

Allocating CSR plant functional types: the use of leaf economics and size traits to classify woody and herbaceous vascular plants

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Summary

1. Three main directions of adaptive specialization are evident in the world flora, reflecting fundamental trade-offs between economics (conservative vs. acquisitive investment of resources) and size. The current method of ordinating plants according to these trade-offs, CSR classification, cannot be applied to the woody species that dominate many terrestrial ecosystems.
2. We aimed to produce a novel CSR classification method applicable to vascular plants in general.
3. Principal components analysis (PCA) of variation in a range of plant traits for 678 angiosperm, gymnosperm and pteridophyte species was used to determine the limits to multivariate space occupied by functionally diverse species. From this calibration, correlations between PCA axes and values of leaf dry matter content (LDMC; as an index of conservatism in life history), specific leaf area (SLA; indicative of acquisitive economics) and leaf area (LA; photosynthetic organ size) were used to produce predictor regressions from which target species could be compared against the multivariate space. A spreadsheet was developed that returned ternary coordinates and tertiary CSR strategies for target subjects based on LA, LDMC and SLA values.
4. The method allowed classification of target species within a triangular space corresponding to Grime's theoretical CSR triangle and was sufficiently precise to distinguish strategies between species within genera and within populations of species. It was also largely in agreement with previous methods of CSR classification for herbaceous species.
5. Rapid CSR classification of woody and herbaceous vascular plants is now possible, potentially allowing primary plant functional types and ecosystem processes to be investigated over landscape scales.

Key-words: adaptive strategies, CSR theory, Grime, life-form, plant functional type, universal adaptive strategy theory

Introduction

CSR classification (Hodgson *et al.* 1999) is a practical method for the categorization of plants according to Grime's (1974, 1977, 2001) theoretical triangular scheme of competitor, stress tolerator and ruderal plant strategies (CSR theory). The CSR classification method uses various functional traits quantified *in situ* (or measured from material collected *in situ*) and has been applied to over a thousand species across Europe in a range of contrasting

situations (Caccianiga *et al.* 2006; Pierce *et al.* 2007a,b; Simonová & Lososová 2008; Massant, Godefroid & Koedam 2009; Cerabolini *et al.* 2010a,b; Kiliç, Karavin & Kutbay 2010; Navas *et al.* 2010; Caccianiga, Bottacin & Cattaneo 2012; Yildirim, Karavin & Cansaran 2012).

Cerabolini *et al.* (2010a) found that the method is widely applicable outside the relatively restricted geographical range where it was originally calibrated. However, they also noted a number of problems that limit the applicability of Hodgson *et al.* (1999) particular methodology. First, despite the fact that woody species dominate a range of key vegetation types world-wide, Hodgson's

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CSR classification can only be applied to herbaceous species. The method categorizes the lateral spread of species according to classes that are only applicable to forbs or graminoids and assigns all species taller than one metre in height the same height class. This approach has already shown its limitations. For example, in a novel remote sensing approach, Schmidtlein, Feilhauer & Bruelheide (2012) were able to map the distribution of CSR strategies over landscapes by linking leaf reflectance to CSR strategies calculated according to Hodgson *et al.* (1999) method. However, due to the reliance on this method, remote sensing of CSR strategies is currently restricted to herbaceous vegetation and has yet to realize its full potential. Truly comprehensive investigation of ecological strategies over large scales would require classification of woody and herbaceous species on an equal footing.

Recent attempts to apply CSR classification to woody species have met with ambiguous results. Navas *et al.* (2010) used revised categories for lateral spread, proposed by Grime, Hodgson & Hunt (2007), to modify CSR classification and include woody species. Hodgson *et al.* (1999) had originally included lateral spread as a strict predictor of competitive ability. However, Cerabolini *et al.* (2010a) noted that lateral spread is also a characteristic of stoloniferous growth in unproductive habitats by stress-tolerant species of low stature and cannot be assumed to reflect competitive ability, concluding that ‘some of the traits currently used in CSR classification must be interpreted with caution’. Furthermore, Navas *et al.* (2010) did not alter height classes, meaning that the modified system would still classify a 94-m-tall *Sequoiadendron giganteum* in the same height category as a tall grass. Other attempts to assign CSR strategies to trees have used very specific traits, such as the rate of radial (secondary) growth, that are not exhibited by all vascular plants and do not allow direct comparison with key plant groups, such as most monocots (Brzeziecki & Kienast 1994; Wunder *et al.* 2008). Norris, Hobson & Ibsch (2012) produced CSR triangles for several forest stands, but cited Hunt *et al.* (2004) as a source of information for CSR strategies, who had used Hodgson *et al.* (1999) method: how the strategies of woody species were calculated was not disclosed.

A further restriction of Hodgson *et al.* (1999) method is a reliance on nominal categories such as classes of flowering period, flowering start, lateral spread and canopy height, rather than specific values along continuous quantitative scales. For instance, the categories used for flowering start and flowering period are only of relevance to Northern Hemisphere temperate biomes (flowering start category 1 encompasses ‘first flowering in March or earlier’, and category 6 includes a range of months spanning ‘August or later, or before leaves in spring’; Hodgson *et al.* 1999). Furthermore, a single value is typically recorded for each reproductive trait, reflecting when a population as a whole starts and finishes flowering, whereas leaf and whole-plant traits are measured from individuals and allow replication of measurements within

populations. This mixture of individual-level and population-level traits, and the combination of nominal classes (lateral spread, height and flowering attributes) with quantitative traits [leaf dry matter content (LDMC), leaf dry weight (LDW), specific leaf area (SLA)], is not ideal for the investigation of how strategies vary between individuals within plant communities. Also, the relatively restricted calibration of the method prompted the following from Cerabolini *et al.* (2010a): ‘there is room for improvement ... collation of a wider range of trait values from a greater range of geographical locations has the potential to produce a globally applicable tool for comparative plant ecology’.

The main objective of the current study was to develop a CSR classification method generally applicable to vascular plants, including woody species, based on a broad calibration and the quantitative traits of individuals. The aim was to produce a method applicable rapidly to large numbers of individuals growing in nature and yet precise enough to compare species coexisting together or even to investigate the variability of strategies within single populations.

This new CSR classification builds on previous measurements of trait variability in plants. The main axis of trait variability evident in the world flora is the ‘economics spectrum’, reflecting a trade-off between the investment of resources in further resource acquisition versus conservation. This is evident as a ‘world-wide leaf economics spectrum’ (Wright *et al.* 2004) and in the overall ‘plant economics spectrum’ (Grime *et al.* 1997; Díaz *et al.* 2004; Freschet, Aerts & Cornelissen 2012). The second main axis of trait variability reflects plant size and is evident both in whole-plant traits such as canopy height and organ-level traits such as leaf size (Díaz *et al.* 2004; Cerabolini *et al.* 2010a; Pierce *et al.* 2012). For example, canopy height, leaf area and LDW all form part of a common size-related axis emerging from multivariate analysis (Cerabolini *et al.* 2010a). Both vegetative and some reproductive characteristics, such as seed mass, covary as part of this plant size axis (Díaz *et al.* 2004; Douma *et al.* 2012a,b). Indeed, multivariate analysis consistently reveals a triangular space that agrees with that predicted by Grime’s (2001) CSR triangle, delimited primarily by plant economics and size traits (Grime *et al.* 1997; Díaz *et al.* 2004; Cerabolini *et al.* 2010a; Douma *et al.* 2012a,b; Frenette-Dussault *et al.* 2012; Kröber *et al.* 2012; Pierce *et al.* 2012). Specifically, three main extreme trait syndromes emerge from these studies, characterized by the following: (i) tall plants with large leaves, intermediate leaf economics and intermediate flowering start and flowering period (C); (ii) short plants with small leaves, conservative leaf economic trait values (e.g. low-specific leaf area and leaf nitrogen concentrations) and a brief reproductive phase (S); and (iii) short plants with small leaves, highly acquisitive leaf economics and early, prolonged reproductive development (R). Crucially, this triangle is also evident if only small numbers of leaf traits are used, so long as traits reflect key components

of the leaf economics spectrum and leaf size (Cerabolini *et al.* 2010a; Pierce *et al.* 2012), providing ‘a dependable common reference frame for the quantitative comparison of the wider primary adaptive strategies of plants from highly contrasting habitats’ (Pierce *et al.* 2012). Notably, Hodgson *et al.* (1999) use of whole-plant traits, which do not allow tall tree life-forms to be compared directly against shorter life-forms, is perhaps the most important drawback of their method. Indeed, ‘the main problem is that of classifying a herb as C-selected because it is 2 m tall, when a woody species with a slower growth rate may eventually overshadow it – the size axis, and how this relates to traits such as relative growth rate, requires careful consideration ... As specific leaf area is correlated with relative growth rate, this measure may also provide a point of common reference by which herbaceous and woody plants may be compared’ (Cerabolini *et al.* 2010a). Thus, the recognition of organ size as a principal component of the ‘size axis’ and the combination of leaf size and economics traits (reflecting relative growth rate) such as SLA are key innovations of the new methodology presented here.

This study analysed trait variation for 678 species available in the FIFTH data base (for herbaceous plant species; Cerabolini *et al.* 2010a) and from our published data on aquatic species (Pierce *et al.* 2012) alongside new measurements for woody species with bush and tree life-forms (i.e. we investigated the principal components of leaf trait variation exhibited by a wide range of ecologically and taxonomically distinct species). This was used to calibrate a novel CSR classification method for vascular plants that uses truly quantitative functional traits and is applicable to leaf samples collected from plants growing *in situ*.

Materials and methods

The steps involved in the development of the new procedure are described in detail in Appendix S1 (Supporting information), but in summary, the main technical problem was to translate measurements of leaf economics and size traits (representing two axes of trait variability) into three values representing the extent of C, S, and R-selection, within the context of the multivariate trait space occupied by a broad range of species. Thus, the method first involved performing a multivariate analysis [principal components analysis (PCA)] of a range of leaf trait data for a variety of species. Secondly, the objective multidimensional space determined by the PCA was translated into a system of coordinates allowing species to be ordinated in a ternary (triangular) graph in which the three axes represented dimensions of variability in particular leaf traits. As this triangular space represents a trade-off between competing traits, species cannot be ordinated on, or near to, the axes themselves. Thus, this ‘trade-off triangle’ was then translated into a ‘CSR triangle’ by expanding all values along the axes until the ternary plot was entirely occupied, allowing representation of the extent of C, S and R-adaptation (i.e. CSR classification). Note that each step in the development of the method is built on the results of the previous step. Details of leaf trait measurement, multivariate analysis and how this was used in the construction of a spreadsheet to automatically return CSR values are given in Appendix S1 (Supporting information).

VALIDATION OF THE METHODOLOGY

Validation aimed to answer two questions: (i) does the method provide an outcome that is in accordance with CSR theory and with previous practical attempts to classify the CSR strategies of plant species; and (ii) is the method sufficiently precise to allow the comparison of the strategies of different species and of different individuals of the same species?

Tertiary CSR strategies were calculated using the new method for 36 of the species included in the Integrated Screening Programme (ISP) (Grime, Hodgson & Hunt 2007) for which we had our own data (i.e. additional populations, not used to calibrate the new method, of species included in the FIFTH data base; B. Cerabolini, unpublished data), and compared against the strategies predicted for these species by Grime, Hodgson & Hunt (2007; based on Hodgson *et al.* (1999) method). Additionally, separate individuals of six species (three lowland and three alpine) all within the genus *Poa* (Poaceae) were classified using the new method based on trait data from additional populations not used in the calibration of the current method (B. Cerabolini, unpublished data).

Results

The first two axes of the PCA together accounted for 72.6% of variability in the data (Fig. 1). The principal axis (PCA1) was an axis of leaf economics determined by, positively, LDMC and leaf carbon concentration, and, negatively, SLA and leaf nitrogen concentration (Fig. 1). These traits were strongly and highly significantly correlated with PCA1 (Spearman’s correlation coefficient; Table 1). The second axis of trait variation was strongly and highly significantly positively correlated with leaf size (i.e. both leaf area and LDW; Fig. 1; Table 1). Thus, species were ordinated in a triangle of multivariate space with

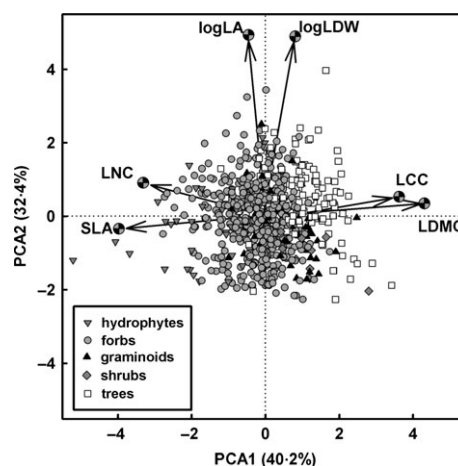


Fig. 1. A principal components analysis (PCA) showing the two main axes of variability in leaf traits amongst 678 wild angiosperm, gymnosperm and pteridophyte species with tree, shrub, graminoid, forb and hydrophyte life-forms from habitats spanning lowland to alpine bioclimatic zones in northern Italy. Leaf traits are leaf nitrogen concentration (LNC), leaf carbon concentration (LCC), specific leaf area (SLA), leaf dry matter content (LDMC), leaf dry weight (LDW) and leaf area (LA). Each data point typically represents the mean of 10 replicates per species (see text). PCA 1 and 2 together account for 72.6% of the variability in the data.

Table 1. Spearman's correlation coefficients between traits and axes 1 and 2 of the principal components analysis (PCA)

Traits	PCA1	PCA2
logLDW	0.139*	0.975***
logLA	-0.092*	0.987***
LNC	-0.635***	0.194*
LCC	0.688***	0.108*
LDMC	0.874***	0.065 n.s.
SLA	-0.778***	-0.018 n.s.

*Denotes significance at the $P \leq 0.05$ level, ** $P \leq 0.01$, *** $P \leq 0.001$. Traits are leaf dry weight (LDW), leaf area (LA), leaf nitrogen concentration (LNC), leaf carbon concentration (LCC), leaf dry matter content (LDMC) and specific leaf area (SLA).

small-leaved species with conservative leaf economics at the positive extreme of PCA1, small-leaved species with acquisitive economics at the negative extreme of PCA1 and large-leaved species with intermediate economics at the positive extreme of PCA2 (Fig. 1).

Absolute trait values ranged from 5.2 to 776815.9 mm⁻² for LA, 4.8 to 53.0% for LDMC and 2.1 to 203.2 mm² mg⁻¹ for SLA (Appendix S2, Supporting information). For logLA and LDMC, the curves of best fit with PCA axes were found to be simple linear regressions ($R^2 = 0.9740$ and 0.7409, respectively; equations shown in Fig. 2a,b). In the case of SLA, the curve of best fit was found to be a five-parameter exponential decay ($R^2 = 0.7031$; equation shown in Fig. 2c). In all cases, the relationships were highly statistically significant ($P < 0.0001$; respective ANOVA results are reported in Fig. 2). The 'trade-off triangle' showing the trade-off between logLA, LDMC and SLA is shown in Fig. 3. This triangle, expanded according to the procedure detailed in Appendix S1 (Supporting information), resulted in a further triangular plot (Fig. 4) showing the CSR classification of the 678 species investigated in the present study. Although it is not feasible to detail the strategies of all species here (these are listed in Appendix S2, Supporting information), the overall distribution of species and the identities of species occupying different regions of the triangle are worthy of note. First, species occupying the R corner of the triangle consisted of fast-growing annual herbs of short stature, such as *Arabidopsis thaliana*, *Cerastium pedunculatum*, *Poa annua*, and *Stellaria media*, and hydrophytes such as *Myriophyllum spicatum* and *Salvinia natans* (Fig. 4). The S-selected corner of the triangle included tough-leaved, slow-growing perennials such as alpine graminoids (e.g. *Agrostis rupestris*, *Carex curvula*, *Festuca halleri*, *Poa alpina*), alpine forbs (e.g. *Cardamine resedifolia*, *Epilobium fleischeri*), numerous gymnosperms (*Pinus* spp., *Cedrus deodara*, *Juniperus oxycedrus*) and woody angiosperms such as *Cistus monspeliensis* and *Rosmarinus officinalis*. Large-leaved hydrophytes, such as *Nelumbo nucifera*, *Nuphar lutea*, *Nymphaea* spp. and *Nymphoides peltata*, occupied the C-selected region of the triangle alongside

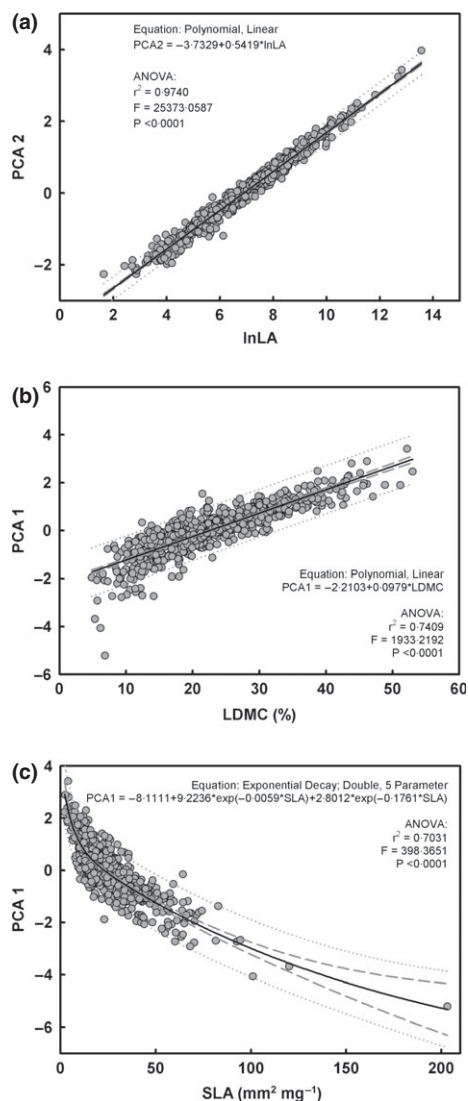


Fig. 2. Regressions between leaf traits and PCA axes used as predictor equations to attain virtual PCA coordinates for unknown target species with known leaf trait values: (a) log leaf area (lnLA) against PCA 2, (b) leaf dry matter content (LDMC) against PCA 1 and (c) specific leaf area (SLA) against PCA 1.

large-leaved herbs that form monospecific stands (e.g. *Arctium* spp., *Cirsium arvense*, *Molopospermum peloponnesiacum*; Fig. 4). The fern species investigated in the present study were classified as CR (e.g. *Athyrium filix-foemina*, *Dryopteris* spp.), SC (*Pteridium aquilinum*) or S/SC-selected (*Asplenium ruta-muraria*) (Fig. 4).

Figure 5 shows the CSR classification of individuals of six species of the genus *Poa* using the new method. The strategies of the individuals of each species were generally ordinated together in a restricted region of the CSR triangle, each individual with a distinct strategy but clustered around a mean strategy for the species. The mean strategy of lowland species was R to R/CSR-selected and for montane species was S-selected (Fig. 5). For instance, the mean strategy of *Poa alpina* was S, but with the strategies of individuals ranging between S and SR/CSR (Fig. 5).

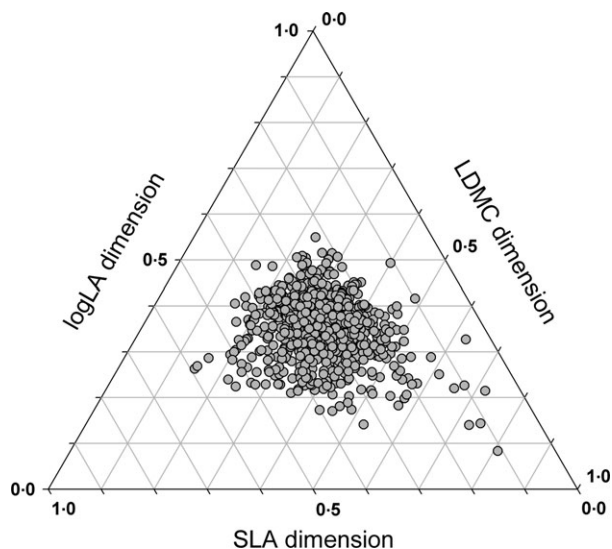


Fig. 3. The ‘trade-off triangle’ showing the trade-off between the ‘logLA dimension’, ‘LDMC dimension’ and ‘SLA dimension’.

Table 2 presents a comparison of tertiary CSR strategies predicted by the ISP (Grime, Hodgson & Hunt 2007) and calculated using the new method. Only 8% of species had precisely the same tertiary CSR strategy as that predicted by Grime, Hodgson & Hunt (2007). However, 56% of species were classified as being highly similar (i.e. 1 strategy class distant), and 97% of species were only two strategy classes or less away from those predicted by Grime, Hodgson & Hunt (2007). One species, *Bromus sterilis*, was three strategies away from that predicted by Grime, Hodgson & Hunt (2007). No species were classified at completely the opposite side of the triangle to the predicted strategy.

Discussion

First, it should be noted that it is difficult to provide a quantitative estimate of the degree of precision of the method, as the predicted CSR strategies of species provided by Grime, Hodgson & Hunt (2007) are based on Hodgson *et al.* (1999) incomplete method. Comparison with these strategies does not necessarily provide a gold standard. Thus, there was no prior baseline against which to compare the strategies of species calculated by the new method. Indeed, the objective multivariate analysis of leaf economics and size variability (Fig. 1) is our attempt to provide such a baseline. Furthermore, data measured at geographically distant sites for widespread species will potentially show differences arising from ecotypic specialization that may confound attempts to unequivocally determine ‘the strategy’ of a species. We would not necessarily expect our *Agrostis capillaris*, measured in alpine pasture and classified as S/SR (Table 2), to occupy precisely the same point in the CSR triangle as *A. capillaris* measured in the Sheffield region (and classified as CSR; Grime, Hodgson & Hunt 2007). Indeed, *Bromus sterilis*, the species exhibiting the most divergent strategy with respect to the ISP, was measured in the present study at a montane site at the upper limit of the altitudinal range of the species and was classified as S/SC (and as R/CR by Grime, Hodgson & Hunt 2007). These particular individuals were characterized by relatively low SLA ($19.6 \pm 0.67 \text{ mm}^2 \text{ mg}^{-1}$) and high LDMC ($44.4 \pm 1.86\%$) which, according to the worldwide leaf economics spectrum (Wright *et al.* 2004), are clear indicators of a conservative compartment, typical of S-selection. These differences in classification are

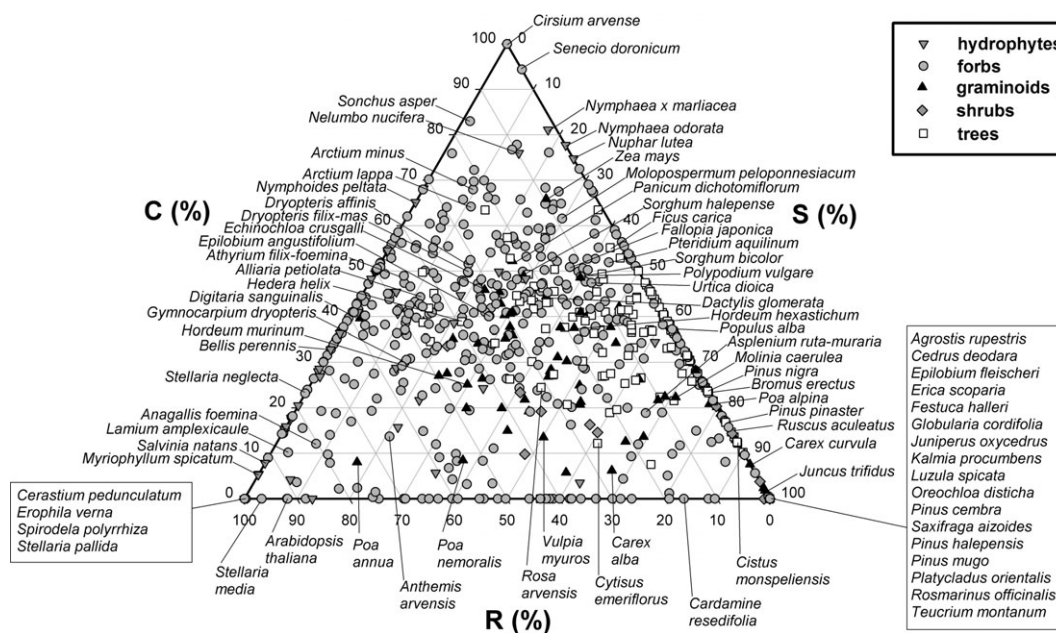


Fig. 4. Expansion of the trade-off triangle to fill the ternary plot, resulting in the CSR classification of 678 wild angiosperm, gymnosperm and pteridophyte species with tree, shrub, graminoid, forb and hydrophyte life-forms from habitats spanning lowland to alpine bioclimatic zones in northern Italy.

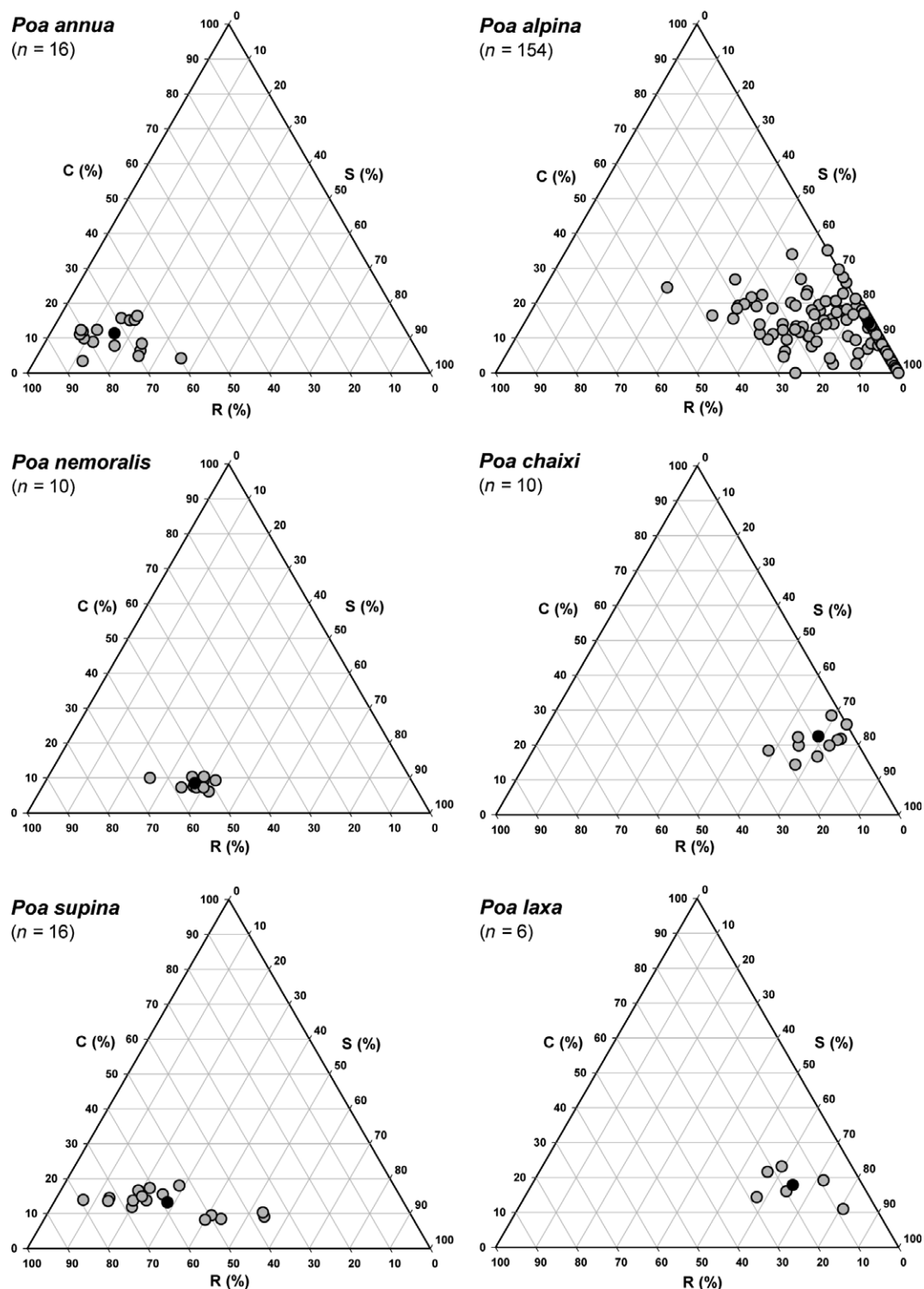


Fig. 5. CSR classification of six species of the genus *Poa* from lowland (left column; *P. annua*, *P. nemoralis*, *P. supina*) and alpine (right column; *P. alpina*, *P. chaixi*, *P. laxa*) northern Italy. Grey circles represent the strategies of individuals, and black circles the mean strategy for the species based on the individuals included in the analysis.

therefore more likely to reflect functional divergence between ecotypes within species, and the tendency of our research group to work in montane and alpine sites characterized by a higher degree of abiotic stress, rather than an error in the methodology. Conversely, if *A. capillaris* and *B. sterilis* were classified as *less* stress-tolerant at

higher altitude, then this would be cause for concern. Our analysis (Fig. 4 and Table 2) suggests that the new CSR classification is in general agreement with CSR theory (Grime 2001) and with the predictions of strategies for each species presented by Grime, Hodgson & Hunt (2007).

Table 2. A comparison of the tertiary CSR strategies of species from the Integrated Screening Programme (ISP), as predicted by Grime, Hodgson & Hunt (2007), with plants of the same species growing in northern Italy using the new CSR classification method in the present study

Species	Tertiary CSR strategy		
	Predicted by Grime, Hodgson & Hunt (2007) [ISP]	Determined by new CSR classification, this study	Distance (no. of tertiary strategies) between strategy classes
<i>Agrostis capillaris</i>	CSR	S/SR	2
<i>Anthoxanthum odoratum</i>	SR/CSR	S/CSR	1
<i>Anthriscus sylvestris</i>	C/CR	CR	1
<i>Arabidopsis thaliana</i>	SR	R	2
<i>Arrhenatherum elatius</i>	C/CSR	SR/CSR	2
<i>Brachypodium rupestre</i>	SC	SC/CSR	1
<i>Briza media</i>	S/CSR	S/SC	1
<i>Bromus erectus</i>	SC/CSR	S/SC	2
<i>Bromus sterilis</i>	R/CR	S/SC	3
<i>Campanula rotundifolia</i>	S/CSR	SR	1
<i>Carex flacca</i>	S	SC/CSR	2
<i>Centaurea scabiosa</i>	SC/CSR	C/SC	1
<i>Chenopodium album</i>	CR	R/CR	1
<i>Dactylis glomerata</i>	C/CSR	CR	1
<i>Deschampsia flexuosa</i>	S/SC	S	1
<i>Dryas octopetala</i>	S/SC	S	1
<i>Epilobium angustifolium</i>	C	CR/CSR	2
<i>Epilobium hirsutum</i>	C	CR/CSR	2
<i>Erigeron canadensis</i>	SR	SR	0
<i>Eriophorum vaginatum</i>	S/SC	S	1
<i>Festuca rubra</i>	CSR	SR	2
<i>Galium aparine</i>	CR	R	2
<i>Helianthemum nummularium</i>	S	S	0
<i>Hieracium pilosella</i>	S/CSR	S/SC	1
<i>Holcus lanatus</i>	CSR	SC/CSR	1
<i>Koeleria cristata</i>	S	S/SC	1
<i>Leontodon hispidus</i>	CSR	SR/CSR	2
<i>Lolium perenne</i>	CR/CSR	R/CR	1
<i>Lotus corniculatus</i>	S/CSR	S/SC	1
<i>Origanum vulgare</i>	SC/CSR	S	2
<i>Plantago lanceolata</i>	CSR	C/SC	2
<i>Poa annua</i>	R	R/CR	1
<i>Poa trivialis</i>	R/CSR	S/SR	2
<i>Rumex acetosella</i>	SR/CSR	R/CR	2
<i>Thymus praecox</i>	S	S/SR	1
<i>Urtica dioica</i>	C	CR	2

Notably, the species shown in Fig. 4 were classified in a way that realistically reflects their ecologies. First, plants from unproductive habitats, particularly slower-growing perennials with tough leaves, were grouped together in the S corner of the triangle. Small, fast-growing annuals and aquatic plants were classified in the R-selected corner. Larger-leaved herbs capable of forming monospecific stands in productive habitats were classified towards the C-selected corner. As predicted by Grime (2001), woody species occupied a region of the CSR triangle from S (typically gymnosperm trees or angiosperm bushes), through CS (angiosperm trees and woody lianas) to C (angiosperm trees with larger leaves): that is S → C. Aquatic species were either small, fast growing and with extremely acquisitive leaves (highly R-selected) or CS to C-selected species with large, broad leaves, such as water lilies, in agreement

with our previous conclusions (Pierce *et al.* 2012). Herbaceous forbs occupied the entire CSR triangle (see also Cerabolini *et al.* 2010a), and graminoids exhibited a broad range of CSR strategies throughout most of the triangle, as also seen by Pierce *et al.* (2007b). Thus, the new CSR classification is a comprehensive method that, despite its simplicity, can be used to compare disparate taxonomic groups and a variety of life-forms within a common framework.

This new approach has a number of advantages over Hodgson *et al.* (1999) method: (i) applicability to vascular plants in general (including trees and other woody life-forms, ferns, hydrophytes, alongside herbaceous angiosperms); (ii) it is based on a broad calibration using hundreds of ecologically diverse species; (iii) trait measurement involves three straightforward, yet fundamental,

leaf economics and size traits measured from plants growing *in situ*, using minimal equipment (a drying oven, balance and digital scanner), and also avoids artificial trait categories; (iv) calculations are included in a spreadsheet that can be used to rapidly calculate CSR scores for thousands of individuals or species (available as Appendix S3, Supporting information; note that Appendix S4 (Supporting information) also provides a spreadsheet tool for the calculation of parameters such as SLA, LDMC, leaf mass per area, leaf succulence and leaf water content, from LFW, LDW and LA data).

Due to the broad calibration of the new method, and its grounding in the world-wide leaf economics spectrum, it should be generally applicable. However, there are many ecological situations, such as desert and rain forest habitats, that are not currently represented and which could in future extend the range of the calibration. For example, Cerabolini *et al.* (2010a) pointed out that extremely large-leaved megaforbs such as the tree-sized herb *Ravenala madagascariensis* could represent the extreme of C-selection and that determining the 'true' CSR triangle would involve the inclusion of such extreme life-forms from around the world. (Note that the range of values detected for each trait in our data set is reported in the Results section). Indeed, the present study should be seen as covering a substantial part of the variability in these traits in European habitats, but by no means, all variability evident in nature and thus provides a general CSR classification tool that may be improved with future international calibration using even larger data sets. For the moment, the CSR classification tool (Appendix S3, Supporting information) truncates any extreme trait values that extend beyond those of the calibration species to provide a reasonable classification of species that would otherwise fall outside the limits of the current calibration.

The development of the new CSR classification method promises several exciting potential applications. For example, Schmidtlein, Feilhauer & Bruehlheide (2012) have demonstrated the utility of remote sensing of plant CSR strategies for mapping the general ecology of herbaceous vegetation at local scales. Now that the CSR strategies of woody species can also be determined this remote sensing method could be extended to rapidly describe the general ecology of entire landscapes, from local to continental scales. This could ultimately lead to four-dimensional representations of global vegetation showing ecological changes in response to large-scale anthropogenic disturbances such as deforestation, species invasions, nitrogen deposition or climate change. Indeed, Grime's CSR strategies are currently used to predict the response of vegetation to climate change (e.g. Abrahams 2008), to describe the development, conservation value and restoration of vegetation in managed ecosystems (Pywell *et al.* 2003; Boatman *et al.* 2011), to chart the response of vegetation to nitrogen pollution (Ling 2003) and abandonment (Prévosto *et al.* 2011), and to describe the ecology and invasion history of alien species (Pyšek *et al.* 2003; Lambdon, Lloret & Hulme

2008a,b). Remote sensing of CSR strategies could extend our knowledge of these aspects of plant community ecology and ecosystem processes over wider regions and imbue plant ecology with greater predictive power at local, regional and global scales.

The theoretical implications of the new method are also worthy of note. Two main historical objections to CSR theory are prevalent in the literature: (i) it is not empirically well supported (e.g. Tilman 1988); and (ii) a simple practical method of application does not exist (Westoby 1998; Westoby *et al.* 2002). First, it should be noted that the main directions of adaptive specialization postulated by CSR theory have now received extensive empirical support from the trait variation evident in nature across national and continental scales (Grime *et al.* 1997; Díaz *et al.* 2004; Cerabolini *et al.* 2010a; reviewed by Grime & Pierce 2012). Separate components of this trade-off, such as the leaf economics spectrum, have received strong support from empirical investigation at the global scale (Wright *et al.* 2004). Thus, clear empirical support for CSR theory now exists. With regard to practical measurement, the method developed in the present study allows vascular plants to be classified in a straightforward, practical manner. This invalidates Westoby's (1998) objection. Furthermore, Westoby's (1998) alternative leaf-height-seed method is necessarily restricted to seed plants, whereas our new method can be applied to any megaphyllous organism. It is difficult to see how, for example, herbaceous vegetation dominated by ferns such as *Pteridium aquilinum* could be classified according to the leaf-height-seed scheme.

To conclude, the new CSR classification method presented here extends the range of organisms that may be classified to include all major components of woody and herbaceous vegetation in terrestrial and aquatic habitats. The classification is rapid to implement, using solely leaf material, and thus can potentially be applied to large numbers of samples representing either individuals within populations or species within plant communities.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Detailed methodology.

Appendix S2. Calibration species data.

Appendix S3. CSR Triangulator VP spreadsheet (CSR classification tool).

Appendix S4. Spreadsheet for the calculation of mean SLA, LDMC, etc. from raw data.