

RESEARCH ARTICLE

Above- and below-ground responses to experimental climate forcing in two forb species from montane wooded pastures in Switzerland

Pierre Vollenweider¹  | Géraldine Hildbrand^{1,2} | Davide De Masi¹ |
Konstantin Gavazov^{1,2,3}  | Vivian Zufferey⁴ | Alexandre Buttler^{2,3}  |
Georg von Arx^{1,5} 

¹Swiss Federal Research Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

²École Polytechnique Fédérale de Lausanne EPFL, School of Architecture, Civil and Environmental Engineering ENAC, Laboratory of Ecological Systems ECOS and Plant Ecology Research Laboratory PERL, Lausanne, Switzerland

³Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Lausanne, Switzerland

⁴Agroscope Changins-Pully, Institut de recherche en production végétale, Nyon, Switzerland

⁵Oeschger Centre for Climate Change Research, University of Bern, Bern, Switzerland

Correspondence

Pierre Vollenweider

Email: vollenwe@wsl.ch

Present address

Géraldine Hildbrand, Bern University of Applied Sciences, Zollikofen, Switzerland

Funding information

WSL internal grant, Grant/Award Number: 201311N0799

Handling Editor: Katie Field

Abstract

1. Mountain ecosystems are particularly threatened by ongoing climate change and the species composition of high elevation grasslands is already changing. An open research question is how these ecosystems will adapt to changes in their key environmental constraints.
2. The responses of wooded pastures to experimental climate forcing were analysed in a transplantation experiment conducted downslope, along an elevational temperature and precipitation gradient on the lee side of Jura Mountains, Switzerland (up to +4.17°C and -35% precipitation). To improve mechanistic understanding of biodiversity and biomass decreases in response to transplantation, changes in functional traits within foliage and roots of one ubiquitous (*Taraxacum officinale*) and one montane (*Alchemilla monticola*) perennial forb species were investigated.
3. In consequence of transplantation, the two studied species raised their temperature optimum for CO₂ assimilation and net photosynthesis yield from 20 to 30°C. During cool periods, the highest rates of leaf gas exchanges were measured at the lower recipient sites. However, an opposite trend was observed during a spring drought and summer warm spell. Regarding the more integrative morpho-anatomical traits, *Alchemilla* primarily acclimated to warmer temperatures at the recipient sites with increased leaf and foliage rosette size. Missing xeromorphic and/or hydraulic adjustments in foliage and roots, its susceptibility to higher vapour pressure deficits and lower soil moisture availability was thus enhanced. *Taraxacum* showed adjustments to both warmer temperature and lower moisture availability, including reduced leaf size, lower hydraulic diameter of xylem vessels and theoretical specific hydraulic conductivity.
4. The anticipated shift in the environmental conditions at high elevation, with reduced coldness limitation but increasingly constraining water economy, could thus become particularly demanding for montane species of wooded pastures. It may

favour perennials with large phenotypic plasticity but leads to maladjustments and loss of the species which are more specifically adapted to montane conditions.

KEYWORDS

altitudinal gradient, climate change, ecophysiology, foliage xeromorphy, functional traits, grasslands, root xylem anatomy

1 | INTRODUCTION

In the recent past, regions at higher latitude and altitude have been warming up at faster rates than the rest of the world (Gobiet et al., 2014; Pepin et al., 2015). In Central Europe (Switzerland), a pronounced warming of 0.13°C per decade has been observed from 1864 to 2017, accelerating to 0.35°C between 1961 and 2017, which is some 1.6 times faster than in the rest of northern hemisphere (Ceppi et al., 2012; Isotta et al., 2019). By contrast, precipitations have shown little change during this period (Isotta et al., 2019). Corresponding to its Central European location, Switzerland is expected to show climate change patterns intermediate between those expected in northern (winter warming) versus southern (summer warming) regions until 2100 (CH2018, 2018). By the end of 21st century, the temperature increase in summer/winter with respect to the 1981–2010 reference period is thus projected to range between 0.7–2.4°C/0.6–2.0°C, in the case of a low emission scenario (RCP2.6), and 4.1–7.2°C/3.1–5.4°C, if the high emission scenario (RCP8.5) should prevail (http://sedac.ipcc-data.org/ddc/ar5_scenario_process/RCPs.html; IPCC, 2014). With this latter scenario, the precipitations are projected to decrease by –5% to –40% in summer (outside the Alps) and increase by 2%–24% in winter.

Native plants in mountain ecosystems have already started to respond to the observed warming trends in different ways (Parmesan & Yohe, 2003). Vascular species have shown upward redistribution shifts throughout mountains of northern hemisphere (Dolezal et al., 2016; Grytnes et al., 2014; Lenoir et al., 2008; Pauli et al., 2012; Vitasse et al., 2021), with recent acceleration of species enrichment on European summits strikingly synchronous with that of warming (Steinbauer et al., 2018). By contrast, the warmer temperatures at the bottom of dry inner alpine valleys have contributed to enhanced rates of tree mortality and species replacement, in relation to recurring droughts (Allen et al., 2010; Etzold et al., 2019; Rebetez & Dobbertin, 2004; Rigling et al., 2013). Considering an intermediate emission scenario (A1B), important changes in plant species composition are projected at low and middle (2000m) elevation by the end of the 21st century (CH2014-Impacts, 2014). Wooded pastures at higher versus lower elevation—similar to montane forests—may thus show contrasted response trends, with an increase in biomass and mostly stable species composition because of milder temperatures versus severe decline and replacement of drought-sensitive, for example, beech and spruce trees (IPCC, 2014; Peringer et al., 2013). Particularly the fate of formations at intermediate elevation and more specifically the species-specific dynamic thus appears uncertain, given the likely shift in

the main environmental drivers—from site coldness to reduced soil moisture availability.

Montane grassland communities, exposed to experimental climate forcing during transplantation experiments have provided insights on the plausible acclimation to forthcoming climate change in mountain ecosystems. Transplanted grassland turfs responses appear to depend on the elevation of donor site, being rather positive for high elevation sites, in apparent relation to lessened site coldness limitation, versus negative for low donor sites (Bruehlheide, 2003; Niedrist et al., 2016; Sebastia, 2007; Yang et al., 2018). With a donor site at 1350m and transplantation down to 570m, species loss up to 30% and above-ground biomass reduction of nearly 40% were thus observed in pasture woodlands (Gavazov et al., 2014). Transplanted plants can also show changes in their functional traits, with the leaf area or specific leaf area ranging among the traits most plastically responsive to changes in temperature (Guittar et al., 2016; Henn et al., 2018). These latter traits together with a few others, also easily assessed using shoot and foliage material, are particularly responsive to environmental filters (Diaz et al., 1998; Westoby & Wright, 2006). They can show strong intercorrelations, indicating functional trade-offs in the context of specific ecological strategies (Gillison, 2016; Pierce et al., 2013; Wright et al., 2004). Beside the leaf size/specific area, physiological and morphological traits responsive to climate filters thus include the leaf dry matter content, life span and photosynthetic pathway, regarding foliage, and the specific root length, fine root diameter or rooting depth, regarding the hypogenous organs (Lavorel et al., 2007). However, our current understanding is more limited for plant reactions below- versus above-ground and furthermore regarding the coordination between root and foliage responses (Fortunel et al., 2012; Liu et al., 2010; Weemstra et al., 2021). Moreover, traits easily assessed, in the framework of so-called parsimony approaches, are best suited with a view to large-scale assessments and modelling in plant community ecology. However, they appear less appropriate with a view to mechanistic understanding of ecophysiological/morpho-anatomical plant responses, as well as for the distinction between acclimation, tolerance or stress reactions (Fahn & Cutler, 1992; Fink, 1999; Vollenweider et al., 2016). Some authors thus have advocated more integrative approaches for deeper understanding of plant responses to environmental drivers (Chapin, 1991; Gillison, 2016).

The main objective in this study was to characterize the responses in situ to experimental climate forcing of two representative forb perennials from wooded pastures at mid-montane elevation and thus better understand the mechanisms behind documented biomass and biodiversity reductions (Gavazov et al., 2014). We

hypothesized that the two distinct forb species: (1) have shown similar responses to the turf transplantation treatment; (2) have adjusted to warmer temperatures and lower precipitation by enhancing their foliage xeromorphy (2.1) and by reducing the risk of hydraulic failure below-ground (2.2). Therefore, we assessed changes in physiological, morphological and anatomical traits in foliage and root organs of selected forb species in response to climate forcing, as a consequence of transplantation along an elevation gradient. We thus aimed towards a comprehensive characterization of cause–effect relationships based on whole-plant trait syndromes (Gillison, 2016).

2 | MATERIALS AND METHODS

2.1 | Experimental design

In the framework of a space-for-time substitution approach (Körner, 2003), a transplantation study was conducted at the Mountland experimental platform established in 2009 (Gavazov et al., 2013, 2014; see Appendix S1). Briefly, the donor site (1350 m a.s.l.) was located in a typical wooded pasture mosaic within the upper montane vegetation belt of southern Swiss Jura (Appendix S2). In three pasture subsites varying in shading intensity, mesocosms made of turf monoliths with topping pasture vegetation were extracted and exposed to either ambient (control treatment) or warmer (climate forcing treatment, two levels) climate conditions by transplantation either locally or at two recipient sites at 1010 and 570 m a.s.l. (Figure S1). At each experimental site—equipped with an automated weather station, the boxes buried to the soil surface were arranged in a linear common garden, recreating the shading conditions and randomizing the pasture subsite types and box position (Appendix S1, Figure S1).

With yearly temperature and precipitation differences of +4.2°C and –35% between the donor (1350 m) and lowest recipient (570 m) site, the experimental settings provided a realistic framework for simulating the warmer and drier climate at the donor site (1350 m), as projected for the years 2050 and 2100, applying the intermediate RCP 4.5 or extreme RCP 8.5 climate scenarios (Table 1). Irrespective of the RCP scenario, already the transplantation of mesocosms to the intermediate recipient site (1010 m) caused generally superior climate forcing than expected

by 2050. By 2100, the climate conditions expected at the donor site (1350 m) should mostly range between those experienced by the transplanted mesocosm turfs at the intermediate (1010 m) and lowest (570 m) recipient site. With regard to the upper wooded pastures of Jura Mountains, the two climate forcing treatments in the Mountland experiment were thus representative of climate conditions expected in the mid- and long term in the case of a rather extreme climate change scenario.

At the beginning of this study (2011), two perennial forb species were selected in the sparsely wooded pasture treatment, on the basis of (1) availability of plant individuals per mesocosm at each site (≥ 2), (2) leaf size allowing gas exchange measurements and (3) representativeness with regard to mesic wooded pastures (no fieldwork permission required). The rather montane *Alchemilla monticola* Opiz and ubiquitous *Taraxacum officinale* F.H. Wigg herbaceous perennials selected showed similar Raunkiaer plant life-form but slightly contrasting ecology (Figure S2; Körner & Diemer, 1987; Körner & Mayr, 1981). 2011 had been the warmest year in Switzerland since the beginning of measurements (1864) and also a markedly dry and sunny year (MeteoSchweiz, 2012). At the experimental sites (1350/1010/570 m), as compared to the 1980–2010 long-term averages, yearly temperature increases of +0.96/1.12/0.99°C and precipitation deficits reaching –37.4%/21.2%/17.8% were recorded (Table S1 vs. Table 1). Following a warm and dry winter, the spring of 2011 had set a new temperature record for the preceding 150 years. The rest of the vegetation season did not deviate from long-term averages (Figure S3). Throughout the 2011 vegetation season and in rather close relation with decreasing elevation, the three study sites showed a positive gradient of temperature (Figure S3) and vapour pressure deficit (VPD; Figure 1a) and a negative trend regarding the soil moisture content (SMC; Figure 1b).

2.2 | Leaf gas exchanges

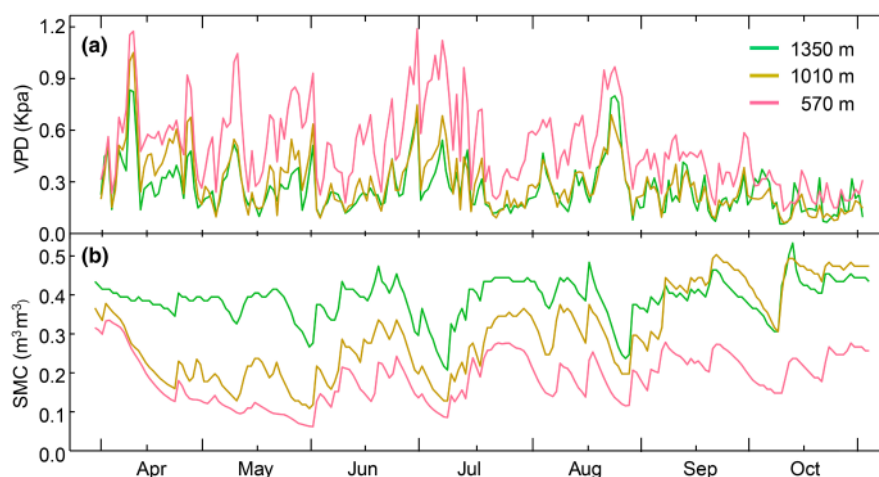
In order to assess the leaf physiology on a seasonal basis, leaf gas exchange measurements (P_N —instantaneous net photosynthesis, E —transpiration, g_s —stomatal conductance and C_i —intercellular CO_2 concentration) were repeated every 1–2 weeks on clear and sunny days from 19 May to 4 October 2011. Therefore, healthy

TABLE 1 Mean seasonal [AMJJAS] and yearly (in brackets) air temperature averages and precipitation amounts at the donor (1350 m a.s.l.) and recipient (1010 and 570 m a.s.l.) sites, as observed for the 1980–2010 reference period and projected at the donor site for 2050 and 2100, based on the RCP4.5 and RCP8.5 climatic scenarios (IPCC, 2014; Jacob et al., 2014)

	Observed—All sites 1980–2010			Projected ^a —Amburnex 1350 m a.s.l.			
	Amburnex 1350 m a.s.l.	Saint-Georges 1010 m a.s.l.	Aubonne 570 m a.s.l.	2050		2100	
				RCP4.5	RCP8.5	RCP4.5	RCP8.5
Air temperature (°C)	9.87 (5.24)	12.03 (7.08)	14.79 (9.41)	11.4 (6.7)	10.6 (6.5)	11.6 (7.3)	12.8 (8.6)
Precipitation (mm)	867.8 (1873)	737.8 (1591)	579.5 (1218)	631.4 (1685.0)	895.6 (2024.0)	677.6 (1825.1)	613.1 (1597.5)

^aEURO-CORDEX projections (<https://doi.org/10.1007/s10113-013-0499-2>) downscaled to 100 m resolution using the interpolation software 'DAYMET' (Thornton et al., 1997).

FIGURE 1 Variation in the hydric constraints (daily averages) at the donor (1350 m a.s.l.) and recipient (1010 and 570 m a.s.l.) sites during the 2011 vegetation season (April–October; Vollenweider et al., 2022). (a) Vapour pressure deficit (VPD) at 2 m above-ground level. (b) Mean volumetric soil moisture content (SMC) at 3 cm soil depth ($n = 5$ plots)



leaves from two plants per box and five boxes per site were selected and their gas exchanges measured by means of a portable photosynthesis system (LI 6400; Li-Cor) equipped with a broad-leaf cuvette. The intrinsic water use efficiency (WUE_i) was calculated as the P_N/g_s ratio (Osmond et al., 1980). At each date, the leaf gas exchanges in all plants at all three sites were measured from 10:00 am to 02:00 pm CEST, to ensure comparable leaf temperature between the different sites (daily temperature gradient between sites over the measurement period: 1.5–5°C). Other measurement conditions in the cuvette at each measurement date were kept constant, with photosynthetic photon flux density (PPFD) typical of sparsely wooded pasture ($830 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) and CO_2 concentrations of 380–390 ppm (minimum 1 min equilibration prior to reading measurements), slightly varying between measurement dates. Light and temperature- CO_2 assimilation curves were measured during distinct assessments, repeated between 13 and 20 September 2012, using three plants per species and site and assessing one site per date (10–40°C temperature increase, PPFD: $1500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, CO_2 concentration: 380 ppm).

2.3 | Foliage dynamic

The foliage dynamics in the two forb species were assessed by monitoring the leaf turnover and determining the total foliage surface, using the same plant individuals as for the ecophysiological assessments. From 23 May to 4 October, pictures of leaf rosettes were taken every 2 weeks (nine assessments) and the total amount of leaves, new leaf emergence and old leaf decay determined. Once during summer (11 August 2011), the foliage surface of plant rosettes was determined on the basis of leaf counts and individual leaf area estimates, as provided by linear models (lm) based on leaf length (*Taraxacum*; $y = 2.8059x - 13.581$, $R^2 = 0.83$) or leaf ellipse data (*Alchemilla*; $y = 1.3587x - 0.6949$, $R^2 = 0.91$). The lm relationships were established by measuring (LI-3100 Area Meter; Li-Cor) fresh leaves randomly sampled at the donor site (1350 m; $N = 88$, *Alchemilla*; $N = 97$, *Taraxacum*).

2.4 | Morpho-anatomical responses in foliage and roots

Morphological and anatomical functional traits in foliage (Table S2) were assessed using nonsenescent and fully developed leaves in two plants per box and five boxes per site, harvested during summer (25–26 August 2011). Structural root traits indicative of root hydraulic capacities and stored carbohydrate reserves (Table S2) were quantified using the same plants, which were uprooted by the end of subsequent winter and vegetative dormancy (recipient sites: 20 March 2012; donor site: 16 May 2012). The anatomical traits in foliar and main root material were measured using leaf discs (Figure S2) and $60 \mu\text{m}$ (leaf, Figure S2) and $20 \mu\text{m}$ thick (root, Figure S2) cross-sections (Appendix S3).

2.5 | Statistical analyses

As a consequence of phenological progress (*Taraxacum*), severe spring drought and other hazards in 2011, the number of plant rosettes available per species and box ($n = 2 \times 2$) within the five box replicates per experimental site was decreased during the vegetation season. The effects of experimental climate forcing on the leaf gas exchanges and root/foliage morpho-anatomical responses in the two studied forb species were analysed using linear mixed effect models (lme). The fixed effect term included the elevation of transplantation site (three levels), species (two levels) and two-way interactions (random factor: mesocosm box). With time series (leaf gas exchanges, leaf turnover), the measurement date was added to the random term. Analysing the effects of environmental drivers on leaf gas exchanges, the continuous predictors VPD and SMC, their two-way interaction and the interaction with categorical elevation and species factors were included in the fixed term of models. However, we proceeded with simpler lm whenever the Akaike information criterion with correction for small sample size (AICc) revealed poorer or indistinct model performance when including random effects ($\Delta\text{AICc} \leq 2$; Ligges, 2009). Additionally, and in order to assess the significance of any elevation/site effect

on the different dependent variables, simple linear regressions against elevation were calculated for each species taken separately. Homoscedasticity and normality of residuals were verified with Bartlett and Shapiro test respectively and log-transformation was performed for all dependent variables to meet the model assumptions. Differences in gas exchange levels between the donor (1350m) and recipient sites (1010 and 570m) at specific assessment dates were tested by means of pairwise Tukey HSD post hoc tests. Differences in the frequency of root starch abundance classes within *Alchemilla* roots were tested by means of χ^2 tests. All data were analysed using R, version 3.6.0 (R Core Team, 2019) and the LMERTEST (Kuznetsova et al., 2017), MuMIn (Barton, 2019) and NLME (Pinheiro et al., 2019) packages.

The effects of experimental climate forcing on the temperature-CO₂ assimilation curves measured in 2012 in the two forb species were analysed by means of repeated measure ANOVA using the GLM procedure of the Statistica software package (Stat Soft. Inc.). Besides the cuvette temperature (within effect factor), the factors included elevation (three levels), species (two levels) and two-way interaction (between effect factors). Violations of the compound symmetry and sphericity assumptions were remedied using Greenhouse-Geisser and Huynh-Feldt univariate adjustment factors and the univariate results were further verified using the multivariate tests for repeated measure. Homoscedasticity and normality of residuals were verified and log-transformation performed, as necessary. Differences between groups were tested by means of Tukey HSD post hoc tests.

The multivariate responses above- and below-ground were analysed by means of principal component analysis (PCA; Statistica, Statsoft Inc.), selecting the morpho-anatomical variables (LS, LMA, Dh, CD) mainly responsive to the experimental factors (transplantation and species). Using data from both forb species taken together or separately, the PCAs were based on correlation matrices, after correcting biases to normality in descriptors according to Legendre and Legendre (Legendre & Legendre, 1998) and testing correlations between descriptors (Pearson's r). The interpretation of axes was confirmed using supplementary species (PCA with the two species) and site elevation variables projected passively in the PCA planes, testing the correlation of latter variables with axes (Spearman's R). The centroids of site and species groups were passively projected in the first factorial plane.

3 | RESULTS

3.1 | Physiological responses in foliage

At all three donor (1350m) and recipient (1010 and 570m) sites, the two forb species showed a similar course of gas exchanges during the 2011 vegetation season, with strong variability between assessment dates but no apparent seasonal trend (Figure 2). Within the leaf gas exchange models (60.7% of total variance on average), the combined explanatory power of fixed effects (species, elevation, VPD, SMC and interactions) reached a maximum of 27.4% of total

variance only (Table 2), while the assessment date was apparently the main contributor to the random term (43.7% on average). Indeed, random terms with only the box factor in the, for example, morpho-anatomical models were generally not retained during the AICc comparisons (results not shown). In May, the spring drought (Figure 1, Figure S3) caused a marked drop in gas exchanges at the two recipient sites (1010 and 570m; Figure 2). Lower gas exchange values at the recipient (1010 and 570m) versus donor (1350m) sites were further observed during other sunny periods in the second half of August and end of September (Figures 1 and 2, Figure S3). However, higher gas exchange rates were generally observed at the low versus high elevation sites during wetter and colder periods. At the species level, *Alchemilla* showed higher assimilation (P_N) and WUE compared to *Taraxacum* and the species factor formed the main fixed effect component in models for the latter gas exchange variables (Figure 2, Table 2). As indicated by mostly missing interactions with the species factor, the elevation, VPD and SMC factors constrained gas exchanges in both forbs in a similar way. Although significant in the case of P_N , E and g_s models, the elevation of the transplantation site played a subordinate role in the models (higher gas exchanges overall at the 1350m donor site; Figure 2, Table 2). The VPD $\times$ SMC interaction formed the first (E , g_s) and second (P_N) fixed effect component in importance within the models, largely exceeding the contribution of VPD $>$ SMC taken separately.

Physiological adjustments in the leaf physiology within plants translocated to lower elevation were indicated by the increased temperature optimum for P_N with decreasing site elevation (Figure 3). The pattern of temperature response curves in the two species by each measurement date at each site was similar (elevation $\times$ species interaction not significant), whereas *Alchemilla* versus *Taraxacum* and the recipient versus donor sites showed higher P_N ($p < 0.0001$). During assessments, the PPFD optima in 2012 versus 2011 showed comparable values (1500 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$; light curve results not shown).

3.2 | Foliage dynamic

The total amount of leaves per *Alchemilla*'s foliage rosette increased linearly over the 2011 vegetation season ($p < 0.001$), reaching 5.1 ± 0.59 leaves per plant by 4 October (range: 2–9.5) versus 3.6 ± 0.44 by 23 May (range: 2–7.5), without significant differences between sites. The number of dead ($p = 0.031$) and new ($p = 0.021$) leaves also increased during this period, with more dead leaves at the recipient (1010 and 570m) than donor (1350m) site ($p = 0.009$ and $p = 0.041$), suggesting a slightly different foliage dynamic in response to transplantation. In *Taraxacum*, there was no apparent change in the foliage dynamic during the shortened observation period (23 May–18 July), due to loss of plant replicates. Only the number of leaves per plant rosette was responsive to the transplantation treatment, showing a decrease at the recipient sites ($p = 0.042$), for phenological reasons probably.

By 11 August and because of the aforementioned losses regarding *Taraxacum* plant replicates, the changes in the foliage surface

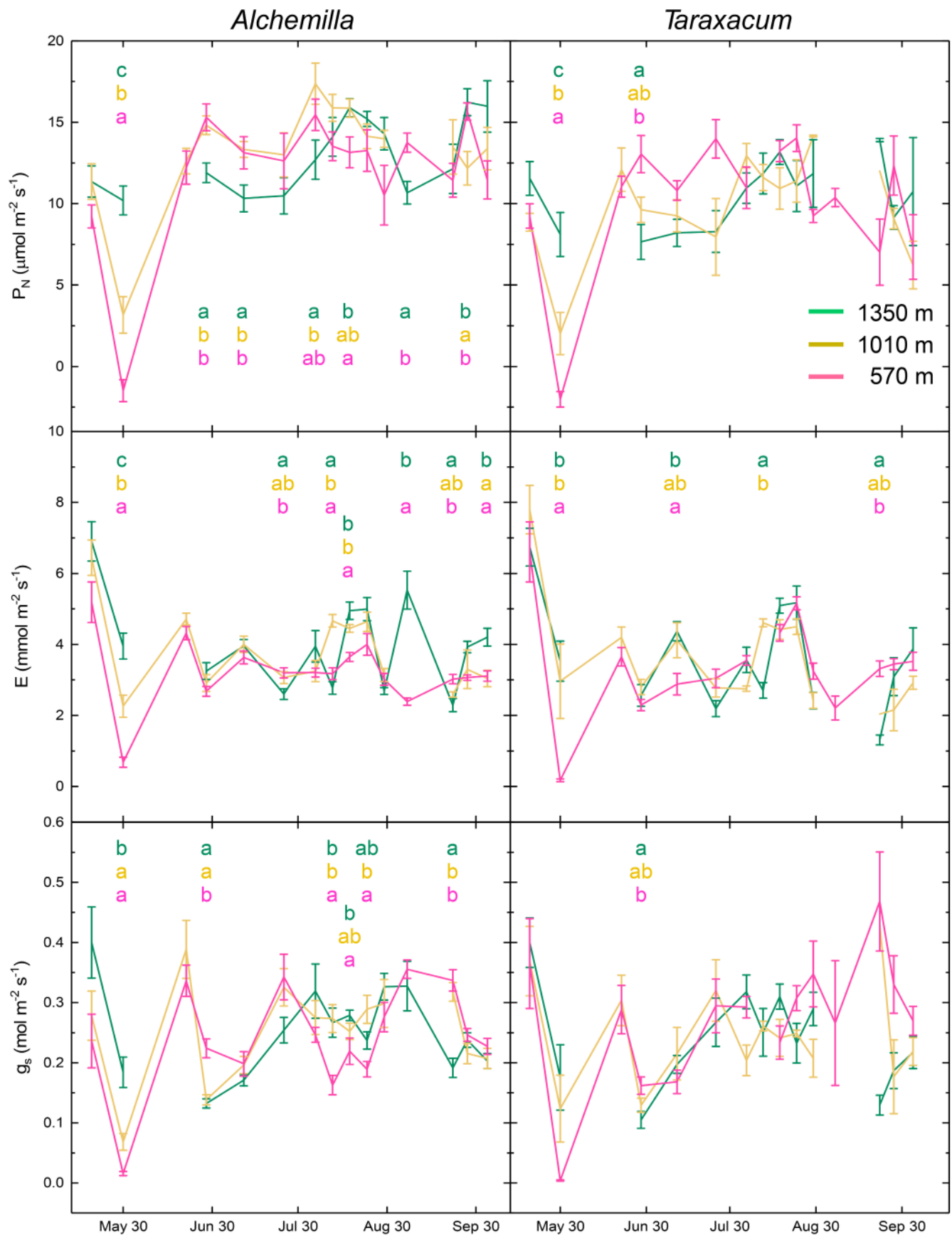


FIGURE 2 Seasonal course of gas exchange ($P_N/E/g_s$: Net photosynthesis/transpiration/stomatal conductance) in *Alchemilla* and *Taraxacum* at the donor (1350 m a.s.l.) and recipient (1010 and 570 m a.s.l.) sites in 2011 (means $\pm$ SE; Vollenweider et al., 2022). Different letters indicate significantly different gas exchange values ($p \leq 0.05$) among sites at each measurement date.

TABLE 2 Main effects of species, elevation, vapour pressure deficit (VPD), volumetric soil moisture content (SMC) and two-way interactions on gas exchange variables ($P_N/E/g_s$, WUE: Net photosynthesis/transpiration/stomatal conductance/water use efficiency; highest main effect contribution to gas exchange model indicated with bold characters) in the two studied forb species during the vegetation season (19 May to 4 October 2011; Vollenweider et al., 2022). For categorical factors, the estimate sign indicates the direction of factor contribution to models for the *Taraxacum* versus *Alchemilla* level (species, species $\times$ VPD effect) and the 1350 m, 1010 m versus 570 m site elevation level (elevation, elevation $\times$ VPD, elevation $\times$ SMC effect). Significance: nr, not retained; ns, not significant; * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

Effect ^a	P_N			E^b			g_s			WUE		
	F	Significance	Estimate sign	F	Significance	Estimate sign	F	Significance	Estimate sign	F	Significance	Estimate sign
Species	102.50	***	–	nr			2.80	(*)	+	43.90	***	–
Elevation	14.68	***	+	4.99	**	+	11.34	***	+	ns		
VPD	11.62	***	–	17.27	***	–	37.64	***	–	4.15	*	+
SMC	7.35	**	–	17.40	***	–	7.67	**	+	7.02	**	+
Species $\times$ VPD	nr			nr			6.05	*	–	nr		
Elevation $\times$ VPD	17.03	***	–	3.39	*	–/+	14.99	***	–	6.08	**	–
Elevation $\times$ SMC	14.78	***	–	5.27	**	–	24.83	***	–	nr		
VPD $\times$ SMC	27.07	***	+	28.08	***	+	68.25	***	+	nr		
R^2 total		0.604			0.619			0.721			0.482	
R^2 fixed factors		0.207			0.111			0.274			0.096	

^aSpecies $\times$ elevation and species $\times$ SMC interaction retained in none of the reduced lmem.

^blmem with the simpler structure out of the best two with indistinguishable performance, according to $\Delta AICc$.

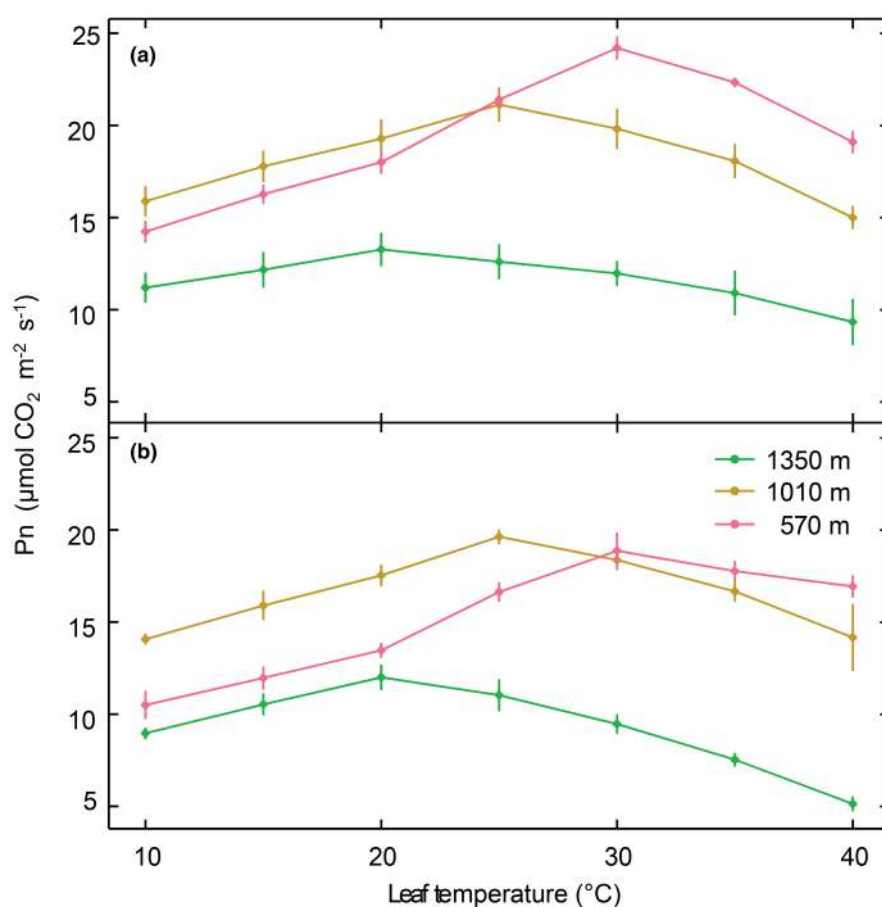


FIGURE 3 Increase in the temperature optima of net photosynthesis (P_N) in response to mesocosm turf transplantation. Temperature response curve of *Alchemilla* (a) and *Taraxacum* (b) at the donor (1350 m a.s.l.) and recipient (1010 and 570 m a.s.l.) sites. Measurements performed on 13 September (1350 m a.s.l., ambient temperature: 10°C), 17 September (1010 m a.s.l., ambient temperature: 18°C) and 20 September (570 m a.s.l., ambient temperature: 15–18°C) 2012, at optimum photosynthetic photon flux density (PPFD, 1500 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) and CO_2 concentration of 380 ppm. Values represent means $\pm$ SE; $n = 3$ plants (Vollenweider et al., 2022). The pattern of temperature response curves in the two species at each site was similar (interaction elevation $\times$ species n.s.), whereas *Taraxacum* versus *Alchemilla* and the donor versus recipient sites showed lower P_N ($p < 0.0001$).

per plant in response to transplantation could only be assessed in *Alchemilla*. In this latter species, the foliar rosettes positively responded to mesocosm transplantation ($p = 0.009$), with their total

surface at the lowest recipient site (570 m; $36.5 \pm 6.08 \text{ cm}^2$) being circa 1.7 $\times$ larger than at the donor site (1350 m; $21.7 \pm 3.06 \text{ cm}^2$; range: 9.6–100.2 cm^2 ; intermediate site at 1010 m: $27.8 \pm 3.04 \text{ cm}^2$).

3.3 | Morpho-anatomical responses in foliage and roots

The leaf morphology and anatomy in the two forb species responded to the transplantation treatment in contrasted ways (interaction site $\times$ species: $p \leq 0.004$ [morphology], $p \leq 0.05$ [anatomy, when retained in models, Table S3]). In *Alchemilla*, an increase in leaf surface (LS) with lower elevation was observed, while the leaf mass per area (LMA) remained unchanged (Figure 4a,c). In *Taraxacum*, both LS and LMA decreased with lower elevation (Figure 4b,d). The LS in both species was similar whereas *Alchemilla* versus *Taraxacum* showed larger LMA ($p = 0.0002$). Regarding the leaf structure, the veinlet network (VN) density tended to be less dense with lower elevation in *Alchemilla* leaves, while the leaf blade tended to be thicker, primarily relating to thicker upper palisade parenchyma (Figure 5a,c; Table S3). In *Taraxacum*, the principal change in response to transplantation was a reduction in leaf blade thickness, primarily relating to thinner spongy parenchyma and lower epidermis (Figure 5b,d; Table S3).

Contrasting responses in the two studied forb species to the transplantation treatment were also observed in the case of root traits. Regarding the hydraulic traits measured in xylem, the mean hydraulic Diameter (Dh, Figure 6a) and Conducting vessel Density (CD, Figure 6c) in *Alchemilla* did not change with decreasing elevation. The mesocosm transplantation caused a decrease in root Dh of *Taraxacum* (Figure 6b) whereas CD remained unchanged (Figure 6d). Because of the strong correlation with Dh (Pearson's r , $p < 0.001$,

$R^2 \geq 0.71$) and in response to the transplantation treatment, the theoretical root specific conductivity (Ks) was reduced in *Taraxacum* ($p < 0.001$) but not in *Alchemilla* (results not shown). Both Dh and Ks—but not CD—thus showed a significant elevation $\times$ species interaction ($p \leq 0.023$). Further comparing the root anatomy in the two forb species, *Taraxacum* versus *Alchemilla* showed higher Dh ($p = 0.001$) but similar Ks and lower CD ($p < 0.001$). Thicker roots contained more xylem ($p = 0.03$) and the percentage area of water conducting versus storage tissues in *Alchemilla* (cortical and pith parenchyma) versus *Taraxacum* (phloem parenchyma) was larger ($p < 0.001$; Figure S2). By the end of winter, starch abundance in root storage tissues of *Alchemilla* decreased with elevation (Figure 7, $p = 0.028$).

3.4 | Above- and below-ground responses to mesocosm transplantation

In the multivariate analysis of morpho-anatomical data from the two studied forb species, taken together, the interspecific differences were identified as the main factor of variation in below-ground (PCA axis 1, 44.8% of total variance, CD+Dh contribution = 0.91) and above-ground organs (PCA axis 2, 31.39% of total variance, LMA+LS contribution = 0.95—results not shown). More PCAs, taking each species separately, confirmed that *Alchemilla* and *Taraxacum* responded to the environmental drivers in a different way (Figure 8). In the case of *Alchemilla*, the main PCA axis was primarily correlated

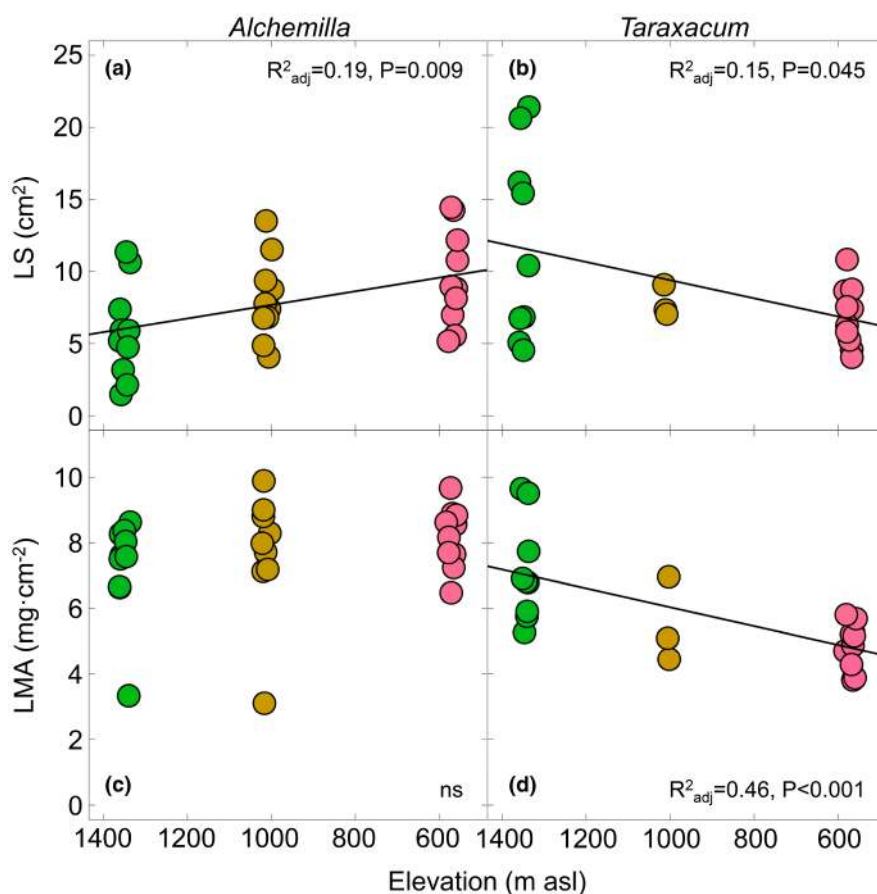


FIGURE 4 Responses of leaf morphological traits, that is, the leaf surface (LS; a, b) and leaf mass per area (LMA; c, d), to mesocosm turf transplantation in the foliage of *Alchemilla* and *Taraxacum* plants at the donor (1350 m a.s.l.) and recipient (1010 and 570 m a.s.l.) sites in 2011 (sampling performed on 25–26 August; means $\pm$ SE, $n = 10$ and 3–10 in *Alchemilla* and *Taraxacum*, total: $n = 52$). Each circle represents data from one plant individual (Vollenweider et al., 2022). Statistics refer to replicated linear regressions using log-transformed response variables, while untransformed data were used for plotting, to ease comparison. Solid lines indicate significant ($p \leq 0.05$) linear regressions. Differences between species were significant for LMA only ($p = 0.0002$).

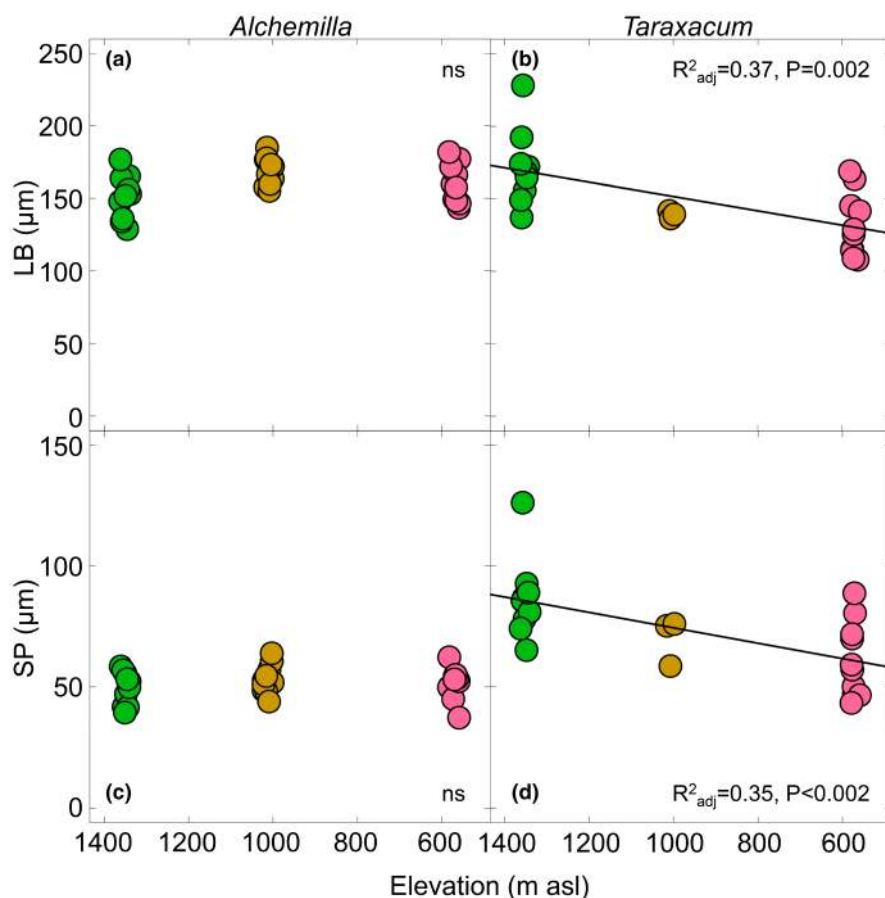


FIGURE 5 Responses of leaf histological traits, that is, the leaf blade (LB; a, b) and spongy parenchyma (SP; c, d) thickness, to mesocosm turf transplantation in the foliage of *Alchemilla* and *Taraxacum* plants at the donor (1350 m a.s.l.) and recipient (1010 and 570 m a.s.l.) sites in 2011 (sampling performed on 25–26 August; means $\pm$ SE, $n = 10$ and 3–10 in *Alchemilla* and *Taraxacum*, total: $n = 52$). Each circle represents data from one plant individual (Vollenweider et al., 2022). Statistics refer to replicated linear regressions using log-transformed response variables, while untransformed data were used for plotting, to ease comparison. Solid lines indicate significant ($p \leq 0.05$) linear regressions. Differences between species for both LB and SP were not significant.

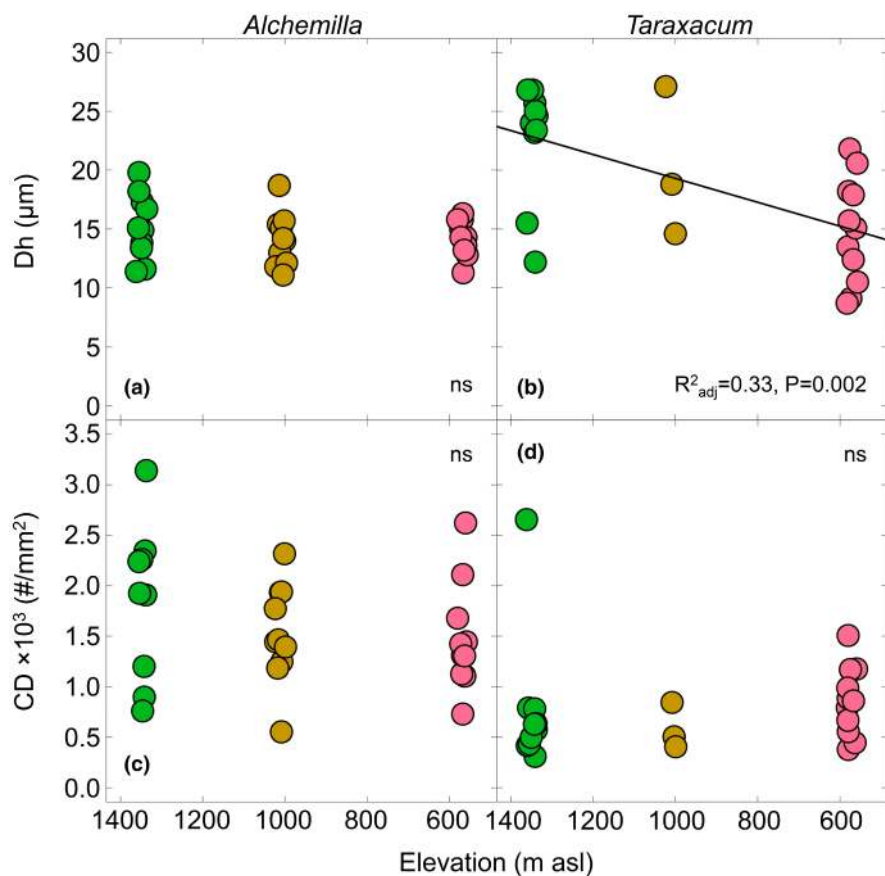


FIGURE 6 Responses of xylem anatomical traits, that is, the mean hydraulic diameter (Dh; a, b) and vessel density (CD; c, d), to mesocosm turf transplantation in the roots of *Alchemilla* and *Taraxacum* plants at the donor (1350 m a.s.l.) and recipient (1010 and 570 m a.s.l.) sites (sampling performed on 20 March 2012 and 16 May 2012 at 570, 1010 and 1350 m; means $\pm$ SE, $n = 10$ and 3–10 in *Alchemilla* and *Taraxacum*, total: $n = 52$). Each circle represents data from one individual plant (Vollenweider et al., 2022). Statistics refer to replicated linear regressions using log-transformed response variables, while untransformed data were used for plotting to ease comparison. Solid lines indicate significant ($p \leq 0.05$) linear regressions. Differences between species for both Dh and CD were significant ($p \leq 0.001$).

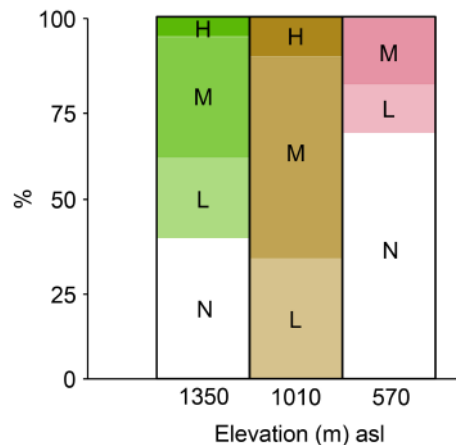


FIGURE 7 Relative frequency of root starch abundance classes at the donor (1350 m a.s.l.) and recipient (1010 and 570 m a.s.l.) sites in *Alchemilla*. Sampling (52 plants) performed on 20 March 2012 at the recipient sites (1010 and 570 m), and 16 May 2012 at the donor site (1350 m). Abundance classes with regard to starch filling per storage tissue averaged per plant: High, H: 67%–100%; medium, M: 33%–66%; low, L: ≤33%; none, N: 0% (Vollenweider et al., 2022).

with the below-ground variables (CD+Dh contribution = 0.78), independent of site elevation (Figure 8a). The second PCA axis was principally correlated with the above-ground variables (contribution of LMA+LS = 0.78). As confirmed by the distribution of site centroids and correlation with the supplementary elevation variable (Spearman's R , $p < 0.05$), it could be interpreted as a site elevation axis. However, it explained only one fourth of variance in the morpho-anatomical dataset for *Alchemilla*. Among all morpho-anatomical variables selected, LS showed the highest responsiveness to the translocation treatment (communality with PCA axis 2 = 0.426), with larger values at lower elevation (Spearman's R , $p < 0.05$). In the case of *Taraxacum* and in contrast to *Alchemilla*, the main PCA axis showed significant correlation with elevation (Spearman's R , $p < 0.05$; Figure 8b). Both above-ground and below-ground variables contributed to this axis (Dh > LMA > CD > LS = 0.39 > 0.25 > 0.20 > 0.15), with Dh most specifically responding to the translocation treatment (communality with PCA axis 1 = 0.760) and the root xylem variables showing a higher relative contribution share than the foliage traits. There was no straightforward interpretation for the second axis. Hence, the root and leaf traits responded independently to the translocation treatment in *Alchemilla*, whereas they showed coordination in *Taraxacum*.

4 | DISCUSSION

4.1 | Physiological responses in foliage to shifts in the main environmental drivers

At the warmer and more water-constrained recipient sites (570 and 1010 m), as compared to donor site (1350 m), the transplanted forb plants showed typical adjustments to higher temperatures in their leaf physiology, in the form of temperature optimum for

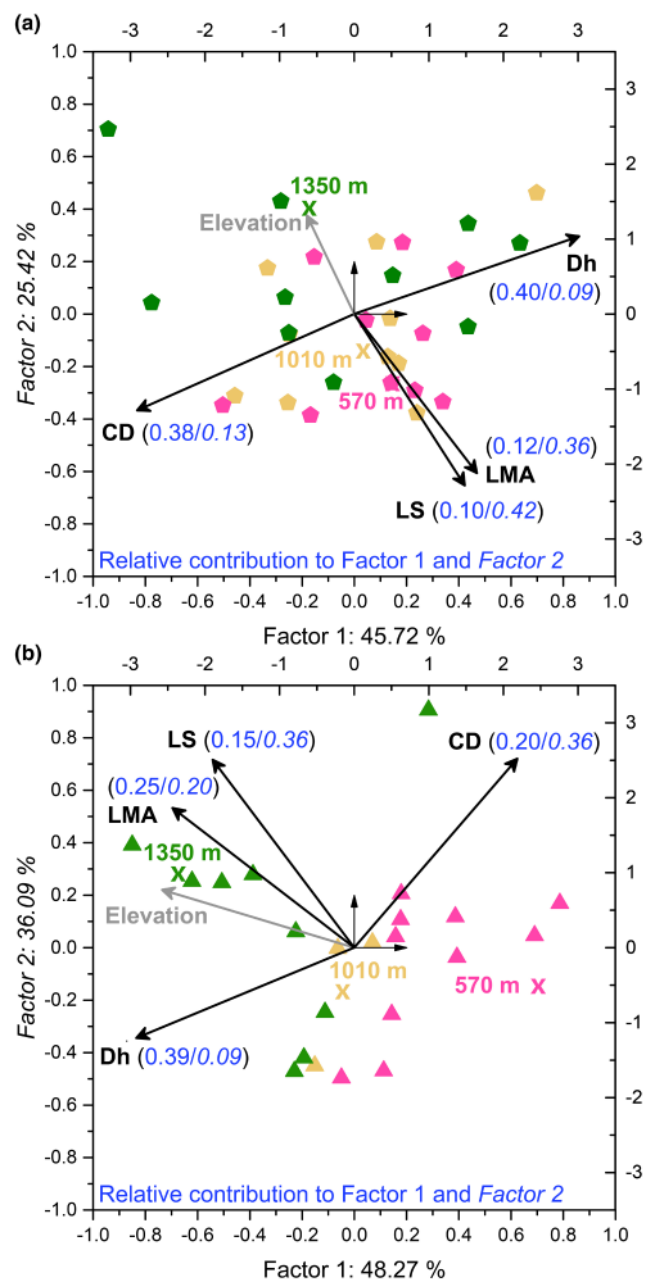


FIGURE 8 Unconstrained ordination (PCA) of above- (LMA, LS) and below-ground (Dh, CD) morpho-anatomical parameters responsive to treatment and species factor in the transplantation experiment (Vollenweider et al., 2022). Ordination of data from *Alchemilla* (a) and *Taraxacum* (b) within the scatter plot formed by the first (45.7% and 48.3% of total variance) and second (25.4% and 36.1% of total variance) principal components. The supplementary variable elevation is projected passively. The centroids of donor and recipient sites (1350, 1010 and 570 m) are indicated with crosses and symbols are given for the sites with the corresponding colours. $N = 30$ (a), 24 (b)

assimilation enhanced up to 30°C and higher assimilation yield (Berry & Björkman, 1980; Körner, 2015). Given the PPFD values for half-shaded habitats ($830 \mu\text{mol photons m}^{-2} \text{s}^{-1}$), the temperature optima of 20°C at the donor site were close to values commonly measured in alpine meadows (22°C at PPFD = 1000; Körner, 2003). However,

no clear gas exchange pattern or trend between sites was found in 2011 and the succession of cold and warm episodes primarily determined whether higher rates of gas exchange would be observed at the lower or higher site, with a low explanation power of the elevation factor in the leaf gas exchange models as a consequence. At the recipient sites during hot spells, the SMC sizably dropped while VPD peaked and the lower gas exchange values indicated that plants suffered under drought stress (Breda et al., 2006; Leuzinger et al., 2005). The VPD×SMC interaction as the main leaf physiology determinant confirmed the importance of water economy in the Mountland experiment, which, particularly during hot spells, exceeded that of temperature—the dominant environmental constraint for the tested perennials at the donor site. Overall, the leaf physiology data thus suggest a shift in the main constraining environmental factors, namely the site coldness at the 1350m donor versus the water economy at the 570 > 1010m recipient sites. Such a shift in the main environmental drivers along the elevation gradient and regarding the leaf gas exchanges is consistent with other experimental (De Boeck et al., 2016) and observational evidence, also including *Alchemilla* and *Taraxacum* (Körner & Mayr, 1981). The same was also observed in the soil compartment (Mills et al., 2014). By 2050 and 2100, the wooded pastures at mid-montane elevations, such as those in the Jura Mountains, may then experience a gradual shift from a mostly temperature- to water-limited environment. In response, the herbaceous species may show some phenotypic acclimation in their leaf physiology and other traits further discussed below, contributing to tolerance and resilience, as observed in 2011 after hot spells.

4.2 | Conflicting morpho-anatomical adjustments to warmer temperatures and low water availability

Both *Alchemilla* and *Taraxacum* showed a consistent spectrum of morpho-anatomical traits, which shed light on less transient responses to transplantation than those observed, analysing the leaf gas exchanges alone. Despite similar life-forms, leaf size and thickness or theoretical root hydraulic conductivity, the two species showed different responses to the transplantation treatment, indicative of contrasts in their respective ecology.

In *Alchemilla*, primarily the foliage was responsive. The increase in leaf size formed a typical adjustment to higher temperatures (Guittar et al., 2016; Körner, 2003; Lavorel et al., 2007; Scheepens et al., 2010), also observed in beech saplings in a follow-up experiment using the same experimental settings (de Carcer et al., 2017). Consistent with the (1) larger total foliage surface, (2) looser VN and (3) tendency to thicker mesophyll tissues, it indicated the development of more productive foliage and plants (Fahn & Cutler, 1992; Sebastia, 2007; Wright et al., 2004). This finding was corroborated by the aforementioned increase in assimilation yield, measuring temperature-CO₂ assimilation curves at the recipient sites and lower starch reserves in roots (Chapin, 1980). It might then be associated with (1) higher, for example, N nutrient content within leaves, (2) higher leaf diffusive conductance, (3) low tissue density,

(4) high rates of C and nutrient uptake and (5) low leaf life span, as typically found with higher habitat fertility (Chapin, 1980; Lavorel et al., 2007; Westoby et al., 2002). One frequent trade-off is a lessened protection of leaf structures with respect to disturbance by, for example, drought stress (Chapin, 1991). Accordingly, the *Alchemilla* plants transplanted at the lower recipient sites showed no xeromorphic adjustments [e.g. higher LMA, increased VN, thicker cuticles, smaller but more numerous stomata and root vessels, increased proportion of root storage tissues (Fahn & Cutler, 1992; Fink, 1999; Lens et al., 2016; Schuldt et al., 2016; von Arx et al., 2012)], which then contrasted with the higher foliage xeromorphy observed in the aforementioned beech saplings (de Carcer et al., 2017). Given their shallow root system, adjustments to warming but not to the also increased hydric constraints at the lower elevation sites strongly suggest that the susceptibility to drought stress of transplanted *Alchemilla* plants had been enhanced. These maladjustments could then contribute to significant drops in gas exchanges during warm and dry spells, as observed during the spring of 2011.

In *Taraxacum*, both the roots and foliage were responsive, not only to higher temperatures, but also to lower water availability. The main responses to translocation were observed in the taproots, where reduced Dh and lower theoretical hydraulic conductivity, given unchanged CD, formed typical adjustments to water stress (Breda et al., 2006; von Arx et al., 2012). Reducing the evaporative surface, foliage adjustments such as smaller leaves were also consistent with acclimation to more constrained water economy (Abrams, 1994; Fahn & Cutler, 1992). However, the leaf xeromorphy of plants transplanted at recipient sites was also reduced, as indicated by the (1) concomitant reduction of LMA, (2) thinning of leaf blade and (3) thinner epidermis (Cunningham et al., 1999; Fahn & Cutler, 1992), contrasting with findings in beech at the same experimental sites (de Carcer et al., 2017). Given *Taraxacum* spring bloom and the phenological acceleration observed along the experimental gradient (Signarbieux et al., 2017), the smaller leaf size and associated spectrum of foliar traits may relate to advanced and accelerated phenophase, as observed for other mid- and high-elevation species and consistent with an escape strategy (Gugger et al., 2015). The higher assimilation yield, as observed during measurements of temperature-CO₂ assimilation curves was similar to findings in *Alchemilla* and formed the only adjustment attributable to acclimation to warmer temperature at the recipient sites. Contrasting with *Alchemilla*, the morpho-anatomical traits thus primarily responded to reduced water availability and secondarily to beneficial warmer temperatures. Hence, the acclimation in *Taraxacum* appeared to primarily rely on both structural and phenological adjustments.

4.3 | Better acclimation of ubiquitous species as a consequence of integrative responses to environmental drivers

Contrasting adjustments at the recipient sites shed light on the unequal acclimation potential of *Alchemilla* and *Taraxacum*. The

rather species-specific overall response pattern was reminiscent of trends observed in several studies in plant community ecology (Albert et al., 2010; Pescador et al., 2015) or during the aforementioned follow-up project (de Carcer et al., 2017). In *Alchemilla* with orthogonal foliage and root response patterns, as indicated by PCA, the functional traits showed little coordination between the above- and below-ground plant parts, similar to findings in tropical trees (Fortunel et al., 2012). However, in *Taraxacum*, both root and foliage traits contributed to the first PCA—in this case an elevation axis, but they did not show correlations (data not shown). Other studies on herbaceous species suggest rather whole-plant responses, with coordinated suites of leaf and root trait (i.e. nitrogen concentration or tissue density; Craine et al., 2005; Craine & Lee, 2003; Liu et al., 2010; Tjoelker et al., 2005). The primary divergence between the two studied species was observed for root hydraulic traits, which may at least partly relate to the prevalence of ontogenetic determinants regarding the xylem structure (Schweingruber et al., 2011, 2013). Thicker palisade parenchyma in *Alchemilla* versus *Taraxacum* probably contributed to higher assimilation yield, in a characteristic way for montane versus ubiquitous species (Körner, 2003; Liu et al., 2020; Niinemets, 2001). Higher responsiveness for changes in the temperatures rather than water economy in *Alchemilla* was also in line with its montane ecology and characteristic acclimation patterns found in high elevation species (Körner, 2003). In their alpine environments, these latter plants thus show numerous adaptations to low temperatures and associated physical constraints (e.g. higher illumination, more frequent fog, recurring frosts; Larcher, 1983) but overall weak xeromorphy, even in the case of thickened and dense leaves (Codignola et al., 1987; Körner, 2003). Responding to changes both beneficial, regarding temperatures, and detrimental, regarding the moisture availability, ubiquitous plants such as *Taraxacum* or beech (de Carcer et al., 2017) appeared to sense multiple changes in environmental drivers more specifically and address their physiological consequences in a more integrative way.

5 | CONCLUSIONS

During the transplantation experiment, the selected ubiquitous *Taraxacum* and montane *Alchemilla* forb species showed rather contrasting responses in their roots and foliage. The hypothesized similarity of responses to translocation in these two forbs had to be rejected (Hypothesis 1). Regarding the hypothesized acclimation to changes in the environmental conditions (Hypothesis 2), none of the two species enhanced its foliage xeromorphy (rejection of 2.1) and only *Taraxacum* showed the expected below-ground reduction of hydraulic failure risk (partial confirmation of 2.2). Other trait responses including the, for example, increase in dark respiration or key macronutrients (N, P) and decrease in leaf life span can be additionally postulated. From a mechanistic perspective, the ubiquitous species from montane wooded pastures may be favoured by the expected climate changes over those restricted to higher habitats, as a consequence of integrative whole-plant acclimation to multiple and

partly combating effects of changes in the main environmental drivers. By enabling the development of more productive foliage, but without further dehydration protection, the higher temperatures may thus promote maladjustments, enhancing the drought stress susceptibility, and thereby the replacement of typical montane species by ubiquitous and more adaptable species.

AUTHOR CONTRIBUTIONS

Alexandre Buttler was PI in the Mountland experiment; Konstantin Gavazov contributed to experiment design and climatic data; Pierre Vollenweider, Alexandre Buttler and Georg von Arx conceived the study's ideas and designed its methodology; Géraldine Hildbrand and Davide De Masi collected the data; Vivian Zufferey supervised the ecophysiological part of study; Georg von Arx and Pierre Vollenweider analysed the data; Pierre Vollenweider wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We thankfully acknowledge technical support by Dirk Schmatz (climatic data), Patrick Landolt (field work), Terry Menard (light microscopy of foliage) and Constant Signarbieux (2012 ecophysiological assessments). This work was supported by WSL internal grant (201311N0799) to G.v.A., P.V. and A.B.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Public access to data used in this study: The climatic data from the experiment (Table S1; Figure S3) are available from the Envidat repository with the identifier <https://www.doi.org/10.16904/envidat.179> (Buttler et al., 2016); The data used for climatic projections (Table 1) are available from the EURO-CORDEX database with the identifier <https://doi.org/10.1007/s10113-013-0499-2> (Jacob et al., 2014); Trait data measured above- and below-ground (Table 2, Table S3; Figures 1–8) are available at the TRY repository with the identifier <https://doi.org/10.17871/TRY.91> (Vollenweider et al., 2022).

ORCID

Pierre Vollenweider  <https://orcid.org/0000-0002-4995-1419>
Konstantin Gavazov  <https://orcid.org/0000-0003-4479-7202>
Alexandre Buttler  <https://orcid.org/0000-0001-5900-4573>
Georg von Arx  <https://orcid.org/0000-0002-8566-4599>

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How to cite this article: Vollenweider, P., Hildbrand, G., De Masi, D., Gavazov, K., Zufferey, V., Buttler, A., & von Arx, G. (2023). Above- and below-ground responses to experimental climate forcing in two forb species from montane wooded pastures in Switzerland. *Functional Ecology*, 37, 432–446. <https://doi.org/10.1111/1365-2435.14212>