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Using the CSR Theory when Selecting Woody Plants for Urban Forests: Evaluation of 342 Trees and Shrubs

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Abstract. Background: The development of a framework for optimising plant selection, with the objective of integrating plant resilience for site and function, is crucial for urban forest managers and designers. The principal objective of this study was to evaluate the leaf economics spectrum of trees and shrubs and to categorise them using the CSR classification system, classifying plants according to 3 principal strategies (Competitors [C], Stress tolerators [S], Ruderal [R]), which represent a spectrum of plant forms and functions arising under conditions of competition, abiotic restriction to growth, or periodic disturbance, respectively. The second objective was to discuss how the CSR classification system applied plant ecological strategies to plant specification in urban environments. Methods: The method for ordinating species in CSR space is based on leaf economic data including Leaf Area, Leaf Dry Matter Content, and Specific Leaf Area. Data were assembled at the Swedish University of Agricultural Sciences Campus Arboretum. Results: A total of 342 taxa (170 tree and 172 shrubs) were examined in this study. The study taxa were distributed along the Competitor-Stress tolerator (CS) axis of the ternary plots. The data analysis indicated that shrubs exhibited a more expansive position in the model, displaying a greater prevalence of stress tolerators and species with a more comprehensive approach to disturbance, competition, and stress compared to trees. Conclusion: The results provided an understanding and rationale for how species-specific selection for urban environments could be carried out. This was based on trait-oriented plant selection using the CSR classification, which was then adapted to different urban situations and functions. As a result, not only can quadratic equations be derived which describe the distribution of shrubs and trees of evolutionary variation, but also the uses of tree and shrub species in urban environments can be quantitatively described.

Keywords. Climate Change; Diversity; Plant Selection; Urban Environments.

INTRODUCTION

Trees and shrubs provide distinctive combinations of ecosystem services (ES) in urban settings. Recent projections suggest that an overreliance on a limited range of species may compromise the ES provided by urban forests (Pauleit et al. 2017). The suboptimal fitness of plants for their climate and the diminished performance of their ES are frequently compounded by the planting of species in locations that are not conducive to their growth and development. In the planning and design of urban green infrastructure, it is of the utmost importance to be able to anticipate the development of different species under a variety of growing conditions. This enables the planning and anticipation of their needs for establishment and long-term maintenance, as well as their long-term development in response to current and future climates. In a changing climate, characterised by increasingly hotter and periodically drier conditions, coupled with the densification of urban structures and the occurrence of severe outbreaks of diseases and pests, there are increasingly challenging conditions for the successful utilisation of plants (Koeser et al. 2014; Allen et al. 2015; Matusick et al. 2018; Yi et al. 2022). This is leading to a high proportion of trees and other plants dying or experiencing impaired development and establishment. (Kianmehr et al. 2024). In addition to the aforementioned factors, the natural mortality of trees in urban environments due to the aging of the urban tree population represents another significant cause of urban canopy loss (Roman et al. 2014). It is therefore crucial to gain a deeper understanding of the resilience of different tree and shrub species to challenging conditions and to anticipate their initial management needs, particularly in light of the potential for nontraditional plant material to be free from serious diseases and pests. When available plant literature directed to urban forestry is reviewed, the descriptions of trees and shrubs are often limited to their aesthetic qualities and size, with minimal attention given to climate and site-related guidance. The climate and site-related information that does exist is primarily based on the authors' personal experiences and observations, rather than on rigorous scientific evaluations of their capabilities or limitations in challenging growing habitats (Sjöman and Nielsen 2010; Sjöman et al. 2018; Watkins et al. 2020), which means that there are many contradictory conclusions within the literature. This contributes to the pervasive reluctance to test unconventional plant material with the aim of diversifying the urban forest.

One type of information that is notably absent from the urban forestry community and seldom considered in the design of public green spaces is trait-oriented plant selection (Watkins et al. 2021). This approach considers the evolutionary properties that different species have developed in order to cope with the growing conditions and competition for resources in their natural environment.

One accessible method for classifying plant investments and thereby their tolerance to different plant environments, as well as for gaining insights into growth rate, is the CSR classification system (Hodgson et al. 1999; Pierce et al. 2017). This classification system is based on Grime's theory of competitor-stress tolerator-ruderal (CSR) plant strategies (Grime 1974, 1977, 2006; Grime and Pierce 2012). In the CSR system, the 3 principal strategies represent viable trait combinations that have evolved in response to competitive pressures, abiotic limitations to growth, or periodic biomass destruction. C-strategists (competitors) are plants that are adapted to stable and productive habitats and are successfully converting available resources into rapid growth and rapid attainment of large individual and organ size, thereby aiding resource pre-emption. S-strategists (stress tolerators) are adapted to resource-limited habitats, investing in the capacity to retain resources and repair cellular components in dense, persistent tissues. R-strategists (ruderals) are disturbance-favoured species that invest in traits not in the individual plant, but in propagules from which the population can regenerate in the face of repeated lethal biomass destruction events or disturbances. The CSR classification method employs a variety of functional traits, which are quantified in situ (or measured in material collected in situ), thereby providing plant users with a comprehensive understanding of the capacity of plant material to thrive in resource-rich or resource-limited habitats.

In the context of urban horticulture, it is essential to have a clear understanding of the evolutionary strategies of different tree and shrub species prior to the planning and design of planting schemes. This provides insight into their suitability for specific conditions, whereby their investments must align with the environments in which they are planted. Furthermore, knowledge of their growth rate is vital for anticipating their requirements for establishment management and for predicting their development (growth) on-site. The process of matching a plant to its designed location integrates multiple sources of information. Conceptual frameworks for this have been proposed for herbaceous plants and small shrubs by Kühn (2011) and for trees by Watkins et al. (2021) (Figure 1). Both of these frameworks connect locations in trait space, illustrating an ongoing trade-off between metabolic pace and stress tolerance in urban environments. The optimal location for a plant is determined by its evolutionary adaptations, which are designed to enhance its fitness.

In a landmark study by Pierce et al. (2017), a plethora of species were positioned within the CSR model through the assessment of an array of traits pertaining to resource investment and environmental adaptation. The study demonstrated that the utilisation of a reduced set of 3 leaf traits, in lieu of the original 14, resulted in a relatively minor loss of information. Moreover, the multivariate plant functional space described by leaf traits alone was found to be representative of whole-plant functional variation. This is further verified in a comprehensive review by Reich (2014), which established a correlation between the investments made by leaves, stems, and roots of plants in order to cope with varying resource availability and climate situations. In the same study, Reich concluded that leaf investments provide a framework for assessing the capacity of different species to manage different habitats and for obtaining guidance on their investment priorities and thus their

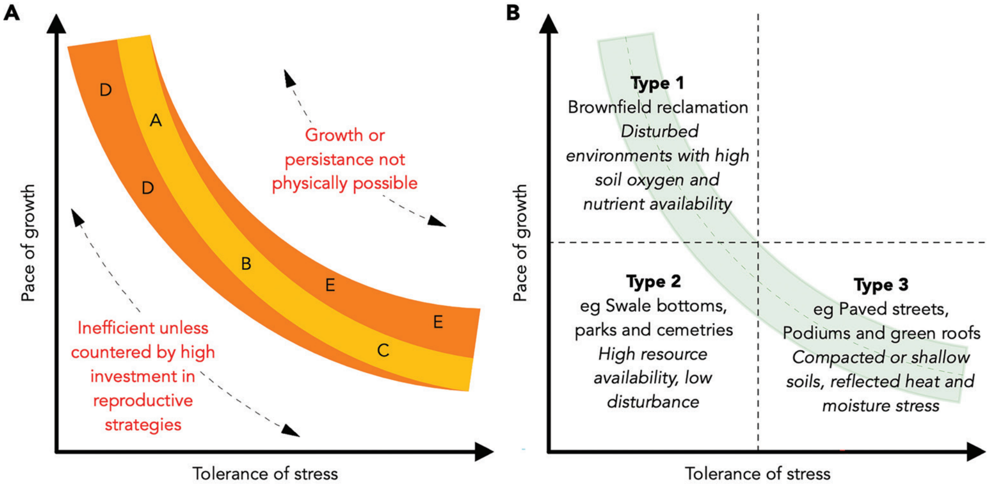

Figure 1. The hypothetical trait-based scheme for urban foresters, as presented by Watkins et al. (2021), builds upon the competitor-stress tolerator-ruderal (CSR) theory. It demonstrates the diversity of viable plant strategies, which are characterised by a trade-off between fast growth and high tolerance of stress. This allows for the identification of tree species that are well-suited to urban forestry sites. (A) Positions A and C represent the 2 extremes of the trade-off between competitive and stress-tolerant strategies, with position B representing a generalist strategy. In disturbed environments, a greater investment in reproduction and faster growth is required, resulting in more ruderal strategies (Position D). In more stressful situations, delayed sexual maturity allows for greater investment in dense structural and photosynthetic tissues (Position E). It should be noted that, in contrast to other similar graphs, the trait trade-off is fitted by a quadratic rather than a linear line of best fit. (B) Overlays environments found in urban forests upon this model, resulting in a method for identifying the most suitable tree species for urban forestry sites.

growth rate. The 3 leaf traits presented in Pierce et al. (2017) are leaf area (LA), leaf dry matter content (LDMC), and specific leaf area (SLA). Leaf area (LA) represents interspecific variation in plant size, while leaf dry matter content (LDMC) represents conservative resource use. Specific leaf area (SLA) represents acquisitive resource use. The combination of these traits provides a robust indication of the classification of the different species in the CSR model. This, in turn, allows for an overview of a large number of species and their plant economic investment, which is based on plant ecological strategies derived from functional traits. This, in turn, explains the trade-off between dry matter investment in leaf structure and the potential rate of resource return.

While these conceptual ecological frameworks offer a valuable means of describing or predicting plant fitness, the challenge of accessing the requisite data to ordain plants in CSR space persists. To date, the majority of published studies in this field have been conducted using either plants that have been cultivated specifically for the purposes of the study in question, or established plants in their planted location. This approach has the effect of constraining the potential for data to be shared between sites or projects. The aggregation of extensive trait databases from disparate studies offers promising avenues for macro-ecological inquiry (e.g., Ely et al. 2021) and the evaluation of hypotheses pertaining to ecological restoration (e.g., Crowther et al. 2022). Nevertheless, it remains uncertain to what extent these data can be employed in fine-grained inquiries, such as plant selection at either interspecific or intraspecific levels in complex stress environments, including urban forests.

The principal objective of this study was to evaluate the leaf economics spectrum for trees and shrubs that are currently used, or have the potential to be used, in urban forests in Northwestern Europe (in total 342 taxa—different species and genotypes) and categorise them using the CSR classification. In this study, the leaf economic spectrum is described through the investment of nutrients and dry mass in leaves. This reflects a mixture of direct and indirect causal relationships between traits independently of growth form, plant functional type, or biome (Wright et al. 2004). The second objective was to discuss how the CSR classification system applied plant ecological strategies to plant specification in urban environments.

MATERIALS AND METHODS

The method for ordinating species in CSR space follows the framework presented in Pierce et al. (2017)

where LA, LDMC, and SLA are integrated in a single model. Data were assembled at the Swedish University of Agricultural Sciences Campus Arboretum in Alnarp, which hosts one of the largest collections of woody plants in Northern Europe. Alnarp is considered to have a fully humid, oceanic temperate climate with warm summers (Cfb in the Köppen-Geiger climate classification system)(Kottek et al. 2006). The trees and shrubs studied in the Arboretum at Alnarp were all established for over 10 years in unconstrained rooting space, were growing in full sun or only subjected to short periods of partial shade, and had no visual symptoms of stress. The species included in the study were limited to taxa with more than 6 individuals in order to achieve an adequate number of replicates—for a complete list of species, see Appendix.

The methodology used for collecting leaf trait data followed the standard presented in Pérez-Harguindeguy et al. (2013) which is a very well experienced methodology. Specific leaf area (SLA) is calculated as the ratio of one-sided area of a fresh leaf to its oven-dry mass and thus indicates how much leaf area a plant builds with a given amount of leaf biomass:

$$SLA = \frac{A}{M_L}$$

where A is the area of a given leaf and M_L is oven-dry mass of that leaf. Typical units are $m^2\ kg^{-1}$ or $mm^2\ mg^{-1}$.

Leaf area (LA) is the most commonly used metric for leaf size and is defined as the one-sided or projected area of an individual leaf, expressed in mm^2. Heat stress, cold stress, drought stress, nutrient stress, and high-radiation stress all tend to select for relatively small leaves, which makes LA a strong trait in the plant economic spectrum.

Leaf dry-matter content (LDMC) is the oven-dry mass (mg) of a leaf divided by its water-saturated fresh mass (g), expressed in $mg\ g^{-1}$. LDMC is widely used as an indicator of plant resource use and has been shown to correlate positively with leaf lifespan (Shipley and Vu 2002).

Sample Collection

The collection of data was conducted over the course of 2 months, specifically from July to August. In this study, a single branch that was exposed to sunlight and did not exhibit any indications of abiotic or biotic stress, such as fungal pathogens infecting leaves, defoliation, or leaf chlorosis, was selected from each species or genotype under investigation. Depending on the availability of trees and shrubs within the collection, leaf material was collected from 6 to 10 individuals between 18:00 and 20:00 h. Excised branches were immediately placed in a humid bag and taken to the laboratory within 20 min. At the laboratory, branches were recut under water at least 2 nodes distal to the original cut and placed in a tube of water without exposing the cut surface to the air. Branches were rehydrated overnight in a dark chamber with > 75% relative humidity as measured by a wet-dry bulb thermometer (wet bulb 15 °C/dry bulb 17 °C) in order to get full turgor. Through this procedure, it was possible to compare different species and genotypes. Mean trait values were then calculated for each species.

The mean trait values for each species in the study were then used to calculate CSR values using the StrateFy tool (Pierce et al. 2017), which were plotted in ternary plots. The StrateFy tool, as described by Pierce et al. (2013; 2017), employs mean trait values for each species to generate a principal components analysis (PCA) utilising XLSTAT 10 software (Kovach Computing Services, Anglesey, Wales). The resulting PCA was rotated via standard Varimax rotation, also using XLSTAT. Based on the outcome of the PCA, the values of LA were regressed against PCA axis 2, LDMC was regressed against PCA 1 (a positive correlation), and SLA against PCA 1 (a negative correlation), in order to produce 3 regression equations. The resulting curves of best fit, derived from a range of models in the SigmaPlot 10 database (Systat Software, Chicago, IL, USA), were fitted and those with the highest R^2 values were selected. Subsequently, the regression equations were employed to generate functions within a Microsoft Excel (Redmond, WA, USA) spreadsheet, thereby enabling the prediction of PCA 1 and 2 coordinates derived from values of LA, LDMC and SLA. Three dimensions were thus assigned to the target species: a "LA dimension" based on PCA2, a "LDMC dimension" based on positive variability along PCA1, and a "SLA dimension" based on negative position along PCA1. Given that PCA values may be either positive or negative, the minimum values along each PCA axis were identified and used as a constant to be added to all values of each trait. This was done in order to translate the LA, LDMC, and SLA dimensions into an entirely positive space (Pierce et al. 2013).

The subsequent function established the maximum values, thereby defining the range of values for each trait. In order to produce ternary coordinates (i.e., 3 coordinates for a triangular graph), a function was then added to the spreadsheet that summed the 3 dimensions and divided by 100. This allowed for the determination of the proportional contributions of LA, LDMC, and SLA for each species. The resulting ternary coordinates represent a trade-off between 3 competing functional traits and thus 3 competing ecological functions. It is necessary for all species to have a minimal capacity for competition, stress tolerance, and survival of disturbance (Grime and Pierce 2012). Furthermore, no leaves were characterised by zero area or zero mass. Therefore, the resulting triangular ordination of species represented a "trade-off triangle." The ternary plots were produced separately using SigmaPlot (Grafiti LLC, Palo Alto, CA, USA). A spreadsheet function was used for all 3 dimensions, resulting in the space occupied by species filling the entire ternary plot and thus achieving a CSR classification. This was achieved by multiplying all values by a rescaling constant that allowed the maximum and minimum values along the axis exhibiting the least variability to occupy 100% of the range of the x-axis of a ternary plot (Pierce et al. 2013; Pierce et al. 2017). The calculations and plot creation were carried out using R software (R Foundation for Statistical Computing, Vienna, Austria) complemented by the Tidyverse and ggtern packages (Hamilton and Ferry 2018).

In order to test the collected leaf data of trees and shrubs and, based on a CSR categorisation, group them according to different urban types, a Principal Components Analysis was conducted. This analysis was performed as Díaz et al. (2016), following a study conducted by Baraloto et al. (2010). The aim was to establish a hypothetical relationship between 2 dimensions of plant functioning: stress tolerance and competitiveness (growth rate). The objective was to identify how this system could be used to select species for urban forests.

RESULTS

In this assessment, the study taxa (170 trees and 172 shrubs) were distributed along the Competitor- Stress tolerator (CS) axis of the ternary plots. Analysis of data gathered in Alnarp Arboretum revealed that shrubs had a broader position in the model with a greater prevalence of stress tolerators and species with a more general approach to disturbance as well as competition and stress (CSR) compared with trees, where 6 shrub species are categorised as CSR compared to 1 tree species (Figure 2). Among the tree species evaluated, there was a large proportion that act as CS strategists: 69 out of 170 species (Figure 3). The S-strategists included tree species that are naturally found in very challenging environments where it is an advantage for a species to equip itself with expensive leaves/needles. Thus, they included many evergreen species that specialise in hot, dry environments, such as *Pinus leucodermis*, or shady environments, such as *Tsuga heterophylla* and *Taxus cuspidata* (Figure 3). In contrast, the tree species categorised as C-strategists were distinct pioneer species in resource-rich habitats, such as *Pterocarya fraxinifolia, Liriodendron tulipifera*, and *Sorbus ullungensis*. Among the species included in the study, there were fewer C-strategists among the shrubs, but significantly

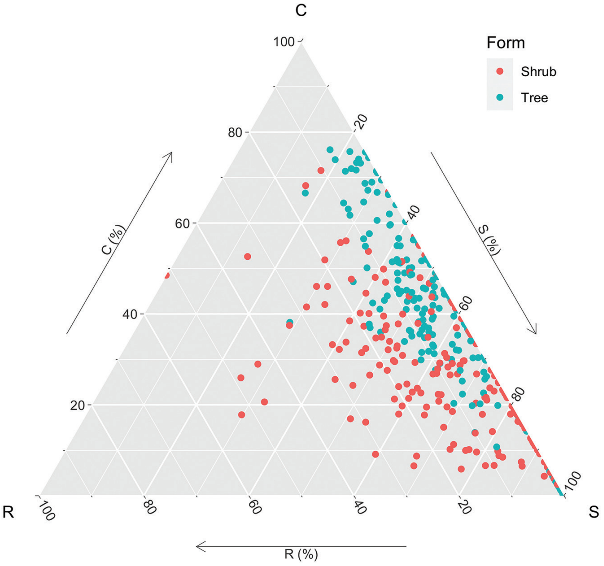

Figure 2. Ordination of trees and shrubs growing in Alnarp, showing the different evolutionary strategies of each life form classifying plants according to 3 principal strategies (Competitors [C], Stress tolerators [S], Ruderal [R]), which represent a spectrum of plant forms and functions arising under conditions of competition, abiotic restriction to growth, or periodic disturbance, respectively. In this assessment, the study taxa of trees and shrubs were distributed along the Competitor-Stress tolerator (CS) axis of the ternary plots. It indicates that long-lived organisms such as trees have a limited tolerance to recurrent disturbances with extensive biomass losses, while this tolerance is somewhat higher in shrubs concerning disturbance, showing that shrubs have a more general approach to disturbance as well as competition and stress (CSR) compared with trees.

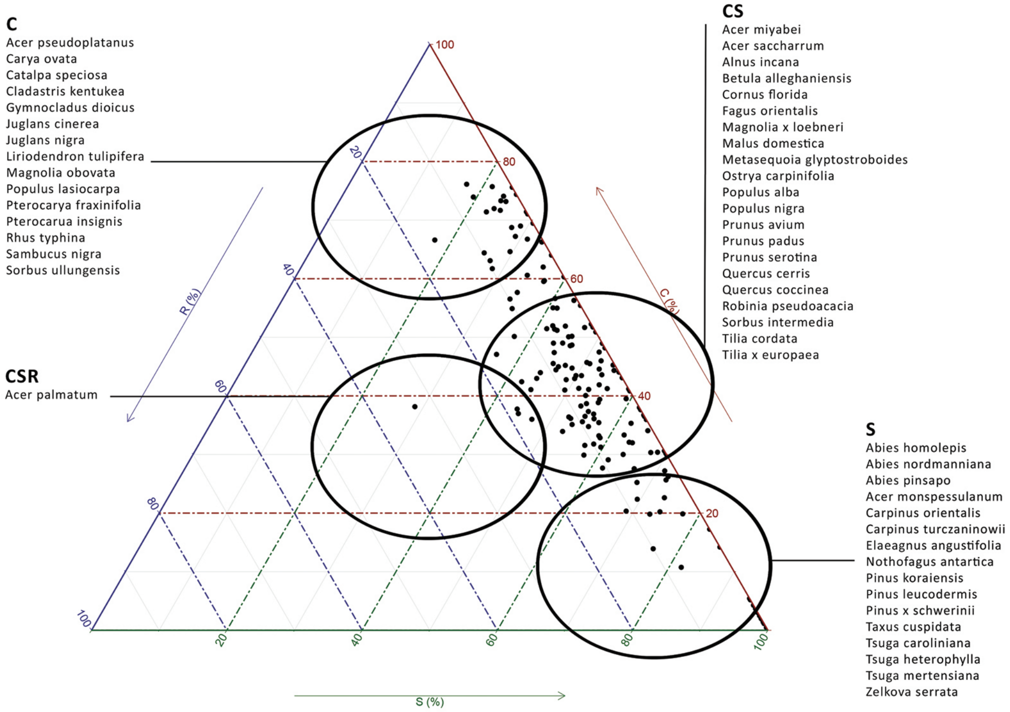

Figure 3. Ordination of trees growing in Alnarp, with examples of species within the different sections of the model according to 3 principal strategies (Competitors [C], Stress tolerators [S], Ruderal [R]) which represent a spectrum of plant forms and functions arising under conditions of competition, abiotic restriction to growth, or periodic disturbance, respectively. This shows a clear concentration of CS strategists with a relatively high tolerance to stress (resource constrained conditions) with a relatively good growth rate. Among the species that are more pronounced C-strategists, there are several pioneer species from resource-rich habitats, while pronounced S-strategists originate from resource-limited habitats such as warm and dry environments to shade late successional phases in forest environments.

more species that are distinct S-strategists and more generalist (CSR-strategists). Even among shrubs, the S-strategist species were those that specialise in dealing with very challenging conditions by having evergreen needles/leaves, such as *Taxus baccata*, *Buxus sempervirens*, and *Berberis* × *fricartii*, which gives them flexibility in shady conditions (Figure 4). The S-strategists among the shrubs also included many species with pronounced high tolerance to exposed and periodically very dry environments, such as *Potentilla fruticosa*, *Rosa rugosa*, and *Spiraea trilobata* (Figure 4). For a full summary of the categorisation within the CSR-classification of the different species in the study, see Appendix.

Figure 5 presents a 2D diagram in which the data collected in the study and their corresponding Competitive Strategy Position (CSR) have been plotted. The diagram includes the variables of stress tolerance and competitiveness (growth rate), which have been used to construct the S-C axis, as illustrated in Figure 2. Position A in Figure 5 encompasses distinct C-strategists that flourish in environments characterised by high resource availability and low disturbance. Such conditions are exemplified by swale bottoms and open park environments, which afford ample space above and below ground. Position B is designated for generalist plants that demonstrate a relatively extensive range of adaptive capacity and are classified as CS strategists. Such environments may be likened to those found in parks and gardens, which offer a somewhat limited supply of resources. These include shaded environments and short periods of drought. Position C refers to plants that are well adapted to high-stress environments, such as paved areas or drought-prone sites where resource constraints can be very pronounced. These species are therefore classified as pronounced stress strategists, which can cope with these resource-limited conditions through expensive and resilient investments, but at the expense of rapid growth. Position D refers to plants with a higher degree of adaptation to disturbed sites, making them more suitable for pioneering roles in new plant communities, such as young micro-forest plantations.

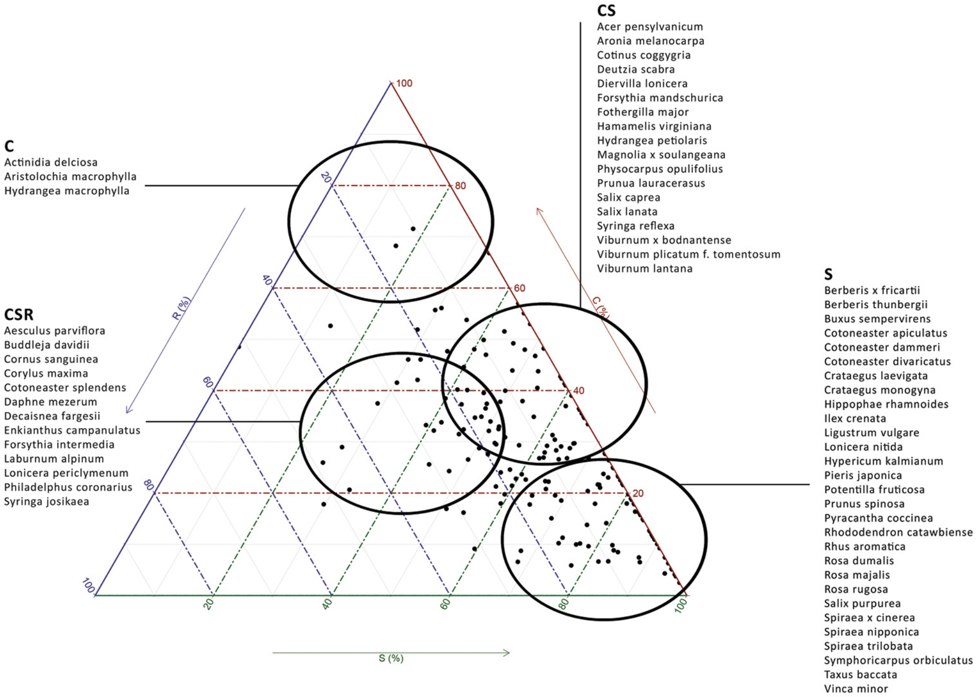

Figure 4. Ordination of shrubs, growing in Alnarp, classifying them according to 3 principal strategies (Competitors [C], Stress tolerators [S], Ruderal [R]), which represent a spectrum of plant forms and functions arising under conditions of competition, abiotic restriction to growth, or periodic disturbance, respectively. This shows a broader spectrum of strategies with the exception of pronounced C-strategies compared to trees. Due to the limited ability of shrubs to compete with trees for sunlight, many species have developed characteristics to cope with more extreme conditions such as hot and dry sites or as undergrowth in mature forest environments, resulting in a large proportion of specialists and thus a large proportion of S-strategists.

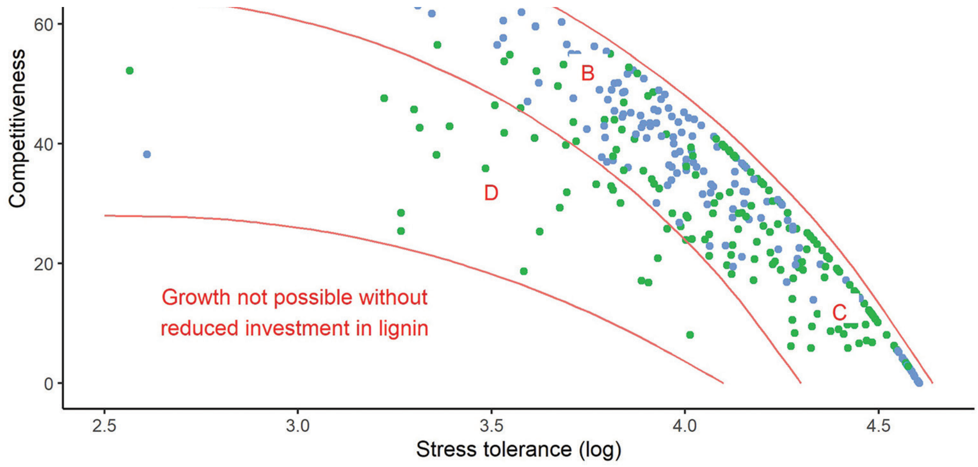

Figure 5. The S-C axis in variation, overlaid with hypothesised fitness in urban environments, where position A relates to situations with high resource availability and low disturbance (e.g., swale bottoms or parks); position B relates to plants with generalist that have a relatively wide range of adaptive capacity; position C relates to plants that are well fitted to high stress environments such as paved areas or sites prone to drought; and position D relates to plants with a higher degree of adaptation to disturbed sites, making them more suitable for pioneer roles within new plant assemblages ($S = \log C^2 + \log C - 76.13$ [1]; $S = \log C^2 + \log C - 104.65$ [2]).

DISCUSSION

Given that a significant proportion of the available guidance for selecting trees and shrubs for urban environments is based on the observations and personal experiences of various authors, rather than on controlled scientific studies, it can be challenging to translate these experiences to other climates or to contexts characterised by more complex urban situations. Such information often originate from arboretums, botanical gardens, or authors' own gardens, which may be the source of many plant literatures towards use of trees and shrubs in a more horticultural approach (Sjöman and Nielsen 2010; Sjöman et al. 2018; Watkins et al. 2020). In order to supplement these recommendations based on observation regarding the selection of an appropriate plant for a specific location and function, it is possible to utilise studies of functional traits that can elucidate why certain species are more suited to, for instance, resource-limited habitats or whether they will undergo a slower establishment and development. Although studies on functional traits focus on how different species have developed traits to cope with different types of climate and growing environments and compete for resources in their natural growing environments, these studies are of great importance when used in urban forestry despite the different competitive situations (Watkins et al. 2021). The inherited attitude to growth and investment of traits to cope with different resource constraints remains strong even when a tree or shrub is planted in a different competitive situation (Laughlin 2023). This makes the plant economic perspective a valuable addition to the more observation-based guidance, as it can explain *why* different species are slower in their growth and *how* they cope with, for example, more stressful environments. There is clear evidence demonstrating that plant economics is a driving factor for the ability of different species to compete within different plant environments (Diaz et al. 2016). Functional traits have thus been used as the main foundation for constructing classifications to identify ecological strategies that indicate how species cope with environmental factors and are assembled in a given community (Grime 1977; Westoby 1998; Westoby et al. 2002; Reich 2014; Pierce et al. 2017). Understanding the investment strategy employed by different species can provide good guidance on their ability to handle different plant environments even in cultivation and predict their development. In this study, we evaluated 342 species and cultivars of shrubs and trees based on 3 leaf traits (SLA, LDMC, LA) with the aim of classifying the species from a leaf economic perspective. Inspired by Pierce et al. (2013), we opted to communicate this through the CSR model based on Grime's theoretical triangular scheme of Competitor, Stress tolerator, and Ruderal plant strategies (Grime 1974, 1977, 2006; Grime and Pierce 2012). These 3 principal strategies represent viable trait combinations arising under conditions of competition, abiotic limitation to growth, and periodic biomass destruction, respectively, and predictions require data on only 3 morphological functional traits representing the extremes of leaf economics and the leaf size spectra (Rosado and de Mattos 2017). Due to its applicability across distinct habitats, CSR theory, despite important shortcomings (Wilson and Lee 2000), has been proven to be powerful because of its efficiency (Caccianiga et al. 2006; Cerabolini et al. 2010; Negreiros et al. 2014; de Paula et al. 2015). The CSR analysis tool proposed by Pierce et al. (2017) can therefore be considered a valuable way to clarify some of the mechanisms explaining plant community assembly and environmental filtering across scales (Rosado and de Mattos 2017). Our analysis of 342 species revealed that the C-strategists comprised many species that have their natural origin as pioneer species in resource-rich habitats, i.e., environments with a very good supply of water, nutrients, and sunlight. They included e.g., 2 species of wing nuts, *Pterocarya fraxinifolia* and *P. insignis*, which originate from river valleys or other moist terrain with a good supply of nutrients from a constant supply of sediment and more or less unlimited supply of sunlight (Maharramova et al. 2018; Song et al. 2020). Other species identified as successful in resource-rich habitats were *Magnolia obovata, Liriodendron tulipifera*, and *Sorbus ullungensis*. This confirms the reliability of the CSR model in positioning these species as distinct C-strategists, as both in nature and in cultivation they show very strong growth in resource-rich habitats (Dirr 2011). It is important to clarify that the role of the competitive strategist is to leverage the resources available through sunlight, water, and nutrition to facilitate vigorous growth and thus create a competitive advantage. This vigorous growth is also evident in the cultural context, with the aforementioned species described as easily established and fast-growing even when free-growing without any competition from other adjacent trees or shrubs (Sjöman and Anderson 2024).

The tree species analysed in the study included a large proportion of species shown previously to be CS strategists (Figure 3). This is explained by the fact that many species of trees invest in deep root systems to create an advantage during drier periods, which makes them a combination of the C-strategists' investments to create an advantage and the S-strategists' investments to manage or avoid a stressful situation which is demonstrated by the hickory species (*Carya* spp.) in the study as having distinct CS strategies, as noted in Grime (2006), and where the ability of the genus to invest in deep taproots that can reach resources at depth and thus escape resource limitation during hot and dry summer months is recognized even in cultivation (Sjöman and Anderson 2024). Species with pronounced Stress tolerance strategies among the trees were dominated by evergreen tree species such as firs (*Abies* spp.), pines (*Pinus* spp.), yews (*Taxus* spp.) and hemlocks (*Tsuga* spp.), all of which are species from different types of resource-limited habitats such as warm, dry environments or cold, shady habitats. The costly investment required for the production of evergreen needles is substantial; however, this strategy has proven to be highly effective in addressing more challenging environmental conditions. The inherent flexibility of evergreen species throughout the year is attributable to their ability to photosynthesise when conditions are most conducive, such as when overgrown and emerging species lack leaves, or in cold climates with a limited growing season, or in warm, periodically dry habitats (Keddy 2007). Even among shrubs, many evergreen species in the study were found to be distinct S-strategists, such as *Lonicera nitida* and *Berberis* × *fricartii*. It is perhaps not surprising that the majority of the shrubs are S-strategists and thus more disturbance-tolerant, since shrubs are present in most vegetation systems globally and extend much farther than trees, occupying tree-free habitats such as high mountain areas, deserts, steppes, and habitats with recurrent disturbances (Rundel 1991; Archibold 1995). A reason for the greater prevalence of shrub species among S-strategists (Figure 4) is their limited ability to compete for sunlight with tall trees and face limited light interception conditions under a compact canopy of overgrown trees. This means that shrubs have developed unique properties and investments in order to handle these sometimes very stressful conditions. Apart from investment in leaf structure, being a low and multi-stemmed shrub also creates resilience to disturbance such as browsing by deer (Tanentzap et al. 2012). Moreover, a single-stemmed tree faces a lethal risk if the stem breaks and dies due to e.g., harsh weather conditions, falling trees/branches, drought through risk of cavitation, disease, or browsing and trampling by animals, whereas a shrub can afford to lose some of its stems and still survive (Wilson 1995; Ryan and Yoder 1997; Scheffer et al. 2014; Götmark et al. 2016).

Many studies have reported extensive intraspecific variation in leaf economic traits (e.g., Poorter et al. 2012; Laforest-Lapointe et al. 2014; Morrow et al. 2022), which can vary between different ecotypes within the same species. These findings must be more carefully explored in the future, to evaluate the capacity of different ecotypes to manage a changing climate. We may increasingly have to depart from treating species as a unified concept and instead move towards considering the unique investment strategy of different ecotypes to manage competition and/or stress (Sjöman et al. 2024). The results in this study show the importance of evaluating unique genetic plant material of different plant collections regarding their functional traits in increasing understanding of how different species and ecotypes prioritise different investments in order to create tolerance and success in their development. This is of critical importance in efforts to match the right plant to the right place and function in urban environments. This intraspecific variation was also obvious in the dataset of this study with variation in leaf traits between different genotypes of the same species in e.g., *Prunus lauracerasus* and *Salix lanata* (see Appendix). It is crucial to recognise that the plant material examined in this study represents a narrow subset of the genetic diversity present across the species' entire geographical range. This is a significant consideration when interpreting the data, as other material may exhibit differing investment priorities, reflecting the specific plant environments and climates from which the unique genetic material originates. A more extensive international screening of a broader genetic pool within species is of significant importance for the enhancement of plant material currently in cultivation, enabling it to be upgraded to better withstand future climate scenarios. The present study has focused on species originating from temperate climates. However, further complementary studies of species and ecotypes in other climates are essential to gain a more comprehensive understanding of the diverse genetic types of a single species across different climatic zones. This is a crucial aspect when attempting to match plants for future climate scenarios, particularly in light of the observed climate shift towards a warmer climate in Northern Europe, which urban plants must adapt to (Lyon et al. 2022).

However, a shortcoming of the CSR framework today is that it does not provide a mechanistic framework for categorising the specific environments in which the different species are likely to be best fitted, especially for stress strategists. This is because their investments can be based on specific stress conditions, such as drought, flood, shade, etc., while competition strategists have a more significant and clearer use of their repertoire of growing environments to achieve successful development, which is mainly in resource-rich habitats. However, in recent studies on drought tolerance of trees and shrubs (e.g., Sjöman et al. 2018; Sjöman et al. 2023), there is a clear correlation between the most drought-tolerant species when assessing estimated water potential at leaf turgor loss with the stress strategists in this study, such as *Acer tataricum, Berberis julianae, Chaenomeles japonica, Cotinus coggygria*, and *Spiraea betulifolia*, indicating that the leaf economical and ecophysiological perspectives are compatible when it comes to drought tolerance between species from different datasets. Further research is however needed to provide a more detailed description of the unique stresses to which the different stress strategies are adapted to. Nevertheless, in this study, we want to test and explore leaf economy perspectives linked to the CSR model and see how this can become a tool for selecting the right plant for place and function in urban environments. In Figure 5, we further explore the axis of variation of the Competitive-Stress tolerator by using the C and S ordinations in a 2D perspective. This arrangement clearly identifies the adaptive limits to growth according to Watkins et al. (2021), as well as the areas of trait space that result in inefficient resource use relative to environmental tolerance. As a result of this step, we can not only derive quadratic equations describing the distribution of shrubs and trees along axes of evolutionary variation, but also refine the hypothesis of Watkins et al. (2021) to quantitatively describe design uses for tree and shrub species in urban environments. Through this model (Figure 5) it is possible to further link the CSR perspective towards use potential of trees and shrubs for urban environments and for specific functions such as for stormwater management.

Another perspective that links plant economics, the CSR model, and plant use is the relative priorities of different species with regard to growth. Species originating from resource-rich habitats with a good supply of water, nutrients, and sunlight have developed the ability to exhibit rapid growth in order to create a competitive advantage. In contrast, species that have developed strategies for more resource-limited habitats exhibit defensive growth in response to resource limitations. This trait of more limited growth based on evolutionary selection where tolerance of habitat is prioritized over vigorous growth in resource limited habitats is an approach that is also maintained in cultivation. In a landmark study by Grime and Hunt (1975) it is shown that species originating from resource-limited habitats (S-strategists) maintained lower growth even in cultivation under 'optimal' conditions, which has since been confirmed by numerous studies (Laughlin 2023). From an urban horticultural perspective, this is of great importance in the establishment and growth of shrubs and trees as extended establishment management with irrigation is necessary for the slow S-strategists, while establishment and growth is significantly faster for the C-strategists (Figure 6). When using vegetation to deliver important ecosystem services, the size of the trees and the shrub vegetation is often important, such as shading over playgrounds, which means that using fast-growing C-strategists is tempting, but in order to reach this rapid growth, it is crucial that resource-rich conditions be offered. This perspective on growth rate based on this CSR summary in the study makes it possible to tailor establishment management and predict how and when different functions can occur where, for example, using shrubs as ground cover in urban plantations, it is important to know which ones are fast and slow in order to predict management and when final function of the plantation will be reached.

The intention of this study was to establish a link between a well-known and widely used model in biology and the utilisation of urban plants. It has been observed that a significant number of trees and shrubs are planted in conditions that do not allow them to flourish, resulting in a considerable proportion of

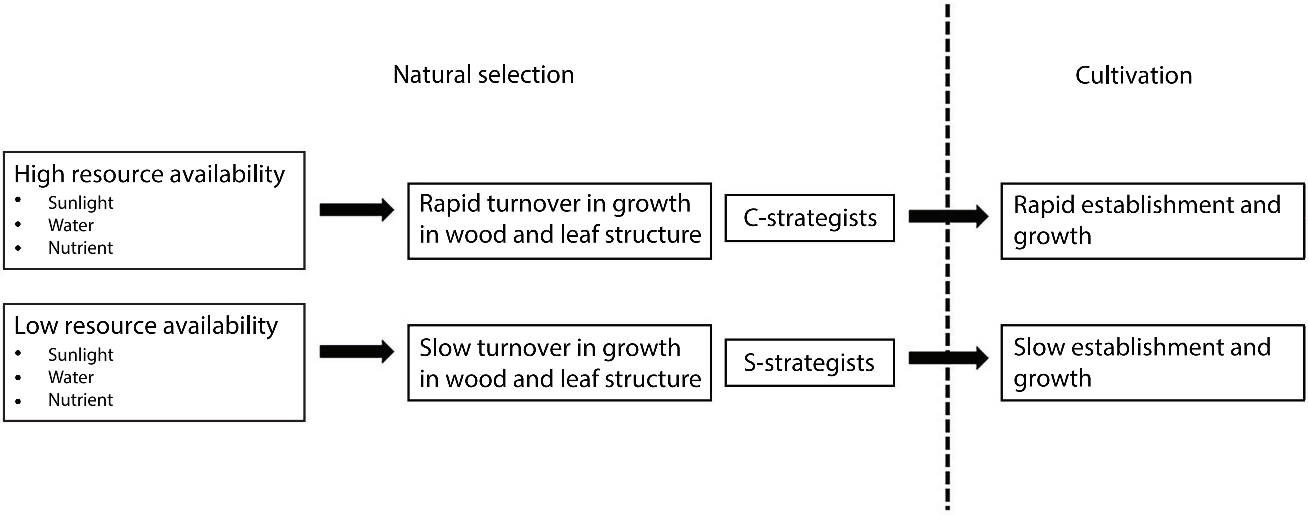

Figure 6. Species originating naturally from resource-rich habitats have developed unique traits with a rapid turnover in growth to create a competitive advantage (C-strategy), traits that they retain in cultivation as they establish and grow rapidly in resource-rich environments such as parks and gardens. Species originating from resource-limited habitats have a slower turnover in growth due to limited resources (S-strategy), a characteristic they also have in cultivation, even on resource-rich habitats, resulting in significantly slower establishment and growth. Figure developed with inspiration from Chapin (1980) and Laughlin (2023).

these plants either dying or exhibiting impaired growth and establishment (Kianmehr et al. 2024), and thus underscores the necessity to enhance the precision of our approach and to embrace diverse ecological and biological perspectives. This entails a departure from the prevailing tradition in urban forestry, which has been largely guided by the experiences and observations of a limited number of individuals to a more trait orientated plant selection (Watkins et al. 2021). The development of a more nuanced language surrounding the selection and utilisation of plants hinges upon the availability of species-specific data, as exemplified by the findings of this study. Currently, such data is scarce, impeding the ability to engage in informed discourse on plant selection with other professional groups, including politicians and construction companies. The integration of a plant economic perspective offers a compelling biological rationale for the selection of specific species in given circumstances. Moreover, it enables a more constructive dialogue during the planning phase, addressing potential challenges in the establishment process. Further research is required to ascertain the specific stress conditions to which the different species are adapted, based on their stress strategies. However, if this can be achieved, the CSR approach can serve as a foundation for communicating the selection of an appropriate plant for a given site and function. This entails identifying the characteristics of the site in the planning phase, including its opportunities and constraints, as well as the investment priorities of different species and their alignment with the site-specific conditions.

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Conflicts of Interest:
The authors reported no conflicts of interest.

Appendix.

Table S1. Compilation of the CSR classification of the studied shrubs, where the calculated percentage for each category is presented in % (using one decimal), with a subsequent final classification using the StrateFy tool (Pierce et al. 2017).

Species (Shrubs)	C (%)	S (%)	R (%)	Strategy
Acer pensylvanicum	56.5	28.8	14.7	C/CSR
Actinidia deliciosa	67.5	32.5	0.0	C/CS
Aesculus parviflora	47.6	25.1	27.3	C/CSR
Amelanchier alnifolia	21.8	68.1	10.1	S/CS
Amelanchier laevis	23.1	61.7	15.2	S/CSR
Amelanchier × lamarckii	27.4	64.4	8.2	S/CS
Amelanchier × spicata	21.4	61.5	17.1	S/CSR
Aristolochia macrophylla	68.4	13.7	17.9	C/CR
Aronia melanocarpa	30.6	69.4	0.0	S/CS
Berberis julianae	11.3	88.7	0.0	S
Berberis thunbergii	11.6	88.4	0.0	S
Berberis verruculosa	5.6	94.4	0.0	S
Berberis × frikartii	6.3	93.7	0.0	S
Buddleja davidii	42.9	29.7	27.4	CSR
Buxus sempervirens	16.4	83.6	0.0	S/CS
Caragana arborescens	8.1	55.3	36.6	SR
Chaenomeles japonica	13.3	86.7	0.0	S
Cornus alba	33.2	43.4	23.3	CS/CSR
Cornus mas	30.1	50.7	19.1	S/CSR
Cornus racemosa	24.9	58.1	17.0	S/CSR
Cornus racemosa 'Green Carpet'	24.5	75.5	0.0	S/CS
Cornus sanguinea	31.9	40.2	27.8	CSR
Cornus sericea	28.5	71.2	0.4	S/CS
Cornus sericea 'Bailadeline' Firedance™	19.3	73.3	7.4	S/CS
Cornus sericea 'Baileyi'	29.6	64.8	5.6	S/CS
Corylus avellana	37.2	45.3	17.5	CS/CSR
Corylus maxima 'Cosford'	41.0	37.0	21.9	CS/CSR
Corylus maxima 'Nottingham'	42.7	27.5	29.8	CSR
Corylus maxima 'Purpurea'	45.7	27.1	27.2	C/CSR
Cotinus coggygria	33.1	52.2	14.7	S/CSR

Table S1 continued on next page

Table S1. Continued.

Species (Shrubs)	**C (%)**	**S (%)**	**R (%)**	**Strategy**
Cotinus coggygria	26.3	66.8	6.9	S/CS
Cotoneaster apiculatus	9.5	75.8	14.6	S/SR
Cotoneaster dammeri	11.9	88.1	0.0	S
Cotoneaster dielsianus	9.7	84.6	5.7	S
Cotoneaster divaricatus	8.1	91.9	0.0	S
Cotoneaster lucidus	21.3	58.1	20.6	S/CSR
Cotoneaster multiflorus	17.5	72.2	10.2	S/CS
Cotoneaster splendens	7.1	87.3	5.6	S
Cotoneaster × *suecicus*	8.2	82.3	9.4	S
Crataegus laevigata	19.7	60.8	19.5	S/CSR
Crataegus monogyna	20.8	73.0	6.2	S/CS
Crataegus rhipidophylla	19.9	68.5	11.6	S/CS
Daphne mezerum	25.4	26.2	48.3	R/CSR
Decaisnea fargesii	28.5	26.2	45.3	R/CSR
Deutzia gracilis	15.0	85.0	0.0	S
Deutzia scabra	32.5	51.1	16.5	S/CSR
Diervilla lonicera	23.9	76.1	0.0	S/CS
Diervilla lonicera 'Dilon'	52.1	37.2	10.6	CS
Diervilla sessilifolia	36.3	63.7	0.0	S/CS
Enkianthus companulatus	18.7	36.0	45.2	SR/CSR
Euonymus alatus	14.3	85.7	0.0	S
Euonymus europaeus	27.7	55.0	17.3	S/CSR
Euonymus fortunei 'Emerald Gaiety'	28.4	58.7	13.0	S/CSR
Euonymus fortunei 'Emerald 'n' Gold'	26.6	69.4	3.9	S/CS
Euonymus fortunei 'Silver Queen'	22.2	77.8	0.0	S/CS
Euonymus fortunei var. *radicans*	25.8	72.8	1.5	S/CS
Euonymus fortunei var. *vegetus*	52.2	13.0	34.7	CR/CSR
Euonymus planipes	37.9	45.3	16.8	CS/CSR
Forsythia 'Lowe Tide'	18.6	81.4	0.0	S/CS
Forsythia mandshurica	49.6	39.3	11.1	CS/CSR
Forsythia 'Maree d'Or'™	17.7	78.3	4.0	S/CS
Forsythia intermedia	24.6	75.4	0.0	S/CS
Forsythia × *intermedia* 'Goldzauber'	41.8	34.2	24.0	CS/CSR

Species (Shrubs)	**C (%)**	**S (%)**	**R (%)**	**Strategy**
Fothergilla major	40.8	47.9	11.4	CS/CSR
Hamamelis virginiana	40.4	41.2	18.3	CS/CSR
Hamamelis × *intermedia*	39.0	45.7	15.4	CS/CSR
Hedera colchica	55.0	45.0	0.0	CS
Hedera helix	44.0	45.5	10.5	CS
Hippophaë rhamnoides	19.5	78.5	2.0	S/CS
Hydrangea arborescens	46.9	46.6	6.5	CS
Hydrangea macrophylla	65.1	25.2	9.6	C/CS
Hydrangea petiolaris	48.6	50.3	1.1	CS
Hydrangea serrata	52.2	44.2	3.6	CS
Hypericum kalmianum ‘Ames’	11.6	76.9	11.5	S/CS
Hypericum kalmianum ‘Gemo’	8.7	79.5	11.8	S
Ilex aquifolium ‘Alaska’	25.1	74.9	0.0	S/CS
Ilex aquifolium ‘J.C. van Tol’	32.2	67.8	0.0	S/CS
Ilex crenata ‘Blondie’	15.4	84.6	0.0	S
Ilex crenata ‘Dark Green’	4.2	95.8	0.0	S
Ilex verticillata	31.9	61.3	6.7	S/CS
Kolkwitzia amabilis	25.8	52.1	22.2	S/CSR
Laburnum alpinum	25.3	37.5	37.3	CSR
Laburnum anagyroides	23.9	54.7	21.5	S/CSR
Ligustrum vulgare	14.3	79.6	6.0	S/CS
Lonicera caerulea	24.0	57.5	18.5	S/CSR
Lonicera caerulea var. *kamtschatica*	20.8	79.2	0.0	S/CS
Lonicera involucrata	34.1	50.1	15.9	CS/CSR
Lonicera maackii	25.7	62.6	11.7	S/CS
Lonicera nitida	9.8	87.1	3.1	S
Lonicera periclymenum	35.9	32.6	31.5	CSR
Lonicera tatarica	28.0	54.8	17.2	S/CSR
Lonicera xylosteum	26.2	54.0	19.7	S/CSR
Lonicera xylosteum ‘Compacta’	23.6	65.7	10.7	S/CS
Magnolia ‘Wada’s Memory’	32.9	45.1	22.0	CS/CSR
Magnolia × *soulangeana*	53.8	34.2	12.0	CS/CSR
Mahonia aquilifolium	28.5	63.2	8.2	S/CS

Table S1 continued on next page

Table S1. Continued.

Species (Shrubs)	**C (%)**	**S (%)**	**R (%)**	**Strategy**
Malus toringo var. *sargentii*	34.2	65.8	0.0	S/CS
Philadelphus coronarius	30.1	46.2	23.7	S/CSR
Physocarpus opulifolius	28.4	52.8	18.8	S/CSR
Pieris floribunda	20.2	73.7	6.1	S/CS
Pieris japonica	19.2	80.8	0.0	S/CS
Pinus mugo var. *pumilio*	3.1	96.9	0.0	S
Potentilla fruticosa	5.9	83.2	10.9	S
Prunus cerasifera	23.0	60.6	16.4	S/CSR
Prunus laurocerasus 'Mano'	48.0	49.6	2.4	CS
Prunus laurocerasus 'Otto Luyken'	39.5	60.5	0.0	CS
Prunus laurocerasus 'Piri'	35.3	64.7	0.0	S/CS
Prunus pumila var. *depressa*	21.2	78.8	0.0	S/CS
Prunus spinosa	16.9	71.0	12.1	S/CS
Pyracantha 'Anatolia'	10.7	89.3	0.0	S
Pyracantha coccinea 'Red Cushion'	10.8	89.2	0.0	S
Rhamnus catharticus	29.3	39.5	31.2	CSR
Rhododendron brachycarpum	38.7	61.3	0.0	CS
Rhododendron 'Catawbiense Album'	38.0	62.0	0.0	CS
Rhododendron catawbiense 'Boursalt'	41.6	52.0	6.3	CS
Rhododendron 'Catawbiense Grandiflora'	37.8	62.2	0.0	CS
Rhododendron luteum	35.6	46.6	17.8	CS/CSR
Rhododendron mucronulatum	22.9	58.2	18.9	S/CSR
Rhododendron 'Rosa Wolke'	33.6	66.4	0.0	S/CS
Rhododendron 'Roseum Elegans'	42.4	46.4	11.2	CS/CSR
Rhus aromatica	19.1	80.9	0.0	S/CS
Rhus typhina	26.8	53.8	19.4	S/CSR
Ribes alpinum	18.2	61.6	20.2	S/CSR
Ribes alpinum 'Compacta'	11.5	88.5	0.0	S
Ribes glandulosum	23.2	76.8	0.0	S/CS
Rosa dumalis	14.1	72.0	13.8	S/CS
Rosa majalis	17.2	65.2	17.6	S/CSR
Rosa pimpinellifolia	20.7	65.3	14.0	S/CS
Rosa rubiginosa	10.6	72.0	17.4	S/SR

Species (Shrubs)	**C (%)**	**S (%)**	**R (%)**	**Strategy**
Rosa rugosa	18.8	81.2	0.0	S/CS
Salix caprea	41.6	48.1	10.3	CS
Salix lanata ‘Hjeltnes’	38.1	61.9	0.0	CS
Salix lanata ‘Nitida’	6.8	88.5	4.7	S
Salix repens	6.7	85.6	7.7	S
Salix × purpurea	9.0	81.2	9.8	S
Sambucus nigra	38.2	13.6	48.2	CR/CSR
Sorbaria sorbifolia	17.1	48.8	34.1	SR/CSR
Spiraea betulifolia	22.4	74.8	2.8	S/CS
Spiraea fritschiana	21.1	78.8	0.1	S/CS
Spiraea japonica	24.1	55.6	20.3	S/CSR
Spiraea miyabei	23.2	76.8	0.0	S/CS
Spiraea nipponica	8.4	72.5	19.2	S/SR
Spiraea trilobata	14.3	78.7	7.0	S/CS
Spiraea × cinerea	5.9	75.6	18.5	S/SR
Spiraea × cinerea ‘Grefsheim’	6.2	71.8	22.0	S/SR
Stephanandra incisa	16.8	49.7	33.5	SR/CSR
Stephanandra tanake	28.4	62.7	8.9	S/CS
Symphoricarpos ‘Arvid’ E.	18.9	69.9	11.2	S/CS
Symphoricarpos ‘Magical Galaxy’	9.8	83.0	7.2	S
Symphoricarpos orbiculatus	10.2	89.8	0.0	S
Syringa josikaea	46.4	33.4	20.3	CS/CSR
Syringa meyeri ‘Palibin’	20.9	50.9	28.2	S/CSR
Syringa microphylla ‘Superba’	27.8	63.9	8.3	S/CS
Syringa patula	30.1	58.9	11.0	S/CSR
Syringa reflexa	43.6	40.9	15.5	CS/CSR
Syringa reticulata	47.6	40.9	11.5	CS/CSR
Syringa vulgaris	43.4	49.0	7.6	CS
Syringa × chinensis	32.3	45.3	22.4	CS/CSR
Taxus baccata	3.4	96.6	0.0	S
Taxus cuspidata	2.8	97.2	0.0	S
Viburnum carlesii	33.2	66.8	0.0	S/CS
Viburnum ferreri	35.5	49.0	15.5	CS/CSR

Table S1 continued on next page

Table S1. Continued.

Species (Shrubs)	**C (%)**	**S (%)**	**R (%)**	**Strategy**
Viburnum lantana	36.2	54.8	9.0	CS
Viburnum opulus	39.8	40.1	20.1	CS/CSR
Viburnum plicatum f. *tomentosum*	38.0	55.7	6.3	CS
Viburnum rhytidophyllum	52.8	47.2	0.0	CS
Viburnum sargentii	33.3	50.4	16.3	CS/CSR
Viburnum × bodnantense	46.0	35.7	18.4	CS/CSR
Viburnum × burkwoodii	38.9	61.1	0.0	CS
Vinca minor	12.2	87.8	0.0	S
Weigela × hybrida	39.9	60.1	0.0	CS
Wisteria sinensis	19.5	61.8	18.7	S/CSR

Table S2. Compilation of the CSR classification of the studied trees, where the calculated percentage for each category is presented in % (using one decimal), with a subsequent final classification using the StrateFy tool (Pierce et al. 2017).

Species (Trees)	**C (%)**	**S (%)**	**R (%)**	**Strategy**
Abies alba	1.9	98.1	0.0	S
Abies homolepis	1.4	98.6	0.0	S
Abies nordmanniana	2.0	98.0	0.0	S
Abies pinsapo	1.1	98.9	0.0	S
Acer campestre	36.5	54.7	8.8	CS
Acer davidii	43.5	49.9	6.7	CS
Acer miyabei	35.3	62.1	2.6	S/CS
Acer monspessulanum	22.4	69.5	8.1	S/CS
Acer negundo	51.2	43.2	5.6	CS
Acer nigrum	51.9	44.1	4.0	CS
Acer palmatum	38.2	28.7	33.1	CSR
Acer platanoides	56.6	40.2	3.2	CS
Acer pseudoplatanus	66.8	31.1	2.2	C/CS
Acer pseudosieboldianum	36.2	52.8	11.1	CS/CSR
Acer rubrum	43.5	50.7	5.8	CS
Acer saccharinum	41.1	52.9	6.0	CS
Acer saccharum	50.2	45.9	3.9	CS
Acer spicatum	50.1	37.4	12.4	CS/CSR

Table S2. Continued.

Species (Trees)	C (%)	S (%)	R (%)	Strategy
Acer tataricum	32.1	63.4	4.5	S/CS
Acer × zoeschense	38.0	62.0	0.0	CS
Alnus glutinosa	42.8	48.8	8.4	CS
Alnus incana	38.7	53.8	7.5	CS
Alnus rubra	44.6	52.8	2.7	CS
Alnus sinuata	41.2	55.6	3.1	CS
Alnus subcordata	53.2	39.9	6.8	CS
Alnus × spaethii	45.5	50.9	3.6	CS
Amelanchier lamarckii	25.2	68.0	6.8	S/CS
Betula albosinensis	36.4	52.4	11.2	CS/CSR
Betula alleghaniensis	38.3	53.2	8.5	CS
Betula pendula	27.7	61.7	10.6	S/CS
Betula populifolia	30.3	67.5	2.2	S/CS
Broussonetia papyrifera	59.7	37.1	3.2	CS
Buxus sempervirens ‘Rotundifolia’	17.2	82.8	0.0	S/CS
Carpinus betulus	33.9	52.7	13.4	CS/CSR
Carpinus caroliniana	30.0	63.6	6.4	S/CS
Carpinus fargesii	29.1	61.8	9.1	S/CS
Carpinus orientalis	13.9	76.1	10.0	S/CS
Carpinus turczaninowii	19.9	77.5	2.7	S/CS
Carya cordiformis	66.3	33.4	0.3	C/CS
Carya ovata	71.4	28.6	0.0	C/CS
Carya tomentosa	71.1	28.9	0.0	C/CS
Castanea sativa	49.0	43.8	7.2	CS
Catalpa speciosa	71.7	24.6	3.7	C/CS
Celtis occidentalis	36.1	56.2	7.7	CS
Cercidiphyllum japonicum	36.0	47.1	16.9	CS/CSR
Cladrastis kentukea	63.1	27.4	9.5	C/CS
Cornus florida	41.1	44.4	14.5	CS/CSR
Cornus kousa	40.1	53.0	6.9	CS
Cornus mas	34.8	56.1	9.1	CS
Corylus avellana	44.0	44.4	11.7	CS/CSR

Table S2 continued on next page

Table S2. Continued.

Species (Trees)	C (%)	S (%)	R (%)	Strategy
Corylus chinense	48.6	46.5	5.0	CS
Corylus colurna	50.1	45.5	4.4	CS
Corylus ferox	43.0	49.9	7.1	CS
Cotinus coggygria	30.4	68.5	1.1	S/CS
Crataegus monogyna	30.2	69.8	0.0	S/CS
Davidia involucrata	57.7	34.1	8.2	CS
Elaeagnus angustifolia	22.6	73.4	4.0	S/CS
Eucommia ulmoides	49.0	45.1	5.8	CS
Fagus orientalis	37.0	44.6	18.4	CS/CSR
Fagus sylvatica	35.4	57.3	7.3	CS
Fraxinus americana 'Autumn Purple'	64.6	29.6	5.8	C/CS
Fraxinus excelsior	67.2	29.1	3.7	C/CS
Fraxinus fallax	69.0	28.9	2.1	C/CS
Ginkgo biloba	47.1	36.3	16.6	CS/CSR
Gleditsia triacanthos	45.3	54.5	0.3	CS
Gymnocladus dioicus	76.1	17.4	6.5	C/CS
Hippophae rhamnoides	14.2	85.8	0.0	S
Ilex aquifolium	29.8	70.2	0.0	S/CS
Juglans cinerea	73.2	24.7	2.2	C/CS
Juglans nigra	72.0	23.5	4.5	C/CS
Juglans regia	75.6	24.4	0.0	C/CS
Koelreuteria paniculata	62.0	35.8	2.2	C/CS
Laburnum angyroides	42.4	42.4	15.2	CS/CSR
Larix × eurolepis	0.0	100.0	0.0	S
Liquidambar styraciflua	45.7	50.4	3.9	CS
Liriodendron tulipifera	64.4	25.8	9.8	C/CS
Magnolia biondii	48.7	46.7	4.6	CS
Magnolia kobus	44.4	46.4	9.1	CS
Magnolia obovata	73.9	19.5	6.6	C/CS
Magnolia sprengeri	56.3	43.2	0.5	CS
Magnolia × loebneri	41.0	49.5	9.5	CS
Malus domestica	46.0	52.3	1.7	CS
Malus sylvestris	39.5	59.3	1.2	CS

Species (Trees)	**C (%)**	**S (%)**	**R (%)**	**Strategy**
Metasequoia glyptostroboides	37.6	62.4	0.0	CS
Morus alba	60.6	34.1	5.3	C/CS
Morus nigra	61.7	28.4	9.9	C/CS
Nothofagus antarctica	10.7	81.8	7.4	S
Nyssa sylvatica	32.8	58.8	8.4	S/CS
Ostrya carpinifolia	31.8	58.3	9.9	S/CSR
Ostrya virginiana	35.1	53.5	11.4	CS/CSR
Picea abies	0.0	100.0	0.0	S
Picea omorika	0.0	100.0	0.0	S
Picea orientalis	0.0	100.0	0.0	S
Picea peuce	3.3	96.7	0.0	S
Picea sitchensis	0.0	100.0	0.0	S
Pinus koraiensis	4.3	95.7	0.0	S
Pinus leucodermis	5.2	94.8	0.0	S
Pinus sylvestris	3.7	96.3	0.0	S
Pinus × schwerinii	5.4	94.6	0.0	S
Platanus × hispanica	59.5	37.1	3.4	CS
Populus alba 'Nivea'	34.1	65.2	0.7	S/CS
Populus balsamifera	51.5	41.6	7.0	CS
Populus lasiocarpa	74.1	23.9	2.0	C/CS
Populus nigra 'Italica'	36.5	63.5	0.0	S/CS
Populus purdomii	55.4	44.6	0.0	CS
Populus tremula	35.6	54.8	9.6	CS
Populus × canadensis 'Robusta'	49.0	51.0	0.0	CS
Populus × wettsteinii	38.9	55.5	5.7	CS
Prunus avium	45.5	45.5	9.0	CS
Prunus cerasifera	31.3	59.7	9.1	S/CS
Prunus laurocerasus	36.0	64.0	0.0	S/CS
Prunus padus	37.3	54.8	7.9	CS
Prunus sargentii	45.2	47.4	7.4	CS
Prunus serotina	33.2	58.4	8.4	S/CS
Prunus spinosa	20.2	73.9	5.9	S/CS
Pterocarya fraxinifolia	73.3	23.9	2.8	C/CS

Table S2 continued on next page

Table S2. Continued.

Species (Trees)	**C (%)**	**S (%)**	**R (%)**	**Strategy**
Pterocarya insignis	75.7	21.4	2.9	C/CS
Pterocarya rhoifolia	71.4	22.7	5.9	C/CS
Pyrus communis	32.0	64.0	4.1	S/CS
Pyrus ussuriensis	31.6	57.1	11.3	S/CSR
Quercus bicolor	48.2	51.8	0.0	CS
Quercus cerris	36.9	55.8	7.3	CS
Quercus coccinea	47.5	51.3	1.2	CS
Quercus dentata 'Carl Ferris Miller'	60.3	39.7	0.0	CS
Quercus frainetto	41.9	54.1	4.0	CS
Quercus macrocarpa	52.3	47.7	0.0	CS
Quercus petraea	43.6	53.6	2.8	CS
Quercus prinus	51.7	47.1	1.3	CS
Quercus robur	44.3	55.1	0.6	CS
Quercus rubra	55.0	40.7	4.3	CS
Rhododendron 'Catawbiense Grandiflorum'	43.1	56.9	0.0	CS
Rhododendron mucronulatum	20.3	68.9	10.8	S/CS
Rhus typhina	68.7	27.7	3.5	C/CS
Robinia pseudoacacia	47.4	44.7	7.9	CS
Salix alba	19.8	72.6	7.6	S/CS
Salix alba var. *sericea*	26.2	72.1	1.6	S/CS
Salix caprea	39.4	55.4	5.2	CS
Salix pentandra	36.7	63.3	0.0	S/CS
Salix viminalis	27.2	71.1	1.7	S/CS
Salix × *fragilis*	29.9	57.8	12.3	S/CSR
Salix × *sepulcralis* 'Chrysocoma'	25.7	72.1	2.2	S/CS
Sambucus nigra	66.6	17.4	16.0	C/CS
Sorbus aucuparia	55.0	41.3	3.7	CS
Sorbus hupehensis	50.9	49.1	0.0	CS
Sorbus intermedia	41.2	58.8	0.0	CS
Sorbus torminalis	44.1	55.9	0.0	CS
Sorbus ulleungensis	64.0	36.0	0.0	C/CS
Styphnolobium japonicum	56.5	33.6	9.9	C/CSR
Syringa reticulata	40.8	59.2	0.0	CS

Species (Trees)	**C (%)**	**S (%)**	**R (%)**	**Strategy**
Syringa vulgaris	51.8	48.2	0.0	CS
Taxodium distichum	27.6	66.4	6.0	S/CS
Taxus baccata	2.5	97.5	0.0	S
Taxus cuspidata	3.0	97.0	0.0	S
Tetracentron sinense	37.8	44.0	18.2	CS/CSR
Tetradium danielii	69.5	30.5	0.0	C/CS
Tilia cordata	45.0	46.5	8.5	CS
Tilia mongolica	41.3	51.4	7.3	CS
Tilia platyphyllos	44.7	48.7	6.6	CS
Tilia tomentosa	52.0	42.2	5.8	CS
Tilia × *europaea* 'Zwarte Linde'	43.0	44.3	12.7	CS/CSR
Toona sinensis	74.4	25.6	0.0	C/CS
Tsuga canadensis	0.0	100.0	0.0	S
Tsuga caroliniana	0.4	99.6	0.0	S
Tsuga heterophylla	0.3	99.7	0.0	S
Tsuga mertseniana	0.2	99.8	0.0	S
Ulmus glabra	51.4	42.8	5.9	CS
Ulmus glaucescens	29.9	70.1	0.0	S/CS
Wisteria sinensis	54.9	34.7	10.4	CS
Zelkova schneideriana	30.6	69.4	0.0	S/CS
Zelkova serrata	33.3	62.1	4.6	S/CS