

## Meetings

## Tracking the origins of the Kok effect, 70 years after its discovery

The 18<sup>th</sup> New Phytologist Workshop 'The Kok effect: beyond the artefact, emerging leaf mechanisms (KOALA)' Angers, France, July 2016

## Introduction

The 18<sup>th</sup> New Phytologist Workshop was dedicated to possible causes of the Kok effect, the typical break in the light response curve of net photosynthesis. Available data obtained since its discovery in 1948 show that the effect is not purely caused by a down-regulation of respiration, contrary to the commonly accepted view. However, estimates of leaf respiratory rates obtained in various ecosystems with techniques including the Kok method appear to be widely consistent across different studies, suggesting that Kok-derived values can be used as a surrogate for actual day respiration values.

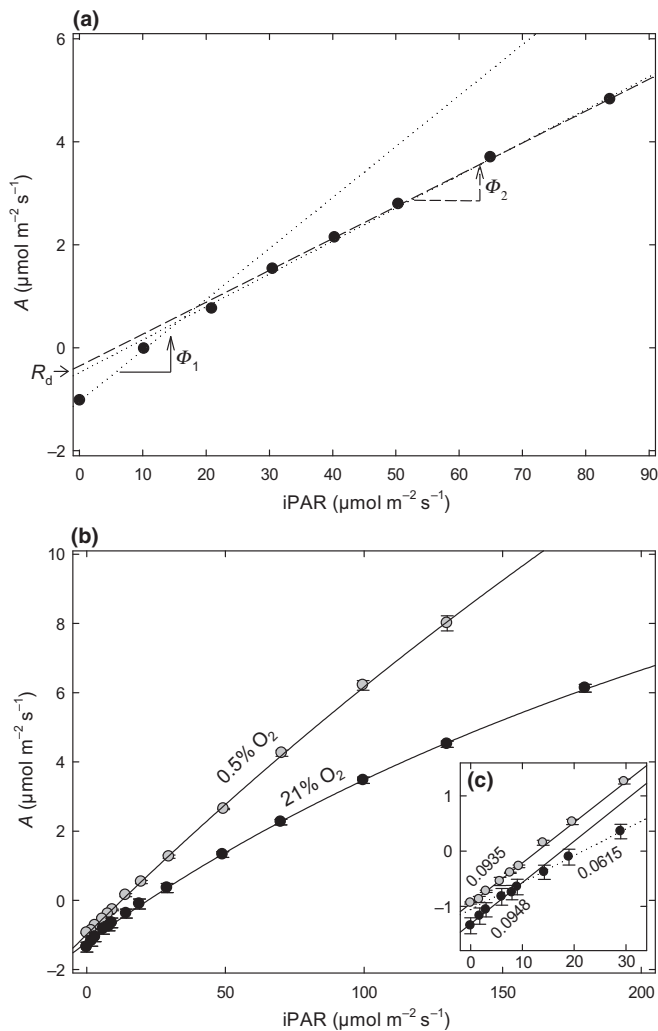
Gross CO<sub>2</sub> assimilation of photosynthetic organs of plants is accompanied by concurrent efflux of CO<sub>2</sub> by photorespiration and day respiration (i.e. nonphotorespiratory CO<sub>2</sub> evolution in the light). While the rate of photorespiration can be predicted using the internal CO<sub>2</sub> mole fraction and equations that describe gas exchange (taking into account the stoichiometry of CO<sub>2</sub> liberation with respect to O<sub>2</sub> fixation by ribulose-1,5-bisphosphate carboxylase/oxygenase), estimating day respiration is much more challenging because there is no equation that can predict its rate as a function of net photosynthesis, CO<sub>2</sub> mole fraction or other environmental parameters. That is, in equations describing gas exchange (or isotopic mass balance), day respiration ( $R_d$ ) has to be determined separately or simply assumed to model net carbon (C) exchange. At the leaf level, day respiration represents a C loss of *c.* 5% of gross-fixed CO<sub>2</sub> but this proportion is highly variable, depending on species and conditions (see, e.g. Atkin *et al.*, 1997). Estimates of day respiratory CO<sub>2</sub> loss rely on specific techniques used to measure  $R_d$ : amongst them, the Kok method is certainly the most popular, because it is easy to implement in the laboratory or in the field using classical gas-exchange systems. This method takes advantage of the 'Kok effect', a phenomenon first described in the 1940s in unicellular algae (Kok, 1948, 1949). This effect is further described later, and in Fig. 1. The Kok effect is believed to be primarily caused by the inhibition of respiration by light and thus provides a direct way to estimate  $R_d$ . At the present date, *c.* 800 published works have used, or cited, the Kok method, representing *c.* 40% of articles that involve a measurement of  $R_d$  or deal with day respiration. However, some persisting doubt remains about the validity of this method, simply because the Kok effect is inconstant

and influenced by environmental conditions (such as O<sub>2</sub> mole fraction) in ways that may not be consistent with day respiratory metabolism. Considering the wide range of applications, and the considerable number of articles that have been published, there is an urgent need to clarify the origin of the Kok effect and to evaluate its relevance to measure  $R_d$ . This was the objective of the 18<sup>th</sup> New Phytologist Workshop that took place in July 2016 in Angers (France).

## What is the Kok effect?

The 'Kok effect' refers to the change in quantum yield of net photosynthesis ( $\Phi$ ) at low light levels: at very low light levels (typically 0–20  $\mu\text{mol m}^{-2} \text{s}^{-1}$  of incident photosynthetically active radiation, iPAR), the quantum yield (denoted as  $\Phi_1$ ) is larger than that observed at higher light levels ( $\Phi_2$ ). In practice, when a light response curve of net photosynthesis is performed, there is a change in the slope and a break point (examples are shown in Fig. 1). In general,  $\Phi_1$  is *c.* 0.1 under standard conditions (25°C, 21% O<sub>2</sub> and 380  $\mu\text{mol mol}^{-1}$ ) while  $\Phi_2$  is *c.* 0.06 (Fig. 2). These values are rather similar when net photosynthesis is measured as CO<sub>2</sub> fixation or O<sub>2</sub> release (but data on the assimilatory quotient at low light, presumably close to 1, are scarce). Thus, the relative change in quantum yield above the break point is about  $(0.1 - 0.06)/0.1 = 40\%$  at ambient CO<sub>2</sub> (380  $\mu\text{mol mol}^{-1}$ ). Note that computing a true value of quantum yield requires a correction for leaf absorbance so as to convert incident radiation into absorbed light. The extrapolated intercept associated with the second portion of the response curve gives an estimate of  $R_d$  (illustrated in Fig. 1a), which is typically lower than  $R_n$ , the rate of respiration in darkness (night respiration). In other words, in this region of irradiance, the response curve of net assimilation is modelled as  $A = \Phi_2 \cdot \text{iPAR} \cdot \alpha - R_d$  while at very low light, it is modelled as  $A = \Phi_1 \cdot \text{iPAR} \cdot \alpha - R_n$ , where  $\alpha$  is leaf light absorbance.

Problems associated with the Kok method itself should be recognized. First, in practice, carrying out a light response curve at very low light can be difficult due to the small difference between inlet and outlet air in open gas exchange systems (since  $A$  is low) and leaks, even very modest, can be an issue. Second, observing the two linear portions of the light response curve (and thus calculating  $R_d$ ,  $\Phi_1$  and  $\Phi_2$ ) can be rather difficult when the number of data points is limited. A good graphical resolution is also necessary to see the break point (e.g. compare the resolution of Fig. 1a and b). Consequently, there is often some uncertainty in the choice of data points to draw linear regressions. Including or excluding points in the presumed neighbourhood of the break point can change  $\Phi$ -values and  $R_d$  significantly. For example, in Fig. 1(a), excluding and including the third point gives  $\Phi_1$  values

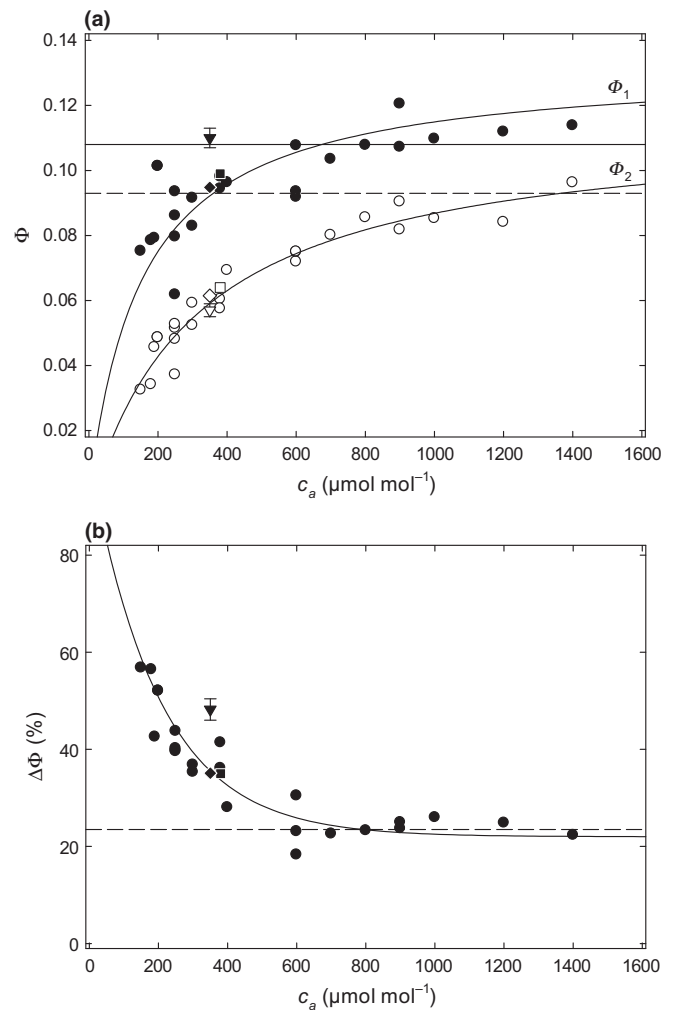


**Fig. 1** Examples of response curves of net photosynthesis to incident light (iPAR) in cucumber leaves, under 21%  $\text{O}_2$ , 23°C and  $380 \mu\text{mol mol}^{-1} \text{CO}_2$  (a) and in *Rumex acetosa*, at 30°C and  $350 \mu\text{mol mol}^{-1} \text{CO}_2$  under 0.5%  $\text{O}_2$  (grey) or 21%  $\text{O}_2$  (black) (b, c). In (a), the first slope (at low light level) is denoted as  $\Phi_1$  and the second slope (at higher light level) is denoted as  $\Phi_2$ . The continuous and dashed lines represent the linear regression obtained when regression regions are 0–25 and 25–90  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (i.e. three points are used to draw the line at low light). Dotted lines represent regressions obtained when regression regions are 0–15 and 15–90  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (i.e. two points only are used to draw the line at low light level). The Kok-estimate of day respiration (denoted as  $R_d$ ) is the intercept of the second regression line and is here found to be c.  $0.35\text{--}0.47 \mu\text{mol m}^{-2} \text{s}^{-1}$ . In (b), continuous lines stand for hyperbolic trends of the curves. In (c), a magnification at low light is shown. Values of quantum yield (corrected for leaf absorbance) are shown for each portion of linear regression. From unpublished data presented at the 18<sup>th</sup> New Phytologist Workshop (mean  $\pm$  SD,  $n = 5$ ).

of 0.099 and 0.085, respectively, and gives  $R_d$  values of 0.47 and  $0.35 \mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively. A recommendation to solve this problem is to have a sufficient number of measurements: typically, at least three in the  $0\text{--}10 \mu\text{mol m}^{-2} \text{s}^{-1}$  region.

### Why is the Kok effect of high significance?

The Kok method is used widely to estimate  $R_d$ , including in wide-spectrum studies carried out in different species or ecosystems



**Fig. 2** Quantum yield of photosynthesis as a function of external  $\text{CO}_2$  mole fraction ( $c_a$ ) in *Rumex acetosa* leaves at 30°C, 21%  $\text{O}_2$ . (a)  $\Phi_1$  (black circles) and  $\Phi_2$  (white circles). (b) Relative difference between  $\Phi_1$  and  $\Phi_2$ :  $\Delta\Phi = (\Phi_1 - \Phi_2)/\Phi_1 \times 100$ . Values (triangles) obtained in leaves kept under constant light for 24 h ( $300 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) before the Kok-curve (mean  $\pm$  SD,  $n = 5$ ). Values associated with Fig. 1 are plotted as a square (cucumber) and a diamond (*Rumex*). Curves represent hyperbolic trends. In (a), the horizontal continuous and dashed lines represent the value of  $\Phi_2$  (measured as the quantum yield of net photosynthetic  $\text{O}_2$  evolution instead of  $\text{CO}_2$  consumption) at high  $c_a$  in Björkman & Demmig (1987) and the average  $\Phi_1$  value found by Long *et al.* (1993) under 0.5%  $\text{O}_2$ , respectively. In (b), the dashed line represents the average value at high  $c_a$  ( $> 600 \mu\text{mol mol}^{-1}$ ). From unpublished data presented at the 18<sup>th</sup> New Phytologist Workshop.

under various conditions. For example, the Kok method has been implemented recently in an unpublished world-wide survey presented at the Workshop by Owen Atkin, Mary Heskell and others, in arctic species (Heskell *et al.*, 2014), in tropical tree canopies (Weerasinghe *et al.*, 2014), in trees in different seasons (Way *et al.*, 2015) and at varying  $\text{CO}_2$  (Crous *et al.*, 2012; Kroner & Way, 2016), or in different species along a vegetation chronosequence (Atkin *et al.*, 2013). The usefulness of Kok-derived estimates of leaf respiration in the light for ecosystem C budget studies has been extensively discussed (Heskell *et al.*, 2013). Interestingly, the Kok effect has been shown to scale up to the

ecosystem, that is, with a break in the response curve of net ecosystem uptake of CO<sub>2</sub> to measured irradiance (Bruhn *et al.*, 2011). At the Workshop, it has been recognized that in general, Kok-derived estimates of  $R_d$  are lower than  $R_n$  by 20–40%, consistent with the well-accepted inhibition of leaf respiratory metabolism by light. Comparisons with  $R_d$  values obtained using other techniques (such as the Laisk method, which takes advantage of response curves to CO<sub>2</sub> mole fraction) have also been shown to be rather satisfactory despite some variability (see, e.g. Villar *et al.*, 1994). Further data presented during the Workshop also showed a relatively good agreement between Kok-, Laisk- and isotope-derived  $R_d$  values in spinach, cocklebur and *Magnolia* leaves (Barbour *et al.*, 2017).

### What are the origins of the Kok effect?

Despite considerable efforts and discussions during the 18<sup>th</sup> New Phytologist Workshop, no simple explanation of the Kok effect could be articulated. Several causes have received attention, related to the different terms that describe net assimilation under light-limited conditions:

$$A = \gamma \frac{J_t \cdot c_c - \Gamma^*}{4 c_c + 2\Gamma^*} - R_d \quad \text{Eqn 1}$$

where  $\gamma$  is the cyclic-pseudocyclic electron flow coefficient,  $J_t$  is the total electron flow,  $c_c$  is the internal CO<sub>2</sub> mole fraction at

carboxylation sites, and  $\Gamma^*$  is the CO<sub>2</sub> compensation point in the absence of day respiration. However, Eqn 1 may be re-arranged easily with  $\Phi_1$  and  $\Phi_2$  (as given earlier) since  $J_t$  can be rewritten as a function of iPAR:  $J_t = \alpha a \Phi_{\text{PSII}} \cdot \text{iPAR}$  (where  $\Phi_{\text{PSII}}$  is the photochemical yield of photosystem II (PSII) and  $a$  is light distribution between PSI and PSII). It is evident from this relationship that the change in slope ( $\Phi_1$  vs  $\Phi_2$ ) in the Kok effect can have diverse origins, with a change in  $\gamma$ ,  $a$ ,  $\Phi_{\text{PSII}}$ ,  $c_c$  or  $R_d$  with light.

The widely-accepted (historical) origin of the effect is the inhibition of respiratory metabolism by light (linear decrease of  $R_d$  with light) and in fact, mechanisms for the down-regulation of respiratory decarboxylation reactions by light have been described (reviewed in Tcherkez *et al.*, 2012). In addition, the pentose phosphate pathway (PPP), which also liberates CO<sub>2</sub>, has been shown to be inhibited by light, even at very low light levels (Singh *et al.*, 1993; Farr *et al.*, 1994). A metabolic steady-state model has also suggested that at low light, the enhancement of the PPP can potentially explain the Kok effect (Buckley & Adams, 2011).

However, a purely respiratory (catabolic) origin of the Kok effect is highly unlikely. In fact, it strongly depends on gaseous conditions whereas  $R_d$  is not expected to be very sensitive to CO<sub>2</sub> and O<sub>2</sub> mole fraction. The Kok effect disappears at low oxygen (Fig. 1b,c; Cornic & Jarvis, 1972; Ishii & Murata, 1978; Sharp *et al.*, 1984), suggesting that photorespiration could be involved. The Kok effect also depends on CO<sub>2</sub>: the relative difference between  $\Phi_1$  and  $\Phi_2$  decreases, but does not disappear, at high CO<sub>2</sub> mole fraction (Fig. 2), suggesting again that photorespiration could explain part

**Table 1** Summary of hypotheses discussed at the 18<sup>th</sup> New Phytologist Workshop to explain the origin of the Kok effect (see the text for further details)

Possible origin	Likely?	Experimental evidence	Comments
Regulation of respiratory decarboxylations (decrease in $R_d$ ) when light increases	Yes	Biochemical evidence of enzymatic down-regulation in the light compared to the dark.	No specific study of respiratory metabolism at (very) low light; not consistent with the negligible impact of respiratory inhibitors on the Kok effect.
Increase in $c_i$ at very low light	No	The Kirshbaum–Farquhar correction introduces minimal correction, and stomatal conductance does not correlate with the Kok effect.	
Increase in $c_c$ at very low light	Yes	Explains the O <sub>2</sub> -dependence, matches observed changes in quantum yield ( $\Phi_1$ , $\Phi_2$ ) and explains the absence of Kok effect in C <sub>4</sub> plants tested so far.	Might not be consistent with a persisting Kok effect at high CO <sub>2</sub> and in unicellular algae with a carbon concentrating mechanism (CCM) (see text); does not explain the breakpoint (discontinuity in the slope) when visible.
Change in the photorespiratory O <sub>2</sub> /CO <sub>2</sub> stoichiometric coefficient to values larger than two, thereby decreasing $\Gamma^*$ at very low light	No?	Isotopic labelling has shown that at (very) low photorespiration rates, the stoichiometric coefficient is not statistically different from two.	However, a small change in the stoichiometric coefficient from very low light to low light due to the change in $c_c$ (oxygenation rate) might contribute marginally to the Kok effect.
Decrease in the cyclic electron flow thereby increasing the apparent photochemical yield at very low light	Yes	The maximal electron flow through photosystem I (PSI) decreases a lot and there is more Mehler reaction.	Potentially, the Kok effect should be sensitive to wavelength, and this has to be tested; further data on the assimilatory quotient CO <sub>2</sub> /O <sub>2</sub> should also be informative.
Increase in the photochemical yield $\Phi_{\text{PSII}}$ at very low light	Yes?	$\Phi_{\text{PSII}}$ has been found to be higher at low light, but variable.	More measurements needed.
State transition in favour of PSII: increase in $a$ at low light	Yes?	State transition of light harvesting complexes (LHCs) from PSI to PSII has been observed at low light.	More measurements needed.

of the effect. It should nevertheless be noted that the Kok effect disappears at extremely high CO<sub>2</sub> ( $\geq 1\%$ ) (Björkman & Demmig, 1987; Evans, 1987) but this observation might not be very conclusive due to side effects of extremely high CO<sub>2</sub> on C metabolism (including cellular acidification and inhibition of respiration).

Potentially, a photorespiratory origin could be due to: (1) a different photorespiratory metabolism at low light (such as a change in O<sub>2</sub>/CO<sub>2</sub> stoichiometry) thereby making the 'scaling factor'  $(c_c - I^*)/(c_c + 2I^*)$  erroneous in Eqn 1. Recently, slight changes in photorespiratory stoichiometry have been found at high O<sub>2</sub> or low CO<sub>2</sub> but significant changes at very low photorespiration rates seem unlikely (Abadie *et al.*, 2016); or (2) changes in  $c_c$  along a light curve. Usually, the classical correction used to adjust  $A$  values to what they would be if intercellular CO<sub>2</sub> ( $c_i$ ) were constant (Kirschbaum & Farquhar, 1987) is minimal and does not suppress the Kok effect. Still, the second hypothesis appears very likely, through the influence of internal conductance so that  $c_c/I^*$  (rather than  $c_i/I^*$ ) increases considerably at low light (see the companion article Farquhar & Busch, 2017).

It is nevertheless improbable that an effect on  $c_c$  only can explain the Kok effect in totality. In fact, the effect persists at high CO<sub>2</sub> (Fig. 2). Furthermore, it has been originally described in unicellular algae with a carbon concentrating mechanism (CCM) (Kok, 1948) and has also been found in other CCM-containing algae (Peltier & Sarrey, 1988). Also, the break in the light response curve, when it happens to be visible (as in Fig. 1c), would not be easy to explain since there is no clear reason for a discontinuous effect of internal conductance on  $c_c/I^*$ . It should also be noted that the effect of gaseous conditions might not be inconsistent with metabolism: under the steady-state hypothesis, the balance of reductive power predicts that PPP activity should depend on CO<sub>2</sub> mole fraction (Buckley & Adams, 2011). Unfortunately, there is presently no published data (of either metabolomics or fluxomics) obtained at very low light along a Kok curve. Therefore, fluxes in catabolic pathways responsible for CO<sub>2</sub> generation at very low light are not very well known. Recent unpublished data obtained using isotopic (<sup>13</sup>C) labelling and presented during the Workshop by Gauthier and co-workers have nevertheless suggested that at very low light, decarboxylation by the pyruvate dehydrogenase is up-regulated. Finally, other mechanisms associated with electron transport cannot be excluded. First, at very low light, there is an abrupt decrease in the cyclic electron flux around PSI that disappears under 2% O<sub>2</sub>, thereby suggesting that  $\gamma$  can change, may be due to the Mehler reaction (Laisk *et al.*, 2005; Kou *et al.*, 2013). Second, both the light partition to PSII ( $a$ ) and the photochemical yield of PSII ( $\Phi_{\text{PSII}}$ ) have been found to increase at low light (Oberhuber *et al.*, 1993; Yin *et al.*, 2014).

## Perspectives

A summary of possible explanations of the Kok effect is shown in Table 1. It is clear that the origin of this effect is not unique, and it is likely a combination of several processes that lead to an increase in

the quantum yield of photochemistry, and cause gaseous (decrease in photorespiration due to the increase in  $c_c/I^*$ ) and metabolic changes at very low light. In an effort to disentangle the mechanism of the Kok effect, more experiments should be done at very low light to ascertain catabolic pathways involved, examine electron transport parameters and the CO<sub>2</sub>/O<sub>2</sub> assimilatory quotient, and use species where the Kok effect does not occur like C<sub>4</sub> plants (Cornic & Jarvis, 1972; Ishii *et al.*, 1979) and perhaps, C<sub>3</sub>/C<sub>4</sub> intermediates. There is little doubt that the rate of day respiration  $R_d$  is lower than  $R_n$  because it has been shown using several methods (for a review, see Tcherkez & Ribas-Carbó, 2012). However, it seems clear that the Kok effect is not purely respiratory and thus, the values of  $R_d$  or  $R_d/R_n$  obtained with the Kok method have to be considered as proxies.

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