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Meta-analysis assessing potential of steady-state chlorophyll fluorescence for remote sensing detection of plant water, temperature and nitrogen stress

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Abstract

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Meta-analysis assessing potential of steady-state chlorophyll fluorescence for remote sensing detection of plant water, temperature and nitrogen stress

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Abstract

Many laboratory studies investigating chlorophyll fluorescence (F) of plants have provided sufficient evidence of the functional link between dynamic changes in photosynthetic activity and F emissions. Far fewer studies, however, have been devoted to detailed analysis of F emission under steady-state conditions, which may be amenable to measurement by passive spectroradiometers onboard airborne or satellite missions. Here, we provide a random-effects meta-analysis of studies using both passively (sun-induced) and actively (e.g. laser-induced) measured steady-state F for detecting stress reactions in terrestrial vegetation. Specifically, we review behaviour of F in red and far-red wavelengths, and also the red to far-red F ratio, for plants physiologically stressed by water deficit, temperature extremes, and nitrogen insufficiency. Results suggest that water stress is, in general, associated with a decline in red and far-red F signal intensity measured at both leaf and canopy level, whereas the red to far-red F ratio displays an inconsistent behaviour. Chilling, for which only studies with active measurements at the leaf level are available, significantly increased red and far-red F, whereas heat stress produced a less convincing decrease in both F emissions, notably in canopies measured passively. The clearest indicator of temperature stress was the F ratio, which declined significantly and consistently. The F ratio was also the strongest indicator of nitrogen deficiency, revealing a nearly uniformly increasing pattern driven by predominantly declining far-red F. Although significant knowledge gaps were encountered for certain scales and F measurement techniques, the analyses indicate that future airborne or space-borne acquisitions of both red and far-red F signals would be beneficial for timely detection of plant stress events.

Keywords: steady-state chlorophyll fluorescence, passive sun-induced fluorescence, active laser-induced fluorescence, photosynthesis, stress, water, temperature, nitrogen, random-effects meta-analysis, FLEX satellite mission

Introduction

The Earth's environment is increasingly exposed to multiple stress agents, due to a combination of exponentially growing human population and associated energy needs (Hughes et al., 2013), as well as naturally occurring stress episodes. Under such conditions, the ability to detect timely stress responses of vegetation at regional and also global scale is necessary for successful mitigation of adverse and potentially irreversible negative impacts.

For over three decades, remote sensing has provided essential inputs for estimation of carbon fluxes and vegetation productivity at various spatial scales (e.g. Running et al., 2004). Increasing spectral resolution and accuracy of instruments has opened up possibilities to assess new characteristics associated with dynamic vegetation functioning (Grace et al., 2007). One such characteristic is the emission of chlorophyll fluorescence (F) under steady-state light conditions, which provides information on the functional status of photosynthetically active leaves (Papageorgiou and Govindjee, 2004). Steady-state F measured by active (laser or pulse-amplitude modulation) fluorometers, commonly termed F_s, and solar-induced steady-state F measured by passive systems (SIF), are the subject of intensive research in recent years (Malenovský et al., 2009). Reliable estimates of global SIF observed from space (Joiner et al., 2011) are expected to reduce uncertainties associated with modelling of gross primary production (GPP) using terrestrial carbon fluxes (Frankenberg et al., 2011; Guanter et al., 2014). Our study investigates another possible use of the steady-state F as an indicator tracking development of vegetation stress reactions and providing early identification of physiological strain prior to appearance of visual symptoms.

Upon absorption of incoming photosynthetically active radiation (PAR) between 400 and 700 nm, the energy of photons is converted into: i) photochemical energy of photosynthesis, ii) heat dissipation related to photoprotection, and iii) F emissions (Demmig-Adams and Adams, 2000). In general, the magnitude of F emission during photosynthesis is inversely related to the efficiency of energy transfer between antenna pigments and electron acceptors (Kok, 1965). Under steady-state light conditions, chlorophyll fluorescence usually constitutes only around 2-3% of red (684–695 nm) and far-red (730–760 nm) light reflected by leaves (e.g. Zarco-Tejada et al., 2003), which is a small yet measurable quantity, if sufficiently sensitive instrumentation and appropriate signal retrieval methods are used. While hundreds of laboratory studies using well

established active F measurement methods and protocols proved the functional link between various F features and photosynthesis (e.g. Maxwell and Johnson, 2000; Papageorgiou and Govindjee, 2004), the information content of the steady-state F signal, especially from passive detectors measuring SIF, is yet to be fully understood and exploited.

The pulse amplitude modulation (PAM) method, developed by Schreiber et al. (1986), is the most commonly used active method to measure F of single leaves in laboratory and also field experiments. The PAM approach enables discrimination of F from extraneous reflected light via selective amplification (Roháček and Barták, 1999). However, the strong saturation flashes applied in high-frequency time series might induce a non-natural behaviour of the plant photosynthetic apparatus altering possibly plant F responses. Other active remote sensing F methods used either pulsed (i.e. laser-induced fluorescence – LIF) or non-pulsed light sources (Kim et al., 2001) for excitation of F. While LIF has the advantage of measuring F in the presence of sunlight, the non-pulse methods tend to acquire more stable F signals, which enable better characterization of F emission peaks. LIF methods can induce F emissions of different intensities depending on the excitation wavelengths of laser sources, which typically range between 300 and 700 nm (Chappelle and Williams, 1987; Middleton et al., 2008). Apart from the excitation wavelength, selection of optical filters and detectors with appropriate spectral resolution affects the quality (i.e. intensity, amplitude, accuracy and signal-to-noise ratio) of the acquired F signal. Recently, a laser or light-emitting diode induced fluorescence transient (LIFT) system, which is based on a fast repetition rate (FRR) fluorometry, was applied for remote sensing of photosystem II fluorescence of tree crowns or small canopies from a distance up to 50 m (Kolber et al., 2005; Pieruschka et al., 2014).

Passive remote sensing methods retrieving the steady-state F signal from air-/space-borne data can be divided into: i) reflectance-based (relative unit) and ii) radiance-based approaches (in physical unit of $W.m^{-2}.sr^{-1}.\mu m^{-1}$). Reflectance-based approaches utilize F signal integrated in vegetation reflectance measured between 650 and 800 nm. According to Meroni et al. (2009), twenty-four F indices based on reflectance differences, reflectance ratios or reflectance derivatives of 2 to 3 spectral bands have been proposed. The rationale behind these indices is to normalize reflectance of F-sensitive wavelengths by the closest F insensitive wavelength (Perez-

Priego et al., 2005). Radiance based F quantities were derived using the Fraunhofer Line Discriminator (or Fraunhofer Line Depth, FLD) technique (Plascyk, 1975), which requires measurements of total solar irradiance (reference standard) and the sample radiance (leaf or canopy) inside and outside the atmospheric oxygen absorption bands or solar Fraunhofer lines located in the red and/or far-red parts of the spectrum. Recently Joiner et al. (2011), Frankenberg et al. (2011), and Guanter et al. (2012) presented global maps of vegetation SIF using Fraunhofer lines at 755 and 770 nm acquired by the high spectral resolution Fourier Transform Spectrometer (FTS) aboard of the Japanese Greenhouse Gases Observing Satellite (GOSAT). Lee et al. (2013) used F estimates from GOSAT to detect drought stress in the Amazon forest. Other satellite platforms usable, but not purposely designed for F observations, include the Global Ozone Monitoring Experiment-2 (GOME-2; Joiner et al., 2013), the Scanning Imaging Absorption Spectrometer for Atmospheric Chartography (SCIAMACHY; Köhler et al., 2014), and the Orbiting Carbon Observatory-2 (OCO-2; Frankenberg et al., 2014).

Mapping terrestrial photosynthetic activity from space is the main objective of one of the current candidate missions for the European Space Agency's (ESA) 8th Earth Explorer program. The Fluorescence Explorer (FLEX) satellite is proposed as a tandem mission with ESA's Sentinel-3 operational mission. FLEX would measure red and far-red vegetation F as a potential key input into GPP modelling of ecosystem vegetation canopies, and also as an indicator of actual vegetation stress status. This study aims to contribute to filling current knowledge gaps about use of remotely sensed steady-state F as a stress indicator. The objective is to analyse scientific literature using passive and active red and far-red steady-state F measurements at both leaf and canopy scales to investigate the potential F detectability of plant water deficit, low and high temperature stress, and nitrogen deficiency. The selected stressors are among the most common natural stress agents, which are expected to intensify with the globally progressing climate change (Tuteja and Gill, 2014; Rennenberg et al., 2009).

Material and Methods

Input data

In total 73 peer-reviewed scientific articles, one dissertation, and two unpublished experimental datasets investigating a link between water, temperature, or nutrition stress and F were collected using the following scientific publishing portals: Web of

Science, Elton Bryson Stephens Company, and Google Scholar. The key words used for the search were: "water", "temperature" ("cold", "chilling", or "heat"), and "nitrogen" in combination with "sun-induced" or "laser-induced" chlorophyll fluorescence and "stress". To include as many relevant studies as possible, we also searched on internet for work of specific researchers by names. Studies were not included if they investigate too extreme (e.g. temperature stress of 100 °C) and very short-term (e.g. few minutes only) stress events, as well as detached leaves, as these were not representative of the gradually developing stress effects that usually occur under natural conditions.

Steady-state F measurements, their standard deviations (σ), and the size of dataset (n) acquired with: i) active approaches measuring F_s induced by laser or light-emitting diodes, and ii) passive approaches measuring solar induced SIF at the leaf and at the canopy scale, were analysed separately in order to ensure compatibility and comparability of input data and subsequent results. To maintain consistency of our analyses, we always selected the endpoints (i.e. the last data points) of the stress treatment. If several stress severity levels were applied, we considered outputs of the most severe case. Whenever the F values were not directly reported, we applied the Plot Digitizer software (University of South Alabama, USA) to retrieve the particular numerical F values from displayed graphs and figures. Multiple experiments from the same author(s) applying just slightly different F excitation wavelengths or expressing F in different units were considered as a single study input. To avoid data autocorrelation, the F measurements conducted on different sub-species or clones, but following the same methodology, were averaged and considered as a single experimental dataset. Finally, we studied only the three stress factors, which represent the majority of published F stress work and are relevant to changing climate conditions such as more frequently expected occurrence of droughts and heat waves. Other biotic and abiotic stressors were not included, as these would introduce too high interpretational complexity. However, a potential ambiguity of results originating from an indivisible multifactorial stress (e.g. combination of high temperature and water deficiency) was noted and discussed.

Standardized difference in means

Since the reviewed experiments were based on specific independent approaches, the methodological differences (e.g. use of various measurement devices and protocols)

resulted in diverse and non-systematic outputs. In order to remove the incomparability of F measurements due to different physical or relative units, we computed the standardized mean difference (*d*) between treated (stressed) and control (unstressed) plant experiments as a common statistical measure entering the subsequent meta-analysis (Borenstein et al., 2005). The standardized mean difference expresses the size of the intervention effect in each study relative to the data variability observed in that study. The effect size is standardised since it is measured as the number of standard deviations, by which the means differ. The standardized mean difference is computed according to the equation:

$$d = \frac{\overline{F_{s1}} - \overline{F_{s2}}}{\sqrt{\frac{\sigma_1^2(n_1-1)+\sigma_2^2(n_2-1)}{n_1+n_2-2}}}, \quad (1)$$

where $\overline{F_{s1}}$ is the mean steady-state chlorophyll fluorescence (F_s or SIF) of n_1 observations of stressed plants with the standard deviation σ_1^2, and $\overline{F_{s2}}$ is a mean steady-state chlorophyll fluorescence of n_2 observations of unstressed (control) plants with the standard deviation σ_2^2.

Random-effects meta-analysis

As described in Borenstein et al. (2005), meta-analyses of various studies can be based on either a fixed-effect model or a random-effects statistical model. Under the fixed-effect model we expect existence of a common true effect shared by all studies entering the analysis. The null hypothesis assumes that differences in observed effects are originating purely from sampling errors, but not from the method itself. By contrast, under the random-effects model we expect the true effect to vary from study to study. A single common effect size of all different experiments cannot be assumed due to the alternations in experimental material (e.g. use of different plant populations or species) and implemented methodologies (e.g. diversity of measurement techniques and instruments). Only an infinite number of studies would provide us with the true effect sizes distributed around a grand mean. Thus effect sizes in the number of performed

studies are representing only a random sample of the infinite dataset, i.e. 'random-effects meta-analysis'.

If each study had an infinite sample size, then the sampling error would be zero and the observed effect would be the same as the true effect for that study. Since the sample size in any study is never infinite, the observed effect Y_i of the study is a sum of the overall grand mean (μ) of all investigated studies, the deviation of the study's true effect from the grand mean (ζ_i), and the deviation of the study's observed effect from the study's true effect (ε_i). Therefore, to predict how far the observed effect Y_i of any given study is likely to fall from μ, we need to consider both the variance of ζ_i and the variance of ε_i. Random-effects meta-analysis is using the collection of Y_i to estimate the overall mean μ by computing a weighted mean, where the weight W_i is the inverse of the total study's variance equal to the sum of the within-study variance (V_{Yi}) and the between-studies variance (T^2). V_{Yi} is defined as squared standard deviation of all observations (σ^2) normalized by the sample size of each study (n), and the between-studies variance T^2 is estimated using the DerSimonian-Laird method of moments (DerSimonian and Laird, 1986). The weighted grand mean effect (M) is then computed as:

$$M = \frac{\sum_{i=1}^{k} W_i Y_i}{\sum_{i=1}^{k} W_i}, \quad (2)$$

i.e. as the sum of the effect size, in our case the standardized mean difference (eq. 1), multiplied by weight and divided by the sum of the weights of the k number of studies. The variance of the summary effect (V_M) is estimated as the reciprocal of the sum of the weights:

$$V_M = \frac{1}{\sum_{i=1}^{k} W_i}. \quad (3)$$

The lower and upper limits of the 95% confidence interval of the summary effect (LL_M and UL_M) are computed according to:

$$LL_M = M - 1.96\, SE_M \quad (4)$$

and

$$UL_M = M + 1.96\, SE_M . \quad (5)$$

where SE_M is the estimated standard error of the summary effect obtained is square root of the variance V_M (eq. 3). Finally, the Z-value testing the null hypothesis that the overall mean effect μ is zero is computed as:

$$Z = \frac{M}{SE_M} \quad (6)$$

and the related probability p-value for a one-tailed test is given by:

$$p = 1 - \Phi(\pm Z), \quad (7)$$

where $\Phi(Z)$ is the normal cumulative distribution function, and '+' or '–' is used if the difference is in the expected direction or in the opposite direction (Borenstein et al., 2005).

The statistically significant random-effects model is recognized by strong summary effect (i.e. M significantly different from zero), narrow confidence intervals of the summary effect, and high Z-value (positive or negative) with low probability of the null hypothesis acceptance. Although study weights are well balanced under the random-effects model, i.e. large studies with a larger sample sets are assigned less relative weight and small studies are assigned more relative weight, both variances (V_{Yi} and T^2) play the key role in overall random-effects meta-analysis assessment. If the number of input studies is too small, only two or three, then the estimate of T^2 has poor precision, which results in statistically less significant summary effect (i.e. lower p-values) and wider confidence intervals. In these cases the meta-analysis suffers from lack of information and cannot be applied correctly. We, therefore, flagged these results with a single cross (†), indicating that they must be regarded as less reliable.

Understandably, a random-effects meta-analysis of a single study has T^2 equal zero, which makes the results completely incomparable with outcomes of multiple study analysis. Hence, we flagged these results with a double cross (††) to notify their incomparability and need to interpret them separately as single studies. All datasets entering the random-effects meta-analyses are summarised in Appendix A.

Basic statistical analysis of stress to control chlorophyll fluorescence ratio

Not all of the reviewed papers provide information about the standard deviation of the actual steady-state F measurements, which is a basic requirement for any meta-analysis. To exploit also a valuable stress indicative potential of mean F values, we performed, additionally to the meta-analysis, basic statistical tests not taking into account the variability within and in-between experiments. Differences in F units, spectral positioning and width of measured spectral bands, excitation wavelengths, and F extraction methods, were eliminated by converting the F_s and SIF values into a stress to control (S/C) ratio. If S/C ratio is lower than one, then the stress factor is causing decrease in F, while the ratio higher than one indicates an F increase due to the stress exposure and S/C ratio equal or close to one indicates no change. To keep results consistent, we transformed into the S/C ratio also the ratio of red to far-red F. Since majority of collected datasets was lacking the normal Gaussian distribution, a non-parametric statistical Mann-Whitney U-test (Mann and Whitney, 1947) was applied to test the significance of a null hypothesis that the S/C steady-state F ratio is equal to one, i.e. that no stress induced F change occurred. The null hypothesis was rejected at two probability levels: i) a highly significant level with p-value ≤ 0.01 (1%) is denoted in figures with a double asterisk (**), and ii) a significant level with p-value ≤ 0.05 (5%), which is denoted with a single asterisk (*). It is important to note, that these results are considered as additional and supportive indicators and were regarded only in cases where the meta-analysis could not be properly applied due to a small number of inputs.

Results

Water deficit analyses

Water deficit random-effects meta-analyses were conducted for red and far-red chlorophyll fluorescence, and also for their ratio acquired by 27 experiments at leaf scale, out of which only 3 investigated SIF signals, and by 14 canopy scale experiments,

where 8 experiments employed active methods and 6 applied passive techniques (see Table A1). Standardized mean differences in steady-state F of water-stressed and non-stressed plants together with corresponding standard errors, variance parameters, and indicators of statistical significance are listed in Table 1.

Fig. 1a shows a negative standard difference in means of leaf active observations, which indicates that red F of drought stressed plants is lower than that of plants growing in optimal environmental conditions. For passive studies of leaf or canopy red F, there was an insufficient number of experiments to conduct the random-effects meta-analysis. However, the simple statistic computed for three independent canopy active and passive trials revealed the stress to control red F ratio was lower than 1 (p=0.049) (Fig. 2a). Analysing all 15 red F experiments together, we found a significantly negative grand mean of standard differences in means (Fig. 1a). Z-value close to −4 and a narrow 95% confidence interval suggest that the null hypothesis of the overall mean effect M being equal to zero can be rejected for red F at the probability level p=0.0001.

Similar, but statistically even stronger results were obtained for far-red F as depicted in Fig. 1b. The leaf active and canopy passive studies reveal a consistent tendency of negative standard differences in means that are accompanied by Z-values between −3 and −4 at the probability level p=0.0001 and p=0.0006, respectively. Although other leaf and canopy studies did not provide enough data to conduct the meta-analysis, the Mann-Whitney U test for the stress to control far-red F ratio of 5 canopy active experiments proved that the null hypothesis suggesting its equality to 1 can be rejected with a high probability p=0.009 (Fig. 2b). Analyses of leaf passive far-red F observations delivered insignificant results due to the low number of inputs. Nevertheless, the random-effects meta-analysis integrating all 16 far-red F studies gained Z-value smaller than −7, which confirmed a generally observed trend that water deficiency induces decline in far-red steady-state F emission at the probability level p<0.0001.

Fig. 1c illustrates that only active fluorescence studies investigating the ratio between red and far-red F of water stressed leaves and canopies provided sufficient inputs to conduct the random-effects analysis. Results were rather ambiguous due to an inconsistent trend in d values of single input studies. Approximately half of investigated studies produced negative d, whereas the other half gained positive d values (Table 1), which resulted in Z-value and the probability level p of all 10 examined studies close to

0.5 and less than 0.6, respectively (Fig. 1c). No additional clarity was obtained from results of the basic statistical analysis showing that mean S/C ratio of 19 reviewed studies is close to 1 (Fig. 2c). The corresponding Mann-Whitney U test approved the null hypothesis that this ratio is statistically equal to 1 at the probability level p=0.79. In other words, we did not find any statistical evidence that red to far-red F ratio of water-stressed plants is significantly different from the same ratio of unstressed plants.

Temperature stress analyses

Similarly to the water deficit analysis, statistical significance of standardized mean differences in steady-state F was tested between plants stressed by high (heat) or low (chilling) temperature and plants growing under favourable temperature. In total, 9 experiments were available for the effects of heat stress and 11 experiments for the effects of cold stress. Out of these 20 experiments, 17 were carried out at the leaf level using active methods, one experiment at the canopy level using active methodology, and two experiments at the canopy level using passive methods (see Table A2). Since heat and chill might be expected to result in different effects, both stressors were analysed separately.

Fig. 3a indicates that cold stress has no significant effect on the red F in the case of leaf active measurements. However, if we disregard the experiment conducted on chill-tolerant species (n=1, negative d), then chilling seems to have a positive effect (n=3, positive d) increasing the red F (Table 2). Heat stress induced an opposite effect on red F, demonstrated by negative standard differences in means and negative Z-values. Unfortunately, only two single studies, one at leaf and one at canopy level, are available, yielding together a statistically insignificant result (p=0.3). Nonetheless, these results are supported by three additional canopy studies showing S/C ratio smaller than 1 (p=0.06), yielding p=0.093 in combination with five other studies using active methods at the leaf level (Fig. 4a).

Similar results were obtained for the far-red F, with low temperatures increasing the F intensity and high temperatures having an opposite effect (Fig. 3b). Although limited number of input studies is challenging the reliability of meta-analyses, outcomes of basic statistical analyses are in line with these limited results (Fig. 4b). Effect of chilling temperatures significantly increased the far-red F signal (n=6, p=0.05). Even though effect of high temperature on far-red F varies, it is prevailingly decreasing when

using active F methods at the leaf scale. The simple statistic of the passive canopy measurements reported an exclusively decreasing F trend under heat treatment, similar to the joint leaf and canopy analysis (n=8, p=0.093).

Studies using the ratio of red to far-red F for the temperature stress assessment pointed out that both low and high temperatures are affecting negatively the active-leaf F ratio (Fig. 3c), but with a less significant statistical probability level p=0.2. The net effect of high temperature stress at both leaf and canopy scales is also decreasing (see negative standard difference in means and Z-values in Fig. 3c), but it did not reach an acceptable statistical significance (p=0.1) either, due to the high variability of the canopy experiment. Results of basic statistics in general supported the trends of meta-analyses with a stronger statistical significance (Fig. 4c). The Mann-Whitney U test rejected the null hypothesis that the F ratio is equal to 1 for low and high temperature stresses observed actively on leaves (p=0.008 and p=0.05, respectively), as well as for all, leaf plus canopy, high temperature stress experiments (p=0.017). Two studies investigating the effects of a high temperature passively at the canopy level also indicated a decreasing effect on red to far-red F ratio.

Nitrogen deficiency analyses

Ten out of 31 identified experiments investigating influence of nutritional (nitrogen) deficit on chlorophyll fluorescence were devoted to the red F, only 5 to the far-red F, and 16 to the red to far-red F ratio. While most of the observations were conducted on leaves, two experiments investigated red and far-red F signals, respectively, at the canopy level (see Table A3). Standardized mean differences in steady-state F of nitrogen stressed and control plants with corresponding standard errors, variance parameters, and indicators of statistical significance are listed in Table 3.

Results of the meta-analyses did not indicate the presence of a consistent (one-directional) scale and methodology-specific effect of nitrogen deficiency on the red F. Fig. 5a shows a negative standard difference in means using active methods at the leaf level, indicating that nitrogen stressed plants produce a lower red F than that of controls (p=0.0003). Opposite results were obtained from studies investigating the red F signal using the passive methods. However, these results are less relevant since they correspond to only two studies. An insufficient number of studies available for leaf-passive and canopy-passive trials, and absence of canopy-active studies indicate that the

leaf-active data is the main driving force behind the summary random effects of all studies shown in Fig. 5a. Analysing all 10 red F experiments together, we found a negative grand mean of standard differences in means, but due to the cancelling effect of different methodologies the hypothesis that Z-value is statistically different from zero cannot be accepted (p=0.1). Similar results were obtained from basic statistical tests, i.e. declining effect at leaf and canopy scales using active methods and an increasing effect when using passive F methods. The overall effect is statistically significant (n=28, p=0.042), but it is dominated by leaf active measurements of the red F (Fig. 6a).

More consistent and statistically stronger results were obtained for the far-red F signal (Fig. 5b). Four leaf-active studies, also when merged with the canopy-passive one, expressed a lower far-red F of stressed plants with Z-values close to –3 at significant probability levels p<0.01. This declining effect is fully supported by results of the S/C far-red F ratio tested for 22 experiments with the Mann-Whitney U test, gaining the probability level p =0.0009 (Fig. 6b).

Finally, the most consistent results were obtained from meta-analyses of the red to far-red F ratio (Fig. 5c). Unfortunately, small number of leaf-passive and canopy-active experiments did not provide any reliable outcome, but unprecedented statistical significance was achieved for leaf-active, canopy-passive and all acquired studies together (p<0.008, p<0.0001, and p<0.0001). Although results of the S/C of canopy-active trials tested by the Mann-Whitney U test were not statistically significant (p=0.11), the consistent effects of the nitrogen stress on the F ratio of 31 leaf-active and 41 studies in total are convincing (p<<0.0001 for both; Fig. 6c).

Discussion

Impact of water deficit on steady-state chlorophyll fluorescence

Results of the statistical analyses testing the ratio of stress to control F support the conclusion of a drought-induced decrease in steady-state red and far-red F. This phenomenon, which was articulated by Medrano et al. (2002) for *Vitis vinifera* (L.), is thought to be associated with stomatal closure. As stomata are closing in proportion to the actual water stress intensity, there is progressive limitation of CO_2 availability in chloroplasts, which is consequently reducing the CO_2 to O_2 ratio. The CO_2-limited environment can intensify photorespiration in C3 plants and increases uptake of O_2 associated with either oxygenase activity or electron transport to oxygen via the Mehler

443 reaction (Flexas et al., 2002a). A series of physiological protection mechanisms promote
444 non-photochemical energy dissipation (NPQ) and lowers F. Outcomes of field
445 experiments conducted by Flexas et al. (2002b) on a vine canopy support the hypothesis
446 of steady-state F being dependant on NPQ. Interestingly, their canopy active F
447 measurements carried out at distance of 1 m revealed less variability, i.e. stronger F_s to
448 NPQ relationship, than single leaf measurements. The authors suggested that canopy
449 observations might average out the spatially heterogeneous photosynthetic rate across
450 heterobaric water-stressed leaf blades, as observed by Osmond et al. (1999), and thus
451 facilitate discernment of F signal behaviour using remote sensing methods.

452 More recently, Zarco-Tejada et al. (2012) demonstrated that although leaf F_s
453 varied diurnally with increasing irradiation intensity, SIF of water-stressed trees
454 remained always lower than SIF of control trees, even during the midday photosynthetic
455 depression. They observed that steady-state F of citrus crowns estimated passively from
456 airborne hyperspectral imagery was in agreement with that from active leaf
457 measurements, i.e. both were lower for trees under water deficiency. These findings
458 indicate that remotely sensed steady-state F might be used as a rationalizing tool to
459 monitor canopy water stress and to optimize water irrigation, especially in water-
460 limited arid agricultural areas (Flexas et al., 2000). Although the statistically significant
461 decline of red and far-red F revealed by our analyses for actively and passively
462 measured water stressed canopies (Fig. 2a, b) supports these conclusions, it should be
463 noted that those observations were conducted on single crowns with dense
464 homogeneous foliage.

465 Our results indicate more consistent and stronger water stress detectability by
466 far-red rather than red F. This corresponds with observations of Daumard et al. (2012)
467 and Fournier et al. (2012), which noticed a confounding influence of canopy architecture
468 on the red F signal. It is important to note that the red and far-red F signals may contain
469 information from different layers of the leaf or canopy (Porcar-Castell et al., 2014;
470 Gitelson et al., 1998). Red F is highly reabsorbed by vegetation, therefore, the measured
471 red F signal tends to represent the contribution from photosystems near the leaf surface
472 or in the upper leaves of the canopy, whereas the far-red F may be representative of
473 deeper layers in the leaf or canopy, particularly when excitation light is able to penetrate
474 deeply into the leaf or canopy. Guanter et al. (2014) demonstrated that the far-red SIF
475 retrieved from spectrometric data of atmospheric space missions (e.g. GOSAT or GOME-

2) is able to increase accuracy of GPP estimates for spatially uniform cropland and grassland ecosystems. Nevertheless, they also acknowledged that utilisation of somehow lower SIF observed for spatially heterogeneous mosaics of forests and agricultural landscapes of Northern Europe is still a scientific challenge. Since the far-red F emission is subject to scattering according to vegetation structural properties (Knyazikhin et al., 2013), vegetation structure affects both red and far-red F, because of reabsorption and scattering effects, respectively. Therefore, water stress detectability of both F signals measured with space-borne sensors with a coarse spatial resolution should be further verified.

Finally, Fig. 1c illustrates that contrary to systematic red and far-red F decline their ratio does not exhibit any consistent response to water deficiency. Although both F emissions are decreasing, the relative intensity of their decrease is unsystematic. This may be due to the particular experimental circumstances, as for example sensitivity to different chlorophyll concentrations and/or vegetation structure (Porcar-Castell et al., 2014). Since the red to far-red F ratio experiments were conducted prevailingly with active techniques on single leaves, further studies especially with passive-canopy methods are warranted.

Impact of temperature stress on steady-state chlorophyll fluorescence

Chilling stress was found to positively stimulate the red F emission in single leaves observed with active methods, with an exception of a cold tolerant species (Table 2, Fig. 3a, and Fig. 4a). Similar results were obtained also for the far-red F (Table 2, Fig. 3a, and Fig. 4b). The rise of chlorophyll F under low temperature treatment was observed previously not only for intact leaves (Neuner and Larcher, 1990), but also for intact cells, isolated chloroplasts, and thylakoid membranes (Murata and Satoh, 1986). The temperature stimulated F increase could be attributed to reduction of photochemical quenching at lower temperatures, when effect on non-photochemical quenching is also much lower (e.g. Neuner and Larcher, 1990). Similarly to our results in Fig. 4, Agati et al. (1998) noticed that temperature decline increases the far-red F signal to a greater extent than the red F signal, leading subsequently to a red to far-red ratio decline. Based on their study of chilling stress effects in conifer stands, Adams and Demmig-Adams (1994) expressed a possibility that low temperature decreases photosystem II (PSII) and increases photosystem I (PSI) F emission. A lower temperature causes a lower

fluidity of the thylakoid membrane, which, through decreased plastoquinone reoxidation, can positively stimulate the fluorescence yield (Havaux and Gruszecki, 1993). Additionally, a long-term chilling induces chlorophyll degradation, which causes lower re-absorption of the red F (Lichtenthaler and Rinderle, 1988). Another relevant factor is overall temperature stress tolerance, which could explain why different species used by Agati (1996) reacted to the same stress exposure differently, as observed later also by Mishra et al. (2011). However, in other studies Agati et al. (1998; 2000) reported that low temperatures increased the F_s for both chilling sensitive and tolerant species.

Dobrowski et al. (2005) found that the maximum leaf temperature measured within a diurnal course coincided with the minimum observed F value. In few studies investigating the down regulating effect of heat stress on the steady-state F, a short-term intense heat exposure was naturally accompanied by a decline in leaf water content (Lang et al., 1996; Krumov, 2008; Pospíšil, 1998). In these cases the F change might be attributed to the NPQ protection mechanism described in Medrano et al. (2002), as well as to the photochemical (qP) quenching that declines in association with a lower photosynthetic rate (Pastenes and Horton, 1996; 1999) and triggers a concomitant F decrease. Lang (1996) found at least a 5-fold decline of F_s after combined temperature and drought stress exposure, when comparing control sun shaded (high chlorophyll content) with stressed sun exposed (low chlorophyll content) leaves. Such a significant decline is not likely to be caused only by temperature and water stress, but also by a noticeable difference in chlorophyll content. This finding corresponds with the canopy studies of Zarco-Tejada et al. (2003) and Middleton et al. (2009) observing a long-term co-occurrence of chlorophyll content and SIF decline. It should be mentioned that the SIF decline published in Middleton et al. (2009) was recorded within a seasonal cycle and as such influenced by other seasonal stressors (e.g. an excessive light stress or a low soil moisture). Since heat stress and water shortage often co-occur under natural conditions, their synergistic effect could induce even greater decrease in F than reported for both stressors separately.

Generally consistent, but statistically less significant responses to temperature extremes were found for the red to far-red F ratio (Table 2), which demonstrated prevailingly a decrease for both chilling and heat stress (Agati et al., 1995; 1998; 2000; Thoren et al., 2010). The opposite behaviour, i.e. increase of the red to far-red F ratio, was found only in two studies, where the first study (Agati et al., 1996) was using cold

tolerant plant species and a heat stress in the second study (Lang et al., 1996) may have resulted in a chlorophyll degradation.

Impact of nitrogen deficiency on steady-state chlorophyll fluorescence

Results of the random-effects meta-analysis and analysis of the simple S/C ratio both indicate the opposite effects of nitrogen deficiency on active and passive measurements of red as well as far-red F (see Fig. 5 and Fig. 6). Tremblay et al. (2012) also noticed variable trend in active red F measurements of nitrogen-deficient plants. Nitrogen deficiency affects many parts of the photosynthetic apparatus, including photosynthetic pigments, thylakoid proteins, and the soluble enzymes (especially Rubisco) involved in carbon fixation and photosynthetic carbon metabolism (e.g. Ciompi et al., 1996), in a complex way. Moreover, plant species differ with respect to allocation of nitrogen to different leaf pools, electron transport capacity, and specific activities of Rubisco (Kozlowski and Pallardy, 1997). Thus, F under nitrogen deficiency might either increase (e.g. in case of significant chlorophyll decline) or decrease (e.g. in the case of a reduced PSII electron transport, or a decline or an inactivity of the carboxylating enzyme Rubisco), depending on which components of the photosynthetic apparatus are affected. Also duration and intensity of the nitrogen deficiency plays an important role. While a short-term stress might reduce only photosynthetic functions, a long-term stress could cause an additional irreversible degradation of chlorophyll.

Gitelson et al. (1998) showed that the red to far-red F ratio strongly correlates with leaf chlorophyll content under 300 $mg.m^{-2}$, but less with higher chlorophyll concentrations. It is possible that the variable F behaviour noted here may arise from differences in chlorophyll content and consequent reabsorption of red F. Stressed plants, characterised by a lower leaf chlorophyll content ranging from 16 to 70% of control plants (e.g. Apostol et al., 2007 or Chappelle et al., 1997), re-absorb less red F photons, which consequently causes increase in the red F flux (Agati, 1998). Additionally, depending on the degree of penetration of incoming light into the deeper layers of leaves and canopies, both light absorption and the red F emission will be affected accordingly. Whereas some studies have found a species-specific, yet significant correlation between chlorophyll reduction and increase in the red F (e.g. Apostol et al., 2007; Kebabian et al., 1999) and the red to far-red F ratio (e.g. Apostol et al., 2007; Campbell et al., 2014; Kebabian et al., 1999; Kuckenberg et al., 2009), other studies have found a decrease in

575 the red to far-red F ratio (e.g. Campbell et al., 2007; Corp et al., 2003; McMurtrey et al.,
576 2002). We used our collected data to test the relationship between leaf chlorophyll
577 content and the S/C red and far-red F (including their ratio) where nitrogen deficiency
578 lasted longer than one-month, but no significant relationship was found (results not
579 shown). Homolová et al. (2013) recently reviewed leaf nitrogen content variability
580 across 27 plant species. They found that a universal correlation between leaf nitrogen
581 and chlorophyll content of various species could hardly be established. While restricted
582 nitrogen availability is for some plants stressful and endangers their survival, for others
583 a low nitrogen supply might be sufficient to support their growth even under a limited
584 chlorophyll production (e.g. symbiotic nitrogen fixing species). Therefore, the link
585 between the steady-state F, a nitrogen deficiency tolerance, and corresponding
586 chlorophyll content cannot be addressed generally, but should be considered for each
587 plant functional type separately.
588 Leaf age also determines the detectability of nitrogen insufficiency, since older
589 leaves are the first to express stress symptoms as a result of nitrogen movement from
590 older to more photosynthetically efficient younger leaves (Himelblau and Amasino,
591 2001). In addition to well known effects on plant productivity such as reduction of leaf
592 area and growth rate (Apostol et al., 2003; 2007; Boussadia et al., 2010; Ciompi et al.,
593 1996; Corp et al., 2006; McMurtney et al., 2003 and Zhao et al., 2005), a reduced leaf
594 photosynthetic rate due to the nitrogen deficiency has also been associated with a low
595 stomatal conductance (e.g., Boussadia et al., 2010; Ciompi et al., 1996; Corp et al., 2006
596 and Zhao et al., 2005). All of these aspects provide strong evidence that nitrogen stress
597 causes an array of plant physiological reactions and interactions with other stressors
598 (Chapin, 1991), which can make its detection by either red or far-red F rather
599 inconsistent. Despite this, we observed that the red to far-red F ratio of plants exposed
600 to a long-term nitrogen deficiency consistently increased (Fig. 5c and Fig. 6c).
601 Consequently, we recommend that this ratio should be further investigated as a
602 potential nutrition stress indicator.
603
604 ***Conclusions***
605 This meta-analysis revealed that a drought stress is, in general, accompanied by a
606 decrease in the steady-state red and far-red chlorophyll fluorescence. Chilling stress
607 tended to induce an increase in both red and far-red F, whereas heat stress, which often

accompanies water stress, caused F to decline. In contrast, the red to far-red F ratio significantly decreased with both chilling and heat. Also nitrogen deficiency produced consistent response of the red to far-red F ratio. The stress indicating character of this ratio suggests that the red and the far-red F measurements are complementary rather than redundant and should be collected simultaneously, if possible. Results of this work also indicate several existing knowledge gaps and inconsistencies. Future remote sensing studies should, therefore, focus on resolving canopy chlorophyll fluorescence changes by scaling structurally simpler experimental designs up to more complex multi-species canopies (e.g. natural forests) and standardizing F signals impacted by combined multi-agent stress events of varying intensities and durations by, for instance, normalisation with incident or absorbed photosynthetically active radiation (e.g. Rascher et al., 2009). Despite an intensive development, more attention should be paid to passive remote sensing methods that are still underrepresented with respect to the spatiotemporal assessment of actual vegetation stress load. Outcomes of these experiments are crucial not only for stress detection, but also for correct understanding of ecosystem functioning in general.

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List of Figure Captions

Fig. 1. Weighted means of standard difference in means between water deficit stressed and unstressed control plant trials computed with the random-effects meta-analysis model for red (FR) (a), far-red (FFR) (b), and red to far-red ratio (c) of steady-state chlorophyll fluorescence measured at leaf and canopy level using active and passive detection techniques. The single study analyses labelled with a double cross (††) are incomparable with the multi-study analyses (n>1). Analysis with a small number of input studies labelled with a single cross (†) should be regarded as less reliable. Error bars represent standard errors (SE_M) of the standard difference in means. Dashes indicate the upper and lower limits of 95% confidence interval and crosses indicate *Z*-values testing the null hypothesis and providing the probability levels (p), under which the null hypothesis is accepted or rejected. Description of the random-effects meta-analysis parameters and indicators is provided in methodological part of the study.

Fig. 2. Steady-state chlorophyll fluorescence (F) ratio of water deficit stressed and unstressed control plants for (FR) (a) and far-red (FFR) (b), and red to far-red F ratio (c) measured at leaf and canopy scales using active and passive detection techniques. Value p indicates the probability level computed by non-parametric Mann-Whitney U test, at which the null hypothesis that the steady-state F stress to control ratio is equal to one can be rejected. Statistically significant differences at probability level $p \leq 0.01$ and $p \leq 0.05$ are denoted with a double asterisk (**) and a single asterisk (*), respectively. The probability level p is not provided for cases having too small number of input studies (n≤2).

Fig. 3. Weighted means of standard difference in means between temperature stressed and unstressed control plant trials computed with the random-effects meta-analysis model for (FR) (a), far-red (FFR) (b), and red to far-red ratio (c) of steady-state chlorophyll fluorescence measured at leaf and canopy level using active and passive detection techniques. The single study analyses labelled with a double cross (††) are incomparable with the multi-study analyses (n>1). Analysis with a small number of input studies labelled with a single cross (†) should be regarded as less reliable. Error bars represent standard errors (SE_M) of the standard difference in means. Dashes indicate the upper and lower limits of 95% confidence interval and crosses indicate *Z*-

values testing the null hypothesis and providing the probability levels (p), under which the null hypothesis is accepted or rejected. Description of the random-effects meta-analysis parameters and indicators is provided in methodological part of the study.

Fig. 4. Steady-state chlorophyll fluorescence (F) ratio of low and high temperature stressed and unstressed control plants for (FR) (a) and far-red (FFR) (b), and red to far-red F ratio (c) measured at leaf and canopy scales using active and passive detection techniques. Value p indicates the probability level computed by non-parametric Mann-Whitney U test, at which the null hypothesis that the steady-state F stress to control ratio is equal to one can be rejected. Statistically significant differences at probability level $p \leq 0.01$ and $p \leq 0.05$ are denoted with a double asterisk (**) and a single asterisk (*), respectively. The probability level p is not provided for cases having too small number of input studies ($n \leq 2$).

Fig. 5. Weighted means of standard difference in means between nitrogen deficit stressed and unstressed control plant trials computed with the random-effects meta-analysis model for (FR) (a), far-red (FFR) (b), and red to far-red ratio (c) of steady-state chlorophyll fluorescence measured at leaf and canopy level using active and passive detection techniques. The single study analyses labelled with a double cross (††) are incomparable with the multi-study analyses ($n>1$). Analysis with a small number of input studies labelled with a single cross (†) should be regarded as less reliable. Error bars represent standard errors (SE_M) of the standard difference in means. Dashes indicate the upper and lower limits of 95% confidence interval (being off the scale, the lower limit for Canopy/Active studies is not displayed) and crosses indicate Z-values testing the null hypothesis and providing the probability levels (p), under which the null hypothesis is accepted or rejected. Description of the random-effects meta-analysis parameters and indicators is provided in methodological part of the study.

Fig. 6. Steady-state chlorophyll fluorescence (F) ratio of nutrition (nitrogen deficiency) stressed and unstressed control plants for (FR) (a) and far-red (FFR) (b), and red to far-red F ratio (c) measured at leaf and canopy scales using active and passive detection techniques. Value p indicates the probability level computed by non-parametric Mann-Whitney U test, at which the null hypothesis that the steady-state F stress to control

ratio is equal to one can be rejected. Statistically significant differences at probability level $p \leq 0.01$ and $p \leq 0.05$ are denoted with a double asterisk (**) and a single asterisk (*), respectively. The probability level p is not provided for cases having too small number of input studies ($n \leq 2$).

Tables and Figures

Table 1

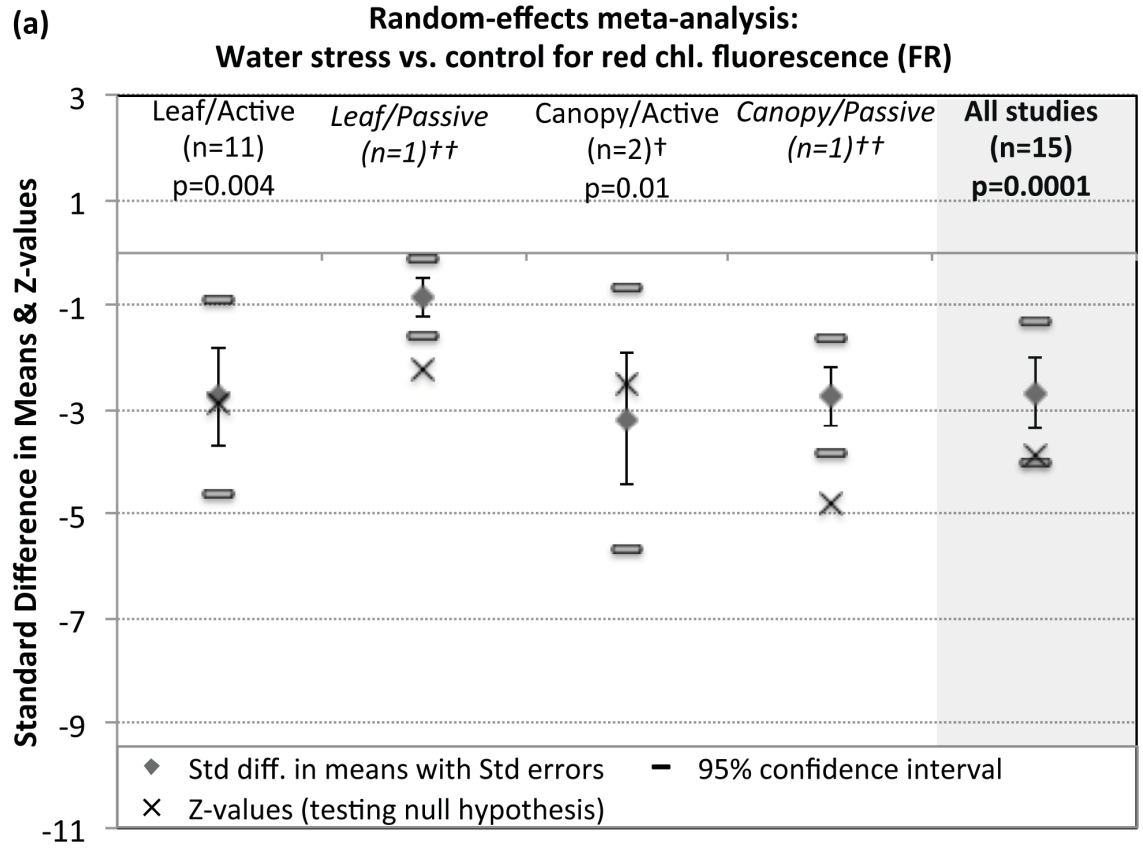
Results of random-effects meta-analysis of standard difference in means for steady-state chlorophyll fluorescence of red (FR) and far-red (FFR) wavelengths measured with active and passive methods for various plant species stressed by water deficit and unstressed (control) plants at leaf and canopy level. Explanation of the statistical indicators is provided in methodological part of this study. Only first authors of investigated studies are mentioned.

Leaf - Active	*Std diff in means*	*Std Error*	*Variance*	*Lower Limit*	*Upper Limit*	*Z-Value*	*p-Value*	*Relative Weight*
FR (n=11)								
Amoros-Lopez 2006	-1.1176	0.3926	0.1542	-1.8871	-0.3481	-2.8465	0.0044	9.3049
Araus 2010a	-2.8200	0.4993	0.2493	-3.7986	-1.8415	-5.6485	0.0000	9.2152
Araus 2010b	-1.2117	0.3972	0.1578	-1.9903	-0.4331	-3.0503	0.0023	9.3015
Araus 2010c	-1.9508	0.4295	0.1845	-2.7926	-1.1090	-4.5421	0.0000	9.2761
Araus 2010d	-2.8159	0.5153	0.2655	-3.8258	-1.8060	-5.4651	0.0000	9.2000
Burling 2014	-6.8562	0.7570	0.5730	-8.3399	-5.3726	-9.0575	0.0000	8.9221
Cendrero-Mateo 2013	-1.5077	0.8013	0.6421	-3.0782	0.0628	-1.8816	0.0599	8.8620
Evain 2004	-5.4766	0.7958	0.6332	-7.0363	-3.9170	-6.8823	0.0000	8.8697
Flexas 2000	-7.6174	0.7678	0.5895	-9.1223	-6.1126	-9.9212	0.0000	8.9077
Leufen 2013	5.6046	0.5549	0.3079	4.5170	6.6922	10.1004	0.0000	9.1607
Ounis 2001	-4.7367	0.7122	0.5073	-6.1326	-3.3407	-6.6505	0.0000	8.9801
Random Eff. (mean)	***-2.7382***	***0.9531***	***0.9083***	***-4.6061***	***-0.8702***	***-2.8730***	***0.0041***	
FFR (n=6)								
Amoros-Lopez 2006a	-0.8693	0.3820	0.1459	-1.6180	-0.1206	-2.2756	0.0229	18.8681
Amoros-Lopez 2006b	-1.1008	0.3918	0.1535	-1.8687	-0.3328	-2.8093	0.0050	18.7766
Flexas 1999	-2.8302	0.6327	0.4002	-4.0701	-1.5902	-4.4735	0.0000	16.2227
Flexas 2002a	-5.5691	0.9016	0.8128	-7.3361	-3.8021	-6.1772	0.0000	13.2166
Flexas 2002b	-3.1240	0.7964	0.6343	-4.6849	-1.5631	-3.9226	0.0001	14.3688
Perez-Priego 2005	-1.7512	0.4158	0.1729	-2.5662	-0.9362	-4.2113	0.0000	18.5472
Random Eff. (mean)	***-2.3396***	***0.5425***	***0.2943***	***-3.4027***	***-1.2764***	***-4.3129***	***0.0000***	
FR/FFR (n=7)								
Da Silva 2012	-4.4017	1.1699	1.3688	-6.6948	-2.1087	-3.7624	0.0002	12.2657
Leufen 2013	0.2409	0.2509	0.0630	-0.2508	0.7327	0.9603	0.3369	18.9049
Leufen 2014	0.9875	0.2648	0.0701	0.4685	1.5065	3.7294	0.0002	18.8489
Lins 2005	-0.6107	0.4575	0.2093	-1.5074	0.2860	-1.3348	0.1820	17.8235
Gouveia-Neto 2011	-6.3008	1.5443	2.3850	-9.3276	-3.2739	-4.0799	0.0000	9.6329
Subhash 2004a	8.8657	2.0809	4.3300	4.7873	12.944	4.2606	0.0000	6.8278
Subhash 2004b	1.7669	0.7457	0.5561	0.3053	3.2285	2.3694	0.0178	15.6963
Random Eff. (mean)	***-0.1413***	***0.6753***	***0.4561***	***-1.4649***	***1.1823***	***-0.2093***	***0.8342***	

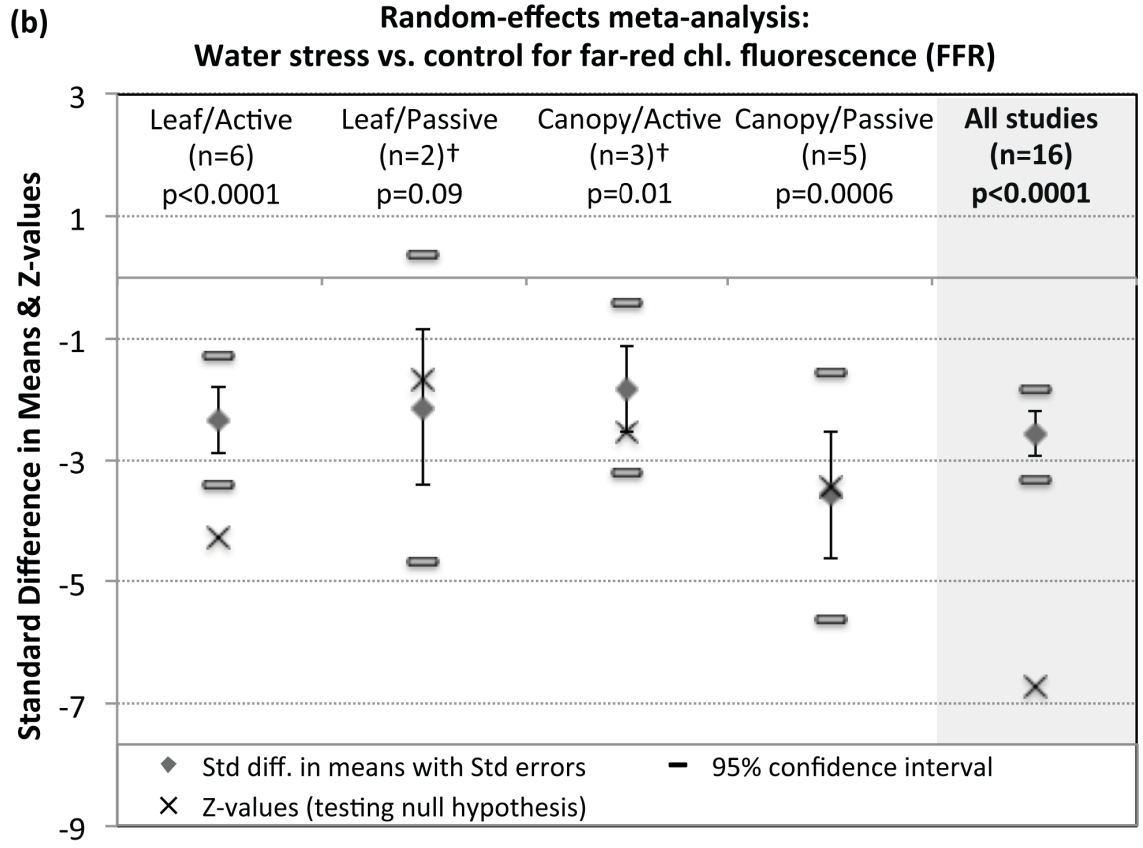
Leaf - Passive								
FR (n=1)								
Amoros-Lopez 2006 ††	-0.8419	0.3810	0.1451	-1.5886	-0.0952	-2.2098	0.0271	100.000
FFR (n=2)								
Amoros-Lopez 2006a	-0.8985	0.3831	0.1468	-1.6494	-0.1476	-2.3452	0.0190	51.4187
Amoros-Lopez 2006b	-3.4569	0.5766	0.3325	-4.5870	-2.3267	-5.9950	0.0000	48.5813
Random Eff. (mean) †	***-2.1414***	***1.2787***	***1.6350***	***-4.6475***	***0.3648***	***-1.6747***	***0.0940***	
Canopy - Active								
FR (n=2)								
Gunther 1994	-1.9559	0.4440	0.1971	-2.8261	-1.0858	-4.4057	0.0000	52.1130
Evain 2004	-4.5034	0.6865	0.4713	-5.8490	-3.1578	-6.5595	0.0000	47.8870
Random Eff. (mean) †	***-3.1758***	***1.2726***	***1.6195***	***-5.6701***	***-0.6816***	***-2.4955***	***0.0126***	
FFR (n=3)								
Gunther 1994	-2.5440	0.4911	0.2412	-3.5066	-1.5814	-5.1800	0.0000	32.6765
Rascher 2009	-0.5345	0.3992	0.1593	-1.3168	0.2479	-1.3389	0.1806	34.5523
Rosema 1998	-2.4921	0.4867	0.2368	-3.4460	-1.5383	-5.1208	0.0000	32.7712
Random Eff. (mean) †	**-1.8327**	**0.7019**	**0.4927**	**-3.2084**	**-0.4569**	**-2.6109**	**0.0090**	
FR/FFR (n=3)								
Dahn 1992	-0.3805	0.6382	0.4072	-1.6313	0.8702	-0.5963	0.5510	32.1133
Valentini 1994a	2.5893	0.5809	0.3374	1.4508	3.7277	4.4575	0.0000	33.1978
Valentini 1994b	0.6497	0.4985	0.2485	-0.3274	1.6268	1.3033	0.1925	34.6889
Random Eff. (mean) †	***0.9628***	***0.8285***	***0.6864***	***-0.6611***	***2.5866***	***1.1620***	***0.2452***	
Canopy - Passive								
FR (n=1)								
Daumard 2010 ††	-2.7342	0.5678	0.3224	-3.8471	-1.6213	-4.8153	0.0000	100.000
FFR (n=5)								
Daumard 2010	-6.5714	1.0326	1.0663	-8.5953	-4.5475	-6.3638	0.0000	17.8508
Rascher 2009	-6.9408	0.6842	0.4681	-8.2818	-5.5998	-10.145	0.0000	19.8092
Lee 2014	-2.0723	0.4527	0.2049	-2.9595	-1.1851	-4.5780	0.0000	20.8140
Zarco-Tejada 2009	-1.3912	0.3940	0.1552	-2.1634	-0.6189	-3.5308	0.0004	21.0152
Perez-Priego 2005	-1.4626	0.5307	0.2816	-2.5028	-0.4225	-2.7560	0.0059	20.5107
Random Eff. (mean)	***-3.5717***	***1.0393***	***1.0801***	***-5.6086***	***-1.5347***	***-3.4367***	***0.0006***	

†† Only one input study, i.e. results are incomparable with the analyses of multiple studies.

† A low number of input studies, i.e. meta-analysis cannot be applied correctly and results are less reliable.


(a)
Random-effects meta-analysis:
Water stress vs. control for red chl. fluorescence (FR)
Leaf/Active (n=11) p=0.004
Leaf/Passive (n=1)††
Canopy/Active (n=2)† p=0.01
Canopy/Passive (n=1)††
All studies (n=15) p=0.0001
Standard Difference in Means & Z-values
3
1
-1
-3
-5
-7
-9
-11
Std diff. in means with Std errors
95% confidence interval
Z-values (testing null hypothesis)

1147


(b)
Random-effects meta-analysis:
Water stress vs. control for far-red chl. fluorescence (FFR)
Leaf/Active (n=6) p<0.0001
Leaf/Passive (n=2)† p=0.09
Canopy/Active (n=3)† p=0.01
Canopy/Passive (n=5) p=0.0006
All studies (n=16) p<0.0001
Standard Difference in Means & Z-values
3
1
-1
-3
-5
-7
-9
Std diff. in means with Std errors
95% confidence interval
Z-values (testing null hypothesis)

1148

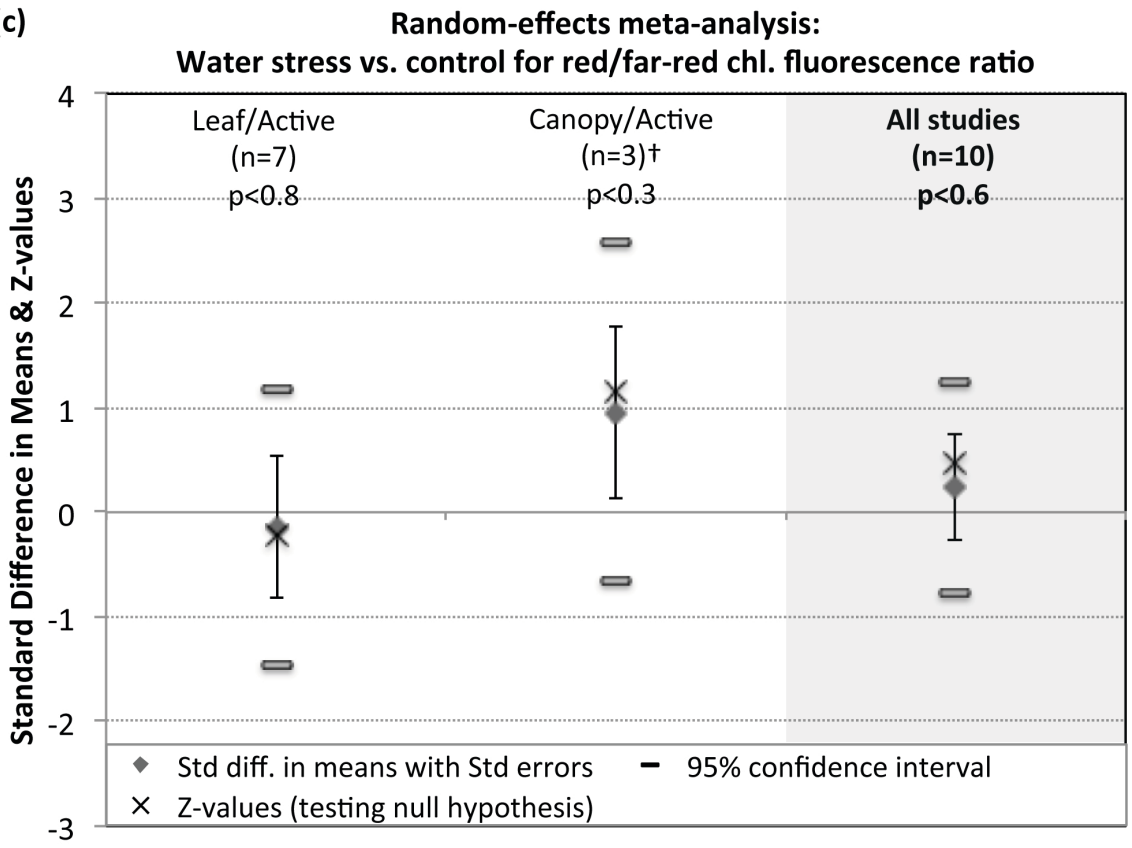
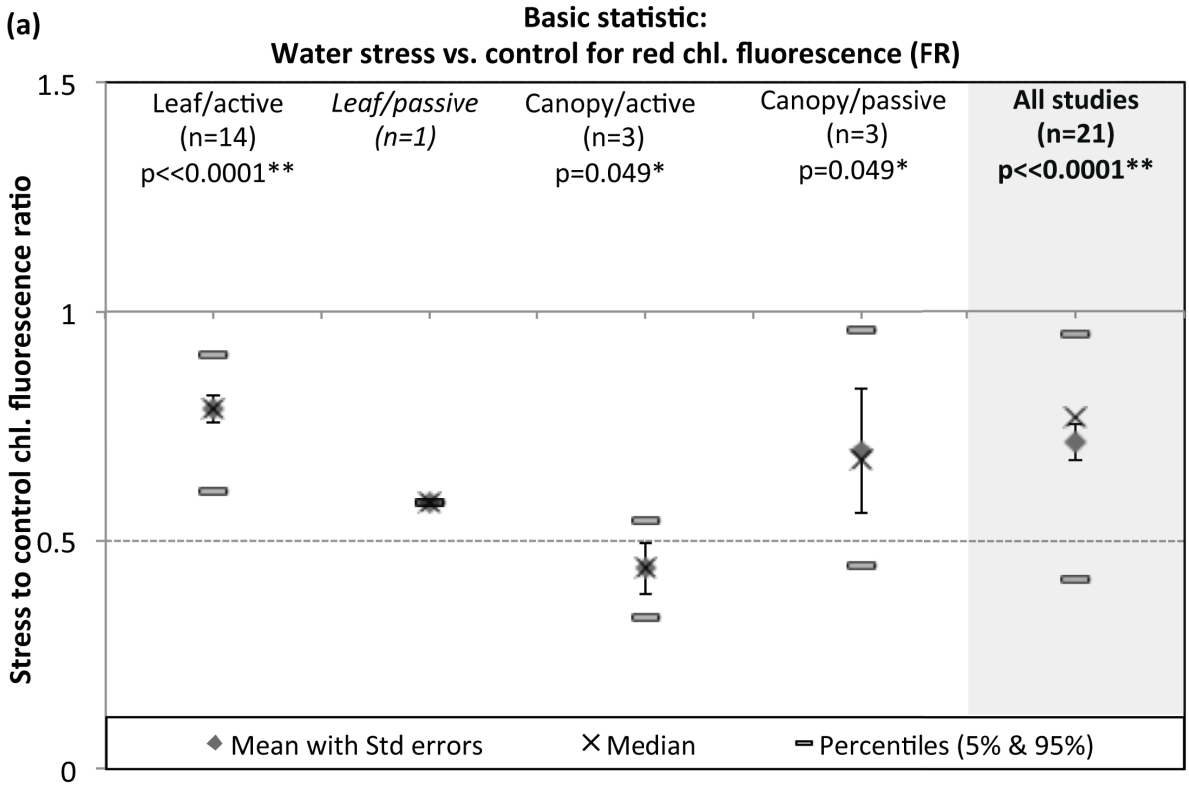
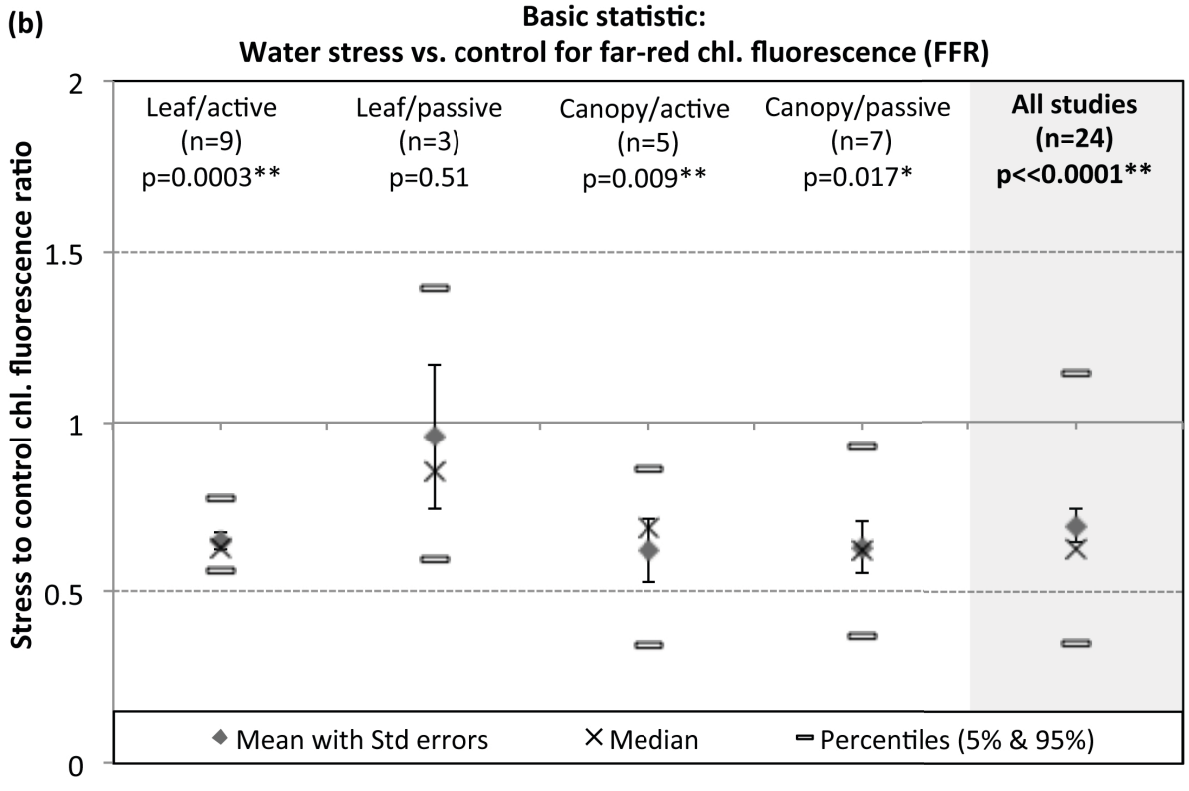


Fig. 1. Weighted means of standard difference in means between water deficit stressed and unstressed control plant trials computed with the random-effects meta-analysis model for red (FR) (a), far-red (FFR) (b), and red to far-red ratio (c) of steady-state chlorophyll fluorescence measured at leaf and canopy level using active and passive detection techniques. The single study analyses labelled with a double cross (††) are incomparable with the multi-study analyses (n>1). Analysis with a small number of input studies labelled with a single cross (†) should be regarded as less reliable. Error bars represent standard errors (SE_M) of the standard difference in means. Dashes indicate the upper and lower limits of 95% confidence interval and crosses indicate *Z*-values testing the null hypothesis and providing the probability levels (p), under which the null hypothesis is accepted or rejected. Description of the random-effects meta-analysis parameters and indicators is provided in methodological part of the study.


(a)
Basic statistic:
Water stress vs. control for red chl. fluorescence (FR)
Stress to control chl. fluorescence ratio
1.5
1
0.5
0
Leaf/active (n=14) p<<0.0001**
Leaf/passive (n=1)
Canopy/active (n=3) p=0.049*
Canopy/passive (n=3) p=0.049*
All studies (n=21) p<<0.0001**
Mean with Std errors
Median
Percentiles (5% & 95%)

1162


(b)
Basic statistic:
Water stress vs. control for far-red chl. fluorescence (FFR)
Stress to control chl. fluorescence ratio
2
1.5
1
0.5
0
Leaf/active (n=9) p=0.0003**
Leaf/passive (n=3) p=0.51
Canopy/active (n=5) p=0.009**
Canopy/passive (n=7) p=0.017*
All studies (n=24) p<<0.0001**
Mean with Std errors
Median
Percentiles (5% & 95%)

1163

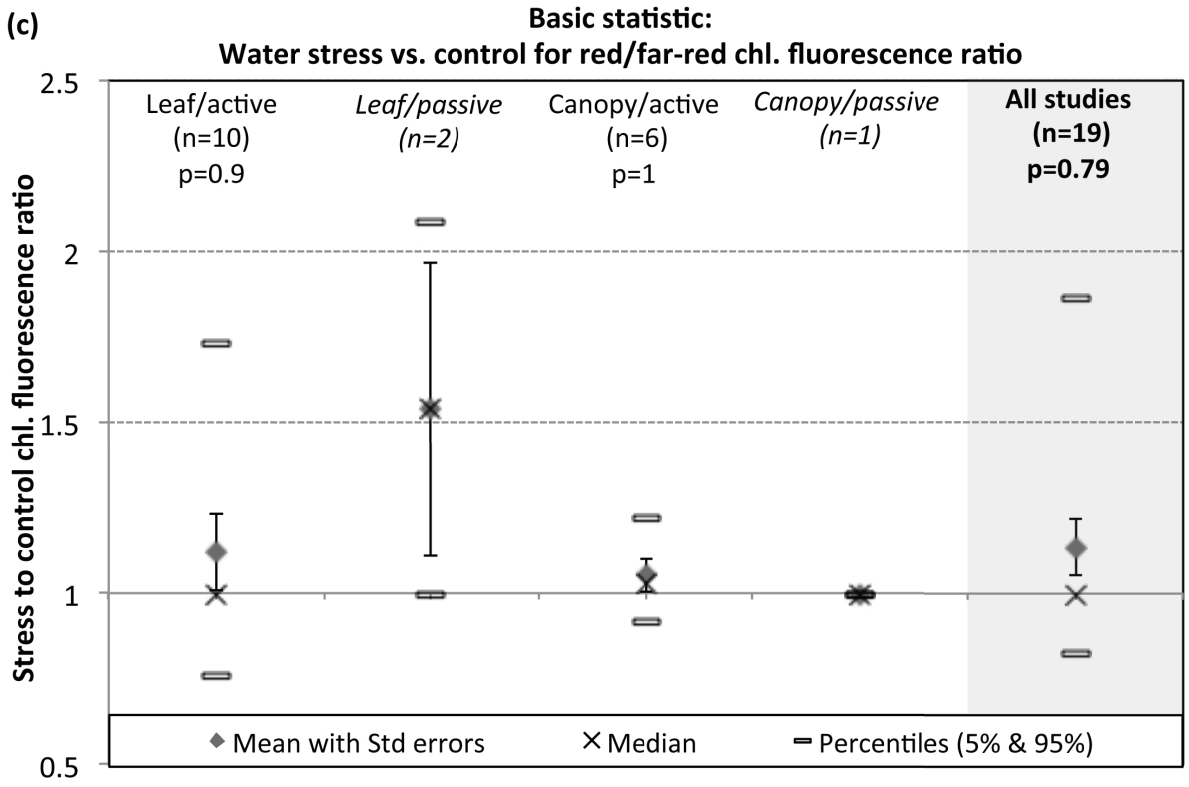


Fig. 2. Steady-state chlorophyll fluorescence (F) ratio of water deficit stressed and unstressed control plants for (FR) (a) and far-red (FFR) (b), and red to far-red F ratio (c) measured at leaf and canopy scales using active and passive detection techniques. Value *p* indicates the probability level computed by non-parametric Mann-Whitney U test, at which the null hypothesis that the steady-state F stress to control ratio is equal to one can be rejected. Statistically significant differences at probability level $p \leq 0.01$ and $p \leq 0.05$ are denoted with a double asterisk (**) and a single asterisk (*), respectively. The probability level *p* is not provided for cases having too small number of input studies ($n \leq 2$).

1175 Table 2

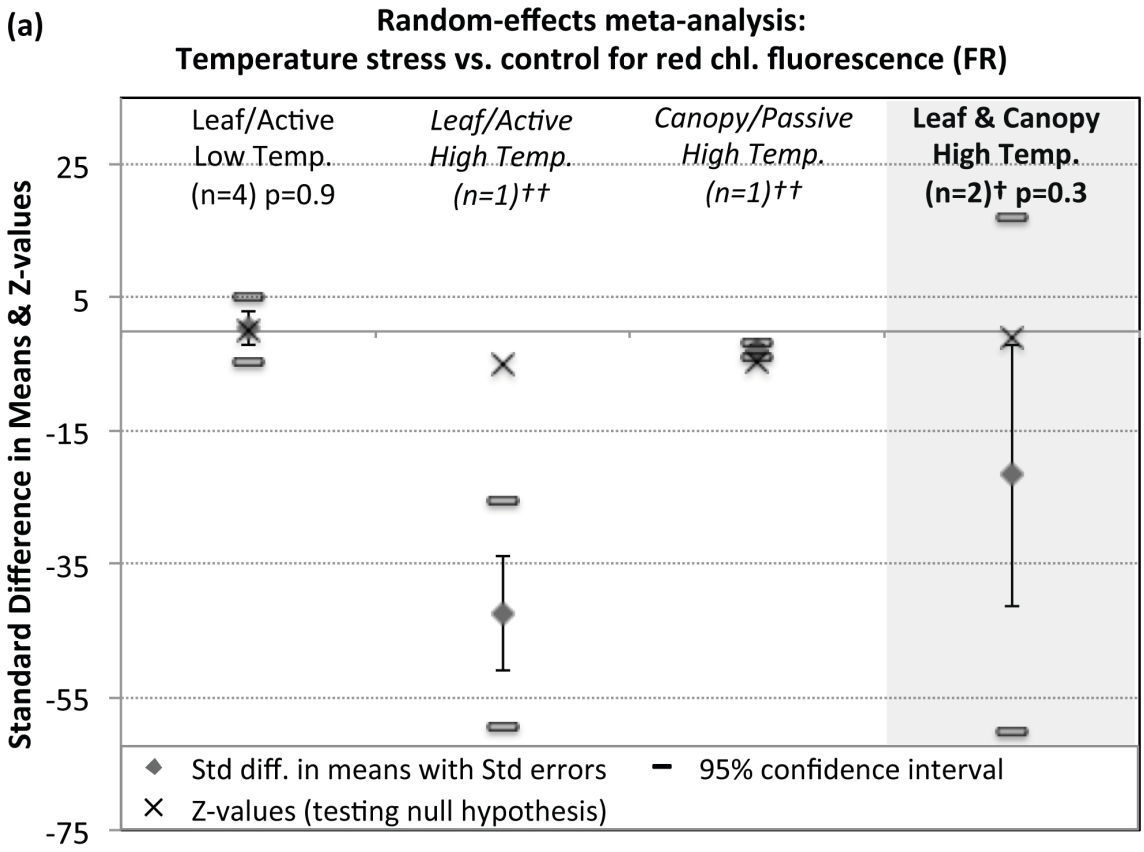
1176 Results of random-effects meta-analysis of standard difference in means for steady-state
1177 chlorophyll fluorescence of red (FR) and far-red (FFR) wavelengths measured with
1178 active and passive methods for various plant species stressed by low or high
1179 temperature (T) and unstressed (control) plants at leaf and canopy level. Explanation of
1180 the statistical indicators is provided in methodological part of this study. Only first
1181 authors of investigated studies are mentioned.

Leaf - Active	*Std diff in means*	*Std Error*	*Variance*	*Lower limit*	*Upper Limit*	*Z-Value*	*p-Value*	*Relative Weight*
FR (n=4+1)								
Agati 1996a (low T)	-34.8125	6.6006	43.5682	-47.7495	-21.8755	-5.2741	0.0000	11.6253
Agati 1996b (low T)	7.9964	1.6029	2.5694	4.8547	11.1381	4.9886	0.0000	25.6925
Agati 2000a (low T)	2.0711	0.7156	0.5121	0.6686	3.4736	2.8943	0.0038	27.3534
Agati 2000b (low T)	3.2024	0.8721	0.7606	1.4930	4.9117	3.6718	0.0002	27.1414
Random Eff. (mean)	***0.4668***	***2.4864***	***6.1823***	***-4.4065***	***5.3400***	***0.1877***	***0.8511***	
Lang 1996 (high T)††	-42.3355	8.6610	75.0123	-59.3107	-25.3603	-4.8881	0.0000	100.000
FFR (n=2+1)								
Agati 2000a (low T)	4.8202	1.1408	1.3014	2.5843	7.0561	4.2253	0.0000	45.1191
Agati 2000b (low T)	3.6862	0.9484	0.8995	1.8273	5.5450	3.8867	0.0001	45.7358
Random Eff. (mean) †	***4.1496***	***0.7293***	***0.5319***	***2.7202***	***5.5790***	***5.6899***	***4.1496***	
Lang 1996b (high T)††	-53.2663	10.8883	118.554	-74.6069	-31.9257	-4.8921	0.0000	100.000
FR/FFR (n=5+4):								
Agati 1996a (low T)	-3.5184	0.9215	0.8491	-5.3245	-1.7123	-3.8182	0.0001	20.2250
Agati 1996b (low T)	4.9302	1.0742	1.1538	2.8249	7.0355	4.5898	0.0000	19.8527
Agati 2000a (low T)	-4.4173	1.0707	1.1463	-6.5157	-2.3188	-4.1257	0.0000	19.8616
Agati 2000b (low T)	-2.9210	0.8300	0.6889	-4.5477	-1.2943	-3.5194	0.0004	20.4266
di Paola 1992 (low T)	-6.7469	1.1567	1.3380	-9.0141	-4.4798	-5.8328	0.0000	19.6341
Random Eff. (mean)	***-2.5315***	***1.8125***	***3.2851***	***-6.0839***	***1.0209***	***-1.3967***	***0.1625***	
Agati 1995 (high T)	-9.4020	2.0041	4.0166	-13.3301	-5.4740	-4.6913	0.0000	16.1556
Balota 1999 (high T)	-1.8850	0.2453	0.0602	-2.3658	-1.4042	-7.6843	0.0000	29.1654
Lang 1996a (high T)	0.0000	0.4472	0.2000	-0.8765	0.8765	0.0000	1.0000	28.3583
Lang 1996b (high T)	2.4876	0.7689	0.5912	0.9806	3.9946	3.2354	0.0012	26.3207
Random Eff. (mean)	***-1.4140***	***1.1970***	***1.4329***	***-3.7601***	***0.9322***	***-1.1812***	***0.2375***	
Canopy - Active								
FR/FFR (n=1)								
Thoren 2010 (high T)††	-31.4438	9.1183	83.1425	-49.3152	-13.5723	-3.4484	0.0006	100.000
Canopy - Passive								
FR (n=1):								
Middleton 2009 (high T)††	-2.8000	0.6293	0.3960	-4.0334	-1.5666	-4.4495	0.0000	100.000

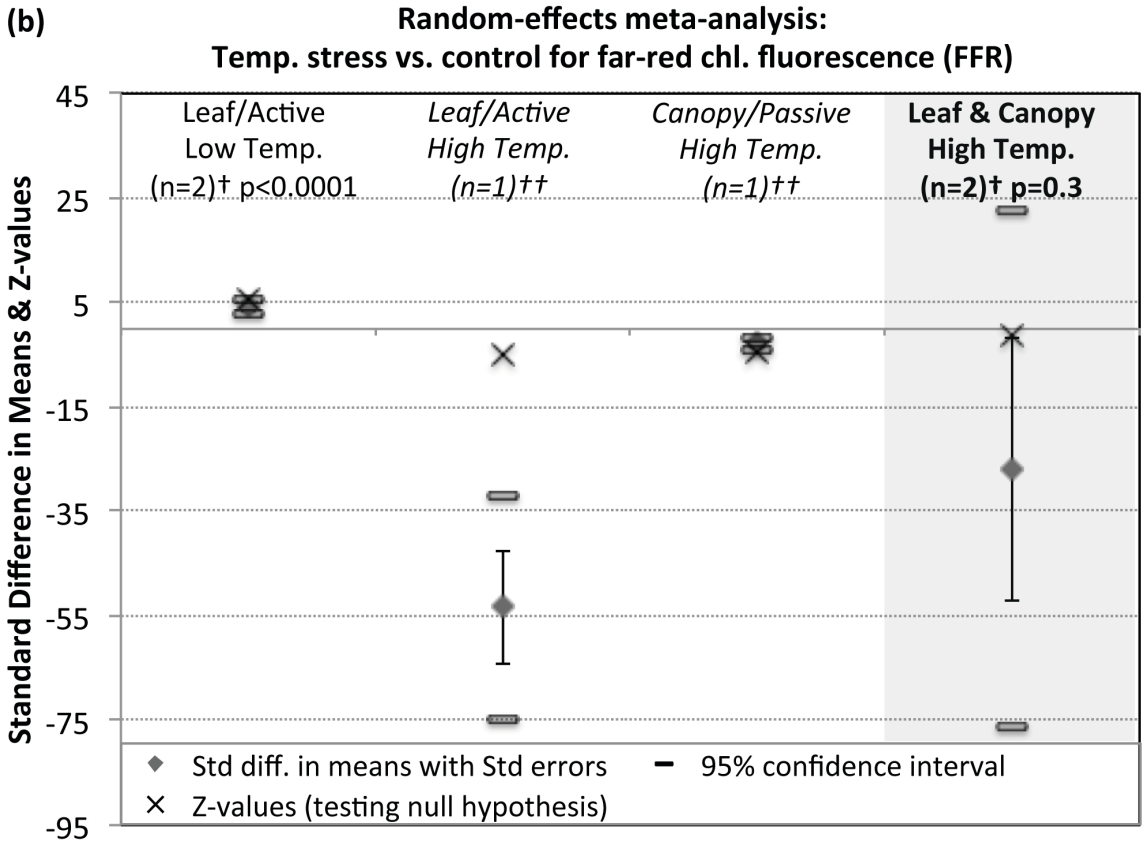
FFR (n=1)								
Middleton 2009 (high T)††	-2.7839	0.6275	0.3938	-4.0138	-1.5541	-4.4365	0.0000	100.000

†† Only one input study, i.e. results are incomparable with the analyses of multiple studies.

† A low number of input studies, i.e. meta-analysis cannot be applied correctly and results are less reliable.


(a)
Random-effects meta-analysis:
Temperature stress vs. control for red chl. fluorescence (FR)
Leaf/Active Low Temp. (n=4) p=0.9
Leaf/Active High Temp. (n=1)††
Canopy/Passive High Temp. (n=1)††
Leaf & Canopy High Temp. (n=2)† p=0.3
Standard Difference in Means & Z-values
25
5
-15
-35
-55
-75
Std diff. in means with Std errors
95% confidence interval
Z-values (testing null hypothesis)

1184


(b)
Random-effects meta-analysis:
Temp. stress vs. control for far-red chl. fluorescence (FFR)
Leaf/Active Low Temp. (n=2)† p<0.0001
Leaf/Active High Temp. (n=1)††
Canopy/Passive High Temp. (n=1)††
Leaf & Canopy High Temp. (n=2)† p=0.3
Standard Difference in Means & Z-values
45
25
5
-15
-35
-55
-75
-95
Std diff. in means with Std errors
95% confidence interval
Z-values (testing null hypothesis)

1185

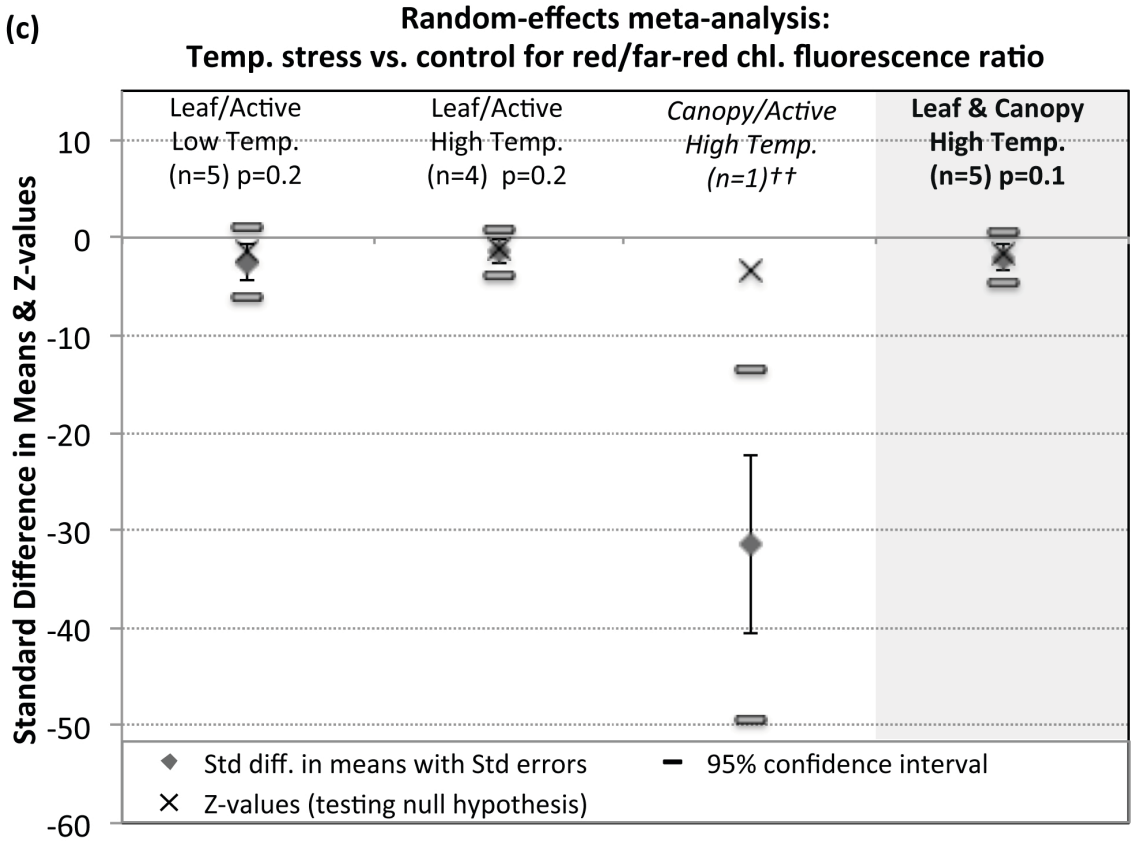
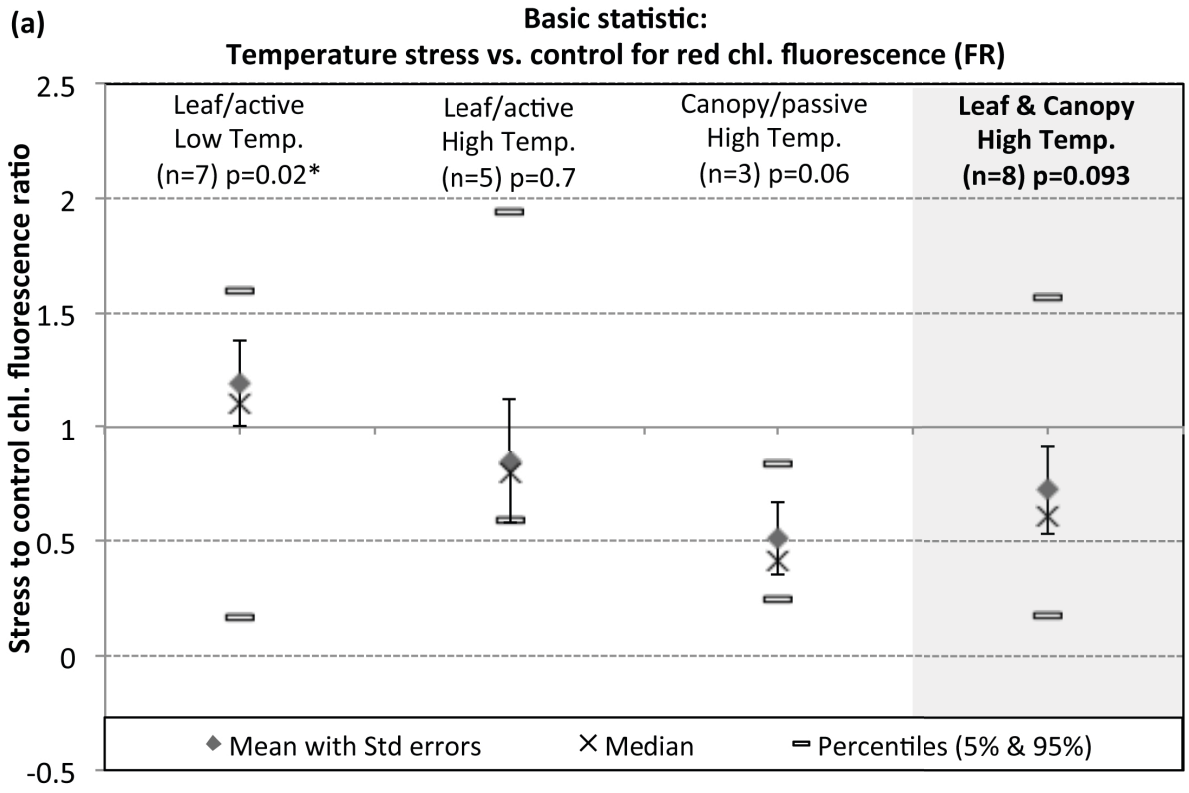
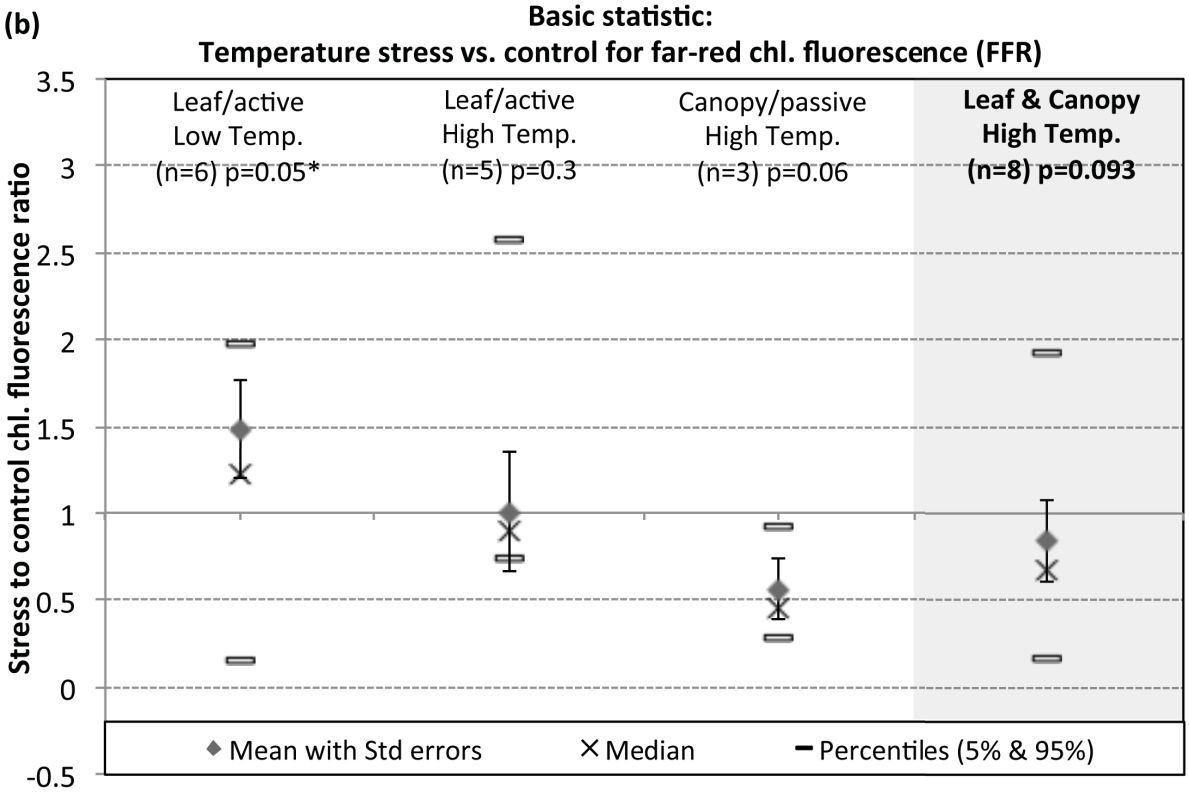


Fig. 3. Weighted means of standard difference in means between temperature stressed and unstressed control plant trials computed with the random-effects meta-analysis model for (FR) (a), far-red (FFR) (b), and red to far-red ratio (c) of steady-state chlorophyll fluorescence measured at leaf and canopy level using active and passive detection techniques. The single study analyses labelled with a double cross (††) are incomparable with the multi-study analyses (n>1). Analysis with a small number of input studies labelled with a single cross (†) should be regarded as less reliable. Error bars represent standard errors (SE_M) of the standard difference in means. Dashes indicate the upper and lower limits of 95% confidence interval and crosses indicate *Z*-values testing the null hypothesis and providing the probability levels (p), under which the null hypothesis is accepted or rejected. Description of the random-effects meta-analysis parameters and indicators is provided in methodological part of the study.


(a)
Basic statistic:
Temperature stress vs. control for red chl. fluorescence (FR)
Stress to control chl. fluorescence ratio
2.5
2
1.5
1
0.5
0
-0.5
Leaf/active Low Temp. (n=7) p=0.02*
Leaf/active High Temp. (n=5) p=0.7
Canopy/passive High Temp. (n=3) p=0.06
Leaf & Canopy High Temp. (n=8) p=0.093
Mean with Std errors
Median
Percentiles (5% & 95%)

1199


(b)
Basic statistic:
Temperature stress vs. control for far-red chl. fluorescence (FFR)
Stress to control chl. fluorescence ratio
3.5
3
2.5
2
1.5
1
0.5
0
-0.5
Leaf/active Low Temp. (n=6) p=0.05*
Leaf/active High Temp. (n=5) p=0.3
Canopy/passive High Temp. (n=3) p=0.06
Leaf & Canopy High Temp. (n=8) p=0.093
Mean with Std errors
Median
Percentiles (5% & 95%)

1200

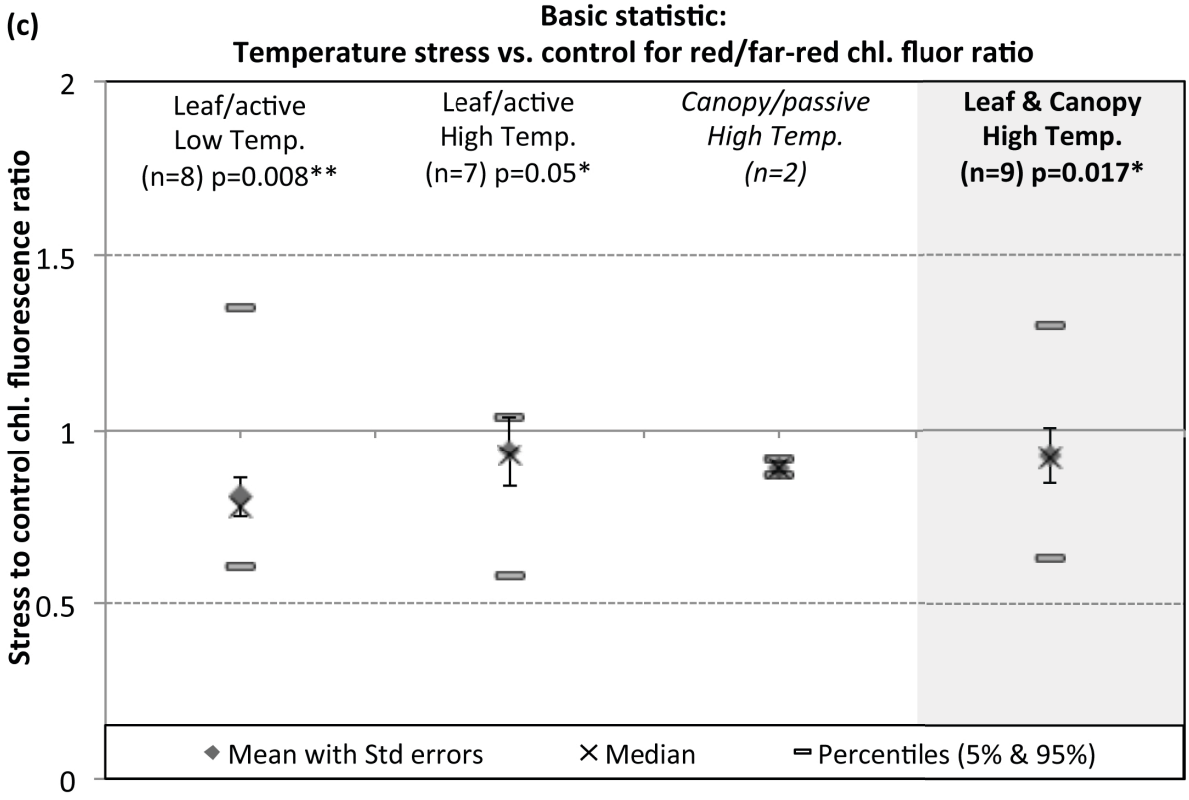


Fig. 4. Steady-state chlorophyll fluorescence (F) ratio of low and high temperature stressed and unstressed control plants for (FR) (a) and far-red (FFR) (b), and red to far-red F ratio (c) measured at leaf and canopy scales using active and passive detection techniques. Value *p* indicates the probability level computed by non-parametric Mann-Whitney U test, at which the null hypothesis that the steady-state F stress to control ratio is equal to one can be rejected. Statistically significant differences at probability level $p \leq 0.01$ and $p \leq 0.05$ are denoted with a double asterisk (**) and a single asterisk (*), respectively. The probability level *p* is not provided for cases having too small number of input studies ($n \leq 2$).

Table 3

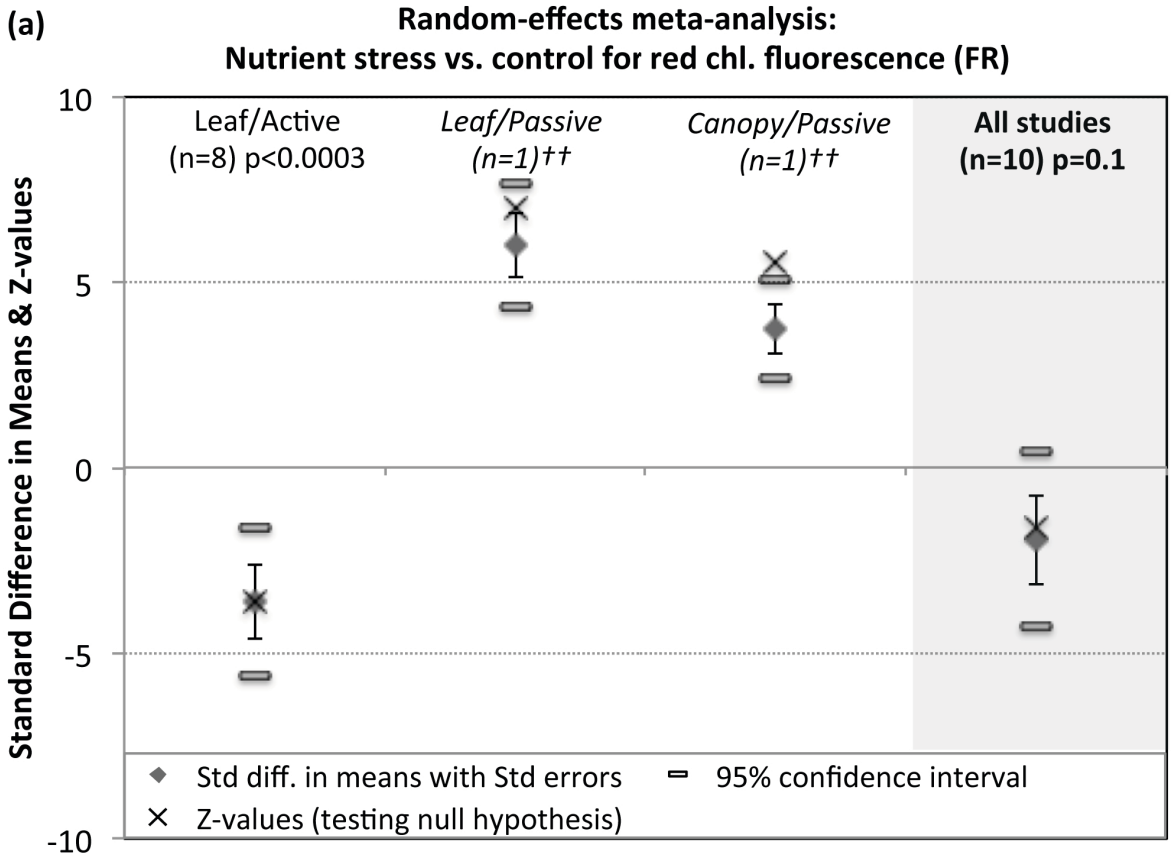
Results of random-effects meta-analysis of standard difference in means for steady-state chlorophyll fluorescence of red (FR) and far-red (FFR) wavelengths measured with active and passive methods for various plant species stressed by nitrogen deficit and unstressed (control) plants at leaf and canopy level. Explanation of the statistical indicators is provided in methodological part of this study. Only first authors of investigated studies are mentioned.

Leaf - Active	*Std diff in means*	*Std Error*	*Variance*	*Lower limit*	*Upper Limit*	*Z-Value*	*p-Value*	*Relative Weight*
FR (n=8)								
Ač unpublished	-1.7660	0.5582	0.3116	-2.8601	-0.6719	-3.1635	0.0016	13.1949
Cendrero-Mateo 2013	-7.1294	2.2141	4.9024	-11.4691	-2.7898	-3.2200	0.0013	8.2742
C-Mateo unpublished	-3.5276	0.7536	0.5679	-5.0046	-2.0506	-4.6811	0.0000	12.7709
Chapelle 1984	-7.7247	0.3755	0.1410	-8.4606	-6.9888	-20.5732	0.0000	13.4932
Konanz 2014	-2.0473	0.6172	0.3810	-3.2571	-0.8376	-3.3169	0.0009	13.0774
Leufen 2014	-1.6247	0.8155	0.6650	-3.2230	-0.0264	-1.9924	0.0463	12.6174
McMurtrey 2002	-4.3841	0.6735	0.4537	-5.7042	-3.0639	-6.5089	0.0000	12.9565
Tartachnyk 2006	-1.9266	0.2706	0.0732	-2.4569	-1.3963	-7.1210	0.0000	13.6154
Random Eff. (mean)	***-3.6188***	***1.0092***	***1.0186***	***-5.5969***	***-1.6407***	***-3.5857***	***0.0003***	
FFR (n=4)								
C-Mateo unpublished	-2.9829	0.6851	0.4694	-4.3257	-1.6401	-4.3539	0.0000	24.3064
Chapelle 1984	-6.7976	0.3361	0.1129	-7.4563	-6.1390	-20.2277	0.0000	25.4489
Konanz 2014	-1.8002	0.5927	0.3513	-2.9618	-0.6385	-3.0373	0.0024	24.6734
Tartachnyk 2006	-2.0653	0.2769	0.0767	-2.6080	-1.5227	-7.4594	0.0000	25.5713
Random Eff. (mean)	***-3.4273***	***1.3892***	***1.9298***	***-6.1500***	***-0.7046***	***-2.4671***	***0.0136***	
FR/FFR (n=10):								
Agati 2013a	6.4395	0.3517	0.1237	5.7503	7.1288	18.3115	0.0000	10.3282
Agati 2013b	3.3869	0.2206	0.0487	2.9545	3.8194	15.3511	0.0000	10.4825
Apostol 2003a	0.7797	0.4728	0.2235	-0.1470	1.7063	1.6491	0.0991	10.1297
Apostol 2003b	1.4355	0.5098	0.2599	0.4364	2.4346	2.8161	0.0049	10.0593
Burling 2011	4.4173	0.7571	0.5732	2.9334	5.9011	5.8346	0.0000	9.4909
Konanz 2014	1.0000	0.3354	0.1125	0.3426	1.6574	2.9814	0.0029	10.3509
Kuckenberg 2009	1.4702	0.6507	0.4234	0.1949	2.7456	2.2595	0.0239	9.7544
Leufen 2014a	0.1697	0.3542	0.1254	-0.5245	0.8638	0.4790	0.6320	10.3246
Leufen 2014b	0.0743	0.3537	0.1251	-0.6189	0.7675	0.2100	0.8336	10.3253
Tartachnyk 2006	5.6117	1.0197	1.0398	3.6131	7.6103	5.5032	0.0000	8.7541
Random Eff. (mean)	***2.4261***	***0.7254***	***0.5262***	***1.0043***	***3.8479***	***3.3445***	***0.0008***	
Leaf - Passive								
FR (n=1)								
Middleton 2008 [††]	6.0000	0.8563	0.7333	4.3216	7.6784	7.0065	0.0000	100.0000

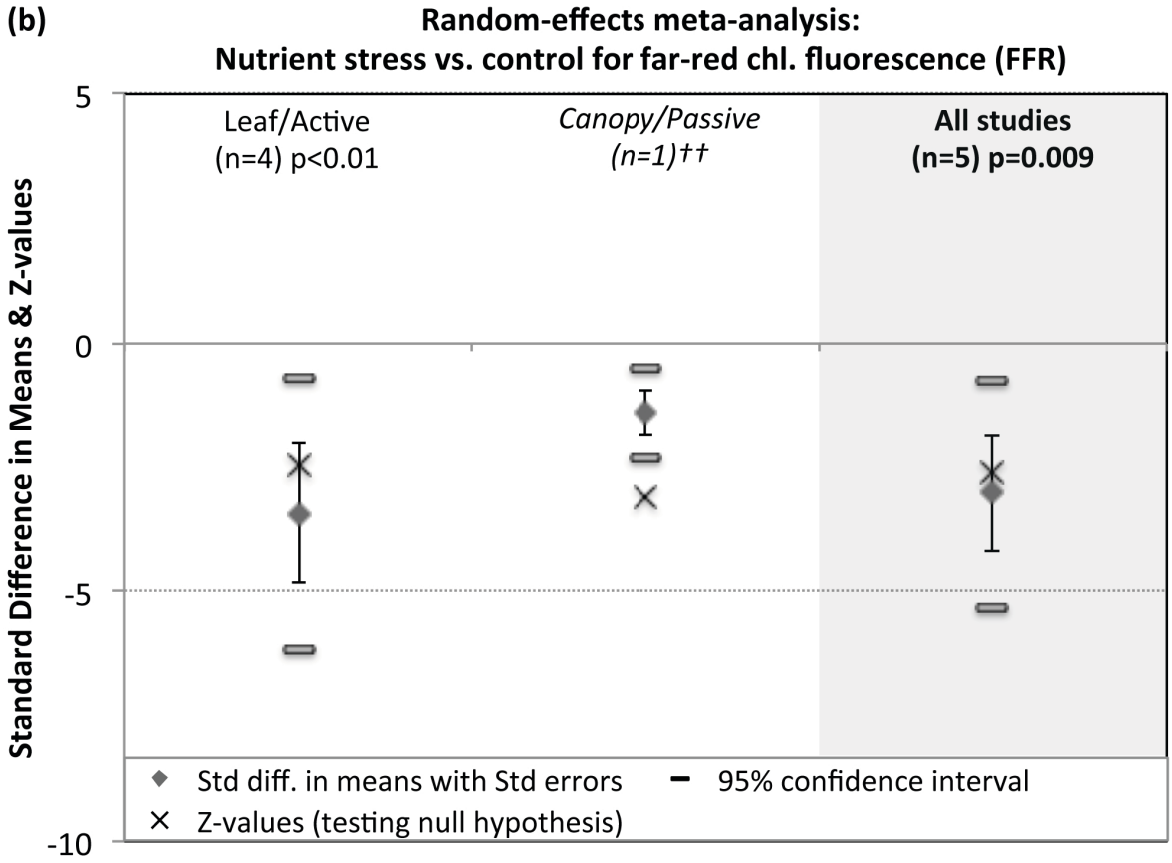
FR/FFR (n=1)								
Campbell 2008 ††	7.2672	0.9748	0.9502	5.3566	9.1777	7.4552	0.0000	100.0000
Canopy - Active								
FR/FFR (n=2)								
Kuckenberg 2009	0.4600	0.5849	0.3422	-0.6864	1.6065	0.7864	0.4316	51.0685
Thoren 2009	17.5907	2.5716	6.6132	12.5504	22.6310	6.8403	0.0000	48.9315
Random Eff. (mean) †	***8.8423***	***8.5634***	***73.3315***	***-7.9416***	***25.6262***	***1.0326***	***0.3018***	
Canopy - Passive								
FR (n=1)								
Kebabian 1999 ††	3.7566	0.6787	0.4607	2.4263	5.0869	5.5348	0.0000	100.0000
FFR (n=1)								
Kebabian 1999 ††	-1.4047	0.4558	0.2078	-2.2981	-0.5113	-3.0817	0.0021	100.0000
FR/FFR (n=3)								
Freedman 2002a	6.6408	1.0418	1.0854	4.5988	8.6827	6.3741	0.0000	31.1744
Freedman 2002b	5.4622	0.8878	0.7882	3.7221	7.2023	6.1523	0.0000	42.9275
Kebabian 1999	7.3969	1.1430	1.3066	5.1566	9.6373	6.4712	0.0000	25.8981
Random Eff. (mean) †	***6.3307***	***0.5817***	***0.3384***	***5.1906***	***7.4708***	***10.8831***	***0.0000***	

†† Only one input study, i.e. results are incomparable with the analyses of multiple studies.

† A low number of input studies, i.e. meta-analysis cannot be applied correctly and results are less reliable.


(a)
Random-effects meta-analysis:
Nutrient stress vs. control for red chl. fluorescence (FR)
Leaf/Active
(n=8) p<0.0003
Leaf/Passive
(n=1)††
Canopy/Passive
(n=1)††
All studies
(n=10) p=0.1
Standard Difference in Means & Z-values
10
5
0
-5
-10
Std diff. in means with Std errors
95% confidence interval
Z-values (testing null hypothesis)

1221


(b)
Random-effects meta-analysis:
Nutrient stress vs. control for far-red chl. fluorescence (FFR)
Leaf/Active
(n=4) p<0.01
Canopy/Passive
(n=1)††
All studies
(n=5) p=0.009
Standard Difference in Means & Z-values
5
0
-5
-10
Std diff. in means with Std errors
95% confidence interval
Z-values (testing null hypothesis)

1222

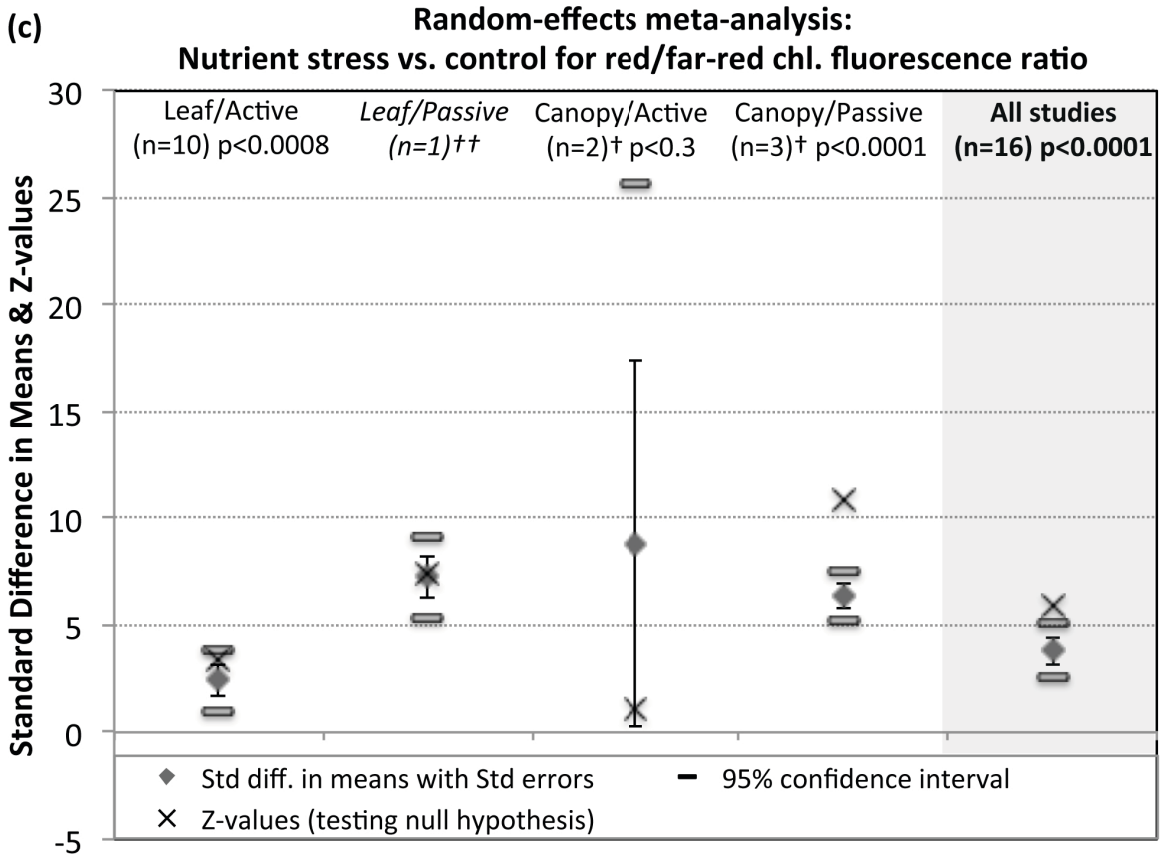
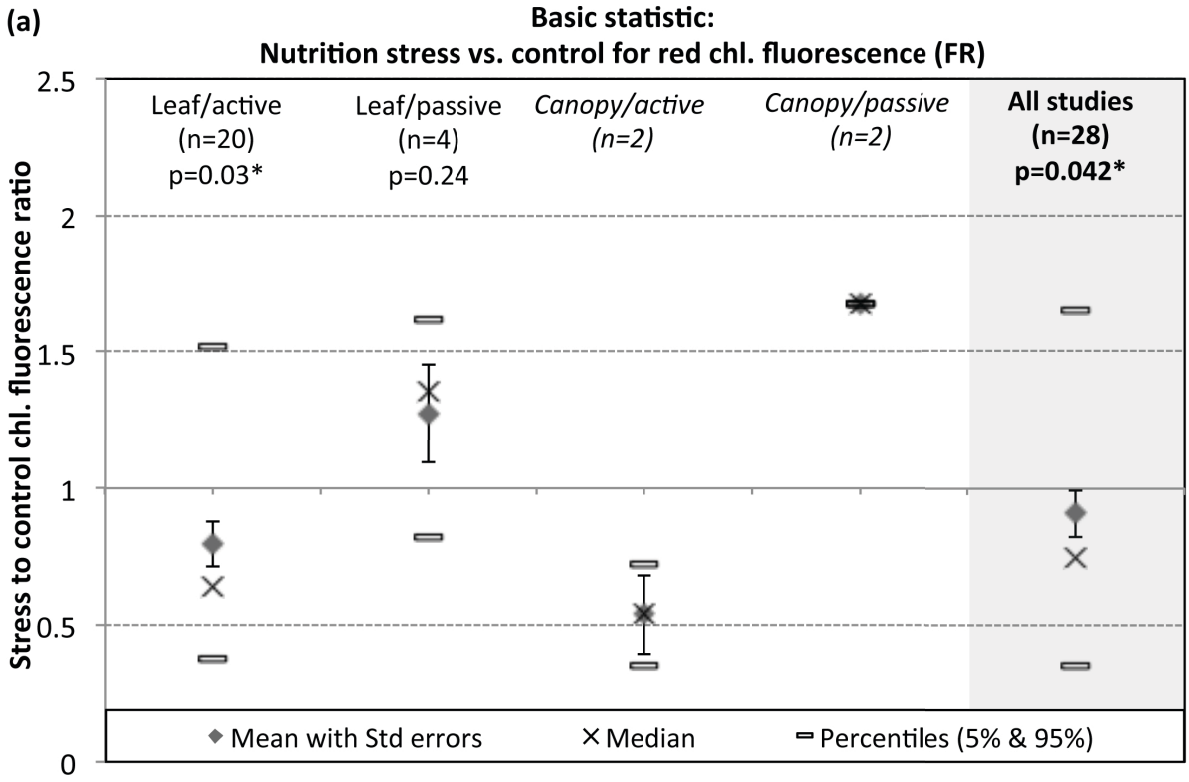
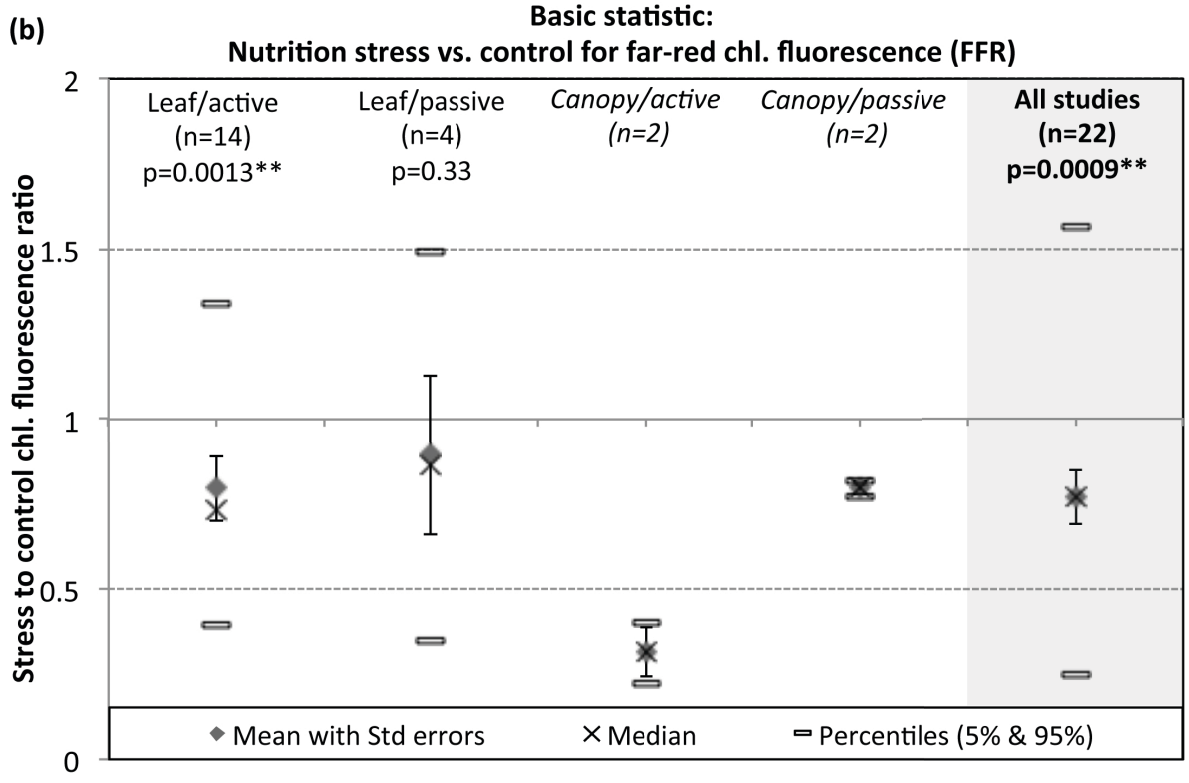


Fig. 5. Weighted means of standard difference in means between nitrogen deficit stressed and unstressed control plant trials computed with the random-effects meta-analysis model for (FR) (a), far-red (FFR) (b), and red to far-red ratio (c) of steady-state chlorophyll fluorescence measured at leaf and canopy level using active and passive detection techniques. The single study analyses labelled with a double cross (††) are incomparable with the multi-study analyses (n>1). Analysis with a small number of input studies labelled with a single cross (†) should be regarded as less reliable. Error bars represent standard errors (SE_M) of the standard difference in means. Dashes indicate the upper and lower limits of 95% confidence interval (being off the scale, the lower limit for Canopy/Active studies is not displayed) and crosses indicate *Z*-values testing the null hypothesis and providing the probability levels (p), under which the null hypothesis is accepted or rejected. Description of the random-effects meta-analysis parameters and indicators is provided in methodological part of the study.


(a)
Basic statistic:
Nutrition stress vs. control for red chl. fluorescence (FR)
Stress to control chl. fluorescence ratio
2.5
2
1.5
1
0.5
0
Leaf/active (n=20) p=0.03*
Leaf/passive (n=4) p=0.24
Canopy/active (n=2)
Canopy/passive (n=2)
All studies (n=28) p=0.042*
Mean with Std errors
Median
Percentiles (5% & 95%)

1237


(b)
Basic statistic:
Nutrition stress vs. control for far-red chl. fluorescence (FFR)
Stress to control chl. fluorescence ratio
2
1.5
1
0.5
0
Leaf/active (n=14) p=0.0013**
Leaf/passive (n=4) p=0.33
Canopy/active (n=2)
Canopy/passive (n=2)
All studies (n=22) p=0.0009**
Mean with Std errors
Median
Percentiles (5% & 95%)

1238

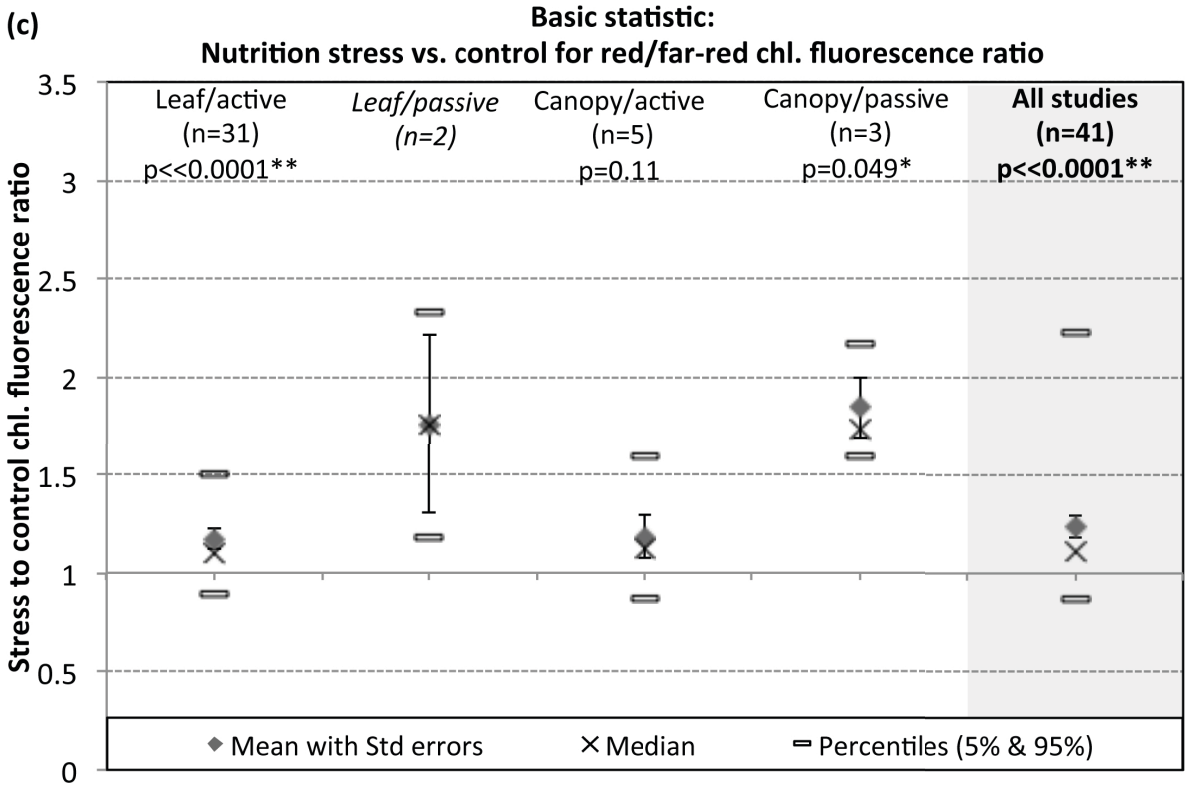


Fig. 6. Steady-state chlorophyll fluorescence (F) ratio of nutrition (nitrogen deficiency) stressed and unstressed control plants for (FR) (a) and far-red (FFR) (b), and red to far-red F ratio (c) measured at leaf and canopy scales using active and passive detection techniques. Value *p* indicates the probability level computed by non-parametric Mann-Whitney U test, at which the null hypothesis that the steady-state F stress to control ratio is equal to one can be rejected. Statistically significant differences at probability level $p \leq 0.01$ and $p \leq 0.05$ are denoted with a double asterisk (**) and a single asterisk (*), respectively. The probability level *p* is not provided for cases having too small number of input studies ($n \leq 2$).

Appendix A. Study input data

Table A1

Input data of the random-effects meta-analysis of standard difference in means for steady-state chlorophyll fluorescence of red (FR) and far-red (FFR) wavelengths measured with active and passive methods for various plant species stressed by water deficit and control (unstressed) plants at leaf and canopy level. Only first authors of investigated studies are mentioned.

Leaf - Active	*Stressed (Mean)‡*	*Standard Deviation*	*Sample Size*	*Control (Mean)‡*	*Standard Deviation*	*Sample Size*
FR (n=11)						
Amoros-Lopez 2006	0.2640	0.0909	15	0.4247	0.1819	15
Araus 2010a	326.6000	50.4000	16	444.8000	31.2000	16
Araus 2010b	269.9000	29.4347	15	305.1000	28.6601	15
Araus 2010c	342.6000	67.2000	16	444.8000	31.2000	16
Araus 2010d	210.4000	37.9552	15	305.1000	28.6601	15
Bürling 2013	63.2300	5.3630	24	100.0000	5.3630	24
Cendrero-Mateo 2013	974.7980	36.3530	4	1026.7600	32.4655	4
Evain 2004	0.1969	0.0260	15	0.3256	0.0207	15
Flexas 2000	126.9286	14.2073	28	244.0357	16.4575	28
Leufen 2013	347.8515	34.3684	32	205.4675	10.4699	32
Ounis 2001	118.2308	18.1482	15	202.1538	17.2764	15
FFR (n=6)						
Amoros-Lopez 2006a	0.6348	0.1198	15	0.7528	0.1500	15
Amoros-Lopez 2006b	0.4091	0.1269	15	0.6231	0.2439	15
Flexas 1999	0.2545	0.0349	10	0.3410	0.0255	10
Flexas 2002a	1.0025	0.0717	12	1.3750	0.0617	12
Flexas 2002b	1.0243	0.0814	7	1.3257	0.1095	7
Perez-Priego 2005	0.2918	0.0556	16	0.3745	0.0370	16
FR/FFR (n=7)						
Da Silva 2012	2.2000	0.1200	5	2.6000	0.0460	5
Leufen 2013	0.2192	0.0950	32	0.1958	0.0992	32
Leufen 2014	0.4243	0.1933	32	0.2631	0.1262	32
Lins 2005	1.0806	0.1614	10	1.5735	1.1300	10
Gouveia-Neto 2011	1.6000	0.0327	5	1.8200	0.0370	5
Subhash 2004a	3.7500	0.1915	5	2.0500	0.1920	5
Subhash 2004b	2.1500	0.2078	5	1.7800	0.2110	5
Leaf - Passive						
FR (n=1)						
Amoros-Lopez 2006	3.1941	1.2788	15	4.4938	1.7695	15
FFR (n=2)						

Amoros-Lopez 2006a	0.3730	0.0529	15	0.4094	0.0220	15
Amoros-Lopez 2006b	0.2663	0.0303	15	0.3921	0.0416	15
Canopy - Active						
FR (n=2)						
Gunther 1994	0.0513	0.0312	15	0.3767	0.2332	15
Evain 2004	1.0808	0.2368	15	2.0538	0.1931	15
FFR (n=3)						
Gunther 1994	0.1713	0.1035	15	1.0944	0.5026	15
Rascher 2009	0.3570	0.0463	13	0.3800	0.0395	13
Rosema 1998	75.4500	25.2400	15	135.0000	22.4700	15
FR/FFR (n=3)						
Dahn 1992	0.6630	0.0550	5	0.6830	0.0500	5
Valentini 1994a	0.5638	0.0336	15	0.4894	0.0148	8
Valentini 1994b	0.8846	0.1117	8	0.8297	0.0497	9
Canopy - Passive						
FR (n=1)						
Daumard 2010	0.0276	0.0064	12	0.0424	0.0042	12
FFR (n=5)						
Daumard 2010	0.0276	0.0042	12	0.0552	0.0042	12
Lee 2013	0.7537	0.0540	30	1.2815	0.0930	30
Rascher 2009	4.3800	0.2140	15	4.8600	0.2480	15
Zarco-Tejada 2009	4.0000	3.4600	9	10.1700	4.8600	9
Perez-Priego 2005	0.0134	0.0035	16	0.0182	0.0034	16

1257 ǂ Values are expressed in various chlorophyll fluorescence physical units or relative numbers.

1258

Table A2

Input data of the random-effects meta-analysis of standard difference in means for steady-state chlorophyll fluorescence of red (FR) and far-red (FFR) wavelengths measured with active and passive methods for various plant species stressed by low or high temperature (T) and control (unstressed) plants at leaf and canopy level. Only first authors of investigated studies are mentioned.

Leaf - Active	*Stressed (Mean)‡*	*Standard Deviation*	*Sample Size*	*Control (Mean)‡*	*Standard Deviation*	*Sample Size*
FR (n=4+1)						
Agati 1996a (low T)	89.9200	4.0000	7	229.1700	4.0000	7
Agati 1996b (low T)	178.4300	5.5600	7	133.9700	5.5600	7
Agati 2000a (low T)	108.0000	2.2000	6	100.0000	5.0000	6
Agati 2000b (low T)	120.6000	7.6000	6	100.0000	5.0000	6
Lang 1996b (high T)	263.0000	11.0000	6	1708.0000	47.0000	6
FFR (n=2+1)						
Agati 2000a (low T)	118.0000	1.7000	6	100.0000	5.0000	6
Agati 2000b (low T)	122.0000	6.8000	6	100.0000	5.0000	6
Lang 1996b (high T)	370.0000	12.0000	6	3268.0000	76.0000	6
FR/FFR (n=5+4)						
Agati 1996a (low T)	0.2900	0.0550	6	0.4400	0.0247	6
Agati 1996b (low T)	1.0400	0.0043	7	0.9550	0.0240	7
Agati 2000a (low T)	0.9200	0.0200	6	1.0000	0.0160	6
Agati 2000b (low T)	0.9500	0.0190	6	1.0000	0.0150	6
di Paola 1992 (low T)	0.7500	0.0350	10	1.0000	0.0390	10
Agati 1995 (high T)	0.6800	0.0280	6	0.8800	0.0110	6
Balota 1999 (high T)	0.5169	0.0240	48	0.5577	0.0190	48
Lang 1996a (high T)	0.7500	0.0800	10	0.7500	0.0700	10
Lang 1996b (high T)	0.7500	0.1100	6	0.5000	0.0900	6
Canopy - Active						
FR/FFR (n=1)						
Thoren 2010 (high T)	1.0700	0.0040	2	1.2400	0.0058	4
Canopy - Passive						
FR (n=1)						
Middleton 2009 (high T)	0.0500	0.0250	10	0.1200	0.0250	10
FFR (n=1)						
Middleton 2009 (high T)	0.0500	0.0230	10.0000	0.1100	0.0200	10

‡ Values are expressed in various chlorophyll fluorescence physical units or relative numbers.

Table A3

Input data of the random-effects meta-analysis of standard difference in means for steady-state chlorophyll fluorescence of red (FR) and far-red (FFR) wavelengths measured with active and passive methods for various plant species stressed by nitrogen deficit and control (unstressed) plants at leaf and canopy level. Only first authors of investigated studies are mentioned.

	Stressed	*Standard*	*Sample*	*Control*	*Standard*	*Sample*
Leaf - Active	*(Mean)‡*	*Deviation*	*Size*	*(Mean)‡*	*Deviation*	*Size*
FR (n=8)						
Ač unpublished	0.3257	0.0720	8	0.4690	0.0876	10
Cendrero-Mateo 2013	229.9280	16.4950	3	415.8700	32.9900	3
C-Mateo unpublished	272.8290	44.8389	9	634.7093	137.9730	9
Chapelle 1984	25.0000	5.0000	120	91.0000	11.0000	120
Konanz 2014	621.0000	87.7000	8	1086.0000	309.0000	8
Leufen 2014	35.9250	18.6851	4	67.4750	20.1260	4
McMurtrey 2002	490.0000	60.0000	15	800.0000	80.0000	15
Tartachnyk 2006	6037.5000	828.5000	40	7699.5000	895.5000	40
FFR (n=4)						
C-Mateo unpublished	0.6036	0.0743	9	2.2088	0.7574	9
Chapelle 1984	25.0000	5.0000	120	101.0000	15.0000	120
Konanz 2014	293.0000	46.0000	8	483.0000	142.0000	8
Tartachnyk 2006	6822.5000	933.5000	40	8600.0000	781.0000	40
FR/FFR (n=10)						
Agati 2013a	0.2222	0.0049	100	0.1538	0.0142	100
Agati 2013b	0.8889	0.0198	100	0.8264	0.0170	100
Apostol 2003a	0.8000	0.0500	8	0.7400	0.0900	12
Apostol 2003b	0.7400	0.0600	8	0.6700	0.0400	12
Bürling 2011	0.9800	0.0080	12	0.9400	0.0100	12
Konanz 2014	0.4700	0.0300	20	0.4400	0.0300	20
Kuckenberg 2009	1.0896	0.1274	6	0.9179	0.1051	6
Leufen 2014a	0.2822	0.1173	16	0.2623	0.1173	16
Leufen 2014b	0.2722	0.0821	16	0.2639	0.1350	16
Tartachnyk 2006	0.6289	0.0193	9	0.5197	0.0196	10
Leaf - Passive						
FR (n=1)						
Middleton 2008	2.0000	0.1000	6	1.4000	0.1000	6
FR/FFR (n=1)						
Campbell 2008	1.1500	0.1100	16	0.4800	0.0700	16
Canopy - Active						
FR/FFR (n=2)						

Kuckenberg 2009	2.0379	2.2115	6	1.2348	1.0977	6
Thoren 2009	0.8170	0.0070	12	0.7100	0.0050	12
Canopy - Passive						
FR (n=1)						
Kebabian 1999	2.6000	0.3250	12	1.5500	0.2250	12
FFR (n=1)						
Kebabian 1999	1.4000	0.1000	12	1.7000	0.2850	12
FR/FFR (n=3)						
Freedman 2002a	0.5700	0.0200	12	0.3600	0.0400	12
Freedman 2002b	0.7800	0.0800	12	0.4500	0.0300	12
Kebabian 1999	1.5400	0.1500	12	0.6950	0.0600	12

1272 ǂ Values are expressed in various chlorophyll fluorescence physical units or relative numbers.