

Environmental variation drives the decoupling of leaf and root traits within species along an elevation gradient

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- **Background and Aims** Plant performance is enhanced by balancing above- and below-ground resource uptake through the intraspecific adjustment of leaf and root traits. It is assumed that these organ adjustments are at least partly coordinated, so that analogous leaf and root traits broadly covary. Understanding the extent of such intraspecific leaf–root trait covariation would strongly contribute to our understanding of how plants match above- and below-ground resource use strategies as their environment changes, but comprehensive studies are lacking.
- **Methods** We measured analogous leaf and root traits from 11 species, as well as climate, soil and vegetation properties along a 1000-m elevation gradient in the French Alps. We determined how traits varied along the gradient, to what extent this variation was determined by the way different traits respond to environmental cues acting at different spatial scales (i.e. within and between elevations), and whether trait pairs covaried within species.
- **Key Results** Leaf and root trait patterns strongly diverged: across the 11 species along the gradient, intraspecific leaf trait patterns were largely consistent, whereas root trait patterns were highly idiosyncratic. We also observed that, when compared with leaves, intraspecific variation was greater in root traits, due to the strong effects of the local environment (i.e. at the same elevation), while landscape-level effects (i.e. at different elevations) were minor. Overall, intraspecific trait correlations between analogous leaf and root traits were nearly absent.
- **Conclusions** Our study suggests that environmental gradients at the landscape level, as well as local heterogeneity in soil properties, are the drivers of a strong decoupling between analogous leaf and root traits within species. This decoupling of plant resource acquisition strategies highlights how plants can exhibit diverse whole-plant acclimation strategies to modify above- and below-ground resource uptake, improving their resilience to environmental change.

Key words: Elevation gradient, intraspecific trait variation, leaf traits, root traits, trait correlations, trait covariation.

INTRODUCTION

Plants can regulate the use and uptake of light, carbon, water and nutrients to grow and survive (Cannell and Dewar, 1994) via an adjustment of functional traits (Sultan, 2000). To better understand this balance in resource use and uptake, several studies examined above- and below-ground trait covariation across species, based on the assumptions that plants adopt the same acquisitive or conservative resource strategy both above- and below-ground, and that analogous traits of leaves and absorptive roots are similarly involved in resource acquisition strategies (Mommer and Weemstra, 2012; Reich, 2014). For example, species with an acquisitive resource strategy need to efficiently intercept both above- and below-ground resources via large, thin leaves with a high specific leaf area (SLA, leaf area per dry mass) and long, thin roots of high specific root length (SRL, root length per root dry mass, i.e. the below-ground analogue of SLA). In contrast, species with a conservative strategy would need both robust and long-lived (e.g. thick, dense) leaves and roots to retain plant resources above- and below-ground (Reich, 2014), leading to interspecific covariation between

SLA and SRL, leaf and root thickness, and leaf and root tissue density (RTD, root mass per unit root volume) (Liu *et al.*, 2010). As plants need both above- and below-ground resources, determining whether leaf and root traits are coordinated along this acquisitive–conservative continuum would lead to a better understanding of whole-plant functioning across environments, compared with examining leaves and roots in isolation (De Kroon *et al.*, 2005).

Several studies have shown that across species these acquisitive–conservative strategies are generally not coordinated above- and below-ground (Fortunel *et al.*, 2012; Valverde-Barrantes *et al.*, 2015; Medeiros *et al.*, 2017; Carmona *et al.*, 2021; Vleminckx *et al.*, 2021; Weigelt *et al.*, 2021). A recent global meta-analysis showed that some analogous leaf and root trait pairs [e.g. leaf and root nitrogen (N) concentration] are correlated but others are not (e.g. SLA and SRL) (Weigelt *et al.*, 2021). A likely explanation of this decoupling is that, while species generally adjust a single syndrome of covarying leaf traits to improve the acquisition of above-ground resources (i.e. high SLA, high leaf N concentration, high photosynthetic rates

and short leaf lifespans), they may adjust a variety of root traits to enhance below-ground resource uptake, e.g. by increasing SRL and decreasing root diameter to enhance soil exploration and exploitation by roots, or decreasing SRL and increasing root diameter to acquire nutrients via the mycorrhizal pathway (Weemstra *et al.*, 2016; Bergmann *et al.*, 2020), so that analogous traits do not correlate (Weigelt *et al.*, 2021). Such recent insights on leaf–root trait covariation (or lack thereof) are primarily established across species (e.g. Weigelt *et al.*, 2021), but traits also vary within species. This intraspecific trait variation allows individuals of the same species to acquire and conserve resources across resource gradients and cope with environmental changes (Sultan, 2000; Hoffmann and Sgrò, 2011; Liancourt *et al.*, 2015; Stotz *et al.*, 2021).

The degree of intraspecific positive covariation between analogous leaf and root traits (i.e. analogous traits changing in the same direction) depends on how and to what extent these traits vary with the environment, and whether this occurs in the same direction. In general, patterns in intraspecific trait variation along environmental gradients are predicted based on plant resource economics (Grime, 1977). Following these principles, as environments become colder, drier and/or less fertile, leaves generally become more conservative (i.e. thicker, denser and with lower SLA), resulting in reduced leaf turnover rates but maintaining resources invested in plant tissue. On more productive sites, leaf traits become more acquisitive (with opposite trait values), so that readily available resources can be rapidly acquired (Grime, 1977; Ordoñez *et al.*, 2009). For root traits, similar hypotheses have been formulated, predicting that root trait expressions shift from conservative (i.e. thicker, denser roots with lower SRL) to acquisitive (i.e. thin, less dense and high-SRL roots) as resource availability increases (Ryser, 1996; Eissenstat, 2000). As resource availability decreases, plants would therefore have lower SLA and SRL and thicker and denser leaves and roots to conserve resources, and on more productive sites opposite traits would be displayed that improve resource acquisition, leading to positive intraspecific trait covariation along resource gradients. Despite these hypotheses, however, the degree of such intraspecific covariation between analogous leaf and root traits remains largely untested, especially among large numbers of species. For example, several studies reported no intraspecific relationships between analogous leaf and root traits (e.g. SRL and SLA; root N and leaf N; leaf tissue density and RTD) along environmental gradients (Freschet *et al.*, 2013; Isaac *et al.*, 2017) or between conspecific plants with different provenances (Hajek *et al.*, 2013), but these studies tested plants from only one (Hajek *et al.*, 2013; Isaac *et al.*, 2017; Martin *et al.*, 2019; Borden *et al.*, 2020) or three (Freschet *et al.*, 2013) woody and non-woody species.

There are several possible reasons behind a lack of intraspecific leaf–root trait covariation. Firstly, it may result from different environmental drivers of variation in analogous leaf and root traits, and if these drivers vary in opposite directions along the same environmental gradient this may decouple the intraspecific covariation between leaf and root traits (Freschet *et al.*, 2013; Isaac *et al.*, 2017; Westerband *et al.*, 2021). Secondly, intraspecific root trait variation along environmental gradients often does not follow the patterns predicted by plant resource economics (but see Hajek *et al.*, 2013; Isaac *et al.*, 2017) and

is usually highly idiosyncratic among species (Kumordzi *et al.*, 2019; Zhou *et al.*, 2019; Weemstra *et al.*, 2021). This disparity in responses is potentially because many root traits can be adjusted to acquire resources depending on the local (biotic and abiotic) soil environment (Freschet *et al.*, 2018; Weemstra *et al.*, 2021). For example, in contrast to leaves, which are mostly optimized for light interception while controlling water loss, roots acquire various nutrients and water, which differ in their mobility and spatial distribution in the soil matrix, which will in turn select for different trait expressions, depending on the most limiting resource (Weemstra *et al.*, 2016). Also, interactions with soil biota, in particular mycorrhizal fungi, further complicate our understanding of below-ground resource uptake and the root traits involved. As a result of this below-ground multidimensionality, a wide range of viable root trait combinations, combined with more consistent and less variable patterns in leaf trait variation, would in turn weaken intraspecific leaf–root trait relationships across environments. Thirdly, intraspecific correlations between leaf and root traits could be reduced further if leaves and roots respond to environmental variations at different spatial or temporal scales but were quantified at the same scales (Read *et al.*, 2017). Spatially, for example, root traits often vary strongly locally (Defrenne *et al.*, 2019; Weemstra *et al.*, 2021), probably because the soil environment can be highly heterogeneous at very small spatial scales (Ettema and Wardle, 2002). If drivers at such a small scale have strong effects on root trait expression, trait patterns can become unclear along larger spatial scales. In a previous study we showed that, along an elevation gradient, intraspecific root trait variation was more strongly determined locally (i.e. between conspecific plants at the same altitude) than at the landscape scale (i.e. between conspecifics at different altitudes), thereby weakening the elevation effect on root traits (Weemstra *et al.*, 2021). In comparison, the drivers of intraspecific leaf trait variation (e.g. temperature, water availability; Poorter *et al.*, 2009) vary more strongly at larger spatial scales, so that intraspecific leaf trait variation might be more consistent across species at the landscape level. Therefore, we hypothesize that along the same environmental gradient, root trait variation displays a strong response to the local environment, but a weak response to landscape-level environmental variables, and vice versa for leaves, which should reduce intraspecific leaf–root trait correlations along a common gradient.

By quantifying intraspecific covariation between analogous leaf and root traits along an elevation gradient, this study seeks to improve our understanding of how plants of the same species balance above- and below-ground resource uptake and to what extent this coupling or decoupling is determined by different leaf and root trait responses to environmental variation. Elevation gradients are considered valuable systems to examine plant responses to environmental change (Sundqvist *et al.*, 2013), because with elevation a multitude of climate and soil variables that impact plant performance change within a relatively small distance. For example, high altitudes are colder, and their soils usually have more heterogeneous nutrient distributions (Holtmeier and Broll, 2005) and are less fertile than soils at lower altitudes (Sveinbjornsson *et al.*, 1995), as cooler temperatures slow down microbial activity (Loomis *et al.*, 2006; Mayor *et al.*, 2017), mineralization

rates (Sveinbjornsson *et al.*, 1995) and litter decomposition (Moore, 1986; Loomis *et al.*, 2006; See *et al.*, 2019). Along a 1000-m elevation gradient, we test three hypotheses related to intra- and interspecific covariation between morphological leaf traits and analogous root traits [SLA and SRL, leaf thickness and root diameter, leaf dry matter content (LDMC, leaf dry mass/leaf fresh mass) and RTD], across 11 species. First, we hypothesize (H1) that within species, leaf traits vary more predictably and consistently along the elevation gradient and with associated climatic changes (e.g. temperature and precipitation) than root traits. We expect that leaf trait adjustments mostly align along a single axis of acquisitive–conservative resource strategies, so that, with increasing elevation (and lower temperatures), SLA decreases, while leaf thickness and LDMC increase, as opposed to root traits showing variable responses among species along the same environmental gradient (Weemstra *et al.*, 2021). Second, we hypothesize (H2) that, overall, leaf traits display lower local variation (i.e. at the same elevation) and greater variation at the landscape scale (i.e. between elevations) than root traits. Third, we hypothesize (H3) that, following on from H1 and H2, analogous leaf and root trait pairs will not be significantly correlated within species along the gradient.

MATERIALS AND METHODS

Study site characterization and sampling

Our study site was situated along an elevation gradient between 1400 and 2400 m a.s.l. on a south-west-facing slope, located in the Belledonne Massif in the French Alps (45°7'1"N, 5°53'35"E). Bedrock along the gradient was composed of Variscan metamorphic rocks and ophiolitic complexes (Ménot, 1988; Guillot *et al.*, 1992). Climatic data [mean annual temperature (MAT) and mean annual precipitation (MAP), including snow] were obtained from the Digitalis database (Laboratoire SILVA, Université de Lorraine-AgroParisTech-INRAE). Mean annual temperature and MAP were modelled and mapped using the Aurelhy model, which estimates climate data to a resolution of 1 km² based on spatially distributed variables that characterize the geography, topography (altitude, slope, exposure, distance to the sea) and land use at our study site (Bertrand *et al.*, 2011; Piedallu *et al.*, 2013, 2016, 2019; Stokes *et al.*, 2021). From 1400 to 2400 m a.s.l., MAT decreased from 8.5 to 5.7 °C, MAP increased from 1024 to 1187 mm, and the length of the growing season (i.e. number of months when the mean monthly temperature exceeded 5 °C; Jones and Briffa, 1995) decreased from 7.7 to 6.5 months (Supplementary Data Table S1) and was highly correlated with MAT (Pearson $r = 1$, $P < 0.001$, $n = 11$). Sites at 2400 m a.s.l. were slightly warmer and received less rainfall than the sites at 2200 and 2300 m a.s.l. (Stokes *et al.*, 2021); this is counterintuitive and may be caused by the resolution of the climate models used, but these differences were small. The treeline lies between 2000 and 2100 m a.s.l. and is defined by the replacement of acidophilous *Picea abies* forests (*Vaccinio myrtilli-Piceetea abietis*) and codominant *Pinus uncinata* and *P. cembra* trees (Petitcolas *et al.*, 1997) by arctico-alpine heath and grasslands dominated by *Vaccinium* spp., *Juniperus communis*, and graminoids including *Carex*

sempervirens, *Festuca* spp. and *Nardus stricta* (Bardat *et al.*, 2004; F. Anthelme, pers. obs.).

Along the elevation gradient (between 1400 and 2400 m a.s.l.), five 20 × 20 m replicate plots were established every 100 m (Stokes *et al.*, 2021). These plots were similar in slope (17.5 ± 5.6°) and aspect (south-west) and were located at an average distance of 100 m from each other below the treeline and 50 m between plots above the treeline. A botanical survey was performed on each plot and vascular plants were identified at the species level following the *Flora Helvetica* (Lauber *et al.*, 2018). The ground cover of trees, shrubs, herbs, bryophytes, rocks and bare soil was estimated, and vegetation ground cover (i.e. the percentage of ground surface covered by vegetation versus bare soil) significantly decreased with increasing elevation (Stokes *et al.*, 2021; Weemstra *et al.*, 2021). Ten soil samples were collected from the top 10 cm of soil below the litter layer in each plot because, in general, most nutrients are concentrated in the topsoil and because at high elevations soils were shallow, making soil samples more comparable across altitudes. Samples were pooled per elevation, air-dried and sieved to 2 mm, and their soil texture (sand, loam and clay content; g kg⁻¹), total soil organic carbon (soil C; g kg⁻¹), nitrogen (soil N; g kg⁻¹) and phosphorus (soil P; g kg⁻¹) contents, soil pH and cation exchange capacity (CEC; cmol⁺ kg⁻¹) were determined as described by Weemstra *et al.* (2021).

Trait measurements

In June and July 2018, we sampled mature plants from 11 vascular species (Table 1). Species were selected to comprise different growth forms (grasses, forbs, shrubs and trees) and to occur across a range of consecutive elevations; the number of species sampled per elevation ranged from five to 11 (Table 1). To only sample exposed leaves, understorey plants (grasses, forbs and shrubs) were mostly sampled from gaps where they were not (fully) covered by trees. For each elevation, we aimed to sample one plant per species in each of the five replicate plots, leading to five individuals per species per altitude. However, not all species were present at all elevations, and we only found three or four individuals of some species per elevation, resulting in a total of 434 plants measured (Table 1).

Collected plants (herbaceous species) or branches (woody species) with leaves attached were stored cooled in moist plastic bags during the field work and were rehydrated overnight in water at 4 °C until further analysis (Cruz-Maldonado *et al.*, 2021). Within 24 h of collection in the field, we selected between 5 and 25 healthy, fully expanded leaves without petioles from each individual. The number of leaves depended on leaf size (*Gentiana acaulis* and *Homogyne alpina*, five leaves; *Peucedanum ostruthium*, six leaves; four grass species, *Vaccinium myrtillus* and *Sorbus aucuparia*, ten leaves; *Picea abies* and *Juniperus communis*, 25 needles). Selected leaves were weighed to determine fresh weight and the flat leaf surface area was scanned with a flatbed scanner at 300 dpi (Canon MG3010 PIXMA). The total area of the scanned leaves was determined using ImageJ software (<http://rsbweb.nih.gov/ij/>). For most species, leaf thickness was measured on the scanned leaves and on one (*J. communis*), two (*Anthoxanthum odoratum*, *V. myrtillus*), or three locations on the leaf lamina using a digital

TABLE 1. Study species, occurrence and sampling range along elevations.

Species	Species abbreviation	MF	Family	Growth form	Elevation (m a.s.l.)	Sampling range (m a.s.l.)	<i>n</i> per trait
<i>Anthoxanthum odoratum</i>	AODOR	AM ^a	Poaceae	Grass	0–3100	1400–2000	34
<i>Carex sempervirens</i>	CSEMP	AM + NM ^{a,b}	Cyperaceae	Grass	1500–2400	1800–2400	35
<i>Deschampsia flexuosa</i>	DFLEX	AM ^a	Poaceae	Grass	300–2800	1400–2400	53
<i>Nardus stricta</i>	NSTRI	AM ^a	Poaceae	Grass	400–3000	1700–2400	39
<i>Gentiana acaulis</i>	GACAU	AM ^b	Gentianaceae	Forb	1400–3000	1700–2400	27
<i>Homogyne alpina</i>	HALPI	AM + EcM ^b	Asteraceae	Forb	0–3000	1700–2400	40
<i>Peucedanum ostruthium</i>	POSTR	AM ^b	Apiaceae	Forb	1000–2900	1500–2400	40
<i>Juniperus communis</i>	JCOMM	AM ^a	Cupressaceae	Shrub	0–2500	1700–2400	40
<i>Vaccinium myrtillus</i>	VMYRT	ErM ^a	Ericaceae	Shrub	0–2800	1400–2400	54
<i>Picea abies</i>	PABIE	EcM ^a	Pinaceae	Tree	0–2200	1400–2000	35
<i>Sorbus aucuparia</i>	SAUCU	AM ^a	Rosaceae	Tree	0–2000	1400–1900	30

^aAkhmetzhanova *et al.* (2012).

^bHempel *et al.* (2013).

MF, mycorrhizal association (AM, arbuscular mycorrhizal; EcM, ectomycorrhizal; ErM, ericoid mycorrhizal; NM, non-mycorrhizal).

Elevation (m a.s.l.): elevation at which a species occurs in the French Alps (www.FloreAlpes.com, 2019).

Sampling range (m a.s.l.): range of elevations at which each species was sampled.

n per trait: number of observations per species per trait.

micrometer (QuantuMike-IP65, Mitutoyo, Japan) and averaged at the individual level, with the number of measurements depending on the leaf size. For species with small, round leaves (*Deschampsia flexuosa*, *Nardus stricta* and *P. abies*), we could not accurately measure leaf thickness with the micrometer, so we calculated leaf thickness as $1/\text{SLA} \times \text{LDMC}$ (Vile *et al.*, 2005). For all other plants, the strong correlation between measured and calculated leaf thickness (Pearson $r = 0.95$, $P < 0.001$) demonstrates that this equation predicts thickness accurately. Leaves were then oven-dried (48 h at 60 °C), and their dry weight was determined. For each plant, SLA was calculated as the total area divided by the total dry weight of the sampled leaves, and LDMC was calculated as leaf dry weight divided by the leaf fresh weight.

Root trait data were obtained from Weemstra *et al.* (2021). In short, roots were collected from the same individuals as the leaves, and carefully dug out from the top 15-cm soil horizon and below the litter layer. For herbaceous species, the whole root system was dug up, while for woody species we collected three to five coarse roots with fine roots attached. From the sampled roots, we selected a subset of healthy absorptive (i.e. first- to third-order) roots with largely intact tips that were representative of the whole absorptive root system of a plant. The selected roots were washed and scanned at 800 dpi using a flatbed scanner (Epson Perfection V800 Photo); for grasses and forbs, roots were stained with methyl violet (5 g L⁻¹) prior to scanning to improve contrast. After root samples were scanned, they were oven-dried (60 °C, 48 h) and their dry mass was determined. Root scans were analysed with WinRhizo Pro (version 2009c; Regent Instruments, Canada) to obtain data on the root length and root volume in different diameter classes (from 0 to 2 mm diameter with 0.1 mm bin size). From these data, we determined SRL, mean root diameter and RTD (root dry mass/total root fresh volume in diameter classes) (Rose, 2017; Freschet *et al.*, 2021).

Statistical analyses

All statistical tests described were conducted here for leaf traits. Root trait analyses were carried out with the same statistical approaches and models as those described by Weemstra *et al.* (2021), to test our hypotheses and compare intraspecific leaf and root trait (co)variation. All analyses were carried out in R Statistical Software (R Core Team, 2021).

For our first hypothesis (H1), we tested intraspecific relationships between leaf traits and elevation, or environmental properties, with a linear regression model with the trait as dependent, and elevation, or a single environmental property, as independent variable. We were unable to apply multiple regression models within non-linear effects, as we lacked *a priori* predictions and information regarding non-linear trait–environment relationships. We applied linear or second-degree polynomial models for each leaf trait and each species depending on their Akaike information criterion (AIC; Akaike, 1974). The environmental variables tested included MAT, MAP, CEC, soil N content, pH, sand content and vegetation ground cover, which all reflect different elements of the plant’s environment (e.g. temperature, water and nutrient supply, and the degree of resource competition among plants). Regarding soil texture, we only included sand content in our analyses, because this was strongly and negatively correlated to soil clay and loam content (Pearson $r = -0.85$, $P = 0.001$ for both sand–clay, and sand–loam correlations across 11 elevations). We also tested the relationships between leaf traits and elevation and environmental variables across all plants of all species ($n = 427$ plants). For these tests, we ran mixed-effects models using the lme4 package (Bates *et al.*, 2015) with trait as dependent variable, and elevation or an environmental property as independent fixed factor, and species identity nested in growth form as random intercepts to account for the dependence between plants of the same species and/or growth form (grasses, forbs, shrubs and trees). We tested the significance of the slopes but not of the intercept.

To test whether leaves and roots responded to environmental variations at different spatial scales (i.e. H2), we partitioned the overall variance (i.e. across all plants) within each trait

across four hierarchical levels: growth form, species, conspecific plants at different elevations (representing the landscape level), and conspecific plants sampled at the same elevations (i.e. the local scale). To this end, we applied a linear mixed model to partition the variance in traits with a given trait as the dependent factor and only random effects ('elevation' (i.e. conspecific plants between elevations) nested in 'species' nested in 'growth form'). The remaining variance was partly explained by trait differences between conspecific plants growing in different replicate plots at the same elevation (Albert *et al.*, 2010; Weemstra *et al.*, 2021) and partly by unexplained variation in data. To determine whether hierarchical levels had different effects on leaf versus root traits, we ran Welch's *t*-test to compare the mean percentage of root and leaf trait variance explained by growth form, species, conspecifics at different elevation, and conspecifics at the same elevation.

For our third hypothesis (H3), we tested bivariate intraspecific relationships between the trait pairs of interest, that is, leaf–root trait correlation. Therefore, we ran standardized major axis (SMA) regression using the *sma* function in the *smatr* package (Warton *et al.*, 2012) across the mean trait values per elevation for each individual species [i.e. averaged among replicate plants at the same elevation, $n = 5–11$, depending on the number of elevations at which a species was sampled (Table 1)]. Furthermore, we used SMA regression to test intraspecific leaf–root trait covariation *within* elevations across conspecific replicate plants (i.e. sampled at the five replicate plots) at the same altitude. We used SMA regressions because, unlike simple linear regressions, they do not assume a unidirectional effect of one parameter over the other; as we focus on the direction and

strength of trait covariation, we tested only the significance of the slope of this relationship. We also tested interspecific leaf–root trait correlations across species' trait means *across* all altitudes ($n = 11$) and *within* altitudes (n depending on the number of species per elevation; Table 1) using SMA regression.

RESULTS

Intraspecific trait variation with elevation and environment

Within species, leaf traits varied significantly with elevation for most species (Fig. 1A–C; Supplementary Data Table S2). With increasing elevation, SLA most often decreased (seven species), and leaf thickness (five species) and LDMC (six species) mostly increased, but within some species certain leaf traits had non-linear or non-significant relationships with elevation. Elevation explained on average 37, 25 and 21 % of the intraspecific variation in SLA, leaf thickness and LDMC across all species, respectively (Supplementary Data Table S2). Intraspecific leaf trait patterns were also related to environmental properties. For more than half of the species, leaf trait variation was significantly related to MAT, MAP and vegetation cover (Table 2; Supplementary Data Fig. S1), explaining on average 18, 25 and 25 % of their variation (Supplementary Data Table S2). For fewer species, leaf traits were significantly related to soil properties (CEC, soil N, soil pH and sand content), explaining 10–15 % of the intraspecific leaf trait variation averaged across all species. These intraspecific leaf trait patterns were largely consistent among species: SLA increased and leaf thickness and

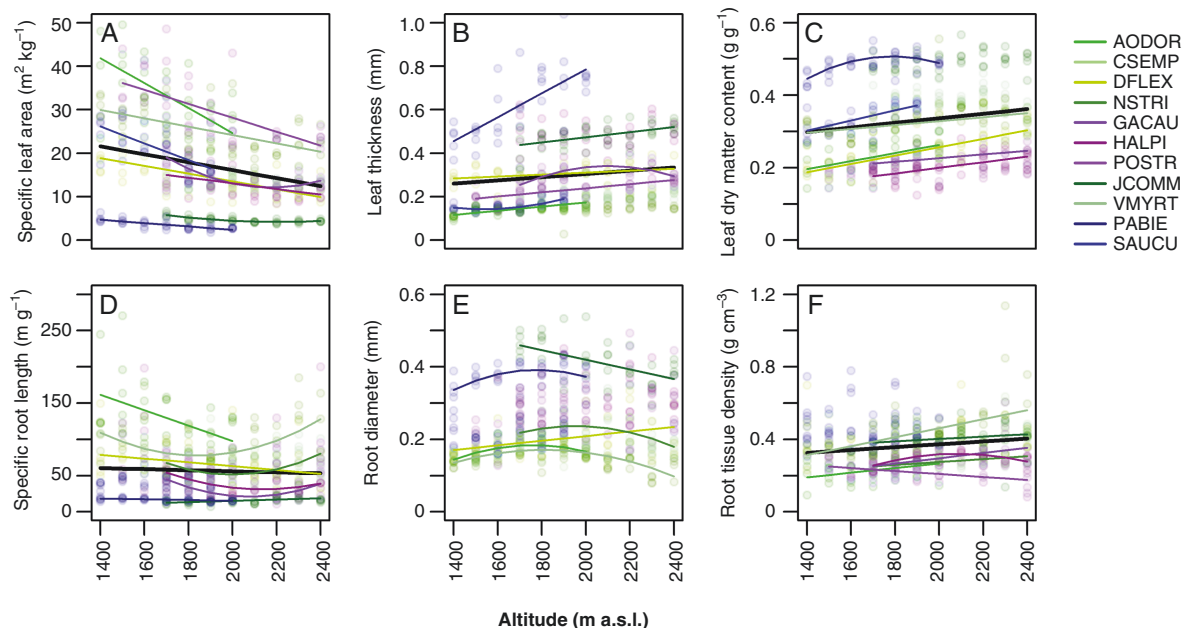


FIG. 1. Across (black line)- and within (coloured lines)-species variation in (A–C) leaf and (D–F) root traits with elevation. Points indicate trait data of individual plants along the elevation gradient, and regression lines indicate significant relationships ($P < 0.05$) between a trait and elevation. Different colours mark different species and different colour hues indicate functional types (light green, grasses; purple, forbs; dark green, shrubs; blue, trees). The black line represents relationships between traits of individuals of all species and all elevations. Non-significant relationships are not shown. Test statistics for leaves are presented in Supplementary Data Table S2, and those for roots were obtained from Weemstra *et al.* (2021). AODOR, *Anthoxanthum odoratum*; CSEMP, *Carex sempervirens*; DFLEX, *Deschampsia flexuosa*; NSTRI, *Nardus stricta*; GACAU, *Gentiana acaulis*; HALPI, *Homogyne alpine*; POSTR, *Peucedanum ostruthium*; JCOMM, *Juniperus communis*; VMYRT, *Vaccinium myrtillus*; PABIE, *Picea abies*; SAUCU, *Sorbus aucuparia*.

TABLE 2. Significant intraspecific relationships between leaf (green lines) and root traits (brown lines) and environmental variables. Line directions indicate the shape of the relationship between traits and environmental properties; line widths indicate the number of species that showed the respective response, as explained in the key. MAT, mean annual temperature; MAP, mean annual precipitation; CEC, cation exchange capacity; Sand, soil sand content; pH, soil pH; Soil N, soil nitrogen concentration; Cover, vegetation cover; SLA, specific leaf area; SRL, specific root length; LTh, leaf thickness; RD, root diameter; LDMC, leaf dry matter content; RTD, root tissue density. Statistics for leaf trait regressions are presented in Supplementary Data Table S2, and data points and regression lines for individual plants in Supplementary Data Fig. S1, and for roots they were obtained from Weemstra et al. (2021).

	SLA	SRL	LTh	RD	LDMC	RTD
MAT						
MAP						
CEC						
Sand						
pH						
Soil N						
Cover						

— 1 – 3 species
 — 4 – 6 species
 — 7 – 9 species

↗ Positive
 ↘ Negative
 ∪ U-shaped
 ∩ Bell-shaped

LDMC decreased, especially with higher temperatures, lower rainfall and greater vegetation cover (Table 2; Supplementary Data Table S2, Supplementary Data Fig. S1). The same trait patterns were observed in relation to soil properties that reflect greater nutrient availability (i.e. higher CEC, lower soil pH and sand content), but these relationships were significant for only one to four species.

Intraspecific variation in root traits was less consistent than in leaf traits: it was significantly related to elevation for six to eight species, depending on the root trait, but among species these patterns differed strongly in direction and were often non-linear (Fig. 1D–F). Relative to leaf traits, elevation explained less of the intraspecific variation in SRL, root diameter and RTD: on average 17, 15 and 13 %, respectively, across all species (Weemstra et al., 2021). Within species, root traits most frequently varied with the same environmental properties as leaf traits, i.e. MAT, MAP and vegetation cover, but these relationships were weaker, explaining on average 12, 14 and 11 %, respectively, across all species (Table 2; Supplementary Data Fig. S1; Weemstra et al., 2021). Like leaves, root traits were significantly related to soil properties within only a few species, and soil variables explained 5–9 % of the intraspecific variation in root traits across all species. Compared with leaf traits, patterns in intraspecific root trait variation with environmental variation were highly variable across species: all root traits showed differential responses to the same environmental properties depending on the species.

Variation in leaf and root traits across hierarchical levels

Overall intraspecific differences (i.e. between conspecific plants both across and within elevations) tended to have a

smaller impact on overall leaf trait variation than on root trait variation (Fig. 2). Intraspecific trait variation between conspecifics at different (i.e. ITV_{between} in Fig. 2) and at the same elevations (ITV_{within} in Fig. 2) together explained 12–20 % of the leaf trait variation versus 22–48 % of the root trait variation (mean across leaf traits, 15 %; mean across root traits, 36 %; $t = -2.55$, d.f. = 2.4, $P = 0.10$). For each of the individual leaf and root traits, the relative effect of local trait differences (i.e. within elevations) on overall trait variation was 2–4 times larger than the contribution of landscape-level (i.e. between elevations) trait differences (Fig. 2: mean leaf ITV_{between} , 4.8 % versus mean leaf ITV_{within} , 10.3 %, $t = -2.9$, d.f. = 3.4, $P = 0.05$; mean root ITV_{between} , 7.4 % versus mean root ITV_{within} , 28.2 %, $t = -3.3$, d.f. = 2.4, $P = 0.06$). The strength of the effects of intraspecific variation at the landscape level did not differ significantly between leaf and root traits (Fig. 2: mean ITV_{between} of leaves versus roots, $t = -1.1$, $P = 0.35$). Intraspecific variation at the local scale tended to have a larger impact on root traits than leaf traits (Fig. 2: mean ITV_{within} of leaves versus roots, $t = -2.9$, $P = 0.09$).

The overall variation in leaf and root traits (i.e. across all plants of all species, represented by coefficients of trait variation in Fig. 2) was highest for SRL, SLA and leaf thickness, and lower for LDMC, root diameter and RTD. It was also predominantly explained by species' identity, but more so for leaves (explaining 44–87 % of overall leaf trait variation, and the mean across leaf traits = 70 %) than roots (23–69 %, with the mean across root traits = 50 %) (Fig. 2). Growth form identity explained no variation in SLA and leaf thickness and played only a small role in the variation of SRL and root diameter, but was one of the major sources of overall trait variation in both LDMC and RTD, explaining 44 and 29 % of their variation, respectively.

Intra- and interspecific trait covariation

Within our 11 study species, analogous leaf and root traits covaried significantly for few species and trait pairs: across elevations, we found significant, positive intraspecific covariations between SLA and SRL for *A. odoratum* and *D. flexuosa*, and between LDMC and RTD for *A. odoratum* but not for any other species, and not for relationships between leaf thickness and root diameter (Fig. 3; Supplementary Data Table S3). Within elevations (i.e. across conspecific replicate plants at the same altitude), we found eight instances of significant, positive trait covariations, and they occurred for all three analogous traits pairs, at five different elevations (1500, 1600, 1900, 2000 and 2200 m a.s.l.), and within five different species (*A. odoratum*,

C. sempervirens, *G. acaulis*, *P. ostruthium* and *V. myrtillus*) (Supplementary Data Table S4). Another five correlations were significant and negative, and these were observed across all three trait pairs, at four altitudes (1800, 1900, 2100 and 2400 m a.s.l.), and within five species (*C. sempervirens*, *D. flexuosa*, *N. stricta*, *P. ostruthium* and *J. communis*).

Interspecific covariation between analogous leaf and root traits was overall (i.e. across elevations) significant and positive for SLA and SRL, and for leaf thickness and root diameter, and marginally significant for LDMC and RTD (Fig. 3; Supplementary Data Table S3). Interspecific leaf–root trait covariation within elevations was also (close to) significant and positive within all altitudes for SLA–SRL, and for leaf

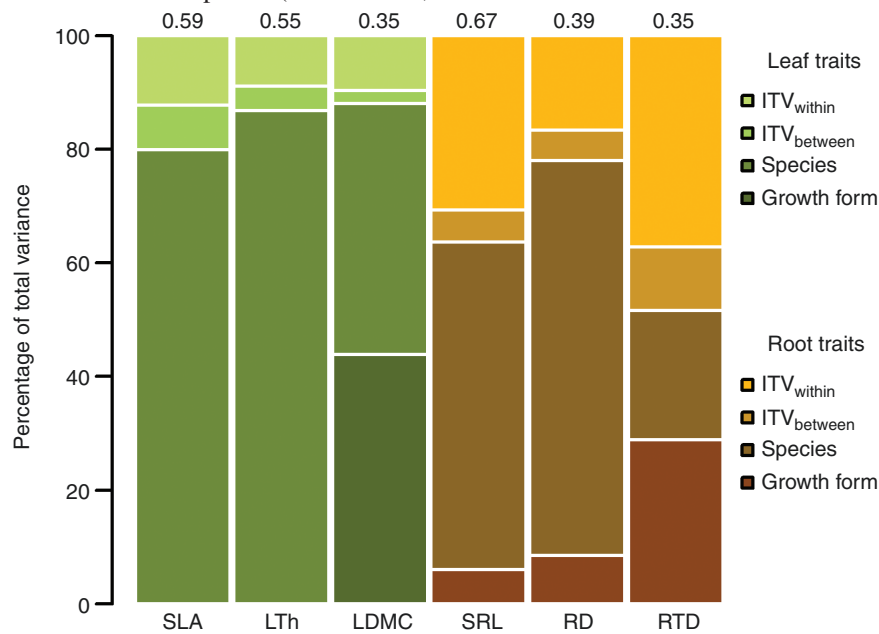


FIG. 2. Percentage of overall leaf (green bars) and root (brown/yellow bars) trait variation explained by different biological levels, indicated in the keys for leaf and root traits. $ITV_{between}$, intraspecific variation between plants at different altitudes; ITV_{within} , intraspecific variation between plants at the same altitudes. Values above each bar indicate the overall coefficient of variation for each trait. SLA, specific leaf area; LTh, leaf thickness; LDMC, leaf dry matter content; SRL, specific root length; RD, root diameter; RTD, root tissue density.

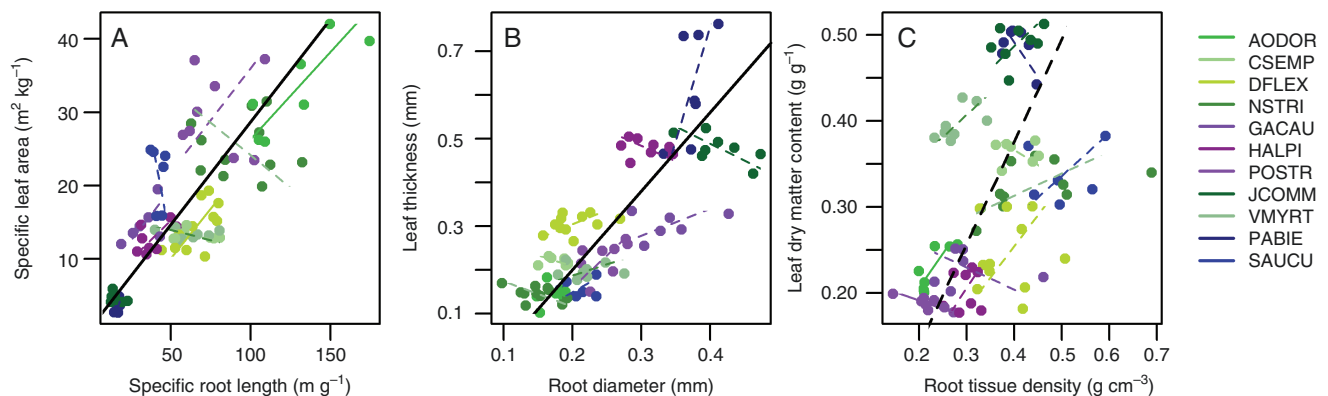


FIG. 3. Intra- and interspecific relationships between analogous leaf and root traits. (A) specific leaf area and specific root length, (B) leaf thickness and root diameter, and (C) leaf dry matter content and root tissue density. Different colours mark different species and different colour hues indicate functional types (light green, grasses; purple, forbs; dark green, shrubs; blue, trees). Data points indicate species mean trait values per altitude (i.e. averaged across replicate plants per species). Black lines indicate interspecific relationships, coloured lines indicate intraspecific relationships, solid lines mark significant ($P < 0.05$) and dashed lines indicate non-significant ($P > 0.05$) relationships between pairs of traits. Test statistics are presented in Supplementary Data Table S3. Species abbreviations are as given in the legend of Fig. 1.

thickness–root diameter, but significant and positive within only two elevations for LDMC–RTD (Supplementary Data Table S5). On average, across species, intra-elevational covariation was similar in direction (positive), strength and explanatory power (i.e. mean slope = 0.25, 1.72 and 1.14; mean R^2 = 0.70, 0.69 and 0.26 for covariations between SLA–SRL, leaf thickness–root diameter, and LDMC–RTD, respectively; Supplementary Data Table S5) to inter-elevation covariation (Supplementary Data Table S3). Across species, SLA was negatively correlated with leaf thickness and LDMC (leaf thickness and LDMC were not significantly correlated), and SRL negatively correlated with root diameter, but not with RTD (root diameter and RTD did not correlate significantly) (Supplementary Data Table S6).

DISCUSSION

Within species, leaf traits varied more consistently than root traits along the elevation gradient

In line with H1, intraspecific trait patterns along the 1000-m elevation gradient were far more consistent for leaves than roots across the 11 species. Whereas root trait patterns were highly idiosyncratic between elevations, leaf traits generally varied as hypothesized, with plants having lower SLA and denser and thicker leaves at higher elevations. Similar and largely consistent intraspecific relationships between leaf traits and elevation were also observed for the majority of species by Cruz-Maldonado *et al.* (2021) and Kichenin *et al.* (2013). Albert *et al.* (2010), however, reported more diverse intraspecific leaf trait patterns across 15 species along a 300- to 1000-m gradient in the French Alps. These authors argued that these variable leaf trait responses to elevation can be attributed to species being sampled at different positions along their distribution range. Assuming that the trait variation of a given species follows a bell-shaped curve along its distribution range, with the highest trait values at the species' environmental optimum, sampling this species at the lower or higher end of its environmental range would thus show a positive or negative trait–environment relationship, respectively (Albert *et al.*, 2010). While our study species have also been sampled at different parts of their elevational distribution range (Table 1), the intraspecific leaf trait patterns observed here were highly similar across species, as we expected.

The patterns that we observed with changing elevation likely reflect leaf trait adjustments to environmental changes along the gradient. For example, plants of almost all species produced thicker, denser and smaller leaves in response to lower temperatures at higher altitudes, which may be associated with the construction of leaves with thicker cell walls (Körner *et al.*, 1989) and a reduction in leaf size to reduce the risk of frost damage (Wright *et al.*, 2017). Such cold-tolerant leaves can reflect a more conservative resource strategy to reduce tissue turnover and thus retain plant resources, but may also result from physiological constraints, as leaf cell division may be temperature-limited (Körner *et al.*, 1989). However, other relationships between leaf traits and environmental properties were not in line with resource economics theory. Leaf resource economics predicts conservative leaf traits on dry sites (Poorter *et al.*, 2009) to reduce water loss through transpiration, and to

lower the risk of wilting (Wright *et al.*, 2001; Ackerly, 2004), and on soils with low nutrient availability (reflected here by low CEC, high soil pH, high sand content and low soil N concentration at high-elevation sites) (Freschet *et al.*, 2015). In contrast, we observed more conservative leaf traits on sites with greater precipitation, and only a few species possessed more conservative leaves on less fertile soils, which supports results from previous studies (Poorter *et al.*, 2009; Walters and Gerlach, 2013). Possibly, along our elevation gradient, temperature effects offset the impacts of the other (a)biotic variables (such as precipitation and soil fertility) on leaf traits since it is generally a stronger driver of intraspecific leaf trait variation than water or nutrient availability (Körner *et al.*, 1989; Poorter *et al.*, 2009; Stotz *et al.*, 2021).

The environmental drivers of leaf and root traits did not explain the consistent versus variable intraspecific leaf and root trait patterns along the gradient as proposed by Westerband *et al.* (2021), because roots varied mostly with the same environmental variables as leaves (i.e. MAT, MAP and vegetation cover). However, compared with leaf traits, fewer species had altered root traits in response to these environmental variables and these relationships were weaker and far more variable. For example, the effect of precipitation on leaf thickness was positive (six species) or U-shaped (one species), while on root diameter it was positive (two species), negative (one species), U-shaped (one species) or bell-shaped (three species). Other studies also reported highly variable root trait patterns along environmental gradients (Kumordzi *et al.*, 2019; Roybal and Butterfield, 2019; Zhou *et al.*, 2019; but see Isaac *et al.*, 2017), and this may result from the various ways in which roots respond to the below-ground environment. Across species, a far greater variety of viable root trait combinations exists (Kramer-Walter *et al.*, 2016), including mycorrhizal symbiosis, compared with leaf traits, which generally covary in tight syndromes (Reich *et al.*, 1997; Wright *et al.*, 2004). This phenomenon may also occur within species, as suggested by our and previous studies in natural and agro-ecological systems (Roybal and Butterfield, 2019; Kumordzi *et al.*, 2019; Zhou *et al.*, 2019; Borden *et al.*, 2020), leading to a variety of intraspecific below-ground adjustments combined with more similar leaf trait responses across elevations with different environments.

Root and leaf traits vary at different spatial scales, leading to divergent trait patterns along an elevation gradient

We hypothesized (H2) that within species, leaf traits display less variability at a local level (i.e. at the same elevation) but greater variability at the landscape scale (i.e. between elevations), compared with root traits. This variability was expected to be due to drivers of leaf trait variation such as temperature varying predominantly at larger spatial scales, while soil-related drivers of root trait variation are highly heterogeneous at small spatial scales. This hypothesis was only partly supported by our data. In contrast to H2, the degree of trait variation at the landscape level was similar for leaves and roots, even though trait patterns along the gradient were far more consistent for leaves than for roots. In line with H2, however, local effects were stronger for roots than for leaves, which may be associated with the small-scale environmental heterogeneity

of soils, owing to micro-topography and plant–soil feedbacks (Ettema and Wardle, 2002; Hutchings *et al.*, 2003; Lü *et al.*, 2012), which affect roots more directly than leaves (Read *et al.*, 2017). Across elevations, the idiosyncratic versus consistent root and leaf trait patterns, respectively, may result more from strong local environmental effects on roots than from strong landscape-level environmental effects on leaf trait variation.

We found that intraspecific leaf trait variation was larger locally (i.e. at the same elevation) than at the landscape level (i.e. across elevations). As observed in previous studies, environmental variations at a local scale, such as heterogeneity in soil nutrients or water availability, may not only be relevant for roots (as we expected), but may also have influenced leaf trait variation within species (Poorter *et al.*, 2009; Messier *et al.*, 2010; Freschet *et al.*, 2013; Wellstein *et al.*, 2017; Kumordzi *et al.*, 2019), which may explain why the local intraspecific variation in leaf traits that we observed here was larger than we expected. For example, while our sampling protocol aimed to control for variation in light conditions affecting leaf traits, plants in the forest understorey at lower altitudes might be exposed to both lower light availability and greater heterogeneity in light levels throughout the day, compared with fully exposed plants above the treeline, leading to greater leaf trait variation within than between elevations. Nonetheless, in our study, these local environmental effects on leaf traits were not strong enough to confound the strong and consistent above-ground trait patterns associated with changes in temperature and precipitation that we observed along the elevation gradient. Our results therefore suggest that although the strength of landscape-level environmental effects on leaf and root traits was similar, local (soil) environmental influences acted also on leaf but more strongly on root traits, contributing to the divergent above- and below-ground trait patterns observed between elevations.

Across the 11 species studied, overall intraspecific variation (i.e. both within and between elevations) was greater for roots than for leaves, which may also be related to the different scales at which environmental drivers influence leaf and root traits. Read *et al.* (2017) also found greater intraspecific variation in root than leaf traits along a climate gradient and they suggested two potential explanations. Firstly, stronger below-than above-ground competition between individuals may lead to niche differentiation and thus greater root trait variation (Read *et al.*, 2017), but our results do not support this explanation since vegetation cover – which may reflect the degree of plant competition – had a greater influence on leaf than root traits. Secondly, intraspecific trait variation may be greater for roots than for leaves due to the relatively large variability in soil properties that drive root trait expressions. In our study, variation in the soil properties measured (i.e. CEC, sand content, soil pH and soil N percentage) between elevations affected leaf trait variation more strongly than root trait variation (i.e. more significant trait relationships and stronger relationships), which contradicts this explanation. However, the greater intraspecific variation in roots compared with leaves mostly resulted from trait differences between conspecific plants at the same rather than at different elevations. As a result, soil heterogeneity may still be larger locally than at the landscape level, and therefore cause greater intraspecific variation in roots than in leaves. Characterizing the soil environment of roots at smaller

spatial scales than we did in our study, e.g. even at the rhizosphere level, would likely provide stronger connections between roots and edaphic factors. Evidence that root and leaf trait adjustments are modulated by environmental variations that predominantly occur at contrasting spatial scales has important implications for our understanding of how plants and plant communities respond to environmental changes. For example, there cannot be one simple picture of when intraspecific variation should be most important across scales, as this will strongly depend on the (leaf or root) trait considered (Albert *et al.*, 2011). Thus, different plant traits, both above- and below-ground, will likely play different roles in the capacity of plant species to survive in a community experiencing environmental changes, depending on the spatial scale at which these changes occur (e.g. Saar *et al.*, 2017).

Environmental effects decouple leaf and root trait variation within species along the elevation gradient

In line with H3, intraspecific analogous leaf–root traits were almost never correlated across or within elevations across the 11 species studied here. The species that did show intraspecific covariation across elevations (i.e. *A. odoratum* and *D. flexuosa*) also did not show consistent or explanatory patterns in trait covariation within elevations. As discussed above, this lack of (positive) covariation within species at least partly results from the consistent leaf trait patterns, and idiosyncratic root trait patterns (H1), so that along the gradient, leaf and root trait patterns diverge, rather than converge, as expected from a resource economics perspective. To some extent, the lack of intraspecific leaf–root trait coordination may result from different functions associated with different traits. For example, having thick roots may be considered a resource-conservative strategy, as thick roots may have longer lifespans (McCormack *et al.*, 2012; Weemstra *et al.*, 2016), but can also be considered as resource-acquisitive as they generally have a greater cortex area and higher (arbuscular) mycorrhizal colonization rates (Kong *et al.*, 2014). Similarly, thick leaves may be more cold-tolerant and thus resource-conservative (Körner *et al.*, 1989; Wright *et al.*, 2017), but they may also be acquisitive as they have more mesophyll layers packed together (de la Riva *et al.*, 2016), contributing to higher photosynthetic rates (Niinemets 2007). Especially root diameter and leaf thickness may therefore not be perfectly functionally analogous. Unravelling the (lack of) coordination among leaf and root traits therefore requires further quantification of their actual functioning, for example, by using anatomical traits that underlie organ morphology.

In this study, the different patterns in intraspecific leaf and root trait variation were in turn, at least partially, attributed to the different scales at which environmental variables influence leaf and root traits within species (H2). As roots responded more strongly to local soil environmental drivers than leaves, they did not clearly vary across the elevation gradient, contributing to the divergence of leaf and root trait patterns along the gradient. In contrast to the absence of intraspecific trait covariation, however, analogous leaf and root traits covaried positively across species, both along the elevation gradient and at

the same elevation, although these relationships were weaker for LDMC–RTD than for the other trait pairs. Our study suggests that environmental variation (at different spatial scales) and the various ways through which roots can adjust to this, decouple intraspecific leaf and root trait variation.

Conclusions

This study provides, across a substantial number of species, further evidence of a decoupling between intraspecific leaf and root trait variation, previously observed among a few species only. This decoupling resulted from largely consistent intraspecific leaf trait variation versus highly idiosyncratic root trait variation along an environmental gradient. These below-ground idiosyncrasies complicate the prediction of plant community responses and composition in a changing environment, at least at a local or landscape scale. It has recently been demonstrated that interspecific relationships between root traits and environmental variables contribute to explaining species' distribution and hence community composition, and that the positive relationship between root diameter and minimum temperature across species suggests that thick roots are beneficial as temperature increases (Laughlin *et al.*, 2021). Our study shows that intraspecific root trait–environment relationships are not general at smaller spatial scales. Therefore, beneficial root traits for greater species abundance under given site conditions may be species-specific, and so do not predict well community composition along (landscape-level) environmental gradients. To unravel how traits underlie community composition, future work should therefore ideally (1) account for both inter- and intraspecific variation in above- and below-ground traits, (2) include a large number of species to identify the different adaptive below-ground strategies of the plant community as a whole, (3) quantify a large number of traits (such as mycorrhizal or anatomical traits) that may also predict plant fitness but that are less frequently quantified, and (4) measure environmental variation at various spatial scales.

Above-/below-ground decoupling indicates that plants possess diverse whole-plant strategies when an environment changes, potentially explaining further how species can occupy different environmental niches. Trait-based models that simulate plant performance, species interactions, community assembly or (agro-)ecosystem functioning across environments therefore cannot be used to extrapolate the mechanisms that drive leaf trait patterns to roots. Instead, the variety of below-ground trait adjustments needs to be modelled independently from above-ground trait adjustments, and the environmental drivers of root adjustments would need to be modelled at smaller spatial scales than those of leaves.

Our results also contribute to improving conceptual plant-ecological models. Intraspecific trait adjustments at the local scale may obscure global, interspecific patterns in leaf and root trait covariation, but the extent of this intraspecific impact is uncertain due to limited data (Weigelt *et al.*, 2021). Studies like ours, where above- and below-ground trait variation is quantified within relatively large species sets, can therefore lead to better predictions of interspecific variation in plant resource strategies, and consequently, of species abundance (Laughlin

et al., 2021). From a more applied perspective, these insights are relevant for agro-ecological systems where above- and below-ground trait information is increasingly used to predict and improve crop responses along often steep environmental gradients at small spatial scales (e.g. in agroforestry; Isaac and Borden, 2019)

Finally, the species-specific patterns observed here result in a daunting prospect in our search for generalizable mechanisms that underlie plant responses to a changing world. However, such a diversity of plant responses to the local environment is encouraging in terms of the propensity of communities that show multiple ways to adjust to climate change.

SUPPLEMENTARY DATA

Supplementary data are available online at <https://academic.oup.com/aob> and consist of the following. Table S1: soil, climate and vegetation data across elevations and their correlations. Table S2: statistical output of regression models relating leaf traits to elevation and environmental variables per species. Table S3: statistical output of standardized major axis regression between analogous leaf and root traits within and across all species and across elevations. Table S4: results of standardized major axis regression between analogous leaf and root trait pairs *within* species. Table S5: results of standardized major axis regression between analogous leaf and root trait pairs across species within elevations. Table S6: trait correlations across species. Figure S1: intraspecific relationships between leaf and root traits and environmental variables.

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