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ÉCLAIRE

Effects of Climate Change on Air Pollution Impacts and Response Strategies for European Ecosystems

Seventh Framework Programme

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Report on ensemble application of DGVMs and DSVMs

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PP	Restricted to other programme participants (including the Commission Services)	☐
RE	Restricted to a group specified by the consortium (including the Commission Services)	☐
CO	Confidential, only for members of the consortium (including the Commission Services)	☐

1. Executive Summary

In ECLAIRE work package 14, several land surface and dynamic global vegetation models (DGVMs) have been used to simulate the impacts on ecosystems of various scenarios of climate change, air quality (exposure to tropospheric O_3 and CO_2) and deposition of nutrients on plant productivity and nutrient cycling. The specific objective of deliverable 14.7 is to report on the result of a modelling experiment performed with an ensemble of four DGVM (LPJ-Guess, OCN, JULES, CLM). These models have been further developed within the framework of ECLAIRE to simulate the impact of O_3 and N deposition on the ecosystem carbon and water budget as summarised in D14.3. The results of the modelling experiment described in D14.4 have been harmonized and analysed to produce a summary of the estimated impacts at European scale. Results show a clear convergence of model predictions concerning the fertilization effect of N deposition, but with different sensitivities between models (large in CLM, limited in OCN). In parallel, all models show the detrimental effect of O_3 exposure on plant productivity and transpiration. The interaction between O_3 and N deposition on the functioning of terrestrial ecosystems proved to be rather complex to model and to interpret. Results show that the interaction term can be either positive or negative according to the area of interest and vegetation type, probably due to the effect of ancillary drivers like water availability. In summary, this analysis represents the very first attempt to simulate the combined effect of climate and multiple air pollutants on the terrestrial C budget and clearly highlights the complexity of the underlying processes and the need for comprehensive modelling frameworks for predicting future trajectories of the terrestrial carbon budget.

2. Objectives:

The objectives of work package 14 were to assess the effects of combined air pollution and climate change scenarios on productivity and ecosystem C/GHG balance for forests, semi-natural and agricultural systems.

This deliverable 14.7 reports on the ensemble application of DGVMs (dynamic global vegetation models) and the inter-comparison of model results on net primary production (NPP), in combination with evapotranspiration (ET) and water use efficiency (WUE), in response to pollution scenarios for the period 1901-2050. The only DSVM included in Eclaire (EUgrow-VSD+) gives other model outcomes and was thus not part of this inter-comparison, but its results are reported in Del 14.8.

Work package 14 has resulted in a database describing ensemble runs of the 4 DGVMs (LPJ-Guess, further denoted as LPJ, OCN, JULES, CLM) on common climate and air pollution scenarios. Comparison between these models and scenarios shows where these models provide more robust projections and where some of the largest uncertainties lie.

3. Activities:

MODELS AND DATA

A number of different modelling groups have contributed to work package 14. In total, these groups have provided simulations for 4 vegetation models (LPJ, OCN, JULES, CLM), under 4 different scenarios of atmospheric conditions. These scenarios, and the different atmospheric conditions which they represent, are described in table 1.

Name	Climate	CO_2	N deposition	O_3
S0	1901-2050	1901-2050	1901-2050	1901-2050
S1	1901-2050	1901-2050	1901-2050	1901
S2	1901-2050	1901-2050	1901	1901-2050
S10	1901-2050	1901-2050	1901	1901

Table 1. Definitions of the 4 scenarios used with respect to transient atmospheric conditions.

As mentioned in previous deliverable reports, not all models have been able to run under all scenarios. Table 2 describes the different model-scenario combinations that have been simulated.

Model	S0	S1	S2	S10
CLM	Yes	Yes	Yes	Yes
LPJ	No	Yes	No	Yes
JULES	No	No	Yes	Yes
OCN	Yes	Yes	Yes	Yes

Table 2. Vegetation models and scenario combinations analysed in WP14.

Essentially, the LPJ model is not yet able to simulate the effect of O_3 and so can only be used to investigate the effect of N deposition on vegetation. At the same time, the JULES model is not yet able to simulate the effect of N deposition on full transient model runs, and so can only be used to assess the effect of O_3 on vegetation. Two versions of JULES are used, one with high sensitivity to O_3, and the other with low sensitivity to O_3. This leads to 4 JULES datasets, as the scenarios S2 (N fixed at 1901 levels, transient O_3) and S10 (both N and O_3 fixed at 1901 levels) are applied to both model versions.

Briefly, the effects of transient N deposition for each model (where possible) are assessed as the difference between scenarios S1 and S10 (transient N vs fixed N, both with fixed O_3). This comparison is possible with CLM, LPJ and OCN models. The effect of O_3 is assessed as the difference between scenarios S2 and S10 (transient O_3 vs fixed O_3, both with fixed N), possible with CLM, JULES (twice, with high and low sensitivity versions) and OCN models. The effects of both N and O_3 together are assessed as the difference between model simulations based on scenarios S0 and S10 (both N and O_3 transient vs. both N and O_3 fixed). This is only possible with CLM and OCN models.

The influence of N *alongside that of O_3* (that is, already given that of O_3, or, alternatively, the combined influence of N and O_3 over and above that of just O_3) is assessed as the difference between scenarios S0 and S2 (that is, the difference between simulations based on transient N and O_3, and simulations using fixed N and transient O_3). The influence of O_3 *alongside that of N* (that is, already given that of N, or, alternatively, the combined influence of N and O_3 over and above that of just N) is assessed as the difference between scenarios S0 and S1 (that is, the difference between simulations based on transient N and O_3, and simulations using fixed O_3 and transient N). Again, these comparisons are only possible with CLM and OCN models.

DGVMs can output many different variables describing (changes in) the state and functioning of vegetation and soils. For the purposes of this report we focus on:

- **Net primary productivity** (NPP) representing the difference between the gross amount of carbon fixed by the vegetation, and the amount of carbon respired by the vegetation (positive values indicate the conversion of more carbon from the atmosphere into plant material, on balance, than from vegetation back into the atmosphere);
- **Evapotranspiration** (ET) representing the cumulative amount of water that evaporates from the land surface and the amount of water transpired by the plant through the stomata to enable the leaf level exchange of gases and ultimately photosynthesis;
- **Water use efficiency** (WUE) here defined as the gross primary productivity divided by the total evapotranspiration, representing the amount of carbon fixed by the vegetation for a 'standardised' amount of water used by the vegetation.

All model outputs were harmonised to have the same units, and describe the same time period.

4. Results:

COMPARISONS OF SCENARIOS AND MODELS

Figure 1 shows the European annual average of NPP as simulated by each of the models for each of the scenarios (where available). A consistent pattern over all of the models and scenarios shows NPP increasing over this period (although CLM under scenarios S0 (transient N and O_3) and S2 (fixed N, transient O_3) show a decline over the first part of the period, and only then a subsequent increase in NPP).

CLM simulations with transient N is clearly separate from the other scenarios, while the results with constant N and O_3 and transient N and fixed O_3 exhibit a comparable but different pattern over the time period as compared to the scenarios with either transient O_3 only or both transient N and O_3. This suggests that CLM is sensitive to transient patterns of N deposition and atmospheric O_3. LPJ and JULES simulations show separation between scenarios, albeit to a lesser extent than for CLM, but the scenarios *within each model* show similar patterns of response over the duration of the simulation. This suggests that LPJ and JULES are sensitive to the effects of N deposition and O_3 (respectively), but that the models still impose similar overall patterns and are therefore not as sensitive as CLM. OCN scenarios are not well separated, and each shows a consistent response pattern, suggesting that OCN may be the least sensitive of the four models.

Figure 2 shows the effects of each of the atmospheric drivers (identified as the differences between scenarios within each model as described above) for European annual average NPP. CLM, LPJ and OCN all show the positive effect of N deposition on NPP (black lines, differences between scenarios S1 and S10 are always positive). CLM, JULES and OCN all show the negative effect of O_3 on vegetation (red lines, differences between scenarios S2 and S10 are always negative; JULES high sensitivity always shows a more negative effect than JULES low sensitivity, as would be expected). The joint effect of N and O_3 together is more subtle. CLM and OCN both show this influence to be closer to zero. However, whilst OCN shows this is consistently varying around the zero line, CLM shows a more systematic negative deviation during the first three quarters of the time period, followed by a more positive deviation over the last quarter of the period. Note that this is the influence of the varying (transient) levels of N deposition and O_3, rather than the specific (combined) effect of N and O_3 itself.

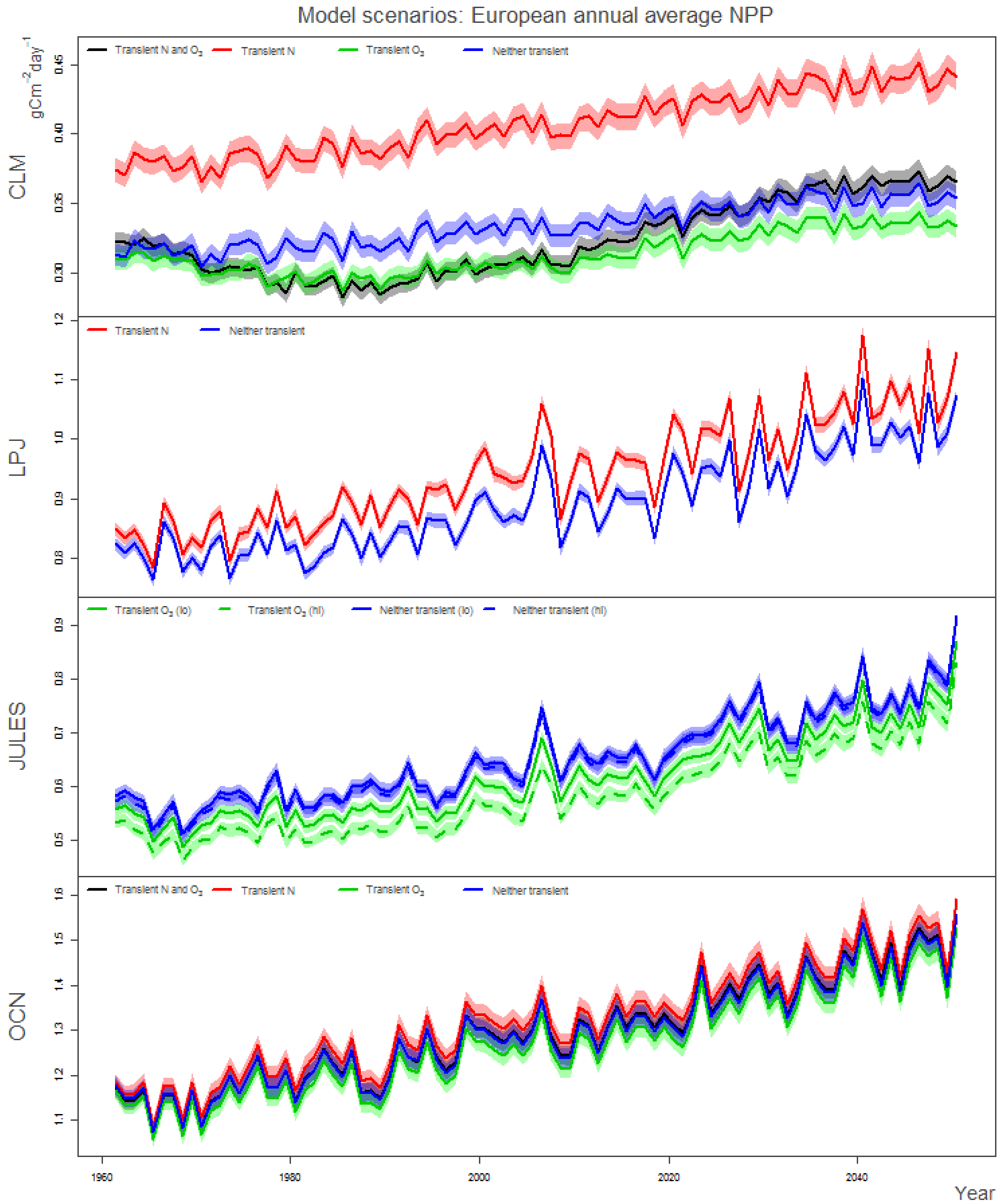

Figure 1. European annual average NPP for each of the scenarios, uncertainty indicated by ± 2 s.e., by model.

The effect of N given O_3 is represented by the blue lines in figure 2 (only present for CLM and OCN models). This is close to zero for much of the time for CLM, which would suggest that when O_3 is accounted for (or, 'allowed' to influence the simulated vegetation), N deposition doesn't have a very large positive effect (as it otherwise has when N deposition is considered *without* O_3). The sum effect, given O_3 whether with or without N, is reduced vegetation NPP. To the contrary, OCN's response for N given O_3 is much more positive, suggesting that regardless of whether O_3 is present and reducing vegetation NPP, the addition of N will serve to increase that NPP. Results from OCN seem to be more in accordance than those from CLM with experimental evidence emerging from the ECLAIRE project.

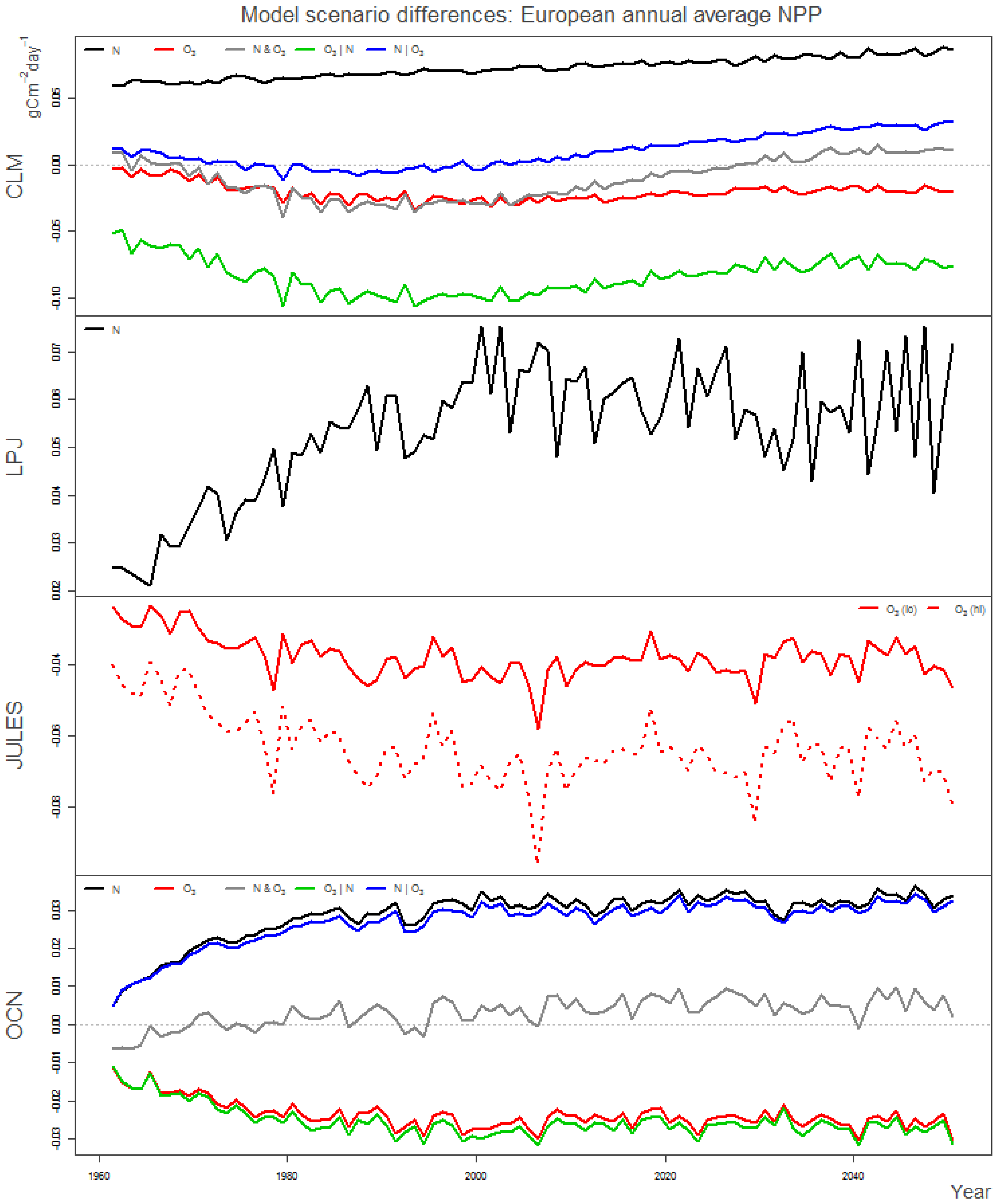

Figure 2. Effects of individual and combined atmospheric drivers on European annual average NPP by model. The effects of the different drivers is calculated as: N = S1-S10; O3=S2-S10; N&O3=S0-S10; O3|N=S0-S1; N|O3=S0-S2.

A similar effect is seen with these models' simulated effect of O_3 given N (the green lines in figure 2). CLM shows a very negative effect of O_3 (in combination with N). What this suggests is that, where there is just the influence of N, the response would be largely positive (as seen for just N), but the presence of O_3 dominates, and inhibits this otherwise positive response. It is not that the influence of O_3 given N is stronger than the influence of just O_3, but rather that O_3 and N do not influence the model individually and independently. N does not increase NPP if there is O_3, and O_3 reduces NPP whether there is N or not. The interaction appears to be asymmetric.

OCN, on the other hand, shows a negative effect for O_3 given N, much the same as the effect of O_3 individually. What this suggests is that the influence of O_3 is reducing the positive influence of N, much as the influence of O_3 by itself reduces the NPP of OCN simulations without N. The effects of N and O_3 in OCN appear to counteract each other. The effect of O_3 appears to be the same whether there is N deposition or not, as the effect of N appears similar whether there is O_3 or not. There is no obvious interaction between N and O_3, as found in experimental work by Mills et al. in Component 3. It is worth noting that the combined effect of N and O_3 (given by S0-S10) is rather similar in CLM and OCN.

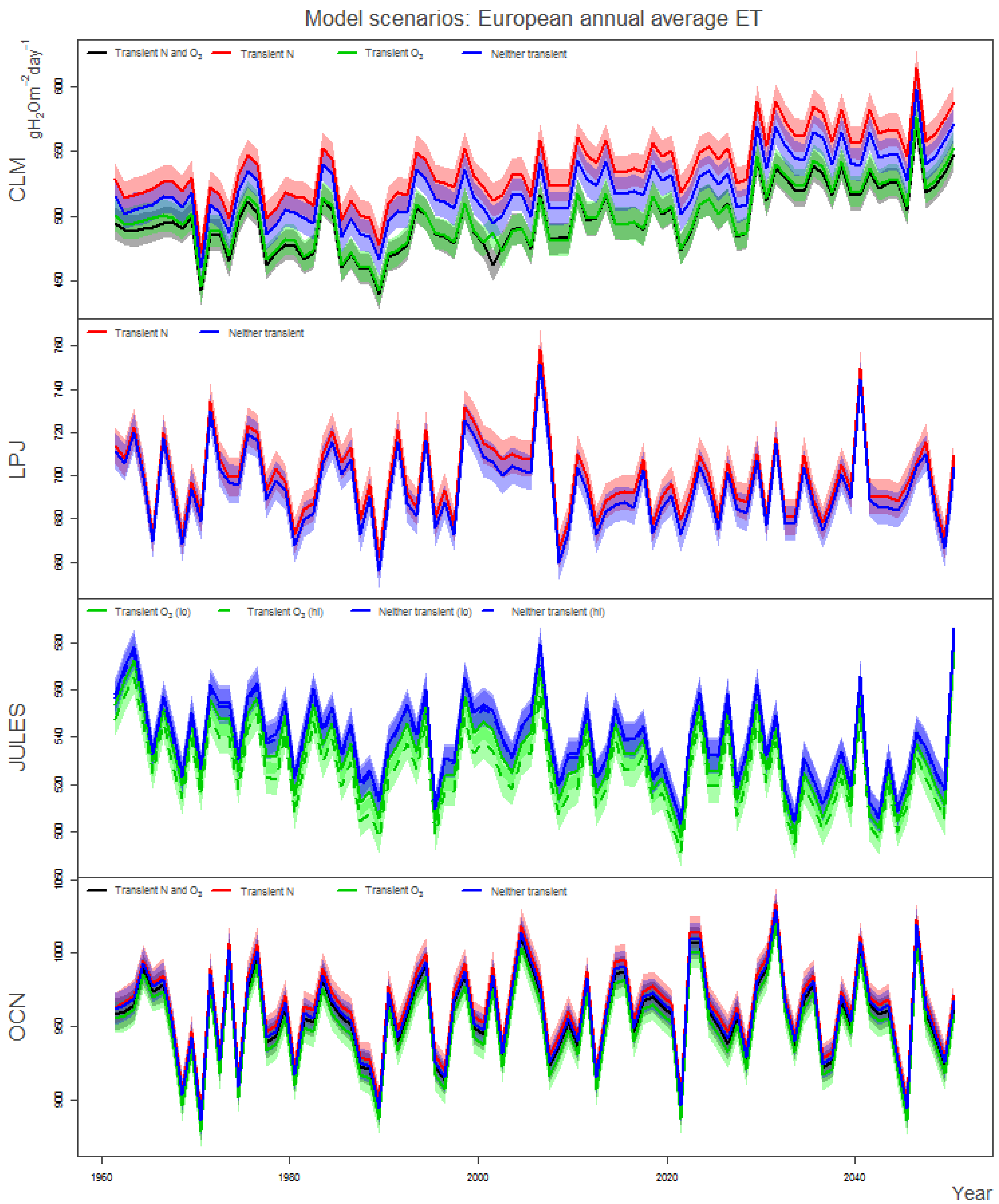

Figure 3. European annual average evapotranspiration for each of the scenarios, uncertainty indicated by ± 2 s.e., by model

Figure 3 shows the response of European annual average evapotranspiration for each of the models and scenarios. Again, CLM separates the scenarios to a larger degree than any of the other models, but compared to NPP the scenarios are less clearly separated considering the much larger standard error of the European average. What's more, whilst these scenarios are somewhat separated, the pattern of evapotranspiration over the time period is clearly similar for all the scenarios. There is a lot of overlap between scenarios for the LPJ and for OCN, suggesting that N deposition and O_3 do not largely affect evapotranspiration in these models (perhaps N deposition increases evapotranspiration, but the effect is marginal). JULES exhibits some limited scenario separation (O_3 reducing evapotranspiration), but the pattern of evapotranspiration over the time period is similar for all scenarios (and model versions).

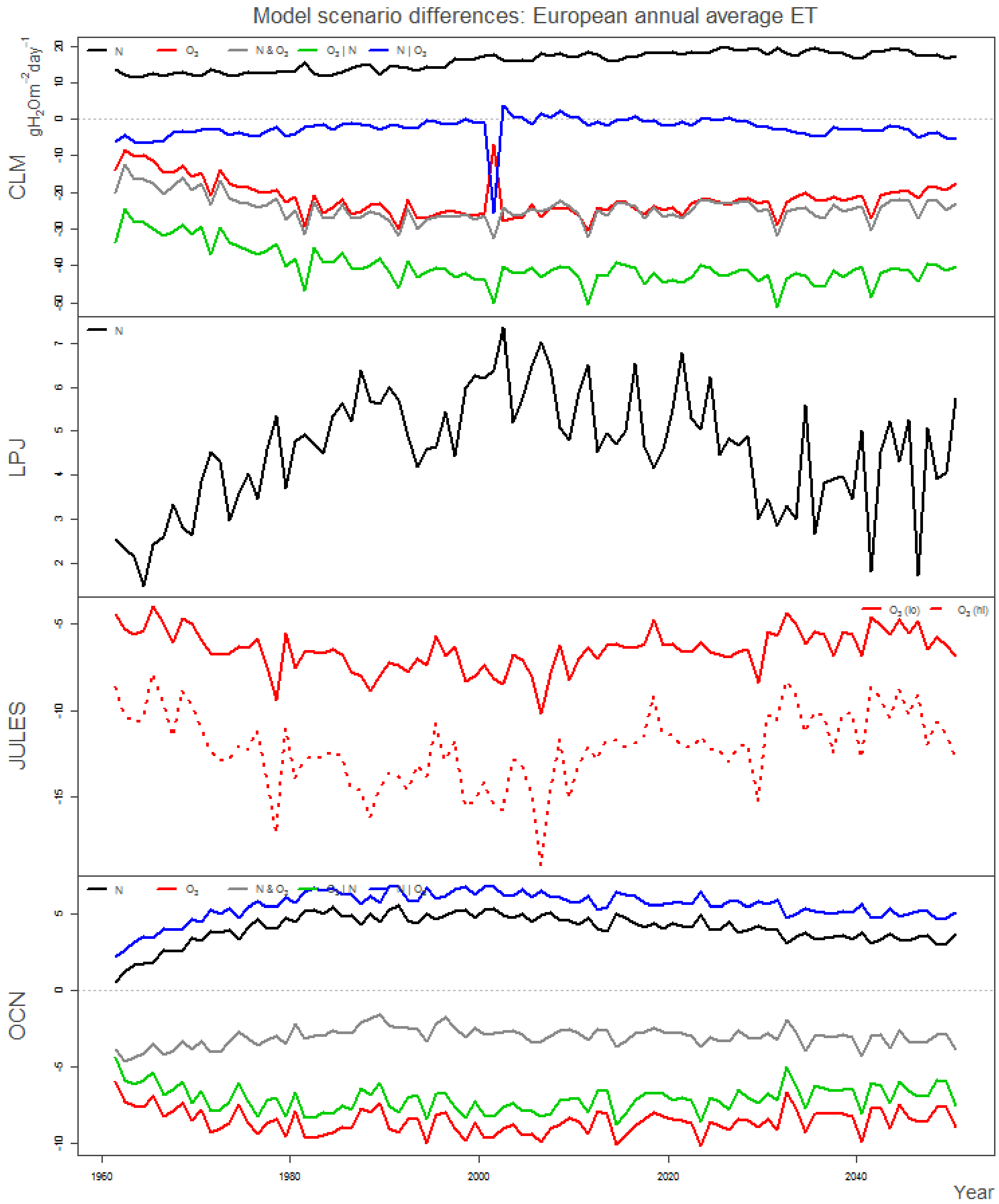

Figure 4. Effects of individual and combined atmospheric drivers on European annual average evapotranspiration, by model. The effects of the different drivers is calculated as: N = S1-S10; O3=S2-S10; N&O3=S0-S10; O3|N=S0-S1; N|O3=S0-S2.

Figure 4 shows the effects of individual and combined atmospheric drivers (identified as the differences between scenarios, as described above). These effects on evapotranspiration in CLM are largely similar to those identified for NPP in CLM. N increases and O_3 decreases evapotranspiration. N and O_3 together reduce evapotranspiration much as O_3 alone does. The effect of N given O_3 is close

to zero for the entire 90 years (there is almost no difference between scenario S0 with transient N and O_3, and scenario S2 with fixed N and transient O_3). The effect of O_3 given N is again a larger decrease, because the model would otherwise simulate a much larger evapotranspiration with the added N.
The effects of these drivers on evapotranspiration in the other 3 models are largely the same as for NPP. N deposition increases evapotranspiration in LPJ and OCN. O_3 reduces evapotranspiration in JULES and OCN. The effects of N given O_3 and O_3 given N are again somewhat symmetrical in OCN, except this time the effect of O_3 seems stronger than the effect of N.

Figure 5 shows the European annual average water use efficiency for each model and scenario.

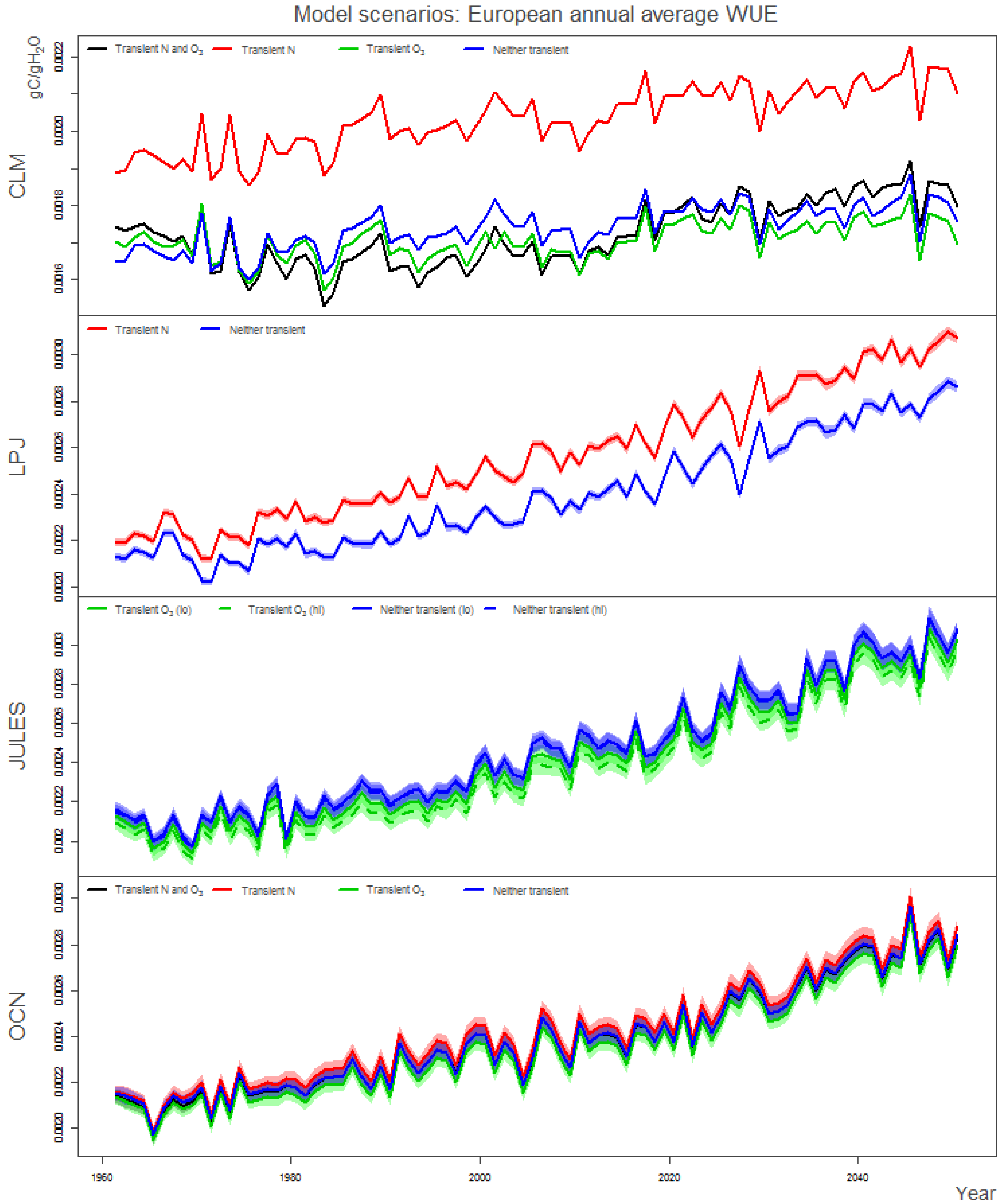

Figure 5. European annual average water use efficiency for each of the scenarios, uncertainty indicated by ± 2 s.e., by model

As for the previous variables there is a clear separation between CLM scenarios, and an increasing trend mostly due to the increasing CO_2 concentration over the 90 year time period. The scenario with N deposition leads to higher water use efficiency. LPJ shows a good separation between scenarios S1 and S10 although their patterns across 90 years are very similar, with higher values for the N deposition case. JULES shows slightly lower water use efficiency with scenarios that include transient O_3, but these are not separated from scenarios with neither N nor O_3. N deposition shows very slightly higher water use efficiency, and O_3 very slightly lower water use efficiency, but there is no real separation between the scenarios in OCN, and patterns are almost identical for all scenarios.

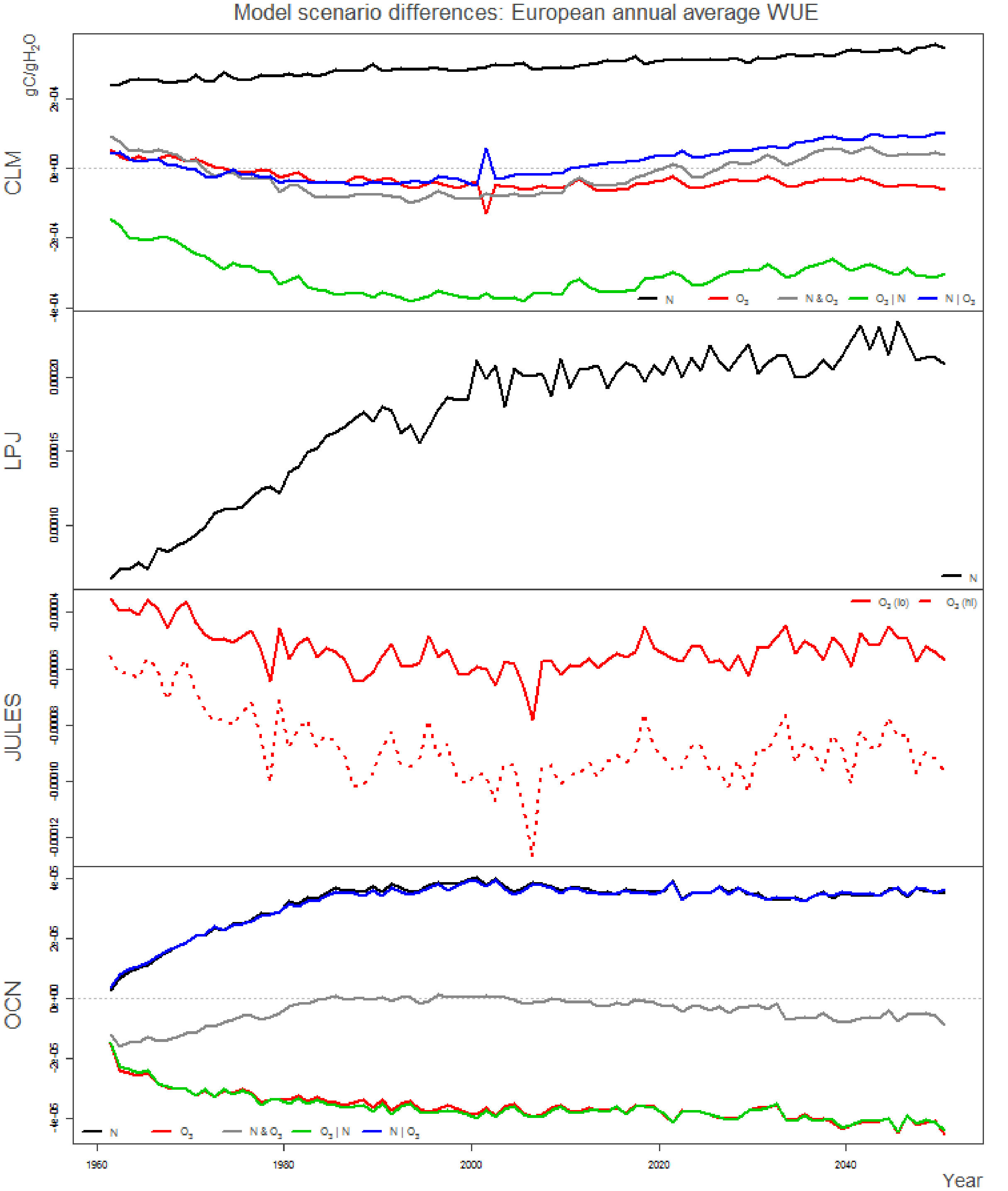

Figure 6. Effects of individual and combined atmospheric drivers on European annual average water use efficiency, by model. The effects of the different drivers is calculated as: N = S1-S10; O3=S2-S10; N&O3=S0-S10; O3|N=S0-S1; N|O3=S0-S2.

In terms of the individual and combined effects of atmospheric drivers on water use efficiency in these models (figure 6), there is a clear pattern in CLM. The effect of N deposition is increasing water use efficiency, and the effect of O_3 given this N increase is to inhibit and reduce water use efficiency (as for NPP and evapotranspiration). OCN again shows symmetric and counteracting effects of N given O_3 and O_3 given N. These effects are again much smaller than for the other models.

DIFFERENCES BETWEEN MODELS AND SCENARIOS SIMULTANEOUSLY

Rather than comparing European averages in models and scenarios, it is also possible to compare all models and scenarios together simultaneously. This allows us to see how they differ, and perhaps to gain an understanding of how N and / or O_3 really influence the different variables simulated by these models.

For each model-scenario combination there is a matrix (number of grids by the number of times) of simulated values for each variable. The similarity between each model-scenario combination and the others can be assessed using the RV coefficient (Robert & Escoufier 1976), a measure of covariance (i.e. similarity) between entire matrices rather than just between rows or columns of 1 matrix.

Once the covariance between all possible pairs of model-scenarios has been calculated, these must be converted into a 'dissimilarity' or distance measure, and formed into a distance matrix. Multidimensional scaling (MDS, e.g. Gower 1966) can be applied to this distance matrix, and we end up with a reduced dimensional representation of the dissimilarity between model-scenario combinations. When this method would be applied to a matrix of Euclidian distances, it would result in a reduced dimensional space identical to that resulting from a principal components analysis.

In this particular case, two adjustments are made. Firstly, it is usually obvious for any data matrix which are the samples (usually the rows) and which are the variables on which those samples are measured (usually the columns). However, with these model-scenario matrices both rows *and* columns can be considered samples and variables, and the RV coefficient is sensitive to which of these is actually used in its calculation. In fact, an analysis considering the rows as samples inherently characterises geographic variation, whilst one considering the columns as samples characterises the temporal variability in the dataset (these are not the same because the matrices are not double-centered). For this analysis we consider the columns as samples, in order to identify the similarity between model-scenarios with respect to the 90 years. Secondly, MDS requires a distance matrix, and so we convert the RV coefficient (which is 0-1 delimited) to a distance by subtracting it from 1.

Once the model-scenarios are placed in the principal coordinates space, we will be able to see from the configurations of model-scenarios how these atmospheric drivers influence vegetation by seeing which lead to more similar outcomes (indicated by which model-scenarios lie near each other in the space). For example, does scenario S0 (transient N and O3) typically lie between scenarios S1 and S2, or perhaps nearer to one than the other? Is a scenario for one model more similar to different scenarios of another model? etc.

Figure 7 shows that for NPP, model-scenarios are clustered in this space by model, that is, they are much more similar by model than by scenario. This suggests that comparisons of NPP between model-scenarios are still overwhelmed by differences in the model, rather than by differences in the scenarios. OCN and LPJ models lie very near each other, suggesting that they lead to similar model output. All the JULES scenarios lie near each other, away from all the other models. Only CLM scenarios appear well spread out, suggesting that this model is more sensitive to the particular atmospheric drivers represented by the different scenarios.

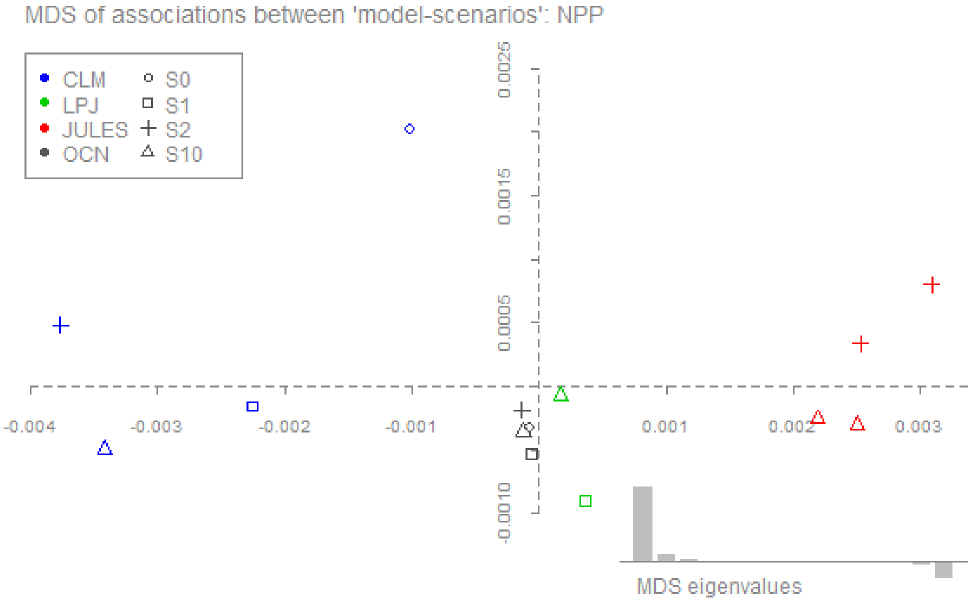

Figure 7. MDS of NPP-based 'RV distances' for all models and all scenarios.

A similar pattern is evident in figure 8, in the MDS based on evapotranspiration. Model-scenarios are clustered by model again, although now LPJ lies nearer to JULES, suggesting that the representation of evapotranspiration in the 2 models is more similar. OCN appears especially clustered, suggesting little variation between scenarios (as also suggested by the European annual average graphs). Mostly, this MDS appears to contrast CLM with the other models (even though the CLM scenarios appear less spread out than for NPP).

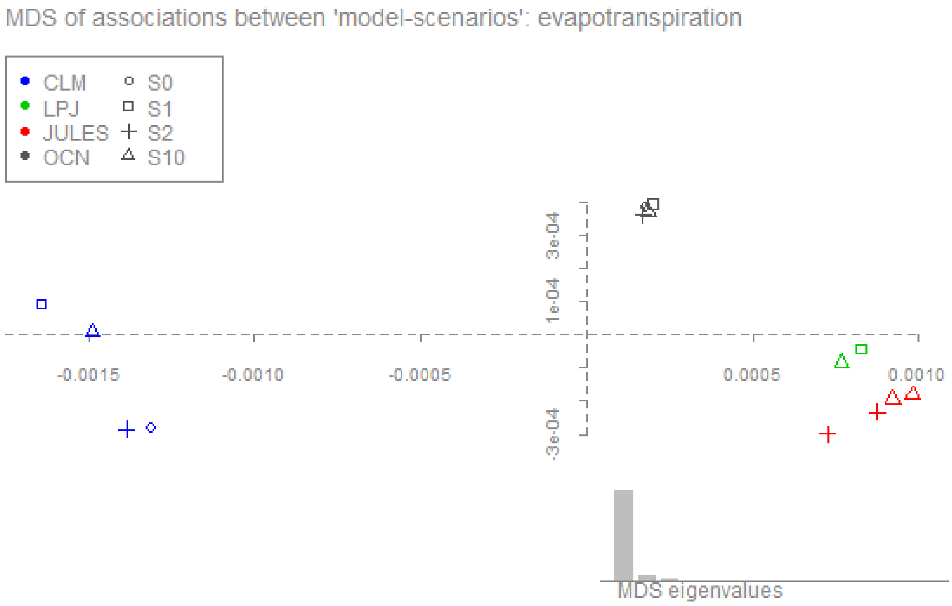

Figure 8. MDS of evapotranspiration-based 'RV distances' for all models and all scenarios.

Variation between CLM scenarios in the MDS based on water use efficiency (figure 9) is overwhelming, and hiding, any variation in the other models. This is probably due to the independent parameterization of photosynthesis and stomatal conductance effect of O_3 deposition in CLM.

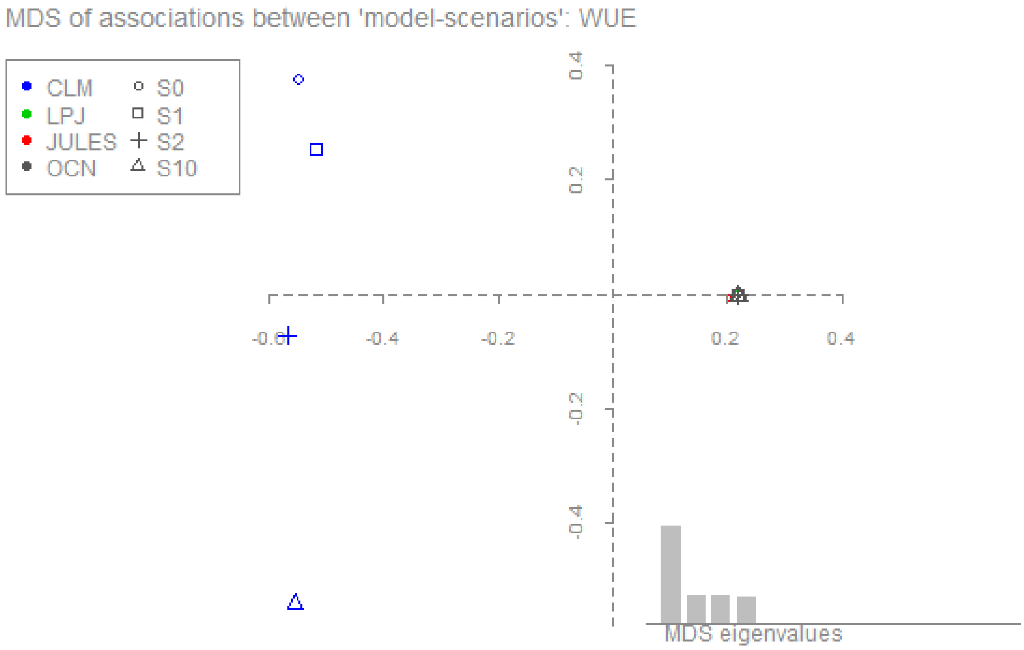

Figure 9. MDS of water use efficiency-based 'RV distances' for all models and all scenarios.

THE INTERACTION BETWEEN N AND O_3

Only two of the models assessed in work package 14 are capable of simulating the influences of N deposition and atmospheric O_3, and it is apparent that these 2 models represent the interaction of N and O_3 in very different ways. How can we characterise this interaction?

If the effect of O_3 and N were additive then model output from scenario S0 (with both transient N and O_3) would equal the average of model output from scenarios S1 and S2 (transient N and fixed O_3, and fixed N and transient O_3, respectively). One possible way to characterise a more complex interaction between N and O_3 is therefore as the deviation of S0 from the average of S1 and S2:

$$interaction = S0 - \frac{S1 + S2}{2}$$

This is possible for both CLM and OCN models. Figure 10 shows this deviation as grey bars, based on model output for NPP. (Note, annual average NPP is calculated for each grid cell for each year, this deviation calculated for each grid cell, and then the European average calculated for each year).

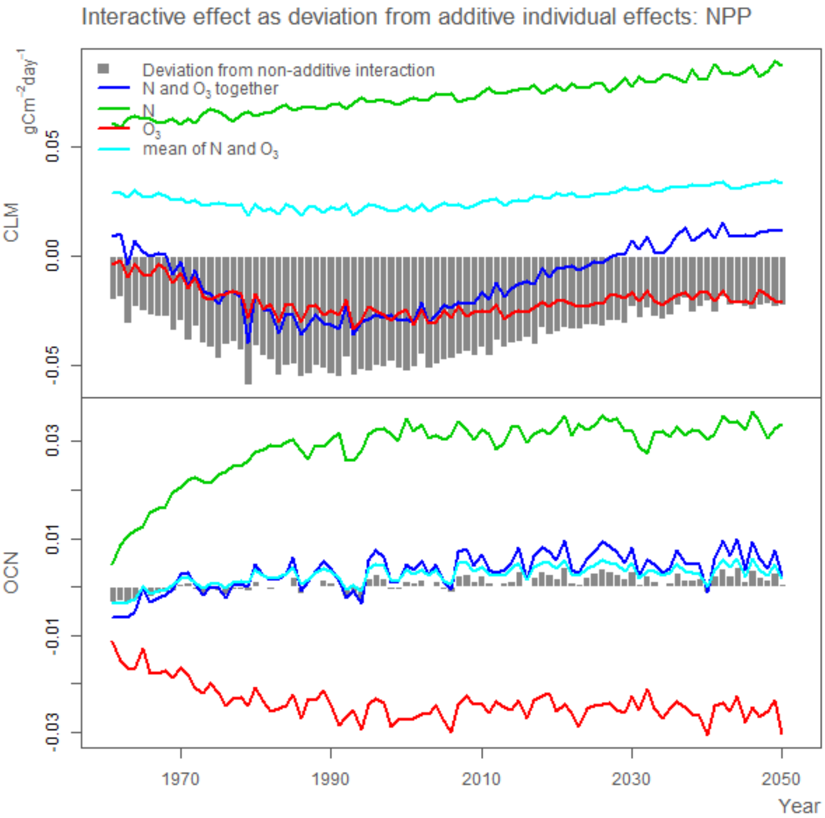

Figure 10. Deviation from additive interaction between N and O_3 based on NPP.

In the top panel of figure 10 (for CLM) the individual effect of N is shown as the green line, whilst the individual effect of O_3 is shown as the red line. The average of these, what we would expect if there were no interaction between N and O_3, is shown as the cyan line. The difference between no interaction, and what is actually found in scenario S0 (simulating transient N and O_3 together, the blue line) are shown as grey bars (one for each year). These are consistently negative, showing that there is a consistent negative effect in this interaction (which was also suggested by earlier interpretation). For OCN, these bars are almost consistently zero. That is, the interplay between N and O_3 in OCN is strongly characterised as an additive effect with no interaction.

To explore if the interaction between the two factors varies spatially we map the deviation from simple additive interaction for each gridcell (as the 1961-2050 average deviation for each gridcell) in figure 11.

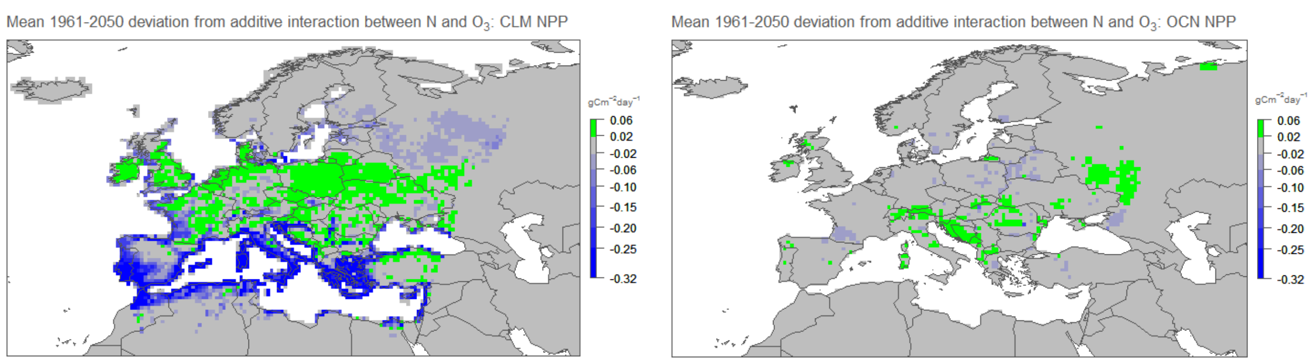

Figure 11. Maps of the deviation from additive interaction between N and O_3 for CLM and OCN NPP.

CLM shows a strong negative deviation from no interaction in much of southern Europe, and in fact many other coastal areas. However, there is also consistent positive deviation in much of central (inland) Europe, and this is obscured when the European average is calculated. This suggests that there is also positive interaction in some places, where O_3 does not completely inhibit the positive N effect, and in fact the resulting NPP is greater than the average of individual N and O_3 simulations. Note, though, that this positive effect is much smaller than the predominant negative effect shown in blue.

The geographic distribution of deviation from no interaction for OCN is much less extreme. There are only a few places with slight negative effect and a few places with slight positive effect, with only slight similarity to the distribution found for CLM. The overall average would indicate no effect.

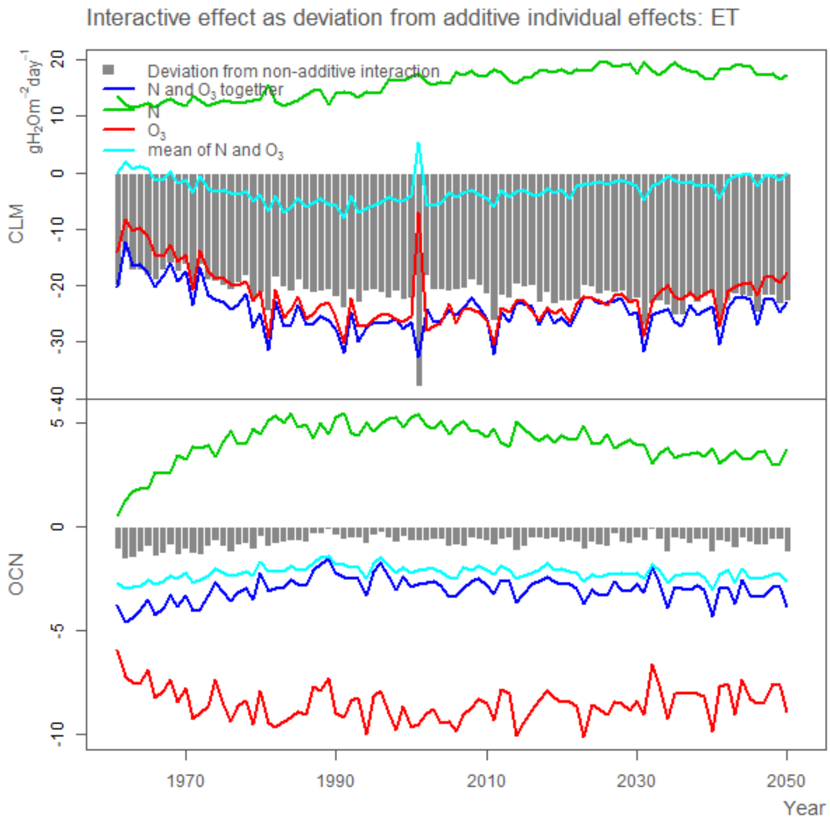

Figure 12. Deviation from additive interaction between N and O_3 based on evapotranspiration.

Figure 12 shows the deviation from simple interaction calculated for evapotranspiration, and figure 13 shows the maps of these deviations. Again, CLM shows a strong negative deviation from simple interactive effect (where the influence of N and O_3 together appears even more similar to that of O_3 alone). The map of these deviations (Figure 13) for CLM shows negative deviation for the majority of Europe (blue). The few positive (green) gridcells show little geographic consistency.

The interaction between N and O_3 with respect to evapotranspiration in OCN is slightly more complex than for NPP, with the interaction being consistently, albeit less strongly, negative. The mapped deviation values for OCN evapotranspiration in figure 13 show consistent (very slight) positive deviations across the Balkan region of SE Europe, rather than consistent negative deviation.

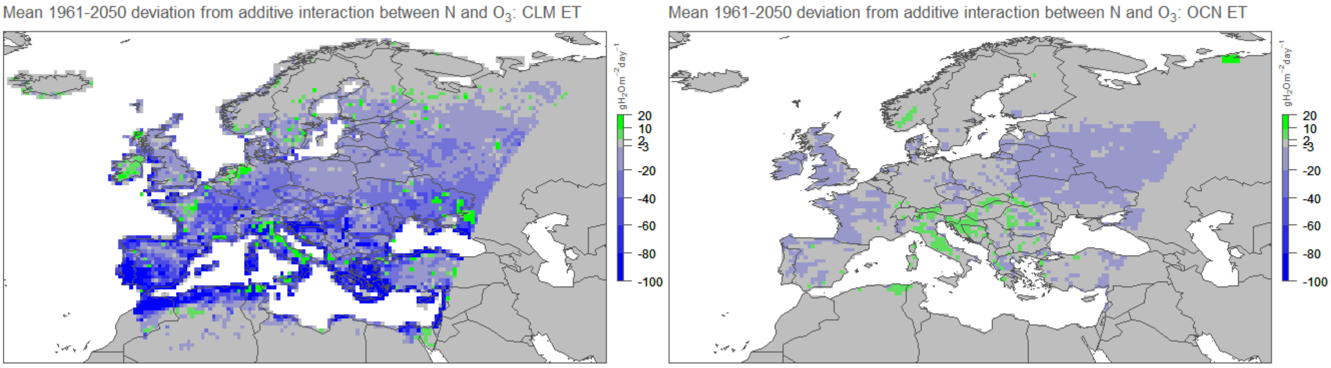

Figure 13. Maps of the deviation from additive interaction between N and O3 for CLM and OCN evapotranspiration.

Figure 14 shows the deviation from no interaction calculated for water use efficiency, and figure 15 the maps of these deviations.

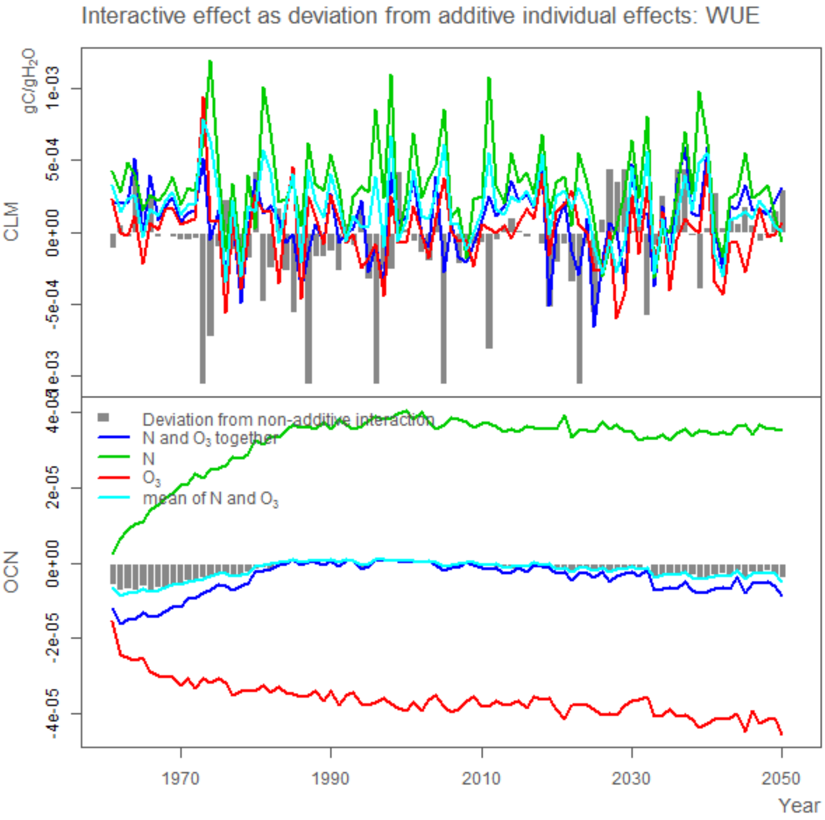

Figure 14. Deviation from additive no interaction effects between N and O3 based on water use efficiency.

There is little pattern in CLM deviations from simple interaction in figure 14, but this might be expected given the patterns that were seen in figure 6. Some years are negative, some are positive, with little consistency between them. However, the mapped deviations in figure 15 show a different, more consistent pattern, where water use efficiency shows positive deviation from simple interaction across much of central Europe, as shown for NPP. Southern Europe is again more strongly negative, with no consistent pattern for northern Europe.

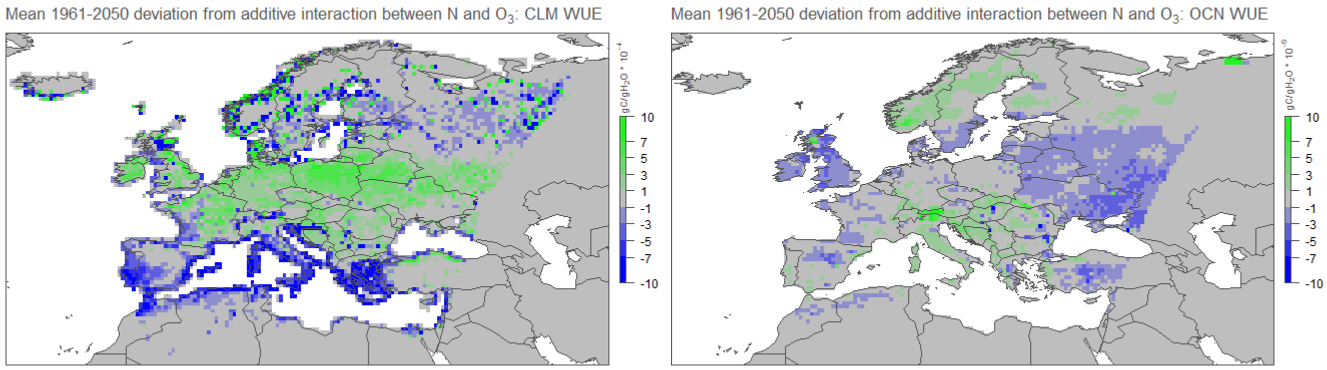

Figure 15. Maps of the deviation from additive interaction between N and O_3 for CLM and OCN water use efficiency.

OCN shows almost negligible deviation from no interaction (in fact, the scale had to be changed by an order of magnitude to see any detail, otherwise, with the same scale as for CLM, there would have been no blue or green whatsoever).

HOW DO THESE MODELLED INTERACTIONS COMPARE TO ANY ACTUAL INTERACTION BETWEEN N AND O_3?

A range in the *complexity* (that is, the deviation from simplicity) of interactions between N and O_3 influencing vegetation can be seen in the CLM and OCN models, although it in not clear through what mechanisms these interactions influence the vegetation in these models.

Experimental observations suggest that these interactions can take many forms, influencing the vegetation on different timescales through different mechanisms (e.g. Sanz et al. 2014). For example, they show that N can enhance the effect of O_3 to induce early senescence that would then decrease vegetation productivity. That is, the N is increasing the effect of O_3 to reduce productivity (which conceivably is then cancelling what might otherwise be a positive effect of N on the vegetation, and thus reducing productivity to 'O_3 only' levels. This may be consistent with the CLM interaction effects, but again, it is not clear by what dominant mechanism in the model).

Is this consistent with potential (albeit minor) positive interactions? Sanz et al. (2014) also found that N and O_3 do not always (positively or negatively) interact. What's more, they found (as have other studies) that O_3 can have a stronger effect on root biomass than above-ground biomass, which might change any photosynthesis (leaves) to evapotranspiration (leaves and roots) regime. Whilst this could conceivably increase water use efficiency, it is hard to see how this might increase evapotranspiration (except perhaps, by increasing evaporation relatively more than decreasing transpiration). This report has not investigated the different components of evapotranspiration (not all the models report these components separately).

5. Milestones achieved:

No milestones were defined in relation to this deliverable

6. Deviations and reasons:

Delay in D14.7

Deliverable 14.7 was completed with a delay of about six months. The main reason was a delay in the development and running of the models including the combined interaction of both N and ozone deposition that was more demanding than originally foreseen.

Human resources in WP14

Several modelling teams involved in WP14 have faced unexpected problems with human resources due to maternity/paternity leave (MPI, MetOffice) or premature termination of temporary contracts (JRC and KIT). For this reason several scientists that were involved in the development and application of DGVMs models were not available to conduct the final analysis of model results (temporary or permanently), which caused delays.

7. Publications:

Cescatti A., Hooker J., Marcado L., Zaehle, Arneth A., de Vries W. et al. Joined effect of nitrogen and ozone depositions on the primary productivity, evapotranspiration and water use efficiency of European ecosystems (in prep).

8. Meetings:

ECLAIRE plenary meetings.

9. List of Documents/Annexes:

None

REFERENCES

Gower JC (1966). Some distance properties of latent root and vector methods used in multivariate analysis. Biometrika 53: 325–328.

Robert P and Escoufier Y (1976). A unifying tool for linear multivariate statistical methods: the RV coefficient. Applied Statistics 25: 257-265.

Sanz J et al. (2014). Ozone and nitrogen effects on yield and nutritive quality of the annual legume Trifolium cherleri. Atmospheric Environment 94: 765-772.