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Seasonal dynamics of the nutritive value of temperate forage trees differ among species

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Abstract There is growing interest in using temperate forage trees to alleviate the effects of summer drought and heatwaves on herbaceous forage. However, forage trees remain understudied in temperate climates. We studied the seasonal variation of the nutritive value of 16 tree species commonly found in Western Europe. We collected 285 samples of tree leaves between spring and autumn (June, August and October) over three years at 14 sites across France. We measured seven nutritive characteristics: in vitro dry matter digestibility (IVDMD) and the contents of crude protein (CP), dry matter (DM), neutral detergent fibre (NDF), acid detergent fibre (ADF), acid detergent lignin (ADL), and ash. We used linear mixed models to analyse their seasonal variation and then clustered the species based on CP and IVDMD. CP content and IVDMD generally decreased from spring to autumn (by 26% and 6 percentage points), while DM and ash contents increased (by 42 and 32%). *Corylus avellana*, *Morus alba*, and *Robinia pseudoacacia* had the greatest CP content (from 138 to 250 g.kg^{-1}), and *M. alba* had the greatest IVDMD (84.7% on average). We observed a trade-off between CP and IVDMD among clusters. The order of clusters based on their nutritive value remained consistent across seasons. Our findings highlight the importance of carefully planning tree use, as their nutritive value varies substantially among species and across seasons. Results provide new opportunities for farmers to compensate for the lack of herbaceous forage in summer, even though yield and palatability aspects remain to be studied.

Keywords Agroforestry · Crude protein · In vitro digestibility · Fodder · Ruminant

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Introduction

Trees were increasingly removed from agroecosystems throughout Europe during the twentieth century to increase agricultural yields (Nerlich et al. 2013). In

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the past few decades, interest in agroforestry has been renewed due to the ecosystem services and goods it can provide. Agroforestry can enhance soil fertility, water quality, biodiversity, and landscape aesthetics, as well as decrease soil erosion and sequester carbon (Jose 2009). Trees also provide goods such as timber, firewood, and fruits (Nerlich et al. 2013), as well as forage for animals (Akeret and Rentzel 2001). In recent years, concerns about climate change and its effects on the yield and quality of herbaceous forage in temperate climates (Staniak and Harasim 2018; Deroche et al. 2020), have increased interest in trees as a supplemental source of forage for ruminants. However, considering woody forage as a potential part of herbivore diets requires investigating their nutritive values across species and seasons. To date, most studies on forage trees have focused on tropical and Mediterranean climates (Vandermeulen et al. 2018a), with little attention paid to temperate species. Tropical forage trees tend to have greater contents of crude protein (CP), neutral detergent fibre (NDF), acid detergent fibre (ADF), and acid detergent lignin (ADL) in the rainy season than in the dry season (Camacho et al. 2010; Basha et al. 2013). Studies in Mediterranean climates found different results: CP, NDF, and ADL contents could increase, remain constant, or decrease across seasons depending on the species, year, and/or site studied (Papachristou et al. 1999; Ainalis et al. 2006; Parissi et al. 2018).

Previous studies in temperate climates highlighted that several forage tree species have a high nutritive value in summer, which can exceed that of herbaceous species such as *Lolium perenne* L. (perennial ryegrass) and *Dactylis glomerata* L. (cocksfoot) (Mahieu et al. 2021). From spring to autumn, the CP content of the leaves of temperate forage trees generally declines while NDF, ADF, and ADL contents increase (Vandermeulen et al. 2018b; Kendall et al. 2021). Previous studies also highlighted that the nutritive value of tree leaves is often influenced by the season and species (Camacho et al. 2010; Vandermeulen et al. 2018b; Luske and van Eekeren 2018; Ravetto Enri et al. 2020). Soil type can influence the chemical composition of the leaves of certain tree species. Luske and van Eekeren (2018) found that *Salix viminalis* L. (basket willow) and *F. excelsior* had greater dry matter (DM) digestibility and calcium content on clay soils than on sandy soils. In addition, tree leaves had greater nitrogen and phosphorus concentrations in flooded areas (Trémolières et al. 1999). Although the studies cited above were conducted in temperate environments, the overall literature on temperate forage trees remains scarce and has often focused on a few species and/or a single site, which may introduce bias when extrapolating results to other species or sites. We hypothesised that CP content and IVDMD would decrease from spring to autumn, while ash and fibre contents would increase. We further expected that the rate and magnitude of these seasonal changes would differ among species. Finally, we hypothesised that, despite interspecific variability, tree species could be grouped into consistent clusters based on their seasonal nutritive characteristics, providing useful guidance for forage tree use.

Very little is known about the influence of season and species on the nutritive value of temperate forage trees. The present study aimed to fill this gap by evaluating the seasonal variation in the nutritive value of 16 common temperate tree species sampled across multiple sites and years. Our goal was to assess their potential as forage for ruminants and to identify consistent species groups to guide agroforestry-based feeding strategies. This multi-site, multi-year analysis makes it one of the first studies to address this topic at such a scale in temperate climates.

Materials and methods

Sample collection

We selected 16 tree species based on their common use as forage and/or their common presence in temperate climates: *A. pseudoplatanus* (sycamore maple, n = 36 samples), *Alnus cordata* (Loisel.) Duby (Italian alder, n = 16), *Castanea sativa* Mill. (chestnut, n = 14), *Corylus avellana* L. (common hazel, n = 14), *Fagus sylvatica* L. (European beech, n = 6), *Fraxinus americana* L. (American ash, n = 6), *F. excelsior* L. (European ash, n = 59), *Gleditsia triacanthos* L. (honey locust, n = 6), *Juglans* x intermedia (hybrid walnut, n = 12), *Morus alba* L. (white mulberry, n = 29), *Paulownia tomentosa* (Thunb.) Steud. (Paulownia, n = 12), *Prunus avium* L. (sweet cherry, n = 18), *Robinia pseudoacacia* L. (black locust, n = 14), *Sorbus domestica* L. (service tree, n = 12), *Ulmus minor* Mill. (field elm, n = 15), and *Ulmus* 'Nanguen' (Lutece elm, n = 16). Tree size was not a criterion in species selection, as ruminants can directly browse shorter trees, while taller trees can be pruned to provide fodder. We collected 285 leaf samples from 125 trees in 2015 (n = 15), 2016 (n = 227), and 2017 (n = 43), in June, August, and October (i.e. respectively spring, summer, and autumn) (Table 1, Online Resource 1). The variability in sample size among species reflects their availability in partner collections. Some species are less common in French agroforestry systems, which limited the number of samples collected (e.g. *Fraxinus americana* or *Gleditsia triacanthos*). We selected only high-stem trees to avoid potential bias, as practices like pruning and pollarding can impact the nutritive value of tree foliage (Burner et al. 2005; Mahieu et al. 2019), and, as much as possible, we re-sampled the same trees over time to ensure temporal consistency. For each leaf sample, we collected a mixture of mature and young leaves (blade and petiole) from several branches at multiple elevations in the tree canopy. No tree was sampled more than once within a given season and year; however, some were re-sampled across different seasons or years.

The fresh weight of each leaf sample ranged from 1–3 kg per tree. Leaves were collected at 14 sites in France, and those that lay within 40 km of each other were grouped for the subsequent statistical analysis (Fig. 1). The sites studied were selected to cover a large gradient of temperate climates (i.e. oceanic, Mediterranean, and mountain) and soil characteristics. Across sites, the mean annual temperatures and precipitation were respectively 11.2 ± 1.42 °C [8.2–13.6 °C] and 815 ± 88.6 mm [690–1031 mm] over the 1970–2000 period, and soil pH was 6.68 ± 0.73 [5.04–7.60] (mean ± SD [min–max]) (Fick and Hijmans 2017; Ballabio et al. 2019).

Table 1 Number of samples collected per species each month

Species	June	August	October	Total
Acer pseudoplatanus	12	12	12	36
Alnus cordata	3	10	3	16
Castanea sativa	3	8	3	14
Corylus avellana	3	8	3	14
Fagus sylvatica	2	2	2	6
Fraxinus americana	2	2	2	6
Fraxinus excelsior	18	23	18	59
Gleditsia triacanthos	2	2	2	6
Juglans x intermedia	4	4	4	12
Morus alba	10	13	6	29
Paulownia tomentosa	3	6	3	12
Prunus avium	6	6	6	18
Robinia pseudoacacia	3	8	3	14
Sorbus domestica	4	4	4	12
Ulmus minor	3	9	3	15
Ulmus 'Nanguen'	3	10	3	16
Total	**81**	**127**	**77**	**285**

Nutritive value analyses

Seven characteristics of leaf nutritive value were determined: in vitro dry matter digestibility (IVDMD, %) and the contents of DM (g.kg^{-1}), CP (g.kg^{-1} DM), NDF (g.kg^{-1} DM), ADF (g.kg^{-1} DM), ADL (g.kg^{-1} DM), and ash (g.kg^{-1} DM). We used the same measurement protocol as Mahieu et al. (2021) did. Leaf samples were dried at 60 °C for 72 h (when their mass stabilised) to calculate their DM content. We measured total nitrogen content using the Dumas method (elemental analyser Flash 2000, Thermo Fisher Scientific, Waltham, Massachusetts, USA) (Hansen 1989). Crude protein (CP) was calculated by multiplying total nitrogen by 6.25 (N × 6.25 = CP).

We determined in vitro dry matter digestibility or degradability (IVDMD) using the enzymatic method (cellDMD) initially described by Aufrère (1982) and Aufrère and Michalet-Doreau (1988), adapted for use with the DAISY incubator (Ankom Technology Corp., Fairport, New York, USA) validated by Le Morvan et al. (2016). The protocol includes three main steps: (1) pre-treatment with pepsin in hydrochloric acid; (2) starch hydrolysis in the same solution; and (3) filtration, rinsing, and incubation with cellulase.

The contents of amylase-treated neutral detergent fibre (NDF), acid detergent fibre (ADF), and acid detergent lignin (ADL) were measured following the method of Goering and Van Soest (1970), with α-amylase added to the neutral detergent solution, but without sodium sulphite. NDF and ADF were measured using a fibre analyser (ANKOM 220, Ankom Technology Corp.), and ADL was measured after the addition of sulfuric acid. All fibre fractions were corrected for residual ash, determined via incineration in a muffle furnace at 550 °C for 3 h.

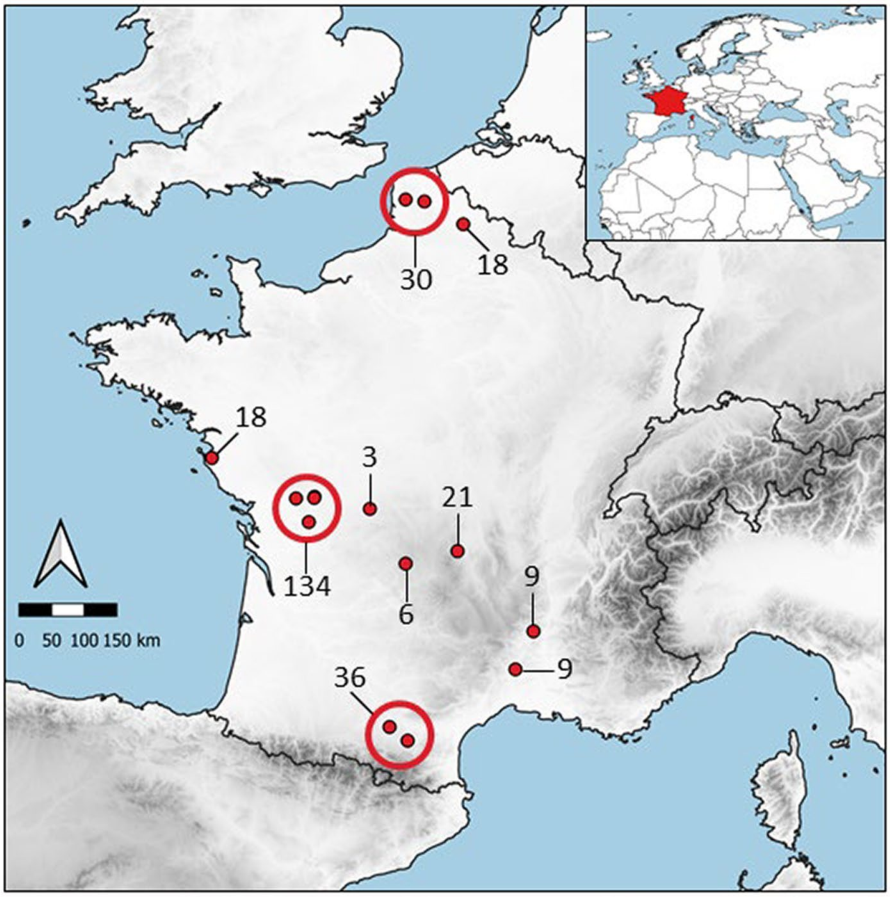

Fig. 1 Sampling sites (n = 14) and number of samples per site (total = 285). Sites in red circles lay within 40 km of each other and were grouped for the statistical analysis

Statistical analyses

All statistical analyses were performed using R software v. 4.3.1 (R Core Team 2023). To ensure that the study can be reproduced, the data and R script are openly available (Mesbahi et al. 2025).

First, we assessed several models to determine whether species, season (i.e. month), or their interaction best predicted the nutritive value. To this end, for each characteristic, we developed a linear mixed model with season, species, and their interaction as fixed effects and the main effects of site and year as random effects. We then derived all possible sub-models, including an intercept-only model (Burnham and Anderson 2002; Grueber et al. 2011), using the 'lme4' package (Bates et al. 2015). We thus obtained five models per characteristic:

- Interaction: $Y = \beta0 + \beta1(species) + \beta2(season) + \beta3(species \times season) + u(site) + u(year) + \varepsilon$
- Main effects: $Y = \beta0 + \beta1(species) + \beta2(season) + u(site) + u(year) + \varepsilon$
- Species only: $Y = \beta0 + \beta1(species) + u(site) + u(year) + \varepsilon$
- Season only: $Y = \beta0 + \beta2(season) + u(site) + u(year) + \varepsilon$
- Intercept only: $Y = \beta0 + u(site) + u(year) + \varepsilon$

where Y is the response variable (e.g. CP, IVDMD); β0 is the intercept; β1, β2, and β3 are fixed effects; u(site) and u(year) are random effects respectively for the site and year; and ε is the residual error.

We visually verified linearity assumptions using the 'performance' package (Lüdecke et al. 2021) and verified the variance inflation factor using the 'corvif' function (Zuur et al. 2009). We selected the best models based on the Akaike weight calculated using the 'MumIn' package (Barton 2018). To assess the selected models' goodness of fit, we calculated conditional and marginal R^2 using the 'performance' package (Lüdecke et al. 2021), the residual standard error (RSE), and the coefficient of variation (CV).

Second, we assessed the effects of species and season on the nutritive value by performing Type III analysis of variance (ANOVA) of the best linear models using the 'stats' package (R Core Team 2023). The ANOVA assessed the significance of each selected fixed effect (season, species, and their interaction), considering random effects of the site and year, which highlighted general trends for all tree species. Then, as a post-hoc test, we estimated marginal means to compare the nutritive value among seasons for each species, among species in each season, and for the combined effects of season and species. To this end, we used the 'emmeans' and 'multcomp' packages (Hothorn et al. 2008; Lenth 2021) and adjusted the *P*-value using the Tukey method.

Agronomic interpretation

To provide farmers easily understandable and workable results, we clustered the tree species based on the seasonal CP content and IVDMD predicted by the models (i.e. six variables). We focused only on CP content and IVDMD for this agronomic interpretation, as they are usually the most important nutritive forage characteristics for farmers. We then performed hierarchical clustering on principal components (HCPC) using the 'FactoMineR' package (Lê et al. 2008). An HCPC consists of principal component analysis (PCA), to separate the signal from the noise, and then clustering based on the results of the PCA. The number of components in the PCA, the hierarchical tree, and the number of clusters were defined automatically using Ward's method and an inertia approach in order to avoid bias. Relations between clusters and nutritive values (seasonal CP content and IVDMD) were characterised by the *P*-values of v-tests (Escofier and Pagès 2008), which compared values of the clusters to the overall mean. Thus, we aimed to provide simplified, group-level recommendations rather than require stakeholders to compare the detailed advantages and disadvantages of individual tree species.

Results

Model selection

All nutritive values were best predicted when including species, season, and their interaction as fixed effects and the main effects of site and year as random effects. All the best models obtained an Akaike weight of 1, and their conditional R^2 ranged from 0.811 to 0.890 (Table 2). The CV of the model used to predict the ADL content exceeded 15%, which indicated high variability in the predictions.

Effects of species and season on tree leaf nutritive value

General trends

The type III ANOVAs of the selected models revealed that species and the interaction between species and season had significant effects on all of the characteristics studied ($p<0.001$). As a main factor, the season significantly influenced IVDMD and CP, DM, and ash contents, but not fibre contents (NDF, ADF, and ADL). From Spring to Autumn, CP content and IVDMD decreased (by a mean of respectively 26% and 6 percentage points

Table 2 Goodness of fit (R^2), residual standard deviation (RSE), and coefficient of variation (CV) of the selected models

Characteristic	Conditional R^2	Marginal R^2	RSE	CV
CP ($g.kg^{-1}$)	0.811	0.701	19	13.1
IVDMD (%)	0.868	0.765	4	6.3
DM ($g.kg^{-1}$)	0.864	0.644	34	9.2
NDF ($g.kg^{-1}$)	0.845	0.607	32	8.5
ADF ($g.kg^{-1}$)	0.872	0.632	24	11.2
ADL ($g.kg^{-1}$)	0.890	0.724	17	17.1
Ash ($g.kg^{-1}$)	0.877	0.658	11	13.3

Conditional R^2 describes the proportion of variance explained by both the fixed and random effects, while marginal R^2 describes the proportion of variance explained by the fixed effects alone. *CP* crude protein content, *IVDMD* in vitro dry matter digestibility, *DM* dry matter content, *NDF* neutral detergent fibre content, *ADF* acid detergent fibre content, *ADL* acid detergent fibre content, and *Ash* ash content.

(pp)), while DM and ash contents increased (by a mean of respectively 42 and 32%). The contents of NDF, ADF, and ADL were statistically unchanged across seasons.

Species × season interaction

Analysing the effect of season across species (Tables 3, 4, and 5, Fig. 2), CP content significantly decreased across seasons for 10 of the 16 species: *A. pseudoplatanus* −29%, *F. americana* 43%, *F. excelsior* −28%, *G. triacanthos* −58%,

Table 3 Effects of season and species on crude protein (CP) content (g.kg^{-1}) and in vitro dry matter digestibility (IVDMD, %) in the leaves of 16 tree species sampled in France in June, August, and October (i.e. spring, summer and autumn)

Species	CP content (g.kg^{-1})			IVDMD (%)		
	June	August	October	June	August	October
A. pseudoplatanus	$_{def}147^{a}$	$_{cd}127^{b}$	$_{e}105^{c}$	$_{bc}69.6^{a}$	$_{cde}66.7a^{b}$	$_{cd}62.8^{b}$
A. cordata	$_{bcd}184^{a}$	$_{b}174^{a}$	$_{abcd}163^{a}$	$_{bc}69.6^{a}$	$_{def}60.2^{b}$	$_{cde}62.6^{ab}$
C. sativa	$_{cdef}154^{a}$	$_{b}173^{a}$	$_{ab}186^{a}$	$_{bcd}64.9^{a}$	$_{cdef}62.2^{a}$	$_{ef}52.0^{b}$
C. avellana	$_{abc}207^{a}$	$_{cd}138^{b}$	$_{a}189^{a}$	$_{de}56.8^{a}$	$_{g}48.5^{b}$	$_{f}46.4^{b}$
F. sylvatica	$_{def}129^{a}$	$_{bcd}131^{a}$	$_{cde}116^{a}$	$_{e}47.6^{a}$	$_{g}46.2^{a}$	$_{f}48.3^{a}$
F. americana	$_{bcdef}158^{a}$	$_{bcd}143^{a}$	$_{e}90^{b}$	$_{bcd}70.6^{a}$	$_{abcd}71.8^{a}$	$_{bcd}67.1^{a}$
F. excelsior	$_{de}160^{a}$	$_{cd}136^{b}$	$_{e}115^{c}$	$_{b}72.0^{a}$	$_{b}72.9^{a}$	$_{b}72.1^{a}$
G. triacanthos	$_{abc}216^{a}$	$_{bcd}124^{b}$	$_{e}90^{b}$	$_{bcd}64.8^{a}$	$_{efg}55.9^{ab}$	$_{def}54.3^{b}$
J. x intermedia	$_{ab}213^{a}$	$_{bc}151^{b}$	$_{cde}120^{b}$	$_{b}74.8^{a}$	$_{bcd}68.9^{a}$	$_{abc}72.0^{a}$
M. alba	$_{a}249^{a}$	$_{b}177^{b}$	$_{abcd}168^{b}$	$_{a}88.4^{a}$	$_{a}83.3^{b}$	$_{a}82.5^{b}$
P. tomentosa	$_{cdef}141^{a}$	$_{cd}114^{a}$	$_{bcde}116^{a}$	$_{cde}58.0^{a}$	$_{fg}55.2^{a}$	$_{cdef}58.1^{a}$
P. avium	$_{def}148^{a}$	$_{cd}113^{b}$	$_{e}95^{b}$	$_{bc}69.4^{a}$	$_{bc}69.7^{a}$	$_{ab}73.5^{a}$
R. pseudoacacia	$_{a}244^{a}$	$_{a}224^{a}$	$_{abc}176^{b}$	$_{bcd}63.6^{a}$	$_{g}47.8^{b}$	$_{f}45.6^{b}$
S. domestica	$_{f}117^{a}$	$_{d}97^{ab}$	$_{e}80^{b}$	$_{cd}63.3^{a}$	$_{bcdef}66.2^{a}$	$_{cde}63.0^{a}$
U. minor	$_{ef}128^{a}$	$_{cd}116^{a}$	$_{de}122^{a}$	$_{bcd}64.2^{a}$	$_{def}60.7^{a}$	$_{def}57.3^{a}$
U. 'Nanguen'	$_{bcd}183^{a}$	$_{cd}129^{b}$	$_{cde}124^{b}$	$_{bcd}68.0^{a}$	$_{cdef}61.7^{ab}$	$_{def}56.1^{b}$

$_{abcdef}$ Shared subscript letters within a column indicate a non-significant species effect. ^{abc} Shared superscript letters within each variable in a row indicate a non-significant seasonal effect

Table 4 Effects of season and species on the contents of dry matter (DM, g.kg^{-1}) and ash (g.kg^{-1}) in the leaves of 16 tree species sampled in France in June, August, and October (i.e. spring, summer and autumn)

Species	DM content (g.kg^{-1})			Ash content (g.kg^{-1})		
	June	August	October	June	August	October
A. pseudoplatanus	$_{cde}302^{a}$	$_{cd}416^{b}$	$_{cde}449^{c}$	$_{cd}64^{c}$	$_{cd}84^{b}$	$_{bcd}99^{a}$
A. cordata	$_{bcde}304^{a}$	$_{abc}366^{b}$	$_{bc}380^{b}$	$_{def}42^{b}$	$_{efg}60^{a}$	$_{gh}57^{ab}$
C. sativa	$_{abc}253^{a}$	$_{a}334^{b}$	$_{ab}297^{ab}$	$_{f}30^{a}$	$_{g}43^{a}$	$_{h}44^{a}$
C. avellana	$_{abcd}256^{a}$	$_{cde}411^{c}$	$_{ab}329^{b}$	$_{cdef}56^{a}$	$_{def}66^{a}$	$_{efgh}70^{a}$
F. sylvatica	$_{e}385^{a}$	$_{f}536^{b}$	$_{ef}540^{b}$	$_{ef}32^{a}$	$_{fg}48^{a}$	$_{gh}57^{a}$
F. americana	$_{abc}246^{a}$	$_{abc}334^{b}$	$_{bcd}390^{b}$	$_{abcd}75^{a}$	$_{bcde}89^{a}$	$_{fgh}63^{a}$
F. excelsior	$_{cd}293^{a}$	$_{cd}403^{b}$	$_{c}406^{b}$	$_{bc}69^{b}$	$_{c}91^{a}$	$_{cdef}93^{a}$
G. triacanthos	$_{abcde}262^{a}$	$_{bcdef}440^{b}$	$_{bcd}406^{b}$	$_{abcde}69^{a}$	$_{cdefg}75^{a}$	$_{cdefgh}80^{a}$
J. x intermedia	$_{ab}208^{a}$	$_{abcd}360^{b}$	$_{bcd}388^{b}$	$_{cdef}57^{b}$	$_{bcd}93^{a}$	$_{abc}110^{a}$
M. alba	$_{a}217^{a}$	$_{a}337^{b}$	$_{ab}318^{b}$	$_{a}93^{b}$	$_{a}133^{a}$	$_{a}141^{a}$
P. tomentosa	$_{abcde}317^{a}$	$_{a}312^{a}$	$_{abcd}352^{a}$	$_{abcdef}65^{a}$	$_{cdef}71^{a}$	$_{cdefgh}66^{a}$
P. avium	$_{cde}309^{a}$	$_{def}439^{b}$	$_{de}472^{b}$	$_{abc}84^{a}$	$_{bc}99^{a}$	$_{bcde}97^{a}$
R. pseudoacacia	$_{abc}228^{a}$	$_{ab}348^{b}$	$_{a}270^{a}$	$_{cdef}57^{a}$	$_{efg}60^{a}$	$_{gh}57^{a}$
S. domestica	$_{de}352^{a}$	$_{ef}489^{b}$	$_{f}576^{c}$	$_{bcdef}62^{a}$	$_{cdef}77^{a}$	$_{defg}72^{a}$
U. minor	$_{abcd}261^{a}$	$_{cde}424^{b}$	$_{bcd}387^{b}$	$_{ab}93^{b}$	$_{a}127^{a}$	$_{a}143^{a}$
U. 'Nanguen'	$_{abcde}277^{a}$	$_{bcd}397^{b}$	$_{bc}372^{b}$	$_{abc}84^{b}$	$_{ab}118^{a}$	$_{ab}123^{a}$

$_{abcdefg}$ Shared subscript letters within a column indicate a non-significant species effect. ^{abc} Shared superscript letters within each variable in a row indicate a non-significant seasonal effect

Table 5 Effects of season and species on the contents of neutral detergent fibre (NDF, g.kg^{-1}), acid detergent fibre (ADF, g.kg^{-1}), and acid detergent lignin (ADL, g.kg^{-1}) in the leaves of 16 tree species sampled in France in June, August, and October (i.e. spring, summer and autumn)

Species	NDF content (g.kg^{-1})	ADF content (g.kg^{-1})	ADL content (g.kg^{-1})						
	June	August	October	June	August	October	June	August	October
A. pse	${}_{bcd}375^{a}$	${}_{bc}365^{a}$	${}_{cd}364^{a}$	${}_{cd}225^{a}$	${}_{de}205^{a}$	${}_{de}218^{a}$	${}_{bcd}81^{a}$	${}_{bc}81^{a}$	${}_{c}90^{a}$
A. cor	${}_{defg}449^{a}$	${}_{ef}447^{a}$	${}_{cdef}414^{a}$	${}_{f}338^{a}$	${}_{h}317^{a}$	${}_{g}302^{a}$	${}_{i}233^{b}$	${}_{h}205^{a}$	${}_{f}201^{a}$
C. sat	${}_{bcdefg}403^{a}$	${}_{def}433^{a}$	${}_{g}510^{b}$	${}_{cde}242^{a}$	${}_{ef}247^{a}$	${}_{fg}279^{a}$	${}_{abcd}73^{a}$	${}_{c}86^{a}$	${}_{bcd}95^{a}$
C. ave	${}_{cdefg}422^{a}$	${}_{ef}464^{ab}$	${}_{fg}499^{b}$	${}_{cd}232^{a}$	${}_{ef}247^{a}$	${}_{efg}262^{a}$	${}_{cdefg}100^{a}$	${}_{def}127^{b}$	${}_{de}136^{b}$
F. syl	${}_{fg}468^{a}$	${}_{cdef}438^{a}$	${}_{defg}447^{a}$	${}_{cdef}260^{a}$	${}_{cdefg}225^{a}$	${}_{cdefg}235^{a}$	${}_{efgh}131^{b}$	${}_{abcd}90^{a}$	${}_{abcd}98^{ab}$
F. ame	${}_{abcde}349^{a}$	${}_{ab}317^{a}$	${}_{abcd}340^{a}$	${}_{cde}250^{a}$	${}_{defg}238^{a}$	${}_{defg}259^{a}$	${}_{bcdefg}97^{a}$	${}_{bcdef}99^{a}$	${}_{abcd}101^{a}$
F. exc	${}_{bc}372^{c}$	${}_{b}339^{b}$	${}_{ab}305^{a}$	${}_{de}256^{c}$	${}_{def}218^{b}$	${}_{bcd}195^{a}$	${}_{fg}120^{c}$	${}_{c}85^{b}$	${}_{ab}64^{a}$
G. tri	${}_{bcdef}362^{a}$	${}_{abcde}386^{a}$	${}_{cdef}393^{a}$	${}_{cdef}267^{a}$	${}_{fgh}277^{a}$	${}_{g}302^{a}$	${}_{gh}146^{a}$	${}_{fgh}157^{a}$	${}_{ef}167^{a}$
J. int	${}_{ab}308^{a}$	${}_{ab}321^{a}$	${}_{ab}290^{a}$	${}_{cde}233^{a}$	${}_{defg}232^{a}$	${}_{cdef}218^{a}$	${}_{bcdef}93^{a}$	${}_{cde}104^{a}$	${}_{bcd}99^{a}$
M. alb	${}_{a}264^{a}$	${}_{a}297^{b}$	${}_{a}265^{ab}$	${}_{ab}141^{a}$	${}_{a}143^{a}$	${}_{a}145^{a}$	${}_{a}39^{a}$	${}_{a}48^{a}$	${}_{a}51^{a}$
P. tom	${}_{g}493^{a}$	${}_{ef}474^{a}$	${}_{defg}452^{a}$	${}_{ef}330^{a}$	${}_{h}325^{a}$	${}_{fg}306^{a}$	${}_{hi}177^{a}$	${}_{g}166^{a}$	${}_{def}157^{a}$
P. avi	${}_{cdef}386^{b}$	${}_{abc}357^{b}$	${}_{ab}301^{a}$	${}_{cd}238^{b}$	${}_{abcd}183^{a}$	${}_{a}151^{a}$	${}_{fgh}134^{b}$	${}_{bc}82^{a}$	${}_{abc}64^{a}$
R. pse	${}_{bc}349^{a}$	${}_{f}486^{b}$	${}_{efg}489^{b}$	${}_{bc}196^{a}$	${}_{gh}295^{b}$	${}_{g}306^{b}$	${}_{abcde}81^{a}$	${}_{efg}147^{b}$	${}_{de}132^{b}$
S. dom	${}_{bc}341^{a}$	${}_{ab}318^{a}$	${}_{abc}330^{a}$	${}_{cd}236^{a}$	${}_{bcdef}208^{a}$	${}_{cdef}220^{a}$	${}_{cdefg}99^{a}$	${}_{bc}87^{a}$	${}_{bcd}97^{a}$
U. min	${}_{efg}451^{b}$	${}_{bcd}387^{a}$	${}_{cde}409^{ab}$	${}_{a}127^{a}$	${}_{abc}153^{a}$	${}_{ab}142^{a}$	${}_{ab}43^{a}$	${}_{ab}53^{a}$	${}_{ab}49^{a}$
U. nan	${}_{bcdefg}399^{a}$	${}_{bc}363^{a}$	${}_{bcd}358^{a}$	${}_{ab}136^{a}$	${}_{ab}153^{a}$	${}_{abc}154^{a}$	${}_{abc}52^{a}$	${}_{ab}55^{a}$	${}_{abc}62^{a}$

${}_{abcdefghi}$ Shared subscript letters within a column indicate a non-significant species effect. ^{abc} Shared superscript letters within each variable in a row indicate a non-significant seasonal effect. Species abbreviations: A. pse, *Acer pseudoplatanus*; A. cor, *Alnus cordata*; C. sat, *Castanea sativa*; C. ave, *Corylus avellana;* F. syl, *Fagus sylvatica*; F. ame, *Fraxinus americana*; F. exc, *Fraxinus excelsior*; G. tri, *Gleditsia triacanthos*; J. int, *Juglans* x intermedia; M. alb, *Morus alba*; P. tom, *Paulownia tomentosa*; P. avi, *Prunus avium*; R. pse, *Robinia pseudoacacia*; S. dom, *Sorbus domestica*; U. min, *Ulmus minor*; U. nan, *Ulmus* 'Nanguen'

J. x intermedia −44%, *M. alba* −33%, *P. avium* −36%, *R. pseudoacacia* −28%, *S. domestica* −32%, and U. 'Nanguen' −32%. Similarly, IVDMD significantly decreased for seven species: *A. pseudoplatanus* −6.8 pp, *C. sativa* −12.9 pp, *C. avenalla* −10.4 pp, *G. triacanthos* −10.5 pp, *M. alba* −5.9 pp, *R. pseudoacacia* −18 pp, and *U.* 'Nanguen' −11.9 pp. The other species exhibited non-significant changes in CP content or IVDMD from spring to autumn, except for *C. avellana*, which was the only species whose CP content significantly decreased from spring to summer (-33%) and then significantly increased from summer to autumn (+37%), which resulted in a similar CP content in June and October (mean of 198 g. kg^{-1}).

DM content significantly increased across seasons for all species except *P. tomentosa* (in which it remained statistically unchanged). Ash content significantly increased for six species (*A. pseudoplatanus*, *F. excelsior*, *J.* x intermedia, *M. alba*, *U. minor*, and *U.* 'Nanguen'). The post-hoc comparisons revealed that NDF content significantly increased across seasons for four species (*C. sativa*, *C. avenalla*, *M. alba*, and *R. pseudoacacia*) but decreased for three species (*F. excelsior*, *P. avium*, and *U. minor*). ADF content increased only for *R. pseudoacacia* and decreased only for *F. excelsior* and *P. avium*. ADL content increased for two species (*C. avenalla* and *R. pseudoacacia*) and decreased for three species (*A. cordata*, *F. excelsior*, and *P. avium*).

Analysing the effect of species across seasons (Tables 3, 4, and 5), CP content was significantly greatest in *M. alba* and *R. pseudoacacia* in spring (mean of 247 g.kg^{-1}), *R. pseudoacacia* in summer (224 g.kg^{-1}), and *C. avellana* in autumn (189 g. kg^{-1}). In contrast, CP content was significantly least in *S. domestica* in spring and summer (respectively 117 and 97 g.kg^{-1}) and *A. pseudoplatanus*, *F. americana*, *F. excelsior*, *G. triacanthos*, *P. avium*, and *S. domestica* in autumn (mean of 96 g.kg^{-1}). *M. alba* was the only species that had the significantly greatest IVDMD in spring (88.4%), summer (83.3%), and

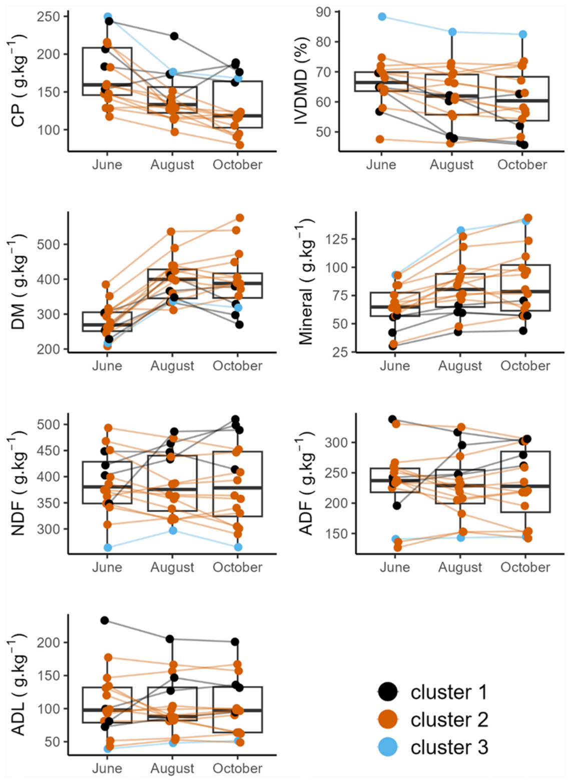

Fig. 2 Seasonal variability in nutritive values of the 16 tree species in June, August, and October (i.e. spring, summer and autumn). Points represent the estimated marginal means of each species, and lines connect species across seasons. Species are coloured according to their cluster for agronomic interpretation. Whiskers equal 1.5 times the interquartile range. *CP* crude protein content, *IVDMD* in vitro dry matter digestibility, *DM* dry matter content, *Ash* ash content, *NDF* neutral detergent fibre content, *ADF* acid detergent fibre content, and *ADL* acid detergent fibre content

autumn (82.5%) and the significantly least DM, NDF, ADF, and ADL contents. In contrast, *C. avenalla* and *F. sylvatica* had the significantly least IVDMD in spring, summer and autumn (respectively 56.8, 48.5, and 46.4%; 47.6, 46.2, and 48.3%). On the other hand, *A. cordata* had the significantly greatest ADF and ADL in spring, summer and autumn (respectively 338, 317, and 302 g.kg^{-1}; 233, 205, and 201 g.kg^{-1}). The ash content was significantly greatest in *M. alba* and *U.* 'Nanguen' in spring, summer and autumn (respectively 93, 133, and 141 g.kg^{-1}; 93, 127, and 143 g.kg^{-1}) and significantly least in *C. sativa* (respectively 32, 48, and 57 g.kg^{-1}).

Analysing the combined effects of season and species (Online Resource 2), CP content and IVDMD were significantly greatest in *M. alba* in June, while ash content was significantly greatest in *M. alba* in August and October, and in *U. minor* in October.

Species clustering

Three clusters of species were identified (Table 6, Fig. 2, Online Resource 3) based on the first three components of the PCA, which explained 95% of the variance. The first dimension was correlated mainly with IVDMD in June, August, and October (r > 0.95), while the second dimension was correlated mainly with CP content in spring, summer and autumn (r > 0.81). The third dimension was slightly correlated with CP content in spring (r = -0.47). Cluster 1 contained *A. cordata*, *C. sativa*, *C. avenalla*, and *R. pseudoacacia*, which had significantly greater CP content in summer and autumn, but significantly less IVDMD in autumn, compared to the overall mean.

Table 6 Mean ± SEM of crude protein content (CP; g.kg^{-1}) and in vitro dry matter digestibility (IVDMD; %) of the three clusters of tree species in June, August, and October (i.e., spring, summer and autumn)

	Cluster	June	August	October
CP content (g.kg^{-1})	1	197 ± 16,4%	177 ± 15,3% **	178 ± 5,1% **
	2	158 ± 9,5% *	126 ± 4,3% **	107 ± 4,4% ***
	3	250 ± 0%	177 ± 0%	168 ± 0%
	Overall mean	174 ± 10%	142 ± 7,7%	128 ± 8,8%
IVDMD (%)	1	64 ± 2,3%	55 ± 3,3%	52 ± 3,4% *
	2	66 ± 2,2%	63 ± 2,4%	62 ± 2,4%
	3	88 ± 0% *	83 ± 0% *	82 ± 0% *
	Overall mean	67 ± 2,1%	62 ± 2,4%	61 ± 2,6%

Asterisks indicate significant differences (using v-tests) between cluster values and overall means: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Cluster 2 contained *A. pseudoplatanus*, *F. sylvatica*, *F. americana*, *F. excelsior*, *G. triacanthos*, *J.* x intermedia, *P. tomentosa*, *P. avium*, *S. domestica*, *U. minor*, and *U.* 'Nanguen', which had significantly less CP content and moderate IVDMD in spring, summer and autumn, compared to the overall mean. Cluster 3 contained only *M. alba*, which had a non-significantly high CP content and a significantly greater IVDMD in spring, summer and autumn, compared to the overall mean.

Thus, cluster 1 grouped species with a high CP content but low IVDMD, cluster 2 species with a low CP content and moderate IVDMD, and cluster 3 species with a moderate CP content and high IVDMD. The order of the clusters based on their nutritive value remained consistent across seasons, as no cluster shifted from significantly high to significantly low for a given characteristic. From June to October, CP content decreased for clusters 1, 2, and 3 by respectively 9, 33, and 33, while IVDMD decreased by respectively 12, 4, and 6 pp.

Discussion

A decrease in tree leaf nutritive value from spring to autumn

General trends indicated a decrease in CP content and IVDMD over the year that resulted in a loss of nutritive value. Vandermeulen et al. (2018b) observed a similar trend in 11 tree species from Belgium, with season having a significant effect on CP content and in vitro organic matter digestibility. However, they also observed that season had a significant effect on NDF, ADF, and ADL contents, which we did not observe across species. Similarly, Kendall et al. (2021) found that season influenced CP content, which decreased from June to September across seven species from the UK. It is noteworthy that all three studies observed a similar trend, even though they shared only *A. pseudoplatanus* and *F. excelsior* in common. Results in Mediterranean climates were also similar to those of the present study: overall forage quality tended to decrease, but specific changes depended on the set of species studied (Ainalis et al. 2006; Parissi et al. 2018). This could be linked by differences in adaptive strategies among species: competitive species may exhibit a sharp decline in nutritive value, while stress-tolerant species tend to show more stability over time (Pierce et al. 2013). It highlights the need for a better understanding of the interactions between species traits and seasonal dynamics. Accordingly, farmers should account for the timing of nutritive value shifts when planning the use of forage trees.

Among multiple studies, the seasonal evolution of nutritive value for a given species differed among locations. For example, digestibility of *F. excelsior* did not change significantly across seasons in the present study, like in Italy (Ravetto Enri et al. 2020), but it decreased in Belgium (Vandermeulen et al. 2018b) and increased in the Netherlands (Luske and van Eekeren 2018). More specifically, both Luske and van Eekeren (2018) and Vandermeulen et al. (2018b) collected samples in the same year (2013) in Belgium and the Netherlands, less than 200 km apart, but observed different trends across seasons. These differences are likely due to differences in soil and microclimate properties. Indeed, soil properties can influence nutritive value strongly, but effects of climate remain little studied for temperate forage trees (but see Eichelmann et al. (2005) for shade effects). Trees growing on soils with greater available water capacity tend to have greater CP content in their leaves (Trémolières et al. 1999; Luske and van Eekeren 2018), suggesting that summer drought stress decreases the nutritive value of forage trees, as observed for herbaceous forage (Deléglise et al. 2015). Soils with a great nitrogen content also promote a greater CP content in tree leaves (Zahreddine et al. 2007). However, soil texture, water content, and nitrogen content are often interrelated, which makes it difficult to isolate the effects of each factor. Because the samples in the present study were collected under multiple soil and climate conditions over three years, we analysed the fixed effects of species and season while considering the site and year as random effects in the model. In this way, we highlighted the general effects of season on several species over a wide range of soil and climate conditions (Gomes 2022). We also observed that the variance explained by the species and season (marginal R^2) was greater than that explained by the site and year (conditional R^2 minus marginal R^2) (Table 2), confirming the strong effect of season and species compared to the environment. Interestingly, despite their low occurrence in the dataset, which could lead to poor statistical results, *F. sylvatica*, *F.*

americana, and *G. triacanthos* exhibited significant seasonal effects.

More specifically, we noted that ADL had less predictability compared to the other characteristics. The high coefficient of variation was mainly due to laboratory variability (CV = 9.5%), which is common for lignin measurements given the typically low lignin content in leaves.

A smaller decrease than that for herbaceous forage

In the present study, the nutritive value of tree leaves decreased from spring to autumn, as commonly observed for herbaceous forage (Bruinenberg et al. 2002). This highlights the importance of selecting species with the least variability in their nutritive value across seasons. It also suggests the potential to combine tree species that differ in leaf phenology at the farm scale to offset the seasonal decrease in forage quality (Navale et al. 2022). Herbaceous forage species have already been classified by their management flexibility, i.e., their capacity to maintain nutritive value after the peak has been reached. However, species whose quality decreases slowly often have a smaller peak in quality (Cruz et al. 2010; Theau et al. 2017). We did not observe this trade-off, as the cluster with the slowest decrease in CP content (cluster 1) also had the greatest CP content (Table 6). More studies are needed to confirm this trend, but trees may offer greater temporal management flexibility than herbaceous species, due to a slower decline in nutritive value over the season. Indeed, the mean IVDMD of trees in the present study decreased by 0.4 percentage points per week over the season, while the organic matter digestibility of the herbaceous forage *L. perenne* typically decreases by 1–2 percentage points per week (INRA 2018). Nevertheless, this decrease in nutritive value can be mitigated in herbaceous forage by well-timed mowing or grazing. Thus, in addition to selecting flexibly managed species with a small seasonal decrease in nutritive value, increasing the frequency of tree pruning or browsing could help maintain good nutritive value from spring to autumn. As in herbaceous forage, younger leaves of trees usually have greater CP content and IVDMD than older leaves, which could be maintained by intra-annual pruning/browsing and regrowth (Larsen et al. 2020). However, doing so could decrease yield and regrowth in the next growing season (Larsen et al. 2020), and few studies have analysed long-term effects of defoliation over several years on tree mortality.

Future opportunities

By assessing the nutritive value of tree leaves, we identified species in clusters 1 and 3 as the most promising to feed ruminants, as they have significantly greater CP content or IVDMD. More specifically, some tree species such as *R. pseudoacacia* and *M. alba* can reach summer CP content and IVDMD comparable to common grass forages like *L. perenne* and *Dactylis glomerata*, although generally less than those of high-value dicotyledonous species such as *Cichorium intybus* (Novak 2020). Vandermeulen et al. (2018b) reported that trees may offer comparable CP content but less IVOMD than herbaceous species, from early spring to late summer. Further studies are needed to compare a broader range of tree and herbaceous species, sampled at the same sites and dates.

Studies on yield, palatability, and voluntary intake are needed to better assess the feeding value of these forage trees. Species with high nutritive value may have low yields and/or low palatability, and thus remain of little importance. Also, it is important to identify livestock feeding preferences. For example, the palatability of *Alnus* spp. and *F. excelsior* (respectively in clusters 1 and 2) seems to be influenced strongly by livestock species and breed, as well as animals' previous experience with woody forage (e.g. Vandermeulen et al. 2018b; Bernard et al. 2020; Mesbahi et al. 2022; Nota et al. 2024). In contrast, *Ulmus* spp., also in cluster 2, is traditionally fed to livestock, which seem to accept it readily (Hejcman et al. 2014). Thus, there seem to be weak relations between the clusters we identified and tree palatability. Palatability can also be influenced by the presence of secondary metabolites, particularly phenolic compounds such as tannins and saponins. However, in our study, tannin content does not appear to be related to the clusters: for example, *R. pseudoacacia*, which has a very high summer tannin concentration (145 $g \cdot kg^{-1}$), belongs to the same cluster as *C. sativa* and *A. cordata*, which have much less tannin levels (3 and 13 $g \cdot kg^{-1}$, respectively; Novak 2020). Data on in vivo digestibility is also needed to accurately calculate the contribution of tree leaves to animals' requirements, such as net energy for lactation and metabolizable protein. This is especially important because current IVDMD equations were developed for herbaceous species and may not apply to other forages. Information is also needed on the nutritive value of tree branches, because cattle also consume those up to 8 mm in diameter (Moore et al. 2003).

The nutritive value of tree forage extends beyond CP content and digestibility. Trees also provide secondary metabolites and micronutrients (e.g. tannins, phenols, vitamins, calcium, selenium), which contribute to animal health, welfare, and product quality (e.g. Martin et al. 2005; Poutaraud et al. 2017). However, some of these compounds can also have antinutritional or toxic effects, particularly condensed tannins and phenols (Trouillard et al. 2024). Also, a trade-off may arise for farmers: as the season progresses, tree leaves tend to accumulate more ash—reflecting greater mineral content—while crude protein and digestibility decline (Fig. 2). Thus, farmers may have to choose between a nutritive forage in spring and early summer, or a mineral-rich forage in late summer and autumn. Additionally, trees provide benefits other than forage provision: they support animal welfare by providing shade, shelter, and dietary diversity (Trouillard et al. 2024).

Conclusion

This study is one of the first multi-species, multi-season, multi-site, and multi-year studies on the nutritive value of tree forage in a temperate climate. It highlighted that the season and species influence the nutritive value of forage trees, which generally decreased from spring to autumn, but less strongly than that usually observed for herbaceous forage species. The clusters' relative strengths and weaknesses remained the same regardless of the season, from spring to autumn. Based on their nutritive value, the most promising species are *Corylus avellana*, *Morus alba*, and *Robinia pseudoacacia*. *C. avellana* is notable, as its CP content remains similar in spring and autumn. However, future studies are needed to assess the yield and palatability of tree species to better understand their potential role in livestock nutrition.

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Data Availability The dataset and the statistical script supporting the findings of this study are openly available at Figshare: https://doi.org/https://doi.org/10.6084/m9.figshare.28270451.v3.

Declarations

Conflict of interest The authors declare no competing interests.

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