remote sensing

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Connection of the Photochemical Reflectance Index (PRI) with the Photosystem II Quantum Yield and Nonphotochemical Quenching Can Be Dependent on Variations of Photosynthetic Parameters among Investigated Plants: A Meta-Analysis

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Abstract: The development of spectral methods of remote sensing, including measurement of a photochemical reflectance index (PRI), is a prospective trend in precision agriculture. There are many works which have investigated the connection between photosynthetic parameters and PRI; however, their results varied and were sometimes contradictory. For this paper, we performed a meta-analysis of works in this field. Here, only linear correlations of PRI with photosynthetic parameters—including quantum yield of photosystem II (ΔF/Fm′), nonphotochemical quenching of chlorophyll fluorescence (NPQ), and light use efficiency (LUE)—were investigated. First, it was shown that the correlations were dependent on conditions of PRI measurements (leaf or canopy; artificial light or sunlight). Second, it was shown that a minimal level of the photosynthetic stress, and the variation of this level among investigated plants, can influence the linear correlation of PRI with ΔF/Fm′ and NPQ; the effect was dependent on conditions of measurements. In contrast, the distribution of LUE among plants did not influence its correlation with PRI. Thus, the meta-analysis shows that the distribution of photosynthetic parameters among investigated plants can be an important factor that influences the efficiency of remote sensing on the basis of the PRI measurement.

Keywords: light use efficiency; meta-analysis; nonphotochemical quenching; photochemical reflectance index; photosynthesis; plant; PRI; quantum yield of photosystem II; remote sensing

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1. Introduction

Plants growing under natural conditions can be affected by various environmental stressors, including drought [1–3], salt stress [4–7], temperature stress [2,8–10], light stress [10,11], etc. The stressors decrease the probability of survival and productivity of plants; in particular, they damage the photosynthetic process [12]. Early monitoring of these damages plays an important role in precision agriculture and ecological monitoring. As a result, remote sensing of the photosynthetic process is an important practical problem [13–15]. There are many methods that can be used for the analysis of the photosynthesis process in plants; in particular, pulse-amplitude-modulation (PAM)-fluorometry [16,17], JIP-test [18–20], and analysis of CO_2 exchange [21–25]. These methods are very effective in the laboratory. However, their use for remote sensing of the photosynthetic process under environmental conditions is very limited. Currently, remote sensing of photosynthetic parameters in plants is often based on reflectance indices. In particular, they include:

- a photochemical reflectance index (PRI), which shows changes in the xanthophyll cycle [26];
- a normalized difference vegetation index (NDVI) [27], an optimized soil-adjusted vegetation index (OSAVI) [28], and an enhanced vegetation index (EVI) [29,30], which quantitatively show a photosynthesizing biomass;
- a chlorophyll index (CI), which shows chlorophyll content in leaves [31,32]; and
- a structural independent pigment index (SIPI), which is connected to the ratio of carotenoids to chlorophylls [33].

There are other reflectance indices, see [34,35].

These indices are important tools for the remote sensing of the photosynthetic process in plants. In respect to the monitoring of fast changes in the photosynthetic process in plants (especially, photosynthetic stress), PRI is the most interesting reflectance index. This index, which is related to the fast transition in the xanthophyll cycle, is based on the rapid decrease of reflectance at 531 nm that is caused by the dissipation of light energy associated with xanthophyll de-epoxidation [26,36]. It is known that the de-epoxidation of xanthophylls plays an important role in the increase of nonphotochemical quenching of fluorescence of chlorophyll (NPQ) under stress conditions [12,37]. Thus, it can be expected that PRI is strongly connected with NPQ (and other photosynthetic parameters) under different environmental conditions.

There are numerous works that investigate the correlation between PRI and NPQ under different stressors [38–44]. Connections between PRI and other photosynthetic parameters, including a quantum yield of photosystem II ($\Delta F/F_m{}'$) [38,41,42,45–49], photosynthetic light use efficiency (LUE) [3,48,50–55], and net CO_2 uptake [47,56–59], are actively being investigated. However, the results of these different works vary considerably, e.g., the linear correlation coefficients between PRI and NPQ can range from -0.90 [38,49,60] to +0.86 [41] in different investigations. It is probable that differences are mostly connected to the various conditions of the investigations, e.g., PRI seems to be more responsive to chlorophyll content then to the xanthophyll cycle over long time periods [48]. As a result, an analysis of factors influencing the connection between PRI and photosynthetic parameters is very important for the practical application of the photochemical reflectance index. A meta-analysis of literature data seems to be an effective method for finding a solution to this problem. There are several works [15,61] that are devoted to the meta-analysis of results of PRI measurements. In particular, these works investigated the influence of different spatial scales (leaves, canopy, or ecosystem) and time scales (daily or seasonal) of PRI measurements on photosynthetic parameters. A determination coefficient (R^2) was used in the works [15,61] as the quantitative criterion for the description of the relationship between physiological processes and the photochemical reflectance index. However, these studies, which were the basis of the meta-analysis, used different regression curves (e.g., linear, logarithmic, or exponential functions), making their comparison with using R^2 more difficult. Analysis of only linear correlation coefficients can eliminate these difficulties. Another weakly studied factor is the influence of the distribution of photosynthetic parameters in investigated plants on PRI.

Thus, our work was devoted to the meta-analysis of the connection between PRI and photosynthetic parameters. Only linear Pearson correlation coefficients were analyzed in this work. Influence of the photosynthetic parameters on the photochemical reflectance index was also investigated.

2. Methods

2.1. Main Principles of Data Analysis

The analyzed works, which investigated the relationship between PRI and photosynthetic processes in plants, are shown in Table 1. For preparation of this list, we performed a wide search of works devoted to PRI investigation (including searching such sources as Web of Science and PubMed, Google searches, and searches in lists of references in articles). After that, we used the following criteria of for the selection of data for further analysis:

- We used only the photochemical reflectance index calculated with an equation $\mathrm{PRI} = \frac{R_{531} - R_{570}}{R_{531} + R_{570}}$ where R_{531} and R_{570} were reflectance at 531 and 570 nm;
- We analyzed correlations of PRI with the quantum yield of photosystem II ($\Delta F/F_m'$), the nonphotochemical quenching of chlorophyll (NPQ), and the light use efficiency (LUE). $\Delta F/F_m'$ and NPQ were used because these parameters show the efficiency of photosynthetic light reactions and the response of photosynthetic machinery to stressors. LUE was used for the estimation of efficiency of photosynthetic assimilation;
- We used only linear correlations between PRI and photosynthetic parameters. These correlations were taken from papers or were calculated on the basis of the determination coefficient (in case of a linear regression) or were calculated on the basis of data from the articles. If correlation coefficients, determination coefficients for linear functions, or graphical data with changes of photosynthetic parameters and PRI were absent, we did not include these works in the analysis;
- We analyzed the investigation of PRI on the levels of leaves and canopy. Data that were registered by satellites were not used in the analysis.

Table 1. List of works, which were analyzed in the meta-analysis, and details of measurement of photochemical reflectance index (PRI) and photosynthetic parameters in each work. LUE = light use efficiency; $\Delta F/F_m'$ = quantum yield of photosystem II; NPQ = nonphotochemical quenching of chlorophyll fluorescence.

Year	Reference	Scale	Source of Light	Species/Vegetation Type	Parameters
1994	Peñuelas et al. [56]	Canopy	Sunlight	Sunflower	LUE *
1995	Peñuelas et al. [62]	Leaves	Artificial light	*Hedera canariensis, Phaseolus vulgaris, Rhus integrifolia, Heteromeles arbutifolia, Agave americana, Opuntia ficusindica* and *Cereus hexagonus*	$\Delta F/F_m'$, LUE ***
1996	Filella et al. [50]	Leaves/Canopy	Sunlight	Barley	LUE *
1997	Gamon et al. [63]	Canopy	Sunlight	*Phaseolus vulgaris,* *Gossypium barbadense,* *Helianthus annuus,* *Zea mays,* *Nicotiana tabacum,* *Trifolium repens,* *Aesculus californica,* *Cercis occidentalis,* *Platanus racemosa,* *Populus fremontii,* *Quercus lobata,* *Vitis californica,* *Vitis girdiana,* *Heteromeles arbutifolia,* *Ligustrum japonicum,* *Quercus ilex,* *Prunus ilicifolia,* *Quercus agrifolia,* *Quercus chrysolepis,* *Hedera canariensis,*	$\Delta F/F_m'$ ***
1997	Peñuelas et al. [3]	Leaves	Sunlight	*Quercus ilex, Phillyrea latifolia*	$\Delta F/F_m'$, LUE *
2000	Méthy [64]	Leaves	Artificial light	*Quercus ilex*	$\Delta F/F_m'$ **
2000	Nichol et al. [51]	Canopy	Sunlight	*Populus tremuloides, Corylus cornutta, Rosa woodsii, Pinus banksiana, Menyanthes trifoliata, Carex and Eriophorum spp, Betula pumila, Larix laricina, P. glauca, Arctostaphylos uva-ursi, Vaccinium vitis-idaea, Cladina spp, Alnus crispa, Picea mariana*	LUE **

Table 1. *Cont.*

Year	Reference	Scale	Source of Light	Species/Vegetation Type	Parameters
2002	Nichol et al. [65]	Canopy	Sunlight	*Pinus sylvestris, Abies siberica, Picea abies, Pinus siberica, Sorbus aucuparia, Abies siberica, and Betel pendula*	LUE **
2002	Strachan et al. [66]	Canopy	Sunlight	Maize	LUE **
2002	Trotter et al. [67]	Canopy	Artificial light	*Hebe townsonii, Carex buchanani Ocoka, Metrosideros excelsa, Pittosporum eugenioides, Hebe 'Otari Delight', Grisilinea littoralis, Hebe pimeleoides, Pittosporum tenuifolium 'Shirley'*	LUE **
2002	Winkel et al. [68]	Leaves	Sunlight	*Chenopodium quinoa*	$\Delta F/F_m'$, LUE **
2004	Evain et al. [38]	Leaves/Canopy	Artificial light	Grapevine	$\Delta F/F_m'$, NPQ ***
2005	Gamon [69]	Leaves	Sunlight	*Anacardium excelsum, Carica papaya, Cecropia longipes, Enterolobium cyclocarpum, Ficus insipida, Luehea seemannii, Piper reticulatum, Pseudobombax septenatum* and *Maclura tinctoria*	$\Delta F/F_m'$ *
2005	Inamullah and Isoda [39]	Leaves	Sunlight	Soybean and cotton	$\Delta F/F_m'$, NPQ *
2005	Nakaji et al. [70]	Canopy	Sunlight	*Larix kaempferi*	LUE *
2005	Raddi et al. [71]	Leaves	Artificial light	*Medicago sativa, Phragmites australis, Rubus fruticosus, Silybum marianum Populus euroamericana, Fraxinus angustifolia, Alnus glutinosa Quercus ilex Pinus pinaster* and *Pinus pinea*	NPQ **
2005	Serrano and Peñuelas [52]	Canopy	Sunlight	*Quercus ilex, Phyllirea latifolia, Arbutus unedo, Erica arborea, Juniperus oxycedrus* and *Cistus albidus*	LUE **
2006	Guo and Trotter [72]	Leaves	Artificial light	*Ackama roseafolia, Brachyglottis repanda, Fejoa selloiana, Rhaphiolepsis indica, Grisilinea littoralis, Corynocarpus laevigatus, Pseudopanax arboreus, Olearia ilicifolia, Pinus patula, Dodonaea viscose, Pinus radiata, Viburnum marisii* and *Populus deltoides*	$\Delta F/F_m'$, LUE ***
2006	Inoue and Peñuelas [73]	Leaves	Sunlight	Soybean	LUE *
2006	Nakaji et al. [74]	Canopy	Sunlight	Japanese larch	LUE *
2006	Nichol et al. [75]	Canopy	Sunlight	*Rhizophora mangle* and *Avicennia germinans*	$\Delta F/F_m'$, NPQ **
2006	Sims et al. [76]	Canopy	Sunlight	*Adenostoma fasciculatum, Adenostoma sparsifolium, Arctostaphylos pungens*	LUE ***
2006	Weng et al. [77]	Leaves	Artificial light	*Mangifera indica, podocarpus nagi, alnus formosana*	$\Delta F/F_m'$***, NPQ**
2008	Hall et al. [78]	Canopy	Sunlight	Douglas fir, western red cedar and western hemlock	LUE **
2008	Nakaji et al. [53]	Canopy	Sunlight	Japanese larch, Japanese cypress, hybrid larch and dwarf bamboo	LUE *

Table 1. *Cont.*

Year	Reference	Scale	Source of Light	Species/Vegetation Type	Parameters
2008	Naumann et al. [79]	Canopy	Sunlight	*Myrica cerifera*	$\Delta F/F_m'$ **
2008	Naumann et al. [80]	Canopy	Artificial light	*Myrica cerifera*	$\Delta F/F_m'$ **
2008	Peguero-Pina et al. [40]	Canopy	Sunlight	*Quercus coccifera*	NPQ ***
2009	Busch et al. [81]	Leaves	Artificial light	Jack pine	$\Delta F/F_m'$, NPQ **
2009	Middleton et al. [82]	Canopy	Sunlight	Douglas fir	LUE **
2009	Naumann et al. [45]	Canopy	Sunlight	*Myrica cerifera* and *Iva frutescens*	$\Delta F/F_m'$ **
2010	Ibaraki et al. [46]	Leaves	Artificial light	Strawberry, lettuce and potato	$\Delta F/F_m'$ **
2010	Ibaraki and Gupta [83]	Leaves	Artificial light	Potato	$\Delta F/F_m'$ **
2010	Naumann et al. [84]	Canopy	Artificial light/ Sunlight	*Elaeagnus umbellata*	$\Delta F/F_m'$ **
2010	Sarlikioti et al. [41]	Leaves	Artificial light	Tomato	$\Delta F/F_m'$, NPQ ***
2010	Shahenshah et al. [42]	Leaves	Sunlight	Cotton and Peanut	$\Delta F/F_m'$, NPQ *
2010	Weng et al. [85]	Leaves	Artificial light/ Sunlight	Mango	$\Delta F/F_m'$ **
2010	Wu et al. [86]	Canopy	Sunlight	Wheat	LUE **
2011	Ripullone et al. [47]	Leaves	Sunlight	*Arbutus unedo, Quercus ilex, Quercus pubescens, Quercus cerris, Quercus robur, Cannabis sativa, Fagus sylvatica and Populus euroamericana*	$\Delta F/F_m'$ **
2012	Ač et al. [87]	Canopy	Sunlight	*(Festuca rubra, Hieracium sp., Plantago sp, Nardus stricta* and *Jacea pseudophrygia*	LUE ***
2012	Osório et al. [43]	Leaves	Artificial light	*Ceratonia siliqua*	$\Delta F/F_m'$ *
2012	Porcar-Castell et al. [48]	Leaves	Sunlight/ Artificial light	*Pinus sylvestris*	$\Delta F/F_m'$, NPQ, LUE *
2012	Rahimzadeh-Bajgiran et al. [88]	Leaves	Artificial light	*Solanum melongena*	NPQ **
2012	Shrestha et al. [60]	Leaves	Artificial light	Rice	NPQ ***
2012	Weng et al. [89]	Leaves	Artificial light	*Pinus taiwanensis, Stranvaesia niitakayamensis*, two *Miscanthus* spp. and mango	$\Delta F/F_m'$ **
2012	Zinnert et al. [7]	Canopy	Artificial light	*Baccharis Halimifolia* and *Myrica cerifera*	$\Delta F/F_m'$, NPQ **
2013	Cheng et al. [90]	Canopy	Sunlight	Maize	LUE **
2013	Liu et al. [54]	Canopy	Sunlight	Maize and winter wheat	NPQ **
2013	Rossini et al. [91]	Canopy	Sunlight	Maize	$\Delta F/F_m'$ **
2014	Hmimina et al. [55]	Leaves	Sunlight	*Quercus robur* and *Fagus sylvatica*	$\Delta F/F_m'$, LUE **
2014	Magney et al. [44]	Leaves	Artificial light	*Sunflower*, wheat, *Quercus macrocarpa, Betula papyrifera,* and *Populus tremuloides*	NPQ **
2014	Soudani et al. [92]	Canopy	Sunlight	*Quercus robur, Quercus petraea, Quercus ilex, Carpinus betulus*	LUE **
2015	Rossini et al. [93]	Canopy	Sunlight	Maize	$\Delta F/F_m'$ **
2015	Šebela et al. [94]	Leaves	Artificial light	Rice	$\Delta F/F_m'$ *
2015	van Leeuwen et al. [95]	Canopy	Artificial light	Douglas fir	LUE **
2015	Wu et al. [96]	Canopy	Sunlight	Wheat	LUE **
2017	Chou et al. [49]	Canopy	Sunlight	Maize	$\Delta F/F_m'$, NPQ **
2017	Zhang et al. [97]	Canopy	Sunlight	*Erica multiflora*	$\Delta F/F_m'$ **
2017	Zhang et al. [98]	Leaves	Sunlight	*Quercus ilex*	$\Delta F/F_m'$ **

* the linear correlation coefficient was shown in this work; ** the linear correlation coefficient was calculated on the basis of the determination coefficient of linear regression in this work; *** the linear correlation coefficient was calculated on the basis of graphical dates from this work.

It should be noted that leaves and canopy levels are widely used scales of PRI measurements [15,61]. Measurements of PRI in leaves are often based on the application of spectrometers and specific systems of PRI measurement (e.g., PlantPen PRI 200) or systems of PRI imaging [15,61]. Measurements of PRI in the canopy of leaves (from single plant or group of plants) can be also based on the application of spectrometers or multispectral and hyperspectral cameras [15,61], which can be placed on a mobile platform (e.g., drone) or fixed at a certain distance from the canopy [35,38]. Photosynthetic parameters in leaves (in particular, ΔF/Fm′, NPQ, and LUE) can be measured by standard methods, including PAM-fluorometry [16,17] and analysis of CO_2 exchange [21–25]. However, the application of these methods on the canopy level is a very difficult problem. In this case, photosynthetic parameters are often measured in only some leaves from the canopy, which are used for PRI measurements [36,40].

In some works, the authors investigated several plants and/or analyzed the influence of different factors separately. In these cases, each connection between PRI and photosynthetic parameters was analyzed independently in each investigated variant. Averaged correlation coefficients and their standard errors were used for analysis. Significance of differences between groups was calculated using the Student's test.

2.2. Analysis of the Influence of Distribution of Photosynthetic Parameters among Investigated Plants on Connection of these Parameters with PRI

Figure 1 shows a common design for analysis of the influence of distribution of photosynthetic parameters among investigated plants on connection of these parameters with PRI. First, in each analyzed variant, all experimental values of photosynthetic parameters (NPQ, $\Delta F/F_m'$, or LUE) were sorted in ascending order, with each experimental value showing NPQ, $\Delta F/F_m'$, or LUE for a single plant or single group of plants. After that, the minimal (P_{min}) and maximal (P_{max}) values of photosynthetic parameters (NPQ, $\Delta F/F_m'$, or LUE) among investigated plants (or groups of plants) were calculated. P_{min} and P_{max} were calculated in each analyzed variant from literature data. P_{min} of NPQ and P_{max} of $\Delta F/F_m'$ and LUE showed the minimal level of photosynthetic stress among investigated plants, because the action of stressors increases nonphotochemical quenching and decreases the quantum yield of photosystem II [7,41,47,99] and light use efficiency [55,56]. Another parameter that was used was the difference between maximal and minimal values of NPQ, $\Delta F/F_m'$, and LUE ($\Delta P_{abs} = P_{max} - P_{min}$). We assumed that the difference reflected the variation of the photosynthetic stress level among investigated plants (or groups of plants) in the analyzed variant.

Second, all analyzed variants were sorted from minimum to maximum of ΔP_{abs} and P_{min} or P_{max}. After that, they were divided into two approximately equal groups. The first group ("low") included ΔP_{abs} and P_{min} or P_{max} with values lower than the median value. The second group ("high") included ΔP_{abs} and P_{min} or P_{max} with values higher than the median value.

Finally, averaged ΔP_{abs} and P_{min} or P_{max} and averaged correlation coefficients of PRI with NPQ, $\Delta F/F_m'$, or LUE, and their standard errors were calculated for each group. Significance of differences between groups were calculated using the Student's test. In a similar manner, we also analyzed data with specific conditions of measurements of PRI (leaves or canopy, artificial light, or sunlight).

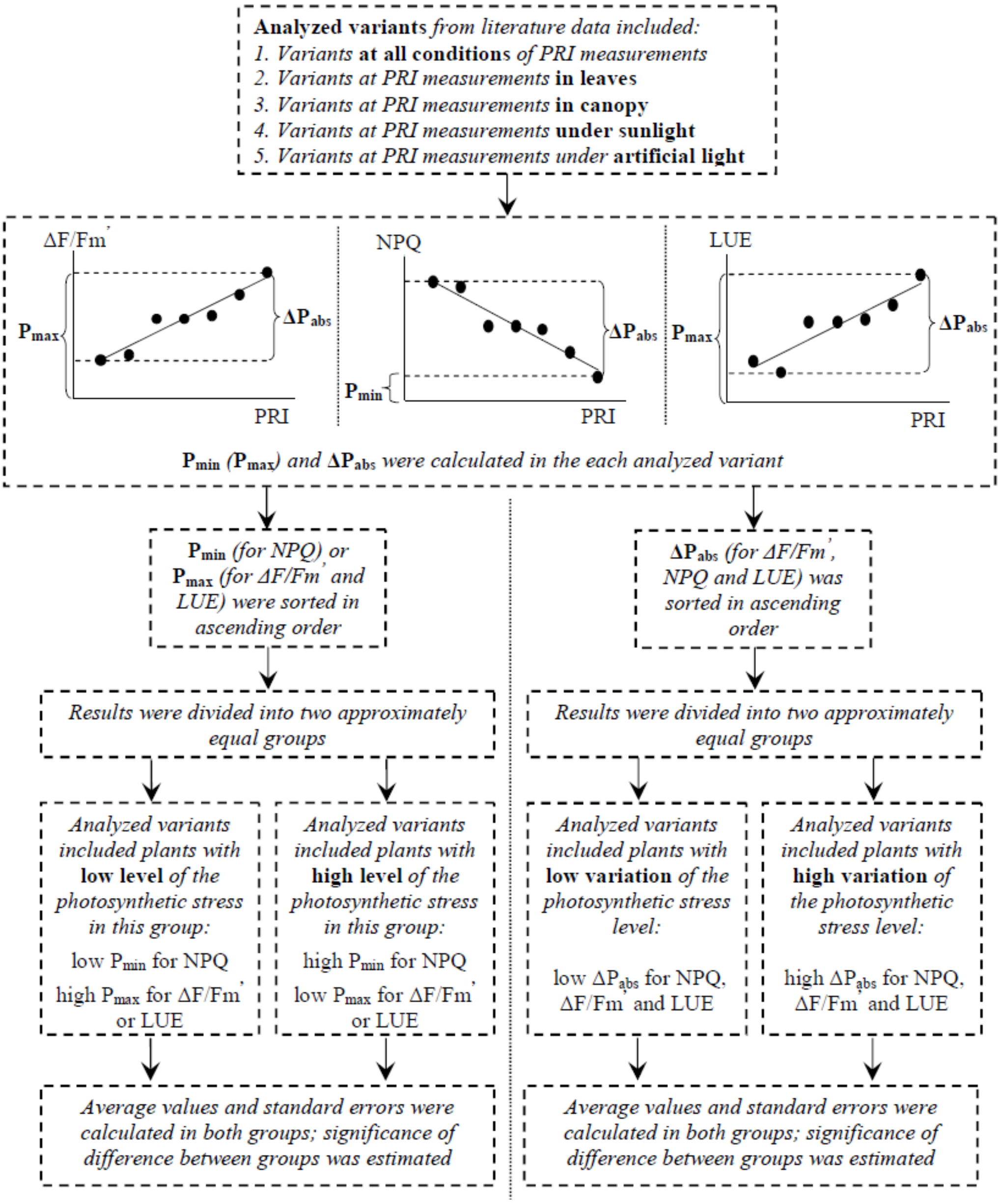
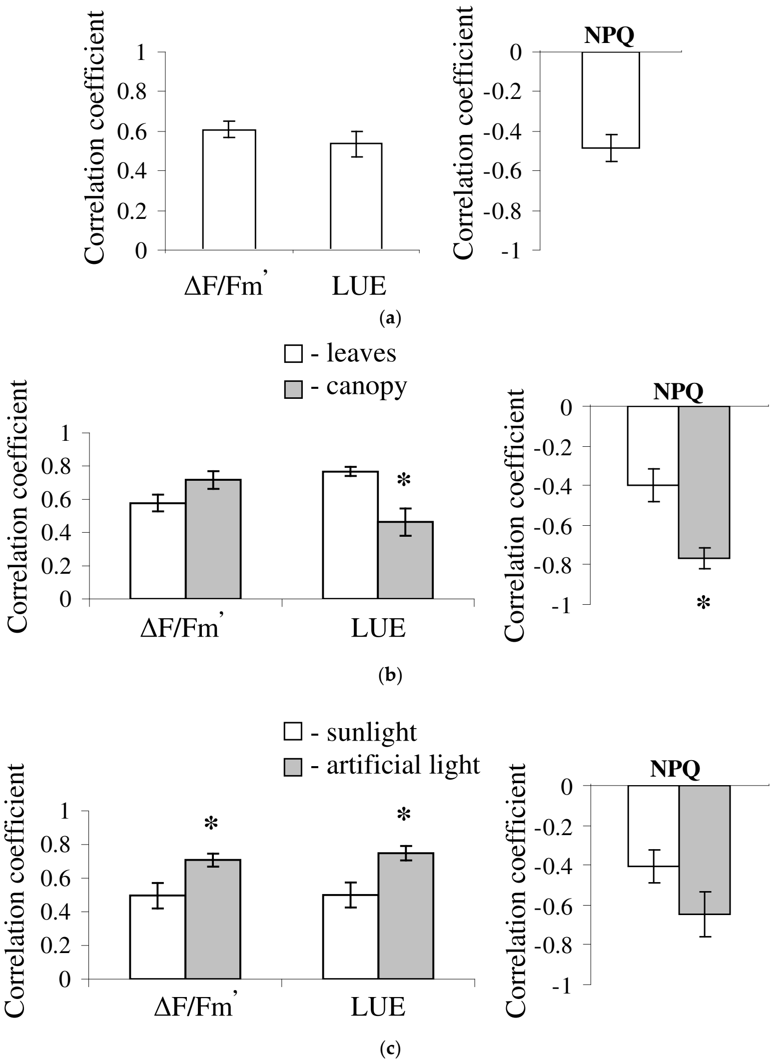


Figure 1. The common design of the analysis of influence of photosynthetic parameter distribution on investigated plants for their connection with PRI. P_{min} is the minimal value of NPQ among plants (or groups of plants) in each analyzed variant; P_{max} is the maximal value of $\Delta F/F_m'$ or LUE among plants (or groups of plants) in each analyzed variant; ΔP_{abs} is the difference between P_{max} and P_{min} for $\Delta F/F_m'$, NPQ, and LUE in each analyzed variant.

3. Results

3.1. Connection of PRI with Photosynthetic Parameters under Different Measurement Conditions

Figure 2a shows that the linear correlation coefficients between PRI and photosynthetic parameters, which were calculated on the basis of all investigated variants, were moderate, and had absolute values from 0.5 to 0.6. Correlations between PRI and $\Delta F/F_m'$ and PRI, and LUE were positive, whereas the correlation between PRI and NPQ was negative.



(**a**)

(**b**)

(**c**)

Figure 2. The connection of PRI with the quantum yield of photosystem II ($\Delta F/F_m'$), nonphotochemical quenching (NPQ), and light use efficiency (LUE). (**a**) Average correlation coefficients of PRI with $\Delta F/F_m'$ ($n = 110$), LUE ($n = 63$), and NPQ ($n = 50$); (**b**) Average correlation coefficients of PRI with $\Delta F/F_m'$, LUE, and NPQ for measurements of the photochemical reflectance index in leaves ($n = 86$, $n = 15$, $n = 38$, respectively) and canopy ($n = 24$, $n = 48$, $n = 12$, respectively); (**c**) Average correlation coefficients of PRI with $\Delta F/F_m'$, LUE, and NPQ with measurements under sunlight ($n = 52$, $n = 54$, $n = 33$, respectively) or artificial light ($n = 58$, $n = 9$, $n = 17$, respectively). * the groups significantly differed from another one ($p < 0.05$, Student's test).

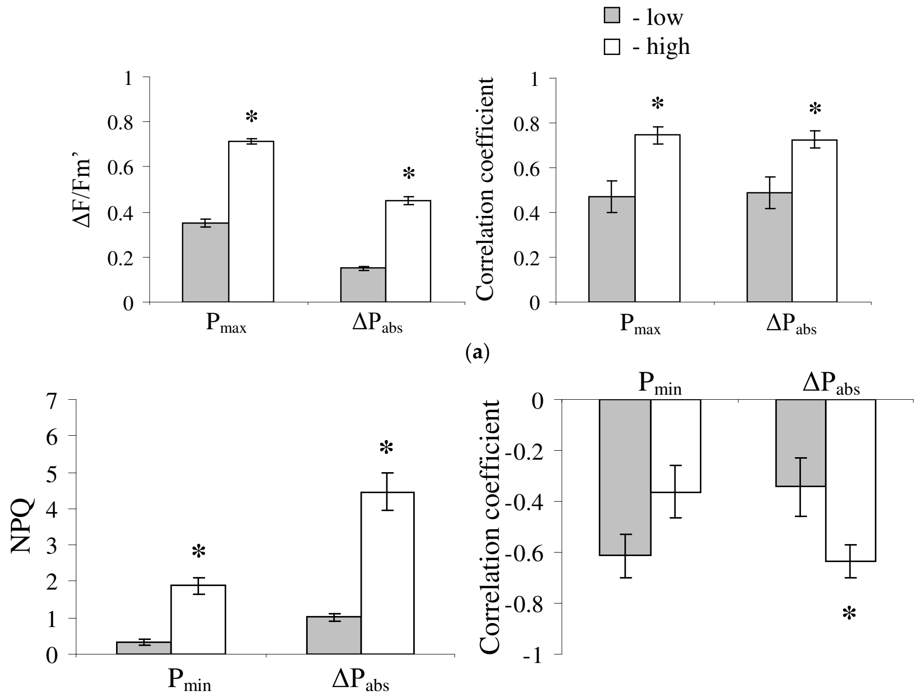
Further, we investigated correlations between PRI and photosynthetic parameters when the reflected light was measured from the leaves or canopy surface. Figure 2b shows that the correlation coefficient between PRI and NPQ for canopy measurements was higher than the coefficient for leaves measurements. A similar tendency was observed for the correlation coefficient between PRI and $\Delta F/F_m'$, although it was not significant. In contrast, the correlation coefficient between PRI and LUE for leaves measurements was higher than the coefficient at canopy measurements.

The analysis of the influence of the light source (artificial light or sunlight) on correlations between PRI and photosynthetic parameters was performed later. It could be seen that the correlation coefficients of PRI with $\Delta F/F_m'$ and LUE were significantly higher under artificial light than under sunlight (Figure 2c). The difference between the correlation coefficients of PRI and NPQ was not significant. However, we did observe a tendency of correlation increase under artificial light (Figure 2c).

3.2. Influence of Distribution of Photosynthetic Parameters among Investigated Plants on Connection of These Parameters with PRI

First, we analyzed the influence of the P_{min} of NPQ and P_{max} of $\Delta F/F_m'$ and LUE, which showed the minimal level of photosynthetic stress among investigated plants in each analyzed variant (see details in Section "Analysis of the Influence of Distribution of Photosynthetic Parameters among Investigated Plants on Connection of these Parameters with PRI" and Figure 1), on the connection of photosynthetic parameters and PRI. All analyzed variants were sorted in accordance to their P_{min} or P_{max} and were divided into two groups: low and high value of these parameters. A similar analysis was performed for ΔP_{abs}, which shows the variation of photosynthetic stress levels among investigated plants in each analyzed variant.

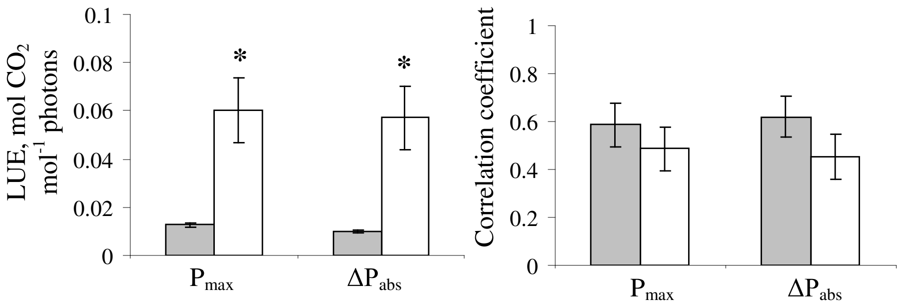
It was shown that the differences of photosynthetic parameters between groups with low and high absolute values of P_{min} (P_{max}) and ΔP_{abs} were significant (Figure 3, on the left). The correlation coefficients between quantum yield of photosystem II and PRI at high P_{max} and ΔP_{abs} (r = 0.75 and 0.73, respectively) were significantly higher than ones at low P_{max} and ΔP_{abs} (r = 0.47 and 0.49, respectively) (Figure 3a). The absolute correlation coefficients between NPQ and PRI at low P_{min} and high ΔP_{abs} (r = −0.61 and −0.63, respectively) were higher than ones at high P_{min} and low ΔP_{abs} (r = −0.36 and −0.34, respectively) (Figure 3b). In the case of LUE (Figure 3c), we did not observe significant differences between the groups with low and high P_{max} and ΔP_{abs}. Thus, it was probable that the correlations between PRI and $\Delta F/F_m'$ and PRI, and NPQ were higher in the analyzed variants that included plants with low photosynthetic stress (low P_{min} of NPQ and high P_{max} of $\Delta F/F_m'$) and had high variation of the photosynthetic stress levels (high ΔP_{abs}). This effect was not observed for correlations between LUE and PRI.



(a)

(b)

Figure 3. *Cont.*

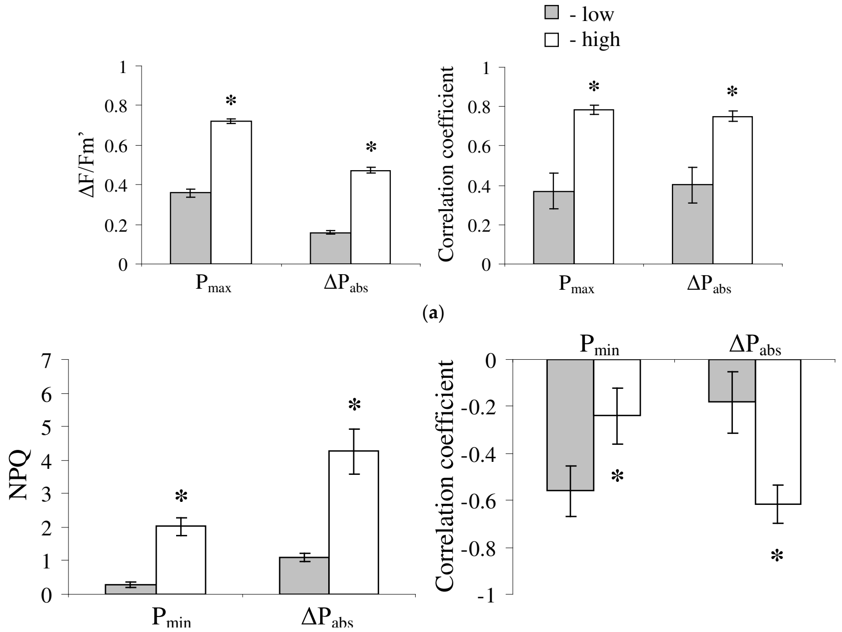


(**c**)

Figure 3. The influence of the distribution of $\Delta F/F_m'$ (**a**); NPQ (**b**) and LUE (**c**) among investigated plants for the connection between these photosynthetic parameters with PRI at all variants of measurements. Average values of P_{min} (P_{max}) and ΔP_{abs} are shown on left panels, average correlation coefficients are shown on right panels. The label "low" indicates groups with low P_{min} (P_{max}) and ΔP_{abs}; the label "high" indicates groups with high P_{min} (P_{max}) and ΔP_{abs}. "Low" groups had $n = 55$ ($\Delta F/F_m'$), $n = 25$ (NPQ), and $n = 31$ (LUE); "high" groups had $n = 55$ ($\Delta F/F_m'$), $n = 25$ (NPQ), and $n = 32$ (LUE). * the group significantly differed from another one ($p < 0.05$, Student's test).

3.3. Influence of Distribution of Photosynthetic Parameters among Investigated Plants on Connection of These Parameters with PRI Measurements in Leaves and Canopy

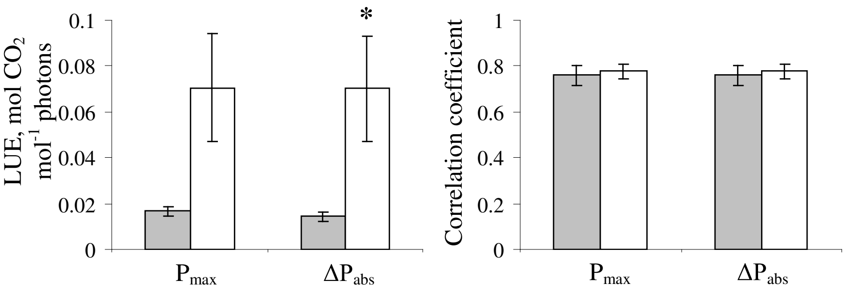
Further, we examined the influence of the photosynthetic parameter distribution among investigated plants on correlations between PRI and $\Delta F/F_m'$, PRI and NPQ, and PRI and LUE with measurements of PRI in leaves and canopy. In this case, we analyzed only experiments that investigated PRI in leaves or only experiments that investigated PRI in canopy. Analysis of each group (leaves or canopy) was analogous to the previous analysis (see above). It should be noted that differences of photosynthetic parameters between groups with low and high absolute values of P_{min} (P_{max}) and ΔP_{abs} were significant for all measurements (Figures 4 and 5, on the left).



(**a**)

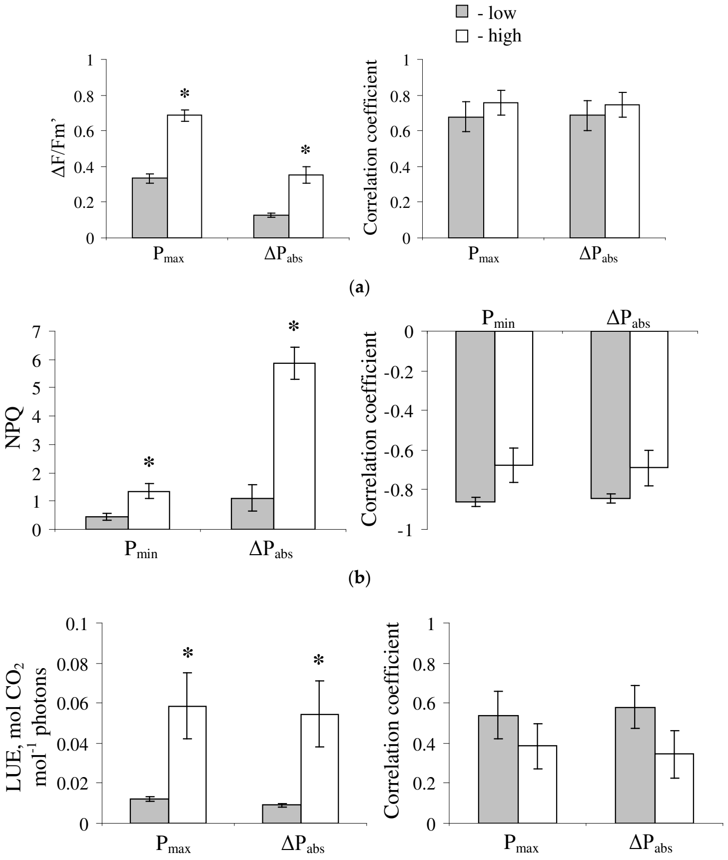
(**b**)

Figure 4. *Cont.*



(**c**)

Figure 4. The influence of the distribution of $\Delta F/F_m{}'$ (**a**); NPQ (**b**) and LUE (**c**) on investigated plants for the connection between these photosynthetic parameters with PRI at measurements of the photochemical reflectance index in leaves. Average values of P_{min} (P_{max}) and ΔP_{abs} are shown on left panels, average correlation coefficients are shown on right panels. The label "low" indicates groups with low P_{min} (P_{max}) and ΔP_{abs}; the label "high" indicates groups with high P_{min} (P_{max}) and ΔP_{abs}. "Low" groups had $n = 43$ ($\Delta F/F_m{}'$), $n = 19$ (NPQ), and $n = 8$ (LUE); "high" groups had $n = 43$ ($\Delta F/F_m{}'$), $n = 19$ (NPQ), and $n = 7$ (LUE). * the group significantly differed from another one ($p < 0.05$, Student's test).



(**a**)

(**b**)

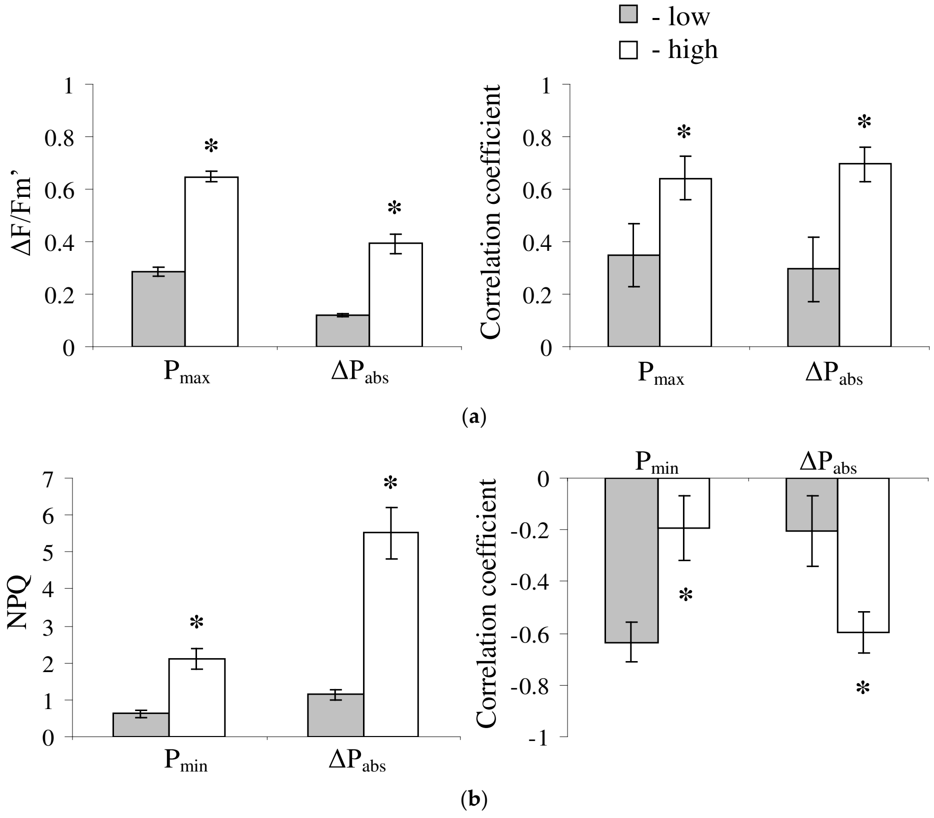
(**c**)

Figure 5. The influence of the distribution of $\Delta F/F_m{}'$ (**a**); NPQ (**b**) and LUE (**c**) on investigated plants for the connection between these photosynthetic parameters with PRI at measurements of the photochemical reflectance index in canopy. Average values of P_{min} (P_{max}) and ΔP_{abs} are shown on left panels, average correlation coefficients are shown on right panels. The label "low" indicates groups with low P_{min} (P_{max}) and ΔP_{abs}; the label "high" indicates groups with high P_{min} (P_{max}) and Δ_{Pabs}. "Low" groups had $n = 12$ ($\Delta F/F_m{}'$), $n = 6$ (NPQ), and $n = 24$ (LUE); "high" groups had $n = 12$ ($\Delta F/F_m{}'$), $n = 6$ (NPQ), and $n = 24$ (LUE). * the group significantly differed from another one ($p < 0.05$, Student's test).

On the basis of works that investigated leaves, we showed that the correlation between PRI and quantum yield was high at high P_{max} and ΔP_{abs} (Figure 4a) and the correlation between PRI and NPQ was high at high ΔP_{abs} and low P_{min} (Figure 4b). In contrast, the correlation between LUE and PRI was high at both values of P_{max} and ΔP_{abs} (Figure 4c). The analysis of works that investigated PRI in canopy showed that significant differences between groups with low and high P_{min} or P_{max} and ΔP_{abs} were absent (Figure 5). It should be additionally noted that absolute values of correlation coefficients of PRI with NPQ and $\Delta F/F_m'$ were high (about 0.75–0.85) in both groups with measurement in canopy. Influence of photosynthetic parameter distribution among investigated plants on correlations between PRI and LUE were absent in all variants.

3.4. Influence of Distribution of Photosynthetic Parameters among Investigated Plants on Connection of These Parameters with PRI at Measurements under Sunlight and Artificial Light

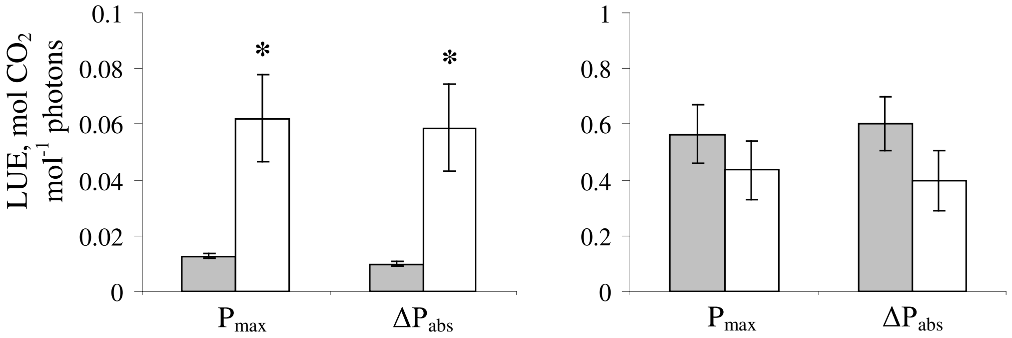
Finally, we investigated the influence of the photosynthetic parameter distribution among investigated plants on correlations of PRI with $\Delta F/F_m'$, NPQ, and LUE with measurement of photosynthetic parameters and the photochemical reflectance index under sunlight and artificial light. The analysis was similar to the analysis that was described in the previous section. It should be noted that differences of photosynthetic parameters between groups with low and high absolute values of P_{min} (P_{max}) and ΔP_{abs} were significant at all light conditions (Figures 6 and 7, on the left).



(**a**)

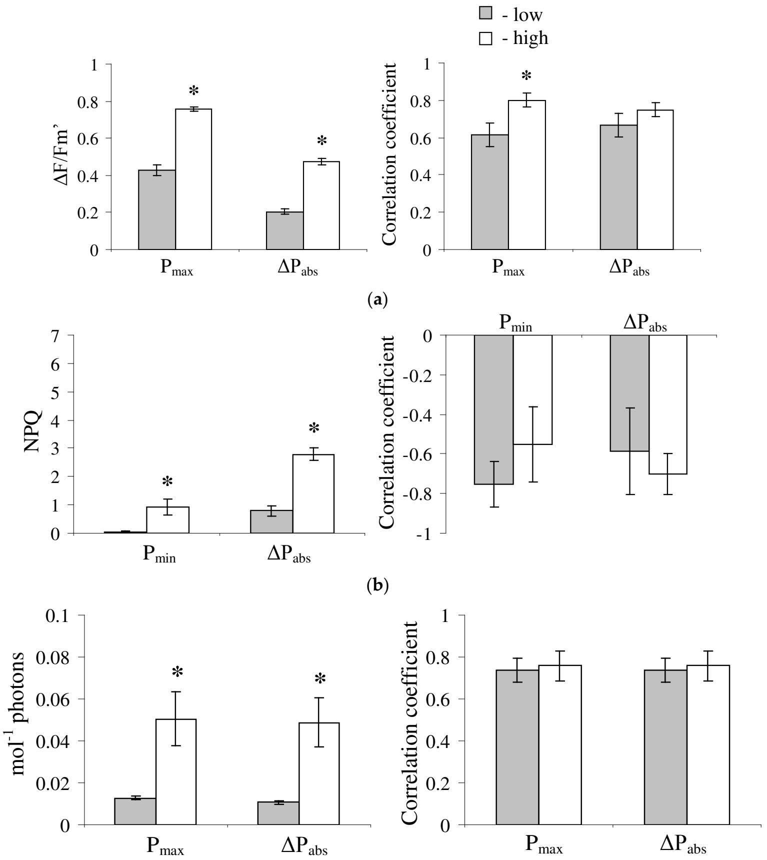
(**b**)

Figure 6. *Cont.*



(**c**)

Figure 6. The influence of the distribution of ΔF/F$_m$′ (**a**); NPQ (**b**) and LUE (**c**) on investigated plants for the connection between these photosynthetic parameters with PRI with measurements under sunlight. Average values of P$_{min}$ (P$_{max}$) and ΔP$_{abs}$ are shown on left panels, average correlation coefficients are shown on right panels. The label "low" indicates groups with low P$_{min}$ (P$_{max}$) and ΔP$_{abs}$; the label "high" indicates groups with high P$_{min}$ (P$_{max}$) and ΔP$_{abs}$. "Low" groups had n = 26 (ΔF/F$_m$′), n = 16 (NPQ), and n = 27 (LUE); "high" groups had n = 26 (ΔF/F$_m$′), n = 17 (NPQ), and n = 27 (LUE). * the group significantly differed from another one (p < 0.05, Student's test).



(**a**)

(**b**)

(**c**)

Figure 7. The influence of the distribution of ΔF/F$_m$′ (**a**); NPQ (**b**) and LUE (**c**) on investigated plants for the connection between these photosynthetic parameters with PRI at measurements under artificial light. Average values of P$_{min}$ (P$_{max}$) and ΔP$_{abs}$ are shown on left panels, average correlation coefficients are shown on right panels. The label "low" indicates groups with low P$_{min}$ (P$_{max}$) and ΔP$_{abs}$; the label "high" indicates groups with high P$_{min}$ (P$_{max}$) and ΔP$_{abs}$. "Low" groups had n = 29 (ΔF/F$_m$′), n = 8 (NPQ), and n = 4 (LUE); "high" groups had n = 29 (ΔF/F$_m$′), n = 9 (NPQ), and n = 5 (LUE). * the group significantly differed from another one (p < 0.05, Student's test).

Under sunlight, we observed dependencies of correlations of PRI with $\Delta F/F_m'$ and NPQ on P_{max} or P_{min} and ΔP_{abs} (Figure 6a,b). Correlation coefficients of PRI with LUE did not significantly differ in groups with different P_{max} and ΔP_{abs} (Figure 6c). Similar trends were observed under artificial light (Figure 7). However, significant differences were shown only between correlation coefficients of PRI with $\Delta F/F_m'$ in groups with low and high P_{max} of the quantum yield of photosystem II. It should be noted that absolute values of correlation coefficients of PRI with NPQ and $\Delta F/F_m'$ under artificial light (about 0.6–0.8) were higher than ones under sunlight (about 0.2–0.7).

These results are in accordance with the results of analysis in the previous section: the correlations of PRI with $\Delta F/F_m'$ and NPQ were affected by the photosynthetic parameter distribution among investigated plants; however, this effect was reduced with a strong connection between PRI and these photosynthetic parameters (investigations under artificial light). Influence of the photosynthetic parameter distribution among investigated plants on correlations between PRI and LUE was absent in all variants.

4. Discussion

Precision agriculture [14,100–103] requires the development of methods of remote sensing of fields and fast analysis of the derived data. The prospective direction of field monitoring is in the application of spectral indices [41,104,105] due to their connection to physiological processes [15,61] and the damage caused by stressors and pathogens in plants [102,106,107]. These indices can potentially be used for the detection of different types of stressors in the early stages of their action [102,107]. The application of a combination of spectral indices can be an additional tool for the improvement of the identification of plant stressors.

Measurement of the photochemical reflectance index is a potentially effective tool for the remote sensing of plants in the field [15,63,108]. There are numerous experimental studies [49,54,66,86,90,93,96] that were devoted to the analysis of the connection between PRI and photosynthetic parameters. The results require theoretical investigations that analyze the current experimental data. The meta-analysis of literature data is an important tool for this analysis [15,61]. In particular, the meta-analysis can reveal the influence of various factors on the connection between PRI and photosynthetic parameters. The meta-analysis in our work shows several important points which are briefly summarized in Table 2.

Table 2. Average correlation coefficients of the photochemical reflectance index with photosynthetic parameters and influence of distribution of these parameters among investigated plants on the connection between PRI and $\Delta F/F_m'$, NPQ, and LUE with different conditions of measurements.

Conditions of Measurement		**Analyzed Parameter or Effect**	**ΔF/Fm′**	**NPQ**	**LUE**
Scale	Leaves	Average correlation coefficient	**0.58±0.05**	**−0.40±0.08**	**0.77±0.03**
		Influence of P_{max} (P_{min})	+++	+++	−
		Influence of ΔP_{abs}	+++	+++	−
	Canopy	Average correlation coefficient	**0.72±0.05**	**−0.77±0.05**	**0.46±0.08**
		Influence of P_{max} (P_{min})	−	+	−
		Influence of ΔP_{abs}	−	−	−
Source of light	Sunlight	Average correlation coefficient	**0.50±0.08**	**−0.41±0.08**	**0.50±0.07**
		Influence of P_{max} (P_{min})	+++	+++	−
		Influence of ΔP_{abs}	+++	+++	−
	Artificial light	Average correlation coefficient	**0.71±0.04**	**−0.65±0.11**	**0.75±0.04**
		Influence of P_{max} (P_{min})	+++	−	−
		Influence of ΔP_{abs}	−	−	−

"+++", the effect was significant ($p < 0.05$); "+", tendency was observed ($0.05 < p < 0.1$); "−", the effect was not significant ($p > 0.1$). Red color shows a low correlation coefficient (0.3–0.5); blue color shows a moderate correlation coefficient (0.5–0.7); green color shows a high correlation coefficient (0.7–0.9).

First, our results showed (Figures 2b, 4a,b and 5a,b, Table 2) that values of correlation coefficients of PRI with $\Delta F/F_m'$ and NPQ, when PRI was registered in canopy, were higher than the coefficients when PRI was registered in leaves. It is probable that this effect was caused by the decrease of noise in PRI measurements due to the averaging of data in the investigation on the canopy level. In contrast, the correlation coefficient of PRI with LUE was minimal for the investigation of the photochemical reflectance index in canopy and maximal at its investigation in leaves. These results may be due to methodological reasons because measurement of CO_2 assimilation, which is the basis of the LUE calculation [62,65], is mainly analyzed in leaves under controlled conditions (CO_2 and H_2O concentrations, light intensity and spectrum, temperature often regulated). That is, the analysis of LUE and PRI at the leaves level tends to be more accurate than the comparison between PRI in canopy and LUE in leaves.

Second, we showed that the correlation coefficients between PRI and photosynthetic parameters under artificial light were higher than those coefficients under sunlight (Figures 2c, 6 and 7, Table 2). It can be presumed that the positive effect of artificial light is caused by the minimization of fluctuations of PRI, $\Delta F/F_m'$, NPQ, and LUE. In contrast, measurements under sunlight can be disturbed by fluctuation of light intensity [42,70,81,85], changes in angle of incidence of light [82,109,110], etc.

Third, the photosynthetic parameter distribution among investigated plants can strongly influence the connection of PRI with $\Delta F/F_m'$ and NPQ (Figure 3, Table 2). However, the influence of the LUE distribution among investigated plants on the connection of PRI with this photosynthetic parameter was not observed (Figures 3c–7c, Table 2).

In particular, it was shown that the correlation coefficients were increased with a decrease of the minimal level of photosynthetic stress among investigated plants in the analyzed variants. The effect may be due to the complex mechanisms of photosynthetic stress in plants. It is known that changes in PRI are mainly connected with redox processes in the xanthophyll cycle [26,36], which is regulated by pH in the lumen of chloroplasts [111]. Transitions in the xanthophyll cycle can influence the nonphotochemical quenching and the quantum yield of photosystem II [111,112]. However, these photosynthetic parameters can be also affected by other mechanisms. In particular, different components of NPQ can be affected by the pH-dependent protonation of PsbS proteins [37,111], state transition [37,113,114], and photoinhibition [115]. The contribution of these processes to the total NPQ depends on environmental conditions [115,116] and the time of their development [117]. The quantum yield of photosystem II is connected with all components of NPQ [113,118,119] as well as with the ratio of the linear and cyclic electron flows [117,120], production of reactive oxygen species [121], etc. Also, there are additional factors which can complicate interaction between photosynthetic parameters and PRI under the action of stressors. In particular, an increase in transthylakoid ΔpH, which can be stimulated during photosynthetic stress, causes chloroplast shrinkage, and this shrinkage probably participates in PRI changes in the range of seconds [15,38]. In contrast, very long-term stress can change the content of chlorophyll and the pool size of the xanthophyll cycle pigments. It is known that similar changes can also influence PRI [48,122].

Thus, it can be speculated that the investigation of plants with high photosynthetic stress (with the high minimal level of the photosynthetic stress among these plants) must be accompanied by numerous mechanisms of changes in NPQ and $\Delta F/F_m'$, including mechanisms which are not connected to changes in PRI. Under these conditions, the connection of PRI with NPQ and $\Delta F/F_m'$ can be disturbed. It is very probable that this effect can be stimulated by fluctuations of environmental conditions at measurement (in particular, changes in light intensity). That is, it should be low at the high correlation between PRI and photosynthetic parameters and it should be high at the low correlation. In reality, our results showed (Figures 4–7, Table 2) that the influence of the minimal level of photosynthetic stress on the connection of PRI with NPQ and $\Delta F/F_m'$ was low at the high correlation between the photochemical reflectance index and photosynthetic parameters (canopy or artificial light). In contrast, the influence was high at the moderate correlation of PRI with NPQ and $\Delta F/F_m'$ (leaves or sunlight).

Influence of variation of the photosynthetic stress level among investigated plants (the difference between maximal and minimal values, ΔP_{abs}) on the correlation of PRI with NPQ and $\Delta F/F_m'$ was also observed (Figure 3, Table 2). The high correlation between PRI and photosynthetic parameters was at high ΔP_{abs} and the low correlation was at the low ΔP_{abs}. This effect was observed (Figures 4–7,

Table 2) at the moderate correlation of PRI with NPQ and $\Delta F/F_m'$ (leaves or sunlight) and was absent at the high correlation (canopy or artificial light). This result seems expected because the influence of fluctuations on the correlation coefficient should be decreased with the increase of variation of the photosynthetic stress level among investigated plants. For the practical problem of field remote sensing, the results show that application of PRI can be more effective in the investigation of the effects of strong stressors than in the investigation of weak stressors. However, the minimal level of the photosynthetic stress among investigated plants should be low (see above), i.e., measurements of control plants, which are not affected by stressors, are also necessary.

The reasons for the absence of the influence of the minimal level of the photosynthetic stress among investigated plants and its variation on the correlation of PRI with LUE (Figures 3–7, Table 2) require future analysis. It cannot be excluded that this absence is caused by a complicated connection between changes in xanthophyll de-epoxidation (i.e., PRI) and changes in CO_2 assimilation (i.e., LUE). The de-epoxidation can directly change NPQ and $\Delta F/F_m'$; however, its influence on CO_2 assimilation is not direct. Changes in linear and cyclic electron flows, transthylakoid proton gradient, and synthesis of Adenosine Triphosphate (ATP) and Nicotinamide Adenine Dinucleotide Phosphate (NADPH) [123] can participate in the induction of changes in CO_2 assimilation after changes in the xanthophyll de-epoxidation.

5. Conclusions

As a whole (Figure 8), our meta-analysis shows that the linear correlation coefficients between PRI and photosynthetic parameters depend on variable conditions of the environment, including scale of measurements (leaves or canopy) and light conditions (sunlight or artificial light). Further, the distribution of photosynthetic parameters among plants (a minimal rate of photosynthetic stress and a variation of the photosynthetic stress level among investigated plants) can influence the linear correlation of PRI with the photosystem II quantum yield and nonphotochemical quenching; the effect is also dependent on conditions of measurements. In contrast, the distribution of light use efficiency among plants did not influence its correlation with PRI.

It is known that the photosynthetic parameters can be modified by numerous factors, including light intensity, temperature, drought, etc. [124]. It is very probable that even a crude guess of the range of photosynthetic parameters can allow one to estimate the efficiency of the PRI in an accurate analysis of photosynthetic stress in plants. The mathematical modeling of photosynthetic processes and PRI can be potentially used for a crude guess of the photosynthetic parameters under specific conditions. Moreover, the modeling can be an additional tool for the analysis of the connection between reflectance indices and photosynthetic parameters [109,125,126]. Development of these models can be used as a solution to the fundamental and applied problems in the field of remote sensing with PRI.

Presently, there are several mathematical models describing the optic properties of leaves and canopy [127–132] and connection of these properties with the content of photosynthetic pigments in leaves [133–136]. Detailed models of PRI, which include a description of the geometry and discontinuity of canopy and different depth penetrations of light into the canopy, are developed on the basis of these models [109,137,138]. Also, linear and nonlinear regressions are widely used to describe the connection between PRI and photosynthetic parameters [62,76,124,137,139]. Development of mechanistic models of PRI and photosynthetic processes is another important method of PRI simulation [109]. In light of the strong connection between PRI and photosynthetic stress [39,40,49], development of detailed models of the relationship between PRI and NPQ is a very important task. Only a few models of the connection between PRI and NPQ have been developed [126]; thus, the problem is very topical.

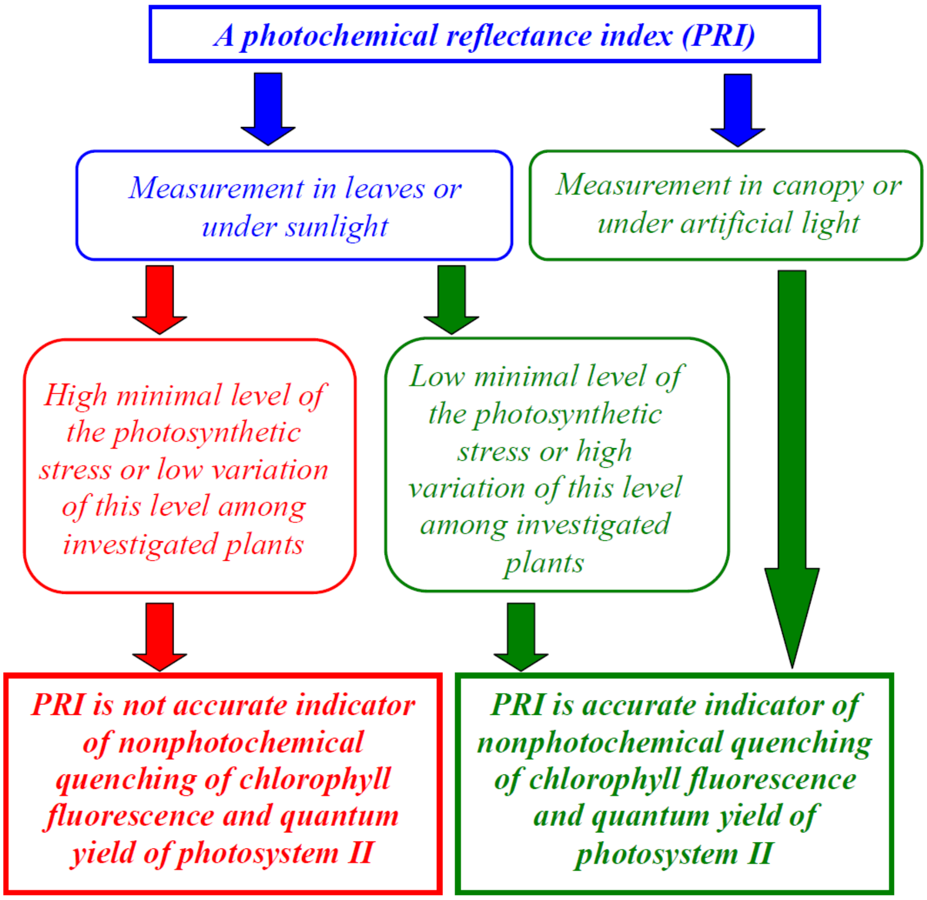


Figure 8. An expected efficiency of application of PRI for investigation of NPQ and $\Delta F/F_m'$ at different conditions of measurements and different distribution of photosynthetic stress levels among investigated plants.

Finally, it should be noted that the development of PRI analysis methods (on the basis of meta-analysis, simulation, etc.) can reveal a new field for use of the photochemical reflectance index. In particular, PRI can potentially be used for fast and remote investigations of systemic photosynthetic responses induced by long-distance stress signals, including electrical [140–147], hydraulic [148], and Reactive Oxygen Species (ROS) [149] signals which strongly influence photosynthetic processes (e.g., the nonphotochemical quenching).

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