Air pollution and forest water use

ARISING FROM T. F. Keenan *et al.* *Nature* **499,** 324–327 (2013)

Forests in North America and northern Europe increased their water-use efficiency (WUE)—the ratio of photosynthetic CO_2 uptake to water loss through evapotranspiration—over the last two decades, according to a recent Letter[1]. Keenan *et al.* attribute the rising WUE to fertilization by increasing levels of atmospheric CO_2 (ref. 1), although biosphere models predict this effect to be much smaller than the observed trend. Here, I show that falling concentrations of ozone and other phytotoxic air pollutants, which were not considered in ref. 1, may explain part of the WUE trend. Future efforts to reconcile biosphere models with field data should, therefore, use integrated modelling approaches that include both air quality and CO_2 effects on forest growth and water use. There is a Reply to this Brief Communication Arising by Keenan, T. F. *et al.* *Nature* **507,** http://dx.doi.org/10.1038/nature13114 (2014).

Tree injuries caused by ozone, the most phytotoxic air pollutant—including visible foliar injury, reduced photosynthesis and diminished biomass—depress global ecosystem productivity[2] and are well documented in field observations from North America and Europe[3,4]. Ozone enters leaves through stomata and causes internal oxidative stress and membrane damage that reduce photosynthetic CO_2 assimilation[5,6]. During ozone injury, transpiration usually falls less than does photosynthesis, but transpiration can sometimes rise because of ozone injury to stomata[6–8]. In either case WUE declines.

Surface ozone concentrations during the summer growing season have fallen significantly in eastern North America and modestly in northern Europe owing to emission controls on vehicles and industrial sources of ozone precursors[9,10]. Figure 1 shows ozone trends in regions around the rural forest sites analysed in ref. 1, evaluated as summer daytime-mean mole fraction (Fig. 1a) and as the accumulated concentration over a threshold of 40 nmol mol^{-1} (AOT40, defined as in the literature[11,12]), which is a common predictor for plant injury (Fig. 1b). I calculated both ozone metrics using only rural sites—from the US Clean Air Status and Trends Network (CASTNET; http://epa.gov/castnet) and the European Monitoring and Evaluation Programme (EMEP; http://www.nilu.no/projects/ccc/emepdata.html)—reporting at least 14 years of hourly ozone data during the period 1995–2010 (Fig. 1c and d). By either metric, ozone significantly decreased at all sites in the midwestern USA ($n = 11$, $P < 0.001$–0.02 for Kendall's τ test) and northeastern USA ($n = 5$, $P = 0.001$–0.004). For averages over all sites within each region, AOT40 fell by half in the period 1995–2010 in both regions ($P < 0.002$). Over northern Europe most sites had negative trends, but with smaller magnitudes, consistent with other recent analyses[10].

The first-order effect of these ozone trends in the Midwest, using sensitivities for broad-leaf trees[6,12,13], would be a 0.6% annual increase in biomass accumulation and a 0.3% annual improvement in WUE. In addition, partial closure of stomata in response to rising CO_2 (ref. 14) and rising vapour pressure deficit[1] reduces leaf uptake of ozone by approximately 0.9% per year regardless of ozone trends. Combining all these effects, improvements in ozone air quality over the period 1995–2010 probably increased forest WUE by approximately 0.33% per year in the midwestern USA and slightly less in the northeastern USA. Using the range of ozone sensitivities reported for tree species[12,13,15], the ozone effect on WUE in the midwestern USA could be 0.1–0.8% per year. This predicted ozone effect is about one-sixth of the observed WUE trend (2% per year, calculated from the Supplementary Information to ref. 1) and larger than the mean simulated effect of CO_2 fertilization in the terrestrial biosphere models surveyed by ref. 1. Measuring ozone mole fractions and fluxes into the forest canopy simultaneously with

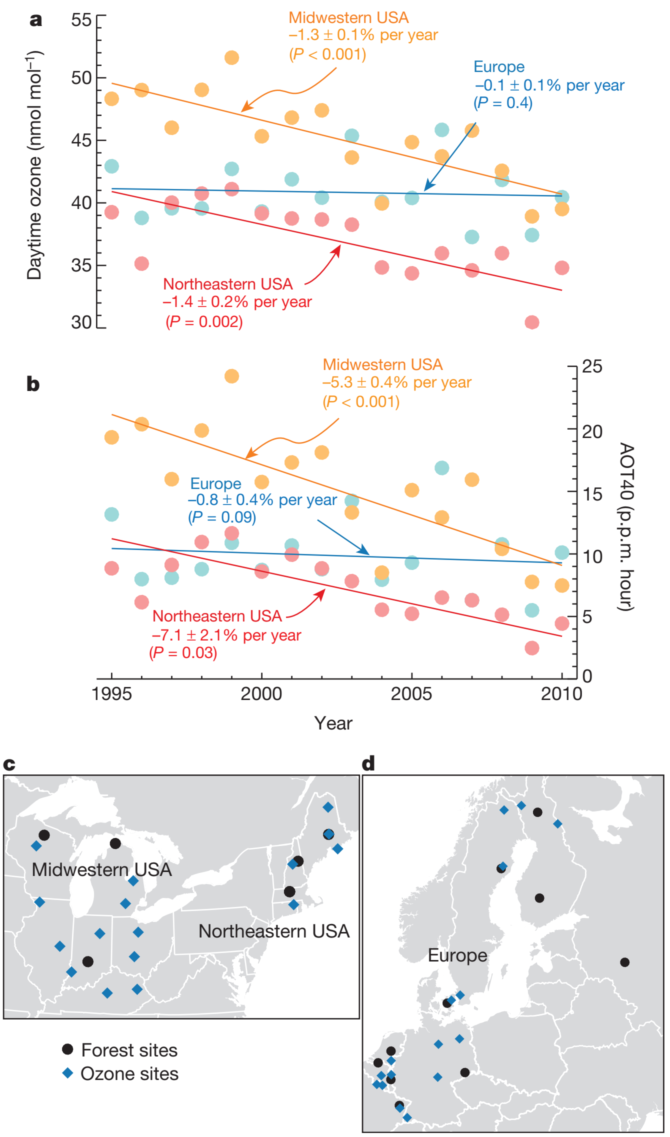

Figure 1 | Trends in ozone exposure metrics that correlate with tree injury. **a**, Daytime-mean ozone mole fraction; **b**, AOT40. Both metrics are calculated in April–September of each year during the hours 8:00–20:00 (local time) at rural sites in the USA (**c**) and Europe (**d**) near forest stations that monitor WUE. Lines show the mean trends (Sen's method) averaged across all stations within each region (±1 standard error, *P* values from Student's *t*-test). The unusually high mole fraction and AOT40 values in Europe in 2003 and 2006 were caused by extreme heatwaves.

WUE should constrain the effect, but the variability of WUE trends across sites and years illustrates that ozone data from multiple forests and many years are necessary to obtain robust results. In addition to the decline in ozone concentration, the concentrations of the air pollutants NO_x and SO_2, which also harm WUE both individually and through synergistic effects with ozone, have fallen quickly but the effects are not included here[11]. Thus, the benefits of improved air quality to forest productivity and WUE may be larger than I have estimated. Keenan *et al.*[1]

suggest that current terrestrial biosphere models underestimate the impact of CO_2 fertilization on WUE. The calculations here show that ozone trends help to reconcile the large differences between models and observations.

Methods

I calculated photosynthesis reductions from ozone AOT40 trends (-0.8 parts per million (p.p.m.) hours per year, where 1 p.p.m. = 1 μmol mol^{-1}, for the midwestern USA) using empirical correlations with ozone exposure for young broad-leaf trees (-0.7% per p.p.m. hour, for beech, birch and maple)[12,13]. Other tree species may be more (poplar) or less (conifers, oak) sensitive: -1.8% to -0.2% per p.p.m. hour (refs 12 and 15). Ozone-induced WUE changes are half those of photosynthesis and of the same sign[6]. Rising CO_2 (2 p.p.m. per year) and rising vapour pressure deficit (11 Pa per year; ref. 1) reduced stomatal conductance and ozone uptake by approximately 0.4% per year and 0.5% per year, respectively, based on empirical sensitivity factors[14] (conductance changes are -0.2% per p.p.m. of CO_2 and -0.05% per Pa).

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Forests have become more efficient at using water over the past two decades[1]. A series of hypotheses exist to explain this trend, but the only credible explanation to date is a response to rising atmospheric CO_2. Keenan *et al.*[1] show that the observed trend is physiologically plausible, but is much larger than expected from conventional theory and experimental evidence. This has led to suggestions that processes other than increased atmospheric CO_2 may have contributed to the observed trend[2]. One such process that has yet to be examined is the effect of tropospheric ozone on forest water-use efficiency (WUE). In the accompanying Comment[3], Holmes reports that ozone concentrations have declined in the northeastern and midwestern USA by about 50% from 1995 to 2010. Using empirical relationships, he estimates that this decline could explain roughly 15% of the reported increase in WUE over North America, and a significantly lower proportion of the trend in Europe.

As a preliminary test of the 'ozone hypothesis', we analyse 20 years of ozone concentration measurements at Harvard forest, in Massachusetts, USA, which were made concurrently with the carbon and water fluxes from which we derived WUE. In agreement with results presented by Holmes[3], extreme ozone concentrations have declined at this forest over the past two decades. Although the 50th percentile of ozone levels has stayed relatively constant, both the 95th percentile and the AOT40 metric show declining trends over the time period ($P = 0.09$ and 0.11, respectively; Kendall's τ test, Fig. 1a).

Despite the declining trend, we found no significant ($P = 0.46$, $r = -0.19$) relationship between annual means of WUE and the occurrence of high ozone concentrations (Fig. 1b). The observations at Harvard forest, therefore, do not support the claim that WUE is being affected by changes in ozone concentrations. That said, we acknowledge that it would be difficult to detect and attribute a change responsible for 15% of the trend we observe given the large influence of other factors.

As an additional test of the ozone hypothesis, we consider the trends of the component fluxes of WUE, published in ref. 1. Decreasing ozone concentrations are primarily expected to increase leaf photosynthesis, with stomatal conductance typically increasing to a lesser extent[3], although conductance responses vary[4]. We would therefore expect a similar response of photosynthesis and conductance in the data of ref. 1. In ref. 1, we report increasing photosynthesis at only 50% of the sites, whereas stomatal conductance showed large declines consistently across all sites.

It is worth noting that global ozone concentrations are increasing[5]. There is no significant trend in ozone concentrations in Europe[3], where half of the sites used in ref. 1 are located. Within the USA, trends vary greatly by region. Ozone in the western USA has increased over the past two decades owing to increased levels of precursors from Asia[5,6]. Globally, ozone concentrations show large declines only in the midwestern and eastern USA[3,7], where 8 of our 21 sites are based. We therefore agree that it is possible, following the calculations of Holmes[3], that changes in ozone concentrations contributed to a small proportion (roughly 15%) of the trend at those sites.

In conclusion, we can neither reject nor accept the ozone hypothesis of Holmes[3], although it is clear that the observed changes in WUE are not primarily driven by changes in ozone concentrations. His estimate[3] of an ozone-induced increase in WUE of 0.33% per year is probably an upper bound for the response at sites in the USA, but an overestimation of the response at European sites. That said, the changes in ozone

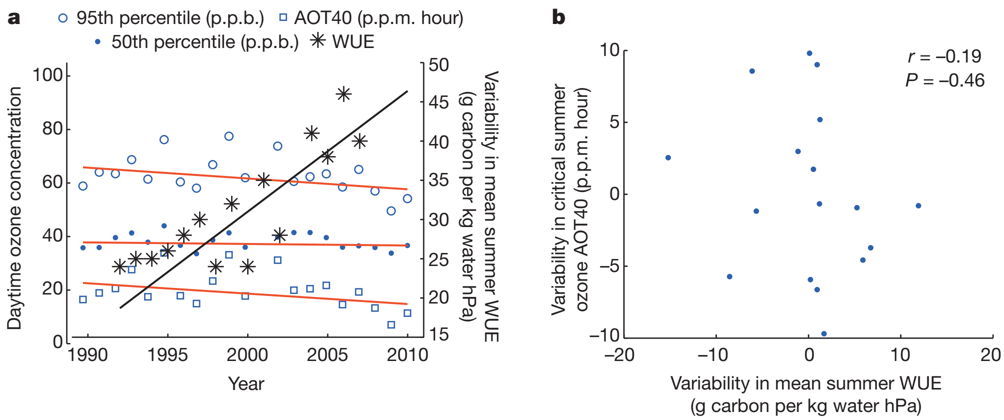

Figure 1 | Ozone and WUE at Harvard Forest. **a**, Long-term trends in ozone concentrations (p.p.b., parts per billion; p.p.m., parts per million) and WUE at Harvard forest, with trends (lines) estimated using the Sen-slope method. **b**, The relationships between variability in critical summer ozone concentrations (AOT40) and variability in mean summer WUE values at Harvard forest from 1992 to 2010.

concentrations reported by Holmes[3] are large in some heavily forested and productive regions, and may beneficially affect ecosystem function. We therefore agree with Holmes[3] that more work is needed to assess the impact of air quality on ecosystems globally, and the resulting change in ecosystem function.

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