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Addressing the altitudinal and geographical gradient in European beech via photosynthetic parameters: a case study on Calabrian beech transplanted to Denmark

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European beech (*Fagus sylvatica* L.) is becoming one of the go-to species in reconstructing declining conifer stands in Europe under climate change. Assisted migration may be considered when looking for suitable beech seedlings. Knowledge about the photosynthetic performance of beech seedlings is fundamental to understanding an essential part of their growth and survival potential in different planting conditions. We investigated the within-provenance variation in photosynthetic performance driven by altitude in contrast to inter-provenance variation given by geographical distance. The experiment was conducted on seedlings replanted in a Danish common garden comprising a cluster of provenances with various altitudinal subgroups transplanted from the Calabria region (Italy) and two local Danish provenances. Provenance and within-provenance variation in chlorophyll fluorescence (ChlF) kinetics, gas exchange (GE), flushing, and senescence were assessed. ChlF measurements revealed within-provenance differences based on altitude of origin and could distinguish between the two Danish provenances. In contrast, GE parameters detected variation in the geographical distance among Italian provenances. High-elevation subgroups of Italian provenances showed the best leaf-level photosynthetic performance in Danish weather conditions with high precipitation levels. Altitude of origin can be a significant source of within-provenance variation. We demonstrated that assessing this variation in young trees may be instrumental in maximizing the potential of provenance variation across diverse planting sites.

KEYWORDS

OJIP transient, photosynthesis, common garden, beech refugia, phenology

1 Introduction

Pure conifer forests in most of Europe are experiencing a decline due to ongoing climate change (Ols and Bontemps, 2021). Introducing broadleaved tree species into pure conifer stands to increase the resistance of forests to windthrow and bark beetle attacks is becoming the main objective of European forestry management (Griess et al., 2012). This effort has increased demand for seedlings of broadleaved species from suitable provenances and ecotypes (Ammer et al., 2008; Hazarika et al., 2021), such as European beech (*Fagus sylvatica* L.).

However, the survival of beech forests has become a great concern. A decline in the growth of most European beech populations is predicted for the following decades, with the only exception being the northern limit range of distribution (Martinez del Castillo et al., 2022). The rapidly changing climatic conditions might pose a challenge, primarily due to the increased risk of more severe drought events (Leuschner et al., 2001; Bolte et al., 2007; Geßler et al., 2007; Fotelli et al., 2009; Aranda et al., 2015). Populations at the southern margin of beech's natural distribution are at the highest risk due to constantly increasing temperatures and prolonged periods of drought (Jump et al., 2006). On the other hand, xeric beech populations exhibit specific morphological and physiological adaptations to overcome unfavorable conditions, such as thicker leaves and increased drought tolerance (García-Plazaola and Becerril, 2001; Aranda et al., 2015). South-eastern European populations also show higher adaptability to different soil water contents and faster growth than north-western provenances (Nielsen and Jørgensen 2003), and higher net assimilation of CO₂ rates (Čater and Levanič, 2019). This geographical trend is apparent in the phenology of European beech as north-western populations tend to flush later during Spring (Robson et al., 2013); the same study also stated that lower elevation populations flush earlier but could not fully separate the effect of elevation from latitude and longitude because most of the south-eastern provenances also originated from high altitudes. Beech displays a limited sensitivity to temperature along the altitudinal and temporal gradient in a study by Vitasse et al. (2009). However, long photoperiods tend to increase their bud growth rates, as reported by Basler and Körner (2014). Additionally, beech is known to maintain flushing patterns after replanting (Robson et al., 2013). Given the variation across the large distribution area, the full potential of provenances should be thoroughly assessed to ensure healthy and prosperous beech forests in the future.

Marginal populations are of great importance, which is well acknowledged and documented (e.g., Hampe and Petit, 2005). In the case of European ash (*Fraxinus excelsior* L.), the populations from the south-eastern edge of the distribution range are of particularly high value because they hold higher genetic diversity (Erichsen et al., 2018). Identifying and preserving such populations in beech might provide a potential source of stress-tolerant planting material suitable for assisted migration to regions experiencing beech decline (Aranda et al., 2015; Dounavi et al., 2016). Most of these diverse populations in Europe persist in the locations of former glacial refugia. The Italian peninsula served as one of the Mediterranean refugia for European beech during the glacial periods (Pott, 1997; Magri et al., 2006). However, new evidence suggests that the beech from the South Italian refugia did not spread much into central and northern Europe. The populations that mainly colonized central and northern Europe after the last glacial period spread likely from relatively northern refugia in

southern France, eastern Alps, and southern Moravia – southern Bohemia (Magri et al., 2006). Therefore, the Mediterranean refugia could provide highly contrasting local phenology and growth adaptations reflected by different photosynthetic rates.

Several physiological parameters, such as photosynthetic assimilation measured by gas exchange (GE) and chlorophyll fluorescence (ChlF), can be used to estimate a tree's leaf-level performance and offer a quick assessment of the physiological status (Bussotti et al., 2010; Niinemets, 2010). ChlF induction (OJIP transient) kinetics indirectly represent the photosynthetic process (Jansen et al., 2009; Jalink and Schoor, 2015) and the adaptive ability to tolerate variable environmental conditions (Baker and Rosenqvist, 2004). Calculated ChlF parameters and the shape of the OJIP curve have shown a high sensitivity to various stress factors (Strasser et al., 2004; Perboni et al., 2012; Kalaji et al., 2016). Each O-J-I-P phase corresponds to different processes in the photosynthetic apparatus – the O-J rise represents the reductions of the acceptor side of PSII, the J-I phase is connected to the oxidation or reduction of the plastoquinone pool, and the I-P phase has to do with re-reduction of plastocyanin (PC)⁺ and P700⁺ in PSI (Oukarroum et al., 2009). Therefore, the calculated parameters have a different sensitivity to different stress factors and environmental conditions (Bussotti et al., 2010, 2020). ChlF kinetics can assess photosynthesis efficiency, responses to changing environments, genetic variation, and ecological diversity (Murchie and Lawson, 2013; Čepl et al., 2016; Mishra, 2018; Akinyemi et al., 2023). Specific studies of the photosynthesis performance of beech provenances under variable environmental conditions confirmed differences depending on the altitude of origin (Pšidová et al., 2018) or climate of origin (Robson et al., 2012; Kučerová et al., 2018; Kurjak et al., 2019). However, studies comparing ChlF kinetics with GE concerning adaptation across altitudes, and thus climatic gradients within provenances, are, to our knowledge, missing.

Our study, based on a common garden experiment, evaluated the differences in ChlF kinetics and GE among beech provenances and provenances' altitudinal subgroups. Specifically, we aimed to investigate the parameters/indexes of each method (ChlF and GE), which could be used to distinguish provenances and their altitudinal subgroups. Further, we assessed leaf flushing and senescence as supporting measurements in the same vegetation season and two years later.

We hypothesized that the leaf-level photosynthetic performance in chosen parameters—P_N (GE method) and PI_{TOTAL} (ChlF method) of Italian provenances would be higher than that of the Danish provenances. In addition, we investigated leaf-level photosynthetic performance among altitudinal subgroups of Italian provenances.

2 Materials and methods

2.1 Plant material

European beech (*Fagus sylvatica* L.) seedlings (1–2 years old) were replanted from Denmark and Italy (Calabria). The established common garden experiment comprised three Italian provenances (distinct mountain ranges) with various altitudinal subgroups and two Danish provenances representing local populations. The seedlings were planted into HerkuPlast boxes—model Quick Pot 12T/18

(plastic tray made by Kubern GmbH, Germany) in September 2016 and placed in an outdoor common garden experiment in the nursery of the University of Copenhagen. Plants from the same provenance subgroup were planted in each box (3×4 plants initially). Each block within the original common garden comprised at least nine Italian provenance subgroups (from three provenances), retaining an incomplete randomized block design (9 boxes in each of 20 incomplete blocks). The Italian provenances were replicated in 9 to 15 boxes. The Danish material was replicated within two blocks in 3 and 4 boxes of 12 seedlings each. Seedling mortality occurred after replanting, which violated the original design before the measurement date. The spatial design of the common garden experiment in September 2018 is visualized in [Supplementary Figure S1](#). The imbalances due to this mortality were accounted for in the REML analysis ([Butler et al., 2018](#)), and the model details are specified in the description of the statistical analysis.

For our study, we selected Italian plant material from provenances Aspromonte and Sila Grande, each containing two within-provenance subgroups: Aspromonte (1,270 and 1,900 m.a.s.l.) and Sila Grande (1,300 and 1,900 m.a.s.l.) and Danish plant material originating from two different seed stands, F13—Stenderup Midtskov and F419—Holstenshuus ([Table 1](#)). The climate data in [Table 1](#) are a selection of the bioclimatic variables from WorldClim version 2.1 climate data for 1970–2000 ([Fick and Hijmans, 2017](#)). All provenance origins and the experimental site are shown in [Figure 1](#).

The main measurements (ChlF and GE) were done at the end of the second growing season of the trees in the common garden setting in September 2018 (10th–14th). There was sufficient precipitation at the end of August 2018 in Copenhagen, and during the measurement week, it was cloudy with occasional rainfall. The trees were not under any apparent stress during that time.

2.2 Chlorophyll fluorescence kinetics

We measured ChlF kinetics using FluorPen FP110 (PSI, Brno, Czech Republic). We included all surviving (320) seedlings of the six provenance subgroups in the ChlF measurements ([Table 2](#)). ChlF induction (OJIP) parameters were measured after dark adaptation (detachable leaf clips placed on leaves 20 min before the measurement). After attaching the instrument to a leaf clip, a saturating light pulse (blue light, 470 nm) of 3,000 μmol·m⁻²·s⁻¹ intensity was applied to the leaf. Rapid fluorescence transient was captured within the first second

of the measurement. We calculated the OJIP parameters according to [Strasser et al. \(2010\)](#) using the FluorPen software (Photon Systems Instruments, Brno, Czechia) and additional parameters from the I-P phase calculated using the raw data according to [Oukarroum et al. \(2009\)](#). All measured and calculated parameters are listed in [Table 3](#).

2.3 Gas exchange

We measured GE (representing net photosynthesis parameters) on randomly selected 84 individuals from all six provenance subgroups: A1270 (14), A1900 (17), SG1300 (19), SG1900 (19), DK-F13 (7), DK-F419 (8). We monitored the light curve using the gas exchange system LI-6400XT (LICOR, NE, United States), where a diode (6400-02B-LED) maintained uniform and stable light inside the chamber. The temperature was adjusted to the external conditions. We sampled leaves from the crown's upper part for light curve measurement. The reference CO₂ concentration was set to 415 μmol·m⁻²·s⁻¹. We monitored the decreasing light as follows: 1,500–1,000–500–250–120–60–40–20–10–0 μmol·m⁻²·s⁻¹. The assimilation rate was displayed against the applied light, and the measured points were fitted according to the equation by [Prado and De Moraes \(1997\)](#) designed for woody species:

$$P_N = \{P_{gmax}[1 - \exp(-k(I - I_{comp}))]\} - R_D,$$

where P_N is the net photosynthesis rate [μmol (CO₂) m⁻²·s⁻¹]; P_{gmax} is the maximum gross photosynthesis rate [μmol (CO₂) m⁻²·s⁻¹]; k is the adjusting factor; I is the photosynthetic photon flux density [μmol (photons) m⁻²·s⁻¹]; I_{comp} is the light compensation point [μmol (photons) m⁻²·s⁻¹]; and R_D is the dark respiration rate [μmol (CO₂) m⁻²·s⁻¹] derived from the curve according to [Prado and De Moraes \(1997\)](#). The constants were optimized by minimizing the residual sum of squares using the Solver function in MS Excel ([Lobo et al., 2013](#)). The GE parameters used in the analyses are listed in [Table 4](#).

2.4 Flushing scores

The first flushing assessment was done in May 2018 at the beginning of the second vegetation season. The second flushing assessment took place in April 2020 at a permanent site in a nearby

TABLE 1 Characteristics of locations of origin and the common garden experimental plot in Copenhagen (C-G CPH), where the study was conducted.

Location	A1270	A1900	SG1300	SG1900	DK-F13	DK-F419	C-G CPH
Altitude [m.a.s.l.]	1270	1900	1300	1900	20	80	8
Latitude (WGS84)	38.11225	38.16074	39.24688	39.28361	55.48083	55.10828	55.68615
Longitude (WGS84)	15.83665	15.91953	16.55135	16.45029	9.6505	10.30975	12.54405
Annual mean temperature [°C]	10.2	7.8	9.8	6.6	7.7	8	8.5
Mean temperature of warmest quarter [°C]	17.8	15.6	17.3	14.1	15.2	15.4	16.6
Mean temperature of coldest quarter [°C]	3.4	1	3	-0.2	0.5	0.9	1
Annual precipitation [mm]	821	849	874	860	722	654	622
Precipitation of wettest month [mm]	112	113	121	113	81	71	67
Precipitation of driest month [mm]	20	22	22	25	39	37	34

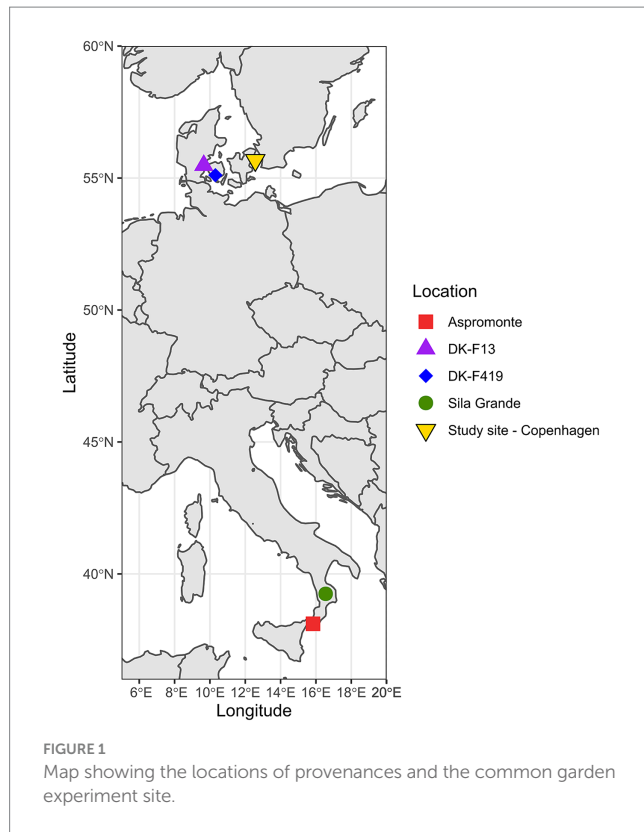


FIGURE 1 Map showing the locations of provenances and the common garden experiment site.

TABLE 2 Seedlings count and survival rate at the end of the vegetation season in 2018 and 2020.

Provenance	Count 2018	Survival 2018	Count 2020	Survival 2020
A1270	41	28%	40	28%
A1900	52	31%	48	29%
DK-F13	20	56%	17	47%
DK-F419	29	60%	28	58%
SG1300	53	49%	52	48%
SG1900	125	69%	59	NA

The survival rate for SG1900 cannot be calculated because not all seedlings from this provenance subgroup were replanted into the new permanent site in 2019 due to a higher seedling count in relation to other provenances.

forest where the seedlings were replanted in 2019. The flushing was scored only on the Italian provenances in 2018 and on all provenances in 2020. In total, 361 individuals were included in the first flushing assessment and 247 in the second. The flushing scores scale is based on a 7-point scale by Robson et al. (2013):

1. Dormant buds
2. Buds swollen and elongated
3. First green visible from bud scales, buds adopt a silver-grey sheen
4. First folded hairy leaves visible but remain partially held by the bud
5. Entire leaves cascade from the bud; the leaves are still folded and flaccid
6. Leaves unfolded but still corrugated, fan-shaped and hairy
7. Leaves fully unfolded, smooth, and flat.

TABLE 3 List of ChlF parameters and their formulas.

F_0	Minimal fluorescence intensity from a dark-adapted leaf (50 μ s)
F_j	Fluorescence intensity at J-step (at 2 ms)
F_i	Fluorescence intensity at I-step (at 30 ms)
F_m	Maximal fluorescence intensity; PSI, photosystem I; PSII, photosystem II; RC, reaction center
F_v	Maximal variable fluorescence $F_v = F_m - F_0$
V_j	Relative variable fluorescence intensity at J-step $V_j = (F_j - F_0) / (F_m - F_0)$
V_i	Relative variable fluorescence intensity at I-step $V_i = (F_i - F_0) / (F_m - F_0)$
t_{Fm}	Time to reach F_m (in ms)
F_m/F_0	
M_0	Approximated initial slope of the fluorescence transient $M_0 = 4 (F_{300} - F_0) / (F_m - F_0)$
S_M	$S_M = \text{Area} / (F_m - F_0)$ (multiple turn-over)
$F_v/F_m (\Phi_{P0})$	The maximum quantum yield of primary photochemistry. $F_v/F_m = \Phi_{P0} = 1 - F_0/F_m$
Ψ_0	The probability that a photon trapped by the PSII reaction center will enter the electron transport chain. $\Psi_0 = 1 - V_j$
Φ_{E0}	$\Phi_{E0} = [1 - (F_0/F_m)] * \Psi_0$
Φ_{D0}	$\Phi_{D0} = F_0 / F_m$
Φ_{Pav}	$\Phi_{Pav} = \Phi_{P0} (S_M / t_{Fm})$
ABS/RC	Average absorbed photon flux per PSII RC (apparent antenna size of an active PSII) (M_0/V_j) ($1 / F_v/F_m$)
TR₀/RC	Maximum trapped exciton flux per PSII RC. $TR_0/RC = M_0/V_j$
ET₀/RC	Electron-transport flux from Q_A to Q_B per PSII RC. $ET_0/RC = (M_0/V_j) (1 - V_j)$
DI₀/RC	Dissipated energy flux per RC. $DI_0/RC = (ABS / RC) - (TR_0 / RC)$
δ_{R0}	Efficiency with which an electron can move from the reduced intersystem electron acceptors to the PSI end electron acceptors. $\delta_{R0} = (1 - V_i) / (1 - V_j)$
Φ_{R0}	Quantum yield of reduction of end acceptors of PSI. $\Phi_{R0} = \Phi_{P0} * \Psi_0 * \delta_{R0}$
PI_{ABS}	Multi-parameter photosynthetic performance index expressing energy conservation from absorption of light by an antenna. $PI_{ABS} = [(V_j/M_0) * (F_v / F_m)] * (F_v / F_0) * [(1 - V_j)/V_j]$
PI_{TOTAL}	Performance index for energy conservation from photons absorbed by PSII antenna until the reduction of PSI acceptors. $PI_{TOTAL} = PI_{ABS} * \delta_{R0} / (1 - \delta_{R0})$
ΔV_{IP}	Decrease of the relative contribution of the I-P phase. $\Delta V_{IP} = 1 - V_i = (F_m - F_i) / (F_m - F_0)$

The parameters used in the analyses are in bold letters.

2.5 Senescence scores

Leaf senescence was assessed at the beginning of November 2020 for all 244 individuals in the permanent experimental site. The senescence assessment was based on a 0–9 point scale assessing the majority of leaves: 0 represents leaves with no

TABLE 4 List of GE parameters.

P_N	Net assimilation of CO ₂ [$\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$]
LCP	Light compensation point [μmol (photons) $\text{m}^{-2}\cdot\text{s}^{-1}$]
LSP₉₅	Light saturation point for $P_N + R_D$, equal to 95% of $P_{N_{\text{max}}}$ [μmol (photons) $\text{m}^{-2}\cdot\text{s}^{-1}$]
R_D	Dark respiration rate [μmol (CO ₂) $\text{m}^{-2}\cdot\text{s}^{-1}$]
ϕ_{10}	Quantum yield at $I = 0 \mu\text{mol}(\text{photon}) \text{m}^{-2}\cdot\text{s}^{-1}$ [μmol (CO ₂) μmol^{-1} (photons)]

Parameters in bold were later used for further analyses.

visible signs of senescence; 1–4 represents leaves with increasing levels of yellowing; 4–8 represents leaves with increasing amounts of necroses, and 9 represents dry and dead leaves.

2.6 Statistical analysis

The statistical analysis was conducted using the R software, version 4.2.1 (R Core Team, 2022).

A linear mixed model (LMM) was fitted to evaluate the photosynthetic parameters with the terms:

$$Y = \mu + Xa + Z_1S_i + Z_2S_j : S_j + e,$$

where Y corresponds to the data vector; μ is the overall mean effect; X is an incidence matrix of a fixed effect; a is the fixed vector of individual provenance; Z_1 and Z_2 are incidence matrices of random effects; S_i is the random effect of a block; S_j ; S_j is the random effect of a box (S_j) nested in a block (S_i); e is the random vector of errors that were normally and independently distributed. The model was analyzed using the ASReml-R software (Butler et al., 2018). After fitting the model, outliers (0–10 per parameter) caused by error measurements were removed from the dataset. Custom R code for pairwise comparisons (least significant difference—LSD) was used for GE and ChlF parameters. We did not use any control for multiple testing.

Wald test (W -value) was implemented to evaluate the fixed effects of country of origin (a is the fixed vector of the country of origin in the model above for this analysis, replacing the fixed vector of individual provenance) when comparing their interaction on all measured traits between pooled Italian and Danish provenances.

For radar chart visualization, the following formula was used to perform a z -score normalization of the model-predicted mean values of photosynthetic parameters:

$$Z - \text{SCORE} = (X - \mu) / \sigma,$$

where X is the mean value of provenance in a given photosynthetic parameter predicted by the linear mixed model; μ is the mean of the data in a given photosynthetic parameter; σ is the standard deviation of the data in a given photosynthetic parameter.

The flushing scores were analyzed using a two-sided Wilcoxon signed-rank test 4.2.1 (R Core Team, 2022).

3 Results

3.1 Photosynthetic performance

The Italian provenances had significantly higher average values compared to the Danish ones in ChlF parameters F_m/F_0 ($W = 1.55e-06$), F_v/F_m ($W = 3.93e-07$), ψ_0 ($W = 1.53e-05$), ϕ_{E0} ($W = 7.27e-08$), δ_{R0} ($W = 0.001$), ϕ_{R0} ($W = 2.76e-07$), PI_{ABS} ($W = 5.16e-08$), PI_{TOTAL} ($W = 6.58e-07$), ΔV_{IP} ($W = 3.75e-06$), and significantly lower average values than the Danish ones in parameters ϕ_{D0} ($W = 3.76e-07$), ABS/RC ($W = 4.24e-07$), TR_0/RC ($W = 1.47e-05$), DI_0/RC ($W = 8.81e-09$). There was no clear observable difference in parameters ET_0/RC ($W = 0.721$), ϕ_{Pav} ($W = 0.259$). The model-predicted means of ChlF parameters for each provenance subgroup are outlined in Table 5. The Italian provenances manifested higher average values than the Danish ones in GE parameters LSP_{95} ($W = 7.90e-08$) and P_N ($W = 2.64e-05$). Under the same irradiation, Italian provenances reached the maximum assimilation rate faster than the Danish ones, and their net assimilation was higher. There was no clear trend or difference in the light compensation point (LCP) ($W = 0.764$) or dark respiration (R_D) ($W = 0.309$). All provenances needed the same photon flux density to assimilate more CO₂ than they respire. No difference was observed in the quantum yield of photosynthesis (ϕ_{10}) ($W = 0.701$), which signifies that the molar ratio between carbon assimilated to photons absorbed in the process does not differ among provenances. The model-predicted means of GE parameters for each provenance subgroup are shown in Table 6. The performance of individual provenance subgroups for each chosen parameter from both types of measurement is visualized in Figure 2.

3.2 Provenance pairwise comparison

All provenance subgroup pairs were compared in photosynthetic parameters of ChlF and GE (Figure 3). Both ChlF and GE parameters distinguished Italian and Danish provenances. ChlF parameters DI_0/RC , ϕ_{R0} , PI_{TOTAL} , and ΔV_{IP} differed among Italian provenance subgroups based on altitude (Figure 3—pink). The GE parameters LSP_{95} and P_N showed differentiation between Italian provenances from Aspromonte and Sila Grande, i.e., different geographical locations (Figure 3—gray and red). In contrast, no altitudinal trend was visible from the GE data, while ChlF measurements could not separate all geographically distant provenances. A different pattern occurred when comparing the two local Danish provenances. The ChlF measurements yielded seven usable parameters (F_m/F_0 , F_v/F_m , ϕ_{E0} , ϕ_{D0} , ABS/RC , TR_0/RC , DI_0/RC) that capture differences between the two Danish provenances (Figure 3—light green). The two Danish provenances could not be separated based on the GE parameters. The only parameter that distinguished the Italian within-provenance variation in altitude of origin and also the Danish provenances was DI_0/RC (Figure 3—pink and light green).

3.3 Bud flushing

In May 2018, provenances from the two mountain ranges, Sila Grande (SG) and Aspromonte (A), varied significantly ($p = 1.92E-15$) in

TABLE 5 Predicted means of ChlF parameters with standard errors (SE) of each provenance subgroup (based on LMM).

	A1270	A1900	DK-F13	DK-F419	SG1300	SG1900
F_m/F_0	4.765 (0.113)	5.065 (0.104)	3.921 (0.194)	4.528 (0.234)	4.804 (0.114)	4.976 (0.092)
F_v/F_m (Φ_{P0})	0.786 (0.005)	0.801 (0.005)	0.742 (0.009)	0.778 (0.011)	0.789 (0.005)	0.797 (0.004)
Ψ_0	0.600 (0.012)	0.625 (0.011)	0.534 (0.020)	0.547 (0.024)	0.602 (0.011)	0.614 (0.009)
Φ_{E0}	0.472 (0.011)	0.501 (0.010)	0.384 (0.019)	0.427 (0.022)	0.474 (0.011)	0.49 (0.087)
Φ_{D0}	0.214 (0.005)	0.199 (0.005)	0.258 (0.009)	0.222 (0.011)	0.211 (0.005)	0.202 (0.004)
Φ_{Pav}	937.1 (2.010)	934.6 (1.813)	941.1 (3.578)	935.7 (3.767)	937.6 (2.020)	932.0 (1.464)
ABS/RC	1.508 (0.034)	1.457 (0.031)	1.842 (0.060)	1.638 (0.068)	1.557 (0.034)	1.493 (0.026)
TR ₀ /RC	1.196 (0.226)	1.165 (0.021)	1.393 (0.041)	1.272 (0.043)	1.228 (0.023)	1.19 (0.018)
ET ₀ /RC	0.701 (0.019)	0.726 (0.018)	0.738 (0.033)	0.690 (0.039)	0.739 (0.020)	0.729 (0.016)
DI ₀ /RC	0.325 (0.014)	0.292 (0.013)	0.474 (0.025)	0.364 (0.029)	0.330 (0.014)	0.303 (0.011)
δ_{R0}	0.558 (0.010)	0.565 (0.009)	0.506 (0.017)	0.504 (0.016)	0.533 (0.010)	0.577 (0.008)
Φ_{R0}	0.258 (0.009)	0.282 (0.008)	0.194 (0.015)	0.214 (0.018)	0.256 (0.009)	0.282 (0.007)
PI _{ABS}	4.039 (0.316)	4.838 (0.294)	1.461 (0.546)	2.465 (0.661)	3.985 (0.324)	4.507 (0.259)
PI _{TOTAL}	5.073 (0.495)	6.464 (0.460)	1.597 (0.854)	2.538 (1.028)	4.905 (0.510)	6.228 (0.405)
ΔV_{IP}	0.333 (0.010)	0.353 (0.009)	0.271 (0.017)	0.275 (0.019)	0.325 (0.010)	0.354 (0.008)

TABLE 6 Predicted means of GE parameters with standard errors (SE) of each provenance subgroup (based on LMM).

	A1270	A1900	DK-F13	DK-F419	SG1300	SG1900
LCP [$\mu\text{mol (photons) m}^{-2}\cdot\text{s}^{-1}$]	6.648 (0.51)	6.332 (0.48)	6.316 (0.87)	5.438 (1.33)	6.256 (0.48)	6.062 (0.47)
R _D [$\mu\text{mol (CO}_2\text{) m}^{-2}\cdot\text{s}^{-1}$]	0.134 (0.033)	0.164 (0.032)	0.100 (0.055)	0.101 (0.077)	0.150 (0.034)	0.104 (0.031)
LSP ₉₅ [$\mu\text{mol (photons) m}^{-2}\cdot\text{s}^{-1}$]	685.9 (30.2)	683.4 (27.7)	373.2 (47.4)	423.6 (46.1)	587.6 (26.7)	598.8 (26.3)
P _N [$\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$]	14.06 (0.64)	13.67 (0.59)	7.61 (1.07)	8.67 (1.11)	12.21 (0.58)	12.05 (0.56)
ϕ_{10} [$\mu\text{mol (CO}_2\text{) }\mu\text{mol}^{-1}$ (photons)]	0.063 (0.0016)	0.061 (0.0015)	0.061 (0.0024)	0.063 (0.0025)	0.063 (0.0015)	0.063 (0.0014)

Provenance effects were significant ($\alpha=0.05$) for parameters shown in bold, later used for further analyses.

bud flushing scoring. The more southern Aspromonte showed more developed buds at the time of assessment. An altitudinal difference could be seen within the Sila Grande provenance, where SG1900 showed significantly less ($p=2.87E-14$) developed buds than SG1300. No such difference could be observed within the Aspromonte provenance. The differences from May 2018 between all individual pairs are outlined in Table 7. The distribution of flushing scores illustrating the magnitude of difference between the provenance subgroups in May 2018 is shown in Figure 4A. The flushing assessment from April 2020 on the surviving trees revealed the same persisting trend (visualized in Figure 4B), although the flushing was in an earlier stage during this assessment. The differences between the provenances and their subgroups in April 2020 (Table 7) remained significant for the same pairs except for SG1300 and A1270. The overall difference between Aspromonte and Sila Grande remained substantial (Figure 4—red vs. green). In addition, in 2020, the Danish provenances were also scored. Both Danish provenances were in a later flushing stage than the Italian ones, except for SG1300, which showed a late flushing pattern more similar to the Danish beech. The significance of the differences is shown in Table 7.

3.4 Senescence

At the beginning of November 2020, all the provenances showed signs of senescence. The majority of leaves were yellowing on almost

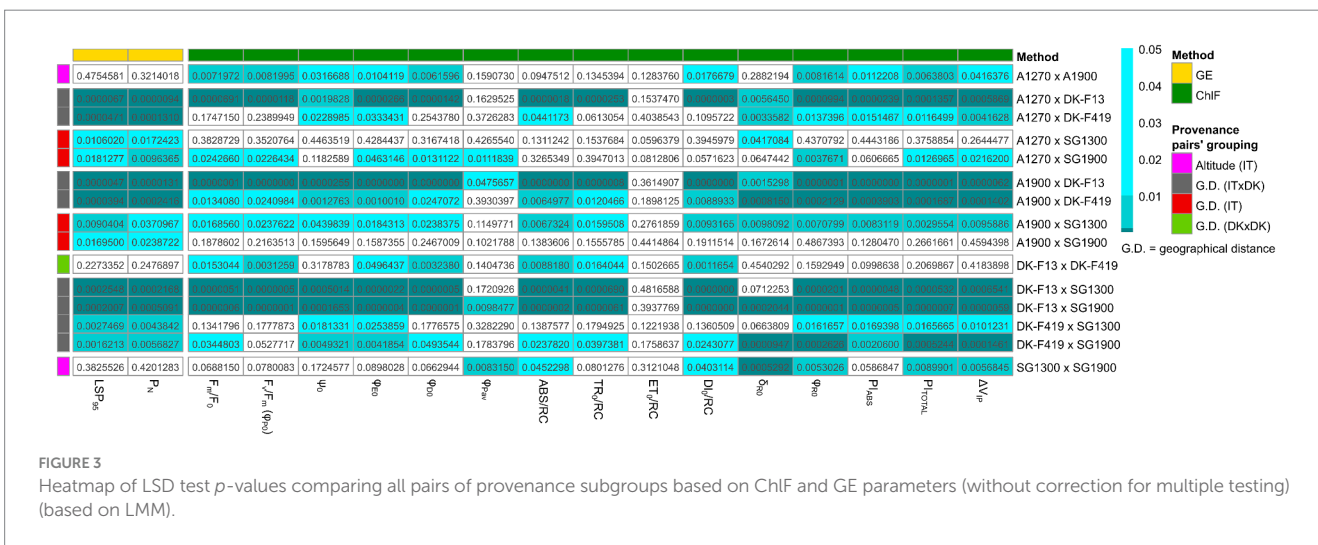
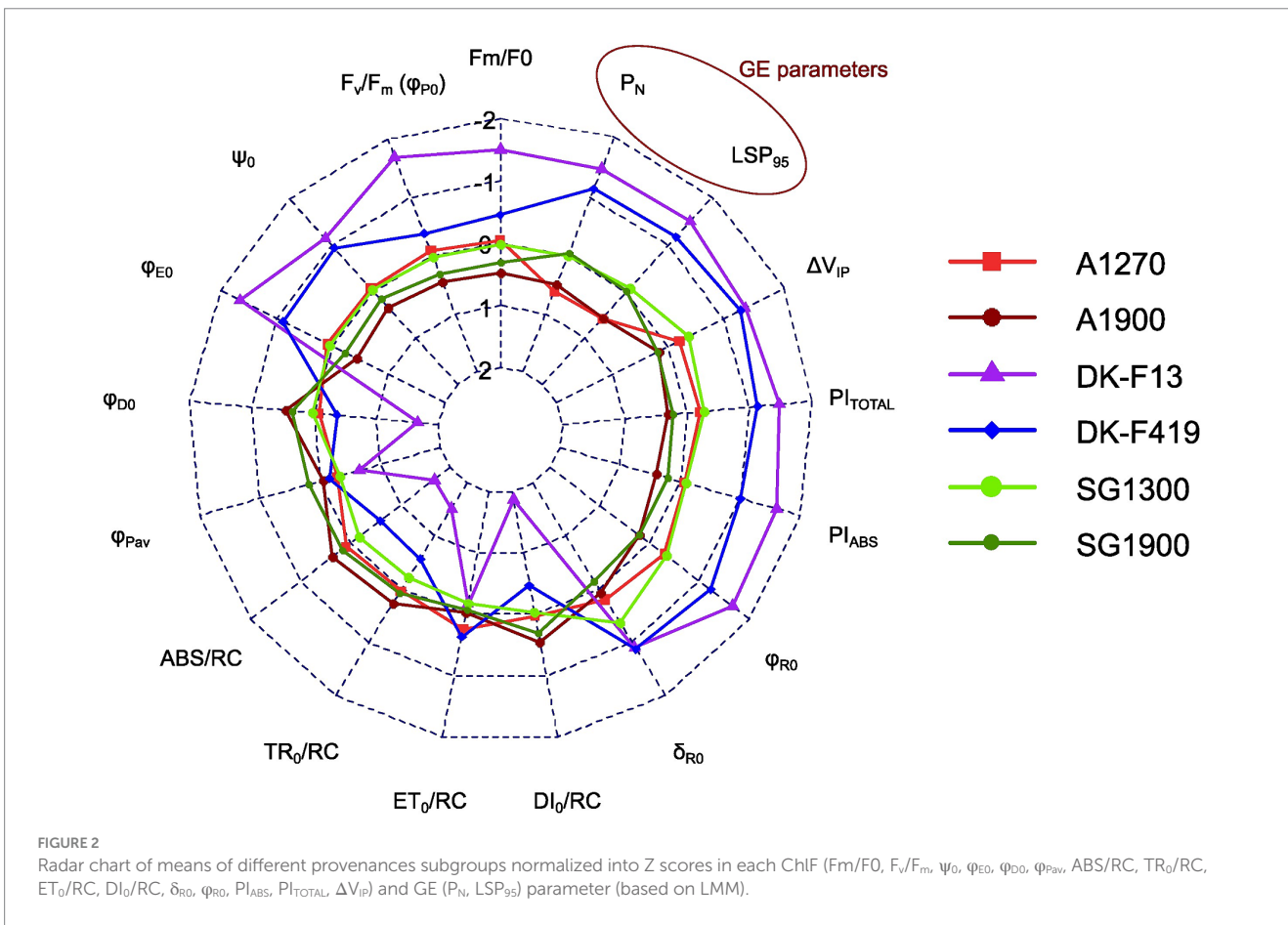
all of the assessed trees. No significant differences were captured between the provenance subgroups. The senescence scores for individual provenance subgroups are visualized in Figure 5.

3.5 Correlations between chlorophyll fluorescence parameters and gas exchange parameters

We highlighted the significant correlations ($\alpha=0.05$) parameters obtained from ChlF and GE methods in a heat map (Supplementary Figure S2). There were mostly weak correlations between ChlF and GE parameters, with the highest positive being 0.41 between PI_{TOTAL} and P_N and the highest negative being -0.40 between TR₀/RC and P_N.

4 Discussion

ChlF and GE can estimate a tree's physiological status based on photosynthetic assimilation rates obtained at the leaf level (Niinemets, 2010). We found significant differences between Italian and Danish provenances in almost all photosynthetic parameters. We confirmed our hypothesis that Italian provenances will perform better in chosen parameters P_N (GE method) and PI_{TOTAL} (ChlF method). Furthermore,



among the Italian provenances, the provenance subgroups from higher altitudes perform better in P_N and PI_{TOTAL} in the Danish climate. Italian trees from higher altitudes react better to the wetter and colder Danish weather, possibly due to adaptation to harsher conditions. This is further supported by a higher survival rate of Italian provenances from higher elevations than the ones from lower elevations, especially in the case of SG1900, which had the highest survival rate in 2018, even surpassing the local provenances. The higher survival rate of SG 1900 could be connected

to later bud flushing of this provenance in 2018, which could have protected it from spring frost damage. On the contrary, both Aspromonte provenances' survival was relatively low at the end of 2018. Between 2018 and 2020, the survival rate of all provenance subgroups remained stable, with only a few trees not surviving (Table 2). The higher initial survival rate of Danish provenances can possibly be explained by adaptation to local conditions and shorter transport time before replanting than in the case of Italian ones.

TABLE 7 Two-sided Wilcoxon signed-rank test of flushing scores between pairs of provenances and provenance subgroups scored in May 2018 and April 2020.

Year	2018	2020
Compared pair	<i>p</i> -value	<i>p</i> -value
SG × A	1.92E-15	0.0008594
I × DK	-	5.316e-07
SG1300 × SG1900	8.80E-13	6.197e-07
SG1300 × A1270	0.01071	0.9836
SG1300 × A1900	0.44400	0.58870
SG1900 × A1900	4.46E-14	7.547e-07
SG1900 × A1270	2.87E-14	0.0001251
A1270 × A1900	0.05032	0.6287
DK-F13 × A1270	-	0.001351
DK-F13 × A1900	-	0.0001237
DK-F13 × SG1300	-	9.407e-05
DK-F13 × SG1900	-	0.1598
DK-F419 × A1270	-	0.0001522
DK-F419 × A1900	-	4.09e-06
DK-F419 × SG1300	-	2.706e-06
DK-F419 × SG1900	-	0.1615
DK-F13 × DK-F419	-	0.7061

p-values in bold are smaller than 0.05.

common garden study, similar by design to ours, southern provenances maintained higher net photosynthesis rates (P_N), water use efficiency, and growth rate throughout the summer (Robson et al., 2012). In contrast, a Romanian provenance of beech showed under different CO₂ treatments lower absolute P_N values than the Danish one in a study by Leverenz et al. (1999). Additionally, xeric provenances are reported to have a faster net photosynthesis rate (P_N) recovery after drought treatment (Arend et al., 2016), which confirms that the differences in GE and ChlF parameters between provenances are magnified when exposed to drought stress (Aranda et al., 2015). In our case, the higher absolute values of photosynthetic parameters in Italian provenances were probably caused by differences in phenology and reflected adaptation. Nielsen and Jørgensen (2003) reported that Danish beech provenances ceased diameter growth sooner than southern European provenances in similar climate conditions as our experiment had.

4.1 Chlorophyll fluorescence kinetics and gas exchange variation of the replanted provenance subgroups

Other studies comparing the photosynthetic performance of European beech that originates from different altitudes include provenances where the trend of elevation is confounded in a shared cardinal direction (e.g., Robson et al., 2012, 2013; Kučerová et al., 2018; Pšidová et al., 2018). Therefore, the latitude and longitude of origin could also drive the differences and cannot be effectively separated. In our study, the geographical distances between provenance subgroups occupying a single mountain range were minimal, meaning that physiological differences within these provenances reflect mainly altitude.

The most common use of ChlF kinetics is to diagnose early stress responses to biotic or abiotic factors before any decline in growth can be observed (Fiorani and Schurr, 2013; Faiseela et al., 2020). DI_0/RC and F_v/F_m are often used as drought or temperature stress indicators (Mathur et al., 2013; Yuan et al., 2013; Fghire et al., 2015). However, the most commonly used parameter, F_v/F_m , is quite robust and sometimes cannot be as sensitive as other ChlF parameters (Bussotti et al., 2020). As the trees in our experiment were under no apparent stress at the time of measurements, these parameters instead reflected provenance variation and overall vitality after replanting. When comparing the subgroups of Italian provenances in ChlF, four parameters could make a distinction based on the altitude (DI_0/RC , ϕ_{R0} , PI_{TOTAL} , ΔV_{IP}). Higher ϕ_{R0} , PI_{TOTAL} , and ΔV_{IP} values were estimated for the high-altitude provenance subgroups in Aspromonte and Sila Grande, and higher DI_0/RC values for the low-altitude provenance subgroups in Aspromonte and Sila Grande (Table 5). ΔV_{IP} is the parameter we found especially interesting in which the relative loss of the I-P phase is related to a loss of PSI reaction centers (Oukarroum et al., 2009), as indices connected to the I-P phase were not much previously explored in European beech. Furthermore, F_v/F_m and ΔV_{IP} are suggested to be the two most suitable OJIP parameters to capture the variability of plant photosynthetic efficiency and their responses to environmental pressures (Bussotti et al., 2020). The ChlF parameter we found most indicative was DI_0/RC , as it was the only one to differentiate between the two Danish provenances as well as between the Italian

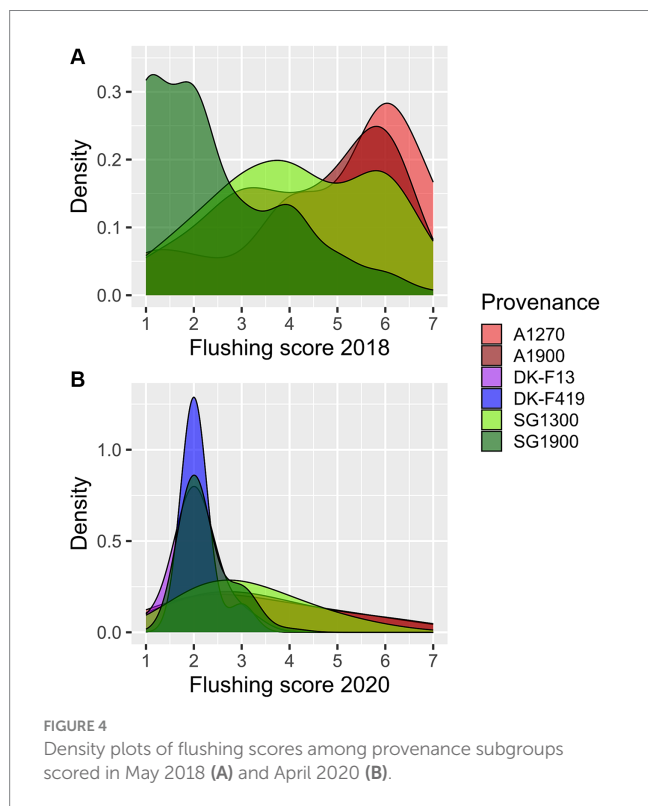


FIGURE 4 Density plots of flushing scores among provenance subgroups scored in May 2018 (A) and April 2020 (B).

Comparable studies focused on altitudinal differences within similar origins are lacking. However, several studies have tackled latitudinal differences in photosynthetic performance. In a beech

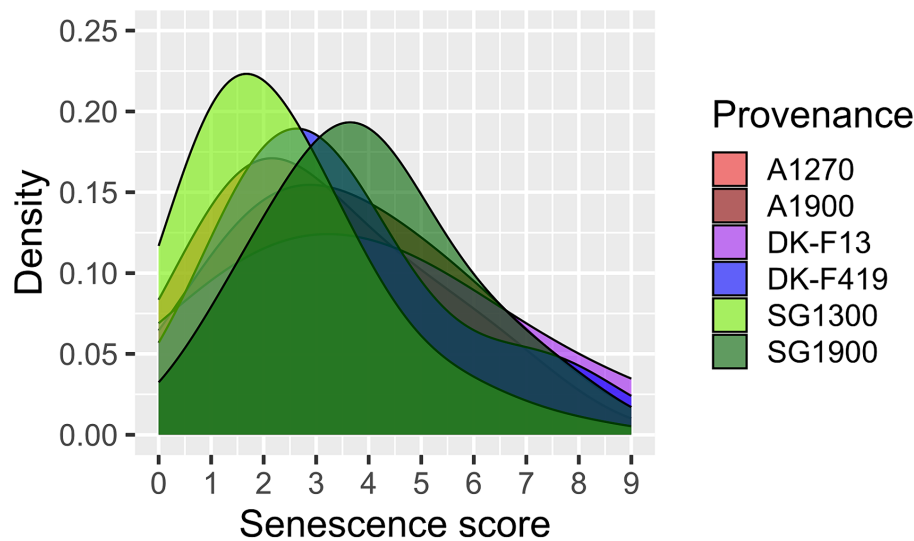


FIGURE 5

Density plots of leaf senescence scores of individual provenances and the altitudinal subgroups assessed at the beginning of November 2020.

provenance subgroups on an altitudinal basis. However, in our study, ChlF parameters could not distinguish provenances based on their geographical origin.

Findings from two studies conducted in a single common garden experiment in Slovakia by Kučerová et al. (2018) and Pšidová et al. (2018) reported mechanistic differences in ChlF kinetics among beech provenances. Kučerová et al. (2018) observed that Austrian and Polish provenances differed from others in the F_v/F_m ratio, although this trend was inconsistent along the altitudinal gradient. Pšidová et al. (2018), focused on provenance performance during heatwaves, finding that ABS/RC and ψ_0 were more limited in lower altitude provenances. Higher altitude provenances showed better PSII photochemistry performance, indicated by PI_{ABS} , under both dry and wet conditions, which aligns with our findings. Kurjak et al. (2019) found significant associations between ChlF parameters (mainly F_v/F_m and PI_{ABS}) and the climate of origin. Provenances from colder, wetter regions exhibited higher PSII performance compared to those from warmer, drier climates. This trend was also linked to the geographical distance from the Slovenian refugium and the common garden site, with closer proximity resulting in better PSII performance. PSII performance decreased towards the north-western margins, supporting our results regarding latitude-related variations in ChlF.

On the other hand, two GE parameters (LSP_{95} and P_N) could reliably distinguish geographical origin (the different Italian mountain ranges, Aspromonte and Sila Grande). We observed no trend in altitude in the GE data. In contrast, Kučerová et al. (2018) reported a significant linear altitudinal trend for the CO_2 assimilation rate between Central European provenances of European beech. Although the provenances used in Kučerová et al. (2018) study originated from different altitudes, they were also geographically distant; therefore, the latitude and longitude of origin could also drive the differences. The GE measurements revealed higher LSP_{95} and P_N values for more southern Aspromonte than Sila Grande. The higher LSP_{95} values from Aspromonte suggest that Sila Grande beech may be more shade tolerant. A study by Meng et al. (2014) showed that shade-adapted plants have lower light saturation levels. However, in beech, the release

of sunlight after a windstorm tends to diminish the differences in LSP between fully released (formerly shade-grown) and sun-grown seedlings (Reynolds et al., 2003). In our study, the different LSP_{95} values of Aspromonte and Sila Grande could most likely be attributed to the local adaptation. For example, Čater and Levanič (2019) report a reduced shade tolerance and higher efficiency of beech towards the south, which supports our results and may correspond to a boost in regeneration.

4.2 Flushing scores related to provenance subgroups' variation

In 2018 and 2020, the southern provenance from Aspromonte exhibited significantly higher flushing scores compared to Sila Grande's provenance. Additionally, in 2020, the Danish provenances showed lower flushing scores than the Italian ones. Previous studies have found that flushing is significantly correlated with latitude, longitude, and altitude, influenced by factors such as chilling, temperature sums, and day length (Nielsen and Jørgensen, 2003). The duration of phenological phases varies annually and mainly depends on temperature (Bednářová and Merková, 2007; Slovíková and Bednářová, 2014). Similarly, research from Slovakia (Schieber et al., 2013), southern Germany (Dittmar and Elling, 2006), and Slovenia (Čufar et al., 2012) showed phenological variation in beech along the altitudinal gradient. In southern Germany, beech leaf unfolding was delayed by 2–3 days for every 100 m of altitudinal increase (Dittmar and Elling, 2006). While the Sila Grande provenance showed variation in flushing along the elevation gradient in 2018 and 2020, this was not observed within Aspromonte. However, our consistent results from 2018 and 2020 suggest that the adaptation of the provenances is linked to flushing variation, as the provenance flushing scores remained stable in Danish climatic conditions over two seasons. Vitasse et al. (2009) noted that beech leaf unfolding is less temperature-sensitive than other European tree species, indicating that other factors are more influential.

Flushing scores did not correlate significantly with photosynthetic parameters. The two data collections in 2018 (flushing vs. GE and ChlF) were conducted at the beginning and end of the vegetation season, respectively, so the expected correlation pattern may have been disrupted due to the various factors influencing the trees during the vegetation season. The weather fluctuations influenced the seedlings' performance in the common garden, and some mortality occurred during the vegetation season. However, both GE and flushing similarly cluster the Italian provenances and their subgroups (Figures 2, 4). In 2020, the Danish provenances were also scored. Both Danish provenances were in a later flushing stage than the Italian ones. The only exception was SG1300, which showed a late flushing pattern similar to the Danish beech. It still had a slightly earlier flushing pattern than the Danish provenances, although not significantly.

4.3 Senescence

There were no visible differences in the senescence of leaves between the provenances and provenance subgroups at the beginning of November 2020 (Figure 5). We conclude that as there were no observable differences in November senescence, the photosynthetic measurements conducted at the beginning of September 2018 were not influenced by the direct onset of leaf senescence. It is widely known that senescence is connected to chlorophyll content. As leaves in deciduous trees lose some chlorophyll content during senescence, the photosynthetic capacity decreases on a leaf area basis (Adams et al., 1990). Leaves that fall later in the season have a better translocation of nutrients, and the translocation is species-dependent (Niinemets and Tamm, 2005). A study in another beech species (*Fagus grandifolia* Ehrh.) documented chlorophyll degradation that was not sudden but continuous, as the slower formation of the abscission layer during senescence allowed beech to translocate more nutrients out of leaves (Primka and Smith, 2019). However, ChlF does not seem to be affected to such a degree by large decreases in chlorophyll content as the yellowing leaves of deciduous trees are still efficiently used in photosynthesis because the photosynthetic capacity on a chlorophyll basis and photosynthetic energy conversion efficiency do not show a decline (Adams et al., 1990). Therefore, we believe that even at the beginning of the senescence process, the ChlF method could still yield relevant results.

4.4 Limitations

This study has potential limitations that need to be stated. Firstly, we only used two provenances from Calabria representing beech refugia, which we separated into two distinct altitudinal subgroups and two local Danish provenances. Secondly, the sample size of GE measurements was smaller than that of ChlF measurements due to the extensive time consumption of the GE method. The main measurements (GE and ChlF) were conducted during one week at the beginning of September, while flushing had to be scored in the Spring (2018 and 2020). Our study did not involve any stress treatment or biomass measurements, which would also be beneficial in understanding the well-being of replanted trees in new conditions. Flushing was not scored for the Danish plant material in 2018. Senescence was only assessed in 2020; however, this

secondary evaluation provided more insight into the potential influence of different onsets of senescence on the measurements taken in September 2018. Our results and conclusions are based on methods applied at various times, as we aimed to observe the differences in spring and autumn phenology. This combined approach helped to verify our main conclusion connected to the variance of photosynthetic performance due to phenology.

5 Conclusion

We found significant differences between Italian and Danish provenances of European beech in almost all photosynthetic parameters. More interestingly, we also detected minor differences among and within Italian provenances. The high-throughput ChlF measurements revealed altitude-based differences within provenances and distinguished the two Danish provenances. As hypothesized, leaf-level photosynthetic performance, indicated by P_N (GE method) and PI_{TOTAL} (ChlF method), was higher in Italian provenances than in Danish ones. Significant differences in photosynthetic performance were also found between altitudinal subgroups within Italian provenances. We conclude that photosynthetic within-provenance altitudinal variation is of similar importance as inter-provenance variation driven by geographical distance and that the sources of variation should be separately addressed. In our study, the photosynthetic parameters reflected phenology connected to broad genetic variation among provenances. We further conclude that the ChlF can uncover variability on a finer scale than GE as it revealed the provenance subgroups' altitudinal differences. Moreover, spring flushing scores repeatedly clustered the Italian provenance subgroups similarly to GE. As the Italian provenances exhibited generally higher photosynthetic rates in Danish conditions than local provenances, we recommend further exploring the beech refugia when assisted migration is of interest.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary material; and in Figshare: dx.doi.org/10.6084/m9.figshare.23736336.

Author contributions

DP: Conceptualization, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. JS: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Supervision, Validation, Writing – original draft, Writing – review & editing. OH: Conceptualization, Data curation, Funding acquisition, Methodology, Project administration, Resources, Writing – review & editing. JČ: Formal analysis, Investigation, Methodology, Validation, Writing – review & editing. EE: Data curation, Funding acquisition, Project administration, Resources, Writing – review & editing. JH: Supervision, Validation, Writing – review & editing. DZ: Formal analysis, Investigation, Writing – original draft. IT: Conceptualization, Data curation, Formal analysis, Methodology, Supervision, Validation, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2024.1369464/full#supplementary-material>

SUPPLEMENTARY FIGURE 1

Spatial design of the common garden experiment in September 2018.

SUPPLEMENTARY FIGURE 2

Heatmap of Pearson correlation coefficient between parameters obtained from ChlF and GE. Only significant ($\alpha = 0.05$) correlations are shown.

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