

1 This study is predicated on a novel way of quantifying CSR plant functional types (PFTs) for
2 species, and comparing these with frameworks including the leaf economics spectrum. This
3 forms the basis of the entire analysis, and so it is fundamental that the way the PFTs are
4 derived represents CSR theory and can be compared against the LES. There are a number of
5 basic problems with the approach used here, however.

6 We cordially thank the reviewer for taking the time to review our manuscript. When
7 comparing the reviewer's perception of our topic with our short summary, we gained the
8 impression that there has been a misunderstanding regarding the main focus of our study. In
9 turn, we believe that this led to a number of misconceptions, which we address in detail in our
10 responses. We are confident that our approach is solid and we hope that our suggested
11 changes to the manuscript as well as the explanations in our author response will help to
12 resolve the issues raised by the reviewer.

13 Using the trait specific leaf area (SLA) to represent both leaf economics and also within the
14 CSR calculations means that to two measures are very likely correlated, potentially leading to
15 a Type 1 statistical error in which the conclusions are accepted despite the statistical test not
16 being sufficient to assign a realistic probability.

17 Thank you for pointing this out, as it shows that our approach was not clearly described. We
18 agree that Type 1 statistical errors need to be avoided. However, we are not representing a
19 statistical but a functional relationship between SLA and leaf longevity here (L175-186 and
20 709-714). The connection between SLA and leaf longevity is well established following leaf
21 economics (LES, Wright et al., 2004), but was so far not implemented as such in the LPJmL
22 model for grasslands.

23 In the original LPJmL model version, SLA was only used to compute the leaf area index
24 (LAI) from the internally computed leaf biomass. In order to represent the establishment of
25 different C-, S- or R-strategists, it is important to represent advantages and disadvantages of
26 the leaf structure in the model. Thinner leaves (high SLA) have a shorter longevity and while
27 they grow quickly to intercept light, they need to be replaced frequently. Neglecting the need
28 to replace thin leaves more frequently would lead to an advantage of high SLA values under
29 all circumstances, which is in contrast to ecological theory and observations (e.g., Díaz et al.,
30 2016; Reich, 2014; Wright et al., 2004). This trade-off had been implemented and applied to
31 tropical (Sakschewski et al., 2015) and European forests (Thonicke et al., 2020) before. The
32 implementation in this study provides a functional relationship of the SLA-LL relationship, as
33 part of the LES, and CSR theory through SLA in grasslands (section 2.3.2 and appendix A2).
34 This newly implemented functional relationship controls the productivity of the different
35 PFTs and the resulting shares of the C-, S- and R-PFTs. However, we do not compare the
36 LES to the C-, S- and R-PFT shares, which would be comparing inputs to outputs and would
37 certainly show a correlation.

38 We will add a paragraph to section 2.3.2 in which we describe

- 39 • the role of the functional relationship between SLA and leaf longevity to distinguish
40 different growth strategies,
- 41 • how this functional relationship together with the resource uptake and distribution
42 (section 2.3.1) as well as reproduction and mortality (2.3.3) provides the basis for the
43 dynamic computation of C-, S-, and R-PFTs' productivity, and
- 44 • how the productivity determines biomass and cover which are used to determine
45 community composition.

46 We will further revise and amend section 2.3.2 and appendix A2 to improve the description of
47 our approach.

48 With regard to stress, the authors state that “According to CSR theory, the stress gradient
49 expresses the level of stress a species is exposed to in a certain habitat. It ranges from
50 unstressed to severely stressed, but does not distinguish individual stress categories (e.g.
51 temperature, water or nutrient)” thus “different strategies for water-resource use can be used
52 to distinguish C- and R-strategists (low stress tolerance) from S-strategists”. Thus the traits
53 used here are specific to water stress, and the definition of stress recognised in CSR theory
54 (constrained metabolic efficiency and thus biomass production) is not cited nor considered.

55 The reviewer raises a valid point. Of course, stress is not restricted to water stress and other
56 traits that are related to (too high or too low) temperature or to nutrient stress could be used to
57 distinguish PFTs. In principle, the LPJmL model also considers stress arising from
58 temperature and nutrient availability in addition to water stress in its phenology and nitrogen
59 acquisition routines. However, the grassland steppe sites that we simulated in our study are
60 predominantly limited by water. Therefore, we decided to focus only on water stress in this
61 first application of LPJmL-CSR. This allows for a better understanding of the underlying
62 processes and the resulting pattern. In addition to the traits related to general stress tolerance,
63 we therefore only include traits related to water stress. However, we agree that the
64 implications of this simplification should be discussed. We will

- 65 • explicitly list the types of stress that are represented or disregarded by LPJmL in
66 section 2.1,
- 67 • add the definition of stress recognized in CSR theory as proposed by the reviewer and
68 the above reasoning for our focus on water stress to section 2.4.1, and
- 69 • discuss the implications of not using traits that are related to temperature and nutrient
70 stress tolerance for our results - especially for our simulation experiments on resource
71 limitation - in section 4.3.

72 Any stress (including water stress - but also factors such as nutrient stress or ‘non-resource’
73 stressors such as temperature) limits metabolic performance and thus growth and biomass
74 production. Internal, inherent metabolic traits (such as photosynthetic capacity and dark
75 respiration rate) or growth traits (such as relative growth rate) would have been acceptable to
76 demonstrate limitation, but the authors provide no evidence that, for instance, that specific
77 adaptations determining canopy-level conductance can represent the extent of general
78 tolerance to stress.

79 We agree with the reviewer that limited metabolic performance is the result of various types
80 of stress. Depending on the complexity of the model, responses to stress can be computed
81 internally (reduced growth rate or reduced photosynthetic capacity) if these are implemented
82 as dynamic functions in the model responding to, e.g., non-optimal temperatures or nutrient
83 limitations. In LPJmL, SLA is important to determine photosynthetic activity and therefore
84 affects the growth rate (L175ff). The leaf-to-root ratio affects the photosynthetic activity as
85 well by controlling the investments into additional leaves. Therefore, we do not only consider
86 traits related to tolerance to water stress but also traits related to a general tolerance to stress.
87 We realize that the original version of the manuscript may not have been sufficiently clear in
88 this regard and will improve the description of the role of the different traits and how they
89 represent tolerance to stress in section 2.4.1. To achieve this, we will include a short
90 paragraph for each trait that provides the following:

- 91 • a definition of the trait,
- 92 • the predominant gradient (stress or disturbance) the trait is associated with through
- 93 the processes it affects, and
- 94 • its use within the computations of LPJmL-CSR including all processes it affects.

95 We also agree with the reviewer that minimum canopy conductance and maximum
96 transpiration rate do only relate to water stress. However, we selected four traits associated
97 with the stress gradient to represent differences between the strategies. Two traits that are
98 associated with general tolerance to stress through their importance for plant growth and two
99 traits that are specific for water stress. As stated in a previous reply in L62f, we did not select
100 additional traits that specifically relate to other types of stress that are represented in the
101 model (temperature and nitrogen). With a better emphasis of our focus on water stress, the
102 selection of traits relevant for water dynamics is hopefully more comprehensible. As already
103 stated in our reply in L55-64, we agree that our description of the representation of different
104 types of stress and our reasoning to focus on water stress needs to be improved. We made a
105 proposal how this can be achieved at the end of the reply in L65-71.

106 [Line 233: the authors state that “plant stature ... can be used to distinguish C- and S-](#)
107 [strategists \(low disturbance tolerance\) from R-strategists”](#). No: S-selected species can be
108 [small \(e.g. *Salix herbacea*\) but some may become large over a long life-span \(i.e.](#)
109 [Sequoiadendron giganteum\). What matters is the C-selected species get large quickly, S-](#)
110 [selected species can become large eventually over a long life-span, and R-selected species](#)
111 [cannot. This is more a reflection of longevity and how rapidly plants achieve adult size.](#)

112 We agree with the reviewer that S-strategists generally show a variety of statures as they
113 nicely illustrated with their examples. This is also clearly stated in Table 2 of Grime (1977) to
114 distinct species of the different strategies. While you can also find tall S-strategists in
115 grasslands (e.g. *Brachiaria brizantha*), generally grassland plant species are of approximately
116 similar height (Gommers et al., 2013; Pontes et al., 2015).
117 Still, the reviewer raises an important point. If one would only consider stature, an S-strategist
118 might not be clearly distinguishable from a C- or an R-strategist and our explanation can be
119 misinterpreted this way. However, we are aware of the importance of growth rate and
120 longevity when distinguishing C-, S- and R-strategists. To account for this, the LPJmL model
121 represents the fast-slow economics of the LES as explained in more detail in our reply in L17-
122 47. Furthermore, we do not prescribe plant stature. Instead, we use a parameter that just
123 represents the potential stature a strategist can attain. Depending on abiotic and biotic factors,
124 the C- and S-strategist can become large but the R-strategist cannot. The C-strategists will
125 grow rapidly if sufficient resources are available. The S-strategist will grow slowly but
126 accumulate large amounts of biomass over a longer time or remain small if it is disturbed or
127 outcompeted. We will amend

- 128 • section 2.4.1 to more clearly explain the distinction between the C-, S-, and R-PFTs
- 129 underpinned by the description of the traits and their use within the model as
- 130 proposed in our reply in L91-94, and
- 131 • section 2.1 to include additional details on the growth dynamics including a
- 132 qualitative description of the photosynthesis, allocation and turnover routines
- 133 implemented in LPJmL-CSR.

134 [In the present study only juveniles were investigated, so using the leaf area index of a sapling](#)
135 [is not going to represent the strategy in the main vegetative phase \(seedling CSR strategies are](#)

136 known to be different from adult CSR strategies; Dayrell et al. (2018) *Functional Ecology* 32,
137 2730-2741).

138 We agree with the reviewer that it is important to not only address CSR dynamics of juvenile
139 plants. However, we would like to stress that we do not focus on juvenile plant dynamics. We
140 assume that this misunderstanding originates in the description of establishment where
141 saplings are established on bare ground. Still the model simulates an average individual that
142 typically represents an adult plant (unless the entire plot has been re-established with new
143 plants). We will add the explanation that LPJmL-CSR simulates adult plants to section 2.1
144 together with the details on the growth dynamics (see details in L131ff).

145 Also, CSR strategies are phenotypic characters (i.e. attributes of the individual plant that are
146 subject to natural selection), but establishment rate (k_{est}) [line 237] is not a character of an
147 individual (the units of measurement are stated in Table 2 as the number of individuals per
148 metre squared per day – a population measure), and so cannot elucidate the individual
149 phenotype or adaptations of the species (i.e. the plant strategy or PFT).

150 We agree that CSR strategies can be defined as a phenotypic characteristic of an individual
151 and it may be counterintuitive that a measure that is not reported as being per individual but
152 per meter squared can be used to represent a phenotypic characteristic. However, the
153 establishment rate is just a parameter used within the model to calculate the actual
154 establishment (appendix A3). This calculation considers several variables including the
155 number of individuals and the resulting actual establishment can be reported as individuals
156 per individual (a phenotypic characteristic). We see the point that this may be misunderstood.
157 Also, LPJmL-CSR does simulate trait plasticity as well evolutionary processes. Therefore,
158 phenotypic adaptation is not accounted for and adaptation only occurs at the community level
159 through changes in its composition.

160 To address the reviewer's concerns, we will

- 161 • provide a more thorough qualitative explanation of the establishment in section 2.3.3,
- 162 • explain the use of k_{est} within the establishment routine of LPJmL-CSR more detailed
163 in appendix A4, and
- 164 • clarify that we do not simulate phenotypic adaptation in section 2.3.3.

165 In Figure 4, the red, green, blue (RGB) color scheme is used both to represent the extent of C,
166 S and R and the experimental treatments rainfed (red), irrigated (blue) and fertilised (green).

167 We agree that the coloring is not enhancing clarity and will remove the colors from the axis
168 labels of the ternary plots.

169 **References**

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