations in leaf traits depends on species and environment.

KEYWORDS

canopy duration, elevation, functional traits, leaf economics spectrum, light use efficiency, nitrogen cycling, nitrogen use efficiency

1 | INTRODUCTION

There are large variations in leaf functional traits between plant species. Since these traits are related directly to photosynthesis, growth and tissue longevity, they are important determinants of plant fitness. Thus, leaf functional traits are subject to natural selection in each habitat, influencing species distribution and community assembly across environmental gradients (Ackerly & Cornwell, 2007; Cornwell & Ackerly, 2009). Large variations in leaf functional traits also occur within species (Messier et al., 2010), and this may be related to the range of distribution for each species (Albert et al., 2011). A recent global meta-analysis by Siefert et al. (2015) showed that, on average, intraspecific variation in plant functional traits explains 25% of the total trait variation within communities and 32% of the total trait variation between communities.

The global convergence of leaf traits was demonstrated previously; at one end of the axis, species have higher photosynthetic capacity (A_{mass}) and leaf nutrient concentration per unit of mass, lower leaf mass per area (LMA) and shorter leaf life span (LLS), and vice versa at the other end. Thus, this axis is directed from fast to slow return on investments of nutrients and dry mass in leaves, known as the leaf economics spectrum (LES; Wright et al., 2004). The LES is influenced by climate; the slope and intercept of the correlations between leaf traits change with climate variables. For example, increased rainfall increases the LLS, when compared at the same LMA, and the slope of the A_{mass} -leaf nitrogen (N) concentration per mass (N_{mass}) relationship becomes flatter with increasing mean annual temperature (Wright et al., 2005).

The altitudinal gradient is a useful natural experimental system for studying environmental responses of organisms, because the environmental gradient is steep within a relatively small spatial scale (Körner, 2007). Many studies have reported that leaf traits change with altitude. In general, species inhabiting higher altitudes have a higher LMA (e.g. Hikosaka et al., 2002; Read et al., 2014; van de Weg et al., 2009), implying the strategy of slow return on investments in dry mass (Read et al., 2014). Such variations have often been observed within a species (Almeida et al., 2013; Cordell et al., 1999; Kamiyama et al., 2014, but see also Fajardo & Piper, 2011). However, the direction of leaf trait variation along altitude is not necessarily the same as that of the LES axis, and the trends often vary among studies. For example, in a world-wide species comparison, Körner (1989) showed that N_{mass} in herbaceous species generally increases at higher altitudes, whereas other studies have demonstrated that

a lower N_{mass} prevails at higher altitudes (e.g. Köhler et al., 2006; Milla et al., 2009; Takahashi & Miyajima, 2008). Several reports have suggested that species inhabiting higher altitudes have lower photosynthetic rates (Cordell et al., 1999; Hikosaka et al., 2002), but no significant difference in photosynthetic activity was found between tropical lowlands and highlands (Bahar et al., 2017). The causes of these discrepancies are unclear.

Several possibilities may explain these inconsistencies in the data. One is that the environmental gradient associated with altitude varies between individual mountains. For example, the gradient of nutrient availability in the soil is inconsistent between mountains (Kitayama et al., 1998; Köhler et al., 2006; Little et al., 2016; Powers, 1990; Rehder & Schäfer, 1978; Tan & Wang, 2016; Wang et al., 2019). The second possibility is that plant trait variation is caused by damage from stress rather than adaptation. For example, LLS may be shortened due to strong winds (Nagano et al., 2009) or herbivory (Zvereva et al., 2014). The third possibility is that the environmental dependence of optimal strategies may differ between species or plant functional types. For example, Wright et al. (2005) showed that the LLS in evergreen species increases with decreasing air temperature, whereas it decreases in deciduous species. The ecological significance of these patterns can be explained by the cost-benefit model (Kikuzawa et al., 2013); a longer LLS is required to maximize carbon gain for evergreen plants when the favourable period for photosynthesis is shorter because plants cannot afford the cost of constructing new leaves. A shorter LLS is required for deciduous plants when the favourable period is shorter because they drop leaves during the unfavourable period. In fact, in snow-bed areas with different snow-melt period lengths, the LLS of evergreen species is longer when the snow-melt period decreases, whereas that of deciduous species is shorter (Kikuzawa & Kudo, 1995; Kudo, 1992). Therefore, the ecological significance of trait value changes may differ between plant functional types.

Variation in the leaf traits is related to whole-plant performance and ecosystem function (Díaz & Cabido, 2001; Reich, 2014). For example, species with higher A_{mass} have higher relative growth rates, leading to higher primary productivities per mass of the stands where the species dominate (Reich et al., 1992). On the other hand, in species with a longer LLS, nutrients remain in the plant body longer, contributing to higher nutrient use efficiency and influencing cycling of carbon and nutrients in the ecosystem (Aerts & Chapin, 2000; Berendse & Aerts, 1987). However, leaf trait variations are not always on the LES axis. For example, LMA influences photosynthetic

capacity in varying ways. In the LES, LMA is negatively related to A_{mass} because of a trade-off in resource allocation between photosynthesis and leaf strength (Hikosaka, 2004; Onoda et al., 2004, 2011, 2017; Reich et al., 1991; Takashima et al., 2004). Such a trade-off occurred across altitudes on Mt Kinabalu (Hikosaka et al., 2002). On the other hand, a higher LMA is necessary to increase photosynthetic capacity per unit leaf area because a larger mesophyll area needs to contain greater amounts of photosynthetic proteins (Oguchi et al., 2003, 2005; Terashima et al., 2001). The leaves of tropical highland plants have both higher LMA and photosynthetic capacities than lowland plants (Bahar et al., 2017). Therefore, the relationships between plant functional traits and ecosystem functions require careful investigation, especially in terms of the ecological significance of the trait variations.

In temperate regions, air temperature and growing season length decrease with altitude, both of which are essential constraints to plant growth and critical drivers of species distribution. In northern Honshu (mainland of Japan), natural forests are generally dominated by deciduous broad-leaved trees and evergreen conifers at lower and higher altitudes respectively. *Fagus crenata* and *Abies mariesii* are the typical dominant species found at low and high altitudes respectively. This distribution will not be fixed in the future, however, since global warming may affect plant functions. In fact, in the Hakkoda mountain range, a study site for the present study, the *A. mariesii* population has moved to a higher altitude over the last three decades (Shimazaki et al., 2011). Information about how plants cope with environmental change is important for predicting ecosystem functioning and conserving biodiversity under climate change.

In the present study, we focus on intraspecific variations in leaf traits, productivity and resource use efficiencies in *F. crenata* and *A. mariesii* along an altitudinal gradient on two independent transects in the Hakkoda mountain range, northern Japan. We addressed the following hypotheses, which are exclusive to each other. Hypothesis 1: Direction of leaf trait variation along altitude within a species is consistent with the LES gradient; at lower altitudes, where growth conditions are favourable, plants have traits that enable them to achieve higher productivity, while at higher altitudes, plants possess

traits that allow them to carry out their conservation strategy. Hypothesis 2: The altitudinal gradient of leaf traits is inconsistent with the LES but contributes to improving productivity or resource use efficiency at respective altitudes; there is an improvement in or compensation for some plant performances at higher altitudes. Hypothesis 3: The altitudinal change in leaf traits does not improve or compensate for plant performance at higher altitudes; both productivity and resource use efficiency decrease with altitude. Leaf trait variations may be caused by other factors, such as the negative impact of environmental stress. We tested these hypotheses by assessing the altitudinal dependence and inter-relationships of leaf traits, productivity and resource use efficiencies.

2 | MATERIALS AND METHODS

2.1 | Site and species

The study area was located in the Hakkoda mountain range in Aomori Prefecture, northern Japan (Figure 1). This range consists of several peaks that are higher than 1,200 m a.s.l., and the highest one (Mt. Ohdake) is 1,584 m a.s.l. (40°41'N, 140°52'E). The annual values for mean temperature, precipitation and maximum snow depth between 1990 and 2009 at the Sukayu meteorological station (40°38.9'N, 140°50.9'E, 900 m a.s.l.) ranged from 4 to 6°C, 1,300–2,300 mm and 3–5 m respectively (see Shimazaki et al., 2011 for details). This region has one of the heaviest areas of snowfall in the world. Snow cover disappears in late April at 400–600 m a.s.l. but remains in June at >1,200 m a.s.l. In this mountain range, the natural vegetation is relatively well preserved between an elevation of 300 m a.s.l. and the peak. At lower elevations, from 400 to 800 m a.s.l., the deciduous broad-leaved forests are dominated by *F. crenata* Blume, which appears to be the natural vegetation. At higher altitudes, from 1,000 to 1,400 m a.s.l., the subalpine coniferous forests are dominated by *A. mariesii* Mast., which is the original vegetation, with a transition between the two types of forest at 800–1,000 m a.s.l. Most subalpine coniferous forests grow within a protected area with little human impact.

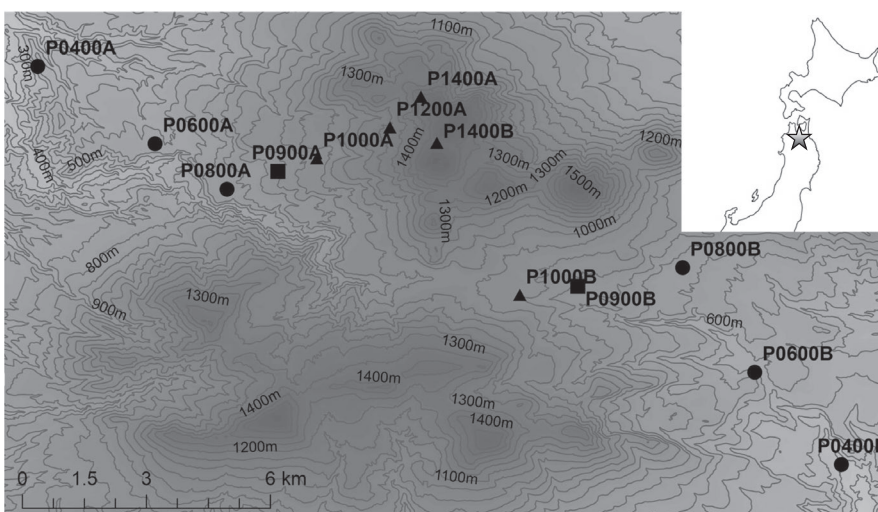


FIGURE 1 Study plots in the Hakkoda mountain range. A series of plots were assigned to line A on the western slope of Mt. Akakuradake, and a series of the plots were assigned to line B on the eastern slope of Mt. Takada-Otake

In this area, we established 13 permanent research plots at every 200 m along the altitude gradient, and in the mixed forests at around 900 m a.s.l. on the west slope of Mt. Akakuradake (a series of the plots assigned to Line A) and on the east slope of Mt. Takada-Ohdake (a series of plots assigned to Line B; Figure 1; Table 1). Plot size ranged 0.05–0.25 ha (Table 1), depending on the difficulties of plot installation and the available forest area, both are limited by topography. In these plots other than those in the mixed forests, either *F. crenata* or *A. mariesii* occupied more than 70% of the forest biomass in terms of basal area (BA), except for 600A (Table 1). In the plots of mixed forests, *F. crenata* and *A. mariesii* collectively occupied more than 90% of the total BA in those plots. The air temperature at 1.3 m above-ground was measured every hour during the 2010 growing season at each plot.

We conducted a tree census annually in summer from 2007. Trunk diameter at breast height of every tree was determined if the diameter was larger than 5 cm. The amount of litter fall during the growing season was measured using five litter traps (0.5 m² each) per plot. For the present study, we used the litter fall collected during July, September, and October or November (depending on altitude) of 2011. The litter was sorted into leaf litter and reproductive organs of *F. crenata*, *A. mariesii* and other species and others (e.g. twigs), to determine their dry mass. Subsamples of the leaf litter were used to measure nitrogen concentration with an elemental analyser (Vario EL III; Elementar).

In the mixed forest plots (900A and 900B), the initial number of litter traps (five) was insufficient for evaluating the leaf litter production of each species because of the heterogeneous distribution of

individual trees in the plots. In 2015, we set 18 and 12 litter traps (including the five original traps) in plots 900A and 900B, respectively, to correct for any deviation in leaf litter production. The corrected litter mass was calculated as follows: (mean litter mass in the five original traps in 2011) × (mean litter mass in 18 or 12 traps in 2015) / (mean litter mass in the five original traps in 2015).

2.2 | Assessed variables

Leaf mass per area (LMA) represents dry mass invested per leaf area. Species with high LMA have a thicker leaf blade or denser tissue, or both. It is related to light interception, leaf toughness (Onoda et al., 2011, 2017), mesophyll cell area and the content of photosynthetic proteins (Oguchi et al., 2003, 2005). Leaf N concentration per unit of dry mass (N_{mass}) and per leaf area (N_{area}) represents investment of N in leaves. Since about half of leaf N is allocated to the photosynthetic apparatus, N concentrations are strongly related to the photosynthetic capacity (Hikosaka, 2004). Leaf life span (LLS) describes the average duration of the revenue stream from each leaf constructed (Wright et al., 2004). Long LLS may require robust construction in the form of high LMA. N resorption efficiency (R_N) is the fraction of N resorbed from living leaves before leaf death, which contributes to recycling of N within the plant (Aerts & Chapin, 2000). Mean residence time of N in the plant body (MRT) describes the average duration between N uptake from roots and N loss with leaf litter (Berendse & Aerts, 1987). MRT may be longer if LLS is longer and/or R_N is higher (Aerts & Chapin, 2000).

TABLE 1 Plot description with climatic parameters. A or B at the end of plot name indicates line A and B in which the plot was set up respectively (see Figure 1). The value for air temperature was mean of daily-mean air temperature during June–October 2010, with the standard error given in parentheses. The value for snow-less duration was mean for 3-year observations (2010–2012) with the standard error given in parentheses. Canopy duration is the length of day when *Fagus crenata* leaves were present in the canopy (see text for details). Basal area was obtained in 2011. NA, not available

Plot name	Plot size (ha)	Elevation (m)	Air temperature (°C)	Snow-less duration (day)	Canopy duration (day)	Dominant species	Total basal area (cm ² /ha)	Total basal area of <i>Abies mariesii</i> (cm ² /ha)	Total basal area of <i>Fagus crenata</i> (cm ² /ha)
400A	0.25	491	18.3 (0.423)	215 (4.73)	179	<i>F. crenata</i>	40.2	0	27.0
400B	0.16	379	17.8 (0.433)	232 (9.91)	188	<i>F. crenata</i>	43.4	0	32.1
600A	0.25	600	17.1 (0.434)	192 (10.5)	156	<i>F. crenata</i>	47.1	0	23.5
600B	0.25	636	16.8 (0.441)	213 (6.93)	156	<i>F. crenata</i>	52.0	0	50.3
800A	0.25	805	16.4 (0.444)	194 (11.8)	130	<i>F. crenata</i>	47.0	0	46.2
800B	0.25	776	16.1 (0.442)	191 (9.24)	122	<i>F. crenata</i>	47.3	0	40.1
900A	0.2	911	15.5 (0.449)	181 (7.09)	118	<i>F. crenata</i> / <i>A. mariesii</i>	30.0	11.3	17.0
900B	0.1	891	15.3 (0.447)	169 (5.77)	118	<i>F. crenata</i> / <i>A. mariesii</i>	54.7	5.9	48.5
1000A	0.1	985	15.0 (0.455)	197 (9.02)	–	<i>A. mariesii</i>	30.8	25.6	0
1000B	0.05	971	15.0 (0.454)	179 (6.24)	–	<i>A. mariesii</i>	43.2	36.4	1.1
1200A	0.1	1,200	14.0 (0.462)	180 (2.03)	–	<i>A. mariesii</i>	23.2	23.1	0
1400A	0.1	1,312	12.9 (0.465)	176 (1.76)	–	<i>A. mariesii</i>	23.9	22.1	0
1400B	0.1	1,440	NA	163 (–)	–	<i>A. mariesii</i>	29.3	28.7	0

Net primary production (NPP) describes the rate of dry mass production per unit ground area. Because NPP was strongly related to standing biomass per unit ground area, we used relative production rate (RPR), which is the production rate divided by the plant biomass (the above-ground vegetative mass), as a measure of productivity. RPR is an analogy of relative growth rate in the classic growth analysis (Lambers & Poorter, 1992). Net assimilation rate (NAR) represents biomass production rate per unit leaf area, which may reflect leaf photosynthetic activity. Leaf area ratio (LAR) describes leaf area per the plant mass. RPR can be expressed as the product of NAR and LAR (Lambers & Poorter, 1992). Leaf mass fraction (LMR) is the ratio of standing leaf mass per the plant mass, which represents biomass allocation to leaves. LAR can be expressed as the LMR divided by LMA.

Light use efficiency (LUE) is defined as the biomass production per unit absorbed light (Hikosaka et al., 1999; Monteith, 1972), which represents the photosynthetic efficiency to use absorbed light. Leaf area index (LAI) is the total leaf area per ground area. Higher LAI contributes to greater light interception. NPP can be expressed as the product of LUE and the absorbed light (Monteith, 1972).

Leaf N productivity (LNP) is defined as the biomass production rate per unit leaf N, which may be higher if photosynthetic N use efficiency is high. N use efficiency (NUE) is defined as the biomass production per unit absorbed N (Berendse & Aerts, 1987; Hirose, 1975; Vitousek, 1982). NUE can be expressed as the product of LNP and MRT (Berendse & Aerts, 1987).

2.3 | Leaf trait measurements

Branches at the top (uppermost) and the bottom (lowermost) of the canopy were collected from mature individuals of *F. crenata* and *A. mariesii* in each plot on 6–10 September 2010 by climbing the trees ($n = 2$ –5). For *F. crenata*, LMA, N_{mass} and N_{area} were determined. For *A. mariesii*, the age of the branch section was defined according to the terminal bud scar, and the survival rate was estimated by counting the number of living leaves and leaf scars at each age. Healthy, typical, mature leaves were collected for each age and scanned on a flatbed scanner (GT-S630, Epson). The number of scanned leaves depended on the available space on the scanner stage. The leaves were then oven-dried at 60°C to a constant weight. The leaf area was measured from the scans using ImageJ image analysis software version 1.45 (National Institutes of Health). The LMA for the whole leaf, including the petioles, was calculated as the dry mass divided by the leaf area. The dried leaves were then ground and used for nitrogen measurement with the elemental analyser (Vario EL III).

Between Autumn 2012 and Spring 2013, a light sensor (HOBO Pendant UA-002-64, Onset Computer Company) was anchored on a trunk surface at the height of 170–180 cm using wire in the plot in which *F. crenata* was dominant. Light intensity was recorded every hour. The date of leaf fall and canopy closure was estimated as the date when light intensity was highest in autumn and lowest in spring respectively (Figure S1). The duration between canopy closure and leaf fall was considered the canopy duration.

2.4 | Calculations

Here we provide a brief explanation of how traits of *F. crenata* and *A. mariesii* were calculated. Further details can be found in the Supporting Information.

For both species, R_N was calculated from the N concentration of living leaves and leaf litter, considering that N is translocated in the form of an amino acid (i.e. not only N but also other elements are resorbed) and part of the leaf mass is lost by respiration during leaf senescence (Yasumura et al., 2005).

Biomass, litter mass, LAI and production were calculated at the species level and expressed on a ground area basis, according to the area of the litter trap. Living leaf mass was calculated from the leaf litter mass, incorporating resorbed or respired mass and N. For *F. crenata*, the sum of living leaf mass was considered the initial standing leaf mass in the spring, assuming that new leaves were not produced after the spring flush. LLS was calculated as the integral of the relative standing leaf mass (initial mass = 1) from the point of canopy closure to leaf fall, assuming a linear decrease in standing leaf mass during the period between litter collections. LAI was obtained from the standing leaf mass and LMA of the top and bottom leaves, assuming an exponential decrease in LMA with cumulative LAI from the top (Davi et al., 2008). The initial standing leaf N was calculated as the sum of the resorbed and leaf litter N throughout the season.

The leaf traits of *A. mariesii* were calculated at the branch level. For LLS, the relationship between the leaf survival rate and the leaf age was fit to a logistic curve, and, assuming steady-state production and fall (Hikosaka & Osone, 2009), the mean LLS for the branch was calculated as the integral of the curve from 0 to the maximal age (Figure S2). The branch-level LMA, N_{mass} and N_{area} were obtained as a survival-weighted mean. We assumed that the standing leaf mass is in a steady state (i.e. the leaf production rate was equal to the leaf shedding rate), and it was calculated as the product of the annual loss of living leaf mass during the year and the mean LLS on the top and bottom branches. The LAI was obtained from the standing leaf mass and the LMA of the top and bottom branches, as in *F. crenata*. Standing leaf N was calculated using the LAI and N_{area} of the top and bottom branches.

Stem mass of *F. crenata* and *A. mariesii* was estimated from the trunk diameter determined at breast height, according to Nakashizuka (1984) and Ohuchi et al. (1968). NPP was calculated as the annual above-ground net primary production per ground area for each of *F. crenata* and *A. mariesii* as the sum of the annual increment in stem mass between 2010 and 2011, annual production of reproductive organs, and the annual loss of living leaf mass in 2011 (trees that were recruited and died during this period were not included in the calculation). The RPR, an analogy of relative growth rate, was calculated as the annual above-ground production divided by the total mass (stem mass + initial standing leaf mass) in 2011. According to classical growth analysis, RPR was expressed as the product of NAR (annual production per leaf area) and LAR (leaf area per above-ground vegetative mass). For the leaf area in *F. crenata*,

the initial LAI was used. LMR was also calculated as leaf mass per unit of above-ground vegetative mass.

Light use efficiency was calculated as annual production per unit of relative absorbed light, assuming that the canopy irradiance was identical among the studied plots. The relative absorbed light was calculated from the LAI, assuming Beer's law for light extinction in the canopy. For *F. crenata*, the canopy duration was considered for the calculation, that is, the amount of absorbed light was lower when the canopy duration was shorter.

Leaf-level NUE was calculated as annual production per unit of annual N allocated to leaves (Yasumura et al., 2002). Assuming a steady-state N cycle in the plants, the amount of N allocated annually was calculated from the amount of annual leaf litter N. NUE was analysed as the product of LNP (annual production per unit of mean leaf N) and MRT (Berendse & Aerts, 1987; Hikosaka & Hirose, 2001). The MRT was calculated as the mean leaf N divided by annual leaf litter N (Berendse & Aerts, 1987). For *A. mariesii*, the mean leaf N was calculated as the amount of leaf N from the LAI and N_{area} of the top and the bottom leaves, assuming an exponential decrease in N_{area} with cumulative LAI from the top (Hikosaka, 2016; Hirose & Werger, 1987). For *F. crenata*, not only N in the leaves but also N resorbed from senescing leaves was considered (Figure S3; Yasumura et al., 2002). N in leaves was calculated as for *A. mariesii*, and resorbed N was calculated from the N in leaf litter and R_{N} . We assumed that resorbed N accumulates in the stems during winter and is used for leaf production in spring. Plants absorb N from roots in spring and allocate it to the leaves, where the amount is the same as the N lost in leaf litter.

For *F. crenata*, the canopy duration was defined as the period when canopy leaves were present (Figure S3). The net assimilation rate and leaf N productivity during this period (NAR_{cd} and LNP_{cd}) were calculated as NAR and LNP divided by the canopy duration respectively.

2.5 | Statistical analyses

All statistical analyses were performed using R version 3.4.3 (R Core Team, 2017). The effects of independent variables on the variables for leaf traits, productivity and efficiency for *F. crenata* and *A. mariesii* were evaluated with a linear mixed-effects model (LMM) using the *lmer* function of the *LME4* package.

The dependent variables estimated from leaves sampled from the canopy ('Leaf variables'; $n = 2-5$) included LMA, N_{mass} and N_{area} for *F. crenata*, and LMA, N_{mass} , N_{area} and LLS for *A. mariesii*. For those variables, the effects of altitude (m), or altitude and stem mass (stem biomass per ground area; g/m^2), and their interaction with leaf position (bottom against top) were evaluated with plot ID/tree ID as a random factor. The dependent variables estimated from the litter traps ('Trap variables'; $n = 5$) included LLS, LAI, MRT and R_{N} for *F. crenata*, and LAI, MRT and R_{N} for *A. mariesii*. For these variables, the effects of altitude or altitude and stem mass were evaluated with plot ID as a random factor. The dependent variables estimated from

the plot ('Plot variables'; $n = 1$) included NPP, RPR, NAR, NAR_{cd} , LAR, LMR, LUE, NUE, LNP and LNP_{cd} for *F. crenata*, and NPP, RPR, NAR, LAR, LMR, LUE, NUE and LNP for *A. mariesii*. For those variables, the effects of altitude or altitude and stem mass were evaluated with line ID (A or B) as a random factor.

The log-transformed and non-transformed values for all dependent variables were tested. The best model was selected based on the lowest Akaike information criterion (AIC) value for each dependent variable, and the significance of the independent variables was tested by a type-II likelihood-ratio test using the ANOVA function in the *CAR* package.

Principal component analysis (PCA) was performed using the averaged values of all the obtained variables described above for each of *F. crenata* and *A. mariesii* in each plot. Thus, LMA_{T} , LMA_{B} , N_{massT} , N_{massB} , N_{areaT} , N_{areaB} , LLS, LAI, MRT, R_{N} , NPP, RGR, NAR, NAR_{cd} , LAR, LMR, LUE, NUE, LNP and LNP_{cd} were included for *F. crenata*. LMA_{T} , LMA_{B} , N_{massT} , N_{massB} , N_{areaT} , N_{areaB} , LLS_{T} , LLS_{B} , LAI, MRT, R_{N} , NPP, RPR, NAR, LAR, LMR, LUE, NUE and LNP were included in the PCA for *A. mariesii*. Here subscripts T and B indicate the top and bottom of the canopy respectively. For the scores of the first three PC axes, the effects of altitude or altitude and stem mass were evaluated with line ID as a random factor with LMM, as mentioned above.

3 | RESULTS

3.1 | Leaf traits

In both *F. crenata* and *A. mariesii*, the LMA, N_{mass} and N_{area} were influenced by the canopy position; the bottom leaves had lower LMA and N_{area} and higher N_{mass} than the top leaves (Figure 2; Table 2). In *F. crenata*, the LMA, N_{mass} and N_{area} rose significantly with increasing altitude, whereas the LLS decreased due to the shortened growing season. In *A. mariesii*, the LMA significantly decreased with increasing altitude, but the LLS showed no altitudinal change. The influence of altitude on N_{mass} was not significant for the top branches, but the interaction between altitude and canopy position was significant. The N_{mass} in the bottom branches tended to decrease with altitude. As the N_{area} is a product of LMA and N_{mass} , it was also affected by the interaction between altitude and canopy position; the N_{area} in the top branches showed a marginally significant decrease with increasing altitude.

If the intraspecific variation is consistent with the LES, leaves with higher LMA would have lower N_{mass} and longer LLS (Wright et al., 2004). However, relationships found in the two species was not consistent with the LES except for the negative correlation between the N_{mass} and LMA in the top leaves of *A. mariesii* ($r^2 = 0.70$, $p < 0.05$). For example, the LLS did not correlate with other leaf traits in *A. mariesii* and negatively correlated with the LMA in the top leaves of *F. crenata* ($r^2 = 0.47$, $p < 0.1$), the latter of which was opposite to the positive relationship found in the LES. These results suggest that the intraspecific variation in leaf traits found in this study is inconsistent with the LES.

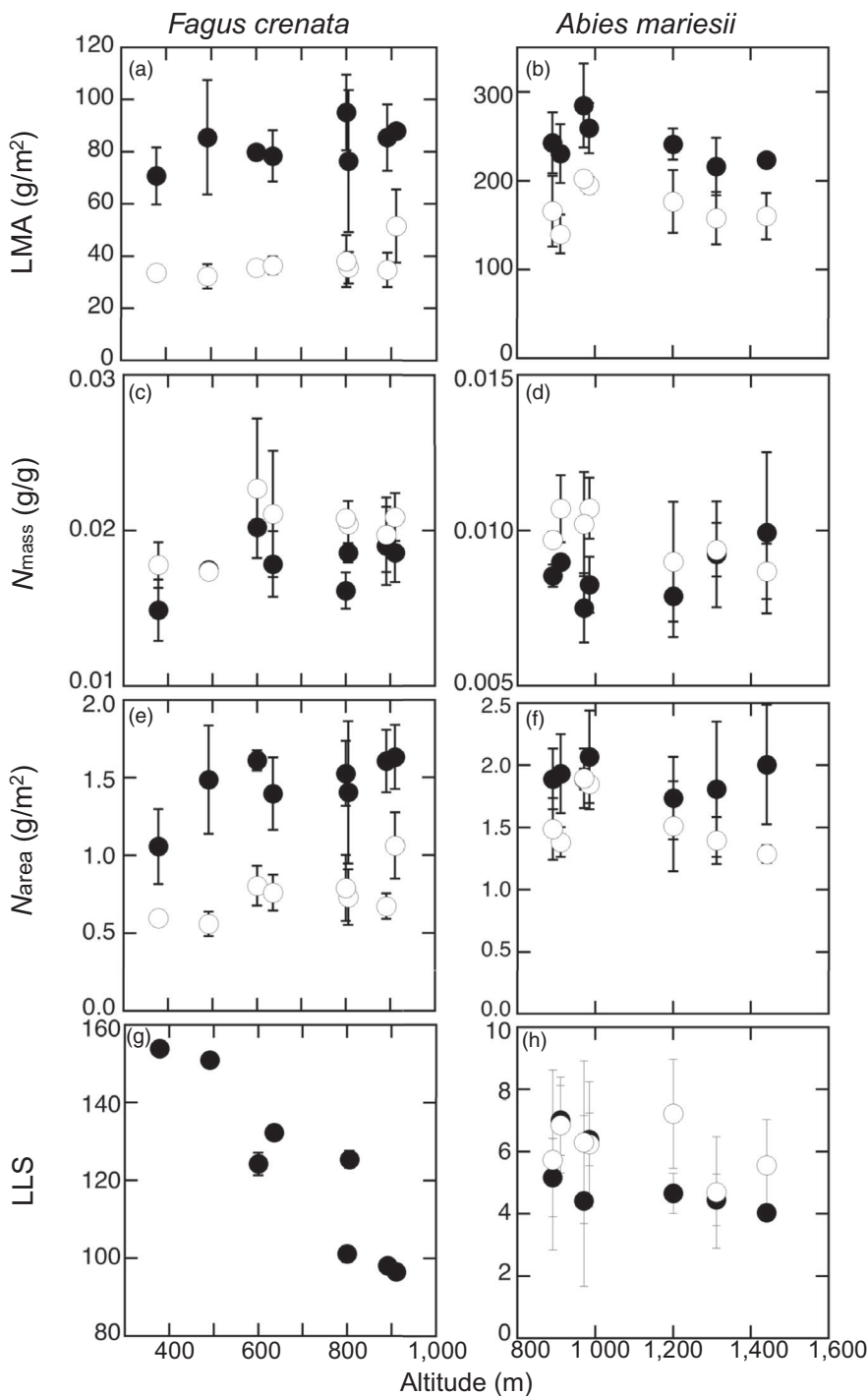


FIGURE 2 Altitudinal dependence of four traits in living leaves of *Fagus crenata* (a, c, e, g) and *Abies mariesii* (b, d, f, h). (a, b) Leaf mass per area (LMA); (c, d) leaf nitrogen concentration per unit leaf mass (N_{mass}); (e, f) leaf nitrogen concentration per unit leaf area (N_{area}); (g, h) leaf life span (LLS). The units of LLS are day and year for *F. crenata* and *A. mariesii* respectively. Closed and open symbols denote top and bottom leaves, respectively, except for LLS in *F. crenata*, which was estimated at a trap level. Bars indicate standard deviation ($n = 2-5$). See Table 2 for statistics

3.2 | Productivity

The stem mass per ground area of the studied species varied among the plots (Table 1), and the NPP of *F. crenata* and *A. mariesii* was strongly related to the total stem mass but not to altitude (Table 2; Figure 3a,b). The RPR was calculated to eliminate the size or abundance effect. In *F. crenata*, the RPR and annual NAR were unrelated to altitude (Figures 3c and 4a; Table 2). This was surprising because the canopy duration was shorter at higher altitudes (Table 1). We also calculated the NAR_{cp} , which was determined from the NAR divided by the canopy duration, and found that it increased significantly with

altitude (Figure 4b). In *A. mariesii*, the RPR decreased with altitude (Figure 3d), which was ascribed to a marginally significant decrease in both the NAR and LAR (Table 2).

3.3 | Resource use efficiencies

LUE was calculated, assuming that irradiance above the canopy was identical among the plots. LUE significantly increased and decreased with altitude in *F. crenata* and *A. mariesii* respectively (Figure 3e,f, Table 2).

TABLE 2 Results of multiple or single regression analysis with a linear mixed model for traits, productivity and efficiency in *Fagus crenata* and *Abies mariesii* trees, as a function of altitude, stem mass and leaf position. Coefficients of the regression, chi-square of the analysis of deviance with significance (ns, not significant; +, $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$) and Akaike information criterion (AIC) values are shown (coefficients are expressed in bold if $p < 0.05$). We tested four models: the dependent variables and stem mass are normal or log-transformed (when the dependent variable is log-transformed, stem mass is also log-transformed), and stem mass is included or not as an independent variable. We selected the best model according to the AIC value. In the full model for leaves sampled from the canopy ('Leaf variables'), independent variables are the leaf variables, altitude (Altitude; m), stem mass per ground area (Stem; g/m²), leaf position (Position; lowermost against uppermost), the interaction of altitude (A) and leaf position (P), and the interaction of stem mass (S) and leaf position. In the full model for variables obtained from the litter trap data ('Trap variables') and those from the plot data ('Plot variables'), the independent variables are altitude and stem mass

Species	Coefficient						Chi-square					AIC
	Intercept	Altitude	Stem	Position	A × P	S × P	Altitude	Stem	Position	A × P	S × P	
<i>Fagus crenata</i>												
Leaf variables												
log LMA	0.903	0.120	–	-1.81	0.0288	–	4.42*	–	287***	0.0714 ^{ns}	–	51.0
log N_{mass}	-1.75	0.0171	–	0.0526	0.0011	–	3.86*	–	15.5***	0.0066 ^{ns}	–	-126
log N_{area}	0.844	0.223	-0.114	-1.69	0.0380	-0.583	11.4***	0.0375*	203***	0.099 ^{ns}	0.340 ^{ns}	64.3
Trap variables												
LLS	3.50	-0.00507	–	–	–	–	53.8***	–	–	–	–	-44.8
log LAI	0.271	-0.00039	0.6633	–	–	–	0.166 ^{ns}	14.0***	–	–	–	92.5
MRT	0.447	-0.00065	–	–	–	–	0.166 ^{ns}	–	–	–	–	99.6
R_N	-0.284	0.000412	–	–	–	–	0.691 ^{ns}	–	–	–	–	102
Plot variables												
log NPP	0.179	-0.00026	0.756	–	–	–	0.048 ^{ns}	10.8***	–	–	–	24.7
RPR	0.217	-0.00031	–	–	–	–	0.030 ^{ns}	–	–	–	–	29.6
NAR	0.728	-0.00106	–	–	–	–	0.349 ^{ns}	–	–	–	–	29.3
log NAR_{cd}	-2.21	0.00321	–	–	–	–	5.01*	–	–	–	–	25.7
LAR	0.413	-0.00060	–	–	–	–	0.114 ^{ns}	–	–	–	–	29.5
LMR	-0.400	0.000581	-0.563	–	–	–	0.157 ^{ns}	4.28*	–	–	–	28.3
log LUE	-2.06	0.002911	0.578	–	–	–	6.00*	6.32*	–	–	–	24.7
NUE	2.17	-0.00314	–	–	–	–	4.69*	–	–	–	–	25.9
LNP	1.43	-0.00207	–	–	–	–	2.02 ^{ns}	–	–	–	–	27.6
log LNP_{cd}	-1.20	0.00174	–	–	–	–	1.30 ^{ns}	–	–	–	–	28.3
Principal component analysis												
log PC1	-0.000	-1.09	–	–	–	–	2.57 ^{ns}	–	–	–	–	42.2
PC2	-0.000	-1.83	–	–	–	–	11.45*	–	–	–	–	35.6
log PC3	0.000	0.170	–	–	–	–	0.051 ^{ns}	–	–	–	–	41.2
<i>Abies mariesii</i>												
Leaf variables												
LMA	0.741	-0.302	0.340	-1.51	0.151	-0.0055	6.08*	12.3***	125***	1.17 ^{ns}	0.002 ^{ns}	74.3
log N_{mass}	-0.408	0.394	-0.310	0.846	-0.745	0.450	0.130 ^{ns}	0.249 ^{ns}	22.8***	14.5***	5.51*	106
log N_{area}	0.491	-0.0555	0.0559	-1.01	-0.466	0.457	3.67 ⁺	4.07*	24.2***	4.51*	4.45*	103
LLS	-0.261	-0.343	–	0.545	0.195	–	2.23 ^{ns}	–	5.68*	0.700 ^{ns}	–	114
Trap variables												
log LAI	-0.738	0.00067	0.276	–	–	–	0.648 ^{ns}	2.68 ^{ns}	–	–	–	104
log MRT	2.72	-0.00247	–	–	–	–	3.05 ⁺	–	–	–	–	70.9
log R_N	2.02	-0.00183	–	–	–	–	1.96 ^{ns}	–	–	–	–	90.9

(Continues)

TABLE 2 (Continued)

Species	Coefficient						Chi-square					
	Intercept	Altitude	Stem	Position	A × P	S × P	Altitude	Stem	Position	A × P	S × P	AIC
Dependent variables												
Plot variables												
NPP	0.805	-0.00073	0.949				1.39 ^{ns}	50.1 ^{***}				14.1
RPR	2.52	-0.00229	-0.553				4.57*	5.73*				21.7
NAR	0.671	-0.00057	0.892				3.31 ⁺	167 ^{***}				9.5
LAR	1.74	-0.00158	-0.741				3.13 ⁺	14.7 ^{***}				19.2
LMR	2.15	-0.00196	-0.734				6.58*	19.9 ^{***}				17.0
LUE	0.866	-0.000785	0.985				4.11*	138 ^{***}				7.7
NUE	1.75	-0.00160	0.960				12.5 ^{***}	97.1 ^{***}				9.6
LNP	-0.104	0.000134	0.846				0.101 ^{ns}	83.9 ^{***}				13.0
Principal component analysis												
PC1	0.0251	-0.110	2.78				0.05 ^{ns}	34.3 ^{***}				31.9
PC2	-0.104	-1.88	0.838				34.6 ^{***}	6.68 ^{**}				29.4
PC3	-0.000	0.228	—				0.16 ^{ns}	—				32.4

Note: LMA, leaf mass per area (g/m²); N_{mass} , leaf nitrogen concentration per dry mass (g/g); N_{area} , leaf nitrogen content per leaf area (g/m²); LLS, leaf life span (year and day for *A. mariesii* and *F. crenata* respectively); LAI, leaf area index (m²/m²; value at season beginning for *F. crenata*); MRT, mean residence time of nitrogen in the leaves (year); R_N , nitrogen resorption efficiency (no dimension); NPP, net primary production per ground area (g m⁻² year⁻¹); RPR, relative production rate (year⁻¹); NAR, net assimilation rate per leaf area (g m⁻² year⁻¹); NAR_{cd} , net assimilation rate in the canopy duration (g m⁻² year⁻¹); LAR, leaf area ratio (×1,000 m²/g); LMR, leaf mass ratio (no dimension); LUE, light use efficiency (g m⁻² year⁻¹); NUE nitrogen use efficiency (year⁻¹); LNP, annual leaf nitrogen productivity (g g⁻¹ N year⁻¹); LNP_{cd} , LNP in the canopy duration (g g⁻¹ N year⁻¹). Note that LMA, N_{mass} and N_{area} for *A. mariesii* are the weighted mean of survival leaves with different leaf age class.

Leaf-level NUE decreased significantly with altitude in both *A. mariesii* and *F. crenata* (Figure 3g,h; Table 2). In *A. mariesii*, the LNP was not related to altitude, whereas the MRT exhibited a marginally significant decrease with altitude, suggesting that the decreased NUE was ascribed to the MRT rather than the LNP (Figure 5; Table 2). The coefficient of altitude for the LLS and R_N was negative but not significant in *A. mariesii* (Figure 5; Table 2). In *F. crenata*, although the MRT, LNP and R_N were not significantly related to altitude (Table 2; Table S1), NUE might be decreased with altitude due to the negative coefficients for MRT and LNP against altitude.

3.4 | Principal component analysis

In *F. crenata*, principal component axes 1, 2 and 3 (PC1, 2 and 3) explained 33.5, 25.5 and 23.2% of the total variation respectively. Whereas altitude had no significant correlation with PC1 and PC3 ($p < 0.1$), it had a significantly positive correlation with PC2 ($p < 0.05$; Table 2), suggesting that the upper side in Figure 6a is oriented to higher altitude. PC1, 2 and 3 were not correlated with the stem mass (Table 2). The NAR, LNP, NAR_{cd} , LNP_{cd} and NUE had highly positive loadings (>0.5) along PC1, whereas the N_{massT} , N_{areaT} , R_N , MRT, LAR and LMR had negative loadings (<-0.5; Figure 6a). The N_{massB} , N_{areaT} , N_{areaB} , LMA_T , LMA_B , NAR_{cd} , LNP_{cd} and LUE had positive loadings along PC2, whereas the LLS had a negative loading (Figure 6a).

In *A. mariesii*, PC1, 2 and 3 explained 48.6, 26.2 and 12.1% of the total variation respectively. PC1 was strongly correlated with

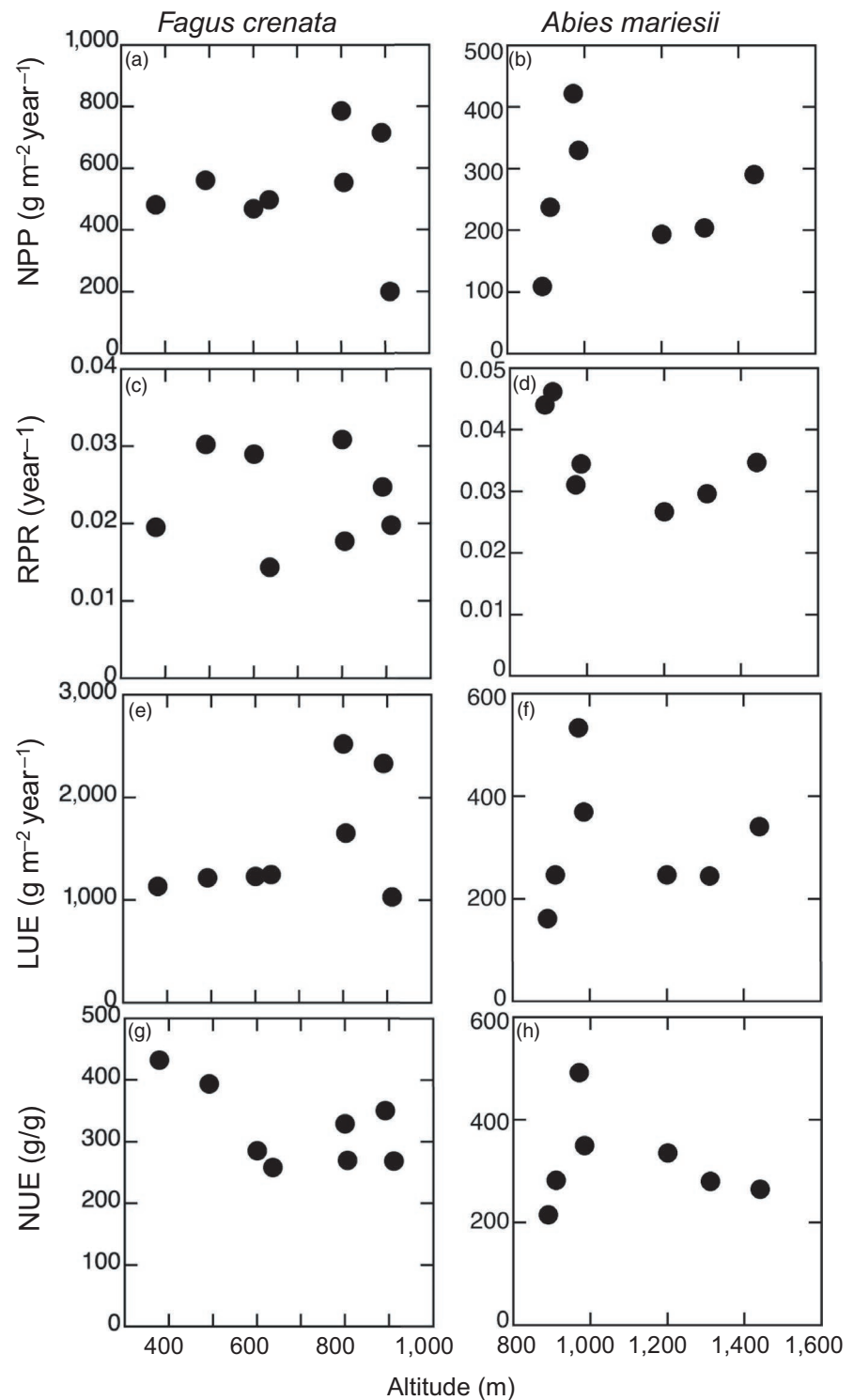
the stand stem mass (Table 2), suggesting that this axis was related to the abundance or size of the trees. PC2 was negatively related to altitude. PC3 was not related to altitude or stem mass. PC1 was strongly related to most of the variables, except the N_{mass} and LLS of the bottom branches and the N_{area} of the top branches (Figure 6b). The MRT, LLS, R_N , LAI, N_{mass} and N_{area} of the bottom branches, and LMA of the top branches had highly positive loadings on PC2, suggesting that they tended to have higher values at lower altitudes, whereas the N_{mass} of the top branches had a negative loading.

4 | DISCUSSION

4.1 | Leaf traits, productivity and resource use efficiency

Leaf trait alterations have been considered an important strategy in adapting to changes in habitat environment. Traits related to fast-return on investment of carbon (C) and N may contribute to higher growth rates in productive or fertile environments. In contrast, those related to slow-return on investment may contribute to a longer residence time of resources in the plant body. Since lower temperatures and shorter growing seasons constrain plant growth at higher altitudes, plants may acclimate or adapt to such environments by the slow-return strategy (Hypothesis 1), where a longer LLS and/or MRT compensate for a lower potential growth rate (Aerts & Chapin, 2000; Berendse & Aerts, 1987). However, in *F. crenata*, the LMA, N_{mass}

FIGURE 3 Altitudinal dependence of productivity and resource use efficiency in *Fagus crenata* (a, c, e, g) and *Abies mariesii* (b, d, f, h). (a, b) Annual above-ground production per unit ground area (NPP); (c, d) Relative production rate (RPR, annual above-ground production per unit above-ground mass); (e, f) light use efficiency (LUE, annual above-ground production per unit relative absorbed light); (g, h) leaf-level nitrogen use efficiency (NUE, annual above-ground production per unit annual nitrogen allocated to leaves). See Table 2 for statistics



and N_{area} increased with altitude, and this trend is not necessarily consistent with the LES. Rather, this trend seems similar to acclimation to high irradiance or low temperature; indeed, a meta-analysis showed that LMA generally increases with increasing irradiance and decreasing temperature (Poorter et al., 2009). Our results are also consistent with previous field observations for different populations of tree species, in that LMA increases with a decrease in the minimum temperature in winter across latitudes or altitudes (González-Zurdo et al., 2016; Jankowski et al., 2017). Muller et al. (2005) also

reported an increase in N_{area} of an evergreen shrub in winter. Hence, altitudinal trends in leaf trait variations of *F. crenata* may partly result from acclimation or adaptation to a cooler environment.

The environmental dependence of N_{area} is explained by the optimality theory. The daily C gain per unit of leaf N (daily PNUE) shows a convex curve against N_{area} , and there is an optimal N_{area} (N_{opt}) that maximizes the daily PNUE (Hikosaka & Terashima, 1995; Hirose & Werger, 1987). The N_{opt} increases with increasing irradiance because a higher N_{area} contributes to increasing the photosynthetic rate

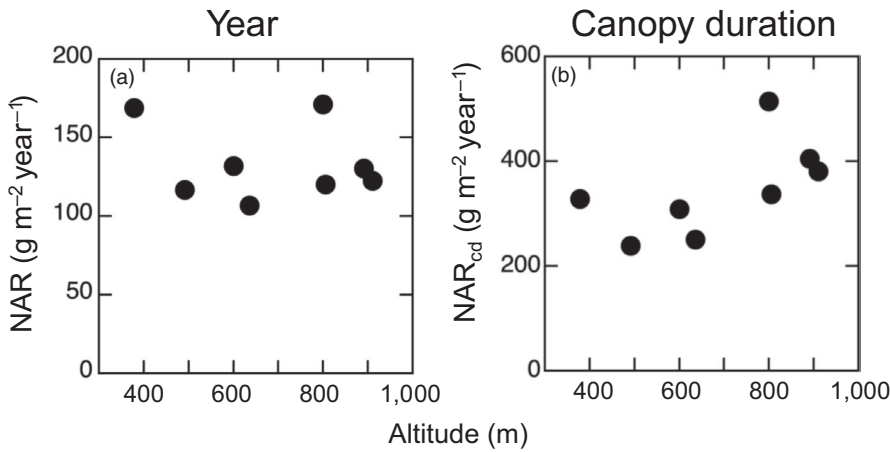


FIGURE 4 Altitudinal dependence of net assimilation rates in *Fagus crenata*. (a) Net assimilation rate (NAR, annual above-ground production per unit leaf area); (b) net assimilation rate for the canopy duration (NAR_{cd}, NAR divided by relative canopy duration). See Table 2 for statistics

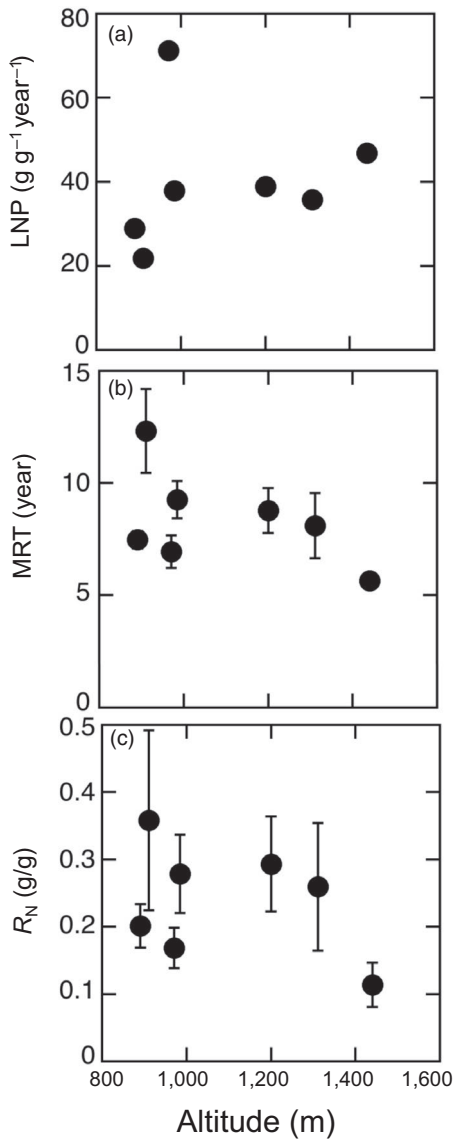


FIGURE 5 Altitudinal dependence of components of nitrogen use efficiency in *Abies mariesii*. (a) leaf nitrogen productivity (LNP, annual above-ground production per unit leaf nitrogen); (b) mean residence time of leaf nitrogen (MRT); (c) nitrogen resorption efficiency (R_N). Bars in b and c indicate standard deviation ($n = 5$). See Table 2 for statistics

only at higher light intensity (Hikosaka & Terashima, 1995; Hirose & Werger, 1987). N_{opt} increases with decreasing temperature to compensate for the decreased instantaneous PNUE (Muller et al., 2011). This theory explained the seasonal variation in the N_{area} of an understory evergreen shrub grown under different light regimes (Muller et al., 2011). Therefore, the increase in N_{area} in *F. crenata* at higher altitudes might contribute to the increase in PNUE at the respective habitat.

Surprisingly, despite the shorter growing season at higher altitudes, *F. crenata* exhibited a similar RPR across altitudes. This might have been made possible by an increasing NAR_{cd}, indicating that productivity in the growing season was greater at higher altitudes. This may be explained partly by an increase in N_{area} with altitude, because there is a positive correlation between photosynthetic capacity and N_{area} within species, including *F. crenata* (Evans, 1989; Hikosaka, 2004; Yasumura et al., 2005). This is consistent with the PCA result, in which NAR_{cd}, LMA and N_{area} were positively related to PC2 (Figure 6a). Therefore, Hypothesis 2 may apply to the intraspecific variations in *F. crenata* associated with the altitude gradient. Increasing LMA and N_{area} with altitude might contribute to increases in both productivity and LUE in the growing season at higher altitudes, leading to similar levels of annual productivity, irrespective of the growing season length. The improved productivity would be beneficial for competition in the mixed zone with other species such as *A. mariesii*.

In *A. mariesii*, the altitudinal dependence of leaf traits was also inconsistent with the LES; the LMA decreased with altitude and other traits had no clear altitudinal trend. Our results suggest that, at higher altitudes, *A. mariesii* plants did not have a fast-return strategy; the RPR and NAR were lower at higher altitudes, suggesting that the lower LMA did not relate to an increase in photosynthetic capacity. Although lower photosynthesis or growth rates occur in species inhabiting infertile environments (Poorter & Remkes, 1990; Wright et al., 2002), such species generally have a longer LLS and longer nutrient residence time (Aerts & Chapin, 2000; Berendse & Aerts, 1987; Reich et al., 1991). The PCA results indicated that most variables had either higher values at lower altitudes (higher PC2 loadings) or no altitudinal trend (Figure 6b). Exceptionally, the N_{mass} of the top branches had a negative loading. Still, its correlation with altitude was not significant, and its contribution was insufficient to compensate for the decrease in LMA, that is, N_{area} ,

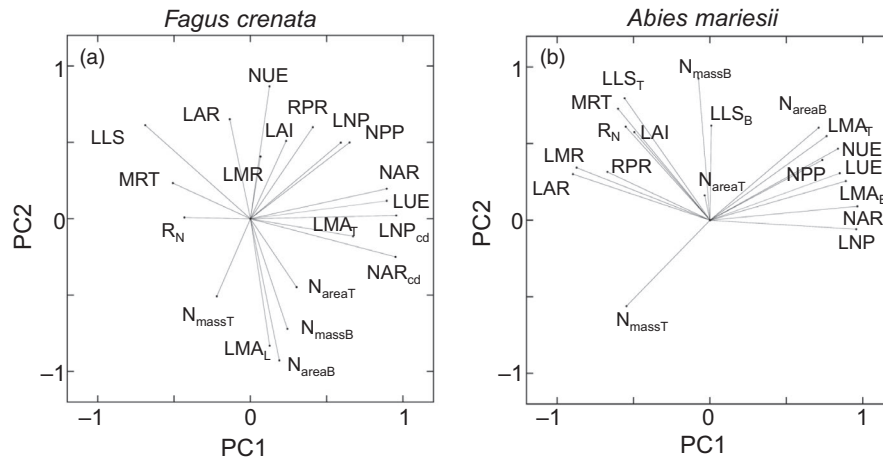


FIGURE 6 Principal component analysis of leaf traits and components of productivity and resource use efficiencies. Vectors representing the trait coefficients on the principal component axis 1 (PC1) and 2 (PC2). (a) *Fagus crenata*, (b) *Abies mariesii*. LMA, leaf mass per area; N_{mass} , leaf nitrogen concentration per dry mass; N_{area} , leaf nitrogen content per leaf area; LLS, leaf life span; LAI, leaf area index; MRT, mean residence time of nitrogen in the leaves; R_N , nitrogen resorption efficiency; RPR, relative production rate; NAR, net assimilation rate; NAR_{cd} , net assimilation rate for the canopy duration; LAR, leaf area ratio; LMR, leaf mass ratio; LUE, light use efficiency; NUE, nitrogen use efficiency; LNP, annual leaf nitrogen productivity; LNP_{cd} , leaf nitrogen productivity for the canopy duration. The subscripted T and B denote top and bottom leaves respectively

which is the product of LMA and N_{mass} , was also lower at higher altitudes (Table 2). Therefore, *A. mariesii* does not realize any improvement in productivity, resource use efficiency or conservation of acquired resources by the alteration of leaf traits (Hypothesis 3).

In the Hakkoda mountain range, the canopy leaves of *A. mariesii* are exposed to wind stress. Nakamoto et al. (2013) reported that, on Mt. Norikura, central Japan, the leaves of *A. mariesii* that are not covered by a snowpack during winter often become brown and die in early spring, suggesting that winter stress can cause leaf death. Furthermore, Nagano et al. (2009) reported that the leaf traits of an alpine evergreen shrub *Pinus pumila* (Pall.) Regel were different between plants growing in wind-exposed and wind-protected areas (both 2,770 m a.s.l.) on Mt. Norikura. They found that plants at the wind-exposed site had a lower LMA, higher photosynthetic capacity, and shorter LLS than plants at the wind-protected site. Nagano et al. (2009) discussed that *P. pumila* at the wind-exposed sites produced low-cost needles with high productivity to compensate for the short LLS, which may be imposed by wind stress when the needles appear above the snow surface in winter. Therefore, in too severe environment where the LLS is short, a slow-return strategy may no longer be effective. If this is also the case for *A. mariesii*, the altitudinal gradient of leaf traits results from the negative impact of environmental stress.

The length of growing season decreases with altitude, which has been considered as an important selecting pressure (Kikuzawa & Kudo, 1995; Kudo, 1992). In snow-bed areas with different snow-melt period lengths, the LLS of evergreen species is longer when the snow-melt period decreases, whereas that of deciduous species is shorter (Kudo, 1992), which was consistent with a cost-benefit model of LLS (Kikuzawa & Kudo, 1995). In the present study, similar trend was found in *F. crenata*, in which LLS was shorter at higher altitude. However, LLS of *A. mariesii* was not longer at higher altitude, which is inconsistent with that of evergreen plants in the snow-bed.

Furthermore, LMA of deciduous plants in the snow-bed was smaller in shorter snow-melt period (Kudo, 1992), whereas that of *F. crenata* was higher at higher altitude in the present study. Therefore, the length of growing season might have some influence, but not be a dominant selecting pressure in our plants.

4.2 | Implications for current and future distribution

Our results showed that *F. crenata* maintains productivity and resource use efficiency, even at its highest altitude limit. Does this mean that low temperature is not a limiting factor for its growth and distribution? Matsui, Yagihashi, Nakaya, Tanaka, et al. (2004) studied the climatic regulation *F. crenata* distribution, using classification tree analysis, and showed that winter precipitation is the most influential factor, followed by the warmth index (cumulative monthly temperature above 5°C), the minimum temperature of the coldest month, and summer precipitation. According to their results, the lower limit of the warmth index for *F. crenata* distribution is c. 40. At our study site, the warmth index was higher than 40 at 1,200 m a.s.l., where *F. crenata* is not currently distributed. Therefore, *F. crenata* has not reached its temperature limitation and might spread towards higher altitudes. Analysing past aerial photographs, Shimazaki et al. (2011) found that the population density of *A. mariesii* is decreasing at its lowest altitude, where it is mixed with *F. crenata* and other deciduous species. This may imply that *A. mariesii* has retreated from lower altitudes as a result of competition with *F. crenata*. In the Hakkoda mountain range, the air temperature has increased by 0.8°C over the past three decades (Shimazaki et al., 2011) and is likely to increase further in the future (Matsui, Yagihashi, Nakaya, Taoda, et al., 2004). Future global warming may, therefore, accelerate the upward shift in *F. crenata* distribution.

In contrast to *F. crenata*, altitudinal variations in leaf traits of *A. mariesii* do not improve productivity or resource use efficiency. This result suggests that *A. mariesii* is not necessarily adaptive to high-altitude environments. However, the analysis of aerial photographs revealed that the population density of *A. mariesii* has increased at higher altitudes over three decades; that is, its distribution has shifted upwards (Shimazaki et al., 2011). This analysis also revealed that *A. mariesii* dominates in the peripheral areas of moorlands, which is an infertile habitat, but its growth rate in these areas was lower than that in other areas (Shimazaki et al., 2011). Therefore, the growth rate or productivity of *A. mariesii* does not necessarily explain its distribution. *A. mariesii* may occupy a niche into which other tree species cannot invade, such as higher altitude areas. This may be realized by some physiological adjustment, rather than by alterations in leaf traits. These points suggest that it may be difficult to predict the future distribution of a species solely from leaf traits or productivity. Physiological tolerance and competitive ability may also need to be incorporated into the analysis.

5 | CONCLUSIONS

Altitudinal gradients in the leaf traits of *A. mariesii* and *F. crenata* oppose each other. The LMA and N_{area} of *F. crenata* increase at higher altitudes, which should contribute to improving productivity and light use efficiency in the growing season and, in turn, to maintaining productivity despite the shorter growing season. On the other hand, the LMA and LLS of *A. mariesii* decrease with rising altitude, probably due to environmental constraints such as wind. There is no compensatory change in leaf traits, and both relative productivity and NUE decrease with altitude in *A. mariesii*. These differences between the two species may be due in part to the difference in environmental harshness; *A. mariesii* is distributed in an area affected by more severe conditions than *F. crenata*, and its leaves may be constrained strongly by the environment, especially in winter. *A. mariesii* is tolerant to such harsh stresses but does not necessarily show superior performance. If the environment becomes milder due to global warming, *A. mariesii* may retreat from lower altitudes due to competition with species that show better levels of performance, such as *F. crenata*, and its distribution will shift upward.

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AUTHORS' CONTRIBUTIONS

K.H., T.N. and H.K. designed the research; H.K., T.N., T.A. and H.O.T. conducted fieldworks; T.A., S.T. and S.N. conducted sample determinations; K.H. and H.K. performed data analyses and wrote the manuscript with input from other authors.

DATA AVAILABILITY STATEMENT

Data used in the analyses are presented on Dryad <https://doi.org/10.5061/dryad.xwbrv1cq> (Hikosaka et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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