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Short communication

Grime's CSR strategies of the invasive plants in Croatia

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Nonstandard abbreviations:
FCD – Flora Croatica Database

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Abstract

Background and Purpose: *Biological invasions are causing serious problems in the environment, often resulting in significant modifications of the landscape structure and ecosystem functioning. J.P. Grime's theory on CSR strategies of plants indicate whether plant species is a good competitor, adapted to disturbance or to limited resources. The goal of this study was to find which CSR strategy (if any) prevails among invasive plants in Croatia.*

Materials and Methods: *Data on CSR strategies were not available, or not consistent, for all invasive plants in Croatia, hence we have allocated CSR strategies to 15 invasive taxa, using the methodology based on several plant traits, which resulted in assignment of CSR type to 57 invasive plants. Distributional records of those 57 taxa in Croatia from the Flora Croatica Database were used to analyse the occurrence of invasive plants among three biogeographical regions (Alpine, Continental and Mediterranean).*

Results and Conclusions: *In total, 10 CSR types were found among the invasive plants of Croatia, mostly CR-strategists, followed by C-strategists and R-strategists. The largest proportion of R-strategists was found in the Mediterranean region, while the largest proportion of C-strategists was found in the Alpine region. Out of the three main strategies, competitive ability and ruderality were found to be frequently present within the Croatian invasive flora, while stress tolerance was almost absent.*

INTRODUCTION

The hostile spread of alien plants outside their native range (i.e., invasion) is nowadays a global problem, causing considerable damage worldwide in terms of ecology, economy and human health *(1–3)*. Three main factors are involved in the invasion process: propagule pressure, the susceptibility of the environment to invasion (i.e., invasibility) and biological characteristics of the newcomer (i.e. invasiveness) *(4)*. Identifying the factors that might play a role in this process is of particular interest to invasion biologists and conservation managers – different mechanisms for the invasion success have already been proposed *(5)*, emphasizing the importance of studying the attributes of invasive plants. Studies have shown that alien species tend to be associated with anthropogenic factors, since human-influenced and/or more disturbed habitats are usually more heavily invaded *(6)*. It is generally believed that disturbance plays a major role in plant invasions *(6, 7)*, relating invasiveness to CSR theory, which assumes that plants invest their resources either in the ability to compete, tolerate stress or survive biomass destruction (disturbance), as an adaptive response to the environment *(8)*. Accordingly, invasive plant

TABLE 1

The procedures used to obtain the values of the plant traits used in the allocation of unknown CSR strategies.

Trait (unit)	Procedure	Exceptions
Canopy height (mm)	Plants were measured in the field	
Lateral spread (six-point classification)	Plants were observed in the field and compared with literature	
Leaf dry weight (mg)	Leaves were oven-dried for 48 h/80 °C, or kept in sealed bags with silica gel for 72 h and weighted	Paspalum paspalodes – two leaves were treated as one because of their size
Leaf dry matter content (%)	Calculated as the ratio between dry and fresh leaf weight	Paspalum paspalodes – two leaves were treated as one because of their size
Specific leaf area (mm^2/mg dry weight)	Fresh leaves were scanned with a Canoscan 2000 scanner and scans were processed with ImageJ software (version 1.43, http://rsbweb.nih.gov/ij/index.html) to calculate leaf area	Carpobrotus edulis – the area was calculated by summing the areas of "basic" and one "lateral" side of the leaf, because of the three-apse leaves. Paspalum paspalodes – two leaves were treated as one because of their size
Flowering period (months in duration)	Data were obtained from literature	
Flowering start (six-point classification)	Data were obtained from literature	

species can be grouped into three main strategies (C – competitors, S – stress tolerators, R – ruderals) and a number of sub-types, based on their preference to environmental factors associated with stress and/or disturbance (for example, disturbance favours the presence of ruderal species while adversely affecting competitors, *9*).

Croatia does not have a long history in surveying invasive plants. Systematic research was initiated only a few years ago, when national standards and criteria for the treatment of alien flora were proposed *(10)*, and a preliminary check-list of invasive alien plant species with analyses of their family affiliation, life forms and origins was prepared *(11)*. An overview on their ecology (in terms of factors that influence their distribution) was first available from the case study of Mt. Medvednica *(12)*, while their distributional patterns on the national level were only recently studied *(7)*.

In the present study we have focused on the invasive flora of Croatia with the aim to allocate CSR strategies to the plant species. In addition, we aimed to determine the current occurrence of invasive species and their composition of CSR strategies in three biogeographical regions (as defined in the NATURA2000 program) present in Croatia. We hypothesised that invasive species will show predominantly ruderal 'behaviour', and expected to find mostly R-component strategies among invasive plants.

MATERIAL AND METHODS

Analyses were performed on the species level, with the exception of *Xanthium strumarium* ssp. *italicum* (Moretti) D.Löve where only this subspecies is invasive. Three species (*Cenchrus incertus* M.A. Curtis, *Epilobium ciliatum* Raf. and *Reynoutria sachalinensis* (F.S.Petrop.) Nakai in T. Mori) were not considered because of the small number of their records in Croatia; therefore, their invasive status may be dubious and should be further checked. We were not able to collect the species *Tagetes minuta* L. from the field during the time frame of this research, and its CSR strategy was not previously known from other sources. Therefore, it was not taken into account. The species *Cuscuta campestris* Yuncker was excluded for similar reasons: its CSR strategy was unknown and we were not able to determine it because of the absence of leaves which are necessary in here used procedure for allocation of CSR type *(13)*. In total we selected 57 taxa for further analyses, and we matched their nomenclature with the FCD (hirc.botanic.hr/fcd, accessed on September, 2013).

The process of assigning CSR strategies to plants (CSR classification) includes measuring a set of traits (Table 1) which can serve as predictors for a specific strategy, and calculating the strategy via previously prepared Excel worksheet *(13)*. Data on CSR strategies *sensu (9)* of invasive plants of Croatia were partly available from on-line databases BiolFlor (http://www2.ufz.de/biolflor/index.jsp, accessed on September, 2013) and FCD (http://hirc.botanic.hr/fcd/, accessed on September, 2013), and from the supplemental material of Hunt *et al. (14)* (http://people.exeter.ac.uk/rh203/csr_lookup_table.xls, accessed on December 2nd, 2013). We did not find any information on the CSR strategies of 13 taxa, and we have used the methodology developed by Hodgson *et al. (13)* to allocate the strategies to those taxa. In addition, we have found that *Erigeron annuus* and *Galinsoga ciliata* had different

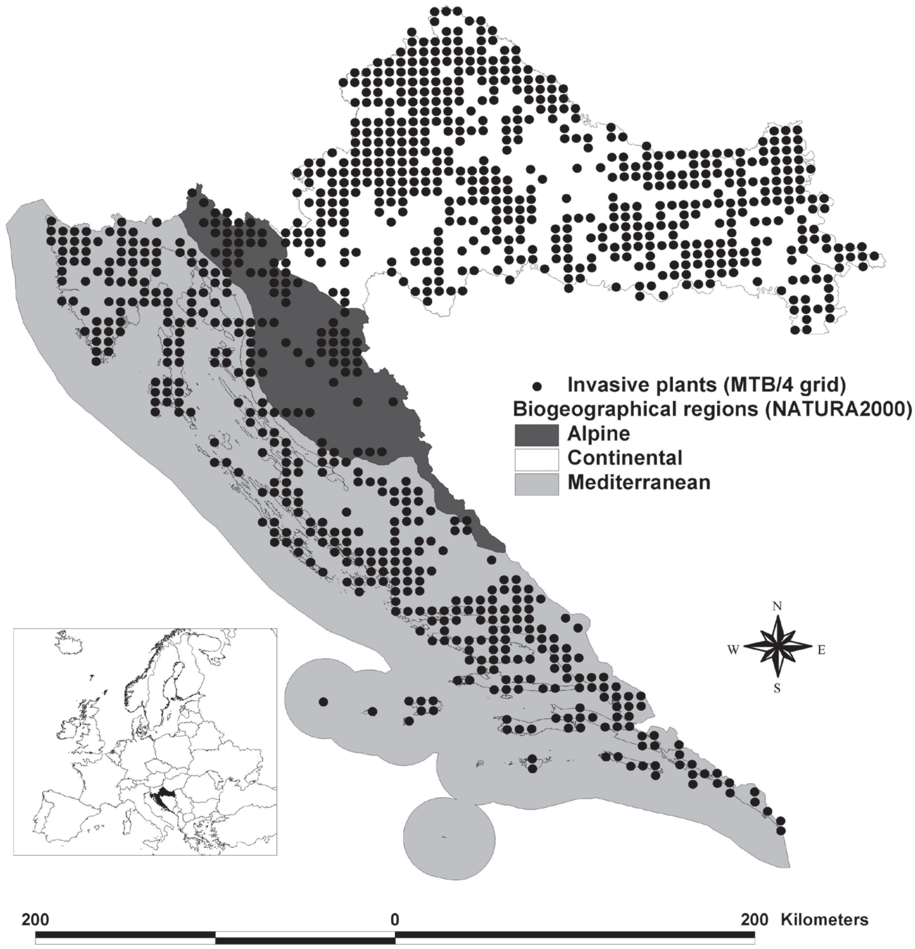

Figure 1. *Inner map: position of Croatia (black polygon). Main map: Croatia with three biogeographical regions and locations of invasive plant species records (for simplicity shown here with centroids of corresponding 1/4 MTB squares – i.e., regular grid proposed for flora mapping in Central Europe).*

entries for CSR strategies across the above-mentioned databases; therefore we have re-calculated their strategies and used our results in the subsequent analyses.

To perform the measurements (Table 1), specimens were collected in the field during the 2010 vegetation season. Only fully developed plants were sampled. For the purpose of keeping the plant tissues water-saturated until measurements could be taken, plants were collected in whole, when size allowed (otherwise, just leaves), wrapped in moist paper and kept in sealed plastic bags. Leaf weighing and scanning took place within 24 hours of collection. For each of the investigated species we sampled five (in some cases, six) leaves from four individuals (in total 20-22 leaves per species), and we selected only healthy leaves, i.e., leaves without any sign of herbivory and/or pathogens. Plant height was measured on the same four individuals.

After the measurements, average values of the plant height, leaf dry matter content, leaf dry weight, and specific leaf area were calculated per species. These values were entered into customized Excel worksheet prepared by Hodgson *et al.* *(13)*, together with the data on the flowering period, lateral spread and flowering start, to calculate the corresponding CSR strategy.

Following the assignment of CSR strategies to the plants, we calculated the percentages of all recorded strategies across biogeographical regions, using records on the localities of invasive taxa from the FCD (Figure 1), combined with corresponding strategies.

RESULTS

A total of 10 CSR types were found among the invasive flora of Croatia, and strategies of 15 taxa were designated in this study (Table 2). The final list of 57 taxa with corresponding strategies is given in Table 4.

The majority of invaders were CR-strategists (22 taxa, 38.60%), followed by C-strategists (15 taxa, 26.32%) and R-strategists (6 taxa, 10.53%). The same pattern was

TABLE 2

Values of the plant traits used in the allocation of unknown CSR strategies. Leaf traits and plant height are expressed in averages.

Taxon name	Height (mm)	Leaf dry matter content (%)	Flowering period (months)	Lateral spread (categorical)	Leaf dry weight (mg)	Specific leaf area (mm2/mg)	Flowering start (categorical)	CSR strategy
Aster squamatus (Spreng.) Hieron	754	34	2	1	54	9	6	C/SC
Bidens subalternans DC.	648	25	4	1	162	18	5	CR
Broussonetia papyrifera (L.) Vent.	3275	38	2	1	1193	11	2	C
Carpobrotus edulis (L.) N. E. Br. in Phillips	230	9	2	6	403	6	2	C/CR
Datura innoxia Mill.	648	11	4	1	704	22	4	CR
Diplotaxis erucoides (L.) DC.	479	16	12	1	91	18	1	R/CR
Erigeron annuus (L.) Pers.	794	28	4	1	77	24	6	CR
Galinsoga ciliata (Raf.) S. F. Blake	156	13	6	1	16	38	3	R/CR
Impatiens balfourii Hooker f.	431	12	2	1	59	31	5	R/CR
Nicotiana glauca Graham	2000	18	12	1	62	15	1	R/CR
Oxalis pes-caprae L.	113	10	7	3	16	28	6	R
Paspalum dilatatum Poir.	473	29	3	2	62	17	5	SC/CSR
Paspalum paspalodes (Michx.) Scribn.	263	23	3	5	19	26	5	CSR
Solanum elaeagnifolium Cav.	645	44	2	4	193	8	5	C/SC
Xanthium strumarium L. ssp. italicum (Moretti) D. Löve	730	19	4	1	684	15	5	CR

TABLE 3

Composition of the CSR strategies of Croatian invasive flora in different biogeographical regions (Alp – Alpine, Con – Continental, Med – Mediterranean) in percentages.

CSR strategy	Alp	Con	Med
C	34.4	33.3	26.9
CS	3.1	2.2	1.9
C/SC	3.1	2.2	5.8
CR	40.6	42.2	36.5
C/CR	–	–	1.9
CSR	3.1	4.4	5.8
R	6.3	8.9	11.5
SR	3.1	2.2	–
R/CR	6.3	4.4	7.7
SC/CSR	–	–	1.9

observed in all biogeographical regions: the dominance of competitors with the prevalence of CR over C strategy (Table 3), followed by R strategy. Comparison of regions, with regard to the three most common strategies, shows that the proportion of species exhibiting the CR strategy was highest in the Continental region, and the percentage of C-strategists was largest in the Alpine region. The Mediterranean was singled out as the region with highest proportion of R-strategists. Other types contributed less than 10% in total and in each region separately. In terms of primary strategies, there are no S strategists among the invasive flora of Croatia while C and R strategists are well represented (Supplement 1).

According to the current distribution data (Supplement 1), all but five invasive plant species have at least one occurrence in the Mediterranean region (91.23%). A high number of invaders can be found in the Continental region (78.95%), while the Alpine region harbours considerably less invasive species (56.14%). A significant portion of invasive plants in Croatia spread across all bioclimatic regions (49.12%), while 28.07% taxa appear in two out of three regions. Twelve taxa (21.05%) can be found in the Con-Med combination, four taxa (7.02%) in the Alp-Con combination and none of the invasive species occur in the Alp-Med combination. Relatively high numbers of invaders are region-specific (22.81%), and almost all of them are exclusively Mediterranean species (21.05%). The species *Elodea canadensis* inhabits only the Continental region, while there are no Alpine-specific invasive plants.

TABLE 4.
List of Croatian invasive plants with their occurences in different biogeographical regions (Alp – Alpine, Con – Continental, Med – Mediterranean), corresponding CSR strategies and sources providing the strategies if previously available. CSR strategies allocated in this study are in bold. For the explanation on the CSR abbreviations see *(13)*.

Taxon name	Region	CSR	Source
Abutilon theophrasti Medik.	Con, Med	CR	BiolFlor
Acer negundo L.	Con, Med	C	FCD, BiolFlor
Ailanthus altissima (Mill.) Swingle	Con, Med	C	FCD, BiolFlor
Amaranthus retroflexus L.	Con, Med	CR	FCD, BiolFlor
Ambrosia artemisiifolia L.	Alp, Con, Med	CR	FCD, BiolFlor
Amorpha fruticosa L.	Alp, Con, Med	C	FCD, BiolFlor
Angelica archangelica L.	Con, Med	CS	FCD, BiolFlor
Artemisia annua L.	Con, Med	CR	FCD, BiolFlor
Artemisia verlotiorum Lamotte	Alp, Con, Med	C	FCD, BiolFlor, (14)
Asclepias syriaca L.	Con, Med	C	FCD, BiolFlor
Aster squamatus (Spreng.) Hieron.	Med	**C/SC**	
Bidens frondosa L.	Alp, Con	CR	FCD, BiolFlor
Bidens subalternans DC.	Med	**CR**	
Broussonetia papyrifera (L.) Vent.	Med	**C**	
Carpobrotus edulis (L.) N.E.Br. in Phillips	Med	**C/CR**	
Chamomilla suaveolens (Pursh) Rydb.	Alp, Con, Med	R	FCD, BiolFlor, (14)
Chenopodium ambrosioides L.	Con, Med	CR	FCD, BiolFlor
Conyza bonariensis (L.) Cronquist	Med	CR	BiolFlor
Conyza canadensis (L.) Cronquist	Alp, Con, Med	CR	FCD, BiolFlor
Conyza sumatrensis (Retz.) E.Walker	Med	CR	BiolFlor
Datura innoxia Mill.	Alp, Con, Med	**CR**	
Datura stramonium L.	Alp, Con, Med	CR	FCD, BiolFlor
Diplotaxis erucoides (L.) DC.	Med	**R/CR**	
Duchesnea indica (Andrews) Focke	Con, Med	CSR	BiolFlor
Echinocystis lobata (Michx.) Torr. et Gray	Alp, Con, Med	CR	BiolFlor
Eleusine indica (L.) Gaertn.	Con, Med	C	BiolFlor
Elodea canadensis Michx.	Con	CR	(14)
Erigeron annuus (L.) Pers.	Alp, Con, Med	**CR**	
Euphorbia maculata L.	Con, Med	R	FCD, BiolFlor
Euphorbia prostrata Aiton	Med	R	BiolFlor
Galinsoga ciliata (Raf.) S.F.Blake	Alp, Con, Med	**R/CR**	
Galinsoga parviflora Cav.	Alp, Con, Med	CR	FCD, BiolFlor
Helianthus tuberosus L.	Alp, Con, Med	C	FCD, BiolFlor
Impatiens balfourii Hooker f.	Alp, Con, Med	**R/CR**	
Impatiens glandulifera Royle	Alp, Con	CR	FCD, BiolFlor, (14)
Impatiens parviflora DC.	Alp, Con	SR	FCD, BiolFlor
Juncus tenuis Willd.	Alp, Con, Med	CSR	FCD, BiolFlor, (14)

Lepidium virginicum L.	Con, Med	R	FCD, BiolFlor
Nicotiana glauca Graham	Med	**R/CR**	
Oenothera biennis L.	Alp, Con, Med	CR	FCD, BiolFlor
Oxalis pes-caprae L.	Med	**R**	
Panicum capillare L.	Alp, Con, Med	CR	FCD, BiolFlor
Panicum dichotomiflorum Michx.	Con, Med	CR	BiolFlor
Parthenocissus quinquefolia (L.) Planchon	Alp, Con, Med	C/SC	(14)
Paspalum dilatatum Poir.	Med	**SC/CSR**	
Paspalum paspalodes (Michx.) Scribn.	Med	**CSR**	
Phytolacca americana L.	Alp, Con, Med	C	BiolFlor
Reynoutria japonica Houtt.	Alp, Con, Med	C	FCD, BiolFlor, (14)
Robinia pseudoacacia L.	Alp, Con, Med	C	BiolFlor
Rudbeckia laciniata L.	Alp, Con	C	FCD, BiolFlor
Solanum elaeagnifolium Cav.	Med	**C/SC**	
Solidago canadensis L.	Alp, Con, Med	C	FCD, BiolFlor, (14)
Solidago gigantea Aiton	Alp, Con, Med	C	FCD, BiolFlor, (14)
Sorghum halepense (L.) Pers.	Alp, Con, Med	C	FCD, BiolFlor
Veronica persica Poir.	Alp, Con, Med	R	BiolFlor, (14)
Xanthium spinosum L.	Con, Med	CR	FCD, BiolFlor
Xanthium strumarium L. ssp. italicum (Moretti) D.Löve	Con, Med	**CR**	

DISCUSSION

The composition of CSR strategies of the invasive flora in Croatia points in several major directions. Although five out of 10 strategies involve the S-component, indicating some level of stress tolerance, these strategies include only a small number of species. In addition, 'pure' S-strategists are completely absent from the invasive flora, generally implying the intolerability of invasive flora toward continuous environmental stress. In comparison with native flora, according to the available data in the FCD, 40 out of 1591 taxa (around 2.5% of those with known CSR strategy), are designated as "pure" S-strategists. On the other hand, the high occurrence of CR and R strategies among invasive flora of Croatia (around 50%) suggests that, not surprisingly, invaders show an affinity toward disturbance, while in natives those two strategies account for around 20% of taxa with known strategies. Studies have shown that disturbed habitats are usually more heavily invaded *(6)*, and it has often been argued that disturbance can promote invasion *(9, 15, 16)*, which would imply that invasive species tend to be ruderals. However, in this study of CSR strategies within invasive flora, a high competitive ability has shown to be even more prominent than ruderality, which was different from our expectations. The C-component strategies generally prevailed, and; moreover, these strategies were assigned to the vast majority of invasive species. In line with our finding, Bakker and Wilson *(17)* proposed that differences in competitive ability may determine which species invade new areas, and Brewer and Cralle *(18)* have demonstrated the ability of the alien *Imperata cylindrica* to outcompete native species for resources. Greater efficiency in the use of resources is certainly an advantage in terms of overcoming the surrounding vegetation; therefore should be regarded as important in the context of invasiveness, as shown by our data.

Human activity (agriculture, mowing, trampling, etc.) introduces disturbance into the environment, consequently increasing landscape heterogeneity and habitat fragmentation. Since alpine zone is the least favourable for human inhabitation, it was least exposed to anthropogenic influence and related disturbances, which could partly explain the lowest proportion of R-strategists, and simultaneously the highest proportion of C-strategists in the Alpine region. Invasive plants seem to generally 'avoid' alpine zones *(19)*, whereas our results show that least invasive plant species in Croatia occur in the Alpine region, and none are Alpine-specific. On the other hand, the Mediterranean was significantly influenced by human population due to millenniums of land use, gradually undergoing an almost complete transformation of the natural vegetation into the variety of semi-natural and human-made habitats, resulting in the formation of a rather heterogeneous landscape *(20)*. This could partly account for the highest proportion of R-strategists and the lowest proportion of C-strategists in the Mediterranean part of Croatia, when compared to other two regions. In addition, invasive plants in Croatia show a certain affinity toward the Mediterranean – almost all species occur within this region, and many of them are region-specific.

In conclusion, out of the three main CSR strategies, ruderality and competitive ability seem to be significantly expressed within invasive plants in Croatia, while stress tolerance is almost absent.

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