

PDF issue: 2025-02-15

# Intraspecific variation in growth-related traits—from leaf to whole-tree—in three provenances of Cryptomeria japonica canopy trees grown in a common garden

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(Citation)

Ecological Research, 38(1):83-97

(Issue Date) 2023-01

(Resource Type) journal article

(Version) Accepted Manuscript

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This is the peer reviewed version of the following article: [Azuma, W. A., Kawai, K., Tanabe, T., Nakahata, R., & Hiura, T. (2023). Intraspecific variation in growthrelated traits—from leaf to whole-tree—in three provenances of Cryptomeria japonica canopy trees grown in a common garden. Ecological Research, 38(1), 83-97.], which ha…

# (URL)

https://hdl.handle.net/20.500.14094/0100478239



1	Special features "Functional biogeography: Lessons from the geographic variations in
2	the most dominant tree species in Japan"
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5	provenances of Cryptomeria japonica canopy trees grown in a common garden
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#### 26 Abstract

27 To elucidate the physiological and morphological factors underlying intraspecific variation in growth rate, we examined the variation in leaf and whole-tree traits for three 28 29 geographical variations of ca. 45-year-old Japanese cedar (*Cryptomeria japonica* D. Don) with contrasting heights and radial growth in a common garden. Traits that reflect leaf-30 31 level photosynthesis, water relations, and whole-tree level crown structure in relation to light use and hydraulic architecture were measured. Overall, intraspecific variation in 32 growth characteristics in field-grown adult trees was regulated by whole-tree properties 33 34 rather than leaf properties. Most leaf traits were similar among provenances. Nevertheless, the leaf traits exhibited highest maximum net photosynthetic rate, dark respiration rate, 35 36 and light compensation point in provenances whose native habitats are most similar to 37 the common garden in the present study. Together with previous reports that this provenance has higher root nutrient acquisition capacity than the other two provenances, 38 39 it can be said that organ-level resource use strategies are coupled in a tandem manner. At the whole-tree level, hydraulic architecture-as explained by axial variation in the 40 41 hydraulically-weighted tracheid diameter-can be linked to leaf distribution with respect 42 to light use strategies as well as water transport capacity, leading to differences in growth characteristics among provenances. The study of intraspecific variation in growth 43

48	<b>Keywords:</b> xylem anatomy, functional trait, photosynthesis, transpiration, hydraulic
47	
46	climate change in each habitat.
45	indicator for predicting changes in growth potential and forest dynamics in response to
44	characteristics in trees with a wide range of native habitats is expected to be a useful

49 architecture

#### 50 Introduction

The patterns and mechanisms of tree growth have long been the core research topics in 51 tree physiology. The rate of tree growth is influenced by 1) the inherited characteristics 52 53 of trees, such as size, phenology, and physiological properties (e.g., Kitajima 1994; Moreira et al. 2014; Obeso 2002; Poorter and Remkes 1990); 2) the surrounding abiotic 54 and biotic factors, such as light availability, mycorrhizal symbiosis, and herbivore 55 pressure (Coley and Barone 1996; Montgomery and Chazdon 2002; Wu and Xia 2006); 56 and 3) their interactions (Nabeshima et al. 2010). To understand the mechanisms 57 underlying the variation in the growth rate of trees, Hunt (1978) introduced the concept 58 of growth analysis, where dry mass-based relative growth rate (RGR) is expressed as the 59 net assimilation rate (NAR) multiplied by the leaf area ratio (LAR, total leaf area per unit 60 61 whole-plant mass). This equation indicates that tree growth is governed by both leaf-level photosynthetic rate and whole-tree carbon allocation. Therefore, it is expected that any 62 plant traits (physiological and morphological characteristics) influencing NAR and LAR 63 could potentially cause variation in growth rate. 64 .

65	Water transport from the roots to leaves is a major determinant of photosynthetic
66	capacity—and thus possibly NAR—because CO2 absorption inevitably induces water
67	loss due to transpiration (Brodribb 2009; Sperry 2003). Previous studies have

68	demonstrated that organ-level hydraulic conductivity strongly influences the maximum
69	photosynthetic rate (Brodribb and Feild 2000; Santiago et al. 2004) and growth rate (Fan
70	et al. 2012; Hietz et al. 2017; Poorter et al. 2010). Hydraulic conductivity is governed by
71	the morphology, dimensions (particularly the diameter), and spatial arrangements of the
72	conducting elements (vessels and tracheids) (Hacke et al. 2017; Tyree and Zimmermann
73	2002). The diameter of conducting elements varies according to tree size (Olson et al.
74	2014), environmental gradients (Arenas-Navarro et al. 2021, Zheng et al. 2022), and
75	position within trees (Petit et al. 2008; Spicer and Gartner 2001). The latter factor
76	determines the pattern of accumulation of hydraulic resistance along tree height, thus
77	influencing whole-tree hydraulic conductivity, especially in large trees (Liu et al. 2019).
78	Theoretical (Enquist 2003; West et al. 1999) and empirical (Anfodillo et al. 2006, 2013;
79	Olson et al. 2018; Williams et al. 2019) studies have shown that the diameter of
80	conducting elements increases from the stem tip to the base as $D = \alpha L^{\beta}$ , where D is the
81	conduit diameter, L is the distance from the tree apex, and $\alpha$ and $\beta$ are coefficients. This
82	increase in diameter possibly mitigates the negative effects of accumulating hydraulic
83	resistance on tree growth and photosynthesis (Ryan and Yoder 1997). Here, if $\beta \ge 0.20$ ,
84	metabolic theory predicts that accumulated hydraulic resistance would be nearly
85	independent of $L$ ; in such cases, trees can maintain their metabolism with an increase in

86	height (Enquist 2003; West et al. 1999). Accordingly, the variations in $\alpha$ and $\beta$ should
87	reflect the differences in whole-tree hydraulic architecture, and thus the growth rate
88	(Rosell et al. 2017).
89	In addition to leaf-level photosynthetic capacity, the LAR also affects the RGR
90	of trees (Givnish 1988; Kitajima 1994; Poorter and Remkes 1990). The LAR can be
91	further decomposed into specific leaf area (SLA) multiplied by the leaf mass fraction
92	(LMF, leaf mass per unit whole-tree mass). Therefore, both leaf morphology and carbon
93	allocation to leaves influence the LAR. Leaf dry mass per area (LMA, the inverse of SLA)
94	is often negatively correlated with RGR across species (e.g., Gibert et al. 2016; Iida et al.
95	2014; Poorter et al. 2006). With regard to LMF, biomass distribution among organs
96	reflects the volume and density of each organ (leaves, stems, branches, and roots). Large
97	trees (> 1,000 kg) generally allocate most of the biomass (> 70%) to stem wood (Poorter
98	et al. 2015). Therefore, for a given amount of photosynthate and SLA, an increase in wood
99	density at the stem increases biomass allocation to the stem (King et al. 2006), thus
100	reducing LMF and RGR. At the whole-tree level, high allocation of biomass to stems
101	reduces LAR, and thus constrains RGR (Onoda et al. 2014).
102	To date, attempts to identify the traits underlying the RGR of trees in relation to
103	NAR and LAR have focused on interspecific variation, mostly using different

104	phylogenies (e.g., King et al. 2006; Martínez-Vilalta et al. 2010; Poorter and Remkes
105	1990; Wright et al. 2010). However, few studies have dealt with intraspecific variations.
106	Because evolutionary processes do not produce extreme phenotypes at smaller temporal
107	scales, intraspecific trait variation is often similar to or lower than interspecific variations
108	(e.g., Asner et al. 2014; Messier et al. 2010). Investigating such within-species variations
109	requires the following: 1) establishing the evolutionary robustness of trait-growth
110	relationships, and 2) investigating an extensive suite of traits that may contribute to a
111	mechanistic and comprehensive understanding of tree growth (Medeiros et al. 2019).
112	Although the importance of LAR-associated traits (e.g., LMA and wood density) on
113	growth is well appreciated, few studies have examined them together with leaf-level
114	physiological traits, particularly for field-grown large trees. In practical terms, this type
115	of within-species approach is ideal for species that show wide distribution ranges-
116	including heterogeneous resource availabilities-because variation in local environments
117	would cause divergent selections in traits and associated growth rates, providing
118	opportunities to test their evolutionary correlations (Cavender-Bares 2019). The Japanese
119	archipelago is a suitable area for this type of study, as it encompasses a wide
120	environmental gradient that causes high intraspecific variation in phenotypic traits (e.g.,
121	Ishii et al. 2018; Osada et al. 2015; Tateishi et al. 2010).

122	Here, we chose the natural geographical variations of the Japanese cedar
123	(Cryptomeria japonica D. Don), which dominates about 20% (including plantation
124	forests) of Japan's forest area (Forestry Agency of Japan 2011) as a study clade. We
125	examined the intraspecific variations in leaf and whole-tree traits associated with NAR
126	and LAR in relation to their growth rate in a common garden. C. japonica is widely
127	distributed in the Japanese archipelago (from 30°15' N to 40°42' N) and comprises
128	genetically differentiated provenances (Tsumura et al. 2012, 2014) that differ in
129	morphology, growth rate, allometries, and other functional traits (Hiura et al. 2021;
130	Nishizono et al. 2014; Osone et al. 2021). Thus, this species is ideal for testing trait-
131	growth relationships at the intraspecific level. A previous study conducted in the same
132	common garden had shown that the root exudation rate and nutrient status of leaves and
133	roots were higher in provenances with a high growth rate, indicating that adaptive
134	divergence in nutrient-uptake strategies among provenances causes a difference in growth
135	rates (Ohta et al. 2019). Based on this, we tested the prediction that provenances in which
136	leaf and whole-tree traits are associated with high NAR (e.g., high photosynthetic rate,
137	conductive tracheid, and high nitrogen content) and high LAR (e.g., low LMA, low wood
138	density, and high fraction of leaf mass) show high RGR in terms of height and diameter.
139	We measured 25 leaf and whole-tree traits that are associated with NAR and LAR through

140	their influence on the resource use strategies of light, water, and nutrients (e.g., leaf
141	photosynthetic rate, crown structure, and tree hydraulic architecture). Using these data,
142	we compared the traits among three provenances of ca. 45-year-old C. japonica with
143	different genotypes and contrasting RGR grown under the same environment.
144	
145	Methods
146	Study site and plant materials
147	The study was conducted in a common garden of C. japonica established at the
148	Wakayama Experimental Forest of Hokkaido University in Wakayama Prefecture, Japan
149	(33°40' N, 135°40' E, and 240 m above sea level). This forest is covered by a very thin
150	and weakly developed mineral soil without horizon differentiation (Regosol, based on the
151	World Reference Base for Soil Resources) (Kanda et al. 2018). The mean annual
152	precipitation and temperature from 1985 to 2019 were 3,564 mm and 14.7°C, respectively
153	(Japan Meteorological Agency).
154	The common garden was located on a south-facing slope, and the soil color
155	(gray), texture (silt and gravel), and depth (< 10 cm) were uniform across the slope. In
156	the common garden, C. japonica grown in various regions of Japan were planted with
157	similar densities (ca. 2,000 individuals per hectare) between 1967 and 1973. The stand

158	had not been managed after planting until our field survey, and the canopy was closed
159	without any gaps. Here, we used clonal stands of the three provenances that had also been
160	used in Ohta et al. (2019): Yoshino, Yanase, and Yaku. These provenances were planted
161	within 50 m of each other at the upper, middle, and lower parts of the slope, respectively.
162	The native habitats of all three provenances are located in the southwestern part of Japan
163	(Figure 1). As in the common garden, all native habitats are covered with very thin soils
164	due to high precipitation and steep slopes, but the basement rock of each native habitat is
165	different (sedimentary rock in Yoshino, sandstone and shale in Yanase, and granite in
166	Yaku) (Geological Survey of Japan 2015). Yoshino and Yanase are known to have
167	relatively high growth rates in the early stage of growth (< ca. 50 years old), whereas
168	Yaku has low growth rates (Itaka et al. 2013; Nishizono et al. 2014). These growth
169	patterns were also observed in the mean tree height and diameter at breast height (DBH)
170	of each provenance measured across the common garden of the present study in 2015:
171	18.3 m and 23.1 cm in Yoshino ( $n = 100$ ), 15.4 m and 19.2 cm in Yanase ( $n = 193$ ), and
172	10.9 m and 18.6 cm in Yaku ( $n = 119$ ), respectively. The age of stands from each
173	provenance in 2015 was 49 years in Yaku, 46 years in Yanase, and 43 years in Yoshino.
174	In this study, three individuals of each provenance were cut down from their
175	stem base at noon on a sunny day in August 2018 and used for the measurements

176	described below. The canopy tops of each sample tree were exposed to direct sunlight.
177	We stretched a tape measure along the stem to measure the tree height, crown depth, and
178	height and diameter of the primary branches attached to the stem of each individual,
179	except for one Yaku tree. The mean height and DBH of the sample trees for each
180	provenance were 21.1 m and 22.7 cm in Yoshino, 20.9 m and 25.6 cm in Yanase, and 11.8
181	m and 15.7 cm in Yaku, respectively. To calculate the stem volume of each individual,
182	stem disks (approximately 1 cm in thickness) were collected at 5 m intervals starting from
183	a height of 1.3 m along the stem. The diameters were recorded, and the stem volume was
184	calculated as the sum of the truncated cones.

### 186 Growth characteristics and tree structures

To estimate the recent growth characteristics of each provenance, the annual stem height and radial growth rates ( $G_h$  and  $G_r$ , cm yr<sup>-1</sup> and mm yr<sup>-1</sup>) from 2013 to 2016 were measured from the annual shoot length at the top of each tree crown (except for one individual from Yoshino, which could not be measured because the tip of the trunk was unclear). These measurements were recorded with an accuracy of 1 mm. The annual ring width was measured from one direction of the stem disk at a height of 1.3 m with an accuracy of 0.001 mm. Based on the above data, we calculated the relative growth rate for height (RGR<sub>h</sub>, yr<sup>-1</sup>) and DBH (RGR<sub>r</sub>, yr<sup>-1</sup>) from 2013 to 2016 using the following
equation (Hunt 1982), assuming that both show exponential growth:

196 
$$\frac{\ln(x_j) - \ln(x_i)}{t_j - t_i}$$
 Eqn. 1

where  $X_j$  and  $X_i$  are the height or DBH at times j and i, respectively (when annual growth ceases), and  $t_j$  and  $t_i$  are the years.  $G_h$ ,  $G_r$ ,  $RGR_h$ , and  $RGR_r$  were calculated for each yearinterval (2013–2014, 2014–2015, 2015–2016) for individual trees.

200 One woody core (ca. 3 cm in length from the cambium) was collected from the 201 main stem at DBH using an incremental borer (5.15 mm in diameter; Haglöf, Langsele, 202 Sweden) from 10–12 individuals per provenance in August 2019. This woody core was used to calculate the sapwood density (WD, g cm<sup>-3</sup>). The sapwood volume was measured 203 204 from the diameter and length of a core (assuming a cylindrical shape), and the bark and heartwood portions (based on the visual check) were removed with a razor blade before 205 measurement. All samples were oven-dried ( $65^{\circ}C$ , > 72 h), and their dry masses were 206 207 recorded. The volumetric density of the sapwood was then calculated as the dry mass divided by its fresh volume. 208 The crown architecture was evaluated by the absolute crown depth (CD, m), 209

and the ratio of CD to tree height (RCD, m  $m^{-1}$ ) was calculated for each individual. In

211

13

addition, we assumed a pipe model, in which the ratio of leaf area to the cross-sectional

area of the branch base is constant (Shinozaki et al. 1964). Based on this, we calculated the total cross-sectional area per stem volume (TBA, cm<sup>2</sup> m<sup>-3</sup>) of primary branch bases for each individual as an alternative index of LAR.

215

#### 216 Tree hydraulic architecture

To analyze the stem anatomy, we excised one sample from the cambium (approximate 217 length, 2 cm; width, 1 cm; depth, 1-2 cm) from all the stem disks we collected, avoiding 218 219 the reaction wood part. Subsequently, transverse sections (approximate thickness, 30-40 220 μm) were prepared using a sliding microtome (Figure 2). The samples were stained with 221 0.5% (w/v) safranin in 50% ethanol and dehydrated using an ethanol series (50%, 99.5%, 222 and 100%). Finally, the samples were dehydrated in xylene and mounted on glass slides with Canada balsam. Images were captured using a digital camera (EOS kiss X3, Canon, 223 224 Tokyo, Japan) coupled to a light microscope (BX50, Olympus, Tokyo, Japan). The resolution of the images was 1919 pixels mm<sup>-1</sup> with a full size of approximately 1.2 mm 225 226  $\times$  0.8 mm. Using these images, we measured the tracheid density (TD, mm<sup>-2</sup>) of earlywood and the mean tracheid lumen area (TLA,  $\mu m^2$ ) for > 650 tracheids per image 227 228 using the Fiji image processing software (Schindelin et al. 2012). The disjunction between 229 earlywood and latewood followed Mork's definition (Denne 1988): latewood was defined

as the wood with the ratio of lumen diameter and double wall thickness < 2. The TLA was convened to the tracheid diameter (D,  $\mu$ m) by assuming circular cross-sections, and the mean hydraulically-weighted tracheid diameter (D<sub>h</sub>,  $\mu$ m) of every stem disk was calculated as follows (Tyree and Zimmermann 2002):

234 
$$D_{\rm h} = \left(\frac{1}{n}\sum_{i=1}^{n}D^4\right)^{\frac{1}{4}}$$
 Eqn. 2

where n is the number of tracheids.

In a soil-plant hydraulic continuum, water flow occurs in proportion to the water potential gradient and is inversely proportional to the hydraulic conductivity according to Darcy's law (Sperry et al. 1998). To estimate the potential water flow in the whole tree, we calculated the water potential gradient from the difference between  $\Psi_{TL}$ and  $\Psi_R$ , as described below. The potential specific xylem conductivity at a certain height (K<sub>p</sub>, kg m<sup>-1</sup> s<sup>-1</sup> MPa<sup>-1</sup>) was calculated according to (Poorter et al. 2010):

242 
$$K_{\rm p} = \left(\frac{\pi \rho_W}{128\eta}\right) TD * D_h^4$$
Eqn. 3

where  $\rho_w$  is the density of water at 20°C (998.2 kg m<sup>-3</sup> at 20°C),  $\eta$  is the viscosity of water at 20°C (1.002 × 10<sup>-3</sup> Pa s at 20°C), and TD and  $D_h$  are as described above.

We calculated  $K_p$  at different heights from every stem disk, and then the axial variation-weighted potential specific xylem conductance ( $K_{ap}$ , kg m<sup>-2</sup> s<sup>-1</sup> MPa<sup>-1</sup>) and potential transpiration rate per unit sapwood area ( $E_p$ , kg m<sup>-2</sup> s<sup>-1</sup>) were estimated. Because of the decrease in  $D_h$  from the stem base to the treetop (Figure S1a),  $K_p$  decreased as sampling height increased in each tree, and its variation was relatively well explained by linear regressions ( $R^2 = 0.53-1.00$ , Figure S1b). These patterns allow us to express the minimum specific resistivity ( $R_{min}$ , an inverse of  $K_p$ ) as a function of height as follows:

$$R_{\min,i} = \frac{1}{a_i H + b_i}$$
 Eqn. 4

where R<sub>min,i</sub> H, a<sub>i</sub>, and b<sub>i</sub> are the R<sub>min</sub>, height, and coefficients of tree i, respectively. 253Integrating R<sub>min</sub> from the ground to the individual tree height yielded the minimum 254 cumulative specific resistivity of the stem (R<sub>cum min</sub>, m<sup>2</sup> s MPa kg<sup>-1</sup>), and potential specific 255 256 xylem conductance ( $K_{ap}$ ) was calculated as the inverse of  $R_{cum min}$ . The  $E_p$  was calculated as K<sub>ap</sub> multiplied by the water potential gradient from the roots to the treetop ( $\Psi_R - \Psi_{TT}$ , 257258 MPa). The above calculations assumed that most water movements occur in the 259 earlywood at the outermost sapwood where large tracheids are observed; thus, we 260 considered our results to be robust to the radial variation of tracheid anatomy.

261

#### 262 *Leaf water relations*

After cutting down the trees in the common garden as described above, the daytime water potential of treetop leaves ( $\Psi_{TL}$ , MPa), lowest-crown leaves ( $\Psi_{LL}$ , MPa), and fine roots ( $\Psi_R$ , MPa) were immediately measured for three replicates per individual using a pressure chamber (Model 1000, PMS Instruments, Corvallis, USA). Branches (ca. 30 cm in length)
were sampled from the treetop of each individual, immediately recut in bucketed water,
and covered with a black plastic bag overnight in the laboratory for the pressure–volume
measurement.

The pressure-volume curve of the leaves (second- and current-year internodes; 270 271 three shoots per provenance) was obtained using the bench-drying approach for the 272 pressure-volume technique (Tyree and Hammel 1972). Using a pressure chamber (Model 273 1000, PMS Instruments, Corvallis, USA), we repeatedly measured the leaf water potential 274 $(\Psi_L, MPa)$  and fresh mass  $(M_F, g)$  of the sampled leaves (repeat pressurization method, 275 Hinckley et al. 1980, Parker and Colombo 1995). After the pressure-volume 276 measurement, all the sample shoots were photographed to measure the total leaf surface area (A<sub>L</sub>, m<sup>2</sup>), as described below. Next, the leaves were oven-dried to constant weight at 277 278 65°C for 48 h to obtain the leaf dry mass (M<sub>D</sub>, g). To estimate the drought tolerance of 279 shoots, we calculated the osmotic potential at saturation ( $\Psi_{sat}$ , MPa), osmotic potential at turgor loss ( $\Psi_{tlp}$ , MPa), and relative water content at turgor loss (RWC<sub>tlp</sub>) at the bulk shoot 280 level using the pressure-volume curve. The saturated leaf water content ( $M_W = MF$  -281 MD) was used to calculate leaf hydraulic capacitance (C<sub>L</sub>, mol m<sup>-2</sup> MPa<sup>-1</sup>) and succulence 282  $(S_L, g H_2 O m^{-2}).$ 283

284 
$$C_{L} = (\delta RWC/\delta \Psi_{L}) (M_{D}/A_{L}) (M_{W}/M_{D}) / MW$$
Eqn. 5

$$S_L = M_W/A_L$$
 Eqn. 6

287

where  $\delta RWC/\delta \Psi_L$  is the slope of the  $\Psi_L$ -RWC relationship calculated from the pressure-286 volume curve before the turgor loss point, and MW is the molecular weight of water. 288

Leaf morphology 289

290 After the pressure-volume measurement, each sample shoot (three shoots per 291 provenance) was placed on a slide viewer, illuminated from below, and photographed to 292 obtain the shoot silhouette images. All leaves were detached from the shoot axis, laid on 293 the slide viewer without overlap, and photographed. The photographs of the shoots and 294 leaves were analyzed using the ImageJ image analysis software (Schneider et al. 2012) to quantify the shoot silhouette area ( $A_s$ ,  $m^2$ ) and projected leaf area ( $A_P$ ,  $m^2$ ). To obtain  $A_L$ , 295 296 the perimeter-to-width ratios obtained from the transverse sections of leaves were 297 multiplied by  $A_P$  (Azuma et al. 2016). We calculated the leaf mass per area (LMA =  $M_D/A_P$ , g m<sup>-2</sup>) and shoot silhouette area to projected leaf area ratio (SPAR = A<sub>S</sub>/A<sub>P</sub>, a 298 measure of leaf overlap within the shoot). 299

#### 301 Leaf photosynthetic traits

302 In August 2019, we sampled a branch (approximate length, 30 cm) from the treetop of 303 each individual tree using a long sickle. The branch was immediately recut under water and fully rehydrated in the laboratory for photosynthetic measurement. The gas exchange 304 305 of second-year shoots was measured in all sampled branches (three branches per 306 provenance) using the LI-6400 portable gas exchange system fitted with an LI-6400-05 307 conifer chamber (Li-Cor Inc., Lincoln, NE, USA). The air temperature and CO2 308 concentration in the cuvette were maintained at 25°C and 380 ppm, respectively. We used 309 an external halogen-type light source fitted with a profile spot projection lens (MHAB-310 150W and ML-50, Moritex Corp., Tokyo, Japan) to provide parallel beam radiation with a maximum photosynthetic photon flux density (PPFD) of 1600  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>. We varied 311 the light intensity to obtain the photosynthetic light response curve for each shoot. 312 Following these measurements, the leaves inside the conifer chamber  $(10 \text{ cm}^2)$ 313 314 were carefully cut out and photographed to measure the projected leaf area using Image J (Schneider et al. 2012). The leaves were then oven-dried to a constant mass to determine 315 the leaf dry mass. We estimated maximum net photosynthetic rate (P<sub>max</sub>, µmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-</sup> 316 <sup>1</sup>), dark respiration rate (R,  $\mu$ mol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>), and light compensation point (L<sub>c</sub>,  $\mu$ mol m<sup>-</sup> 317 <sup>2</sup> s<sup>-1</sup> PPFD) from the relationship between light intensity and net photosynthetic rate. 318

319 These measurements were conducted using the Light Response Curve software developed 320 by Li-Cor Inc. (Norman et al. 1992). We also calculated maximum photosynthetic rate per leaf dry mass ( $P_{max mass}$ , nmol CO<sub>2</sub> g<sup>-1</sup> s<sup>-1</sup>) by dividing  $P_{max}$  by LMA. 321 322 To evaluate the long-term photosynthetic water-use efficiency, we measured the leaf carbon isotope ratio ( $\delta^{13}$ C,  $\infty$ ) in 9–10 individuals of each provenance from which 323 324 we had collected stem cores (Farquhar et al. 1989). The leaves were oven-dried (65°C, > 72 h) and then ground using a mill. Then,  $\delta^{13}$ C was measured using an isotope ratio mass 325 326 spectrometer (DELTA V Plus and DELTA V Advantage, Thermo Fisher Scientific, 327 Massachusetts, USA) at the Center for Ecological Research (CER), Kyoto University. 328 Simultaneously, the dry mass-based leaf nitrogen and carbon concentrations (Nmass and C<sub>mass</sub>, %) were measured using an elemental analyzer (Flash 2000, Thermo Fisher 329 330 Scientific) coupled to an isotope ratio mass spectrometer.

331

### 332 Statistical analysis

All analyses were performed using R (R Core Team 2019, R version 3.6.1). To calculate K<sub>ap</sub> and E<sub>p</sub>, we first estimated coefficients *a* and *b* in Eqn. 4 for each tree with nonlinear least square regression analyses using the R function 'nls'. Using these values, we integrated Eqn. 4 from 0 (ground) to tree height for each tree to yield  $R_{cum_{min}}$  using the

337 'integrate' function in the R package 'stats' (version 4.1.2).

338 To examine the differences in the leaf, stem, and whole-tree traits among provenances, we used one-way ANOVA followed by Tukey's HSD post hoc tests. We also 339 340 examined the residual plots of linear regressions for each trait. When the data did not meet 341 the assumptions of ANOVA (normality and homogeneity of variances), we instead 342 conducted the Kruskal-Wallis test followed by the Steel-Dwass test. To compare Gh, Gr, 343 RGR<sub>h</sub>, and RGR<sub>r</sub>, we first calculated the average provenance-by-year values to consider the variation in growth among years, and then examined the differences among 344 345 provenances based on the linear mixed model analyses with a restricted maximum 346 likelihood (REML) estimation, where provenance was fixed effect and year was a random intercept, using the R package 'lme4' (Bates et al. 2015). Following this, we examined 347 348 the differences among provenances using linear mixed model analyses (with provenance as a fixed effect and year being a random intercept) using the R package 'lme4' (Bates et 349 350 al. 2015). The model parameters were calculated by REML estimation. To examine the axial variation of D<sub>h</sub>, we converted the sampling height to the 351

heights. We estimated the slope (basipetal conduit widening rate,  $\beta$ ) and intercept (log D<sub>h</sub>

352

at 1 m below the treetop,  $\alpha$ ) of L–D<sub>h</sub> relationships among provenances based on linear

distance from the tree apex (L), thus enabling comparisons among trees of different

355	mixed model analyses, where L, provenance, and their interaction were fixed effects and
356	individual trees had a random intercept. The model parameters were calculated using
357	REML estimation. Here, we $log_{10}$ -transformed $D_h$ and L prior to analyses to reflect the
358	scaling relationship of $D_h$ with L (see Introduction). The same analysis was performed by
359	substituting L with the relative distance from the treetop or stem diameter at sampling
360	height to estimate the effect of size differences among provenances on tracheid tapering.
361	We also calculated marginal and conditional $R^2$ ( $R_m^2$ and $R_c^2$ , respectively, Nakagawa and
362	Schielzeth 2013) to evaluate the model fit using the R package 'MuMIN' (Barton 2016).
363	We set a significance level of 0.05.

#### 365 **Results**

366 Growth characteristics and tree structures

Gh, Gr, RGRh, and RGRr were the lowest in the Yaku provenance, followed by Yoshino 367

and Yanase (Table 1). Correspondingly, WD was highest in Yaku, followed by Yoshino, 368

- 369 and then Yanase (Table 2). CD was larger in Yanase than in Yaku. RCD was not
- significantly different among the provinces; however, there was a trend of Yanase having 370
- a higher RCD compared to the other two provenances (Table 2). TBA was significantly 371
- 372 higher in Yaku than in Yanase and Yoshino.

#### 374 Axial variation of tracheid diameter and whole-tree hydraulics

For all provenances, the D<sub>h</sub> was generally smallest near the top of the tree, and the largest 375 D<sub>h</sub> was found near the stem base (Figure 3, Table 3). The slope (basipetal conduit 376 377 widening rate,  $\beta$ ) and intercept (log D<sub>h</sub> at 1 m below the treetop,  $\alpha$ ) in the L-D<sub>h</sub> 378 relationship were significantly different between provenances (Table 3): β was higher in 379 Yanase and Yoshino than in Yaku, whereas  $\alpha$  was higher in Yaku than in the other two. Yanase had a marginally higher  $\beta$  than Yoshino (p = 0.076). In addition, provenances with 380 381 high  $\beta$  tended to exhibit low  $\alpha$ . The overall model fit was relatively good (both  $R_m^2$  and  $R_c^2 = 0.85$ ). We also found that on average, provenances with higher  $\beta$  had longer CD ( $R^2$ 382 = 0.999, p = 0.021, n = 3), indicating a link between hydraulics and crown architectures 383 384 at the whole-tree level (Figure 3). However, when we substituted L with the relative 385 distance from the tree top or stem diameter at the sampling height, the slope was not significantly different among provenances in either case ( $R_m^2$  and  $R_c^2 = 0.73$ , Table S1, 386 for relative distance;  $R_m^2 = 0.72$ ,  $R_c^2 = 0.76$ , Table S2 for diameter). This suggested that 387 388 the results in the L–D<sub>h</sub> relationship may reflect different sizes among provenances. 389 A decline in D<sub>h</sub> caused a decline in K<sub>p</sub> along tree height with indistinguishable

390 slopes among provenances (p = 0.77, Figure S1). These patterns led to significant positive

391 correlations between total tree height and  $R_{cum_min}$  across trees (p = 0.003, Figure S2). 392 Consequently, despite having the lowest  $\beta$ , Yaku had the highest  $K_{ap}$  because it also had 393 the lowest tree height. Despite the high  $K_{ap}$  in Yaku,  $E_p$  was not significantly different 394 among provenances (p = 0.28), as it was offset by the relatively small  $\Psi_{TL} - \Psi_R$  in Yaku 395 (Table 2).

396

#### 397 Leaf water relations, morphology, and photosynthetic traits

Leaf water relations and leaf morphology were similar, with no significant differences among provenances (Table 2). Although most leaf photosynthetic traits were not significantly different between provenances, there were significant or marginally significant differences in R (p = 0.042), Lc (p = 0.053), and  $\delta^{13}$ C (p = 0.054) among provenances. R and Lc were highest in Yoshino and lowest in Yanase, whereas  $\delta^{13}$ C was highest in Yaku and lowest in Yanase (Table 2).

#### 405 **Discussion**

Here, we compared the traits of three provenances of ca. 45-year-old *C. japonica* with different genotypes and contrasting RGR (Yaku, Yanase, and Yoshino) grown under the same environment. Our results partially supported our prediction that the trees in the 409 resource-acquisitive provenance achieved higher growth rates. Among the traits affecting 410 NAR and LAR that lead to differences in RGR, leaf traits had similar values among 411 provenances, whereas canopy structure and hydraulic architecture at the whole-tree level 412 were different between provenances.

The life-history theory suggests that organ-level resource use strategies are 413 coupled in a tandem manner (Grime et al. 1997; Reich 2014). The previous studies 414 conducted in the same common garden showed the highest rate of root exudation in 415 Yoshino whose native habitat was most similar to the common garden (Ohta et al. 2019). 416 417 It has been speculated that this is a result of adaptation to the basement rock in its native 418 habitat. In support of the life-history theory, Yoshino showed resource-acquisitive leaf 419 traits, such as the highest P<sub>max</sub>, R, and L<sub>c</sub> among the three provenances in the present study 420 (Table 2). In turn, the lowest Lc in Yanase may allow Yanase to distribute their leaves in the lowest position relative to tree height. In C. japonica, photosynthetic parameters such 421 422 as P<sub>max</sub>, V<sub>cmax</sub>, and nitrogen content in the second-year (former current year) shoots 423 decrease after summer and primary photosynthetic sites shift to current-year shoots as the 424 seasons changed (Inoue et al. 2018, Kobayashi et al. 2010, Tobita et al. 2014). 425 Considering that the P<sub>max</sub> in the present study was measured on the second-year shoots, it 426 would be reasonable that Pmax was lower than that measured on the current year shoots of

427	C. japonica in general (Osone et al. 2021). $P_{max}$ was similar among provenances, but the
428	leaf water-use efficiency (estimated by $\delta^{13}$ C) tended to be higher in Yaku with lower
429	growth rate (Tables 1 and 2). Leaf water-use efficiency estimated by $\delta^{13}$ C represents long-
430	term accumulation of the photosynthesis per unit stomatal conductance (Farquhar et al.
431	1989). The high leaf water-use efficiency in Yaku may be partially due to low basipetal
432	conduit widening rate ( $\beta$ ), which negatively affects photosynthesis and growth at the
433	whole-tree level through the accumulation of hydraulic resistance from stem anatomical
434	traits as discussed below. However, most leaf water relations, morphology, and
435	photosynthetic traits were similar among provenances (Table 2), indicating that growth-
436	related traits at the leaf level alone did not describe differences in RGR among
437	provenances.
438	In terms of growth characteristics, Yaku trees showed the lowest stem height,
439	radial growth rate, and RGR, corresponding to the highest sapwood density (Tables 1 and
440	2). The high WD in Yaku was also associated with a small tracheid diameter at the same
441	height compared to the two other provenances (Figure S1a). WD is negatively related to
442	volumetric growth and positively related to strength (e.g., van Gelder et al. 2006; Poorter
443	et al. 2003); therefore, the high WD in Yaku may represent a genetically differentiated

444 trait in response to the limited tree size due to typhoon-induced canopy disturbance in its

445	native habitat (Ishii et al. 2010; Takashima et al. 2009). In addition, WD can influence
446	LAR, which is related to tree growth rate (Givnish 1988; Kitajima 1994; Poorter and
447	Remkes 1990). High biomass allocation to the stem affected the variation in WD and
448	could be predicted to reduce LAR, leading to constrained RGR (Poorter et al. 2010;
449	Wright et al. 2010). However, the large TBA in Yaku (Table 2) indicated that assuming a
450	pipe model, the biomass allocation to leaves was higher (Shinozaki et al. 1964) when
451	assuming no difference in leaf area relative to the cross-sectional area of the branch base
452	among provenances. However, the foliage was concentrated at a relatively higher position
453	on the stem. Coniferous trees generally allow light to penetrate deeper into the canopy
454	compared to broadleaf trees because of the arrangement of shoots and branches (Ishii and
455	Asano 2010). Multi-layered trees with branches distributed throughout the crown
456	typically show lower efficiency of light interception compared to that in single-layered
457	trees with branches distributed in the upper canopy. However, the productive leaf area is
458	theoretically maximized by maintaining a deep canopy in conifer trees (Onoda et al. 2014;
459	Niinemets 2010; Stenberg 1996). In turn, the crown structure with low light-use efficiency
460	may be related to the low RGR in Yaku trees.
461	At the whole-tree level, the tree hydraulic architecture affecting photosynthetic

462 capacity also differed between Yaku and the other two provenances. The rate of basipetal

463	conduit widening ( $\beta$ ) describes how conduits widen from the treetop per unit stem length.
464	The value of $\beta$ converges to 0.2 as the predicted exponent in the WBE (West, Brown and
465	Enquis) model in a very broad-leaved plant species. In contrast, $\beta < 0.2$ results in a
466	decreased conduit widening rate and increased resistance to sap flow within the whole
467	tree (Rosell et al. 2017). In the present study, $\beta$ was 0.17 in Yanase, 0.13 in Yoshino, and
468	0.07 in Yaku (Figure 3, Table 3). These values were lower than the optimal value for water
469	transport $(0.2)$ , which may be partly due to the need for coniferous tracheids to perform
470	water transport and achieve mechanical stability. However, the $\beta$ converges to 0.2 in the
471	world's tallest tree species-Sequoia sempervirens and Sequoiadendron giganteum
472	(height, 86-105 m)-suggesting the significant contribution of basipetal conduit
473	widening as a hydraulic compensation mechanism with increasing tree height. In other
474	words, trees that can achieve the optimal $\beta$ show a higher maximum height (Williams et
475	al. 2019). Because the size-dependence of cumulative water resistance decreases as $\beta$
476	approaches 0.2, Yanase trees can maintain a high potential for tree growth, resulting in a
477	high maximum height. In Yaku, $\beta$ was significantly smaller than in the other two
478	provenances, and thus tree height could be constrained as the tree size increased. In
479	addition, there was a negative correlation between $\beta$ and $\alpha$ (log $D_h$ at 1 m below the
480	treetop) in the L-D <sub>h</sub> relationship among the three provinces (Figure 3, Table 3),

481	suggesting that the possible hydraulic architecture of the whole tree is intraspecific
482	constrained. If the water requirement is high (for example, if the leaf area is large), the
483	tracheid diameter at the treetop ( $\alpha$ ) is predicted to be large even at the same stem length
484	(Olson et al. 2021). The advantage of a high $\alpha$ would be that a large tracheid diameter can
485	be maintained, such that the crown can have high water demand even in the upper part of
486	the stem. Indeed, foliar branches were concentrated at relatively high positions in Yaku,
487	whereas Yanase and Yoshino had a wide and sparse distribution deep into the stem (Table
488	2). We found that the higher $\beta$ in Yanase was related to the long vertical distribution of
489	foliar branches along the stem (Figure 3). Thus, whole-tree hydraulic architecture—as
490	explained by axial variation in the hydraulically-weighted tracheid diameter-can be
491	linked to leaf distribution with respect to light use strategies as well as water transport
492	capacity, leading to differences in growth characteristics among provenances. In the
493	present study, only trees originating from Pacific regions with high precipitation were
494	used. However, comparisons with provenances with low precipitation may also be helpful
495	in understanding the wider patterns of variation in the functional traits of a tree species.
496	Interestingly, although there were evident differences in the tree hydraulic
497	structure, the potential transpiration rate per unit sapwood area (E <sub>p</sub> ) did not differ
498	significantly among the provenances (Table 2). Despite having the lowest $\beta$ value, Yaku

499	had the lowest tree height, that is, a shorter L and less cumulative resistance of the whole
500	tree. As a result, the potential specific xylem conductance $(K_{ap})$ was higher in Yaku trees
501	than in Yanase and Yoshino; however, this was offset by a smaller water potential gradient
502	from the roots to the treetop ( $\Psi_R - \Psi_{TT}$ ). It remains to be seen whether $E_p$ is constant in
503	response to the growth environment, or whether it just happens to be constant as a result
504	of the integration of genetic trait differences in each provenance. Future comparative
505	studies on growth-related traits are required at the leaf and whole-tree levels in native
506	habitats.

508 Conclusion

C. japonica is geographically widespread in Japan. In this species, intraspecific variation 509 in growth characteristics in field-grown adult trees is regulated by whole-tree properties. 510 511 Leaf traits were similar among the provenances in the same environments; nevertheless, 512 in provenances whose native habitats were most similar to the common garden used in 513 the present study, resource-acquisitive leaf traits were achieved through a combination of the high nutrient acquisition capacity of roots. Furthermore, the high rate of basipetal 514515 conduit widening was correlated with the long crown depth, suggesting that the light capture strategies at the whole-tree level are coordinated with hydraulic architectures, 516

517	possibly to achieve the optimal growth rate for each provenance. Based on our findings,
518	we suggest that of the mechanisms underlying intraspecific variation in the growth
519	characteristics of trees with a wide range of native habitats can be a useful indicator for
520	predicting changes in growth potential and forest dynamics in response to climate change
521	in each habitat.
522	
523	Acknowledgements
524	We thank Dr. T. Ohta, and staff members of Wakayama Experimental forest, Hokkaido
525	University, for help of field measurement on this study. The present study was
526	conducted using Cooperative Research Facilities (Isotope Ratio Mass Spectrometer) of
527	Center for Ecological Research, Kyoto University. This research was funded by JSPS
528	KAKENHI Grant Number to TH (21H02227 and 21H05316) and JSPS Research
529	Fellowships for Young Scientists to WAA (17J05154) and KK (20J01359).
530	
531	Conflict of interest
532	None declared.
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**Table 1**. Comparisons of growth and relative growth rate (RGR) for height and diameter at breast heigh (DBH) in trees from 2013 to 2016, including mean values, standard errors, and the results of linear mixed model analysis for three provenances (Yaku, Yanase, and Yoshino) of *Cryptomeria japonica*. G<sub>h</sub>: growth rate for height, Gr: growth rate for DBH, RGR<sub>h</sub>: relative growth rate for height, RGR<sub>r</sub>: relative growth rate for DBH.

	$G_h$	Gr	RGR <sub>h</sub>	RGR <sub>r</sub>
Unit	$\mathrm{cm}~\mathrm{yr}^{-1}$	mm $yr^{-1}$	$10^{-3}  yr^{-1}$	$10^{-3}  yr^{-1}$
Yaku	5.6 (1.6) b	0.36 (0.11) b	6.08 (1.76) b	2.70 (0.80) c
Yanase	20.5 (6.1) a	1.00 (0.29) a	10.72 (3.16) a	5.60 (1.62) a
Yoshino	15.1 (4.5) a	0.95 (0.28) a	9.12 (2.72) ab	3.92 (1.14) b

Different letters indicate significant differences between parameters among provenances (p < p

0.05).

Table 2. Comparisons of leaf, stem, and whole-tree traits among three provenances of Cryptomeria. japonica, including mean values, standard errors,

			Cultivars of <i>C. japonica</i>			
Trait	Symbol	Unit	Yaku	Yanase	Yoshino	<i>p</i> value
Tree structures						
Crown depth	CD	m	3.18 (0.89) b	10.89 (1.23) a	7.53 (0.80) ab	0.012
Ratio of crown depth to tree height	RCD	$m m^{-1}$	0.27 (0.09)	0.52 (0.08)	0.36 (0.05)	0.142
Total branch cross-sectional area per stem volume	TBA	$\mathrm{cm}^2\mathrm{m}^{-3}$	929 (170) a	594 (36) ab	439 (46) b	0.021
Sapwood density	WD	g cm <sup>-3</sup>	0.39 (0.01) a	0.34 (0.01) b	0.33 (0.01) b	< 0.001
Whole-tree hydraulic architecture						
Daytime water potential of treetop leaves	$\Psi_{\text{TL}}$	MPa	-1.14 (0.09)	-1.33 (0.06)	-1.31 (0.06)	0.182

and results of one-way ANOVA or Kruskal-Wallis test.

Daytime water potential of lowest-crown leaves		MPa	-1.05 (0.10)	-1.20 (0.10)	-1.24 (0.04)	0.322
Daytime water potential of fine-roots <sup>1</sup>	$\Psi_{R}$	MPa	-0.34 (0.08)	-0.20 (0.06)	-0.19 (0.01)	0.146
Water potential difference between root and treetop	$\Psi_{ m R}$ — $\Psi_{ m TL}$	MPa	0.80 (0.13)	1.13 (0.12)	1.12 (0.05)	0.113
Axial variation-weighted potential specific xylem	Kan	$kg m^{-2} s^{-1} MPa^{-1}$	1.19 (0.06) a	0.68 (0.02) b	0.63 (0.04) b	< 0.001
conductance	Tap	5				
Potential transpiration rate per unit sapwood area	Ep	$kg m^{-2} s^{-1}$	0.93 (0.13)	0.77 (0.05)	0.71 (0.06)	0.278
Leaf water relations						
Osmotic potential at turgor loss <sup>1</sup>	$\Psi_{tlp}$	MPa	-2.08 (0.20)	-1.64 (0.17)	-2.06 (0.13)	0.430
Osmotic potential at saturation <sup>1</sup>	$\Psi_{\text{sat}}$	MPa	-1.43 (0.08)	-1.09 (0.26)	-1.45 (0.02)	0.731
Relative water content at turgor loss	<b>RWC</b> <sub>tlp</sub>	gH <sub>2</sub> O gH <sub>2</sub> O <sup>-1</sup>	0.76 (0.03)	0.76 (0.01)	0.69 (0.02)	0.068

Leaf hydraulic capacitance	$C_L$	mol m <sup><math>-2</math></sup> MPa <sup><math>-1</math></sup>	1.52 (0.22)	1.85 (0.30)	1.94 (0.24)	0.524
Leaf succulence	$S_L$	$gH_2O m^{-2}$	204 (38)	228 (23)	241 (25)	0.687
Leaf morphology						
Leaf dry mass per area ratio <sup>1</sup>	LMA	g m <sup>-2</sup>	411 (36)	321 (1)	385 (40)	0.061
Shoot silhouette area to projected leaf area ratio <sup>1</sup>	SPAR	$m^2 m^{-2}$	0.64 (0.01)	0.68 (0.03)	0.74 (0.05)	0.113
Leaf photosynthesis						
Maximum net photosynthetic rate	P <sub>max</sub>	$\mu mol \ CO_2 \ m^{-2} \ s^{-1}$	3.56 (0.26)	3.17 (0.28)	4.05 (0.14)	0.095
Maximum net photosynthetic rate per leaf dry mass	P <sub>max_mass</sub>	nmol CO <sub>2</sub> $g^{-1} s^{-1}$	8.69 (0.14)	9.87 (0.84)	10.76 (1.28)	0.319
Dark respiration rate <sup>1</sup>	R	$\mu mol \ CO_2 \ m^{-2} \ s^{-1}$	0.62 (0.02)	0.48 (0.09)	0.80 (0.09)	0.042
Light compensation point <sup>1</sup>	L <sub>C</sub>	$\mu$ mol PPFD m <sup>-2</sup> s <sup>-1</sup>	21.5 (1.1)	12.5 (4.9)	46.7 (12.9)	0.053
Stable carbon isotope ratio	$\delta^{13}C$	%0	-28.8 (0.27)	-29.7 (0.21)	-29.5 (0.33)	0.054

Dry-mass based carbon concentration <sup>1</sup>	C <sub>mass</sub>	%	54.0 (0.24)	53.3 (0.35)	53.2 (0.47)	0.200
Dry-mass based nitrogen concentration	N <sub>mass</sub>	%	1.10 (0.04)	1.28 (0.06)	1.21 (0.07)	0.111

Significant differences between provenances are denoted by different letters (Tukey's HSD or Steel–Dwass test, p < 0.05)

<sup>1</sup> Differences in means among provenances were examined by Kruskal–Wallis test.

**Table 3.** Estimation of slopes ( $\beta$ ) and intercepts ( $\alpha$ ) for the relationships between  $\log_{10}$ -transformed distance from tree apex (L) and hydraulically-weighted tracheid diameter (D<sub>h</sub>) based on the linear mixed models for three provenances (Yaku, Yanase, and Yoshino) of *Cryptomeria japonica*.

	Slope (β)	Intercept (a)
Yaku	0.070 (0.016) b	1.354 (0.012) a
Yanase	0.171 (0.023) a	1.272 (0.021) b
Yoshino	0.130 (0.022) a	1.292 (0.019) b

Values in parentheses represent standard errors.

Different letters indicate significant differences in parameters among provenances (p < 0.05).



**Figure 1**. Location (latitude and longitude), mean annual temperature, and mean annual precipitation of the common garden of the present study (Wakayama Experimental Forest) and the native habitats of three provenances (Yoshino, Yanase, and Yaku). The location of the native habitats of three provenances shows the source location of each sapling planted in the common garden. The mean annual temperature and precipitation were calculated from observations from 1985 to 2019 at the nearest Japan Meteorological Agency weather station to that location.



**Figure 2**. Optical microscopic images of stained transverse sections of the xylem at the stem tips (a, c, e) and bases (b, d, f) of three provenances of *Cryptomeria japonica*: Yaku (a, b), Yanase (c, d), and Yoshino (e, f). All images are at the same magnification (bar =  $500 \mu$ m). The pith is on the right side in each image.



**Figure 3.** (a) Scaling relationships between  $log_{10}$ -transformed hydraulically-weighted tracheid diameter (D<sub>h</sub>) and distance from tree apex (L) for three provenances (Yaku, Yanase, and Yoshino) of *Cryptomeria japonica*. Solid, dashed, and dotted lines indicate the trends for Yaku, Yanase, and Yoshino, respectively. On average, the provenance with a steeper slope ( $\beta$ ) had a longer crown depth (CD) ( $R^2 = 0.999$ , p = 0.021, n = 3). (b) The same data in non-transformed axes. The vertical solid, dashed, and dotted lines indicate the average CD (see also Table 1) for Yaku, Yanase, and Yoshino, respectively. Each symbol is a composite of multiple individuals (n = 3 for each provenance).