



Physiological Features of Potato (*Solanum tuberosum* L. Var. Diacol Capiro) Canopy Reflectance Changes under Different Levels of Water Stress

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Abstract

Plant spectral signatures can reveal specific metabolic responses through variations in reflectivity. However, the link between canopy reflectance and photosynthetic behaviour under water stress has been scarcely studied in potato, especially concerning xylem water potential. This study investigated the relationships between xylem water potential, gas exchange variables (net photosynthesis, stomatal conductance, and transpiration), and changes in the spectral signature of the visible region. Measurements were performed at the tuber differentiation and maximum tuberization phenological stages under three water stress intensities. There was a strong relationship between visible-range reflectance and gas exchange variables across all stress levels and growth stages. The Blue/Red Index (400R/690R) and the Blue/Green Index (450R/550R), along with their foundational spectral bands (550 nm and 710 nm), were powerful predictors of gas exchange dynamics and for the detection of moderate-to-severe water stress in potatoes. These results contribute to the monitoring of photosynthetic performance and the detection of water stress in potato plants, providing a direct pathway to integrate these visible-range indicators into precision agriculture platforms.

Keywords Canopy reflectance · Leaf gas exchange · Vegetation indices

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Introduction

Water stress induces physiological changes in plants, such as reduced chlorophyll content, smaller leaf area, premature senescence, and stunted growth, all of which alter the leaf's spectral reflectance (Maimaitiyiming et al. 2017; Sun et al. 2008). Consequently, spectral reflectance measurements are widely used to assess plant water status (Kovar et al. 2019; Peñuelas and Inoue 1999; Sytar et al. 2017). These measurements sense radiation reflected in the visible (VIS, 400–700 nm), near-infrared (NIR, 700–1200 nm), and short-wave infrared (SWIR, 1300–2500 nm) regions. Each region correlates with specific plant properties: leaf pigments (VIS), cell structure (NIR), and water content (SWIR) (Caturegli et al. 2020). Reflectance data are used to calculate vegetation indices (VIs) by combining spectral bands from the visible and NIR regions (Thenkabail et al. 2000; Tucker 1979). Specifically, VIs based on visible bands are sensitive to decreases in plant water content (Kovar et al. 2019; Suárez et al. 2009, 2008). A key example is the Photochemical Reflectance Index (PRI), which indicates the de-epoxidation state of xanthophyll pigments and is closely tied to photosynthesis (Gitelson and Gamon 2015). The PRI is calculated using reflectance at 530 nm (where xanthophyll absorption occurs) and a reference band at 570 nm. This index is directly related to the photosynthesis rate (Suárez et al. 2009; Nichol et al. 1999; Sims et al. 2006), chlorophyll fluorescence, and non-photochemical quenching (Suárez et al. 2009, 2008; Nichol et al. 1999).

As a drought-sensitive species, monitoring the water status of potato is critical (Almanza-Merchán et al. 2016; Díaz Valencia Paula 2016; Karafyllidis et al. 1996; MacKerron and Jefferies 1986; Michel et al. 2019; Rodríguez et al. 2016). Traditional assessment methods, such as leaf water potential and relative water content (RWC), are accurate but time-consuming and destructive. In contrast, non-destructive approaches using spectral reflectance have become a fundamental tool for diagnosing plant physiological status (Kovar et al. 2019). However, these reflectance-based methods remain underdeveloped for potato cultivation. In potato research, spectral methods have primarily been used to assess N rates (Bowen et al. 2005; Evert et al. 2012), water content, and canopy cover (Bouman et al. 1992). While common indices like Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI) are effective for estimating biomass and yield (Mukiibi et al. 2023; Lin et al. 2023), they have limitations. Specifically, they are poor at detecting early-stage water stress in dense canopies because they saturate at high Leaf Area Index (LAI) values (Tenreiro et al. 2021). Furthermore, these indices require the near-infrared (NIR) range, which was not used in this work. Therefore, our study focuses exclusively on the visible spectrum (400–760 nm) to detect subtle changes in pigments and optical properties that are directly linked to xylem water potential and gas exchange. Previous studies in potato have shown that narrow-band VIS indices, such as the Blue/Red Index (BRI) and the Blue/Green Index (BGI), or those in the red-edge region are more sensitive to physiological variations in potato than NDVI or EVI, particularly during critical phenological stages (Romero et al. 2017; Gerhards et al. 2016), which supports the experimental design chosen in the present research.

Currently, there is no available information about reflectance variations and their relationship with water stress (*Stricto sensu*) and physiological status. Gerhards et al.

(2016) used indices like Crop Water Stress Index (CWSI), Moisture Stress Index (MSI), Photochemical Reflectance Index (PRI), and spectral emissivity in potato variety Cilena (*Solanum tuberosum* L. cv. Cilena), demonstrating thus that water stress detection is feasible using indices depicting leaf temperature, leaf water content, and spectral emissivity. Romero et al. (2017) compared the physiological and spectral traits between Diacol Capiro and Perla Negra genotypes under two drought levels and found out that the spectral information was correlated with physiological variables such as foliar area, total water content, relative growth rate of potato tubers, leaf area ratio, and leaf area index. A key limitation of existing approaches is that they link spectral data to indirect measures like soil water deficit rather than the plant's true water status determined by xylem water potential. Consequently, the actual intensity of water stress and its precise influence on canopy reflectance remain poorly understood.

Therefore, the objective of this study was to investigate the relationship between physiological and spectral responses in potato under water stress. Specifically, we sought to establish correlations between visible-spectrum reflectance indices, xylem water potential, and photosynthetic performance. The following questions are addressed in this study: (1) What is the link between canopy-level reflectance and plant physiological status under water stress? and (2) which vegetation indices could be useful to detect water stress in potato plants?

Methodology

Plant Material and Experimental Design

The experiment was conducted at the AGROSAVIA (Corporación Colombiana de Investigación Agropecuaria) research centre in Tibaitatá, Colombia, at an elevation of 2,516 m above sea level, under greenhouse conditions, with an average temperature of 14.6 °C, and a relative humidity of 78.5%. The photosynthetic photon flux density (PPFD) ranged from 101.4 to 1618 $\mu\text{mol m}^{-2} \text{s}^{-1}$, averaging 575 $\mu\text{mol m}^{-2} \text{s}^{-1}$. To determine the effect of water stress on spectral responses and gas exchange of potato (*Solanum tuberosum* L. “Diacol Capiro”) plants, a randomized complete block design distributed in 3 blocks, each one with 7 treatments was established. Each treatment was the combination of one stress level (light, moderate, and severe) and two plant growth stages: tuber differentiation (TD) and maximum tuberization (MT), plus a control group (well-hydrated plants). Potato plants were sown in loam soil that was kept at field capacity (soil water potential did not decline below -0.033 MPa) by drip irrigation from sowing until each growth stage was reached. At each growth stage, the stress treatments were induced by suspending irrigation until reaching each level of stress. The water stress levels were determined based on (Hsiao 1973; Tschaplinski et al. 2019) and using the xylem water potential (ψ_w) measured in the terminal leaflet of the 3rd or 4th fully expanded leaf. Control plants (well-watered plants) had a water potential (ψ_w) ranging from 0 to -0.49 MPa ; the light water stress treatment corresponded to a ψ_w range of -0.50 to -0.59 MPa , moderate water stress has a ψ_w between -0.60 and -0.89 MPa , and severe water stress was defined as ψ_w lower than -0.90 MPa .

Leaf-level Measurements

All physiological measurements were conducted on both stressed and control plants during two key phenological stages: tuber differentiation (week 9 post-sowing) and maximum tuberization (week 13 post-sowing). Daily measurements began at the onset of water stress induction and continued until the target stress levels were achieved.

Xylem Water Potential (ψ_w)

Pre-dawn ψ_w was measured between 04:00 and 07:00 h using a Scholander pressure chamber (PMS Instrument Company, Oregon, USA). For each measurement, the terminal leaflet from the third or fourth fully developed leaf was excised and immediately placed in the chamber, with a reading taken within 2 min (Ortiz-Álvarez et al. 2023; Rodríguez-Pérez et al. 2017).

Gas Exchange

Net photosynthesis (A), stomatal conductance (g_s), and transpiration (E) were recorded between 09:00 and 11:00 h using an infrared gas analyzer (LI-6800, LI-COR Biosciences, USA). All measurements were performed with a constant CO_2 concentration of $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the chamber.

Spectral Reflectance Measurements

Spectral images were captured from a height of 3 m above the plant canopy, with the camera oriented downwards. Image acquisition campaigns were conducted at approximately the same time of day, using a 710-VP Surface Optics Corporation camera with a resolution of 520×696 pixels and 128 spectral bands covering the 400–1000 nm range. In total, 70 hyperspectral images were obtained. In each image acquisition, a Spectralon white reflectance panel was systematically included to convert the hyperspectral intensity data to reflectance, ensuring measurements were independent of the illumination level. The same illumination conditions applied to both the plant canopy and the Spectralon panel (except for shaded areas), providing consistency across captures. To segment the Spectralon panel from the spectral image, the average of the red, green, blue, and NIR bands was calculated and divided by the maximum intensity, applying a threshold above 0.5.

The reflectance of each spectral imagery was computed using:

$$\rho(x, y, \lambda) = \frac{I(x, y, \lambda) \rho_s(\lambda)}{I_s(\lambda)}$$

where $\rho(x, y, \lambda)$ is the reflectance image at pixel coordinates x, y and waveband λ , $I(x, y, \lambda)$ is the raw intensity image at pixel coordinates x, y , and waveband λ , $\rho_s(\lambda)$ the known reflectance of the Spectralon panel at λ wavelength (0.99 at visible and NIR ranges) and $I_s(\lambda)$ the mean intensity of the Spectralon panel at waveband λ . To segment the canopy from its background, the Soil-Adjusted Vegetation Index (SAVI)

was used following the methodology reported by Duarte-Carvajalino et al. (2021). Two image campaigns on tubers differentiation and maximum tuberization growth stages were performed, acquiring images starting from the water supply suspension to each level of stress (light, moderate, severe). The 710-VP camera records spectral information in the full wavelength range of 400–1000 nm; however, only the 400–760 nm range was used for this study. Simple and multiple linear regressions between xylem water potential (ψ_w), gas exchange variables (A_n , E , and g_s), and reflectance responses in terms of specific bands and vegetation indices (Table 1) were performed. Pearson correlation coefficient (r) and coefficient of determination (R^2) were used to explore the significant relationships between all parameters and indices.

Reflectance Variability

The analysis of reflectance variability within stress treatments indicates that during the tuber differentiation stage, the average coefficient of variation (CV) was highest for the moderate stress treatment (CV=20.87%), followed by severe stress (CV=17.18%) and mild stress (CV=16.95%). During the maximum tuberization stage, variability among replicates was slightly higher in the mild stress treatment (CV=17.06%) compared to severe stress (CV=15.19%) and moderate stress (CV=14.15%). Since the data did not meet the assumptions of normality (Shapiro-Wilk test, $p < 0.001$), the non-parametric Kruskal-Wallis test was applied to assess differences among stress treatments. The results showed statistically significant differences in reflectance distributions across treatments during both the tuber initiation ($p = 3.25 \times 10^{-10}$) and peak tuberization stages ($p = 0.0083$). These findings suggest that stress conditions elicit distinct spectral responses that are detectable even in the presence of high variability among replicates, highlighting the sensitivity of spectral analysis for discriminating physiological stress levels in plants.

Results

Spectral Behaviour

Water stress induced a general increase in canopy reflectance across the visible spectrum, a response that became pronounced once xylem water potential (ψ_w) fell below -0.7 MPa (Fig. 1). The most significant changes were concentrated in the green (520–570 nm), red (650–660 nm), and red-edge (700–750 nm) regions, particularly during the maximum tuberization phase. At this stage, the green region showed the most prominent reflectance increase under all stress intensities, while the red region responded more clearly under moderate and severe stress. Concurrently, in the red-edge, lower water potentials resulted in a steeper reflectance slope. In contrast, the violet-blue region (400–500 nm) only showed a clear response to moderate and severe stress during the earlier tuber differentiation phase, with no discernible changes observed during maximum tuberization.

Table 1 Vegetation indices used in this study

Vegetation Index	Equation	Reference
Carotenoid Reflectance Index (CRI)	$CRI = 1/R510 - 1/R700$	Gitelson et al. 2002
Chlorophyll Index (CI)	$CI = (R750 - R705)/(R750 + R705)$	Gitelson et al. 1996
Triangular Vegetation Index (TVI)	$TVI = 0.5 \times (120 \times (R750 - R550) - 200 \times (R670 - R550))$	Haboudane et al. 2004
Normalized Phaeophytinization Index (NPQ) (Haboudane et al. 2004)	$NPQI = (R415 - R435)/(R415 + R435)$	Barnes et al. 1992
Photochemical Reflectance Index (sPRI)	$PRI = ((R531 - R570)/(R531 + R570)) + 1)/2$	Sims and Gamon (2002)
Simple Ratio Pigment Index (SRPI)	$SRPI = R430/R680$	Peñuelas and Filella 1995
Blue/Red Index (BRI)	$BRI = R400/R690$	Zarco-Tejada et al. 2005
Blue/Red Index (BRI2)	$BRI2 = R450/R690$	Zarco-Tejada et al. 2005
Blue/Green Index (BGI)	$BGI = R400/R550$	Zarco-Tejada et al. 2005
Blue/Green Index (BGI2)	$BGI2 = R450/R550$	Zarco-Tejada et al. 2005
Modified Red Edge Simple Ratio Index (mRESR)	$mRESR = (R750 - R445)/(R705 + R445)$	Sims and Gamon (2002)

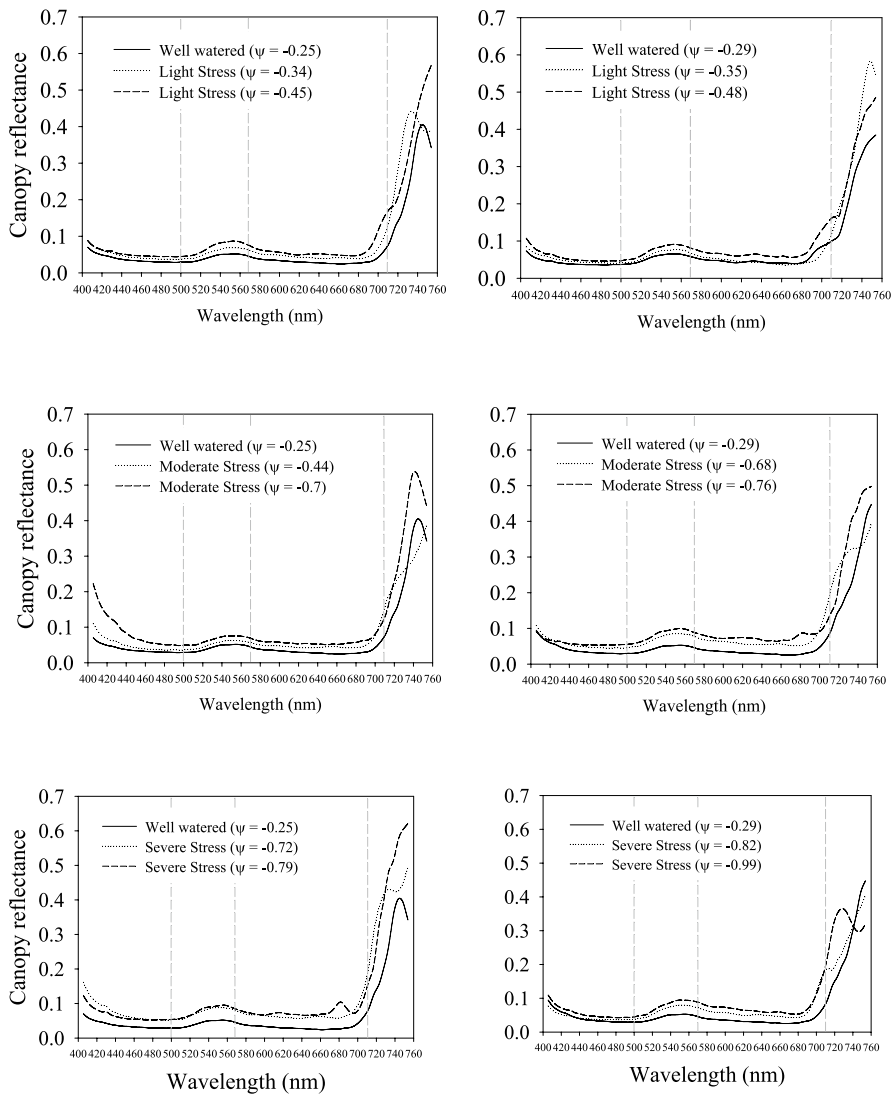


Fig. 1 Potato canopy reflectance measured in two growth stages, TD (tuber differentiation, left) and MT (maximum tuberization, right), for well-watered plants and light, moderate, and severe stress levels on the 400 to 760 nm wavelengths

Relationship Between ψ_w , A_n , g_s , E and the Main Absorption Bands in the Visible Spectrum

We observed a non-linear relationship between xylem water potential and reflectance in the main pigment absorption bands: as ψ_w decreased, reflectance increased. This trend was consistent across both the tuber differentiation (TD) and maximum tuberization (MT) growth stages. Specifically, the reflectance at 550 nm and 670 nm showed

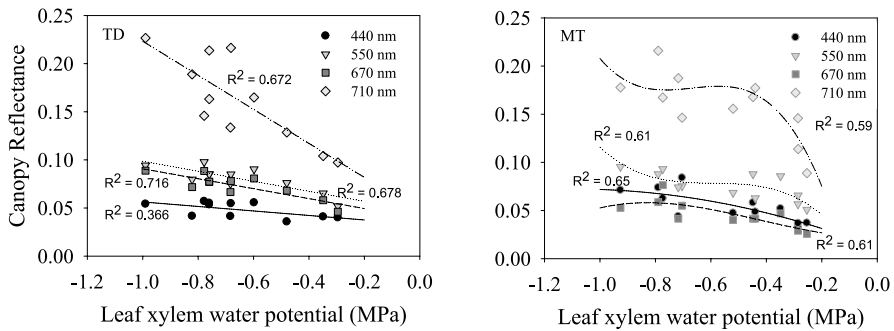


Fig. 2 Relationships between xylem water potential and reflectance in the blue (440 nm), green (550 nm), red (670 nm), and red edge (710 nm) bands of the spectrum in potato leaves for two growth stages, TD (tuber differentiation, left) and MT (maximum tuberization, right). Well-watered plants have hydric potential in the 0 to -0.49 MPa range, light water stress range -0.5 to -0.59 , moderate water stress range -0.6 to -0.89 MPa, and severe water stress range < -0.9 MPa

a similar, strong response to water stress (correlation coefficients > 0.6). However, the 710 nm band exhibited the greatest sensitivity to changes in water potential (Fig. 2).

A consistent inverse relationship was found between canopy reflectance and gas exchange parameters: as photosynthesis, stomatal conductance, and transpiration decreased due to stress, reflectance in key spectral bands increased. Decreased photosynthetic rates were strongly correlated with increased reflectance. Across both phenological stages, the 550 nm and 710 nm bands showed the strongest relationships, with determination (R^2) and correlation (r) coefficients exceeding 0.5 and 0.7, respectively. The 710 nm band consistently exhibited the highest sensitivity to changes in A_n (Fig. 3).

Similarly, stomatal closure (decreased g_s) was associated with increased reflectance, particularly in the 550 nm (green) and 710 nm (red-edge) bands. This indicates that the green and red-edge regions are highly sensitive to stomatal-driven stress

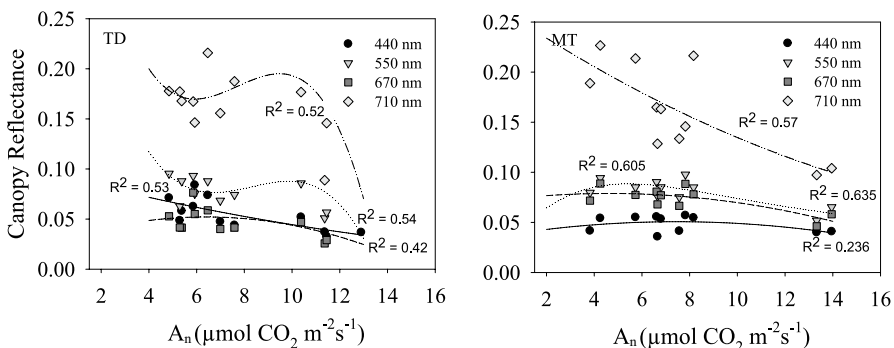


Fig. 3 Relationships between net photosynthesis (A_n) and reflectance in the blue (440 nm), green (550 nm), red (670 nm), and red edge (710 nm) bands of the spectrum in potato leaves for two growth stages, TD (tuber differentiation) and MT (maximum tuberization). Determination coefficients (R^2) are inserted inside graphs

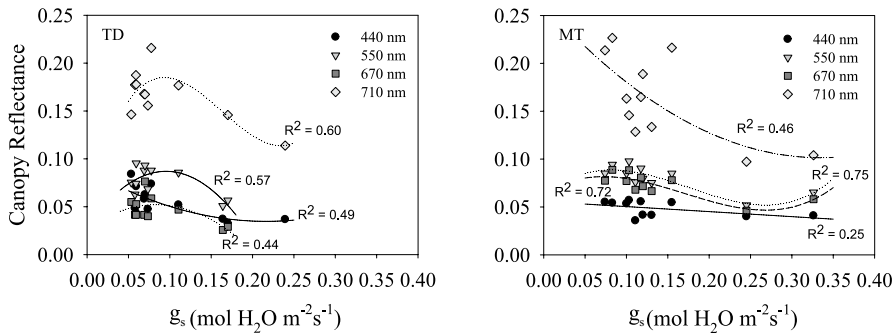


Fig. 4 Relationships between stomatal conductance (g_s) and reflectance in the blue (440 nm), green (550 nm), red (670 nm), and red edge (710 nm) bands of the spectrum in potato leaves for two growth stages, TD (tuber differentiation) and MT (maximum tuberization). Determination coefficients (R^2) are inserted inside graphs

responses in both growth phases. Again, the 710 nm band showed the largest reflectance variations (Fig. 4).

The relationship between transpiration and reflectance varied significantly between the two growth stages. During tuber differentiation, a strong non-linear trend was observed. All tested bands showed high correlation ($r > 0.7$) and determination ($R^2 > 0.5$) coefficients. The 710 nm band had the strongest association with changes in E ($r = 0.87$, $R^2 = 0.76$). During maximum tuberization, the 710 nm band showed a poor correlation with E . Instead, the 550 nm and 670 nm bands became the most reliable indicators of transpiration changes, exhibiting strong correlations similar to those seen in the earlier growth stage (Fig. 5).

Relationship Between Vegetation Indices and ψ_w , A_n , g_s and E

The relationships between vegetation indices and physiological parameters varied significantly depending on the phenological stage, as detailed in Table 2. During

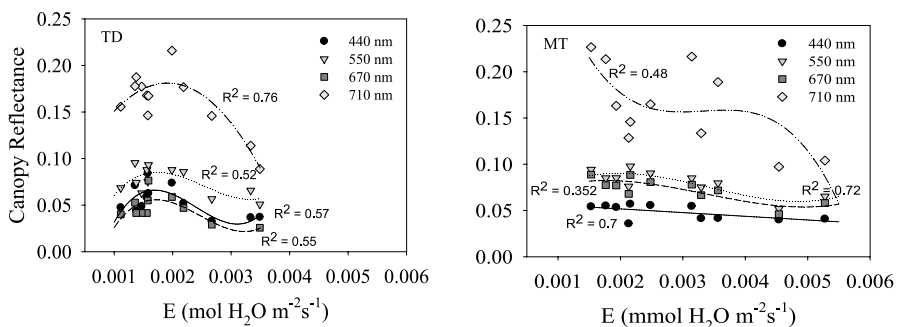


Fig. 5 Relationships between transpiration (E) and reflectance in the blue (440 nm), green (550 nm), red (670 nm), and red edge (710 nm) bands of the spectrum in potato leaves for two growth stages, TD (tuber differentiation) and MT (maximum tuberization). Determination coefficients (R^2) are inserted inside graphs

Table 2 Pearson's correlation coefficient (r) and coefficient of determination (R^2) between calculated vegetation indices from reflectance spectra and leaf xylem water potential (ψ MPa), net photosynthesis (A_n), transpiration (E), and stomatal conductance (g_s)

Vegetation index	Leaf xylem water potential ψ (MPa)				A_n ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)				E (mmol $\text{H}_2\text{O m}^{-2} \text{ m}^{-2} \text{ s}^{-1}$)				g_s (mol $\text{H}_2\text{O m}^{-2} \text{ m}^{-2} \text{ s}^{-1}$)			
	Tuber differ- tiation		Maximum tuberization		Tuber differen- tiation		Maximum tuberization		Tuber dif- ferentiation		Maximum tuberization		Tuber dif- ferentiation		Maximum tuberization	
	r	R^2	r	R^2	r	R^2	r	R^2	r	R^2	r	R^2	r	R^2	r	R^2
Carotenoid Reflectance Index (CRI)	0.864	0.717*	<0.5	<0.5	0.766	0.588*	0.747	0.558*	0.807	0.651*	0.762	0.85**	0.861	0.741*	<0.5	<0.5
Chlorophyll Index (CI)	<0.5	<0.5	0.877	0.770*	<0.5	<0.5	0.740	0.557*	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5
Triangular Vegetation Index (TVI)	<0.5	<0.5	0.914	0.836**	<0.5	<0.5	0.883	0.780**	<0.5	<0.5	0.814	0.66*	<0.5	<0.5	0.857	0.735*
Normalized Phaeophytinization Index (NPQI)	<0.5	<0.5	0.880	0.77*	<0.5	<0.5	0.888	0.79**	<0.5	<0.5	0.874	0.765**	0.763	0.582*	0.899	0.809**
Photochemical Reflectance Index (sPRI)	0.745	0.555*	0.930	0.865**	<0.5	<0.5	0.825	0.681*	0.749	0.562*	0.735	0.54*	0.710	0.504*	0.650	0.432
Simple Ratio Pigment Index (SRPI)	<0.5	<0.5	0.860	0.739*	<0.5	<0.5	0.786	0.618*	<0.5	<0.5	0.845	0.714*	<0.5	<0.5	0.905	0.819**
Blue/Red Index (BRI)	0.871	0.758**	0.840	0.705*	0.904	0.818**	0.913	0.835**	0.762	0.580*	0.910	0.829**	0.753	0.567*	0.946	0.895**
Blue/Red Index (BRI2)	<0.5	<0.5	0.820	0.680*	<0.5	<0.5	0.793	0.628*	<0.5	<0.5	0.730	0.53*	<0.5	<0.5	0.657	0.738*
Blue/Green Index (BGI)	<0.5	<0.5	0.876	0.767**	<0.5	<0.5	0.943	0.889**	<0.5	<0.5	0.936	0.876**	<0.5	<0.5	0.970	0.942**
Blue/Green Index (BGI2)	0.856	0.733*	0.819	0.671*	0.911	0.831**	0.895	0.802**	0.732	0.530*	0.768	0.59*	0.753	0.567*	0.869	0.756**
Modified Red Edge Simple Ratio Index (mRESR)	<0.5	<0.5	0.909	0.827**	<0.5	<0.5	0.82	0.677*	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5

*** $R^2 > 0.75$ * R^2 between 0.5 and 0.75

the maximum tuberization (MT) stage, multiple indices showed strong correlations with plant stress indicators; these included mRESR and PRI with ψ_w ; SRPI with g_s ; TVI with both ψ_w and A_n ; and NPQI, BGI, and BRI with A_n , g_s , and E . In stark contrast, during the tuber differentiation (TD) stage, high correlations ($R^2 > 0.75$) were sparse, observed only between BRI and ψ_w , and BGI2 and A_n . When assessing performance across both stages, the BRI and BGI2 indices consistently emerged as the most robust predictors, generally showing higher correlation and determination values ($R^2 > 0.5$ or > 0.75) for all physiological parameters. Most other indices demonstrated weaker relationships, with r and R^2 values typically at or below 0.49.

Both the 400R/690R (BRI) and 450R/550R (BGI) ratios proved to be strong indicators of xylem water potential, with correlation coefficients exceeding 0.8 in both growth stages (Fig. 6). Crucially, the nature of this relationship was stage-dependent, with the correlation slope inverting from the tuber differentiation to the

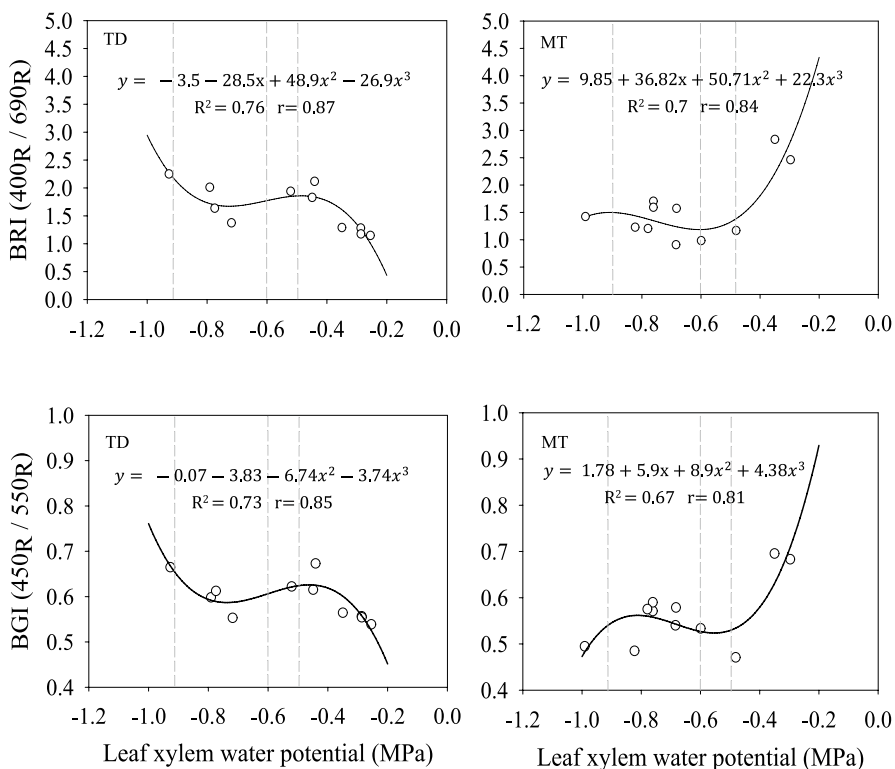


Fig. 6 Relationship between Blue Red Index (BRI), Blue Green Index (BGI), and Leaf xylem water potential for two growth stages, TD (tuber differentiation, left) and MT (maximum tuberization, right). Solid lines represent the relationship between variables. Equations and determination coefficients (R^2) are inserted inside graphs. Well-watered plants have hydric potential in the 0 to -0.49 Mpa range, light water stress (LWS) range -0.5 to -0.59, moderate water stress (MWS) range -0.6 to -0.89 MPa, and severe water stress (SWS) range < -0.9 MPa. Dotted lines indicate stress levels thresholds. Y-axes show the spectral index value (unitless)

maximum tuberization phase. For the 400R/690R ratio, a BRI index value of 1.5 served as a reliable stress threshold ($\psi_w < -0.6$ MPa); values rising above 1.5 indicated stress during tuber differentiation, while values falling below 1.5 indicated stress during maximum tuberization. The 450R/550R ratio (BGI) behaved similarly, with a threshold of 0.6 separating stressed and unstressed plants, and the directional relationship likewise inverting between the two stages (Fig. 6).

The BRI and BGI2 indices were found to be powerful estimators of net photosynthesis (A_n), as indicated by their high coefficients of determination ($R^2 > 0.8$) across both growth stages (Fig. 7). While this confirms their suitability for monitoring photosynthetic activity, the relationship's direction was inverted between the two stages. During tuber differentiation, the correlation was negative, with declining photosynthetic rates leading to higher index values. Conversely, during maximum tuberization, the correlation became positive, meaning that lower rates of photosynthesis corresponded to lower index values.

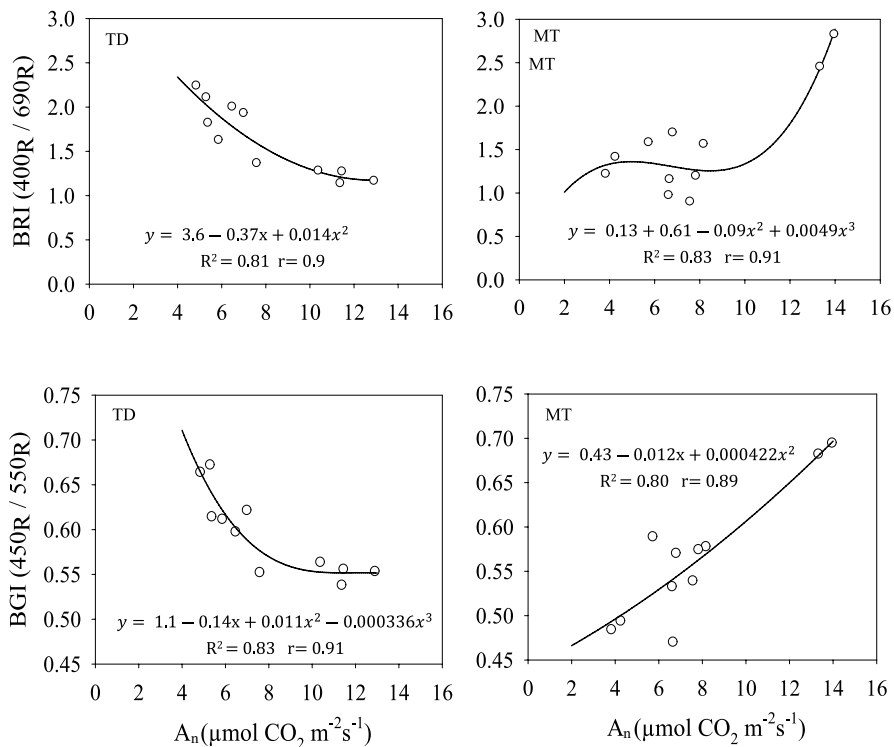


Fig. 7 Relationship between Blue Red Index (BRI), Blue Green Index (BGI), and Net Photosynthesis (A_n) for two growth stages, TD (tuber differentiation) and MT (maximum tuberization). Solid lines represent the relationship between variables. Equations and determination coefficients (R^2) are inserted inside graphs. Y-axes show the spectral index value (unitless)

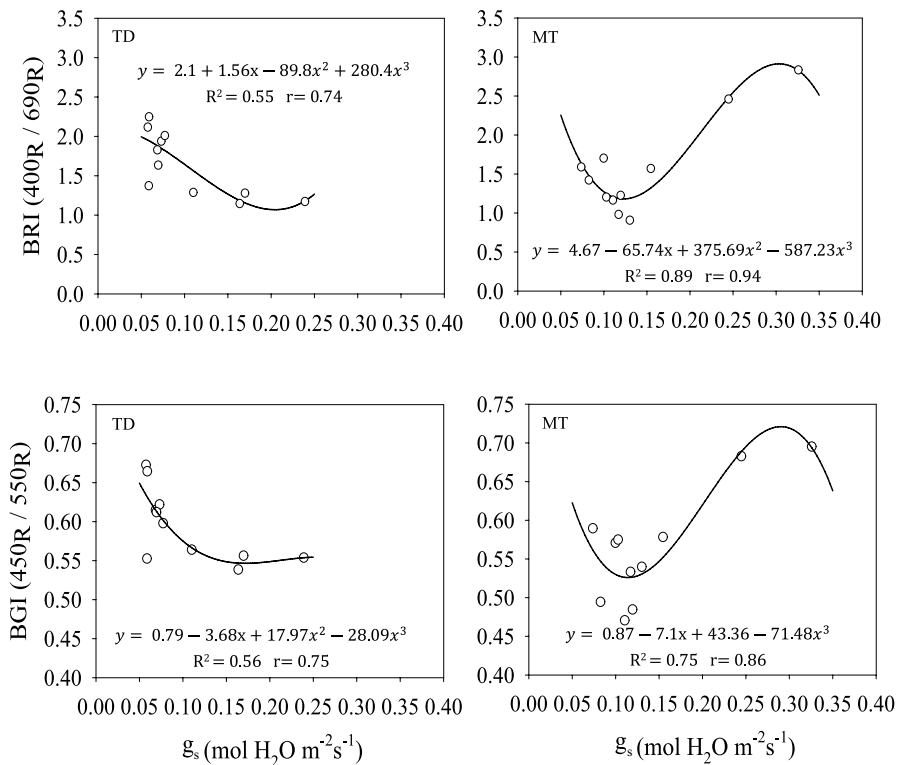


Fig. 8 Relationship between Blue Red Index (BRI), Blue Green Index (BGI), and stomatal conductance (g_s) for both growth stages, TD (tuber differentiation) and MT (maximum tuberization). Solid lines represent the regression relationships between the variables. Equations and determination coefficients (R^2) are inserted inside graphs. Y-axes show the spectral index value (unitless)

The predictive power of the BRI (400R/690R) and BGI (450R/550R) indices for stomatal conductance (g_s) changed dramatically between phenological stages. Initially, during tuber differentiation, these indices showed their weakest correlations of the entire study. However, during maximum tuberization, the BRI became the strongest predictor, with correlation and determination coefficients of 0.90 and 0.89, respectively. This relationship also mirrored the behaviour observed with net photosynthesis, as the correlation slope inverted between the two growth stages (Fig. 8).

The relationship between the BRI and BGI indices and transpiration (E) mirrored the results observed for stomatal conductance (g_s), which is expected given the strong physiological coupling between these two variables. Reinforcing this pattern, the BRI (400R/690R) was again the strongest predictor during maximum tuberization, with correlation and determination coefficients of 0.90 and 0.81, respectively. The relationship also followed the same inversion, showing a negative correlation during tuber differentiation and a positive correlation during maximum tuberization (Fig. 9).

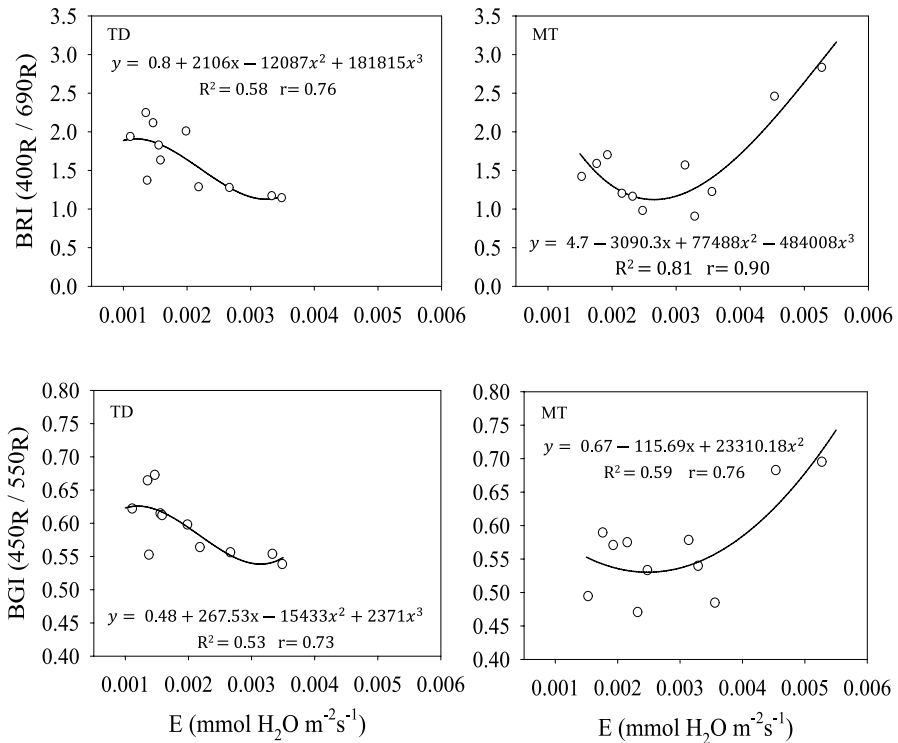


Fig. 9 Relationship between Blue Red Index (BRI), Blue Green Index (BGI), and Transpiration (E) for both growth stages, TD (tuber differentiation) and MT (maximum tuberization). Solid lines represent the linear relationship between variables. Equations and determination coefficients (R^2) are inserted inside graphs. Y-axes show the spectral index value (unitless)

Discussion

Data analysis in this study indicated that progressive water stress caused changes in photosynthesis and in the visible optical properties of potato canopy. The spectral curves showed some slight variations in the regions around 550 nm and 710 nm, but distinguishing these differences from well-hydrated plants is not easy. Under moderate and severe water stress events, the impact on reflectance is much more evident. Although increases in reflectance are observed in the violet-blue region (400–500 nm), considerable increases in the canopy reflectance of stressed plants are mainly observed in the region from 530 to 570 nm, red (660–670 nm) and red edge (around 700 nm). Typically, absorption in the red range is high due to the action of both chlorophyll-a and -b. On the other hand, the sensitivity of absorption and reflectance in the green and red edge spectral regions is higher than in the blue and red regions of the spectrum (Gitelson 2011). Our findings reveal a strong connection between canopy reflectance and the gas exchange processes governed by water stress. The inverse relationship—where decreases in ψ_w , A_n , g_s , and E

corresponded with increased reflectance at 550 nm and 710 nm—can be explained by the plant's initial response to drought. Under light to moderate stress, the primary defence mechanism is rapid stomatal closure. This action reduces stomatal conductance, transpiration, and CO₂ uptake for photosynthesis. Our results demonstrate that reflectance in the green and red-edge regions is highly sensitive to these stomatal-driven changes, suggesting these bands can serve as a reliable proxy for monitoring early-stage water stress (Li et al. 2007; Mafakheri et al. 2010).

Although the near-infrared region (760–1000 nm) is conventionally associated with canopy structure and water status, in this study, we focused on the visible spectrum (400–760 nm) to capture small-scale variations in pigments and gas exchange processes directly linked to xylem water potential. This choice is supported by previous findings in potato, which indicate that narrow-band VIS and red-edge indices (e.g., BRI and BGI) are more sensitive than traditional NIR-based indices (such as NDVI or EVI) for detecting early water stress under dense canopies (Gerhards et al. 2016; Romero et al. 2017). We acknowledge that the omission of the NIR range may limit the direct generalization of the results to larger-scale applications; however, the correlations obtained in the VIS domain confirm its diagnostic value and suggest that these indices could complement NIR-based approaches in future multispectral or hyperspectral monitoring platforms.

The functional relationships between the BRI and BGI2 vegetation indices and gas exchange parameters followed third-order polynomials, demonstrating the non-linear nature of these relationships. Nonlinear relationships were also found by Zarco-Tejada et al. (2005) for BRI and BGI indices in vine. Changes in the 400R/690R and 450R/550R ratios were more evident under more negative water potential during severe water stress events. The correlation results during the tuber differentiation phase (DT) indicate a trend of increasing 400R/690R and 450R/550R ratio values as the water potential becomes more negative due to intensified water stress. This is because, even when the reflectance at 690 nm and 550 nm increases due to the lower absorption in these bands, the increase in the 400–450 nm region is much greater, which can be seen in Fig. 1. This increase in reflectance values in the blue-violet region inverts the sense of the correlations during DT, generating a negative association between the variables. However, during maximum tuberization (MT), there are no such increases in reflectance in the 400–450 nm region, which maintains a positive correlation between the variables. Thus, the response of the 400R/690R and 450R/550R indices to water stress in potatoes depends on the growth stage, and these differences are due mainly to the physiological non-stomatal limitations and structural changes that are specific to each stage. During tuber differentiation, the plants are fully leaf-expanded, with greater meristematic activity and active cell division. Water stress at this stage interrupts the formation of chloroplasts and the synthesis of pigments, especially chlorophylls, before the photosynthetic apparatus has fully developed. The resulting lower concentration of chlorophylls reduces absorption in the blue range and increases reflectance in the 400–450 nm bands (Romero et al. 2017). Similarly, changes in mesophyll cell structure and turgidity modify light scattering and increase reflectance, particularly in the blue range (Romero et al. 2017; Hu et al. 2023). During maximum tuberization, water stress accelerates chlorophyll loss and leaf senescence. Cell damage and tissue

decomposition increase light scattering, especially at wavelengths of ~550–690 nm. This shifts the increase in reflectance towards the green and red wavelengths, where chlorophyll is strongly absorbed under normal conditions (Romero et al. 2017). The process of chlorophyll breakdown (during complete leaf dehydration) may cause a corresponding decreasing 400R/690R and 450R/550R ratios since chlorophyll contributes mainly to the 650 nm absorption band (Suárez et al. 2008, 2012; Dobrowski et al. 2005; Seelig et al. 2008) and the higher sensitivity of the 550 nm band with chlorophyll contents. Therefore, the rise in reflectance in the green and red spectrums during tuber filling under water deficit indicates the progression of leaf senescence, chlorophyll degradation, and the loss of leaf functionality.

The blue/green/red ratio indices included blue/green indices ($BGI1 = 400R/550R$; $BGI2 = 450R/550R$) and blue/red indices ($BRI1 = 400R/690R$; $BRI2 = 450R/690R$). These indices were initially proposed and used by Zarco-Tejada et al. (2005) and Zarco-Tejada et al. (2012) for monitoring the physiological condition of *Vitis vinifera* L. and for the remote detection of water stress in a citrus orchard, finding that the $BGI1$ index (blue/green ratio) showed the highest correlation for both g_s ($R^2 = 0.62$) and Ψ_w ($R^2 = 0.49$), suggesting it could serve as a good estimator of water stress. In this study, both the blue/green and the blue/red indices showed correlations greater than 0.7 and R^2 greater than 0.75 with the xylem water potential, stomatal conductance (g_s), net photosynthesis (A_n), and transpiration (E), which postulates them as good indicators of water stress in potato. These results are consistent with the correlations found between gas exchange parameters and the specific absorption bands at 550 nm, 670 nm, and 710 nm (the “*Relationship Between ψ_w , A_n , g_s , E and the Main Absorption Bands in the Visible Spectrum*” section), where the association and dependence of these spectral regions on variations in xylem water potential, stomatal conductance (g_s), net photosynthesis (A_n), and transpiration (E) are evident.

Conventionally, variations in these indices have been interpreted primarily as indicators of chlorophyll degradation and other non-stomatal limitations, such as reductions in pigment biosynthesis and alterations in light absorption capacity. The present results demonstrate that these indices are also closely linked to stomatal-driven processes, implying that 400R/690R and 450R/550R integrate signals from both non-stomatal limitations (e.g. pigment depletion) and stomatal limitations (e.g. g_s and E reductions), making them sensitive indicators of the combined impacts of drought on leaf optical properties and physiological function. Thus, these indices hold potential as multi-dimensional proxies for monitoring plant water stress, capturing both biochemical and gas-exchange limitations across different growth stages.

Conclusions

While visible-spectrum reflectance is conventionally interpreted as an indicator of non-stomatal factors such as pigment content, our findings establish a robust link between this spectral domain and the physiological markers of stomatal limitation. We demonstrated a strong relationship between visible-range reflectance

and classic indicators of stomatal closure, including reduced transpiration and conductance. This work confirms that visible-spectrum analysis can therefore serve as a powerful proxy for non-destructively assessing the onset and magnitude of stomatal-driven photosynthetic limitations under water stress.

Among the tested spectral indicators, the Blue/Red Index (BRI; 400R/690R) and Blue/Green Index (BGI; 450R/550R) consistently emerged as the most powerful predictors of gas exchange dynamics. Their robust performance across varying stress intensities and phenological stages underscores their diagnostic utility. This study therefore validates the potential of these indices and their foundational 550 nm and 710 nm spectral bands, as a comprehensive method for assessing water stress in potato by effectively capturing the integrated effects of both stomatal and non-stomatal limitations.

From a practical standpoint, this study successfully identified operational thresholds for the BRI and BGI indices to detect moderate-to-severe water stress in *Solanum tuberosum* L. var. Diacol Capiro. This finding is pivotal for Colombian potato production, as it provides a direct pathway to integrate these visible-range indicators into precision agriculture platforms. By deploying these indices on proximal field sensors or UAV-mounted hyperspectral systems, farmers can optimize irrigation scheduling, thereby reducing yield losses and enhancing water use efficiency. Given the economic and cultural importance of this variety, adopting such remote sensing tools is a key step towards strengthening resilience against climate variability and developing advanced platforms for sustainable potato cultivation. Although these results were obtained under greenhouse conditions, their strong consistency suggests a high potential for transferability to open-field scenarios, provided that further validation is conducted under natural variability of light and temperature.

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Data Availability The datasets generated during and/or analysed during the current study are not publicly available due to they are protected under the copyright of AGROSAVIA but are available on reasonable request.

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