Radiative transfer modelling reveals why canopy reflectance follows function

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Optical remote sensing is potentially highly informative to track Earth’s plant functional diversity. Yet, causal explanations of how and why plant functioning is expressed in canopy reflectance remain limited. Variation in canopy reflectance can be described by radiative transfer models (here PROSAIL) that incorporate plant traits affecting light transmission in canopies. To establish causal links between canopy reflectance and plant functioning, we investigate how two plant functional schemes, i.e. the Leaf Economic Spectrum (LES) and CSR plant strategies, are related to traits with relevance to reflectance. These traits indeed related to both functional schemes, whereas only traits describing leaf properties correlated with the LES. In contrast, traits related to canopy structure showed no correlation to the LES, but to CSR strategies, as the latter integrates both plant economics and size traits, rather than solely leaf economics. Multiple optically relevant traits featured comparable or higher correspondence to the CSR space than those traits originally used to allocate CSR scores. This evidences that plant functions and strategies are directly expressed in reflectance and entails that canopy ‘reflectance follows function’. This opens up new possibilities to understand differences in plant functioning and to harness optical remote sensing data for monitoring Earth’s functional diversity.

Through natural selection plants have diversified in various functions in order to adapt to environmental conditions, including abiotic factors (e.g. precipitation or nutrient gradients) and biotic interactions (e.g. competition or herbivory). Assessing patterns of plant functioning in space and time is a prerequisite to understand biosphere-atmosphere interactions and ecosystem dynamics such as community assembly or nutrient cycles. With accelerated global change the data demand on patterns of plant functioning has increased, as the latter is heavily affected by anthropogenic impacts. However, due to vast temporal and spatial variation in plant functions, and the complexity to retrieve the latter in an explicit, consistent and spatially exhaustive way, data of Earth’s plant functional diversity remain limited. To close this gap optical Earth observation data is potentially highly informative. During recent years, various studies have demonstrated that optical Earth observation data allows mapping variation in plant functioning, functional types and strategies. However, it often remains unclear why we can remotely sense differences in plant functioning. To fully harness the potential of Earth observation data and to improve available algorithms, it is crucial to understand the underlying processes that enable us to monitor plant functioning. The key to such understanding are the traits that contribute to canopy reflectance.

The mechanics of solar radiation in plant canopies, including light emitted from plant canopies and thus retrievable from Earth observation sensors, is already well understood and formulated in process-oriented models, i.e. canopy radiative transfer models (RTMs). Although radiative transfer is determined by traits with relevance for plant functioning, few studies have explicitly linked RTMs and plant functioning. Such RTMs are particularly determined by canopy characteristics defining the amount of light being intercepted or scattered by the foliage as well as foliage properties (e.g. leaf constituents or structure) defining leaf internal scattering, absorption and transmission rates. Here, we assess the distribution of these traits along plant functional gradients, because knowing more about the links between optically relevant traits and plant functioning allows for mapping and monitoring plant functions in a more mechanistic way. This could dramatically improve the robustness and transferability of our models. Furthermore, it can be assumed that bridging plant functioning and canopy reflectance with radiative transfer theory can increase our understanding of how environmental factors and biotic interactions shape plant functional diversity (Fig. 1).

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As optically relevant traits we addressed those traits that are incorporated in PROSAIL, which is the most widely applied RTM for plant canopies. It couples two models, firstly PROSPECT modelling the leaf optical properties (e.g. pigment or water content), and secondly 4SAIL taking into account the structural properties of a canopy (e.g. leaf orientation) and its relative orientation to the sun and sensor. We also considered traits that can be directly deduced from the original PROSAIL trait space (e.g. leaf pigments by leaf mass or fAPAR). A summary of traits and assumed links to plant functions is provided in Table 1.

We assessed the distribution of these traits across plant functional gradients using in-situ measurements acquired in an outdoor experimental setting with plants grown in pots. The species pool comprised 45 herbaceous species from Central Europe and covered a broad functional spectrum.

Instead of looking at individual functions such as carbon sequestration or evapotranspiration, we referred to more general expressions of plant functioning provided by two well-established schemes: the Leaf Economic Spectrum (LES) and Grime’s CSR model of plant strategy types (CSR). Both schemes are general approximations of principal functional differences between species that bundle many individual functions to metrics characterising their overall performance towards abiotic and biotic environmental selection pressures.

The LES was derived from analysing various leaf traits (leaf lifespan, leaf mass per area, photosynthetic capacity, dark respiration rate, nitrogen, and phosphorus concentration) and describes the spectrum of leaf resource investments ranging from fast and acquisitive (low investment) to slow and conservative growth (high investment) (Fig. 2a). We compared optically relevant traits to the LES, as resource economics in leaves have been found to reflect a main axis of functional differences in plants and can thus assumed to be directly linked to the optical leaf traits in PROSAIL. The CSR model characterises plant species by means of three axes, defining their competitive (C), stress tolerating (S) and ruderal abilities (R) (Fig. 2b). Competitors are adapted to nutrient-rich sites featuring rapid growth to preemp resources. Stress-tolerators compensate environmental conditions limiting metabolic function through slow and robust growth, whereas ruderals are small-sized with short life cycles to counteract lethal events of disturbance or biomass removal. We compared optically relevant traits to the CSR scheme as it, in contrast to the LES, further integrates differences in function at the whole plant level and, thus, may be more appropriate for assessing optically relevant traits that are related to the canopy structure.

Results

Optically relevant traits versus Leaf Economic Spectrum. Which role do optically relevant traits play in relation to the LES? The set of optically relevant plant traits (compare Table 1) can be summarised using a three-dimensional feature space (Fig. 3), built by a principal component analysis, with component 1, 2 and 3 explaining 28%, 26% and 16% of the total variation, respectively. The LES was projected to this three-dimensional trait space to visualise relationships with optically relevant traits. As expected, LMA, as one of the original constituents of the LES, showed the highest correlation with the LES (r = −0.68 Pearson’s r). A lower yet positive correlation (p < 0.05) existed with pigment contents measured on a mass basis, i.e. Cabmass (r = 0.42), Carmass (r = 0.53), Antmass (r = 0.52), indicating decreasing pigment concentrations with increasing resource investments. Pigments measured on an area-basis also correlated significantly but negatively with the LES, i.e. Cabarea (r = −0.45), Cararea (r = −0.44), so that pigment contents predominantly increased with slow and conservative growth. Mesophyll thickness Nmeso correlated negatively with the LES (r = −0.45), reflecting higher mesophyll thickness with increasing resource investments. Traits linked to leaf water content (EWT, EWTcanopy, LDMC) and canopy structure (LAI, ALA, fAPAR, APARcum) were not significantly correlated to the LES. A table with all correlations is provided in S5.

Optically relevant traits versus CSR plant strategies. The distribution of optically relevant traits within the three-dimensional CSR scheme of plant strategies was assessed using thin plate regression splines and Generalized Additive Models (GAM). Neither EWT nor EWTcanopy correlated to plant strategies among forbs or graminoids. In contrast LAI, LMA, LMAcanopy, LDMC, pigmentmass, fAPAR and APARcum showed significant and consistent relationships across forbs and graminoids (Fig. 4). Pigmentarea, Nmeso, Cbrown and ALA exhibited no consistent relationship to CSR plant strategies across growth forms and thus related differently among forb and graminoid strategies (Figs 4–6). A table summarising the results for all traits is given in S6.
### Traits incorporated in PROSAIL-D

| Trait/Parameter [unit] | Abbr. | Description/functional role |
|------------------------|-------|-----------------------------|
| Chlorophyll content [µg/cm²] | Cabarea | Leaf pigments chlorophyll a + b, primary molecule for light harvesting²⁷ |
| Carotenoid content [µg/cm²] | Cararea | Leaf pigments including xanthophyll and carotenoids; photoprotection and light harvesting²⁶ |
| Anthocyanin content [µg/cm²] | Antarea | Leaf pigments of the flavonoid family; photoprotection, protection from pathogens⁶²,⁷² |
| Leaf Area Index [m²/m²] | LAI | Ratio of total one sided leaf area per unit ground; dominant control of primary productivity and transpiration⁴⁴,⁵⁰ |
| Leaf Inclination Distribution Function [deg.] | LIDF | Variation of leaf angles in the canopy; controls light harvesting efficiency, leaf temperature and transpiration⁶⁴,⁶⁵ |
| Leaf Mass per Area [g/cm²] | LMA | Inverse of Specific Leaf Area (SLA); Aggregates leaf constituents such as sugar, starch, cellulose or lignin; well-known proxy for resource allocation and plant strategies⁴⁸ |
| Equivalent Water Thickness [mg/cm³] | EWT | Water content per leaf area; determines thermal regulation, drought resistance and flammability⁵⁷–⁵⁹ |
| Mesophyll structure coefficient [‐] | Nmeso | Artificially designed PROSPECT parameter, relating to the thickness of the mesophyll layer, which affects light harvesting and light transmission as well as CO₂ diffusion⁶⁸,⁷⁰ |
| Brown pigment content [‐] | Chrown | Artificial PROSPECT parameter, relates to polyphenols such as tannins and other secondary metabolites with functions such as UV protection or defensive compounds against herbivory and pathogens⁵⁰ –⁶⁰ |

### Traits derived from PROSAIL-D trait space

| Trait/Parameter [unit] | Abbr. | Description/functional role |
|------------------------|-------|-----------------------------|
| Canopy Leaf Mass per Area [g/m²] | LMA canopy | Total leaf mass per canopy area [m²] calculated as the product of LAI and LMA |
| Canopy water content [g] | EWT canopy | Total water content per canopy area [m²] calculated as the product of LAI and EWT |
| Chlorophyll conc. [%o] | Cabmass | Chlorophyll mass per leaf dry mass |
| Carotenoid conc. [%o] | Carmass | Carotenoid mass per leaf dry mass |
| Anthocyanin conc. [%o] | Antmass | Anthocyanin mass per leaf dry mass |
| Fraction of Absorbed Photosynthetically Active Radiation [%] | fAPAR | Fraction of photosynthetically active radiation (PAR) absorbed in canopy; Integrates absorption by pigments and canopy structural traits (LAI, ALA); reflects gross photosynthetic capacity of the canopy. Simulated using PROSAIL (S3) |
| Accumulated Absorbed PAR [kWh/m²] | APARcum | PAR absorbed within the growing season; derived from multiplying fAPAR with course of direct and diffuse radiation during species specific growth length (S3) |

Table 1. The optically relevant plant traits considered in the present study and their functions. These are traits implemented in PROSAIL and derivatives thereof.

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### Discussion

Vegetation canopies can be considered as solar power plants and various functions and traits are coordinated to ensure an efficient energy assimilation by adapting to environmental factors (e.g. nutrient availability, temperature) and biotic interactions (e.g. competition)¹¹,⁴⁸. Indeed, our results confirmed that plant functions and strategies are expressed through traits that directly affect or are directly related to optical processes in plant canopies and thus determine their reflectance. This relationship of ‘reflectance follows function’ firstly provides the physical basis for retrieving differences in plant functions by means of optical Earth observation data, and underlines the potential to track Earth’s functional diversity. Secondly, linking plant functions and strategies with radiative transfer provides a different and additional perspective on how environmental factors and biotic interactions shape plant functional diversity.

Why does reflectance of plant canopies follow function? Our results showed strong links between optically relevant plant traits and the two schemes used as baselines for plant functioning, i.e. the Leaf Economic Spectrum (LES) and CSR plant strategies. Originally the LES has been captured through leaf lifespan, LMA, photosynthetic capacity, dark respiration rate, nitrogen and phosphorus content¹. Indeed, variation of observed LMA showed a strong correspondence to the LES, whereas we also found significant correlations with pigment_{meso} and pigment_{meso}, both of which are directly linked to photosynthetic capacity and nitrogen content⁹. Our results further suggest that pigment content (pigment_{meso}) generally increases with leaf lifespan, whereas the concentration of pigments (pigment_{meso}) decreases. Thus, plant investment in leaf tissue proportionally outweigh investment in leaf pigment, which can be explained as with increasing chlorophyll content light absorption follows a saturating curve, since chloroplasts become increasingly stacked in the palisade cells resulting in intraleaf shading⁵⁶–⁵⁸. Accordingly, plants with short leaf lifespan invest fewer pigment to optimise energy revenue. However, the LES reflects only one primary dimension of plant functioning, ranging from a quick to slow return on leaf resource investments. Accordingly, the canopy-structure-related traits (LAI, LMA canopy, ALA, fAPAR or APAR cum) showed no significant correspondence to the LES, suggesting that these traits are indeed related to other functional axes (Fig. 3). With the ‘global spectrum of plant form and function’ Diaz et al. have identified two major axes of plant functional convergence, with one axis reflecting leaf resource investments (LES) and the other axis reflecting plant and organ size-related traits. Accordingly, we expected that optically relevant traits integrating canopy properties are associated with the size-related axis. We actually observed such association between canopy-structure-related traits and the multidimensional CSR space, which characterises plant functioning in terms of competitive, stress tolerant and ruderal abilities at the whole plant level⁵¹. Accordingly, multiple traits that did not exhibit an association with the LES (e.g. LAI, LMA canopy or fAPAR), in turn showed a notable correspondence to the CSR space. Our results confirmed previous relationships between traits and the CSR space and exhibited gradients that have not been assessed before.

In agreement with pivotal formulations of the CSR scheme²⁹ and the allocation by Hodgson et al.³⁹, LMA was lowest for ruderal species and highest for stress tolerators, closely followed by competitors (Fig. 4). Leaf mass per canopy area, i.e. LMA canopy (LMA • LAI), which was to our knowledge not compared to CSR strategies before,
reflects total leaf carbon assimilation per canopy area. We found highest \( LMA_{\text{canopy}} \) for competitive species, followed by intermediate \( LMA_{\text{canopy}} \) for stress tolerators and intermediates and lowest values for ruderals. This gradient reflects the primary principles of the plant strategies\[29\]: stress tolerators feature a conservative growth with a long leaf lifespan resulting in a steady accumulation of dry matter in the canopy, whereas ruderals are adapted to disturbance events and thus have short lifecycles in which they accumulate few resources. Competitors feature both high productivity and a relatively long lifespan and therefore highest resource accumulation (\( LMA_{\text{canopy}} \)). Both leaf and canopy water content, i.e. \( EWT \) [g/cm\(^2\)] and \( EWT_{\text{canopy}} \), did not show a clear relationship with plant strategies. In contrast \( \text{LDMC} \), which is the ratio of leaf mass and leaf water content (\( \text{LDMC} = \frac{\text{LMA}}{(\text{LMA} + \text{EWT})} \)), showed a clear coherence towards plant strategies and was therefore already used by Hodgson \textit{et al.}\[39\].

**Figure 2.** Schemes of plant functional gradients that were compared to optically relevant traits of cultivated plants: (a) Leaf Economic Spectrum (LES), and (b) CSR plant strategies.

**Figure 3.** Two perspectives of the transformed trait space (principal component analysis) and relation to the Leaf Economic Spectrum (LES in red). Significant correlations between traits and the LES are highlighted in blue.
to allocate CSR scores. This suggests that functional characteristics are expressed through the relative water concentration in leaf tissue, rather than the absolute leaf water content.

A more complex pattern was found for LAI, where intermediate species (CSR) have highest LAI values followed by competitors, ruderals and stress tolerators invest more resources towards their strategy-specific trait-expressions and functions. Competitors occur primarily in nutrient rich sites, where competition for sunlight is most pronounced and triggers increased height growth to overtop neighbouring individuals. Increased canopy height in turn requires additional resource investments in support tissues, e.g. in the stem for vertical plant growth itself as well as in enhanced leaf robustness (higher LMA), to compensate for increased exposure to wind (compare LMA gradient, Fig. 4). An increased LMA was also found for plants adapted to high light intensities (competitors) through increased palisade parenchyma to maximise photosynthetic capacity and thus quantum yield per unit leaf area and reduce potential light saturation. This suggests that relative to intermediate strategies, competitors invest fewer resources in the development of total foliage area (LAI). Therefore, competition for sunlight might enforce a trade-off between the maximisation of height growth and light interception. This agrees with Porter et al., who have reported higher accumulation of leaves for shade tolerant species leaves with smaller canopy heights among tropical tree species.

Leaf inclination (ALA) did not show a trivial correspondence to the CSR spectrum, but differed between growth forms, reflecting generic differences in the canopy architecture of graminoids and forbs. Variation in leaf angles across graminoid strategies showed no explicit pattern. For forb strategies ALA increased from competitive forbs to stress tolerant and ruderal forbs (Fig. 5). This agrees with Hikosaka & Hirose, who have simulated leaf angle distributions for plant canopies and found lower leaf angles with increasing competition. Competitive forbs, which aim to overtop and shade out the surrounding and competing plants, develop rather flat leaf angles to deplete or scatter most of the light before it is available for rivals. However, a horizontal leaf position requires increased support costs for petioles and branches, and is generally less efficient for light absorption as self-shading and light saturation increases. Leaf angles hence increase with decreasing competition to scatter light between leaves and hence distribute light into the lower canopy.

Similar to the LES-based analysis, the derived distributions of chlorophylls, carotenoids and anthocyanins across the CSR space are very alike (Figs 4, S6), since pigments are usually highly correlated in mature leaves. Yet, the relationships differed greatly among pigments measured on an area basis (pigment area) and measured on a mass basis (pigment mass) (Fig. 6). The relationship between pigment area and CSR strategies further differed between forbs and graminoids (Fig. 6), which agrees with Tjoelker et al., who has found differences in leaf photosynthetic activity between grasses and forbs. For forbs ruderals and intermediates feature highest pigment area. Among graminoid strategies pigment area showed a low and inconclusive variation across the CSR space apart from a strong increase for extremely stress tolerant graminoids (Festuca ovina and Nardus stricta).

Pigments normalised by mass (pigment mass) showed a very consistent gradient across growth forms (S8), which however almost exclusively mirrors the LMA gradient (r² of 0.74, 0.80, 0.85 for Cab mass, Carmass, Antmass, respectively). This is further confirmed as the modelled pigment mass values across the CSR-space were highly

Figure 4. Distribution of optically relevant plant traits in the CSR- feature space of forbs and graminoids based on GAM extrapolations. Observations are displayed as transparent grey dots (partly overlapping) with a size proportional to the trait expression.
correlated with pigment values based on a null-model, in which we sampled random pigment values that were subsequently divided by LMA and thus mass normalised ($r^2$ of 0.80, 0.91, 0.64 for Cab$_{mass}$, Car$_{mass}$, Ant$_{mass}$, respectively). Accordingly, we found that pigment values indeed do not reflect pigment variation per se, but rather the LMA gradient, which varies in higher magnitudes than traits with photosynthetic function. Likewise the strong correspondence between pigments and the LES can largely be attributed by the high variation in LMA, as indicated by the null-model (S9). This indicates that the characterisation of plant canopies through pigments on a mass basis is greatly redundant with LMA and therefore appears to be not expedient, despite its frequent use in the remote sensing community.

The distribution of simulated fAPAR across the CSR space showed a strong correspondence to LAI (Fig. 4), suggesting that variation in light harvesting is particularly determined by LAI (in line with 44,46,52) and therefore highest for intermediate strategies followed by competitors. Yet, fAPAR solely represents the potential energy gain at a point in time and thereby does not consider phenological differences between plant strategies. Accordingly we modelled the accumulated photosynthetic active radiation (APAR$_{cum}$). This measure integrates fAPAR and the course of absorbed direct and diffuse radiation (assessed from HelioClim-3 archives53) during a plants phenological season (recorded for the cultivated plants). APAR$_{cum}$ thus reflects the accumulated photosynthetic and carbon assimilation during a plant’s growth period. APAR$_{cum}$ showed a very consistent and clear pattern across growth forms. Corresponding to their short growth period ruderals featured the lowest APAR$_{cum}$. Intermediate APAR$_{cum}$ was found for stress tolerators, as these can compensate conditions that limit productivity through robustness and persistence, resulting in a comparably low but prolonged light harvesting. Highest APAR$_{cum}$ was found for competitors, as competitive abilities require long-term investments (e.g., height growth) that are rewarded with long-term returns. These results thus showed that the phenology-dependent variation in energy acquisition directly reflects established plant strategies and functions. Moreover, the comparable strong relationship with APAR$_{cum}$ emphasised that gradients in plant productivity are not fully reflected by a single biochemical or structural trait, but relate to the integrated response of pigments, LAI, ALA as well as phenology.22 This particularly highlights the potential of multi-temporal Earth observation data to map functional gradients. The overall strong correlation between gradients derived from APAR$_{cum}$ and LMA$_{canopy}$ ($r^2 = 0.88$) underlines the plausibility of the models, as a large share of the absorbed energy is used for carbon assimilation in leaves. The minor discrepancy between APAR$_{cum}$ and LMA$_{canopy}$ existed for competitors, where photosynthetic assimilation (APAR$_{cum}$) is highest, but LMA$_{canopy}$ showed a slight bias towards C-CSR, which could result from competitors investing a considerable part of their resources in height growth rather than total leaf tissue.

According to our results Cbrown and Nmeso did not show a consistent relation with the CSR strategies across growth forms. Both traits only corresponded to CSR strategies among graminoids (S7). In agreement with Jacquemoud & Baret Nmeso correlates with LMA. The distribution of Cbrown could not be explained in an
correlations with CSR plant strategies (LAI, LMA canopy, APAR cum) than traits used originally to allocate the CSR complement the suite of determinable proxies to describe spatial variation in plant functioning and community anthocyanin content (Ant area), mesophyll structure coefficient (N meso) and brown pigment content (Cbrown) PROSPECT-D was based on a look-up-table approach and wavelets. Further details on the inversion process of the traits space implemented in PROSAIL.

Material and Methods Retrieval of the traits space implemented in PROSAIL. We derived the PROSAIL trait space from outdoor cultivated plants, including 45 forb and graminoid species covering the full range of the CSR spectrum (Table 2). We performed seed propagation in greenhouses and moved the plants outdoor for a week of acclimatisation once they were grown to an adequate size. Afterwards the plants were planted out in four repetitions in separate pots with a size of 0.4 m × 0.4 m and 30 l volume filled with a standardised substrate. Fewer repetitions had to be planted for species where seedling propagation was less successful. All pots were regularly fertilised, weeded and irrigated.

For each species we measured the considered traits on a weekly basis for each pot. We determined the species-specific trait expressions by averaging the measurements among pots and subsequently calculating the median for the whole season. We only considered measurements that were performed in non-senescent canopies of adult plants (here defined as plants with closed canopy).

In view of the envisaged amount of measurements per species traditional approaches for pigment retrieval such as the spectrophotometer method by Lichtenthaler was not feasible. Furthermore, N meso and Cbrown are specific parameters of PROSPECT. We measured leaf chlorophyll content (Cab leaf), carotenoid content (Car leaf), anthocyanin content (Ant leaf), mesophyll structure coefficient (N meso) and brown pigment content (Cbrown) using leaf reflectance spectra and their inversion using the leaf radiative transfer model PROSPECT-D. We acquired leaf spectra of 5 individual leaves per cultivated pot using an ASD FieldSpec III (ASD, Inc. Boulder, CO, USA) attached with a plant probe and leaf clip. If the area of a leaf was smaller than the opening of the plant probe (3.14 cm²) we seamlessly, and without overlap, placed the leaves side by side on an adhesive tape. The inversion of PROSPECT-D was based on a look-up-table approach and wavelets. Further details on the inversion procedure and its validation are given in S1.

We estimated LAI using an Accu-PAR LP-80 ceptometer equipped with an external reference sensor to account for the current photosynthetic active radiation (PAR). For each pot we recorded and subsequently averaged 18 individual measurements.

To limited the destructive impact over time, we measured leaf mass per area (LMA) and equivalent water thickness (EWT) per species rather than per pot. Samples consisted of leaflets only without petioles and rachis. Fresh leaf mass of around 10 g of whole leaves per species was measured on site. Total leaf area of these leaf samples was retrieved using a flatbed scanner. The LMA [g/cm²] was derived from weighing the sample material at 70°C for at least 72h. EWT [mg/cm²] was derived by subtracting LMA from leaf fresh mass per area.
Graminoids (n = 20) | Forbs (n = 25)

- Alopecurus geniculatus (4, R/CSR); Alopecurus pratensis (4, C/CSR); Anthoxanthum odoratum (4, CSR/SC); Apera spica-venti (4, R/CSR); Agrostis capillaris (4, CSR); Arvenatherum elatius (4, CSR/SC); Brachypodium sylvaticum (4, SC/CSR); Bromus hordeaceus (3, R/CR); Calamagrostis epigeios (4, C/SC); Deschampsia cespitosa (4, S/CSR); Digitaria sanguinalis (4, R/CSR); Festuca arvina (4, S); Holcus lanatus (4, CSR, Lapsana communis (4, C/CSR); Lolium multiflorum (4, CSR); Molinia caerulea (3, SC); Nardus stricta (4, S); Phalaris arundinacea (4, C); Poa annua (4, R); Scirpus sylvaticus (4, C/SC); Tritium flavescens (4, CSR);

- Agropyron cryptostegium (4, CR/CSR); Anthyllis vulneraria (2, S/SC); Actinidia arguta (4, CR); Centaurea erythraea (4, CR); Cirsium arvense (4, CR); Cirsium vulgare (4, C/CSR); Digitalis purpurea (4, CR/CSR); Filipendula ulmaria (1, C/CSR); Geum urbanum (4, CSR); Geranium pratense (4, C/CSR); Geranium robertianum (R/CSR); Plantago major (4, R/CSR); Plantago media (4, C/CSR); Scorpiurus rupicola (4, CR); Solidago canadensis (4, C/CSR); Serratula carduifolia (4, C/CSR); Thesium arvense (3, CR);

Table 2. List of all cultivated species. The number in parentheses indicates the number of repetitions per species followed by the allocated CSR strategy.

The ALA was retrieved from leaf inclination distributions that we determined using levelled digital photograph and the procedure described by Ryu et al.69. For each species we measured not less than 50 angles of leaves parallel to the viewing direction. Leaf angle distributions and ALA were only retrieved once due to logistic constrains.

We deduced additional traits from the PROSAIL traits space to further exploit its information content: leaf dry matter content (LDMC = LA/GEVI + EWT); canopy leaf mass per area (LMA = LMA ⋅ LAI); canopy pigment content (pigment = pigment ⋅ LAI); fraction of absorbed photosynthetic active radiation (fAPAR) simulated using PROSAIL (details in S3);35 cumulative absorbed photosynthetic active radiation (APARcum) in kWh/m², which corresponds to the total absorbed energy within the growing season of each species. The APARcum was calculated as the product of APAR, direct and diffuse irradiance averaged for April–October (data assessed from HelioClim-3 data35, details in S3) and the length of the growing season, (here defined as the observed number of weeks between maturity and senescence). A statistical summary of the trait space is given in S2.

**Linking the Leaf Economic Spectrum and optically relevant plant traits.** Wright et al.3 determined the LES using the first component of a principal component transformation of six leaf traits, i.e. LMA, photosynthetic assimilation rate, leaf nitrogen mass, leaf phosphorus mass, dark respiration rate, and leaf lifespan. From these traits we only measured LMA (or SLA respectively) within the above described plant experiment. We therefore requested the remaining traits from the TRY-database, where sufficient data was available for 26 of the 45 species (see S4 for a list of the 26 species) and two further traits, leaf nitrogen mass, leaf phosphorus mass. We determined the LES for the 26 species using the log10 transformed expressions of these three traits and the loadings reported by Wright et al.3. The LES retrieved this way was compared to each of the optically relevant traits using Pearson’s correlation coefficient. Additionally, the relationship among the different optically relevant traits and their relation to the LES was visualised by means of a principal component analysis (PCA). Therefore, we built a PCA of the PROSAIL trait space on which the LES was projected using the function ‘envfit’ of the vegan package. Prior to the PCA the PROSAIL traits were centered and scaled.

**Linking CSR plant strategies and optically relevant plant traits.** The position of a species in the CSR space is defined by three axes expressing competitive, stress tolerant and ruderal abilities (scores). We used the CSR scores provided by Hodgson et al.39, who allocated CSR strategies for a multitude of European plant species using trait expressions of canopy height, LDMC, flowering period, flowering start, lateral spread, LMA and specific leaf area (Table 2). For some species we adopted the allocation from the BioFlor database39 and expert knowledge.

We assessed the relationship between each PROSAIL trait and the CSR space using Generalized Additive Models (GAM)38 and thin plate regression splines32. As input for the GAM we used the first two PCA components (cumulative variance 97%) instead of the raw CSR scores to facilitate the interpretability of the results. The results were visualised in ternary plots (R-package ‘ggtern’).36

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Author Contributions

T.K. performed the data acquisition. T.K. and S.S. performed the analysis and wrote the manuscript.

Additional Information

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