Biogeosciences Discuss., doi:10.5194/bg-2016-182, 2016
Manuscript under review for journal Biogeosciences
Published: 1 June 2016

Under a new light: validation of eddy covariance flux with light response functions of assimilation and estimates of heterotrophic soil respiration.

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Keywords: ecosystem respiration, light response, autotrophic respiration, assimilation, heterotrophic soil respiration, leaf area index, semi-arid woodland, basal soil respiration, bushfire

Type of Paper: Primary Research Article

Abstract. Estimation of the basal or heterotrophic soil respiration is crucial for determination of whether an ecosystem is emitting or sequestering carbon. A severe bushfire in January 2014 at the Calperum flux tower, operational since August 2010, provided variation in ecosystem respiration and leaf area index as the ecosystem recovered. We propose ecosystem respiration is a function of leaf area index and the y-intercept is an estimate of heterotrophic soil respiration. We calculated an assimilation rate from eddy covariance data for light response functions to calculate ecosystem respiration incorporating suppression of the daytime autotrophic respiration. Ecosystem respiration from light response functions correlated with data processing calculations of ecosystem respiration by OzFluxQC (y_0 = 0.161x + 0.0085; Adj. r^2 = 0.698). The relationship between ecosystem respiration and leaf area index (y_0 = 1.43x +0.398; Adj. r^2 = 0.395) was also apparent. When this approach was compared to field measurements of soil respiration and mass balance calculations from destructive leaf area, leaf area index calculations and litter fall, the year of data corresponding

to the year of soil respiration measurements, the y-intercept was 0.432 µmol m^{-2} s^{-1} or 163.44 gC m^{-2} $year^{-1}$ ($y_0 = 1.37x + 0.432$, Adj. $r^2 = 0.325$). The mass balance approach for the net primary productivity when subtracted from the tower NEE estimated heterotrophic soil respiration of 134.59 gC m^{-2} $year^{-1}$. This is only 28.9 gC different, therefore the y-intercept approach indeed provides an estimate of heterotrophic soil respiration.

1 Introduction

The flux of CO_2 determined from eddy covariance (EC) measures and calculations is a net value because sequestration by photosynthesising vegetation and emission from respiration within a soil plant ecosystem occurs concurrently. The total of this flux over a day is called the net ecosystem exchange (NEE). Partitioning EC determined NEE to quantify the contributions of sequestration and emission of CO_2 is challenging. Ideally, independent measures of both daytime and night-time ecosystem respiration are needed to make reliable estimates of net ecosystem productivity (NEP), the amount of C retained in the ecosystem. However, very few independent measures of respiration are made and so other methods of estimation are used. This paper describes one approach to improve the estimate of NEP.

At night when photosynthesis is not occurring, the flux of CO_2 from the ecosystem into the atmosphere is the measure of ecosystem respiration. However the often calm night-time atmospheric conditions are not ideal for measures of CO_2 flux to and from an ecosystem. Quality EC measures depend on adequate mixing of the atmosphere moving over the soil plant system. This is generally not an issue during daylight hours when near surface atmospheric mixing is usually large (Burba 2013). During the night however, air within the vegetation layer cools and decouples from the layer of air above the plant canopy. With little turbulent mixing, sensors at the top of the EC tower do not fully indicate near surface fluxes. When this happens the estimate of night time CO_2 flux will be an unreliable measure of ecosystem respiration (ER). To minimise the bias that this measurement limitation may induce in full day exchange values, various data filters are applied. Most commonly, minimum thresholds for average half hourly values of friction velocity, u^* (Goulden et al., 1996) are used for removing measurements when it is deemed that there is insufficient mixing. Van Gorsel et al. (2007) identified a maximum value of CO_2 flux in the early evening as the appropriate value for night-time respiration at their undulating site. This may not be an

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appropriate or reliable method for flat to moderate topography sites.

In the absence of independent measures or estimates of ER, many researchers extrapolate from night-time CO_2 flux into the daytime (Gilmanov et al., 2007; Lasslop et al. 2010; Wohlfhardt et al., 2005; Reichstein et al., 2005). However it is known that daylight suppresses autotrophic respiration (Heskel et al., 2013) and hence application of night-time derived respiration estimates during the daytime, will lead to an underestimate of plant C sequestration, often referred to as net primary production (NPP). The reason why foliar autotrophic respiration in the light is suppressed compared to respiration in the night is not completely understood (Ayub et al., 2014). Not with standing this, developing improved methods of estimating ER is important. To assist with this it is important to recognise that ER is deemed to be the sum of two components – heterotrophic (HR) and autotrophic respiration (AR). Autotrophic respiration is the efflux of CO_2 emanating from otherwise photosynthesising organisms that fix C while heterotrophic respiration is the efflux of CO_2 from all organisms that derive the C from other sources. Soil respiration has an efflux of CO_2 from living plant roots (autotrophic) and from a plethora of soil organisms (heterotrophic) occurring concurrently. Kuzyakov and Larionova (2005) concluded that the main reasons why NEE and NEP are often not equal is that the C input into the rhizosphere (part of the below ground carbon (BGC) when estimating NPP) is ignored and often there is no accounting or limited accounting of HR.

Estimates of HR have been made from extrapolation of linear regressions between total soil respiration and root biomass back to the y-intercept value i.e. at zero root mass (Koerber et al., 2010; Kuzyakov, 2006; Kucera and Kirkham, 1971). The causal link between LAI and ER is self-evident (Xu et al., 2004; Lindroth et al., 2008; Cleverly et al., 2013) and we propose that another method of deriving an estimate of HR is to extrapolate this function to the y-intercept with LAI = 0. However to quantify this relationship there needs to be variation in both ecosystem respiration and leaf area index, preferably with a wide range of both values to establish a robust relationship. In this study a wide range of LAI resulted from measurements made before and after the woodland ecosystem was burned in a bushfire.

The procedure used in this study to develop an improved estimate of ER and in turn HR was as follows. Daylight CO_2 flux values from half hourly EC measures were adjusted by subtracting an estimate of ER derived from the immediately preceding night-time flux values. The ratios of associated daytime to night-time soil temperature and daytime to night-time soil water content were used to scale the expected increased respiration as daytime temperatures were generally greater and soil water contents slightly lower than those at night. The adjusted

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daytime CO_2 flux was an estimate of ecosystem assimilation (A, µmol m-2 s-1). Then the relationship between A and photosynthetically active radiation (PAR, µmol m-2 s-1), more generally known as light response functions (Cleverly et al., 2013; Wohlfahrt et al., 2005; Lasslop et al., 2010), for each month was plotted. The use of A instead of NEE (Gilmanov et al., 2007; Lasslop et al. 2010; Wohlfhardt et al., 2005) in the light response function is an attempt to account for suppression of the daytime AR by light (Heskel et al., 2013; Kok, 1949; Kok, 1956). The relationship between A and PAR fits a rectangular hyperbola function that then enables extrapolation to PAR = 0 and hence an estimate of night-time ER.

The research null hypotheses of this paper are: (i) Ecosystem respiration will not be a function of leaf area index. (ii) Direct night-time respiration and respiration in the night derived from light response functions (using daytime data) will not correlate with each other and (iii) HR from NEE + NPP will not agree with HR estimated as a y-intercept from ER versus LAI.

2 Materials and methods

2.1 Site description and tower instrumentation

The flux monitoring site was a semi-arid mallee woodland on Calperum Station approximately 20 km from Renmark in South Australia (34˚00.163S, 140˚35.261E; Fluxnet site abbreviation: AU-Cpr). A 20m high EC tower, as part of the OzFlux Terrestrial Ecosystem Research Network (TERN) was erected in June 2010 (Flight Bros. Adelaide SA) and measurements began August 2010. The surrounding mallee ecosystem (Noble and Bradstock, 1989) is typical of semi-arid ecosystems, adapted to long term annual median rainfall (242 mm) encompassing drought years (Meyer, et al., 2015) and survives by accessing occasionally replenished water stores deep in the soil profile (Mitchell et al., 2009). The characteristic sand hills of the region run west to east with rolling undulations from swale to crest of 5 to 8 m. The area has the largest (>1 million hectares), continuous remnant of mallee habitat in Australia (Nulsen et al., 1986). Mallee surrounds the tower at least 10 km in every direction. The sand hills are stabilized by eucalypt species (*Eucalyptus Dumosa, Eucalyptus incrassata, Eucalyptus oleosa* and *Eucalyptus socialis*) with sparse plants of *Eremophila, Hakea, Olearia, Senna* and *Melaleuca* genera in the mid-storey and *Triodia spp.* in the understory.

The mean air temperature is 25 ˚C (data accessed from http: //www.bom.gov.au/) with hot summers including days with maximum temperatures greater than 40 ˚C. The area often experiences significant summer rainfall events of 20-60 mm in November to March after lengthy dry periods during the year. Soils are alkaline sand (94% sand, 4% silt and 2% clay) with an Australian classification of Tenosol (Isbell, 2002) and US Soil Taxonomy classification of Aridisol (Soil Survey Staff, 1996). Total organic carbon, nitrogen and carbonate (0-300 mm) are 0.5%, 0.04% and 0.25% respectively. Additional site detail and soil properties are given in Sun et al., (submitted) and Sun et al., (2015).

The site experienced a bushfire during 15 to 19 January 2014 burning 52 713 ha with a perimeter of 140 km according to the Country Fire Service, South Australia. The majority of instruments on the OzFlux tower were destroyed by the fire. These were restored within three months to monitor ecosystem recovery. A detailed description of the EC and ancillary instrumentation is in Meyer et al. (2015). Briefly, measurements of three-dimensional wind speed (CSAT3 sonic anemometer, Campbell Scientific Inc., Logan, UT, USA), virtual temperature (CSAT3), water vapour density in air and CO_2 density in air using an open-path IRGA (Licor LI7500, LiCor Biosciences, Lincoln, NE, USA), were recorded at a frequency of 10 Hz.

Auxiliary observations of solar irradiance (Es), air temperature, vapour pressure deficit (D) and rainfall, soil temperature and soil water content were also collected concurrently. Incident Es was observed from a four component radiometer that was positioned at a height of 20 m (CNR4, Kipp and Zonen, Delft, the Netherlands). D was determined as the difference between atmospheric vapour pressure (kPa) and saturation vapour pressure at air temperature (HMP45C, Vaisala, Helsinki, Finland) at a height of 2 m. An additional pyranometer (Licor LI2003S, LiCor Biosciences, Lincoln, NE, USA) was mounted at 20 m and cup anemometers and wind direction sensors (RM Young, Traverse City MI, USA) at 2 and 8.6 m. Onsite rainfall (CS7000, Hydrologic services, Warwick, NSW, Australia) was measured with the tipping bucket gauge (0.2 mm resolution) mounted on a stand of height 0.65 m in a clear area 8 m from the tower. Soil temperature and water content sensors (CS650, Campbell Scientific, Townsville, Australia) were buried 10 metres away from the tower base with multiple depths, ranging from 0.1 m to 1.8 m. Sensors were placed in bare soil (inter-canopy) or beneath eucalypt canopies (under canopy). The collars for measuring soil respiration in burnt Mallee were within 200 m from the tower base.

Covariances were computed every 30 min to generate fluxes following standard data processing and quality assurance and correction procedures (Isaac et al., (In preparation for this Special Issue); Cleverly et al., 2013; Eamus et al., 2013), hereafter referred to as OzFluxQC. A friction coefficient (u^*) threshold was then calculated and set to 0.26 m s^{-1}, 0.21 m s^{-1}, 0.23 m s^{-1}, 0.25 m s^{-1}, 0.26 m s^{-1} and 0.26 m s^{-1} for the years 2010, 2011, 2012, 2013, 2014 and 2015 respectively.

To calculate the effective sampling footprint of the tower we used the Kormann-Meixner method (Kormann and Meixner, 2001), employing a modified version of the ART Footprint Tool of Neftel et al. (2008). The Kormann-Meixner footprint determines the two-dimensional density function for an ellipse upwind from the tower. The predominant wind direction here is from the south-westerly quarter. For every 30 minute measurement of wind speed and direction, mixing and buoyancy parameters the data is filtered according to the Kormann-Meixner constraints. Analysis of the seasonal effects exhibited a smaller footprint in summer which reflected the increased mixing in summer as well as the influence of more frequent winds from the northerly quarter. The annual average of the footprint area for 2014 displayed a distance from the tower of 500 m for at least 10% of the maximum contribution (1300 m for at least 1%).

The regression of latent energy plus sensible heat (LE + H) against net radiation plus soil heat flux (Rn + G) was used to check energy balance closure. From 1 August 2010 to 31 August 2013 the relationship was (LE + H) = 0.8769 (R_n + G) + 2.5095, r^2 = 0.9159. This indicated that energy balance was not completely achieved, as is commonly observed with the eddy covariance method (Twine et al., 2000).

2.2 Light response functions

The light response function needed was the relationship between the assimilation rate (A) and the incoming radiant energy. Assimilation was partitioned from NEE as shown in the schematic flow chart (Fig. 1). To calculate A from NEE the daytime values of NEE were increased in absolute magnitude by the expected rate of CO_2 emission from the soil and plant system. The daily night-time 30 minute respiration (AR + HR) values were adjusted using the ratio of average daytime soil temperature to the night-time soil temperature. A further, generally minor adjustment was made using the ratio of average daytime to night-time soil water content measured at 100 mm depth. The adjusted night-time average value was then subtracted from each daytime 30 minute flux to give an assimilation (A) rate with an absolute value greater than NEE. The calculation of A for every 30 minutes of the daytime in each month was then regressed against short wave radiant energy converted to photosynthetically active radiation (PAR) in µmol m^{-2} s^{-1} according to Meek et al., (1984) and McCree (1972) as detailed in Biggs (1984).

A rectangular hyperbola was fitted to the 30 minute data each month (Eqn. 1, Wohlfahrt et al., 2005; Lasslop et al., 2010; Cleverly et al., 2013) with starting values of -10, 300 and 0.5 for the net saturated A (V_{max}), saturating PAR (K_m) and constant (c) respectively, all in µmol m^{-2} s^{-1}. The value of A when PAR = 0 was assigned as the night-time respiration (R_{night}) value for that month. Further, rearranging the same equation and solving for the value of PAR when A = 0 (Eqn. 2) gave the compensation point when low PAR and hence photosynthesis no longer compensated respiration (Heskel et al., 2013). When PAR was greater than this compensation point, ER was deemed to be supressed by the incoming radiant energy.

$$A = V_{max} \times (PAR / (K_m + PAR)) + c \qquad \text{Eqn. 1}$$

Where V_{max} is the light saturated net photosynthetic rate
K_m is the saturation light intensity
c is a constant

$$PAR = (K_m (A - c)) / (V_{max} - A + c) \qquad A = 0 \qquad \text{Eqn. 2}$$

Fitting the rectangular hyperbola model used the SPSS procedure (IBM SPSS Statistics V. 21 New York, US) of nonlinear weighted least squares fitting using the Levenberg-Marquardt algorithm.

2.3 Leaf area index

During May 2013 to September 2015, plant area index (PAI) of the canopy above 0.5 m from the ground was measured optically using the digital cover photography method (DCP) (Pekin and Macfarlane, 2009, Macfarlane et al., 2007) as described in Eamus et al., (2013). A 1 ha (100 m x 100 m) area immediately to the north west of the tower was marked and 10 x 100 m transects were identified along which photographs were taken at 10 m intervals. Photographs were taken using a Sony Nex-7 DSLR camera fitted with a lens of 25 mm focal length. The camera settings were automatic exposure, aperture-priority mode, F-stop of 9.0 and ISO 400. The camera was oriented to 0° nadir (viewing upward). Calculation of PAI used an extinction coefficient of 0.5. For eight months after the fire the photographs taken were of the trunks and branches without leaves. This area could be subtracted from the previously determined plant area to obtain LAI.

For cross calibration purposes leaf area was determined directly by destructively collecting epicormic stem and leaf regrowth of five trees in April 2015, approximately one year after the bushfire. Leaves from a stem were removed, and a subsample of leaves was measured with a leaf area meter. The subsample and main leaf sample were weighed after oven drying at 60˚C for 48 hours, and the specific leaf area of the subsample was used to calculate the whole tree leaf area.

2.4 Soil respiration, litter collection, tree spacing and biomass

Soil CO_2 efflux was measured monthly from July 2014 to June 2015 (total 12 sampling campaigns) with a manual chamber connected to an infra-red gas analyser (LI-8100, LI-COR Inc., Lincoln, Nebraska, USA). Details are in Sun et al., (accepted May 2016).

In May 2013, 3 litter trays (450 × 340 × 55 mm aluminium BBQ trays) were placed in the 1 ha area adjacent to the tower. These were dug in and secured so that the upper edge was flush with the ground surface. Litter was collected monthly, dried at 60 ˚C for 48 hours and weighed. The carbon content was assumed to be 35% of plant material dry mass (Hadley and Causton, 1984).

On 17 June 2014 remnant (burnt) tree trunks within the 1 ha area adjacent to the tower were viewed aerially, without the obstruction of any leaf canopy using a 3D Robotics RTF Y6 conservation drone. Images were captured at 70 metres above ground at a resolution of 21.6 mm per pixel in RGB colour. Images were mosaicked with Pix4Dmapper and improved by referencing to an existing ortho-rectified aerial photographic image. The central point of each mallee tree was marked with a digital dot while viewing the imagery at scale of 1:100 in ArcGIS. The mean distance between trees could then be calculated and this spacing used to scale up biomass and LAI from the sub sample measurements.

The total carbon associated with the 1 ha area was estimated from the measurements of tree numbers and dry mass of eight destructively sampled trees. This enabled an estimate of aboveground carbon (AGC). An estimate of belowground carbon (BGC) was made using soil respiration measurements and litter amounts (Koerber et al., 2009; Clark et al., 2001; Raich and Nadellhoffer, 1989; Nadellhoffer et al., 1998).

3 Results

The results were determined primarily from the light response functions and the extrapolated values of respiration in the night from daytime A. These values reflect the environmental conditions the mallee ecosystem was experiencing each month of a year.

3.1 Net ecosystem exchange

During the four years prior to 2010, the annual average rainfall was 215 mm, with each year being consistently below the long term median annual rainfall of 242 mm. These dry years were part of a prolonged dry period generally referred to as the "Millennium drought". Significant rain (259 mm) fell in the last five months of 2010, the Millennium drought ended and the mallee ecosystem became a C sink with monthly NEE of -15.49 g C m^{-2} $month^{-1}$ for December 2010. During 2011, with further rain (511 mm for the year) the mallee responded and recovered as indicated by an increase in NEE to -25.70 g C m^{-2} $month^{-1}$ for July 2011 and a maximum of –44.46 g C m^{-2} $month^{-1}$ in April 2011. This increased uptake of C corresponded to an observed increase in green leaf canopy of both trees and grass cover that was reflected in increased remotely sensed NDVI values and inferred LAI back calculated from latent energy exchange determined by the EC measurements (Meyer et al. 2015). This response is consistent with the wide area response during March to May 2011 of Australian arid and semi-arid vegetation to the summer rainfall of 2010 – 2011 (Poulter et al., 2014; Cleverly et al., 2016). During 2012, the recovered ecosystem was sustained during the first half of the year with maximum NEE of -42.83 g C m^{-2} $month^{-1}$ in April 2012. The second half of 2012 was dry (62 mm of rain) and this lower than average rainfall continued into most of 2013. In 2013 the maximum NEE was only -17.82 g C m^{-2} $month^{-1}$ in August. This rate is similar to that recorded at the end of the Millennium drought in late 2010. In January 2014 the destruction of the vegetation in the bushfire resulted in the ecosystem becoming a carbon source, with a maximum emission of 13.53 g C m^{-2} $month^{-1}$ recorded in May 2014. Signs of vegetation recovery were evident in July 2014 as the mallee trees sprouted epicormic stems and juvenile leaves from the lignotubers. In the months of August and September 2014, NEE was -7.73 and -7.59 g C m^{-2} $month^{-1}$ respectively. In 2015, the ecosystem was a sink with a maximum NEE of -20.75 g C m^{-2} $month^{-1}$ in June. Annual NEE from OzFluxQC for each year along with the partitioning into gross primary productivity (GPP) and ER are given in Table 1.

Biogeosciences Discuss., doi:10.5194/bg-2016-182, 2016
Manuscript under review for journal Biogeosciences
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3.2 Assimilation light response functions

The half hourly assimilation (A) values and associated radiation (PAR) values for each month of the entire measurement period were plotted and the assimilation light response function fitted (Table 2). In the summer of 2012, throughout 2013, and the spring and summer of 2015, when the mallee ecosystem was dry, regression r^2 were higher with PAR threshold < 1500 µmol m^{-2} s^{-1}. Even so the regressions had higher coefficients during the winter months and were lower in summer months. This likely indicates that assimilation was more constrained by available radiation in the cooler, less evaporative winter months, while in summer, assimilation was constrained by greater stomatal control as water availability to meet high evaporative demand was limiting (Ayub et al., 2011; Meyer et al., 2015).

The relationship between night-time respiration, derived from the flux tower measurements using OzFluxQC processing against night-time respiration determined indirectly from the y-intercept of daytime A and PAR response functions (Fig. 2) are significantly correlated and approximately similar in the years preceding the bushfire although 2013 was experiencing drought (Pearson correlations, 2010: $r = 0.873$, $P \leq 0.05$; 2011: $r = 0.58$, $P \leq 0.05$; 2012: $r = 0.615$, $P \leq 0.05$; 2013: $r = 0.27$, $P = 0.396$, Fig. 2). In 2014 after the bushfire, all values were small (< 0.7 µmol m^{-2} s^{-1}) with the flux tower values generally being larger than those derived from the light response functions. In 2015, night-time respiration from the tower and from light response curves continued to be small. The spread of respiration values determined from the assimilation light response function is similar in 2014 and 2015 but was smaller than those estimated in the years before the bushfire.

3.3 Comparison of ER from (NEE – A) and ER from OzFluxQC

Calculation of ER as (NEE – A) was significantly correlated to ER from the processing by OzFluxQC, Pearson $r = 0.838$ $P \leq 0.0001$ (Fig. 3). From the equation of the line ($y_0 = 0.1612x + 0.0085$, $r^2 = 0.6977$), the OzFluxQC is underestimating ER with smaller positive rates compared to ER from a calculated A. The larger positive ER corresponds to a more negative ER if using the convention of negative rates for respiration (Atkin et al., 2013) and is in line with their statements that not incorporating supressed daytime respiration underestimates ER.

3.4 Relationship between ER and LAI and estimates of HR

The relationship between ER derived from (NEE – A) and LAI for 25 months around the bushfire was highly significant (Fig. 4; y_0 = 1.43x +0.398; Adj. r^2 = 0.395, Pearson correlation, r = 0.648 $P \leq 0.0001$). From this relation the inferred ER for this period is 0.398 µmol m^{-2} s^{-1}. The ecosystem respiration was standardized to 20 ˚C and 0.03 g g^{-1} soil water content to remove seasonal variation. There are three outlier points with apparently suppressed ER for the months of April, May and June 2014, immediately after the bushfire. For the period from July 2014 to June 2015 that corresponds to the year that in-situ soil respiration measurements were made post fire, the y-intercept is 0.4316 µmol m^{-2} s^{-1} (y_0 = 1.365x + 0.4316, Adj. r^2 = 0.3249, Pearson correlation r = 0.570 P = 0.053). The value at LAI = 0 gave an estimate of ER and more particularly HR of 163.44 gC m^{-2} year^{-1}.

An alternative approach to estimate HR is to calculate the sum of AGC and BGC, that is effectively net primary production (NPP), and subtract OzFluxQC derived NEE. Using the mean ground area per tree of 16 m^2 derived from drone imagery, the annual increase in AGC was estimated to be 105.68 ± 27.37 gC m^{-2} year^{-1}. For July 2014 to June 2015, soil respiration was estimated to be 490.72 gC m^{-2} (details in Sun et al., 2016), litter fall was 566.17 ± 62.57 gC m^{-2} and hence BCG was 75.45 gC m^{-2} year$^{-1.}$ The sum of AGC and BGC and therefore NPP is 181.13 gC m^{-2} year^{-1}. With NEE for the year of -46.54 ± gC m^{-2} year^{-1} the estimate of HR is 134.59 gC m^{-2}. This compares very favourably with the estimate (163.44 gC m^{-2}) from light response functions and is 44% of NEE. This coincidence indicates that the method of extrapolation of the assimilation (A) and incoming energy (PAR) relationship to PAR = 0 (i.e. the y-intercept) provides an estimate of ER each month incorporating AR.

4 Discussion

In this paper we have demonstrated another way to partition NEE recorded by EC towers into the C sequestered by photosynthesis and the efflux of C from respiration. Calculation of daily NEP using an estimate of ER from extrapolation of ecosystem light response functions using A instead of NEE, indicates that derived NEP is inevitably larger i.e. the NEE light response function usually overestimates daily respiration (Ayub et al., 2011; Heskel et al., 2013). The method of estimating HR from the extrapolation of the ER (NEE-A) versus LAI, is similar to that of estimating HR from the y-intercept of soil respiration and root mass (Koerber et al., 2010; Kuzyakov, 2006; Kucera and Kirkham, 1971). The concept of the y-intercept providing an estimate of heterotrophic soil respiration from the assimilation light response function is novel and hasn't been used to assist partitioning EC derived NEE.

The estimates for HR of 163.44 gC m^{-2} $year^{-1}$ from light response function derived ER versus LAI or 134.59 gC m^{-2} $year^{-1}$ from (NEE + NPP) are equivalent to 1.63 tC ha^{-1} $year^{-1}$ and 1.34 tC ha^{-1} $year^{-1}$ respectively. As expected, these are lower but of the same order of magnitude as that estimated (8.13 tC ha^{-1} $year^{-1}$) in much wetter and more plant productive vegetable farming regions in the UK (Koerber et al., 2009).

Partitioning of NEE derived from EC measurements indicates that in semi-arid environments, the timing of rainfall relative to preceding drying greatly influences the outcome of the dynamic balance between sequestration and respiration. For example, Xu et al. (2004) found that in a Mediterranean grassland the early onset of rain in the winter growing season resulted in C assimilation i.e. gross primary productivity (GPP) to be greater than ER and NEE was negative i.e. the ecosystem was a carbon sink. However if significant rainfall did not occur until late in spring or early summer and the water stressed grass was dead, ER was greater than GPP and NEE was positive i.e. the ecosystem was a carbon source. Monthly values of NEP and ER derived in this study suggest that the timing of rainfall in relation to the preceding dry or wet period was more important in determining the net C balance of the ecosystem than the total amount over the course of a year. Paul Jarvis's research (Jarvis et al., 2007) on soil respiration pulses after rain, carrying on the discovery by H.F. Birch 50 years ago (the "Birch" effect) showed the same effect. His research and that of Xin Wang et al (2014) suggests that increased rainfall in summer, along with increasing ambient temperature from global warming will increase the contribution of HR in soil respiration. Soil respiration pulses following rainfall may be enhanced by the availability of organic breakdown materials coming from photo-degradation during drought periods (Ma et al., 2012). Rainfall that irregularly occurs in persistently arid areas such as the *Corymbia* savanna and Mulga ecosystems of inland Australia seems to cause net carbon loss at least in the short term (Cleverly et al., 2016).

The relationship between direct and indirect derived night-time respiration shown in Fig. 2 was close to 1:1 during 2010 and 2011. Drying in 2012 persisted into 2013 and this seems to have affected this relationship. With the bushfire in 2014 there was no active

Biogeosciences Discuss., doi:10.5194/bg-2016-182, 2016
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photosynthetic canopy and only a small but increasing amount in 2015, the amount of respiration declined presumably because both AR and HR declined – AR because the majority of the above ground growth was dead and HR because there is no supply or little supply of photosynthetically derived C from the above ground system to below ground. The reasons why EC estimates of night-time respiration in 2014 appear to be large relative to the light response function is uncertain. With loss of the tree, mid story and ground canopy the atmospheric exchange and mixing would be different. It is not clear why this may cause what appears to be an over-estimate of the CO_2 flux. However it is equally possible that the light response functions are underestimating the flux since active leaf area is very low and hence assimilation is very limited.

After careful consideration, two more problems had to be reconciled. The first is calculations of assimilation were an underestimate in the outset. With ER equilibrated in the night and the day from a ratio of the soil temperature and soil water content in the night and the day, subsequent subtraction covers over some of the A seen as respiration in the day is in fact suppressed (Heskel et al., 2013). For example if ER was constant in the night and the day at 3 μmol $m^{-2}s^{-1}$ and the photosynthetic rate is -8 μmol $m^{-2}s^{-1}$, when the night is subtracted away from the day we are left with an assimilation of -2 μmol $m^{-2}s^{-1}$ however if ER is 1 μmol $m^{-2}s^{-1}$ in the day then assimilation will be -4 μmol $m^{-2}s^{-1}$. Therefore we had an assimilation rate that was an underestimate. In the future we aim to develop methods for conducting linear regressions to estimate autotrophic respiration in the daylight (Heskel et al., 2013; Kok, 1949; Kok, 1956) for correcting the underestimate of A (Koerber et al., unpublished).

The second problem is whether our calculations of A require correction like *in vivo* construction of light response functions requiring A versus CO_2 partial pressure (p_i) curves at three low light intensities (Villar et al., 1994; Kirschbaum and Farquhar, 1987). As p_i is increased at low light intensity, measurements of A increase. Therefore p_i should be standardized for all light intensities and A adjusted to ensure foliar AR provides a correct estimate of the Kok effect and hence A is not an overestimate. Our tower measurements provided multiple A estimates at each light intensity with an external CO_2 partial pressure that was reasonably constant. With this setting the EC derived light response functions do not require standardization.

5 Conclusion

The advantage of using the light response function approach to determine respiration when PAR = 0 is that it is non-destructive. The ecosystem remains intact, soils are not disturbed and there is no need to measure respiration of the plants directly with all of the attendant problems of sufficient sampling to assure representativeness. In this study we did field measurements that were destructive but only to the extent of AGC necessary for the NPP. The BGC was estimated from litter collections and soil respiration. This study highlights the importance of measuring soil respiration as an adjunct measurement.

The similarity in heterotrophic soil respiration estimated by field measurements and from the determination of assimilation from partitioning the NEE as described here is encouraging, only 28.85 gC m^{-2} difference. This result indicates that the NEE and NEP are balanced at our site and we did not underestimate NEP from our field measurements. From our initial calculations, our measurements provide rarely available evidence of the large contribution of basal soil respiration (44%) to the total C balance. Management of the land by land use managers needs to minimize the formation of ecosystems susceptible to larger emissions of basal soil respiration arising from our changing climate. There is much to gain from understanding dry and arid ecosystem functioning of the plants within the sandy alkaline soils of southern Australia. Mallee's are an important biomass crop, potentially providing an increasing income from payments for carbon sequestration, for landholders.

This study has been able to reject all three null hypotheses. When the hypotheses are addressed in reverse order, firstly, we were able to estimate the heterotrophic soil respiration from field measurements and the y-intercept of ecosystem respiration versus leaf area index. Secondly, light use efficiency functions for the respiration in the dark from rectangular hyperbola agree with direct night time data. Lastly, ecosystem respiration is a function of LAI.

Table 1. Annual GPP, ER, NEE in gC m^{-2} $year^{-1}$ and rainfall for 2011 to 2015. Values are from OzFluxQC. Measurements started at the tower in August 2010 and GPP, ER, NEE and rainfall are sums for August to December 2010 (5 months).

Year	GPP	ER	NEE	Rainfall mm
2010	100.74	29.84	-70.9	259.0
2011	432.05	114.37	-317.68	510.8
2012	377.84	93.68	-284.16	211.2
2013	237.15	68.73	-168.41	242.4
2014	52.03	32.57	-19.46	211.6
2015	155.02	56.55	-98.47	241.4

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Table 2. Coefficients from assimilation light response functions. Units are µmol m^{-2} s^{-1}. Rainfall in brackets is from Renmark when the EC measurement system was not in operation after bushfire.

	Rainfall mm	Compensation point when Fc = 0	Vmax	Km	ER in **night**, r^2 and n from rectangular hyperbola
		Units are all µmol m^{-2} s^{-1}			
2010					
July	6.0	76.3	-3.2	456.8	0.47 r^2=0.74 n=25
August	24.0	96.5	-3.9	392.8	0.78 r^2=0.41 n=520
September	48.0	110.2	-4.5	558.3	0.74 r^2=0.40 n=565
October	67.0	140.8	-4.7	825.5	0.68 r^2=0.26 n=633
November	35.0	160.4	-4.4	331.4	1.44 r^2=0.28 n=615
December	86.0	115.3	-4.8	316.5	1.28 r^2=0.25 n=749
2011					
January	87.4	135.5	-7.3	577.9	1.39 r^2=0.36 n=743
February	109.0	153.4	-9.9	522.9	2.24 r^2=0.46 n=604
March	63.4	114.7	-12.1	887.6	1.39 r^2=0.61 n=613
April	4.4	73.3	-12.1	1024.0	0.81 r^2=0.52 n=541
May	14.2	86.4	-11.2	576.3	1.46 r^2=0.52 n=445
June	4.8	72.7	-9.7	647.3	0.98 r^2=0.61 n=459
July	13.4	85.7	-7.8	493.2	1.15 r^2=0.56 n=497
August	25.0	102.0	-7.6	492.7	1.30 r^2=0.38 n=510
September	8.2	..108.9	-5.7	460.5	1.09 r^2=0.28 n=577
October	29.8	99.4	-5.0	316.8	1.20 r^2=0.26 n=656
November	59.4	166.2	-5.6	515.8	1.37 r^2=0.29 n=667
December	91.8	98.4	-6.8	793.0	0.75 r^2=0.27 n=769
2012					
January	27.4	122.7	-7.0	423.9	1.56 r^2=0.40 n=777
February	86.8	85.7	-5.8	689.1	1.65 r^2= 0.24 n=657
March	9.4	150.7	-10.4	215.5	1.86 r^2=0.49 n=643
April	5.4	86.7	-9.0	456.9	1.44 r^2=0.36 n=550
May	9.0	86.5	-8.8	380.6	1.64 r^2=0.52 n=503
June	11.0	89.3	-10.3	743.7	1.10 r^2= 0.61 n=452
July	23.6	109.5	-9.3	753.2	1.18 r^2=0.56 n=485
August	8.2	89.2	-8.6	743.5	0.92 r^2=0.64 n=571
September	5.8	96.2	-6.1	353.2	1.31 r^2=0.14 n=488
October	3.8	88.6	-4.7	626.5	0.59 r^2=0.15 n=445
November	14.0	65.1	-3.5	222.7	0.79 r^2=0.29 n=432
December	6.8	61.8	-4.8	726.1	0.38 r^2=0.22 n=318

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2013					
January	1.0	44.1	-3.7	613.6	0.25 r^2=0.14 n=305
February	36.8	105.0	-3.9	772.8	0.47 r^2=0.08 n=275
March	2.2	184.9	-7.6	1065.8	1.12 r^2=0.31 n=465
April	13.6	48.3	-10.5	1578.7	0.81 r^2=0.31 n=266
May	35.4	81.8	-6.5	1792.4	0.61 r^2=0.39 n=208
June	32.0	138.3	-9.7	617.5	1.77 r^2=0.63 n=275
July	24.4	88.1	-10.8	1249.5	0.71 r^2=0.60 n=392
August	10.6	90.8	-9.5	1045.7	0.78 r^2=0.58 n=353
September	26.2	160.4	-6.0	578.3	1.30 r^2=0.30 n=396
October	9.2	60.2	-4.0	350.7	0.59 r^2=0.24 n=221
November	3.6	23.6	-3.9	508.1	0.17 r^2=0.14 n=435
December	27.2	46.3	-3.8	339.0	0.46 r^2=0.16 n=303
2014					
January	(6.8)	45.8	-5.2	1087.1	0.41 r^2=0.14 n=165
February	(84.4)				
March	(15.0)				
April	(35.6)	-1695.8	-0.4	532.1	0.55 r^2=0.00 n=66
May	28.4	-0.8	0.7	39.8	0.02 r^2=0.01 n=334
June	13.8	2364.7	-1.0	1371.1	0.65 r^2=0.02 n=368
July	4.6	333.3	-1.0	1204.0	0.22 r^2=0.02 n=382
August	18.8	131.6	-4.2	1973.6	0.27 r^2=0.23 n=477
September	6.6	89.4	-2.8	1331.1	0.18 r^2=0.12 n=317
October	0.6	92.3	-1.4	171.4	0.50 r^2=0.06 n=618
November	9.2	95.5	-1.2	378.4	0.24 r^2=0.03 n=686
December	13.8	135.6	-2.0	520.8	0.40 r^2=0.08 n=696
2015					
January	68.8	104.4	-2.9	584.1	0.44 r^2=0.30 n=722
February	0.6	93.0	-2.7	459.3	0.45 r^2=0.21 n=378
March	0.0	106.2	-2.1	271.2	0.60 r^2=0.16 n=420
April	65.4	129.3	-2.7	411.3	0.65 r^2=0.20 n=448
May	9.8	97.2	-6.8	638.2	0.90 r^2=0.61 n=376
June	17.8	80.7	-7.5	671.4	0.80 r^2=0.38 n=280
July	6.0	84.7	-6.0	562.0	0.78 r^2=0.57 n=362
August	20.4	110.7	-5.8	524.6	1.01 r^2=0.41 n=469
September	17.0	102.8	-4.2	368.5	0.92 r^2=0.28 n=561
October	1.5	16.3	-3.4	2480.4	0.02 r^2=0.08 n=232
November	23.0	21.0	-2.4	774.2	0.06 r^2=0.10 n=419
December	0.0	91.4	-1.6	661.5	0.19 r^2=0.07 n=419

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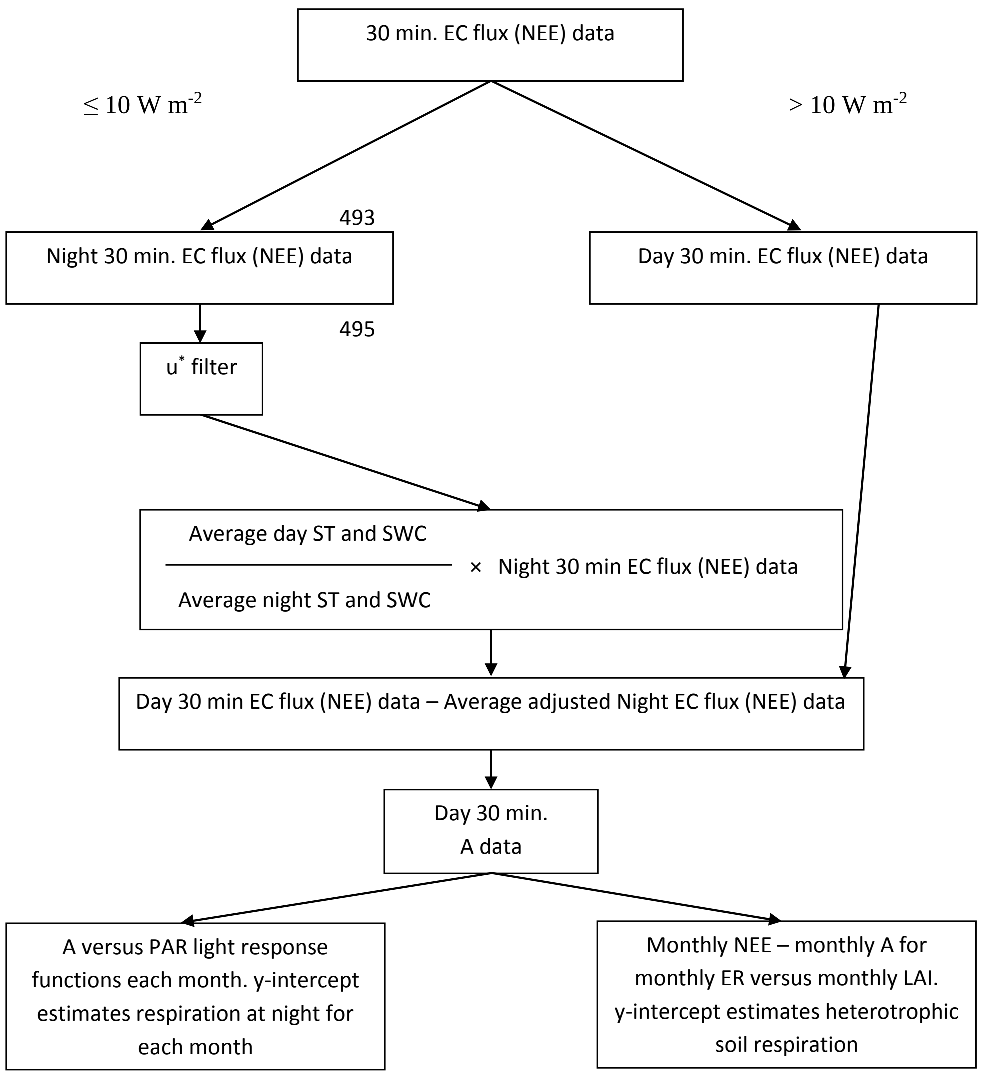

Figure 1. Schematic flow chart showing the method for partitioning carbon fluxes.

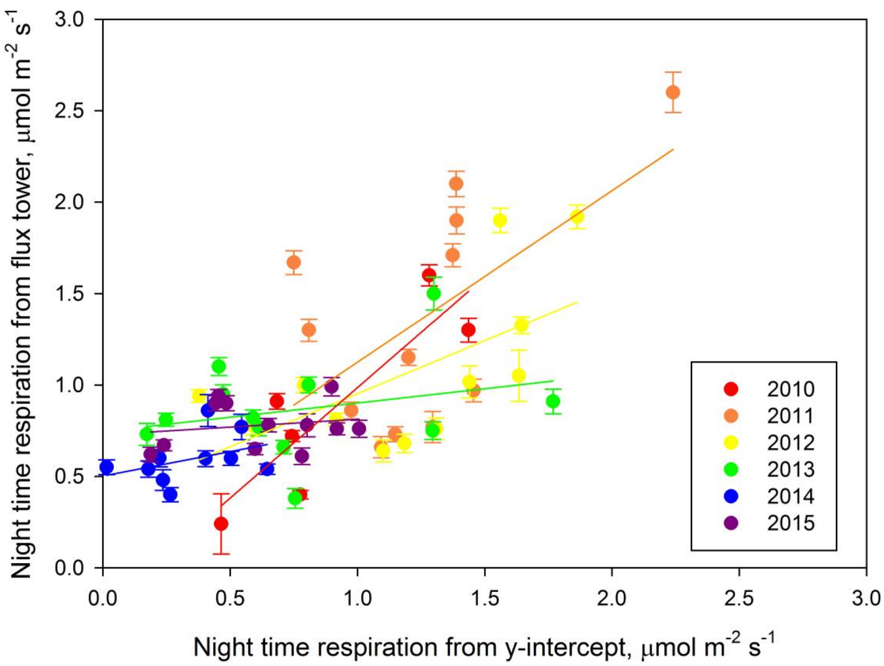

Figure 2. Night respiration from the EC tower measurement system and the y-intercept approach with daytime data.

2010: y_0 =1.20x – 0.22 Adj. r^2 = 0.7617

2011: y_0 = 0.94x + 0.19 Adj. r^2 = 0.34

2012: y_0 = 0.58x + 0.37 Adj. r^2 = 0.3783

2013: y_0 = 0.16x + 0.75 Adj. r^2 = 0.07

2014: y_0 = 0.27x + 0.50 Adj. r^2 = 0.1477

2015: y_0 = 0.09x + 0.73 Adj. r^2 = 0.0312

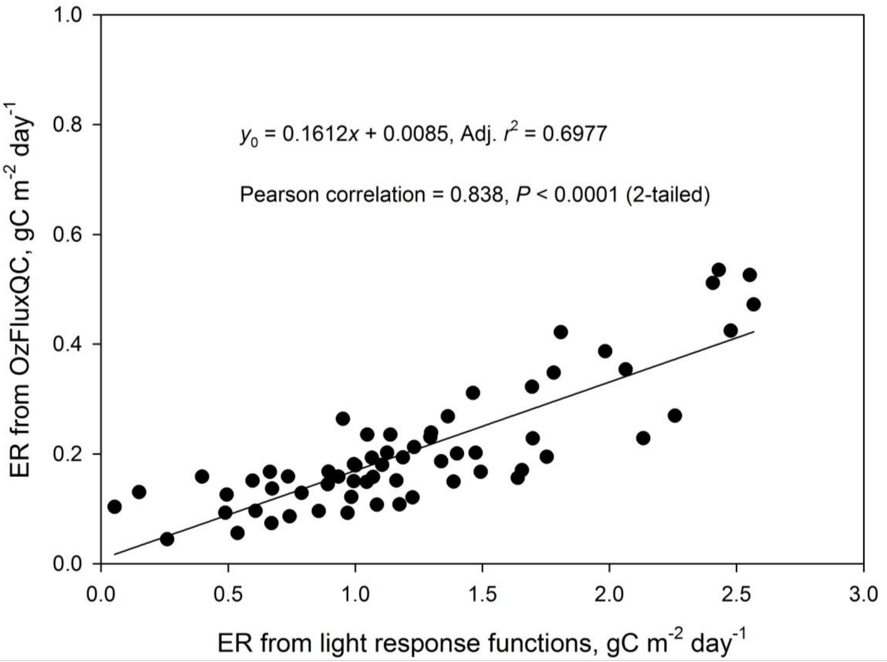

Figure 3. Comparison of ecosystem respiration from the OzFluxQC processing and the light response function of calculated assimilation.

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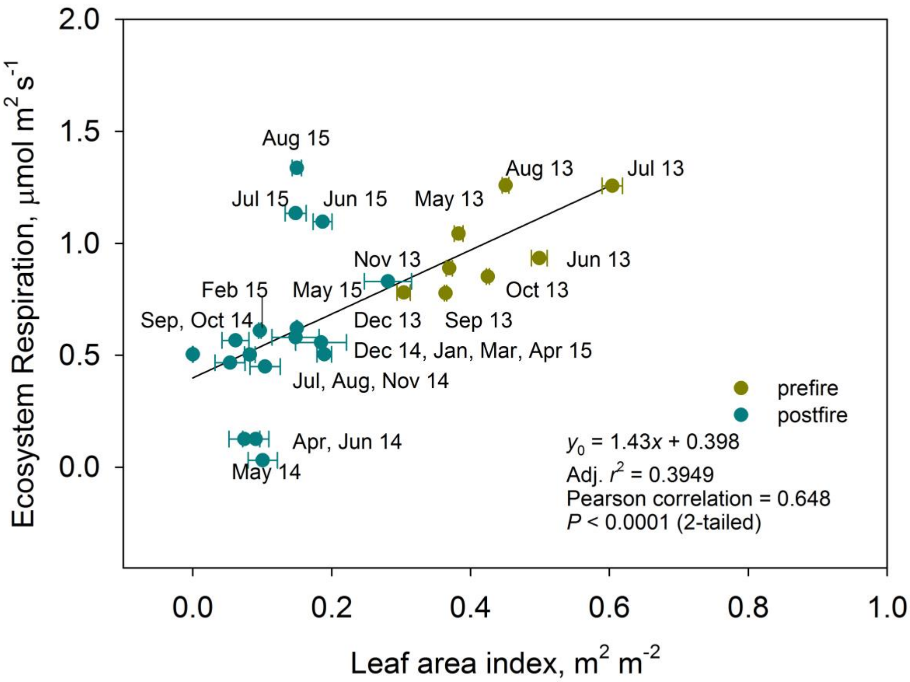

Figure 4. Comparison of ecosystem respiration from the light response function with calculated assimilation extrapolated to LAI = 0 and LAI from digital cover photography. The ecosystem respiration was standardized to 20 ˚C and 0.03 g g^{-1} soil water content.

Author contributions. G.R. Koerber and W.S. Meyer designed the experiment and carried it out. G.R. Koerber, P. Cale, Q. Sun, W.S. Meyer and C. M. Ewenz performed field work. G.R. Koerber, W.S. Meyer and C. M. Ewenz performed data collection and processing. G.R. Koerber and W.S. Meyer prepared the manuscript with contributions from all co-authors.

Acknowledgements. This work was partly supported by grants from the Australian government's Terrestrial Ecosystems Research Network (TERN) (www.tern.org.au). TERN is a research infrastructure facility established under the National Collaborative Research Infrastructure Strategy (NCRIS) and Education Infrastructure Fund, Super Science Initiative, through the Department of Industry, Innovation, Science, Research, and Tertiary Education. Thank you to 12 National Australia Bank employees under the support and expert guidance of Cassandra Collins from the Earthwatch Institute and Peter Cale from the Riverland Australian Landscape Trust.

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