

Chlorophyll fluorescence and its relationship with physiological stress in *Chenopodium quinoa* Willd.

Miguel GARCIA-PARRA^{1*}, Roman STECHAUNER-ROHRINGER¹,
Diego ROA-ACOSTA², Daniel ORTIZ-GONZÁLEZ³,
Jorge RAMIREZ-CORREA¹, Nubia PLAZAS-LEGUIZAMÓN⁴
Andrés COLMENARES-CRUZ⁵

¹Universidad del Cauca, Facultad de Ciencias Agrarias, Departamento de Ciencias Agropecuarias, Popayán, Colombia; miguelgarcia@unicauca.edu.co (*corresponding autor); rstechauner@unicauca.edu.co; j.ramirez@unicauca.edu.co

²Universidad del Cauca, Facultad de Ciencias Agrarias, Departamento de Agroindustria, Popayán, Colombia; droa@unicauca.edu.co

³Corporación Colombiana de Investigación Agropecuaria - AGROSAVIA, Área de fisiología vegetal y cultivos, Palmira, Colombia; dfortiz@agrosavia.co

⁴Fundación Universitaria Juan de Castellanos, Facultad de Ciencias Agrarias y Ambientales, Tunja, Colombia; nplazas@jdc.edu.co

⁵Universidad Nacional Abierta y a Distancia UNAD, Escuela de Ciencias Ambientales Pecuarías y del Medio Ambiente, Tunja, Colombia; ramiro.colmenares@unad.edu.co

Abstract

Photosynthetic activity is a fundamental process in the physiology of plants, and its regulation plays an important role in determining the effect of abiotic factors. Quinoa is a plant species of agronomic and nutritional interest that has been recognized for its adaptability to extreme environmental conditions, however, climate change may result in unfavorable conditions capable of affecting the natural development of this species, which is of great interest culture and research in South America. To evaluate the response of quinoa to stress, techniques could be used that quantify the loss of light energy through its dissipation in the form of heat. However, the measurement of chlorophyll fluorescence is the most widely used and accessible technique for field research, which allows to recognize the relationships between the plant and agroclimatic factors. This review summarizes the physiological effects of heat, radiation, salinity, and nutrient and water availability, as well as their possible interactions on quinoa.

Keywords: photosystem II; quinoa; quantum efficiency; reactive oxygen species; stress tolerance

Introduction

Quinoa, *Chenopodium quinoa* Willd., belongs to the Amaranthaceae family and is a pseudocereal native to South America (Bedoya-Perales *et al.*, 2018). This crop is important for human and animal nutrition, as well as for its medicinal and agro-industrial properties (Ahumada *et al.*, 2016; Navruz-Varli and Sanlier, 2016). This is due to the fact that its seeds have a high content of proteins, carbohydrates, lipids and bioactive compounds that favour nutrition of those who consume it (Vazquez-Luna *et al.*, 2019; Roa-Acosta *et al.*, 2020).

Among the adaptability characteristics of quinoa are its resistance to drought, waterlogging, reduce nutrient availability, radiation changes, edaphic salinity, temperature fluctuations and pests and diseases (García-Parra *et al.*, 2020). That resistance may be due to this plant presents C3 photosynthetic metabolism and genetic rusticity associated with considerable phenotypic plasticity, which allows it to adapt to adverse climatic and edaphic conditions, through modifications in its tissues, organs, productive cycles and therefore, in the physiological and biochemical routes (Becker *et al.*, 2017; Bunce, 2018). However, as other plant species, the quinoa has a range of agroclimatic conditions in which this species develops better, and within this range, an optimal point where, along with its genetic patterns, the best growth and development is attained (Pérez-Bueno *et al.*, 2019).

Outside its optimal range, the stress conditions modify the main physiological activities of plants, mainly their gas exchange through the stomata, which is reflected in the activity of photosystem II (FSII) (Chen, Burke and Xin, 2018). The disturbance of FSII generates reactive oxygen species (ROS), through the accumulation of free radicals in the thylakoid membrane (Kalaji *et al.*, 2014). To avoid the over-excitation of the FSII under conditions of biotic or abiotic stress and the consequent damage of the photosynthetic machinery, part of the energy captured by the reaction centres of the photosystems (photosynthetic pigments) does not take the photochemical pathway, but follows different pathways such as the dissipation of energy in the form of heat and that emitted as light energy through fluorescence. These events occur simultaneously and lead to a decrease in the efficiency of the other two processes (Chen *et al.*, 2018; Maxwell and Johnson, 2000).

The reason to study the fluorescence of chlorophyll is evaluate the function of FSII, mainly during the transport of electrons in the photosynthetic machinery, as well as identify the sensitivity of plants to an external factor through the analysis of the changes in the emission of the red fluorescence of chlorophyll α after subjecting dark adapted plants to lighting, as reported by Kautsky and Hirsch (1931). This methodology has allowed to estimate the photochemical efficiency and thermal dissipation of the photosynthetic reaction centers, becoming an ecophysiological evaluation tool used in cultivable plants such as rice (*Oryza sativa*), wheat (*Triticum aestivum*), corn (*Zea mays*) and pseudo-cereals such as amaranth (*Amaranthus sp.*) (Bermúdez-Cardona *et al.*, 2014; Wu *et al.*, 2015; Jamalluddin *et al.*, 2018; Tsai *et al.*, 2019). Since then, this technique has been widely used to study the physiological performance of plants, and no research on photosynthesis activity seems complete without chlorophyll fluorescence information (Pérez-Bueno *et al.*, 2019). Thus, this high sensitivity variable allows us to provide information about the interaction between plants and stress-generating environmental factors.

Quinoa has been recognized for its adaptability to extreme agroclimatic conditions (Hinojosa *et al.*, 2018), however, the cultivation of this species outside its environmental range leads to the affectation of the FSII and may favour changes in the fluorescence activity (Murphy and Matanguihan, 2015; Eustis *et al.*, 2020). This study aims to compile existing research information about the fluorescence of chlorophyll as an indicator of stress in quinoa, addressing possible threats to this crop such as water stress, waterlogging, nutritional deficit, salinity, radiation and heat.

Chlorophyll Fluorescence (F-Clo)

The F-Clo corresponds to the spectrum of light between 680 and 720 nm, emitted by chlorophyll α . F-Clo is used to diagnose the physiological state and photosynthetic activity of the plant, allowing to evaluate adaptability responses or to recognize damage (Kalaji *et al.*, 2014). Thus, the plant responds to external factors through changes in the amount of electromagnetic energy that the photochemical pathway follows, by which it is dissipated in the form of heat or fluorescence, in such a way that when measuring the F-Clo it can be estimated the intrinsic activity of the other two processes (Guidi *et al.*, 2019).

The activation of routes to facilitate the adaptation of plants to different types of stress allow a higher efficiency in energy dissipation through the increase in the cooling capacity in the non-photochemical route,

without generating alterations in the maximum quantum efficiency of FSII (ratio between variable fluorescence and maximum fluorescence F_v / F_m). Additionally, when the stress level in plants rises considerably, permanent photoinhibition occurs in the F_v / F_m , while when stress is prolonged, the effects are reflected in the effective quantum yield of FSII (Φ_{FSII}) and photochemical dissipation (qP), which results in a reduction in the electron transport chain and functional detriment of FSII under severe conditions (Murata *et al.*, 2007; Sasi *et al.*, 2018) (Figure 1).

In this way, it is possible to measure fluorescence parameters qualitatively and quantitatively, through non-destructive methods (Maxwell and Johnson, 2000; Pérez-Bueno *et al.*, 2019) which are mostly based on light saturation pulses that excite the antennas of the FSII reaction centres, or on the analysis of images captured with the help of LED lamps or lasers, which estimate the activity of the fractions of fluorescence, allowing to evaluate the response to stress. This is of great interest for crops of alimentary importance, which are produced, in many cases, in areas with marginal conditions (Qin *et al.*, 2013; Zhou *et al.*, 2018; Song *et al.*, 2019; Xu *et al.*, 2020).

Several studies highlight the activity of the fluorescence of chlorophyll under various agri-environmental stress conditions in quinoa that lead to changes in photosynthetic activity (Table 1). However, the physiological versatility of this species is an advantage of productive, academic and scientific interest when compared with other cultivable species, and for which it is highlighted as a promising crop in the face of the effects of climate change (Ruiz *et al.*, 2014; Korres *et al.*, 2016).

The abiotic factors that have the greatest impact on quinoa plants are radiation, heat and nitrogen availability, which surely have an influence in the photosynthetic parameters of the crop under specific agroclimatic conditions (Table 1). Thus, identifying the appropriate cultivars that adapts to specific stress conditions is required when the diversity of biotic and abiotic factors that can affect the species individually or as a whole is uncertain (Hinojosa *et al.*, 2019) (Figure 1).

Table 1. Effect of influencing agroclimatic factors on the performance of chlorophyll fluorescence

Factor	Cultivar	F_v / F_m	Φ_{FSII}	qNP	Reference
Radiation	Control	-	0.82	0.73	Huaranca Reyes <i>et al.</i> (2018)
	60 min UV-B * 3 days	-	0.71	0.54	
Salinity and drought	Salinity (300 mm of salt)	-	0.77	0.25	Killi and Haworth (2017)
	Drought (30% of field capacity)	-	0.84	0.6	
	Control	-	0.86	0.7	
Salinity	300mm NaCl	'Titicaca'	0.8	-	Amjad <i>et al.</i> (2015)
	Control		0.81	-	
Heat	45 °C day	17GR	0.73	-	Eustis <i>et al.</i> (2020)
	Control		0.62	-	
	40 °C	QQ74	0.84	-	Hinojosa <i>et al.</i> (2019)
	Control		0.84	-	
Nitrogen	High nitrogen	Lighthouse	0.81	0.49	Bascañán-Godoy <i>et al.</i> (2018)
	Low nitrogen		0.76	0.3	
Irrigation	Irrigated	-	0.8	*	Hinojosa <i>et al.</i> (2019)
	Not irrigated	-	0.83	*	

*: variable over time

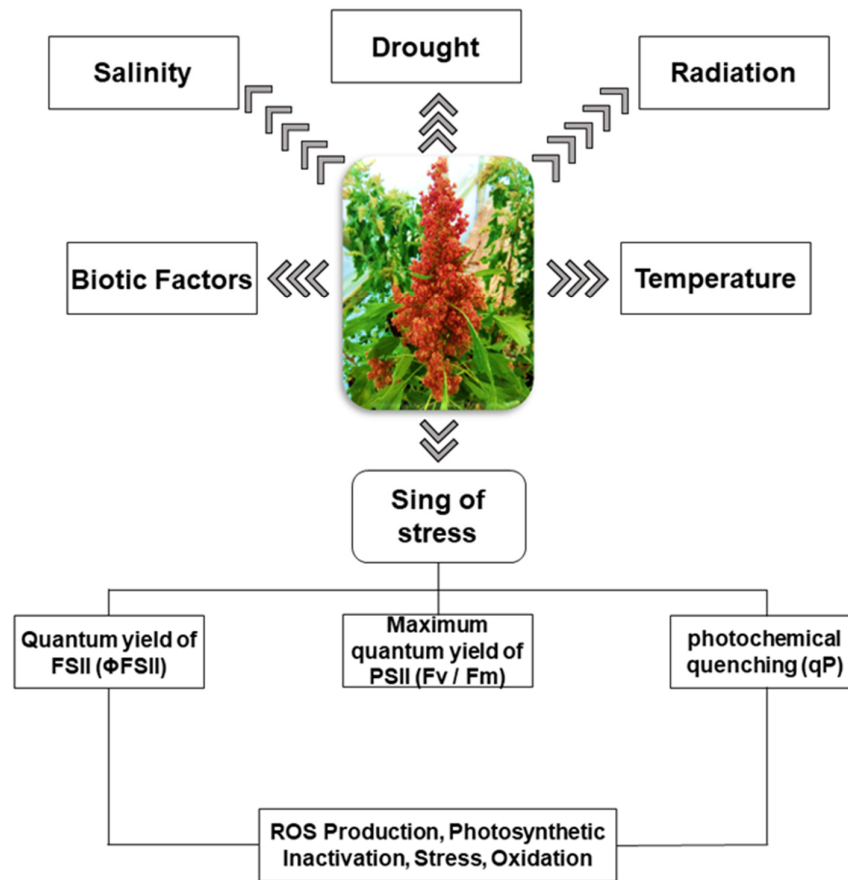


Figure 1. Photosynthetic response of quinoa plants to stress by salinity, drought, radiation, temperature and other biotic factors
Source: Authors.

Water Deficit Stress

Climate change is causing periods with extreme weather extremes in terms of temperature and water deficit (IPCC, 2018), especially in arid regions where quinoa is predominately cultivated, forcing to trust on the genetic diversity of this species to produce in such scenarios (Ruiz *et al.*, 2014). For this reason, quinoa is considered a drought-tolerant species, as it grows in arid regions with annual rainfall of less than 200 mm (Jacobsen *et al.*, 2006; Alcivar *et al.*, 2018). Its tolerance to drought is attributed to different morphological, physiological and biochemical traits achieved during its evolutionary process under adverse environmental conditions (Issa-Ali *et al.*, 2019). This hardiness makes quinoa a suitable species for cultivation in regions with extreme climatic conditions, where irrigation is not available and farmers depend only on seasonal rains.

It has been reported that the reduction in soil moisture leads quinoa to a decrease in the relative water content of the leaves, which causes the stomatal to close impacting the exchange of gases (González *et al.*, 2009). Therefore, it reduces the rate of photosynthesis, photorespiration, transpiration and absorption of nutrients, along with a decrease in the rate of consumption of ATP and NADPH for CO₂ assimilation. This affects the balance between photochemical activity in the FSII and the demand for electrons for photosynthesis, generating an over-excitation in the photosynthetic system and photo-inhibitory damage in the reaction centres (Fghire *et al.*, 2015; Killi and Haworth, 2017). In drought conditions, *in vivo* chlorophyll fluorescence analyses have provided extensive information on the structure and function of the photosynthetic machinery

(Hinojosa *et al.*, 2018), mainly about the photochemical phase of FSII, which is strongly influenced by water stress. An additional approach, based on the Bruno and Reto Strasser (JIP) light intensity analysis test in quinoa, has been developed that interprets to identify the fluorescence transit using the continuous excitation fluorometer (Yang *et al.*, 2016). This technique has been used to analyse the rapid transit chlorophyll, which reflects the behaviour of the primary photochemical activity (Kalaji *et al.*, 2014).

In some experiments in quinoa under controlled conditions, the indicators of the photosynthetic capacity of the leaf, such as the maximum quantum efficiency of FSII and the non-photochemical dissipation of chlorophyll α (qNP and NPQ) showed no sensibility to water stress (Winkel *et al.*, 2002; Killi & Haworth, 2017). Bosque-Sanchez *et al.* (2003), reported in the "Real" variety that the values of F_v / F_m and qP did not show significant differences in the drought stress treatments between -0.159 Mpa and -0.279 Mpa with respect to the irrigated plants, and in all the in cases, F_v / F_m values were higher than 0.812. Therefore, quinoa shows adaptation to drought conditions. However, these adaptability strategies result in a marked drop in grain yield. Also, Killi and Haworth (2017), found that the plants of the Red Head variety that were brought to germination under controlled conditions, and were subsequently subjected to agroclimatic conditions typical of the central region of Italy (Cesano Morderno) did not present differences in 16 chlorophyll fluorescence parameters (for example: F_v / F_m , Φ_{PSII} and NPQ) between the drought and control treatments. The same happened with variables such as the minimum fluorescence yield under adapted dark conditions (F_o), the quantum yield of energy dissipation (Φ_{Do}), the absorption of chlorophyll antennas per reaction center (ABS / RC) and the energy flux dissipated for each reaction center (DIo / RC).

Although the fluorescence of chlorophyll does not express the water stress in quinoa, other photosynthetic variables are sensible. However, studies have not yet been able to determine its effect on qP and QPN activity, and analyses have focused on other techniques such as proline quantification (Yaqoob *et al.*, 2019). In an experiment under greenhouse conditions and with different temperature levels, the Titicaca variety showed a reduction of the F_v / F_m mean value to 0.78 in response to the volumetric water content of the soil, corresponding to deficit irrigation and irrigation alternative (Yang *et al.*, 2016). Similar studies demonstrated a rapid recovery of young quinoa plants after a period of drought stress, finding a significant increase in F_v / F_m to 0.84, which suggests that quinoa maintains a high photochemical efficiency in despite the water deficit (Winkel *et al.*, 2002).

Other complementary studies to chlorophyll fluorescence would allow corroborate the effect of drought stress in quinoa, such as the OJIP test, which analyse the activity of the FSII, FSI and cytochrome b6f fraction. In the case of quinoa, it has made possible to identify the most sensitive parameters that describe drought stress, making it a tool to investigate differences in physiological behaviour at the most sensitive sites of action of the photosynthetic machinery. The results obtained by Fghire *et al.* (2015) during two successive seasons of cultivation of quinoa in Morocco, showed that stress induced changes in the OJIP test.

The OJIP parameter involved several sensitive sites of the FSII and FSI to drought stress. For example, in phenomenological fluxes per time excited cross section (CSm), electron transport (ET_0 / CSm) and energy trapping per cross section (TR_0 / CSm) were lower under drought stress than in the control. Likewise, the energy fluxes of the acceptor electron (Φ_{R_0}) and the quantum efficiency of the electron transport to plastokinase (Φ_{E_0}) and performance index (PI) of the FSII were lower under drought stress and were organized according to its decreased sensitivity to water deficit in the sequence $\Phi_{R_0} > \Phi_{E_0}$. Another very sensitive indicator of the physiological state of plants was the performance index (PI), which describes the conservation of energy between the photons absorbed by the FSII and the reduction of electron acceptors between systems. Finally, the study concluded that plants at the vegetative stage was more tolerant to drought stress than at growth stages.

There is not available a holistic analysis of the resistance of quinoa to drought since drought treatments have been established using different methodologies (volumetric and gravimetric humidity, soil water tension and crop evapotranspiration). Additionally, the genetic character of each cultivar or variety of quinoa has not been taken into account, which can significantly influence the ecophysiological response and adaptability to

drought (García-Parra *et al.*, 2020). Consequently, additional studies that include a greater number of genotypes and simultaneous measurements of a physiological, morphological and anatomy should be performed to allow obtaining a more complete knowledge of the response to drought, since the use of chlorophyll fluorescence as indicator variable of stress of water deficit is not enough and could generate inconclusive data to determine the effect of stress by another biotic or abiotic factor. More information can provide possible genotype selection routes within the great diversity that exists in order to maintain their photosynthetic function, exhibiting highly effective protective mechanisms to dissipate excess energy and neutralize oxidative stress. This would allow identifying cultivars with greater resistance to drought stress.

Waterlogging Stress

Despite that one of the main consequences of climate change is the increasing of droughts in some regions, the years in which the Southern Oscillation (El Niño / La Niña phenomenon) leads to floods affecting the agricultural production by favouring anoxic and hypoxic conditions in the soil (Ramirez-Villegas *et al.*, 2012), limiting the intake of nutrients, the release of exudates and in many cases, the interaction with microorganisms (Kim *et al.*, 2020). Thus, modifications in the amount of water in the soil of the quinoa crops, either by rain or irrigation, can generate effects of agronomic relevance such as alterations in the parameters of growth, development and production (García-Parra *et al.*, 2019).

Jacobsen *et al.* (2006) report that floods during rainy seasons in tropical quinoa crops cause a significant decrease in production. This, probably due to the low availability of O₂ in the root zone, the rot of roots and even the reduced photosynthetic activity in periods of high cloud cover, for example, when years of La Niña phenomenon occur in Colombia (Fajardo-Rojas, 2019). This climatic factor is of great relevance, since the restrictions in terms of light energy reduce the activity of the FSII, in addition to the energy losses due to heat or fluorescence, so the availability of chemical energy used in the fixation phase of CO₂ is significantly low compared to which occurring in plants under ideal agroclimatic conditions. Thus, there is an alteration of the photosynthetic machinery, the formation of reactive oxygen species and the denaturation of the protein complexes of the thylakoid membranes (Murata *et al.*, 2007).

A waterlogging experiment under controlled conditions had showed a decreases in the agronomic performance of quinoa, highlighting a reduction in the dry weight of foliage and roots, leaf area, leaf nitrogen, chlorophyll content α and β , as well as a significant increase in the content of starch and soluble protein (González *et al.*, 2009). Under field conditions, the 'BRS Piabiru' quinoa cultivar performed better in terms of plant height, development of basal area, stem weight and number of leaves when it was cultivated in a water regime of up to 563 mm during its productive cycle. However, under the 647 mm regime there was a considerable reduction in phenological variables, which indicates sensitivity of quinoa to waterlogging (Jayme-Oliveira *et al.*, 2017). The same results were obtained in Morocco, where high rainfall and low solar radiation generate problems in the growth of quinoa plants cultivar DO708, and favoured the presence of diseases and weeds (Hirich *et al.*, 2014). This can be attributed to the low absorption of nutrients due to waterlogging, which affects the transport of electrons in the FSII, favouring the dissipation of energy in the form of heat and fluorescence (Kalaji *et al.*, 2018). However, there are other factors associated to high rainfall that affect quinoa, especially during the milky grain phase and physiological maturity, since it favours accelerated germination of the seed in the inflorescence and its production loss (Romero *et al.*, 2018).

Previous studies had showed that the damage to the photosynthetic apparatus is reflected in the growth and development parameters. Also, as mentioned Wu *et al.* (2015), there are notable reductions in Fv / Fm, electron transport rate (ETR), Φ FSII and qP. It is important to recognize that there is very little research evaluating the effect of waterlogging on the quinoa crop. Given the changing effects of climate, it is necessary to recognize the incidence of this type of stress in the activity of the photosystem. This may favour the cultivation of this species in areas that are influenced by bodies of water at different times of the year.

Nutritional Deficiency Stress

An adequate and timely supply of nutrients facilitates the normal plant development. External factors that affect the capture of nutrients by the plant reduce the physiological and productive performance of crops. Various nutrients and micronutrients are involved in the success of plant biochemical and metabolic pathways (Marschner, 2012). Some micronutrients are required in the photosynthetic apparatus, being part of the O₂ evolution complex (Ca, Cl and Mn), which carries out the oxidation of water and the subsequent transport of electrons towards the cycle of the quinone, plastocyanin and ferredoxin; proteins that structurally contain Fe and Cu, and consequently, their absence would favour thermal dissipation and fluorescence (Belatik *et al.*, 2013). P is a fundamental component of energy activity and the consolidation of genetic chains, K as a regulator of stomatal activity and enzymatic synthesis, favouring energy functioning, finally Ca is as a fundamental element for structuring cell walls, as well as a metabolic signaller (Murphy and Matanguihan, 2015).

Nitrogen makes up the majority of the nutritional requirements of the plant (Fonseca-López *et al.*, 2020). Several studies indicate that stress due to low availability N in quinoa variety UdeC9 before the senescence phase generates changes in FSII activity, mainly in Φ PSII, Fv / Fm, NPQ and damage to the photosynthetic apparatus (Bascuñán-Godoy *et al.*, 2018). This damage is attributed to Fo and Fm, which could be highly sensitive in response to the change in the content of chlorophyll *a* between the beginning of flowering and proximity to senescence. These variables are indicators of stress in plants of alimentary interest, such as rice (*Oryza sativa*), corn (*Zea mays*), wheat (*Triticum*) and barley (*Hordeum vulgare*) (Huang *et al.*, 2004; Jin *et al.*, 2015; Wang *et al.*, 2016; Carstensen *et al.*, 2018; Tränkner *et al.*, 2018). However, no information is available to explain the availability and absorption of elements in quinoa plants and their relationship with photosynthetic activity. This makes difficult to recognize the particular function of each element, even more when fertilization plays a decisive role in crop management (García-Parra *et al.*, 2019).

Salinity Stress

Among the causes of salty soils are the characteristics of the parental material of the soil, the presence of saline water bodies, volcanic emanations, and wrong agronomic practices that give rise to the accumulation of chlorides, sulfates, nitrates and carbonates (Machado and Serralheiro, 2017). Salty accumulation in the soil decreases the photosynthetic potential through the alteration of the osmotic balance of cells, stomatal closure, nutrient uptake, and the increase of ROS production, which can be the main cause of oxidative damage to proteins, lipids and DNA.

Quinoa is a facultative halophyte species, an aspect that has been validated through different and highly variable physiological responses among the quinoa genotypes studied. Thus, plants can tolerate electrical conductivity levels from 15 dS.m⁻¹ up to 75 dS.m⁻¹ (Bosque-Sanchez *et al.*, 2003; Hinojosa, 2018; Yan *et al.*, 2020). Salinity significantly affects the tissues and cells of quinoa, and with it, the activity developed in the chloroplasts. This is how in the thylakoid membrane, where the photochemical phase of photosynthesis takes place, important variations have been identified due to the effect of salinity, changes in the photosynthetic rate, transpiration rate, efficiency of the use of photosynthetic water and in the fluorescence activity of chlorophyll (Bosque-Sanchez *et al.*, 2003; Eisa *et al.*, 2012). These alterations have also been reported in rapeseed (*Brassica napus*), lettuce (*Lactuca sativa*), barley (*Hordeum vulgare*), curuba (*Passiflora tripartita*) and quinoa (*Chenopodium quinoa*) (Belkhodja *et al.*, 1994; Bacarin *et al.*, 2012; Casierra-Posada *et al.*, 2013; Adhikari *et al.*, 2019; Cai & Gao, 2020).

Killi and Haworth (2017) recognized that NaCl contents higher than 300 mM significantly affected Fv / Fm, Φ PSII, qNP and NPQ as well as OJIP in the Red head quinoa variety, which was attributed to the damage of the pigment-protein complex in the thylakoid membrane. However, several studies recognized that these variables were not significantly affected by soil salinity in quinoa cultivars such as 'Titicaca', 'Pasankalla',

'Puno' and 'Amarilla marangani' (Hariadi *et al.*, 2011; Adolf *et al.*, 2012; Shabala *et al.*, 2013; Bonales-Alatorre *et al.*, 2013).

Radiation Stress (UV-B)

Solar radiation is one of the main environmental factors that determines the existence and predominance of most plant species since it regulates activities such as growth, development, photosynthesis, photoperiod and even the effect of other environmental factors such as temperature and humidity. The radiation that reaches the earth comprises a range of electromagnetic spectra of violet, blue, green, yellow, orange and red colours that cover wavelengths between 400 and 700 nm (Photosynthetic Active Radiation (PAR), Carrasco-Ríos, 2009).

The anthropic effect and the changes in biogeochemical cycles have generated the deterioration of the ozone layer during the last decades, and with it, a higher incidence of electromagnetic radiation ranging between 280 and 1000nm. UV-C (200 and 280 nm) directly affects the genetic structure of organisms. UV-A radiation (330 and 400 nm) has been found that it is poorly absorbed by O₃, implying a high biological risk. Finally, UV-B radiation (280 and 320 nm) cause alterations in biomolecules such as proteins, nucleic acids and lipids, thus generating effects in tissues that are manifested as morphophysiological modifications in plants (Mandi, 2017). When the UV-B radiation penetrates in the interior of the leaf and is absorbed by the chromophore there is a damage in the FSII, due to it generates alterations in the Mn⁴Ca cluster through an elongation in atomic distances due to the reduction of Mn, causing the destruction of the metalloprotein group present in the photosystem and production of ROS (Yano and Yachandra, 2014).

UV-B radiation affects the activity of FSII in quinoa. A significant decrease in Φ PSII and Fv / Fm had been reported in plants of the Real variety exposed to UV-B radiation, as well as a strong damage in the leaves (Huaranca Reyes *et al.*, 2018). These results were also presented in the cultivar Sajama, which also presented a significant reduction in chlorophyll contents (α and β) and alternation in the photosynthetic system (Hilal *et al.*, 2004). A reduced solar radiation also affects the photosynthetic activity, since it is not possible to excite the accessory pigments of the reaction centres of the FS and consequently, the reduction of chlorophyll molecule does not lose the electron and there is an inactivity process in the photochemical chain (Furbank *et al.*, 2020).

Hinojosa *et al.* (2018) reported that the UV-B radiation generated a negative effect on chlorophyll fluorescence, pigment synthesis, ROS accumulation and consequently on performance, as well as on the agroclimatic adaptability of quinoa. However, they highlighted the importance of determining the maximum UV-B thresholds that limit the behaviour of quinoa, as well as its influence on other agri-environmental variables.

Heat Stress

Due to climate change, studies focused on the effect of thermal variations on the physiological and productive performance of quinoa has increased (Ruiz *et al.*, 2014; Bazile *et al.*, 2016). The effect of heat stress is determined by a significant increase in the maximum temperature threshold on plants, causing damage and limitations in growth and development, as a result of the denaturation of proteins and the increase in the fluidity of the membranes (Garcia-Parra *et al.*, 2020) (Figure 2).

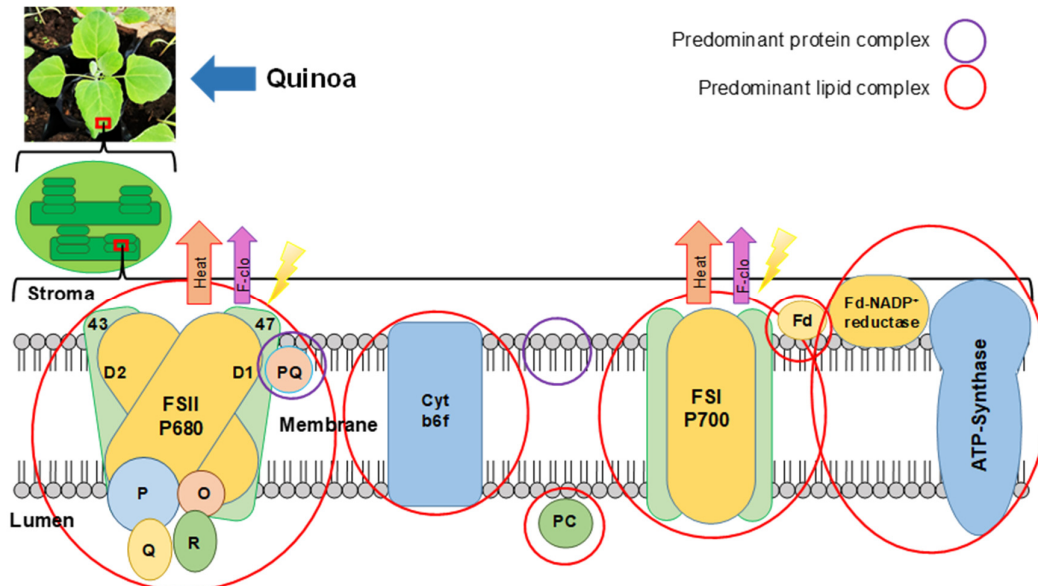


Figure 2. Photosynthetic apparatus and machinery composition
PQ: Plastoquinone, PC: Plastocyanin, Fd: Ferredoxin; Source: Authors.

The Figure 2 schematizes the composition of the photosynthetic apparatus in quinoa leaves, from the thylakoid membrane to the protein and lipid complexes that are affected by heat stress. Wahid *et al.* (2007) reported that the increase in temperatures favours the dissipation of energy in the form of heat and fluorescence, inducing the production of ROS, to the detriment of the stability of the membranes and even affecting the enzymatic reactions, mainly the RuBisCO.

In this sense, Eustis *et al.* (2020), found that the heat stress tolerance capacity in quinoa changes depending on the cultivar, and tolerance levels stand out up to 45 °C when the plants are not affected by other types of stress. Thus, the increase in heat is largely related to the photosynthetic rate, stomatal conductance, and Fv / Fm, and inversely related to the intrinsic activity of water and nocturnal respiration (behaviours that were more marked in cultivars such as 'Kaslaea'). The results of heat adaptability in different quinoa cultivars were reported by Hinojosa *et al.* (2019), who did not find significant differences in Fv / Fm in cultivars such as 17GR and QQ74, but did find a significant effect on grain production.

Garcia-Parra *et al.* (2020) established the physiological criteria for the selection of heat-tolerant quinoa cultivars. The following parameters should be taken into account: (a) tolerance to cell damage, (b) photosynthetic activity and stomatal conductance, (c) chlorophyll fluorescence, mainly Fv / Fm and (d) activity of RuBisCO, factors that according to the authors could vary significantly in quinoa plants under desirable conditions, thanks to C3 metabolism.

Conclusions

F-Clo can be widely used to assess the stress level in quinoa plants, which makes it an important tool for obtaining information about the effect that abiotic factors such as radiation, water deficit, low nitrogen availability and heat. Salinity is not recognized as a factor that decisively affects chlorophyll fluorescence variables; however, it is considered a secondary factor that conditions other factors that limit the normal physiological activity of this species. F-Clo has been recently evaluated as physiological parameter in quinoa, making difficult to evaluate the effects that waterlogging, salinity, and even some other biotic factors have on quinoa, and thus present a complete view of the limiting factors of this crop.

Authors' Contributions

All authors read and approved the final manuscript.

Acknowledgements

The authors express gratitude to Minciencias (Ministerio de Ciencia, Tecnología e Innovación) invitation for bid Nr. 779/2017. We are also grateful with the Boyacá Department Government, Cauca University and project CIUC-01- 2018 carried out by the AOF-JDC.

Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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