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**Comparing the performance of different stomatal conductance models using modelled and measured plant carbon isotope ratios (δ13C): implications for assessing physiological forcing.**

**Running Title: On measured and modeled plant δ13C.**

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**Abstract**:

Accurate modelling of long-term changes in plant stomatal functioning is vital to global climate change studies because changes in evapotranspiration influence temperature via physiological forcing of the climate. Various stomatal models are included in land surface schemes, but their robustness over longer timescales is difficult to validate. Here we use three stomatal models, varying in their degree of complexity, coupled to a land surface model to simulate the carbon isotope ratio of tree leaves (δ13Cleaf ) over a period of 53 years and we test their performance by comparison with carbon isotope ratios obtained from tree rings (δ13Cstem) measured at six sites in northern Europe. All three stomatal models fail to capture the observed inter-annual variability in the measured δ13Cstem time series. However, the Soil-Plant-Atmosphere (SPA) model performs significantly better than the Ball-Berry (BB) or Cox (COX) models when tested for goodness of fit against measured δ13Cstem. The δ13Cleaf time series simulated using the SPA model are significantly positively correlated with measured results over the full time period tested, at all six sites. The SPA model underestimates inter-annual variability measured in δ13Cstem, but is no worse than the BB model and significantly better than the COX model. The inability of current models to adequately replicate changes in stomatal response to rising levels of CO2, and thus to quantify the associated physiological forcing, warrants further investigation.

**Introduction**

The annual rings of trees provide the source for some of the most powerful and widely used of the high temporal resolution environmental proxies. Trees are long-lived and widespread globally and thus hold great potential for reconstructing climate across the seasonal parts of the planet (McCarroll and Loader 2004). Various measures of annual tree growth, including ring width, wood density and height increment are commonly used for the reconstruction of climate, most commonly through the last two millennia (e.g. Briffa *et al*. 2004; Trouet *et al*., 2009; Campbell *et al*. 2007; McCarroll et al. 2013). Recently, stable isotope measurements have also begun to feature as a strong dendroclimatic proxy, extending the information that can be obtained using the more traditional methods (e.g. Treydte *et al*. 2006). Fractionation of carbon in trees is controlled by stomatal conductance and photosynthetic rate, and the dominant environmental signal varies geographically, seemingly providing a proxy for sunshine and cloudiness in the Arctic (Young *et al*. 2010; 2012b; Gagen *et al*. 2011), summer temperature in moist mid latitudes (Loader *et al*. 2008; Young *et al*. 2012a; Loader et al 2013) and hydroclimate in dry areas (Gagen *et al*. 2004; Kress *et al*. 2010), and, where replication is high, carbon isotopes also have the advantage of retaining climate information at multi-decadal timescales at some sites (Gagen *et al*. 2007; Young *et al*. 2011).

In addition to climate information, tree-ring stable carbon isotope (δ13C) time series also contain information on the response of trees to post-industrial changes in atmospheric carbon dioxide concentration and stable isotope composition, (see McCarroll and Loader (2004) for a discussion). Whilst the impact of atmospheric CO2 changes on the climate signal retained in tree-ring δ13C can be quantified and removed (Saurer *et al*. 1997; McCarroll *et al*. 2009), this signal component contains valuable information on tree response to rising CO2. Where this information can be scaled up to forest level, changes in forest response to CO2 through time might be explored (Gagen *et al*. 2010).

The fractionation of stable carbon isotopes by trees can be linked to physiological processes within the tree that are relatively well understood and modelled (Farquhar *et al*. 1982). The δ13C ratio in trunk cellulose is connected to leaf stomatal conductance (gs) and assimilation rate (Anet) and, as such, tree-ring δ 13C can be used to explore long term changes in plant physiology (Farquhar *et al*. 1982).

Plants regulate their stomata in order to maximize carbon gain while minimizing water lost via transpiration (t) (Williams *et al*. 1996). In doing so the relationship between stomatal conductance and the tree’s carbon and water balance is archived within the δ13C of cellulose revealing that, as CO2 rises, many trees adapt their water loss to carbon gain accordingly. The most common way to explore these relationships is by using tree-ring δ13C data as a proxy for intrinsic (potential) Water Use Efficiency (iWUE or Anet/gs) calculated using well established physiological relationships. iWUE changes through time, reconstructed from measurements of tree-ring δ13C, show an increase in the post industrial period, following the rising trend in atmospheric CO2 (Saurer *et al*. 2004; Waterhouse *et al*. 2004; Gagen *et al*. 2010; Loader *et al*. 2011). This widely described relationship seems logical given that the stomatal apertures of plants tend to close, decrease in number and alter their geometry when plants are exposed to elevated CO2 (Woodward 1987; Woodward and Kelly 1995; Kürschner *et al*. 1997; Gray *et al*. 2000; Lake *et al*. 2001). The potential climate forcing impact of such changes are substantial when considered at forest level, given the significance of a reduction in transpired water vapour (a radiatively active gas) as CO2 levels rise.

Tree-ring δ13C has been used to explore iWUE changes in trees from across Europe with indications that iWUE has risen in recent decades in a variety of forests (e.g. Waterhouse *et al*. 2004, Gagen *et al*. 2011). If such changes are genuinely widespread they have the potential to impact strongly upon the temperature response of the planet to rising CO2 as water vapour is a strong greenhouse gas. The temperature changes derived from shifts in evapotranspiration under raised CO2 are referred to as plant physiological forcing. Physiological forcing is an important but poorly quantified process in the land surface models (LSMs) of General Circulation Models (GCMs) (Doutriaux-Boucher 2009). One of the most significant variables in calculating physiological forcing involves the modelling of stomatal conductance, which must be characterised properly if derived estimates of physiological forcing are to be accurate. Here, we assess the accuracy of stomatal conductance models by comparing measured δ13Cstem with simulated δ13Cleaf.

It is widely assumed that plant response to rising CO2 will see a continuing stomatally induced reduction in evapotranspiration (Field et al. 1995; Gedney et al. 2005; Betts et al. 2007). However, there is an emerging body of evidence which suggests that trees can reach a plateau in gs induced rises in water use efficiency, as an acclimation point in plant response is reached. Waterhouse *et al*. (2004) find examples of plateaus in rising iWUE (derived from tree-ring δ 13C) across northern Europe. Kürschner *et al.* (1997); and Royer (2001) suggest a response limit in stomatal adjustment to rising CO2 from studies of stomatal frequency changes. Gagen *et al*. (2011) also present evidence for a plateau in tree-ring δ13C derived iWUE in northern European *Pinus sylvestris*, generally noting a levelling off in iWUE detected via a shift in the observed decrease in tree-ring δ13C in recent decades. The ability of the various stomatal models used in LSMs to reproduce such features would provide a useful independent test of their efficacy. It is important that tree-ring and LSM derived changes in δ13C fractioning are reconciled if LSMs are to be used with confidence for simulating future physiological forcing under elevated CO2. Here we test the Soil-Plant-Atmosphere (Williams, 1996), Cox (Cox *et al*. 1998) and Ball-Berry (Ball *et al*. 1987) stomatal models via their ability to simulate δ13Cleaf time series with the central tendency and variance characteristics of six measured δ13Cstem time series from tree-ring cellulose.

A large number of stomatal models exist (for a review see Damour *et al*. 2010) with a varying range of complexity. The most commonly used models (e.g. Ball *et al* 1987; Wang and Leuning, 1998) are based on the *g*s-Anet relationship. These models include few model parameters and their simplicity makes them suitable for use in LSMs. Several studies use these physically-based models to examine modelled δ13C fractioning in trees or in respired carbon (Baldocchi and Bowling 2003; Suits *et al*. 2005; Aranibar *et al*. 2006; Chen *et al*. 2006; Cai *et al*. 2008; Hidy *et al*. 2009; Ogee *et al* 2009). However, to the best of our knowledge none have tried to validate long term changes in simulated δ13Cstem against measured time series from tree-ring cellulose. Here we present a unique study where we use the known link between the δ13C of trees (as measured in tree-ring cellulose) and leaf stomatal conductance (Farquhar *et al.* 1982) to simulate fractionation of carbon isotopes in leaves (δ13Cleaf) to compare with measurements of δ13C discrimination in pine or oak tree-ring cellulose(δ13Cstem) at six Northern European sites. The measured stable carbon isotope series are part of a developing dendroclimatic archive produced over the last ten years.

Our aim is to examine the performance of different stomatal models in terms of how well they represent the variability in observed δ13Cstem. Three different models are tested: the Cox model (Cox *et al*. 1998), the Ball-Berry model (BB, Ball *et al*. 1987) and the Soil-Plant-Atmosphere(SPA) model (Williams *et al*. 1996). The BB and SPA models have previously been found to give similar results relating to evapotranspiration (Alton *et al*. 2009). The stomatal models were incorporated into the UK Meteorological Office ‘Joint UK Land Environment Simulator’ (JULES) and the model run for 53 years to overlap with the period for which measurements of δ13Cstem are available.

**Materials and methods**

The JULES model is based on the UK Meteorological Office Land Surface Exchange Scheme (MOSES; Cox *et al*. 1999). JULES uses the standard Penman-Monteith approach for energy calculation (Monteith, 1965) to ensure a closed energy budget. Surface albedo is simulated using the two-stream model of Sellers *et al*. (1996). Several changes have been made to the original version of the model relating to leaf orientation, diffuse sky radiation and sun fleck penetration (Alton *et al*. 2007; Mercado *et al*. 2007; Alton 2008) and to plant respiration (Ryan 1991). The model separates vegetation into 5 different plant functional types (PFTs), including two tree PFTs: broadleaf (BL) and needle leaf (NL). Required forcing includes local meteorology: downwelling shortwave (SW) and longwave (LW) radiation, precipitation (PPT), air temperature (T), windspeed (WIND), air humidity (SH) and pressure (PRES). The model also requires atmospheric CO2 concentration, Leaf Area Index (LAI) and a set of soil parameters. A more detailed description of the version of JULES used in this study (JULES-SF) can be found in Cox *et al* (1999) and Alton and Bodin (2010).

In this study we used the three existing stomatal models in JULES-SF: (1) The Cox model (Cox *et al*. 1998), (2) the state-of-the-art Ball-Berry model (BB: Ball *et al*. 1987), and a more mechanistic approach stemming from the SPA model (Williams, 1996). In the Cox model the internal CO2 concentration (ci) depends on the CO2 concentration outside the leaf (ca) and the humidity deficit at the leaf level. Stomatal conductance is then dependent on the resulting photosynthesis (down regulated to take into account soil moisture deficit) following:

 *1*

 where R is the perfect gas constant and T\* is leaf surface temperature.

In the BB-model (equation 2) stomatal conductance is dependent on net photosynthesis (Anet), internal CO2 concentration (ci) and relative humidity (RH):

 *2*

where b and m are empirical constants. The SPA model simultaneously maximizes carbon gain and water loss, which are the main controlling factors on stomatal conductance (Williams, 1996). This is done through a stepwise process where stomata are opened incrementally until the resulting increase in assimilation is below a certain threshold or if leaf water potential reaches its specified cavitation limit.

The δ13Cof leaves (*δ13Cleaf*) was simulated using the standard formula (equation 3) (Farquhar *et al*. 1982):

 3

where *a* (4.4‰) and *b* (28‰) are constants representing fractionation due to diffusion and carboxylation respectively, ca being atmospheric CO2 concentration (ppm), cc being the CO2 concentration at the site of carboxylation and δ13Catm being the δ13Cof atmospheric CO2. Here we assume a constant δ13Catm of -6.4‰ because the measured δ13Cstem values are expressed relative to this pre-industrial δ13Catm value. In this study we also use the common assumption that cc is equal to ci. Evidence suggests that this assumption might not always be valid as internal conductance (the process determining the discrimination between ci and cc) varies with both cc and leaf temperature (e.g Flexas et al. 2008). The understanding about the physical processes behind these effects is however limited and the inclusion of these processes to the model would add further uncertainties. The Anet weighted average δ13Cleaf was calculated for the growing season (JJA) and compared against measurement data.

*Datasets*

The tree-ring data analysed are derived from published δ13C series from the annual rings of multiple Scots pine (*Pinus sylvestris* L.) or oak (*Quercus robur* L.) at six Northern European sites between 52° and 69°N and 3°W to 27°E. Some are tree line sites whilst others are from less environmentally stressed locations. In most cases (Sandringham and Turku as the exception) samples were analysed at the Swansea University stable isotope laboratory. Full methodological information can be found in the original data sources (Table 1).

The most northerly Scots pine site is at Forfjorddalen, beyond the Arctic Circle, in the Vesterålen archipelago of northwestern Norway. Scots pine was sampled from near to its northern limit. Core samples were collected using a 12 mm diameter increment borer, dried at room temperature, surfaced and annually dated by dendrochronology against the local master chronology (Kirchhefer, 2001). The chronology is an n =8-10 mean comprised of annually measured latewood α-cellulose (see Young *et al*. 2010 for full site description and methodology). Laanila is also located north of the Arctic Circle, south of the Scots pine limit, in a research area that has been used to develop tree ring isotope and associated methodologies for many years (McCarroll *et al*. 2011). The Laanila δ13Cseries is comprised of latewood cellulose extracted from rings of 8 mature *P. sylvestris* trees over 200 years in age sampled in 2001. The time series is fully described elsewhere (Gagen *et al.* 2007). Trees were sampled using a 12 mm increment borer and processed to α-cellulose using standard methods. Rovaniemi, also in Finland, lies south of Laanila close to the Arctic Circle. Sixteen *P. sylvestris* trees were sampled at a single site. Disks from breast height were cut in the field, dried and the latewood from annual rings was separated and processed to α-cellulose using standard methods. The series represents the mean of n=16 annual latewood measurements. Turku falls within 100km of the northern distribution limit of oak in Finland. Five *Quercus robur* L. were cored using a 12mm diameter increment borer. Annual latewood samples were removed and samples were processed to α-cellulose before measurement. The series represents an n=5 mean from latewood α-cellulose (see Robertson *et al*. (1997b) for full site details and methodology). A further oak site is represented by Sandringham Park in the UK. The Sandringham site is a dry to mesic location in south east England. The oaks sampled at Sandringham are found growing in open stands of mixed native and non-native hardwoods. Five individuals were sampled with 12mm diameter increment borers. Annual latewood samples were removed and samples processed to α-cellulose using standard methodologies. The Sandringham series represents an n=5 mean. A further Scots pine site is located in the UK, in the Southern Glens region of central Scotland. The Southern Glens tree-ring δ13C series is fully discussed in Woodley *et al.* (2012) and represents an n=6 annual latewood α-cellulose mean δ13C series. In all cases extracted α-cellulose was measured for δ13C ratios using standard stable isotope ratio mass spectrometric methods following absolute dating of tree-ring samples using standard methodologies.

The measured (stem) and simulated (leaf) δ13C series were first corrected for changes in the δ13C of atmospheric CO2. The correction was applied according to McCarroll and Loader (2004) by normalising against the preindustrial δ13Cin the atmosphere of -6.4‰. Corrected δ13Cstem can thus be compared directly with simulated δ13Cleaf, although it should be noted that these variables will always be offset slightly (Waterhouse *et al*. 2004).

A 53 year, 3-hourly reconstructed meteorology dataset at 1 degree resolution (Sheffield *et al*. 2006) (available at http://hydrology.princeton.edu, accessed 15 Mar 2009) was used to force the model using the 1º gridcell in which each of the sites were located. Annual average CO2 concentrations were taken from the Mauna Loa (Keeling *et al*. 2009) and Law Dome (Etheridge *et al*. 1998) datasets. We assessed the bias in the re-analysis climatology against data from nearby meteorology stations. For Laanila and Rovaniemi data from Sodankylä (67○24’N 26○37’ E) were used, for Turku local climate was used (60○31’ N 22○16’ E), for Forfjorddalen data from Andöya (69○17’ N 16○9’ E), for Southern Glens data from Eskdalemuir (55○18’N 3○12’ W), and for Sandringham from X (). In general the bias in monthly mean temperature was very small (less than 1.0 C on average) and with Root Mean Square Error (RMSE) smaller than 0.1. For Rovaniemi there is a warm bias and Forfjorddalen a cold bias compared to station data. For Rovaniemi this bias is not surprising as the Ivalo meterology station is located 300 km to the north of Rovaniemi.

For precipitation the bias in monthly precipitation was smaller than 25 for all sites except Forfjorddalen which had a wet bias of 45 mm. The greater noise in observed precipitation generated a smaller fit between re-analysis and site data ranging with a RMSE ranging from 0.29 (Rovaniemi) to 2.3 (Forfjorddalen). Water is however not expected to be limiting to growth for the sites with highest RMSEs.

Soil parameter values were taken from the GSWP2 1 degree dataset (Dirmeyer *et al*. 1999). Monthly LAI for each grid cell was based on calculations made using observed relationships between FAPAR and temperature and precipitation (Los *et al*. 2006). Grid average leaf area index was normalized to the fractional cover of plant functional types within each grid cell.

*Analysis methods for comparing measured δ13Cstem and simulated δ13Cleaf*

For each site and stomatal model JULES was run for 53 years (AD 1948-2000). The first three years were used as a spin-up of the soil water pool and were not used in the analysis. Model parameters, including BB model parameters, were taken from Alton and Bodin (2010) using the BL parameter values for the Sandringham and Turku sites and NL parameter values for the remaining sites. For the SPA model the same parameter values as in Alton *et al*. (2009) were used, and for the Cox model the JULES default parameter values. Although the full growing season will vary between sites, the mean summer period (June-August) was used for convenience and, since the average δ13Cleaf was weighted based on Anet, any error caused by this assumption is minimised.

In comparing the measured δ13Cstem and simulated δ13Cleaf results we are interested in the ability of the models to replicate changes in the absolute isotope value over time and to reproduce the observed magnitude of inter-annual variability. However, the procedure is complicated by the fact that stem and leaf values will always be offset. The mechanisms behind this offset are not yet clear (Cernusak *et al.* 2009). However, the offset has been shown to be systematic across sites and species (Badeck *et al.* 2005, Bowling *et al.* 2008). Our solution to the problem with an offset borrows from split-period verification techniques developed in palaeoclimatology (National Research Council (NRC), 2006). Each data set is split into two time periods for calibration (1951-1975) and verification (1976-2000). The measured δ13Cstem and simulated δ13Cleaf results are then shifted so that they both have a mean of zero over the early calibration period. The variance of the series is not adjusted. Since the measured and simulated values now have no offset over the early calibration period, the absolute values of any offsets in the later verification period can be regarded as an indication of goodness of fit, which can be quantified using the Reduction of Error (RE) and Coefficient of Efficiency (CE) statistics. The Reduction of Error statistic is used to verify palaeoclimate reconstructions by dividing the Mean Squared Error (MSE) in the verification period (MSEver) with the MSE that is obtained by simply taking the mean observed value of the calibration period and applying it to every year in the verification period (MSEre so that RE = 1- MSEver / MSEre). The CE statistic, which is more difficult to pass, uses the mean observed value of the verification period. Both RE and CE scale between one and minus infinity. Negative values are viewed as failure and the magnitude of positive values provides a measure of predictive skill that can be used to compare different predictors. We apply the same logic here, using isotope ratios rather than climate parameters and use RE and CE as measures of the relative predictive skill of the three stomatal models. This simple method is sensitive to offsets in absolute values, changes in trend through time, and to differences in variance between the two data sets.

**Results**

Average growing season climate is variable across the network of sites (Table 2). The sites receiving the highest incoming short wave radiation are located at Sandringham in the UK and Turku in southern Finland. The wettest are the Scottish (Southern Glens) and Norwegian (Forfjorddalen) sites. Growing season mean temperature varies across the network of sites by 6 K with Forfjorddalen the coldest and Sandringham the warmest site. The Southern Glens and Turku sites were significantly wetter (p<0.05, Wilcoxon test) for the most recent time period (1976-2000) (by 150 and 100 mm respectively) and the Sandringham site had significantly higher SW radiation (by 2.4 W m-2).

The measured δ13Cstem time series for all six sites are shown in Figure 1. Measured δ13Cstem displays a significant (p<0.05, Wilcoxon test) difference between the two time periods before and after 1975 at the Laanila and Sandringham sites (-0.6 and -0.5 respectively). The only model which displays a significant difference of a similar order of magnitude is the SPA model for the Laanila (-0.15) site.

Comparison between the δ13Cleaf simulated with various stomatal models and the measured δ13Cstem was carried out using the RE and CE statistics. In 5 out of the 6 cases the SPA model gives a positive RE (Table 3), whereas for Cox there are only three positive values and for BB only one. Comparing the relative strength of the RE results for each site reveals that, in 5 out of the 6 cases the SPA model gives the best result and in 5 of the 6 cases the BB model gives the worst result. A Friedman 2-way analysis of variance by ranks test (Table 3) suggests that the difference in the RE results obtained from the three models is statistically significant (p< 0.05). The CE test, which uses the mean value of the verification period as the constant value for each year, is much more difficult to pass, so it is not surprising that there are several negative values. However, the rank order of the CE results is still a useful measure of the relative skill of the stomatal models. The SPA model again performs the best with the highest value in 5 of 6 cases and the BB model is the weakest, coming last in 5 cases. The Friedman test again suggests that these differences are statistically significant (p< 0.05).

We also used the split-period design to test the skill of the models as measured by correlation. We considered the calibration and verification time periods separately because we are interested in the ability of the models to capture change over the two time periods (given that several of the measured δ13Cstem time series contain shifts). Considering the two time periods separately (n=12) we again used the Friedman ANOVA statistic to assess the relative skill of the models in capturing the variability in the measured δ13Cstem time series in the two time periods (Table 4).

Over the full period the SPA model is significantly positively correlated with measured values for every site (p<0.05, one-tailed). The BB model gives a significant positive correlation in only 3 cases and the Cox model in only 2 cases. The numerical average of the six correlations fall in the order SPA>BB>Cox. Taking the two separate time periods gives an n of 12 and in this case the difference between the three models is significant (Friedman = 7.17, p<0.05) and the SPA model performs best. Taking the average of the six correlations for the first time period the models fall in the order SPA>BB>Cox and for the later period SPA>Cox>BB. Wilcoxon Matched Pair signed-rank test results suggest that the results obtained using the SPA model are significantly different from those obtained using BB, but the other two pairs (BB/Cox and SPA/Cox) are not significantly different (p>0.05). Using correlation as the measure of goodness of fit also suggests that the SPA model performs best, but the relative skill of the Cox and BB models is not clear. In general there is a decrease in fit between the earlier and the later time period.

All three models fail to capture the observed inter-annual variability in the δ13Cstem values (Table 5). Taking the standard deviation of the whole period as a measure of variability it is clear that the Cox model is the worst in this regard, grossly underestimating the observed variability in every case and on average producing standard deviation values only about 10% as large as those from the δ13Cstem data. The SPA and BB models also fail to capture the full variability in most cases with average standard deviation values only about 50% as large as the δ13Cstem data. Treating the two periods separately does not change the results appreciably. It is reasonable to conclude that all three models underestimate the variability that is seen in the δ13Cstem values. The Cox model consistently performs the least well of the three models and the difference between the performance of BB and SPA is not statistically significant (p > 0.05, Wilcoxon test).

**Discussion**

There are significant model differences in terms of the quality of representation of the interannual signal in measured δ13Cstem. The strongest correlation between simulated δ13Cleaf and measured δ13Cstem was found using the iterative SPA model. The correlation for the more empirical BB and Cox models are in general poorer suggesting that these stomatal models fail to capture long term variation in observed δ13C discrimination. Despite displaying a significant correlation for all sites for the entire simulation period, the SPA model, similarly to the other two models, also fails to reproduce the magnitude of the inter annual variation in measured δ13Cstem. As data only exists for four sites with stands of *P. sylvestris and* two sites with *Q. robur* no conlsusions can be made regarding species differences in model fit. Model fit however did vary with climate (Table 6), for the Cox model, where model fit was strongly positively correlated with SW radiation (R=0.87; p< 0.05). For the BB and SPA model there was no significant change in model fit with climate. A climate bias, in particular related to temperature could also affect model fit. The two sites with the highest absolute temperature bias (Forfjorddalen and Rovaniemi) display the lowest correlation even though some of the observed bias between the re-analysis and site data for Rovaniemi is expected due to the fact that the meteorology station is located 130 km to the north of the reanalysis gridcell used in this study.

The climate sensitivity of δ13Cstem has been extensively studied, and the chronologies used in this study have been tested for their climate sensitivity against local climate drivers. One possible explanation for the underestimation of interannual variability in simulated δ13Cleaf would be if modelled δ13Cleaf is less sensitive to climate than is δ13Cstem. Across sites and years, measured δ13Cstem correlates positively with SW radiation and temperature and negatively with precipitation (Table 7). For the Cox model, the climate signal was in general both weak and with low correlation (R2<0.20) which explains the low interannual variability in modelled δ13Cleaf. For the the BB model climate signals varied strongly between sites and, across sites these signals therefore became spurious with either low correlations or opposing signs to the observed climate signals. The climate sensitivity of modelled δ13Cleaf in the SPA model was roughly three times larger than that of measured δ13Cstem for SW radiation and temperature and of similar order of magnitude for precipitation (Table 3).

There is also a general decrease in the fit between δ13Cleaf and δ13Cstem from the early to the later time period suggesting that the processes controlling δ13Cstem is changing over time. This general decrease in fit is mainly caused by a large decrease in fit for the two *Q. robur* chronologies. For two of the sites (Laanila and Sandringham) there is a significant decrease in average δ13Cstem between the earlier and later time period. The only model to reproduce a small decrease in δ13Cleaf is the SPA model (for the Laanila site). The strong climate signal in the SPA model and the lack of a significant difference in climate between the two time periods at these two sites suggests that this decrease is caused by a non-climatic effect.The inability of the model to simulate the interannual variability in δ13C and the decrease in model fit over time for the SPA model must be caused by a missing process in the model, likely not linearly related to climate.

Several factors have been suggested as causing the commonly seen shift in iWUE as measured from δ13Cstem in recent decades. One hypothesis is that with increasing ca a threshold is reached in the stomatal response to CO2 (Gagen *et al*. 2010), which is clearly not reproduced in our simulated δ13Cleaf values. Results from Free Air CO2 Enrichment (FACE) experiments (Uddling *et al*. 2009) give some support for this suggesting that, over longer timescales, an increase in CO2 leads to an increase rather than a decrease in stomatal conductance although this behavior is not observed universally in all tree-ring based iWUE studies (Waterhouse *et al*. 2004, Loader *et al* 2011). Different species also display a different response to an increase in CO2 related to the stomata index (ratio of stomata to epidermal cells; Haworth *et al.* 2010). This has implications for future projections of, for example, transpiration. If an observed levelling off in iWUE (caused by a shift in measured δ13Cstem) translates into actual WUE, then current LSMs may underestimate future trends in transpiration and thus underestimate the increase in climatic forcing caused by an increase in water vapour (Gagen et al. 2011). If this is the case, a saturation effect of increasing CO2 should be included in stomatal models.

A third possible explanation would be an increase in the importance of internal (mesophyll) conductance with increasing CO2 ­or a change in the rate of respiration or use of stored photosynthates in wood formation. However we did introduce a simple linear model for internal conductance to the SPA model with no positive effect on the fit of the modelled to measured δ13Cstem (results not shown). Many other factors are known to affect internal conductance at varying timescales (e.g. Flexas *et al*. 2008) and the mechanisms behind these effects are still unknown. As we simulate δ13Cleaf and not δ13Cstem we also make the assumption that the discrimination difference between leaf and stem is constant over time. This assumption is supported by the literature (Badeck *et al.* 2005, Bowling *et al*. 2008), but a change in this discrimination could have an impact on model fit. Tropospheric ozone and atmospheric pollution (SO2) changes could also affect stomatal functioning over both shorter and longer timescales (Uddling *et al*. 2004; Rinne *et al*. 2010; Haworth *et al.* 2012). As the model does not incorporate the effects of pollutants an increase in the atmospheric concentrations of these and other pollutants over time could also affect the model fit in our study.

If the ability of current stomata models to correctly account for carbon discrimination in plants is indeed decreasing with rising atmospheric CO2 levels there may be serious implications for the accuracy of simulations of future physiological forcing. Further physiological studies and tests of stomatal models are needed to explore this further and develop the necessary land surface model improvements.

This study is a novel attempt to use tree-ring δ13C data to evaluate stomatal models incorporated into a land surface model over multi decadal timescales. Although the available data is limited to three sites in Finland, two in the United Kingdom and one in Norway the results are encouraging with regards to using tree-ring δ13C data for validation and constraining purposes. Of the three stomatal models used, the more complex iterative SPA model performed better than the BB model which in turn performed better than the simpler Cox model. The SPA model gives positive RE results and the highest CE results of the three models assessed. The SPA model is also the only one that is significantly positively correlated with the measured δ13Cstem time series over the full (53 year) period at every site. The SPA model underestimates the inter-annual variability measured in the stem, but it is no worse than the BB model and significantly better than the Cox model. The BB model gives the lowest verification statistics and the correlation results are erratic. The Cox model performs better than BB in terms of verification statistics but the loss of inter-annual variance is extreme.

The process responsible for the observed shift in δ13Cstem after 1975 can be said to be missing from JULES-SF, regardless of the choice of stomata model (although smaller shifts in the same direction can be seen for the SPA model). Possible explanations for this include the lack of a detailed model for internal conductance, a shift in the discrimination of δ13C from the leaf to the stem, a shift in respiration or increased accessing of stored photosynthates in wood formation or via an increase in tropospheric ozone reaching a threshold level for damaging leaf stomata. However, the simplest explanation is a shift in the stomatal response to very high rates of increase in atmospheric CO2 concentration.

We have a robust and interesting result, namely that one of the stomatal models simulates the long-term trend in measured tree-ring δ13C (even if underestimated) whilst other stomatal models, one of which is used extensively (BB) in land-surface simulations, do not. The inability of current models to adequately predict changes in stomatal response to rising levels of CO2, and thus to quantify the associated physiological forcing, is a cause for concern.

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**Table 1. Measured tree-ring δ13Cstem data analysed in this study with original sources.**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Site** | **Location** | **Species** | **Source** | **n/years** |
| Forfjorddalen, Norway | 68°N 15°E | *Pinus sylvestris* | Young *et al*., 2009 | 8-10/50 |
| Laanila, Finland | 68°N 27°E | *Pinus sylvestris* | Gagen *et al.*, 2007 | 8/50 |
| Rovaniemi, Finland | 66°N 26°E | *Pinus sylvestris* | McCarroll and Pawellek 2001 | 16/45 |
| Sandringham,England | 52°N 0°E | *Quercusrobur* | Robertson *et al*., 1997a | 5/44 |
| Southern Glens,Scotland | 55°N 3°W | *Pinus sylvestris* | Woodley *et al*., 2012 | 6/50 |
| Turku,Finland | 60°N 22°E | *Quercusrobur* | Robertson *et al*., 1997b | 5/44 |

**Table 2 Average summer (JJA) climate variables including inter-annual variability (CV: % for all variables except T (K)). SW (short wave radiation), PPT (precipitation), T (temperature), SH (air humidity), PRES (air pressure).**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | **Species studied** | **SW****(W m-2)** | **PPT****(mm y-1)** | **T****(K)** | **SH****(kg kg-1)** | **PRES****(Pa)** |
| Forfjorddalen | *Pinus sylvestris* | 180 (1.8%) | 1070 (35%) | 283 (1.0K) | 0.007 (6.4%) | 99700 (0.1%) |
| Laanila | *Pinus sylvestris* | 175 (1.6%) | 780 (24%) | 285 (1.1K) | 0.008 (7.5%) | 98300 (0.1%) |
| Rovaniemi | *Pinus sylvestris* | 175 (1.7%) | 800 (28%) | 287 (1.1K) | 0.008 (7.9%) | 98900 (0.1%) |
| Sandringham | *Quercus robur* | 196 (3.8%) | 740 (32%) | 289 (0.8K) | 0.009 (4.6%) | 101100 (0.1%) |
| Southern Glens | *Pinus sylvestris* | 164 (2.9%) | 1080 (26%) | 286 (0.7K) | 0.008 (3.6%) | 98600 (0.2%) |
| Turku | *Quercus robur* | 194 (2.4%) | 830 (31%) | 288 (0.9K) | 0.008 (5.8%) | 10070 (0.1%) |

 **Table 3. Reduction of Error (RE) and Coefficient of Efficiency (CE) results obtained for the three stomatal models at each site.**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  |  | Cox | BB | SPA |
| **Forfjorddalen** | RE | 0.02 | -0.02 | 0.24 |
| CE | -0.08 | -0.13 | 0.16 |
| **Laanila** | RE | -0.06 | 0.15 | 0.37 |
| CE | -1.72 | -1.19 | -0.63 |
| **Rovaniemi** | RE | -0.11 | -0.56 | 0.05 |
| CE | -0.27 | -0.77 | -0.08 |
| **Sandringham** | RE | -0.05 | -0.38 | 0.08 |
| CE | -0.92 | -1.50 | -0.68 |
| **Southern Glens** | RE | 0.10 | -0.06 | 0.26 |
| CE | 0.06 | -0.10 | 0.23 |
| **Turku** | RE | 0.04 | -0.14 | -0.08 |
| CE | 0.02 | -0.16 | -0.10 |

**Table 4 Correlation coefficients (Pearson’s r) between δ13Cleaf values obtained using the three models and δ13Cstem derived from tree rings. Statistically significant (p < 0.05) values are underscored.**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | **Cox** | **BB** | **SPA** | **Cox** | **BB** | **SPA** |
|  Forfjorddalen | Sandringham |
| Full period r | 0.16 | 0.25 | 0.39 | -0.19 | 0.44 | 0.43 |
| 1951-1975 r | 0.06 | 0.27 | 0.33 | 0.14 | 0.72 | 0.63 |
| 1976-2000 r | 0.32 | 0.20 | 0.40 | -0.14 | 0.36 | 0.21 |
|  Laanila | Southern Glens |
| Full period r | -0.07 | 0.43 | 0.63 | 0.58 | 0.01 | 0.50 |
| 1951-1975 r | 0.09 | 0.56 | 0.60 | 0.61 | -0.12 | 0.34 |
| 1976-2000 r | 0.33 | 0.25 | 0.50 | 0.64 | 0.16 | 0.71 |
| Rovaniemi | Turku |
| Full period r | 0.14 | 0.02 | 0.29 | 0.56 | 0.23 | 0.42 |
| 1951-1975 r | 0.22 | 0.14 | 0.28 | 0.65 | 0.48 | 0.63 |
| 1976-2000 r | 0.28 | -0.05 | 0.31 | 0.62 | -0.16 | 0.05 |
|  Overall mean |
| Full period r | 0.17 | 0.20 | 0.38 |
| 1951-1975 r | 0.30 | 0.34 | 0.47 |
| 1976-2000 r | 0.29 | 0.11 | 0.31 |

**Table 5. Standard deviation of δ13Cleaf and δ13Cstem values over the full period and over the two split periods. Early period (1951-1975), late period (1976-2000).**

|  |  |  |  |
| --- | --- | --- | --- |
| Full period |  |  |  |
|  | **Cox** | **BB** | **SPA** | **Stem** |
| **Forfjorddalen** | 0.03 | 0.25 | 0.18 | 0.39 |
| **Laanila** | 0.04 | 0.19 | 0.16 | 0.53 |
| **Rovaniemi** | 0.07 | 0.17 | 0.19 | 0.28 |
| **Sandringham** | 0.03 | 0.59 | 0.24 | 0.58 |
| **Southern Glens** | 0.04 | 0.13 | 0.16 | 0.42 |
| **Turku** | 0.04 | 0.18 | 0.29 | 0.68 |
| Early period |  |  |  |
|  | **Cox** | **BB** | **SPA** | **Stem** |
| **Forfjorddalen** | 0.03 | 0.26 | 0.18 | 0.36 |
| **Laanila** | 0.04 | 0.20 | 0.20 | 0.42 |
| **Rovaniemi** | 0.06 | 0.17 | 0.21 | 0.28 |
| **Sandringham** | 0.03 | 0.64 | 0.24 | 0.28 |
| **Southern Glens** | 0.04 | 0.13 | 0.15 | 0.36 |
| **Turku** | 0.05 | 0.19 | 0.31 | 0.70 |
| Late period |  |  |  |
|  | **Cox** | **BB** | **SPA** | **Stem** |
| **Forfjorddalen** | 0.03 | 0.24 | 0.16 | 0.42 |
| **Laanila** | 0.04 | 0.18 | 0.17 | 0.47 |
| **Rovaniemi** | 0.05 | 0.15 | 0.16 | 0.27 |
| **Sandringham** | 0.02 | 0.53 | 0.23 | 0.58 |
| **Southern Glens** | 0.03 | 0.12 | 0.16 | 0.47 |
| **Turku** | 0.03 | 0.16 | 0.25 | 0.67 |

**Table 6. Climate sensitivity of model fit, measured as the linear regression (with correlation coefficients) between modelled/measured correlation (R); and each climate driver (W m-2, mm yr-1, K).**

|  |  |  |  |
| --- | --- | --- | --- |
|  | SW Wm2 (R) | Precipitation mm-1 yr (R) | Temperature K-1 (R) |
| Cox | 0.025 (0.97) | -0.001 (-0.52) | 0.094 (0.64) |
| BB | -0.009 (-0.59) | 0.000 (0.52) | -0.048 (-0.55) |
| SPA | 0.000 (0.09) | -0.000 (-0.30) | -0.002 (0.05) |

**Table 7. Climate sensitivity of measured δ13Cstem and modelled δ13Cleaf measured as the linear regression (with correlation coefficients) between δ13C discrimination (in ‰) and each climate driver (W m-2, mm yr-1, K).**

|  |  |  |  |
| --- | --- | --- | --- |
|  | SW Wm2 (R) | Precipitation mm-1 yr (R) | Temperature K-1 (R) |
| Meas | 0.015 (0.30) | -0.001 (-0.54) | 0.119 (0.40) |
| Cox | -0.003 (-0.41) | 0.000 (-0.26) | 0.007 (0.14) |
| BB | -0.066 (-0.59) | 0.000 (-0.05) | -0.274 (-0.41) |
| SPA | 0.047 (0.56) | -0.001 (-0.44) | 0.424 (0.85) |

**Figure 1. a-f) Measured δ13Cstem (black line) and simulated δ13Cleaf (Cox: red; BB: yellow; SPA: blue) for six sites all normalised to the mean.**

**Figure 2 – Mean iWUE for all sites over the common period (AD 1951-1994), measured δ13C stem (A) Cox (B), BB (C) and SPA (D) modelled δ13Cleaf.**