

Interactive comment on “Stable isotope and modelling evidence that CO₂ drives vegetation changes in the tropics” by F. J. Bragg et al.

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Anonymous referee #2

We agree with the referee’s point that the pollen data add little additional information to support our case. Indeed, the scarcity of pollen data from the LGM in Africa is precisely what makes the offshore leaf-wax record particularly valuable. We have simplified the text and Figures as the referee suggests. The available pollen data (as biomes) are now in Supplementary Fig. S2.

Anonymous referee #3

The referee states that we don’t provide ‘quantification’ of climate change and CO₂ effects.

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It is true that our result is essentially qualitative: i.e., without the CO₂ effect it is not possible to simulate the nature of the vegetation shifts. This in itself is a very strong result. To estimate the effects more quantitatively would be possible in principle, given higher-resolution measurements that would allow us to exploit the partial decoupling of temperature and CO₂ signals in the time series of changes between glacial and interglacial states. It cannot be done based on a comparison of two time periods. We do intend to pursue quantification via the temporal decoupling of the two signals in future. High-resolution analysis of two deep-sea cores for land-plant wax components spanning the Holocene and the LGM is in progress. But this would be considerably beyond the scope of the present paper.

The referee suggests that effects of precipitation ‘should be looked at more closely’. But our results already comprehensively consider the effects of climate change, including changes in the amount and seasonal distribution of precipitation, as well as solar radiation and temperature. Our modelling approach explicitly takes account of the potential effects of precipitation changes, not only on the C₃/C₄ plant balance, but also on the extent of isotopic discrimination by C₃ plants. Therefore, our results already rule out precipitation changes as major drivers of the vegetation shift.

The referee also mentions that ‘²H in sediment leaf wax n-alkanes might provide further insights’. Hydrogen isotope ratios have been intensely studied by various groups but the results are often inconsistent. There has also been an attempt by Vogts (2011). This manuscript draft has undergone major revision but still needs refinement in the discussion and conclusions and, thus, is not yet ready for publication. The findings of Vogts (2011) are that the principal information likely to be obtained from these measurements would be about the isotopic composition of the precipitation, which is only very indirectly related to the amount of precipitation.

The referee (like referee #2) points out the weakness of the pollen data to support our case.

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The referee asks why we didn't use the data of Vogts (2011) and Vogts et al. (submitted; meanwhile published in 2012). These were not available when our study was carried out. Moreover the Vogts et al. (2012) data are from surface samples only; no samples of LGM age included. The study of Vogts et al. (2012) was mainly undertaken to rule out any effects of transport distance and time (all sediment samples are from close to 1300 m water depth) and of the carbon isotope and n-alkane chain length end member data (with a greatly increased statistical data base from additional southern African plants). Vogts et al. (2012) confirmed the findings of Rommerskirchen et al. (2003, 2006) that there is a strong spatial relationship between contemporary leaf-wax n-alkane ^{13}C signatures and aridity. The Rommerskirchen et al. (2003, 2006) data are therefore quite sufficient for our purpose.

We agree to adopting a more specific, 'conservative' title. We have changed the title to: 'Stable isotope and modelling evidence for CO_2 as a driver of glacial-interglacial vegetation shifts in southern Africa'.

We have taken account of the referee's other points as listed above, in the following ways: â€” Clarified the wording in several places (including Appendix A) to stress that precipitation changes are fully accounted for in the model. â€” Included material in the Discussion clarifying the difference between the overall comparison we are making between the LGM and Holocene, and the quantitative breakdown that might be possible with higher-resolution isotopic records. â€” Removed the map based on pollen data, as also recommended by referee #2, and reduced the corresponding part of the text.

Additional minor points by this referee, regarding the labelling of axes in Figs 1 and 2 (and the overall quality of the former) and the citation of Prentice et al. (2011b), have been attended to.

Interactive comment by J.A. Collins

Collins' comments go straight to a fundamental point which we seek to address in this paper – which is the false dichotomy that exists in the literature, about the roles of

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climate versus CO₂ as controls on vegetation changes. We welcome this opportunity for clarification. Here we address the interpretations in a number of papers cited by Collins. We did not mean to deny a role for climate change (as opposed to CO₂ change) on this time scale to bring about large changes in vegetation, in Africa or anywhere else. Perhaps this will be clearer already as we have adopted a more focused title as suggested by Anonymous Referee #3. But we have also taken the opportunity to modify the text, to make quite sure that readers don't misinterpret us as saying that only CO₂ changes can be important on this time scale. We have added two new paragraphs in the Discussion to make it clear that we are not, in fact, 'ignor[ing] a large body of work which indicates that vegetation distribution has changed independently of CO₂ in the past'. Additional references have been inserted although, obviously, this is not the place for an extensive review of the subject.

We agree that our interpretation implies an overprinting of any putative 'southward shift' of the rainbelt by the CO₂ effect. Indeed the data as presented by Collins et al. (2011) don't point to any such shift. We presume that if a large enough southward shift of the rainbelt occurred, it should be evident in the data, CO₂ effects notwithstanding. It is outside our scope to assess all of the evidence that has been presented in the past several decades in favour of a southward shift of the intertropical convergence zone, and thus the rainbelt. But we are not presenting any evidence ourselves that points in this direction, either. So we have toned down our statement on the subject, and eliminated the last sentence of the relevant paragraph.

New material provided in the Discussion briefly revisits some previously published work which, we suspect, may have either contributed to or been influenced by a belief that the main driver of vegetation change (globally) between glacials and interglacials must be either climate change or CO₂ change. From an ecophysiological modelling perspective this belief is untenable. We know that the present-day distribution of the major photosynthetic pathways on land is related to precipitation and temperature, and we know the mechanistic basis. The 'crossover' temperature, above which C₄ pho-

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tosynthesis is advantageous, is modified by aridity (through the control of stomatal conductance: low stomatal conductance at high vapour pressure deficits leads to low leaf-internal concentrations of CO₂), as well as by CO₂ concentration. Furthermore, in warm-temperate climates with winter-dominant precipitation, C₃ grasses can predominate even in climates that are apparently dry and warm enough to support C₄ dominance. All of these features are represented in the BIOME4 model. We also now refer to a paper by Collatz et al. (1998) which clarifies the underlying principles.

Let's now consider the much-cited paper by Huang et al. (2001). That study contrasted two sites, one in tropical Central America, one in NW Mexico. The former showed a 'tropical' pattern with C₃ vegetation favoured in the Holocene, C₄ in the glacial. The latter showed the opposite pattern, consistent with the well-known enhancement of rainfall in SW North America during glacial times – a feature shown by the existence of huge palaeolakes, and explained in climate models as a consequence of the southward displacement of the jet stream by the Laurentide ice sheet (COHMAP Members, 1988). In this situation, it is likely that the effect of greatly enhanced precipitation in glacial times outweighed the effect of CO₂ on C₃-C₄ plant competition. Indeed, simulations using the LPX dynamic vegetation model (Prentice et al. 2011a) have succeeded in reproducing the observed vegetation shift in this region. The modelling of competition between C₃ and C₄ plants in LPX depends on almost exactly the same set of carbon and water balance equations as BIOME4. LPX simulates a large component of trees (C₃) at LGM in SW North America, where C₄ plants are dominant (and modelled as such) today.

In other words, there is no inconsistency at all between our ecophysiological modelling approach and the findings of Huang et al. (2001). Nevertheless, Huang et al. (2001) concluded their paper with rather strong statements, appearing to contradict earlier papers (by some of the same authors) in which a major role had been ascribed to CO₂ in driving glacial-interglacial vegetation shifts. We have briefly explained this key point. We now cite Huang et al. (2001) and explain how its results have been over-interpreted.

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Here, but not in the text (to avoid unwarranted lengthening), we address some of the other papers cited by Collins.

Vidic and Montañez (2004) described a situation in the Chinese loess plateau, where C3 vegetation was more abundant during the (glacial) periods of loess deposition. They interpreted this as indicating dominant control by temperature. This too is not in conflict with our modelling approach, because temperature effects on the C3/C4 plant balance are explicitly modelled in BIOME4 and we would expect temperature effects to be important in glacial-interglacial vegetation changes near to the present-day crossover temperature.

The results presented by Agrawal et al. (2012) are less clear because their isotopic analyses from soil organic matter and carbonates gave inconsistent results. Furthermore, we would not expect to see effects of CO₂ changes during the period of very slight variability in CO₂ that was studied in this paper. The paper nevertheless provides some indication of variations in the C3/C4 plant balance, presumably reflecting changes in aridity, as the authors suggested. Aridity is one of the major controls on the distribution of C3 and C4 plants, whose effects can be seen in spatial distributions today. They are included in the BIOME4 model.

The paper we cite by Sinninghe Damsté et al. (2011) indeed presents evidence of vegetational effects of the Younger Dryas, which obviously cannot be attributed to changes in CO₂. This paper recognizes both climate and CO₂ effects and while it supports a major role for the latter, it certainly does not ignore the former. We now cite this paper for what it shows about the Younger Dryas, as well as its conclusion regarding CO₂ effects.

Collins goes on to note that several authors have used the C3/C4 plant balance directly as an indicator of precipitation changes. However, this does not mean they were right to do so! The two papers by Castañeda et al. (2007, 2009), for example, appear to simply ignore CO₂ effects. This is not consistent with current understanding.

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We wish to stay out of the arguments concerning the controls of C4 plant expansion during the Miocene (Huang et al. 2007) although we note that Huang et al. (2001) – about which see our remarks above – is cited as evidence against the involvement of CO₂ changes, although the environment and timescales considered are very different.

More intriguing is the paper by Schefuß et al. (2003), which attributed antiphasing of C4 plant abundance and tropical SSTs on 41 ka and 100 ka orbital timescales to variations in aridity (caused by low evaporation from the sea surface; leading to conditions favouring C4 plants), and not CO₂. The record analysed by Schefuß et al. (2003) extends back in time from about 400 ka over many previous glacial cycles. It is important to recall that at the time when this paper was published, there was no record of atmospheric CO₂ extending back beyond 400 ka. Schefuß et al. (2003) tried briefly to rule out CO₂ as the key agent, but this part of their paper is not its greatest strength. Now that there is a detailed record of CO₂ back to 800 ka, it would be worth revisiting this topic, particularly as there appears on inspection to be some degree of coherent antiphasing between Schefuß et al.'s (2003) C4 reconstruction and the EPICA record of atmospheric CO₂ concentration during the last 400 ka of their record.

We now move on to consider Collins' citation of a number of papers showing vegetation changes in Africa during the Holocene, and specifically between the mid- and late Holocene. We will not consider these one by one, and we are aware of others (see e.g. the review by Prentice et al. 2000 and references therein). Instead we have modified our Introduction and Discussion sections so as to be careful not to overstate the case for there being little vegetational change during the Holocene. Several papers cited (including Collins et al. 2011) show that such changes did occur, in southern Africa as elsewhere, even if the glacial-interglacial changes were more dramatic. Indeed, by choosing coarse time slices (Collins' last paragraph notes that our Holocene time slice includes sediments from the mid-Holocene) we have intentionally focused on the LGM-interglacial difference, and thus on a time scale where CO₂ effects could in principle have an influence. We have made this clear in our revision.

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We part company from Collins where he suggests that BIOME4 might be insensitive to climate change effects, and oversensitive to CO₂ effects. On the first of these suggestions, the same model, or its close precursor BIOME3, have been used – again, driven by outputs from climate models – with no change in CO₂, to mimic vegetation changes between the mid-Holocene and pre-industrial time. Large changes have been shown, consistent with those shown by palaeoecological data (e.g. Kaplan et al. 2003). On the other hand, previous work with these models, and more recent work with LPX, have demonstrated correspondence between modelled biome distribution (particularly the extent of forest cover) and pollen-derived biome shifts between LGM and Holocene at a global scale, when (and only when) CO₂ effects are taken into account (Harrison and Prentice 2003, Prentice et al. 2011a). Collins cites apparent disagreements between the African LGM pollen data and the biome simulation (tropical forest recorded at sites modelled as non-forest) but this is not accurate – there are modelled forest refugia shown in Fig. 3 in the region in question. Thus the pollen evidence does not support the idea that the CO₂ effect is overestimated by the model. Comparison with the simulation at pre-industrial CO₂, however, makes clear that the ‘climate-only’ approach is not realistic for tropical Africa at the LGM, because the simulated tropical forest area then increases, an obviously unrealistic result whatever the data source.

We finally turn to the core issues of disagreement.

“ Collins states that ‘a re-interpretation of Collins et al. (2011) is not necessary’. Collins et al. (2011) based their argument on an interpretation of isotopic evidence which ignores the effect of CO₂. But our results show that the effect of CO₂ for this timescale and region was large. Therefore, we contend that the results of Collins et al. (2011) need to be re-interpreted. We have made minor changes to the way in which we express this conclusion, but the conclusion is inescapable.

“ Collins states ‘The argument that CO₂ alone controls C3-C4 vegetation type is ... not explicitly evident ... The vegetation contraction could easily be a response to a combination of ... climate and CO₂ ...’ On the contrary: we have shown that the

vegetation contraction cannot be explained by climate change at all – indeed, the simulation with pre-industrial CO₂ shows an expansion of rainforest, in direct conflict with the available evidence.

Collins also states here that ‘The relative magnitude of the effects of precipitation, CO₂ and temperature . . . is not discussed’. This appears to be a separate point, which we have addressed in our response to Referee #3 regarding ‘quantification’. Of course it would be possible to separate precipitation and temperature effects in the model but it would not be helpful, as their combined effect is shown to be in the wrong direction to account for the observations.

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