**We greatly appreciate the comments and feedback in improving the quality and clarity of our manuscript. Please find our detailed responses below.**

Referee: 1  
  
Comments to the Author  
Review of “Drought frequency predicts life history strategies in Heliophila”  
  
This paper uses herbarium occurrence records with satellite-based drought measurements to examine associations between life history (annual and perennial strategies) and drought frequency. They conduct analysis controlling for phylogenetic relationships. They discover that annuals are associated with environments that experience more drought and that collection dates of annuals occur preferentially in the more wet months, suggesting that annuals are avoiding growth during the seasons with more frequent drought.  Overall, I enjoyed reading this paper, but I think that it could have had more nuance and novelty.  Although they claim that no-one has studied this association (line 58), this isn’t true. For example, classic literature by Stebbins established the association between annuality and drought environments. In this vein, I feel like the paper did a poor job of motivating what is new about their research, and what it adds to our understanding.

**Thank you for the thorough review. We are glad that you enjoyed reading the paper and we have made extensive revisions to address your concerns. Regarding the novelty of our approach and results, we have added a more in-depth discussion about the broader context of life history theory/research that this work contributes to. First, we provide a more thorough of review previous work and highlight the lack of phylogenetically constrained analyses and lack of large-scale species/climate observations to address classic theory. Next, we have added an additional analysis: ancestral state reconstruction of life history strategy in Heliophila. This analysis revealed that Heliophila has experienced a greater number of transitions from annuality to perenniality. Because the majority of previous theoretical and empirical work has focused on explaining the evolution of annuality, Heliophila thus presents a valuable opportunity to study the climatic drivers of the alternative evolutionary transition – from an annual to perennial life history. The results suggest that perenniality is favored over annuality in systems with infrequent drought, suggesting that drought may play an important role as a climatic agent of disturbance necessary for the establishment of annual species. We feel that these results yield a more complex understanding of the climatic factors that explain the relationship between climate and life history with important implications in the context of contemporary climate change. Specifically, we discuss these findings in relation to recent work forecasting changes in precipitation across western South Africa, which we have shown is currently inhabited by derived perennial *Heliophila* species.**

One of my main concerns with the paper is that the authors never actually define drought, or what effect it might have on plants. There are lots of different components to drought – duration, predictability, frequency – and these might affect plants differently. On line 80, the authors simply say they ‘quantify the frequency of drought…” and that is the extent of their explanation.  What does this actually mean? It also seems that they may have access to more nuanced data in their dataset (ie. could they tease apart frequency and duration) and would this lead to more insight?

**Thank you for making this important point. We agree that the original manuscript did a poor job defining drought both conceptually and technically. The revised manuscript contains numerous changes to clarify our approach and discusses the nuances of drought for plant ecology and evolution. As now described in the manuscript, we employ the definition of drought proposed by J.B. Passioura which emphasizes droughts as “circumstances in which plants suffer reduced growth or yield because of insufficient water supply, or because of too large a humidity deficit despite there being seemingly adequate water in the soil.” (Passioura 1996 *Drought and drought tolerance*). The revised manuscript now clarifies how we have quantified such droughts across landscapes and used it to study drought as an agent of selection. In this vein, the revised manuscript goes into further detail to explain how we calculated drought frequency and combined this with another important dimension of drought, timing, to study drought in a nuanced way. We now highlight how these analyses have allowed us to tease apart different components of drought to reveal both drought frequency and predictability as important for explaining Heliophila life history patterns.**

It also seems inherently circular that drought is defined by the “vegetative health index”, this seems to automatically bias their data to finding that annuals are associated with drought, because if drought means no above-ground vegetation, then by definition there can’t be any perennial plants there. However, there are perennial long-lived plants that are associated with desert conditions and use an alternate strategy of water conservation and tolerance to get though periods of dryness. However, these type of plant strategies would never show up using their index of drought. Perhaps I am mis-understanding the index of drought, but the equations used are never properly explained. 

**After re-reading the methods section regarding the Vegetative Health Index, we agree that it failed to describe how drought is quantified using this approach. Your concern is sound given the information provided. We have made major changes to this section to clarify how the VHI was developed and controls for such factors as ecosystem type to generate an unbiased quantification of drought conditions. Specifically, we explain how the VHI is calculated by comparing values between years at the same pixel and season rather than between pixels or different times of the year. For example, the VHI does not function by comparing plant cover during the summer of 1982 between different locations. Rather, it compares summer of 1982 a given location to every other summer at that same location. Accordingly, under conditions of ecological drought stress a location dominated by perennial species will be detected by the VHI. We have also added citations and figures (Figure S1) demonstrating the efficacy of the VHI across a number of ecosystem types in southern Africa.**

Below I outline several other concerns, associated with particular line numbers  
  
Line 58-59 is very odd. The paragraph preceding it gives multiple examples of studies demonstrating that annuality is associated with environments that experience drought. It is then very strange to conclude the paragraph with a sentence saying that whether drought predicts the distributions of annual/perennial strategies has never been tested. This seems like a poor choice of motivation for this paper.  (There also seem to be some grammatical issues with this sentence, so perhaps I am missing a more subtle point). Nonetheless, I think it would be more interesting to better identify the missing component in the literature and how your work builds on these previous studies.

**We agree, this sentence was unclear and poorly worded. As part of a larger restructuring and rewriting of the introduction, it has been removed.**   
  
The Introduction could better motivate this particular study. As it stands now, it describes some classic life history theory and basic (ie. crude) expectations for annual/perennial strategies. However, there is a lot of nuance and novelty that has not been set up.  For example, the PREDICTABILITY of drought might be very important. How would this effect life histories?  Similarly, how might the frequency and/or duration of drought effect life histories? 

**Thank you for the valuable suggestion. In light of this comment, we have made substantial revisions to the introduction which now better articulates the motivation for this study. We now more clearly identify gaps in the literature that this work addresses and discuss a much more nuanced perspective of drought adaptive life history as you suggested. For example, the beginning of paragraph 3 in the revised manuscript now reads, “It is also critical to consider another dimension of drought adaptation: the expectation that annuality is most adaptive when droughts are not only frequent but also predictable.”**

The equations listed between lines 88 and 89 are never explained or really discussed. As they stand, they’re unlikely to be particularly useful to the reader. I can figure out what Tmin and Tmax mean, but it would be better if you told the reader.

**We agree that the description of the VHI lacked clarity. As part of major revisions to this section, these lines have been removed.**  
  
Line 92. What do you mean by “historically”? Because you never describe the equations, the reader has to deduce what the “Thus” on line 92 refers to. Is 1981 the baseline ‘historical’?

**As part of major revisions to the section describing VHI, this line has been removed.**  
  
Line 93. What do you mean by “these measurements”?  What does “these” refer to?

**As part of major revisions to the section describing VHI, this line has been removed.**

Line 100 “16km2 resolution”.  At this point you haven’t told us the scope of the data or the distribution of the focal species.  What is the geographic extent of your dataset at 16km2 resolution? (ie. how many total kms, are we talking at the regional level or the continental level?)

**This issue has been resolved in the revised manuscript. The study area is described before the VHI in the materials and methods section.**

The start of the paragraph on line 118 was very odd to me. The section is titled “Heliophila occurrence records” , and then you go on to describe global herbarium specimens.  I had to go back and check the distribution of your species. What is the relevance of telling us about global specimens when this is an endemic with a restricted range?  The important information is how many records you obtained, and from what years, but that crucial data is missing on line 125.  You also don’t mention the number of species and whether they were annual or perennial

**We agree. This section has been rewritten. It also now includes the number of annual and perennial species.**

Line 128.  For how many species did you obtain genetic data? Annual or perennial?

**The revised manuscript now includes this information (21 annual, 21 perennial)**  
Line 135. What do you actually mean by “drought”? What definition are you using? This relates back to never actually explaining the VHI equations.

**Thank you for making this important point. We now define drought in the manuscript both in the introduction and methods section. As described above, we employ the ecological definition of drought as an episode of plant stress caused by elevated aridity.**  
  
Line 138. What do you mean by “drought frequency” – the frequency within a year or between years? What about the duration or severity of drought?

**We now clarify in the methods section that we are calculating frequency between years. For the purposes of this work, we are focusing on frequency and seasonality, which are valuable for studying life history adaptation in the context of drought predictability.**

Line 151. How many species?   What alignment software?

**The revised manuscriupt states the number of species (21 annual, 21 perennial) here and cites the alignment software in the methods section.**  
  
Line 165. Were these paired t-tests between each season? Did you adjust for multiple comparisons?

**We now clarify that these were t-tests between annual and perennial rather than between seasons. The results are unchanged if multiple testing is considered to adjust pvalues.**

Line 170. The geographical location of species might be important too. It would be useful to also include geographical distance as a covariate.

**The revised manuscript now includes a line that clarifies the purpose of phylogenetically constrained analysis to account this. “This statistical approach is designed to control for the confounding effects of geographic relationships explained by demographic history rather than processes of natural selection.”**  
  
Line 270. Classic life history theory predicts that perenniality (or iteroparity) will be associated with high adult survival, which is typical of stable habitats. It seems that this is the kind of environment of your infrequent drought habitats.  It would be good to discuss the occurrence of perennials in this context.

**Thank you for the suggestion. We have added further discussion to this point here, “This is supported by the theoretical prediction that perenniality is advantageous is stable habitats…” Additionally, the manuscript additional discussion around this prediction, including in the introduction. These new discussions are largely motivated by insights gained from adding ancestral state reconstruction as suggested below.**Line 271. I don’t see how you can infer the evolutionary order of transitions from looking at the phylogeny. The pattern is not \*obvious\* and without actually conducting analyses on ancestral trait reconstruction, these assumptions are on shaky ground. I recommend you either remove these statements, or you actually run some ancestral state reconstruction analyses and see if you can determine the order of events. That would be very interesting, and could contribute substantially to the novelty of the paper.

**We are very grateful for this suggestion. We have added ancestral state reconstruction analysis to the revised manuscript (Fig. 1a) and feel it has considerably elevated the quality of this work. We find evidence of multiple independent transitions to perenniality, which, given the phylogenetically constrained association between perennial species and environments with infrequent drought, has afforded greater power to make inference about the role of drought in the evolution of perenniality.**   
  
Line 265. Typo: environemnts → environments  
Line 270. Typo: morality → mortality  
Line 274. Typo: complete → compete

**Fixed, thank you!**  
  
  
Referee: 2  
  
Comments to the Author  
Thank you very much for the highly interesting article. Your article tackles a – on theoretical grounds – widely discussed, and fairly well understood topic. I see the merits of your work in the new (empirical) approach that largely supports the views and theory revolving the (dis-) advantages of annual vs. perennial life histories and potential environmental drivers of their evolution. The data upon which your study is based is impressive and you have chosen a potentially highly revealing genus of plants for your questions at hand: Is drought-frequency driving life history distribution?  
Altogether, your work is confirming widely accepted theory in that sense not highly novel. However, as mentioned above, I see the merits and novelty of your work in the applied approach combing several (large scale) sources of environmental and ecological data, and your creative approach of using these sources for shedding light on a theory which defies straightforward mechanistic / empirical approaches on meaningful spatial and temporal scales.

**Thank you for the valuable feedback and generous suggestions. We are pleased to hear that you found the work interesting and appreciated the novelty of our approach and insights. We have made major revisions to the introduction to highlight how this work provides novel contributions toward empirical support for classic life history theory.**

The study and methods employed appear to be sound and robust. However, please see my comments in line 163 and following regarding the use of an ANOVA (or analysis of deviance) rather than the currently adopted t-test approach. The suggested approach of analysis differences in drought frequencies by means of a mixed-effect model, using life history and season, as well as their interaction as fixed factors and species as random factor may yield additional insights (e.g. interaction of the two fixed factors) and may also be less affected by the varying (and often large) sample sizes.

**Thank you for this excellent suggestion. We have added this analysis to the revised manuscript. Interestingly, we find a significant association between drought frequency and the interaction between life history and season. This result has provided novel support for the hypothesis that seasonal drought frequency is an important driver of life history strategies.**  
  
The article is very well written, easy to follow, and suggests a high quality of analyses (but see comments regarding statistical analysis) and presentation (including tables and figures).  
Importantly, you did not oversell your results as ultimate “proof” of the theory that the annual vs. perennial life history is an adaptive strategies to environmental harshness and unpredictability, but were well aware of the correlative nature of your results.  
For future work, you may consider to refine the dichotomous classification of annual vs. perennial to also reflect differences in the perenniality (e.g. weak perennial or bi-annual, …).

**We love this idea! We too hope that this work inspires future investigations to study life history evolution at higher phenotypic resolution.**  
  
Referee: 3  
  
Comments to the Author  
In this manuscript, Grey and colleagues demonstrate that life history strategy is significantly associated with drought frequency in a lineage of Brassicaceae from South Africa. The study makes excellent use of natural history collections and satellite data, and analyses the association in a clear phylogenetic framework. As it is the manuscript will benefit from some key revisions, but ultimately will be an excellent contribution and I suspect highly sited.

**We greatly appreciate your encouraging review and are grateful for the valuable revisions you have suggested. As described below, we have incorporated these changes into the revised manuscript and feel that it has considerably improved the quality of this work.**

I suggest the following major revisions to improve the overall quality of the manuscript.  
1. The authors use existing DNA sequence data to estimate phylogenetic relationships across Heliophila. The methods are clearly stated, but more attention to the results of these analyses should be provided in the results section. How does this tree compare to previous studies? What are the posteriors on relationships? Etc.

**We agree that reporting results from the phylogeny construction was needed. We have added a new paragraph to the results section describing the phylogeny and how it compares to previous work. We find that this phylogeny is consistent with previous studies. In addition, following the suggestion below to include ancestral state reconstruction, we have included a summary of this analysis in the results section.**

2. The study would be improved by an analysis of ancestral state reconstruction. What is the predicted ancestral condition for the genus? How many transitions, and where on the phylogeny? Line 271-272 of the discussion hints at the importance of this question.

**We are very grateful for this suggestion. We have added ancestral state reconstruction analysis to the revised manuscript (Fig. 1a) and feel it has considerably elevated the quality of this work. We find evidence of multiple independent transitions to perenniality, which, given the phylogenetically constrained association between perennial species and environments with infrequent drought, has afforded greater power to make inference about the role of drought in the evolution of perenniality.**

3. The phylogenetic logistic regression analysis is solid. However, how the data are presented needs improvement. Table 1 demonstrates that there is an association between life history and drought, even when correcting for phylogeny. In some ways, this could be the end of the data presentation on this point. But the authors have chosen to visualize this result graphically in Fig. 3a. I have some issues with how this was done. Data on the Y axis are not phylogenetically corrected. In fact, the data presented in Fig. 3a is simply a re-presentation of the data presented in Fig. 2g but with new indicators of significance based on phylogenetic correction. I think the most honest way to visually illustrate the association between life history and drought would be to present 4 separate graphs of the logistic regression; predictor (drought) phylogenetically corrected on the X axis and response variable (life history) on the Y axis. As an example see <https://stackoverflow.com/questions/43441467/plot-phylogenetic-logistic-regression-with-binary-response-variable>  
  
**Thank you for the valuable suggestion and useful resource. We have followed this recommendation and the revised manuscript now includes an additional panel in figure 3 graphically displaying the results of the phylogenetic logistic regression as you describe above.**

4. In Fig. 3b, please clarify how data were binned across the X axis, presumably not by season. I would also recommend the X axis be more finely divided (by month? Week?) to better reflect how data were binned.

**We have changed the axis title in this figure to indicate the appropriate units (days).**

Minor suggestions:  
5. The Abstract/Summary is not in New Phytologist format (at least, I think that’s the case)

**Fixed, thank you.**  
6. I found it difficult that the software used are only listed as a block in the supplemental. As a reader, I prefer to see what software packages are used for which individual analyses as I read the methods section of a paper. I recommend using the more standard format of software information integrated into the methods.

**Thank you, we have removed this section and added the necessary citations to the materials and methods section.**7. Line 93: location, not locations

**Fixed, thank you.**  
8. Line 149: outgroup not out group

**Fixed, thank you.**  
9. Line 151: aligned not aaligned

**Fixed, thank you.**  
10. Lines 201-202, 221: replace p=0.00 with p<0.001 (or similar)

**Fixed, thank you.**  
11. Line 209: differences ‘in’

**Fixed, thank you.**