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MAGNA PEREIRA DOS SANTOS

ALTO SUPRIMENTO DE NITRATO ATENUA EFEITOS ADVERSOS DA SALINIDADE EM MUDAS DE CAJUEIRO

FORTALEZA
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Dissertação apresentada ao Programa de Pós-Graduação em Ciência do Solo da Universidade Federal do Ceará, como requisito parcial à obtenção do título de Mestre em Ciência do Solo. Área de concentração: Química, fertilidade e biologia do solo.

Orientador: Prof. Dr. Joaquim Albenisio Gomes da Silveira.
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A Deus.

Aos meus pais José e Maria Rita.

Aos meus irmãos João, Paulo, Amanda e Mikaele.

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Ao professor Joaquim Albenísio.

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RESUMO

O cajueiro (*Anacardium occidentale* L.) é uma espécie originária da região Nordeste do Brasil. Apesar de sua grande importância socioeconômica, essa cultura enfrenta uma série de desafios ambientais como alta luz, altas temperaturas, escassez hídrica e excesso de sais no solo, decorrente das condições edafoclimáticas da região. Testamos a hipótese de que a alta oferta de NO_3^- atenua os efeitos adversos causados pelo excesso de Na^+ e Cl^- na eficiência fotossintética por meio da estimulação de drenos de elétrons alternativos à assimilação de nitrato. O experimento foi conduzido em delineamento inteiramente casualizado em esquema fatorial (2x2), em que plântulas de caju (espécie adaptada ao baixo teor de nitrato e salinidade do solo em regiões semiáridas) foram expostas a alta salinidade (0 e 100 mM de NaCl) na presença de dois níveis contrastantes de NO_3^-, 0,1 mM (baixo) e 10,0 mM (alto), por 35 dias em condições de casa de vegetação. O alto fornecimento de nitrato estimulou a expansão foliar e diminuiu o comprimento das raízes na ausência de salinidade, mas não afetou essas variáveis sob estresse salino. O alto teor de nitrato foi capaz de reduzir danos à membrana associados ao menor acúmulo de Na^+ e Cl^- e menor relação Na^+/K^+ em folhas sob estresse salino. O alto teor de nitrato não afetou as taxas de transporte de elétrons fotossintéticos, enquanto a limitação do lado aceitador PSI diminuiu sob estresse salino. As taxas de assimilação de CO_2 não mudaram devido ao efeito dos níveis de nitrato. Em contraste, as taxas de fotorrespiração foram aumentadas por níveis elevados de nitrato na ausência de salinidade, enquanto, independentemente dos níveis de nitrato, a salinidade induziu um aumento proeminente nas taxas de fotorrespiração. Curiosamente, quando a fotorrespiração foi abolida artificialmente ou intensamente diminuída pela eliminação de O_2, níveis elevados de NO_3^- induziram grandes aumentos em V_{cmax}, J_{max} e P_{Nmax} em plantas sob estresse salino. A elevada oferta de NO_3^- é capaz de mitigar alguns efeitos adversos da salinidade nas plântulas de cajueiro. A fotorrespiração é a maior alternativa de dreno de elétrons em comparação ao uso de nitrato, o que poderia ser mais importante em situações de baixa fotorrespiração.

Palavras-chave: *Anacardium occidental* L.; fotorrespiração; fotossínteses; salinidade.

ABSTRACT

The cashew tree (*Anacardium occidentale* L.) is a species native to the Northeast region of Brazil. Despite its great socioeconomic importance, this crop faces a series of environmental challenges such as high light, high temperatures, water scarcity and excess salts in the soil, resulting from the region's edaphoclimatic conditions. We tested the hypothesis that high NO_3^- supply might attenuate adverse effects caused by excess of Na^+ and Cl^- on the photosynthetic efficiency by stimulation of alternative electron sinks to nitrate assimilation. The experiment was conducted in a completely randomized design in a factorial scheme (2x2), in which cashew plantlets (species adapted to low soil nitrate and salinity in semiarid regions) were exposed to high salinity (NaCl 0 and 100 mM) in the presence of two contrasting NO_3^- levels, 0.1 mM (low) and 10.0 mM (high), for 35 days in greenhouse conditions. High nitrate supply stimulated leaf expansion and decreased root length in the absence of salinity, but did not affect these variables under saline stress. The high nitrate was able to reduce membrane damage associated with lower Na^+ and Cl^- accumulation and lower Na^+/K^+ ratios in leaves under saline stress. High nitrate content did not affect photosynthetic electron transport rates, while PSI acceptor side limitation decreased under salt stress. CO_2 assimilation rates did not change due to the effect of nitrate levels. In contrast, photorespiration rates were increased by high nitrate in the absence of salinity, whereas, regardless of nitrate levels, salinity induced a prominent increase in photorespiration rates. Interestingly, when photorespiration was artificially abolished or intensely decreased by O_2 scavenging, high NO_3^- induced large increases in V_{cmax}, J_{max} and P_{Nmax} in salt stressed plants. The high supply of NO_3^- is capable of mitigating some adverse effects of salinity on cashew plantlets. The photorespiration is the largest alternative electron sink compared to the use of nitrate, which could be more important in situations of low photorespiration.

Keywords: *Anacardium occidental* L.; photorespiration; photosynthesis; salinity.

LISTA DE FIGURAS

LISTA DE ABREVIATURAS E SIGLAS

A	Taxa líquida de assimilação de CO_2
E	Transpiração
ETRI	Taxa de transporte de elétrons do PSI
ETRII	Taxa de transporte de elétrons do PSII
ETR/P_N	Taxa de transporte de elétrons do PSII/razão líquida de fotossíntese
EROS	Espécies reativas de oxigênio
F_o	Rendimento de fluorescência basal
Fm	Rendimento máximo de fluorescência
Fv/Fm	Rendimento quântico potencial do PSII
g_s	Condutância estomática
GS	Sintetase da glutamina
GOGAT	Glutamina-oxoglutarato aminotransferase
LN	Baixo suprimento de nitrato
HN	Alto suprimento de nitrato
J_c	Taxa de fluxo de elétrons para carboxilação da rubisco
J_{max}	Fluxo máximo de elétrons para regeneração da RuBP
J_o	Taxa de fluxo de elétrons para oxigenação Rubisco
NRTs	Transportadores de nitrato
PPFD	Densidade de fluxo de fótons fotossintéticos
P_N	Razão líquida de fotossíntese
P_r	Taxa de fotorrespiração
PSI	Fotossistema I
PSII	Fotossistema II
RD	Respiração no escuro
V_{cmax}	Atividade máxima de carboxilação da Rubisco
WUE	Eficiência do uso da água
Y(NA)	Limitação do lado aceitador do PSI
Y(ND)	Limitação do lado doador do PSI
Y(I)	Rendimento quântico efetivo do PSI
Y(II)	Rendimento quântico efetivo do PSII

SUMÁRIO

1 INTRODUÇÃO

O cajueiro (*Anacardium occidentale* L.) é uma espécie amplamente cultivada na região Nordeste do Brasil, onde desempenha um papel vital na economia agrícola, sendo uma fonte significativa de renda para agricultores como uma cultura de grande importância socioeconômica. Considerada uma das mais importantes espécies cultivadas das regiões tropicais no mundo, o cajueiro ocupa uma área de aproximadamente 3,4 milhões de hectares com uma produção estimada de 3,7 milhões de toneladas de castanha em 2020, destacando-se o a Índia, Costa do Marfim e o Vietnã como principais países produtores mundiais. O Brasil é o sexto maior produtor mundial, com área plantada de 439,2 mil hectares e a produção atingiu 149 mil toneladas de castanhas, tendo como maiores produtores os estados do Ceará, Rio Grande do Norte e Piauí.

Apesar de sua importância, as plantas de cajueiro enfrentam uma série de desafios ambientais, decorrente das condições edafoclimáticas da região. O aumento da salinidade do solo representa uma ameaça substancial a sustentabilidade dessa cultura. O estresse salino, proveniente da salinização do solo, ou da água, compromete o desenvolvimento saudável das plantas de cajueiro, afetando diretamente a produtividade e qualidade dos produtos, pode afetar diretamente a absorção de água e nutrientes. O cajueiro, como muitas outras espécies vegetais, está sujeito a esse fenômeno, que pode ser causado por fatores naturais, como climas secos com baixas precipitações, alta taxa de evaporação e má drenagem ou por práticas agrícolas, incluindo o uso de água salobra na irrigação de pomares e uso excessivo de fertilizantes ricos em sais. A compreensão dos mecanismos pelos quais as plantas de cajueiro respondem ao estresse salino torna-se fundamental para desenvolver estratégias eficazes de manejo. Nesse contexto, destaca-se a importância de compreender os impactos do estresse salino, bem como as respostas adaptativas a condições salinas das plantas de cajueiro.

Aumentar a disponibilidade de N nos solos através da utilização de fertilizantes pode melhorar a produtividade das culturas e mitigar alguns fatores estressantes (Albassam 2001). O nitrato é frequentemente a principal fonte de nitrogênio no solo agrícola, e a absorção e assimilação de nitrogênio são fortemente afetadas pela salinidade (Silveira et al. 2001). Diante do exposto hipotetizamos que uma alta oferta de N-NO_3^- é capaz de aliviar os efeitos danosos da salinidade no crescimento através da estimulação da assimilação de N-NO_3^-. O processo de assimilação de nitrogênio é um forte consumidor de energia atuando como um dreno da cadeia fotossintética de transporte de elétrons diminuindo a redução excessiva na membrana dos tilacóides de folhas de *A. occidentale*.

2 OBJETIVOS

2.1 Objetivo geral

O objetivo do presente trabalho é avaliar como o aumento da assimilação de N-NO_3^- pode atenuar efeitos nocivos da salinidade pelo consumo do excesso de energia na membrana dos tilacóides em plantas de *A. occidentale* L.

2.2 Objetivos específicos

- Avaliar os efeitos do alto suprimento de nitrato nas trocas gasosas de plantas de cajueiro quando expostas as condições de alta salinidade;

- Avaliar a evolução fotorespiratória como mecanismo para minimizar ou evitar o fotodano;

- Avaliar a fluorescência da clorofila a

- Avaliar indicadores de estresses fisiológicos (área foliar e comprimento da raiz principal);

- Avaliar indicadores de estrasse iônico (vazamento de eletrólitos, conteúdos de Na^+, K^+, Cl^- e relação Na^+/K^+) em folhas de plantas de cajueiro;

- Determinar o conteúdo de nitrogênio total e nitrato em folhas de plantas de cajueiro.

3 REVISÃO DE LITERATURA

3.1 Cajueiro e sua importância econômica

O cajueiro (*A. occidentale* L.) é classificado botanicamente como membro da família Anacardiaceae, que é composta por cerca de 60 a 74 gêneros e 400 a 600 espécies (Bezerra et al., 2007). É uma planta típica de clima tropical, originária do Brasil, mais especificamente do litoral nordestino. No Brasil os tipos de cajueiros mais difundidos são o comum (*A. occidentale* L.) e o cajueiro anão precoce *(A. occidentale* var. nanum). O cajueiro comum e mais predominante no Nordeste e ocorre de forma natural sem necessidade de plantio.

O caju é constituído pelo pedúnculo floral ou pseudofruto e pelo fruto verdadeiro, também chamado de castanha. O pseudofruto tem um crescimento lento, em relação ao fruto, atingindo o tamanho máximo somente perto da completa maturação, devido à grande variação da relação peso do fruto/peso do pseudofruto (Arruda, 2023). O pseudofruto representa a parte suculenta e carnoso, podendo apresentar cores que variam do amarelo ao vermelho, seu crescimento e amadurecimento ocorre entre 56 e 60 dias após à emissão do fruto (Sousa et al., 2021).

O cajueiro é uma cultura com grandes perspectivas econômicas no mercado internacional e participa de forma expressiva na atividade socioeconômica do semiárido, destacando-se como uma importante opção na geração de emprego e renda (Muianga et al., 2016; Silva et al., 2018; lima et al., 2020b). O Brasil é um dos principais produtores de castanha de caju do mundo, com uma produção de 111.103 toneladas em 427.144 hectares (Arruda et al., 2023). A produção de castanha de caju no Brasil foi de aproximadamente 110.5 mil toneladas em 2021, e 146.6 mil toneladas em 2022 (IBEGE, 2022). Em 2022 os principais estados produtores são Ceará (95.7 mil t), Piauí (21.6 mil t) e Rio Grande do Norte (18.1 mil t).

A cajucultura é direcionada para a produção de castanha e do seu pseudofruto, além do consumo in natura (Bezerra et al., 2007; Lima et al., 2020a; Sousa et al., 2023). A amêndoa do caju é o principal e mais importante produto comercial do cajueiro devido ao seu auto valor agregado (Rossetti et al., 2020). A venda das amêndoas é umas das principais atividades da agricultura familiar local. O pseudofruto (pedúnculo), mesmo representando a maior parte do caju (90%), é o produto com menor seguimento industrial, representando 12% a 15% do aproveitamento total, seu processamento é destinado principalmente para a indústria de sucos, polpas e consumo in natura (Maia et al., 2000; Paiva et al., 2000; Figueiredo et al., 2010). O caju apresenta alto valor nutritivo na forma de vitaminas, taninos, sais minerais e ácidos orgânicos, apresentando também cálcio, ferro e fósforo, entre outros (Lima et al., 2007).

3.2 Salinidade

3.2.1 Salinidade no solo

Em todo o mundo, a salinidade do solo é considerada um dos principais fatores ambientais restritivos; limita severamente a eficiência do uso da terra, prejudica o crescimento e desenvolvimento das plantas e limita a produtividade das culturas, especialmente em regiões áridas e semiáridas (Delang, 2018; Parihar et al., 2015; Schroeder et al., 2013; Zhu, 2016).

Como as águas disponíveis para irrigação nestas regiões nem sempre são de boa qualidade, estas áreas estão sujeitas à utilização de água salobra como alternativa para irrigação, principalmente com a expansão das áreas irrigadas (Veloso et al., 2023). Consequentemente, o uso de águas salinas representa um desafio constante, e tem sido considerado uma restrição severa à produtividade agrícola (Nadeem et al., 2019). Caracterizando um problema que atinge a economia, a sociedade e o ambiente (Medeiros et al., 2012; Nascimento et al., 2017).

A à alta concentração de sais resulta na salinização do solo de extensas áreas, além de comprometer o desenvolvimento das culturas (Alencar et al., 2021). No solo os sais se acumulam nas camadas superficiais afetando a dinâmica de organização espacial das populações, resultando em perdas da cobertura vegetal e redução da produção agrícola (Castro & Santos, 2020). Além dos efeitos sob as plantas, a elevada concentração de sais causa sérios problemas físicos no solo, podendo levar a salinização e perda de extensas áreas produtivas.

3.2.2 Efeito dos sais nas plantas

A salinidade é um dos principais estresses abióticos que afetam o crescimento das plantas e a produtividade das culturas, ocorrendo principalmente em regiões áridas e semiáridas, onde o teor de sal no solo é naturalmente alto e as chuvas podem ser insuficientes para lixiviar o excesso de sal (Taiz et al., 2015). A salinização do solo inibe o crescimento das plantas, o rendimento e a qualidade do produto (Yang e Guo, 2018). Sendo considerado um dos estresses abióticos mais significativos na agricultura.

O estresse salino restringe o crescimento das plantas por meio do estresse osmótico e da toxicidade iônica. O primeiro é desencadeado pela redução da absorção de água mediada pelas raízes devido à alta pressão osmótica (Acosta-Motos et al., 2017; Zhu, 2002) afetando o potencial hídrico entre o solo e a planta (Alencar et al., 2015, Praxedes et al., 2010).

Os principais componentes do estresse salino nas plantas são o estresse osmótico, o estresse iônico e de forma secundaria a superacumulação de ROS (Parihar et al., 2015; Morton et al., 2019). O estresse osmótico é o primeiro estresse experimentado quando uma planta é exposta a solo salino e afeta instantaneamente o crescimento da planta (Horie et al., 2011). O efeito osmótico é imediato devido à diferença de potencial osmótico entre os ambientes externo e interno da célula, enquanto o efeito iônico ocorre mais tarde quando a concentração de Na^+ e/ ou Cl^- atinge níveis tóxicos no citosol (Shavrukov, 2013), acima do qual a planta não consegue manter a homeostase iônica e o crescimento (Munns e Tester 2008).

A salinidade elevada reduz o potencial hídrico ao redor das raízes das plantas, limitando a absorção de água (Negrão et al., 2017). O excesso de Na^+ na corrente de transpiração exacerba a toxicidade iônica e prejudica a homeostase dos íons foliares, afetando ainda mais o crescimento das plantas (Gao et al., 2022). A acumulação excessiva de sódio e cloreto nas plantas dificulta a absorção eficiente de elementos como Ca^{2+}, resultando na falta de nutrientes essenciais nas plantas (Li et al., 2022; Zhu, 2002; Zhang et al., 2017; Wu, 2018; Li et al., 2021). A toxicidade iônica causada pelo estresse de salinidade resulta do aumento de Na^+/K^+, Na^+/Ca^{+2}, Na^+/Mg^{+2} e Cl^-/NO_3^- no tecido vegetal, causando distúrbios celulares relacionados à função fisiológica desses nutrientes essenciais (Zhu 2003; Praxedes et al., 2010; Abbaspour et al., 2014; Bessa et al., 2017). Altas concentrações de íons principalmente Na^+ e Cl^- na região radicular das plantas inibe a absorção de K^+ e Ca^{+2}, pois o Na^+ compete com K^+ e Ca^{+2} pelos sítios de absorção na membrana celular, causando distúrbios nutricionais (Silva et al., 2022).

O K^+ é um macronutriente que participa de diversas funções celulares, atuando no potencial osmótico como osmossoluto nas células guardas e no funcionamento de vias metabólicas devido ao seu papel como cofator enzimático (Wang e Wu, 2013).

Uma relação K^+/Na^+ mais baixa em resposta ao sal está associada a outros distúrbios metabólicos, como limitação fotossintética e dano fotooxidativo (Rodrigues et al., 2013**).** A salinidade afeta o processo de absorção ao restringir o acúmulo de K^+ em diferentes partes das plantas, uma resposta que já observada em cajueiros (Ferreira-Silva et al., 2009).

A toxicidade iônica e o estresse osmótico são estresses primários que podem causar estresse oxidativo e uma série de estresses secundários (Liang et al., 2018). O estresse oxidativo induzido pelo acúmulo de espécies reativas de oxigênio (EROS) nas plantas que afeta negativamente a estrutura de enzimas, ácidos nucleicos e lipídios (Li et al., 2022), limita as trocas gasosas, danifica a integridade celular e a estrutura da clorofila afetando negativamente o crescimento e o desenvolvimento das culturas (Liang et al., 2018). No entanto, a resposta das plantas ao estresse salino depende da espécie e/ou clone, do estágio de desenvolvimento do mesmo genótipo, da intensidade e duração do estresse e das condições edafoclimáticas da região (Munns e Tester, 2008). A salinidade afeta o crescimento e desenvolvimento do caju, mas a espécie é moderadamente tolerante ao estresse salino (Ferreira-Silva et al., 2010).

3.2.3 Mecanismo de tolerância a salinidade

As plantas desenvolvem estratégias fisiológicas e bioquímicas para lidar com o estresse (Pastori e Foyer 2002). Alguns dos principais mecanismos de tolerância ao estresse salino são, o controle da absorção de íons tóxicos (Na^+ e/ou Cl^- em excesso) pelas raízes, o transporte e sua distribuição pela planta, bem como a capacidade de compartimentá-los no vacúolo (Ashraf e Harris, 2004; Liang et al., 2018).

A alta salinidade causa toxicidade iônica nas células vegetais por meio de um grande influxo de Na^+, podendo resultar em desequilíbrio iônico intracelular (Liang et al., 2018). O excesso de Na^+ se torna tóxico devido aos seus efeitos adversos na nutrição do K^+, nas atividades enzimáticas citosólicas, na fotossíntese e no metabolismo (Flowers, 2004; Zhu, 2001). A capacidade seletiva das plantas, de compartimentalizar os excessos de Na^+, e de manter uma alta proporção de K^+/Na^+ no citosol são alguns dos principais determinantes da tolerância ao sal (Maathuis e Amtmann, 1999).

A resposta ao estresse osmótico envolve principalmente ajustes nas concentrações de solutos (Ashraf e Harris, 2004, Liang et al., 2017; Liang et al., 2018). O ajuste osmótico é crítico para manter o turgor celular, o que permite a manutenção da atividade metabólica e, por sua vez, o crescimento e a produtividade das plantas (Sharp et al., 1990). As plantas sintetizam solutos orgânicos (prolina, N-amino solúvel, açúcares solúveis) glicina, betaína e outros osmólitos no citosol para promover o equilíbrio osmótico no nível celular (Kishor et al., 1995; Taji et al., 2002; Ashraf e Harris 2004, Liang et al., 2018).

Além dos efeitos sobre o estado da água e homeostase iônica da célula vegetal, a salinidade pode originar secundariamente o estresse oxidativo resultante do aumento da concentração de espécies reativas de oxigênio (EROs) (Miller et al., 2010, Gadelha et al., 2017). Para sobreviver a essas condições desfavoráveis, as plantas desenvolvem diferentes estratégias de tolerância ao estresse salino através da eliminação dessas EROs, para aliviar os danos causados pelo estresse em processos que envolvem mensageiros secundários como Ca^{2+}, H_2O_2, H_2S e NO (Fancy et al., 2017; Petrov et al., 2015; Zhu, 2002). A produção de EROs é uma alteração metabólica comum induzida pelos estresses salino, hídrico e de alta temperatura, e a proteção oxidativa na célula vegetal ocorre por mecanismos antioxidantes aparentemente comuns para esses diferentes estresses (Mittler, 2002; Gondim et al., 2012).

A produção do radical superóxido ($O2^{\bullet-}$) pode ocorrer em qualquer sítio celular que possui cadeia de transporte de elétrons, como as mitocôndrias e os cloroplastos, e onde ocorrem reações redox, como os microssomos, glioxissomos, peroxissomos, apoplasto e citosol (Foyer e Noctor, 2005). Na célula, as enzimas antioxidativas dismutases do superóxido (SODs), são responsáveis pela dismutação do $O_2^{\bullet-}$ para H_2O_2 e O_2, sendo consideradas a primeira linha de defesa antioxidante enzimática (Silva, 2009). As enzimas peroxidases do ascorbato (APXs) compõem uma família de isoenzimas localizadas em diversos sítios celulares, como citosol, cloroplastos, mitocôndrias, peroxissomos e glioxissomos (Shigeoka et al., 2002). Todas as APXs utilizam o ascorbato como doador específico de elétrons para reduzir o H_2O_2 para H_2O e O_2 (Asada et al., 1992). As catalases (CATs) são enzimas que catalisam a redução do H_2O_2 para H_2O e O_2, protegendo a célula dos danos oxidativos oriundos da acumulação excessiva do H_2O_2 (Sánchez-Casas e Klessig, 1994). Estão associadas principalmente com a remoção do H_2O_2 nos microcorpos (Willekens et al., 1995). As CATs estão presentes nos peroxissomos, glioxissomos e organelas relacionadas. Além destas a gluiacol peroxidase (G-POD) e glutationa redutase (GR).

3.2.4 Salinidade no cajueiro

Apesar de sua importância, o cultivo do cajueiro, enfrenta diversas limitações que dificultam seu crescimento e desenvolvimento. A maioria dos pomares de cajueiros no Brasil está localizada no semiárido, em condição de sequeiro. Estas regiões são caracterizadas por reduzidas pluviosidades e altas taxas de evaporação ocasionando naturalmente, um déficit hídrico que a produção das culturas sob condições naturais (Cabral et al., 2019; Souza et al., 2019). Aliado a este condicionamento climático, é comum nesta região a predominância de águas com elevada concentração de sais (Dalchiavon et al., 2016). Essa escassez qualitativa e quantitativa dos recursos hídricos torna-se um fator limitante para o estabelecimento desta espécie frutífera (Lima et al., 2020b).

3.3 Metabolismo do nitrato

3.3.1 Importância do nitrogênio para as plantas

O nitrogênio é o nutriente essencial para as plantas, e é demandado em maior quantidade entre os nutrientes minerais. É considerado um dos fatores mais importantes para o crescimento das culturas. As principais formas inorgânicas de N que predominam nas terras agrícolas são NO_3^- e NH_4^+, mas sua disponibilidade no solo é limitada devido a condições ambientais adversas, como salinidade, déficit hídrico, baixa intensidade de luz, calor (Dubey et al., 2021).

Vários processos fisiológicos e bioquímicos são afetados pela salinidade, particularmente a assimilação de nitratos, que influencia em grande parte o crescimento das plantas (Gouia et al., 1994; Dluzniewska et al. 2014). A eficiência fotossintética e a assimilação de nitratos nas plantas são sobretudo importantes sob condições de alta salinidade, que pode afetar de forma diferente algum destes componentes. A melhoria desses processos, especialmente sob alta oferta de nitrato, pode estimular o consumo de açúcar e a exportação de aminoácidos dos cloroplastos (Busch et al., 2018). A assimilação de nitrato e a fotorrespiração podem contribuir para a assimilação de CO_2, evitando o desequilíbrio energético nos cloroplastos induzido pelo poder redutor excessivo e pelo acúmulo de ATP (Busch et al., 2018). Consequentemente, sugere-se que quanto maior a sensibilidade imposta pela salinidade na assimilação de nitrogênio, mais severos são os efeitos nocivos do sal no crescimento das plantas (Viégas e Silveira, 1999). Aumentar a disponibilidade de N nos solos através da utilização de fertilizantes com nitrogênio mitiga os efeitos do estresse salino, corrigindo os desequilíbrios de nutrientes nas espécies de plantas (Albassam, 2001); Gomez et al. 1996, Dluzniewska et al. 2007, Ehlting et al. 2007).

Em ambientes semiáridos, frequentemente as plantas são expostas a condições salinas. Essa exposição causa perturbações no metabolismo, como a redução da fotossíntese. Um equilíbrio adequado entre a entrada de energia no aparato fotoquímico e o consumo pelas rotas bioquímicas assimilatórias (saída) é essencial para a eficiência fotossintética (Foyer et al., 2012). Um dos efeitos secundários da salinidade é o acúmulo excessivo de EROs (Miller et al., 2010; Gadelha et al., 2017). Por sua vez, o excesso de EROs pode afetar a estrutura e atividade do PSII, causando fotoinibição e comprometimento da fotossíntese (Kale et al., 2017), o que pode desencadear efeitos adversos generalizados no crescimento das plantas (Guilherme et al., 2019a). Acredita-se que o enriquecimento de compostos contendo N contribui para o processo de osmoproteção, protegendo a estrutura das proteínas macromoleculares dobradas e reduzindo o estresse oxidativo, eliminando espécies reativas de oxigênio (Mansour 2000).

A atenuação do estresse salino por NH_4^+ e NO_3^- é dependente da espécie (Liu et al., 2024). A influência da forma de N na aptidão da planta está relacionada a muitos fatores, como as preferências da planta por diferentes formas de N, estágio de desenvolvimento ou condições de crescimento (Britto e Kronzucker, 2013). A este respeito, o nitrato tem sido geralmente a forma preferida de N pelas plantas em solos agrícolas temperados, uma vez que o amónio pode tornar-se tóxico quando em excesso no meio radicular, interferindo na absorção de outros cátions (Britto e Kronzucker, 2013), ou acumula-se na planta. células (Esteban et al., 2016).

3.3.2 Absorção e assimilação de nitrato

Do solo, o NO_3^- é absorvido pelas raízes das plantas através de NRTs (transportadores de nitrato do tipo simporte nitrato-próton); posteriormente, NO_3^- é assimilado em compostos orgânicos pela ação de enzimas assimiladoras de NO_3^-. Os processos de captação de NO_3^-, sua translocação dentro dos tecidos e sua redução são regulados de forma coordenada. A captação de nitrato é mediada por uma proteína transportadora de NO_3^- induzida pelo próprio íon (Campbell, 1999). A nitrato redutase (NR, E.C.1.6.6.1) catalisa a redução de NO_3^- para NO_2^- e sua atividade é induzível por nitrato (Silveira et al. 2001). A redutase do nitrato (RN) é a enzima limitante da via de redução do nitrato assimilatório e sua atividade e expressão gênica são fortemente dependentes da disponibilidade de luz e açúcar (Campbell, 1999; Huarancca Reyes et al., 2018).

A assimilação do nitrogênio começa principalmente a partir do nitrato que é reduzido a nitrito e posteriormente a amônio pela redutase do nitrato e redutase do nitrito, respectivamente (Xu et al., 2012). O amônio é usado para produzir glutamina, a amida ácida do Glutamato, catalisada pela glutamina sintetase (GS) (Krämer et al., 2022). A síntese líquida de aminoácidos é então realizada pela enzima glutamina-oxoglutarato aminotransferase (GOGAT) (Krämer et al., 2022). Assim, as duas enzimas GS e GOGAT criam um ciclo de síntese e aminação de Glutamato que consome amônio, α-KG, ATP e equivalentes redutores (Selinski e Scheibe, 2019). O ciclo GS/GOGAT produz glutamina e glutamato, que podem atuar como iniciadores de aminoácidos em diversas vias envolvidas na síntese de aminoácidos, proteínas e outros compostos essenciais ao crescimento das plantas (Rocha et al. 2012; Selinski e Scheibe, 2019). A maioria dessas reações são consumidoras de energia e elétrons como NAD(P)H, ferredoxina reduzida e ATP (Aragão et al., 2012). Assim, todo o processo de assimilação de nitrato é um forte consumidor de elétrons na cadeia fotossintética de transporte de elétrons (Osmond e Forster 2006).

A maioria das condições estressantes causa diminuição na captação de NO_3^- e inibição das atividades das enzimas assimiladoras de N redutase do nitrato e sintetase da glutamina (Dubey et al., 2021). A atividade redutase do nitrato nas folhas é largamente dependente do fluxo de nitrato das raízes (Ferrario et al., 1998) e é severamente afetada pelo choque osmótico induzido pelo NaCl (Rao e Gnanam, 1990, Viégas e Silveira, 1999; Abd-El Baki et al., 2000).

3.4 Fotossíntese

A salinidade afeta a planta de forma multivariada, atingindo principalmente o crescimento além de vários processos metabólicos como fotossíntese, síntese de proteínas e metabolismo lipídico (Praxedes et al., 2010, Silva et al., 2015, Mansour et al., 2016). A limitação fotossintética está entre as primeiras respostas fisiológicas exibidas pelas plantas submetidas à salinidade (Shaheen et al., 2013). A redução desse processo pode estar associada tanto a limitações estomáticas (Hussain et al., 2012) quanto a fatores não estomáticos (Rodrigues et al., 2013). A salinidade afeta a assimilação fotossintética de CO_2 inicialmente causando diminuição da condutância dos estômatos, que é induzida principalmente pelos efeitos osmóticos do excesso de sal nas raízes, envolvendo o transporte de ABA e resultando em uma redução da entrada de CO_2 nas células fotossintéticas e num baixo fornecimento de CO_2 para a Rubisco (Lima-Neto et al., 2014). Diminuições na difusão de CO_2 no mesofilo foliar têm sido estudadas e são responsáveis por induzir importantes alterações na fotossíntese (Souza et al., 2019). Numa segunda fase, a salinidade pode causar efeitos bioquímicos na fotossíntese que podem restringir as reações fotoquímicas e do ciclo de Calvin (Duarte et al., 2013). Para a enzima chave da fixação de carbono, ribulose-1,5-bifosfat-carboxilase/-oxigenase (Rubisco), a relação entre a taxa de carboxilação e a taxa de oxigenação depende das concentrações de CO_2 e O_2 do cloroplasto (Farquhar et al., 1980). Assim, o fornecimento contínuo de CO_2 para a carboxilação da Rubisco é necessário para manter a fotossíntese em condições normais e especialmente sob estresse como salinidade (Xu et al., 2015).

A restrição fotossintética sob condições de estresse salino pode estar associada a um aumento na relação NADPH/NADP no estroma do cloroplasto devido a uma diminuição no consumo de equivalente redutor pelo ciclo de Calvin (Souza et al., 2019). Em situações de estresse abiótico, é comum ocorrer um excesso de elétrons e uma redução excessiva das membranas dos tilacoides (Aragão et al., 2012). Além do excesso de energia produzida devido à menor pressão de CO_2 nas células fotossintéticas sob salinidade, pode ocorrer um aumento no processo fotorrespiratório devido à menor relação CO_2/O_2 na folha e à estimulação da atividade da oxigenase Rubisco (Xu et al., 2015). Nessas condições, as plantas podem implantar diversos mecanismos para evitar ou minimizar o fotodano, a fotoinibição e o estresse oxidativo (Silva et al., 2010). Estes mecanismos de proteção estão associados a diversas reações a nível fotoquímico (regulação negativa na captação de luz, dissipação excessiva de energia por extinção não fotoquímica, aumento no ciclo água-água e no fluxo cíclico de elétrons) e outras vias bioquímicas importantes, como a ligação ascorbato-glutationa ciclo, fotorrespiração e assimilação de nitrato e amônia (Osmond et al., 1997; Niyogi, 1999; Flexas e Medrano, 2002; Takahashi e Murata, 2008; Aragão et al., 2012, Lima-Neto et al., 2014).

3.5 Fotorrespiração

O CO_2 é o substrato para a fotossíntese das plantas e uma alteração no nível de CO_2 tem um impacto direto no metabolismo (Krämer et al., 2022). A enzima Rubisco catalisa a fixação de CO_2, mas também pode usar O_2 como substrato, resultando na produção de 2-fosfoglicolato, que é então processado na via fotorrespiração (PR) (Shih et al., 2015). Como a carboxilação é preferida à oxigenação (Sharkey, 1988), concentrações elevadas de CO_2 (eCO_2) reduzem a probabilidade de oxigenação da Rubisco (Sharkey, 1988) e, assim, o fluxo através da via PR diminui. Especificamente, a carboxilação da Rubisco em plantas C3 é abaixo do ideal em concentrações reais de CO_2 atmosférico (aCO_2), e o aumento previsto no CO_2 ambiente, decorrente das mudanças climáticas, aumentará as taxas de fotossíntese (Jauregui et al., 2022). No entanto, a estimulação inicial da fotossíntese é geralmente revertida a longo prazo: um fenômeno conhecido como aclimatação fotossintética a concentrações elevadas de CO_2 (eCO_2) ou regulação negativa fotossintética (Sage et al., 1989).

A via fotorrespiratória em plantas C3 tem como principal função a recuperação do carbono perdido pela atividade da Rubisco oxigenasse (Souza et al., 2019). No decorrer da PR, duas moléculas de 2-fosfoglicolato (2-PG) são convertidas em uma molécula de 3-fosfoglicerato, que é realimentada no Ciclo de Calvin-Benson (Huma et al., 2018). Mais precisamente, o 2-PG é convertido em glicolato que é posteriormente oxidado em glioxilato, produzindo H2O2 como subproduto nos peroxissomos. Uma etapa fundamental na fotorrespiração é a conversão de glicina em serina com liberação de CO_2 e amônia (Busch et al., 2018). Grande parte do CO_2 liberado sai da folha e, portanto, representa uma perda de carbono (Busch et al., 2013), enquanto a reciclagem da amônia é energeticamente dispendiosa, pois requer ATP e redução da ferredoxina (Busch et al., 2018).

A fotorrespiração é considerada prejudicial devido à redução nas taxas de assimilação de CO_2. Este processo representa uma perda de aproximadamente 25% do CO_2 fixado durante a fotossíntese em plantas C3 em condições ambientais normais (Souza et al., 2019). Contudo, o metabolismo fotorrespiratório também pode ser benéfico, considerado uma forma importante de dissipação de excesso de energia consumindo redutor (quatro elétrons por reação de oxigenação) (Wingler et al., 2000). Quando a proporção de CO_2 para O_2 diminui nos cloroplastos, a aceleração da fotorrespiração requer uma maior demanda de ATP/NADPH (Walker et al., 2014). A fotorrespiração é uma forma importante de dissipação de excesso de energia, principalmente sob condições de estresse abióticos (Wingler et al., 2000; Guilherme et al., 2019b; Aragão et al., 2012, Lima-Neto et al., 2014). A resposta ao processo fotorrespiratório pode ser aumentada em plantas submetidas a estresse abiótico, como a salinidade (Foyer et al., 2009). O excesso de energia pode afetar a integridade do PSII mas, em oposição, pode favorecer sinergicamente assimilação de nitrato e fotorrespiração Guilherme et al., 2019b. A integração dos metabolismos do carbono e do nitrogênio na via fotorrespiratória pode resultar no aumento das taxas de assimilação de CO_2, compensando alguns dos aspectos negativos da fotorrespiração (Busch et al., 2018, Guilherme et al., 2019b). A melhoria desses processos, especialmente sob alta oferta de nitrato, pode estimular o consumo de açúcar e a exportação de aminoácidos dos cloroplastos (Busch et al., 2018). Além disso, a assimilação de nitrato e a fotorrespiração podem contribuir para a assimilação de CO_2, reduzindo o acúmulo de poder redutor e ATP evitando o desequilíbrio energético nos cloroplastos (Aragão et al., 2012, Lima-Neto et al., 2014; Busch et al., 2018; Guilherme et al., 2019b).

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APÊNDICE A – ARTIGO SUBMETIDO AO PERIÓDICO PLANT AND SOIL JOURNAL: HIGH NITRATE MITIGATES SALT STRESS AND INDUCES CONTRASTING EFFECTS ON PHOTOSYNTHESIS AND PHOTORESPIRATION IN CASHEW PLANTS

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REGULAR ARTICLE

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ABSTRACT

Aims – We tested the hypothesis that high NO_3^- supply might attenuate adverse effects caused by excess of Na^+ and Cl^- on the photosynthetic efficiency by stimulation of alternative electron sinks to nitrate assimilation.

Methods – Cashew plantlets (species adapted to low soil nitrate and salinity in semiarid regions) were exposed to high salinity (NaCl 100 mM) in the presence of two contrasting NO_3^- levels, 0.1 mM (low) and 10.0 mM (high), for 35 days.

Results – High nitrate supply stimulated leaf expansion and decreased root length in the absence of salinity, but did not affect these variables under saline stress. The high nitrate was able to reduce membrane damage associated with lower Na^+ and Cl^- accumulation and lower Na^+/K^+ ratios in leaves under saline stress. High nitrate content did not affect photosynthetic electron transport rates, while PSI acceptor side limitation decreased under salt stress. CO_2 assimilation rates did not change due to the effect of nitrate levels. In contrast, photorespiration rates were increased by high nitrate in the absence of salinity, whereas, regardless of nitrate levels, salinity induced a prominent increase in photorespiration rates. Interestingly, when photorespiration was artificially abolished or intensely decreased by O_2 scavenging, high NO_3^- induced large increases in V_{cmax}, J_{max} and P_{Nmax} in salt stressed plants.

Conclusions – The high supply of NO_3^- is capable of mitigating some adverse effects of salinity on cashew plantlets. The photorespiration is the largest alternative electron sink compared to the use of nitrate, which could be more important in situations of low photorespiration.

Keywords - *Anacardium occidental* L., photorespiration, photosynthesis, salinity.

ABBREVIATIONS

Ci – Intercellular CO_2 concentration
ETR – Electron transport rate
ETR/P_N – Electron transport rate of PSII/net photosynthesis ratios
Fv/Fm – Potential quantum yield of PSII
g_s – stomatal conductance
Jo – Electron flux rate to Rubisco oxygenation
Jc – Electron flux rate to Rubisco carboxylation
J_{max} – Maximum electron flux to RuBP regeneration
P_N – Net photosynthesis rate
P_{Nmax} – Maximum potential photosynthesis
Pr – Photorespiration rate
PSI – Actual quantum yield of PSI
PSII – Actual quantum yield of PSII
V_{cmax} – Maximum Rubisco carboxylation activity
WUE – Water use efficiency
Y(NA) – Limitation of the acceptor side of PSI
Y(ND) – Limitation of the donor side of PSI

INTRODUCTION

Salinity induces deep metabolical alterations in the plant homeostasis capable to reduce greatly the crop yield. Salt stress affect direct and indirectly several physiological processes, especially growth, stomatal restriction, energy balance, and CO_2 assimilation (Silveira & Carvalho, 2016). Despite being a huge problem for agriculture worldwide and there is a large number of published articles on that subject, several gaps involving salt tolerance mechanisms remain yet (Silva et. al., 2012). An issue relatively neglected in the last years is understanding how the intensity of N supply in soils could mitigate some adverse effects caused by salinity involving improvement of the balance between the photosynthesis phases (Aragão et al., 2012; Lima-Neto et al., 2014; Guilherme et al., 2019a).

N assimilation and utilization of amino acids for synthesis of proteins and other biomolecules are important sinks for consumption of photosynthetic energy in the forms of electrons, carbon skeletons and ATP (Alencar et al., 2019; Guilherme et al., 2019a). Moreover, N is quantitatively the most important inorganic nutrient involved direct and indirectly in several aspects of the photosynthesis since the composition of important chloroplast proteins until its involvement as an alternative electron acceptor from photochemical phase during nitrate and nitrite reductions and, ammonia assimilation (Alencar et al., 2019; Guilherme et al., 2019b; Lima-Neto et al., 2021).

The N assimilation processes are closely linked to the photorespiratory cycle, which represents the most important photosynthetic electron alternative sink in C3 plants, especially under restriction of CO_2 assimilation as those that occur under salt stress (Silveira & Carvalho, 2016). The main relationships between nitrate supply, photosynthetic efficiency, photorespiration, and salt stress are complexes and essentially unknown (Aragão et al., 2012; Guilherme et al., 2019b). Some works have evidenced that high N supply might mitigate adverse effects caused by salinity, but the underlying mechanisms and metabolical involved processes are poorly understood yet (Aragão et al., 2012; Liu et al., 2024). Nitrate supply might increase nitrate uptake and assimilation by stimulation of transporters expression favoring the growth under salt stress conditions (Liu et al., 2024).

The relationships between N assimilation and photorespiration in C3 plants are complexes and debated yet (Krämer et al., 2022). Photosynthesis and respiration can supply malate to cytosol for NADH production and improvement of nitrate reduction by nitrate reductase activity (Bloom, 2015). The nitrite formed might be transported to chloroplast to be reduced by nitrite reductase consuming four electrons from reduced ferredoxin to produce free ammonia. This N-source is immediately assimilated into amino acids by the chloroplastic GS/GOGAT cycle, consuming one molecule of ATP, NADPH and ketoglutarate and producing glutamine and glutamate, which can participate of the photorespiratory cycle (Krämer et al., 2022).

Besides its capacity to supply metabolic intermediaries for stimulate the photorespiratory cycle, thus, mitigating adverse effects caused by excess energy in chloroplasts (Silva et al., 2015), N assimilation is crucial to protein synthesis and plant growth. Actually, the increase in growth, represented by incorporation of new dry matter, is the most important sink to consumption of excess photosynthetic energy, favoring to an adequate energy balance in plants, especially under salt stress conditions (Silveira and Carvalho, 2016). This circumstances are particularly important under high salinity conditions when some plant species restrict or even cease their growth especially in leaves (Silveira and Sousa, 2024).

In stress conditions, the excess energy produced in chloroplasts tend to increase the formation and overaccumulation of reactive oxygen species, inducing oxidative stress and generalized physiological disturbances (Sousa et al., 2023). Our group have previously reported that cashew (*Anacardium occidentale* L.), a semiarid adapted species, is relatively tolerant to moderate salinity since it is originated from coastal areas of Brazil (Voigt et al., 2009). That species employs an avoidance mechanism to face salinity, strongly restricting the leaf growth and avoiding excess salt accumulation. In parallel, the cashew plants salt-induced impairment in nitrate reduction and transport from root to leaf is accompanied by decrease in N accumulation, protein proteolysis and disturbances in amino acids metabolism (Viégas et al., 1999a; Silveira et. al., 2003; da Rocha et al., 2012).

In parallel, cashew plants display great down-regulation in PSII activity, stomatal conductance, photorespiration activity, accompanied by intense stimulation in non-photochemical quenching and electron cyclic flux (Ferreira-Silva et al., 2011; Lima et al., 2018; Souza et al., 2019). Together, these integrated mechanisms allow avoid oxidative stress, contributing to salt resistance. In this current work we tested the hypothesis that a high NO_3^- supply is capable to mitigate adverse effects caused by high salinity in cashew plantlets by stimulation in consumption of photosynthetic electrons via increased photorespiration and nitrate reduction and assimilation.

Our results evidence that intense salt stress induces complexes responses in N utilization and photorespiration relationships and their consequences on salinity resistance and photosynthesis. Despite the high nitrate supply has clearly mitigated salt stress effects on the leaf Na/K homeostasis and membrane damages, its effects on photorespiration and photosynthesis were slight under photorespiratory conditions and intense salt stress circumstances. We are proposing here that under high salinity and growth restriction the photorespiration is the most important process to dissipate excess photosynthetic and nitrate supply displays a secondary role in these circumstances.

MATERIAL AND METHODS

Experimental and plant growth conditions

Seeds of cashew nuts (*Anacardium occidentale* L.), dwarf clone CCP09, were supplied by Embrapa Agroindústria Tropical, Fortaleza, Ceará, Brazil. The clone CCP 09 is widely cultivated in commercial plantations in the Brazilian semiarid regions (Ferreira-Silva et al., 2010). The cashew nuts were germinated on a 1:1 mixture of sand and vermiculite (v/v) in natural greenhouse conditions. After germination, homogeneous seedlings exhibiting primary four expanded leaves (15 day-old) were transplanted to 3.75 L plastic pots containing ¼ diluted Hoagland-Arnon's nutrient solution (Hoagland and Arnon, 1950). During five days the plants received NO_3^- 2.5 mM as the unique N-source for acclimation. After this pre-acclimatization period, plantlets were separated into two groups: 10 mM NO_3^- (high supply) in the form of 3 mM of $Ca(NO_3)_2$ and 4 mM KNO_3, which corresponded to the high nitrate (HN) treatment, or 0.1 mM NO_3^- (low supply) in the form of 0.05 mM $Ca(NO_3)_2$, which corresponded to the low nitrate (LN) treatment, dissolved in the complete nutrient solution. Ca^{2+} and K^+ concentrations were maintained at 3.0 mM and 6.0 mM, respectively, in all nutrient solutions using $CaCl_2$, K_2SO_4 and K_2HPO_4 salts. The control solution presented Cl^- concentrations of 6 mM from the 3 mM $CaCl_2$ supplied to nutrient solution. All nutrient concentrations were used according to the Hoagland-Arnon (1950)'s nutrient solution.

The plantlets were separated in four groups (treatments): (1) plants supplied with high nitrate in absence of NaCl; (2) plants supplied with low nitrate in absence of NaCl; (3) plants supplied with high nitrate in presence of NaCl 100 mM and, (4) plants supplied with low nitrate in presence of NaCl 100 mM. The plants remained in these conditions for thirty-five days. Nutrient solutions were completely changed twice a week and pH of the solutions was daily adjusted to 6.0 ± 0.5. The study was conducted in a randomized design, in a factorial scheme (2 x 2) with four replications (an individual pot containing a plant) in a greenhouse localized at 3°44′44.2″S 38°34′ 29, 2″W, under natural conditions. The environmental conditions throughout the experimental period change as: air average temperature from 28 °C to 30 °C; average air relative humidity from 52% to 65%; and average of maximum photosynthetic photon flux density from 480 to 850 $\mu mol\ m^{-2}\ s^{-1}$. The leaf samples for photosynthesis and chemical analyses were represented by completely expanded leaves without exhibit toxicity visual symptoms.

Morphological characterization

The growth of cashew plants was evaluated by principal root heigh measured directly and leaf area (LA) employing the width (W) and length (L) measurements and calculated using the following equation and expressed in cm²/plant: LA= 0.21+ 0.69 x W x L as described by Murthy et al., (1985).

Determination of nitrate and total nitrogen contents

Nitrate and total nitrogen were determined in leaf tissues after complete drying in an oven at 45 ºC. Leaf nitrate was extracted with hot water (100 °C), and the concentration was determined by the salicylic acid colorimetric method according to Cataldo et al., (1975). Total- N content was measured according to the Baethgen and Alley (1989) method after complete dry matter digestion.

Stress indicators: electrolyte leakage, sodium, chloride, and potassium contents

The electrolyte leakage (EL) was determined based on the electrical conductivity, as proposed by Shanahan et al., (1990). Twenty discs of cashew leaves were added to 20 ml of distillated water and mixed overnight. After 24h, electrical conductivity (C1) was determined, the extract was boiled for 1h and the new electrical conductivity (C2) was determined. Electrolyte leakage was expressed in % of membrane damage according to the following equation: %EL = (C1 / C2) * 100. The Na^+ and K^+ contents were determined by flame photometry. The extract was read in flame photometer calibrated, the content was calculated according to pattern curve and results were expressed as µmol g^{-1} dry mass. The Cl^- content was determined by Mohr method, according to Viégas et al., (2001). Cl^- content was expressed as µmol g^{-1} dry mass.

Gas exchange and chlorophyll a fluorescence measurement

In vivo photosynthetic parameters were measured using a portable infrared gas analyzer system (LI-6400XT, LI-COR, Lincoln, NE, USA). The amount of blue light was adjusted to 10% of the PPFD (PAR of 800 m^{-2} s^{-1}) in order to maximize stomatal opening (Flexas et al. 2008). The other environmental conditions were 28 °C and 400 ppm CO_2. Measurements were taken on fully expanded and mature leaves. A-Ci curves were performed using increasing CO_2 intensities from 0 to 1,400 ppm. Day respiration (RD) was estimated from A-Ci curves according to Thornley and Johnson (1990). Maximum Rubisco carboxylation rate (V_{cmax}) [$A = (V_{cmax} (pi - \Gamma^*)/(pi - Km)) - Rd$] and maximum electron transport rate for RuBP regeneration (J_{max}) [$A = (J_{max} (pi - \Gamma^*)/(4pi + 8\Gamma^*)) - Rd$]. In these equations pi is the intercellular CO_2 partial pressure, Γ^* is the CO_2 compensation point (taken as 3.69 Pa at 25ºC) in the absence of dark respiration, Rd, and Km is effective Michaelis-Menten constant for CO_2 (75.05 Pa at 25ºC), calculated using the temperature conversions according to Farquhar et al., (1980) and the Michaelis-Menten constant for CO_2 and O_2 according to von Caemmerer et al., (1994).

In vivo chlorophyll fluorescence parameters were measured using a Dual-PAM 100 fluorometer (Walz, Effeltrich, Germany). Fluorescence parameters were measured by the saturation pulse method (Klughammer and Schreiber, 1994) and leaves were previously acclimated to the dark for 30 min. The intensity and duration of the saturation pulse were 8,000 µmol m^{-2} s^{-1} and 0.6 s, respectively. The photochemical parameters PSII and Psi were measured in response to a fast light curve from 0 to 2,200 µmol m^{-2} s^{-1}, with 1 min exposure per light intensity. The maximum quantum yield of PSII [Fv/Fm = (Fm - Fo)/Fm] and the effective quantum yield of PSII [Y(II) = (Fm’-Fs)/Fm’] were evaluated. PSI photochemical measurements were carried out on a DUALPAM 100 and the following parameters were measured: limitation on the donor side of PSI [Y(ND) = 1 - P700 red], limitation on the acceptor side of PSI [Y(NA) = (Pm - Pm')/Pm] as described by (Klughammer and Schreiber, 1994). The electron flow for Rubisco carboxylation was calculated as J_c = 1/3[ETRII + 8(A + RD)], where RD is the daytime respiration parameter calculated from the A-Ci curve. The following photorespiration parameters were calculated: electron flow for Rubisco oxygenation, J_o = 2/ 3[ETRII - 4(A + RD)] and photorespiratory evolution of CO2, P_r = 1/ 12[ETRII - 4(A + RD)], according to Valentini et al. (1995).

Experimental design and statistical analyses

The experiments were carried out in a completely randomized design in a 2 x 2 factorial scheme with two principal treatments (absence and presence of NaCl) and two sub-treatments (high nitrate and low nitrate), with four replicates represented by an individual pot containing one plant. The statistical analyses were performed by ANOVA including Tukey’s test. The grouping and multivariate analysis was performed by PLS-DA system using the MetaboAnalyst platform.

RESULTS

High nitrate supply mitigates membrane damage and salt toxicity decreasing Na^+ and Cl^- accumulation and favoring Na/K ratios in leaves

In order to evaluate the role and importance of N supply to growth and salt resistance of cashew plantlets, initially we evaluated the leaf area index and the principal root length changes in response to two contrasting nitrate levels in a nutrient solution: (1) low nitrate concentration (0.1 mM) and (2) high and adequate nitrate supply (10.0 mM). Low NO_3^- supplied plantlets in absence of salinity showed N deficiency symptoms after 21 days of treatments, represented by chlorosis on the oldest leaves and these symptoms were generalized after 28 days and after 35 days the oldest leaves were completely death (data not shown). After 23 days of salt treatment, plantlets grown in low nitrate begin show salt toxicity symptoms represented by generalized chlorosis followed by necrotic areas in all leaves. In high NO_3^- supplied plantlets these symptoms began only after 30 days of salt treatment (Figure S1).

Cashew plantlets grown under high nitrate in absence of salinity displayed higher leaf area index and lower principal root length after 35 days compared with low nitrate supply. However, these growth indicators did not change by effect of nitrate levels in salt-treated plants despite the high nitrate level had significantly decreased membrane damage in leaves (Figure 1A-B). The leaf area in high nitrate-treated plants was positively related to the NO_3^- and total-N contents in leaves (Figure 2A-B), whereas the intensity of membrane damage and toxicity visual symptoms were inversely associated with accumulation of Na^+ and Cl^- and Na/K ratios in leaves after 35 days of treatments (Figure 3A-C). Nevertheless, despite the high NO_3^- level has contributed to mitigate salt toxicity and ionic homeostasis, after that long-term exposure to high salinity (100 mM NaCl), both low- and high-nitrate supplied plants exhibited severe salt-toxicity symptoms in their leaves.

Salt stress induces strong impairment on photochemical activity and CO_2 assimilation and greatly stimulate photorespiration

After a long-term high salinity exposure for 35 days, cashew plants didn’t exhibit any alterations in the potential quantum yield of PSII (Fv/Fm), independently of the nitrate level, and a same trend was followed by other photochemical parameters electron transport rates of PSII and PSI (ETRI and ETRII) (Figure 4A-C). Interestingly, high nitrate supply decreased the limitation of the PSI acceptor side (YNA) in presence of salt stress, a parameter associated with oxidative capacity of PSI. Conversely, the limitation of the donor side of PSI, a parameter related to electron flux from PSII to PSI, was slightly increased in this condition. The effects of nitrate levels on photochemical activity in absence of salinity were unexpected since high nitrate reduced ETRII and ETRI, increased YNA and did change YND (Figure S2 A-C). The ETR/P_N ratios, an indicator parameter of excess energy in chloroplast available to alternative electron sinks such a photorespiration, did change by effect of nitrate levels under salinity but it was decreased by high nitrate in absence of salinity (Figure S2 A-C).

The net CO_2 assimilation was drastically reduced by salt stress independently of nitrate levels and this response was tightly associated with reductions in stomatal conductance (Figure 5A-B). High nitrate supply did not favor CO_2 assimilation in both situations of absence and salinity, despite has favored stomatal conductance on the first condition and, then contributing to increase the water use efficiency (WUE), as expressed by the P_N/gs ratio (Figure 5C). Salt stress greatly stimulated photorespiration as estimated by the gas exchange parameters electron transport rate to Rubisco oxygenation (Jo), photorespiration rate (Pr) and the ratio between electron transport rate to Rubisco oxygenation and electron transport to Rubisco carboxylation (Jo/Jc). These effects on photorespiration were practically independent of nitrate levels, despite in absence of salinity high nitrate did significantly stimulate photorespiration in comparison low nitrate one (Figure 6-C).

High nitrate supply displays contrasting effects on the photosynthetic efficiency of salt-stressed plants in response to photorespiration level

In order to understand the interactions between nitrate level x salt stress x photosynthetic efficiency x photorespiration intensity, we performed some P_N – Ci curves varying artificially the Ci (intercellular CO_2) concentrations in two environmental conditions: (1) ambient photorespiration and (2) low photorespiration induced by low O_2 levels provoked by excess N_2 gas inside the analysis cuvette. The obtained results were very surprising since under low photorespiration condition the high nitrate supply greatly improved all photosynthetic efficiency analyzed parameters, that is, Vcmax (maximum carboxylation rate of Rubisco), J_{max} (maximum electron transport rate to RuBP regeneration), and P_{Nmax} (maximum potential photosynthesis rate), compared with high nitrate level in stressed plants in ambient photorespiration and with low nitrate in all experimental conditions (Figure 7A-F).

Actually, high nitrate level also stimulated P_{Nmax} in both salt-stressed and control plants in low photorespiration compared with ambient photorespiration.

Interestingly, the trend of the P_N – Ci curves under ambient photorespiration versus low photorespiration was very clear, highlighting the great differences among curve types and, consequently, the derivatives parameters (Figure S2). The medium time for each point of P_N measurement in presence of N_2 inside the cuvettes was approximately 30 minutes and incidence of a photosynthetic photon flux intensity (PPFD) of 800 μmol m^{-2} s^{-1}. Remarkably, in that time and experimental conditions, the low extern O_2 circumstances, interacting with high nitrate supplied plants, was enough to trigger a rapid and intense improvement in CO_2 carboxylation, specifically under salt stress condition.

Thus, our results strongly suggest that the photosynthetic carboxylation system represented by Rubisco activity, Calvin cycle reactions and electron supply to CO_2 assimilation, was greatly stimulated. These responses suggest existence of some type of regulation which could involve partitioning of electron fluxes among Calvin cycle, photorespiration, and nitrate assimilation. The correlation and grouping analysis results by PLS-DA (Figure S3) reinforce that the four treatments (low nitrate in absence of salinity, high nitrate in absence of salinity, low nitrate in presence of salt stress, and high nitrate in presence of salt stress) displayed distinct and contrasting responses, corroborating that these conditions induced different physiological acclimations to cashew plants.

DISCUSSION

In this current study we are demonstrating that a high nitrate level supplied to cashew plants exposed to severe salt stress is capable to mitigate toxic effects by reduction in the accumulation of Na^+ and Cl^- ions, associated with great decrease in Na/K ratios in leaves. These favorable effects on the ionic homeostasis are related to reduction in leaf membrane damage and toxicity visual symptoms. Possibly, high nitrate supply could have downregulated the expression and/or activity of Na^+ transporters (Assaha et al. 2017; Rubio et al., 2020). Despite these clear favorable effects, the role of high nitrate supply on photosynthesis improvement was not so evident in this study as was clearly demonstrated for *Jatropha curcas* plants grown under two levels of nitrate and salinity (Aragão et al., 2012).

Several works have demonstrated that supply of high level of nitrate or N is capable to favor CO_2 assimilation despite the underlying metabolic mechanisms are scarcely known (Huang et al., 2016; Busch et al., 2018; Guilherme et. al., 2019b). However, in this current study the cashew plants there were in a development stage characterized by very low growth rates associated with a severe salt stress what strongly restrict the N demand (Voight et al., 2009). Indeed, recent evidences suggest that the most important favorable role of nitrate supply on photosynthesis in stress conditions is indirect involving its assimilation and acting as an alternative sink and stimulating photorespiration for consumption of excess photosynthetic electrons (Busch et al., 2018; Guilherme et. al., 2019a).

Recently, we have demonstrated that salt-stressed cashew plants display accentuated decrease in photosynthesis (Souza et. al., 2019). Interestingly, when these plants were exposed to low photorespiration induced by high CO_2 concentrations, they displayed reduction in photosynthesis as under control as well as in salt-stressed conditions. These results can suggest that photosynthesis in cashew plants could be naturally favored by high photorespiration rates. Indeed, cashew is a plant species adapted to semiarid conditions, such as drought, heat, salinity and high light intensity, which greatly can favor photorespiration (Ferreira-Silva et. al., 2011; Souza et. al., 2019).

Photorespiration can favor photosynthesis in C3 plants exposed to adverse environmental conditions (Sousa et. al., 2023). On the other hand, high nitrate supply can stimulate photorespiration favoring nitrate reduction in cytosol and nitrite reduction and ammonia assimilation in chloroplasts (Bloom, 2015; Guilherme et. al., 2019a; Bush et al., 2018; Krämer et. al., 2022). In this current study our data evidence that high nitrate supply is capable to greatly stimulate photorespiration in absence of salinity and that salt stress, independently of nitrate levels, is capable of stimulate photorespiration in an extent much higher. In other words, under severe salt stress high nitrate supply has a limited capacity to stimulate photorespiration.

These responses displayed by cashew plants could indicate that under severe salt stress the photorespiration is the most important mechanism acting as alternative sink for photosynthetic electrons in parallel to CO_2 assimilation (Souza et. al., 2019). Thus, in these circumstances the effects of nitrate supply on photosynthesis and photorespiration should be occur in lower extent. Indeed, it has been evidenced that positive effects caused by high nitrate supply on photosynthesis under severe stress conditions should be essentially associated with consumption of excess energy from photochemical phase (Aragão et al., 2012). However, in these circumstances, cashew plants should display very low nitrate uptake and assimilation (Viégas et. al., 1999a; Viégas et. al., 1999b).

Our current results involving interactions between high nitrate supply, photorespiration and photosynthesis improvement under severe salt stress are very complexes. Indeed, the effects of high nitrate supply on photosynthetic efficiency parameters in low photorespiration conditions are unexpected and intriguing. Clearly, when photorespiration is artificially inhibited by low O_2 concentrations, high nitrate supply greatly improves photosynthesis efficiency under salt stress, compared with ambient the photorespiratory condition and with low nitrate supply in same situations. These unexpected responses suggest an intricate regulation between photorespiration and photosynthesis under salt stress situation in cashew plants. Possibly, cashew is adapted to environmental conditions which greatly favor photorespiration over photosynthesis (Souza et., al., 2019).

It’s possible to speculate that those adaptive conditions for cashew plants, including a rigid stomatal regulation induce a tight regulation among these two processes where photorespiration greatly favor protection against excess energy and benefit photosynthesis against oxidative stress and other disturbances caused by excess energy. In conclusion, these results suggest that cashew plants exposed to adverse environmental conditions such as salt stress, display a close interaction between photosynthesis and photorespiration capable to contribute for adaption to adverse environmental conditions such as those displayed in semiarid regions. The high nitrate supply is capable to mitigate adverse effects caused by high salinity possibly contributing to maintain a favorable Na/K ionic homeostasis in leaves.

CONCLUSIONS

The high supply of NO3- is capable of mitigating some adverse effects of salinity on cashew plantlets. The photorespiration is the largest alternative electron sink compared to the use of nitrate, which could be more important in situations of low photorespiration.

Acknowledgments

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Conflict of interest

The authors declare no conflict of interest.

FIGURES AND CAPTIONS

Figure 1 – High nitrate supply mitigates leaf membrane damage but not growth indicators. Changes in (A) leaf area, (B) shoot height, and (C) leaf electrolyte leakage in cashew plantlets after 35 days of high salinity exposure (NaCl 100 mM) in presence of two contrasting nitrate levels (0.1 mM NO_3^- – LN and 10 mM NO_3^- – HN). The treatments were applied after 15 days of seedling emergency (DAE). Data represent means of four replications ± SD and letters represent differences by Tukey's test ($p<0.05$). Different capital letters represent differences among LN and HN whitin treatments (control and salt), and different lower cases indicate significant differences among all treatments.

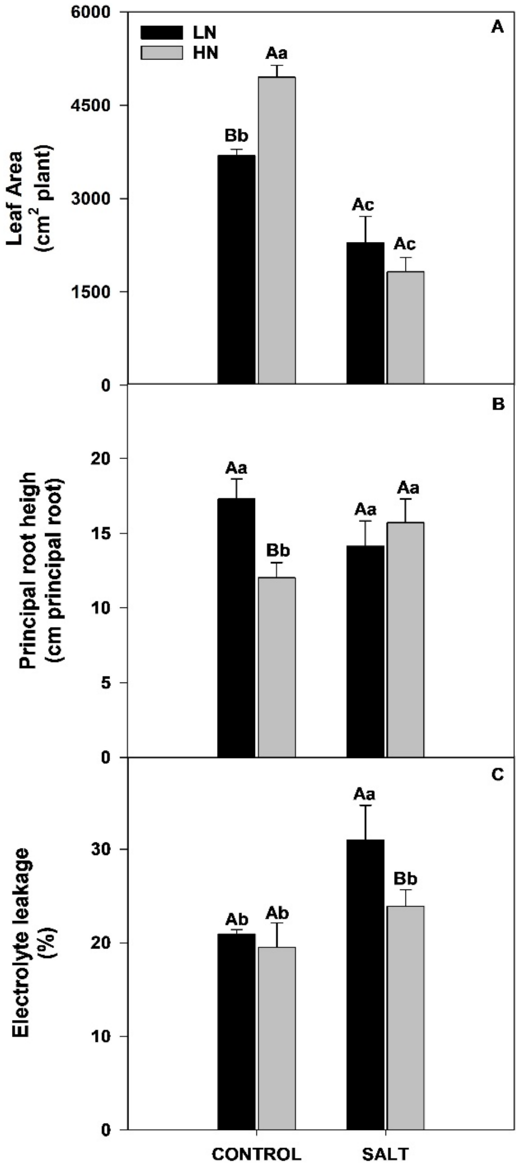


Figure 2 – HN supply induces higher accumulation of NO_3^- and N-total in leaves only in absence of salinity. Contents of (A) nitrate and (B) total-N in leaves of cashew plantlets after 35 days of high salinity exposure (NaCl 100 mM) in presence of two contrasting nitrate levels (0.1 mM NO_3^- – LN and 10 mM NO_3^- – HN). Treatments and statistic comparisons are described in figure 1.

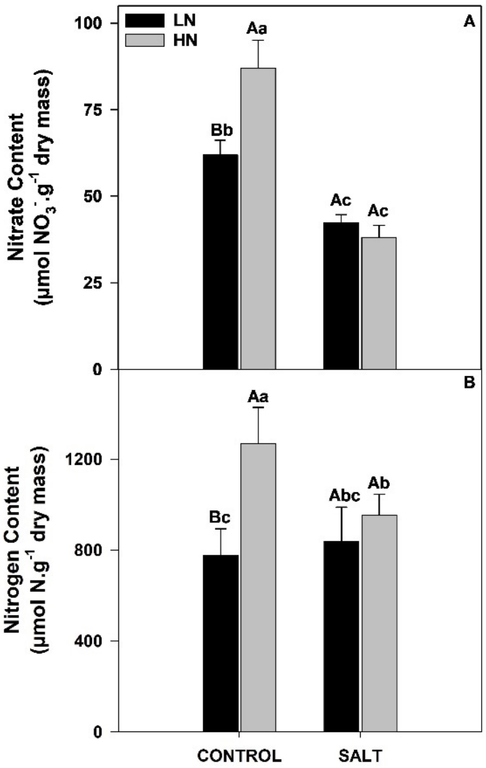


Figure 3 – HN supply favors ionic homeostasis of salt stressed plants. Changes in the contents of (A) Na^+ and (B) Cl^-, and (C) leaf K^+/Na^+ ratios in in leaves of cashew plantlets after 35 days of high salinity exposure (NaCl 100 mM) in presence of two contrasting nitrate levels (0.1 mM NO_3^- – LN and 10 mM NO_3^- – HN). Treatments and statistic comparisons are described in figure 1.

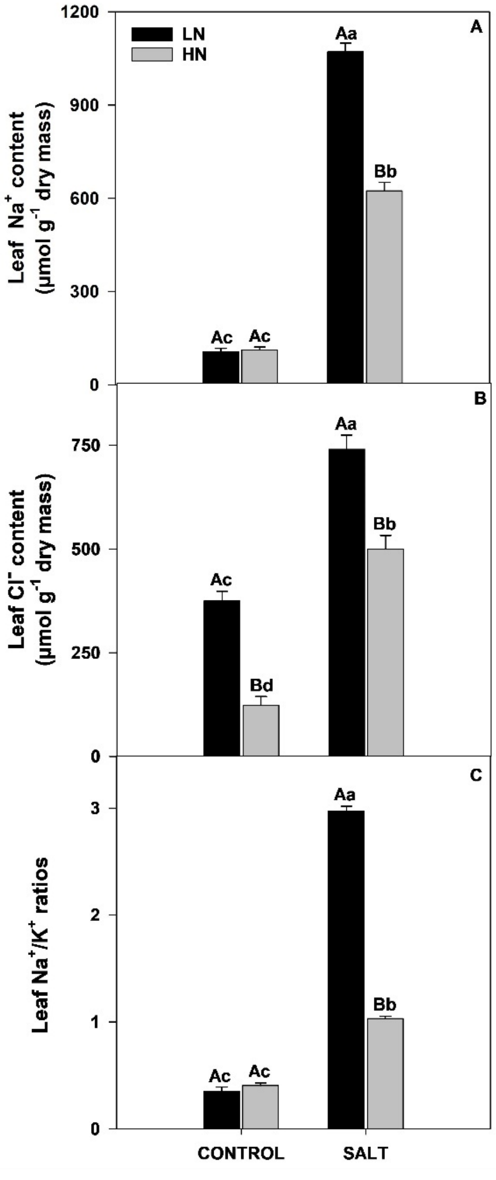


Figure 4 – HN supply doesn't alter the electron transport rates of PSII and PSI in salt stressed plants. Changes in (A) potential quantum yield of PSII, (B) electron transport rate of PSI, and (C) electron transport rate of PSII in leaves of cashew plantlets after 35 days of high salinity exposure (NaCl 100 mM) in presence of two contrasting nitrate levels (0.1 mM NO_3^- – LN and 10 mM NO_3^- – HN). Treatments and statistic comparisons are described in figure 1.

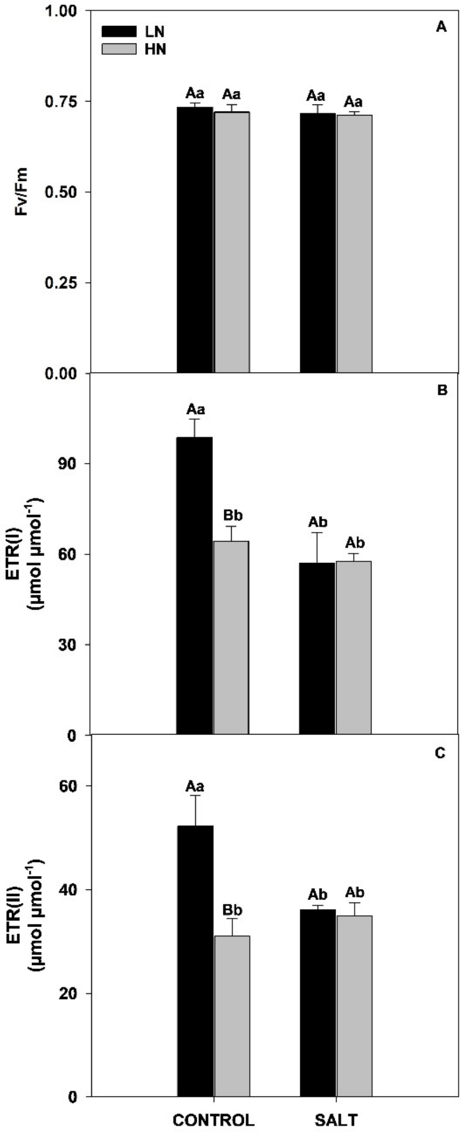


Figure 5 – Salt stress greatly decrease CO_2 assimilation under both LN and HN levels. Alterations in (A) net assimilation of CO_2, (B) stomatal conductance, and (C) water use efficiency in leaves of cashew plantlets after 35 days of high salinity exposure (NaCl 100 mM) in presence of two contrasting nitrate levels (0.1 mM NO_3^- – LN and 10 mM NO_3^- – HN). Treatments and statistic comparisons are described in figure 1.

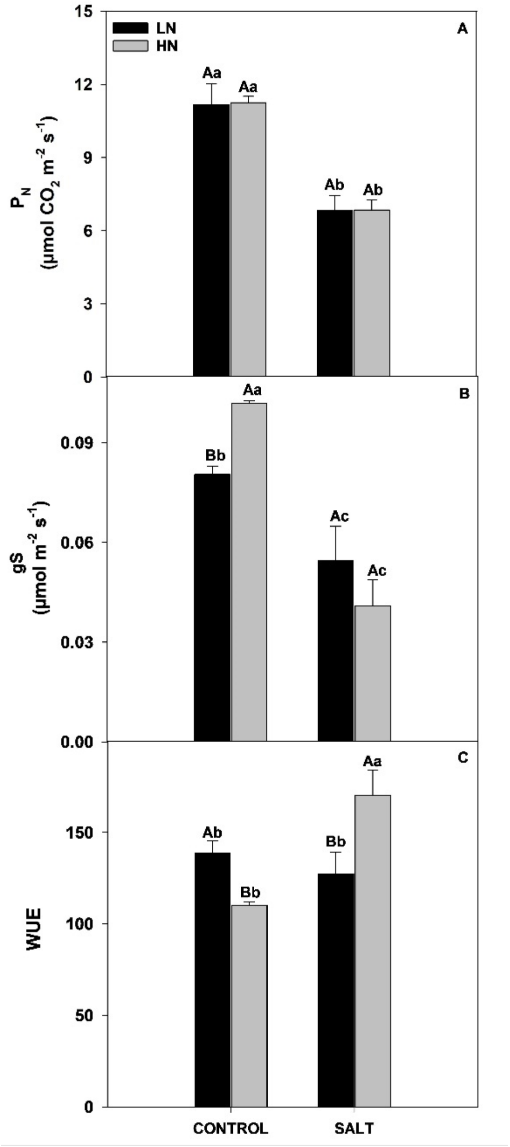


Figure 6 – Salt stress prominently stimulate photorespiration activity. Changes in intensity of photorespiration indicators (A) Pr, photorespiration rates, (B) Jo, electron flux to rubisco oxygenation (B), and (C) Jo/Jc ratios in leaves of cashew plantlets after 35 days of high salinity exposure (NaCl 100 mM) in presence of two contrasting nitrate levels (0.1 mM NO_3^- – LN and 10 mM NO_3^- – HN). Treatments and statistic comparisons are described in figure 1.

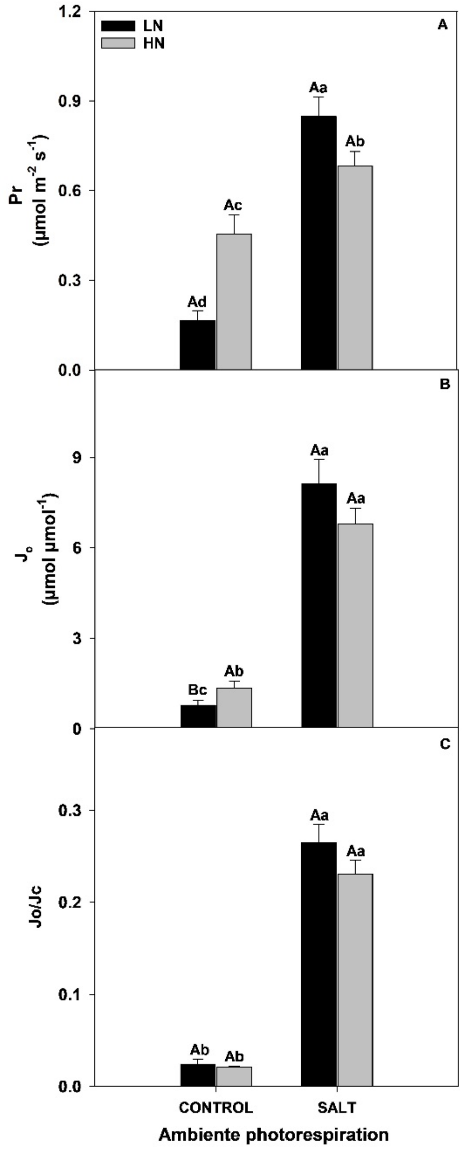
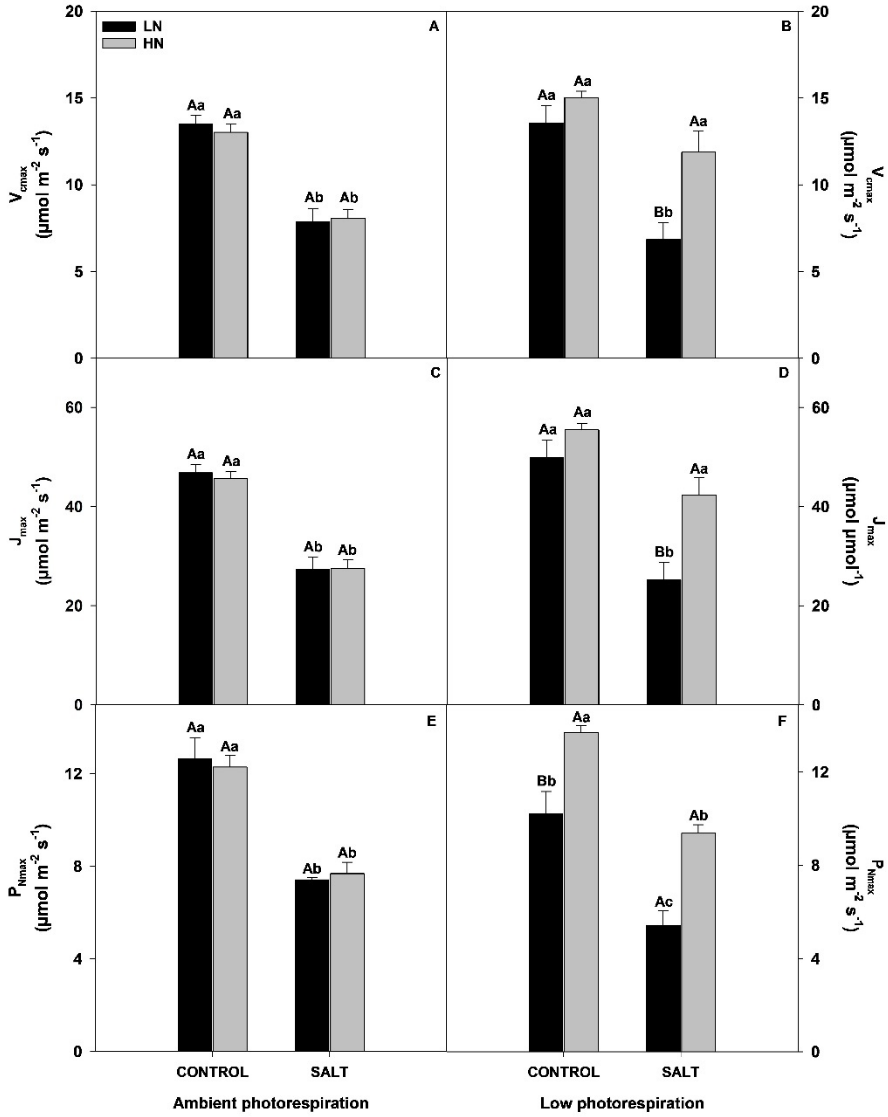


Figure 7 – Photosynthetic efficiency is strongly stimulated by HN in salt stressed plants under low photorespiratory conditions. Changes in photosynthetic efficiency parameters (A) and (B) V_{cmax}, maximum carboxylation rate of Rubisco (C) and (D) J_{max}, maximum electron transport rate for RuBP regeneration and, (E) and (F) P_{Nmax} potential maximum photosynthesis under ambient and low photorespiration conditions in leaves of cashew plantlets after 35 days of high salinity exposure (NaCl 100 mM) in presence of two contrasting nitrate levels (0.1 mM NO_3^- – LN and 10 mM NO_3^- – HN). Treatments and statistic comparisons are described in figure 1.



SUPPLEMENTARY MATERIAL

Figure S1 – HN supply mitigates visual symptoms of salt toxicity on leaves. Morphological aspects of shoot and leaves of cashew plantlets exposed to high salinity under two contrasting nitrate levels, low (0.1 mM NO_3^- – LN) and high nitrate (10 mM NO_3^- – HN) after 35 days of treatments. (A and E) 10 mM NO_3^- in absence of NaCl, (B and F) 0.1 mM NO_3^- without NaCl, (C and G) 10 mM NO_3^- + 100 mM NaCl, and (D and H) 0.1 mM NO_3^- + 100 mM NaCl. Individual plants are representative from four replicates.

Figure S2 – HN supply decreases the limitation of the acceptor side of PSI in salt stressed plants. Changes in (A) limitation of the acceptor side of PSI, (B) limitation of the donor side of PSI, and (C) and ETRII/P_N ratios in leaves of cashew plantlets after 35 days of high salinity exposure (NaCl 100 mM) in presence of two contrasting nitrate levels (0.1 mM NO_3^- – LN and 10 mM NO_3^- – HN). Treatments and statistic comparisons are described in figure 1.

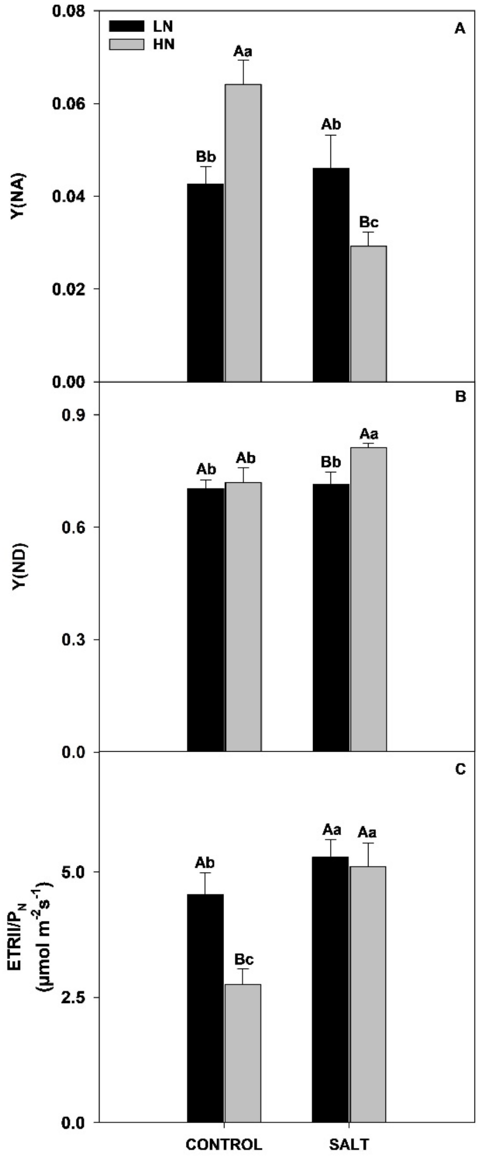
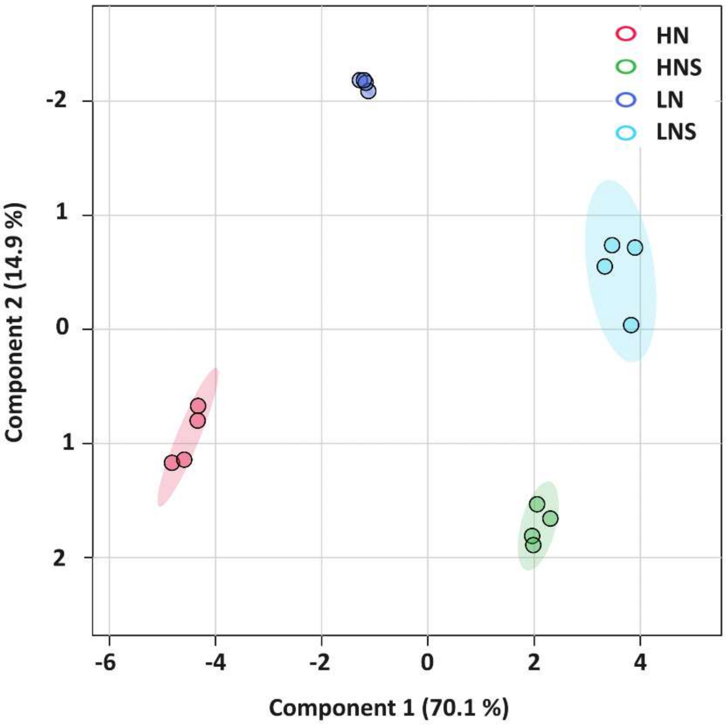


Figure S3 – Grouping and multivariate analysis reveal high contrast displayed by different treatments. Grouping responses of the treatments as indicated by PLS-DA (partial least squares discriminant analysis). Different localization of treatments in quadrants represents contrasts in the grouping and multivariate perfomance. The analysis was performed using the MetaboAnalyst platform.



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APÊNDICE B – OUTROS RESULTADOS ENCONTRADOS NA DISSERTAÇÃO

Figure 1 – Response of net CO_2 assimilation as a function of CO_2 concentration (AP – ambient photorespiration and LP – low photorespiration) of cashew seedlings exposed to high salinity under two contrasting nitrate levels, low (0.1 mM NO_3^- – LN) and high nitrate (10 mM NO_3^- – HN) after 34 days of treatments (DAT) and 49 days after plant emergence (DAE). (A) 0.1 mM NO_3^- + 0 mM NaCl, (B) 10 mM NO_3^- + 0 mM NaCl, (C) 0.1 mM NO_3^- + 100 mM NaCl and (D) 10 mM NO_3^- + 100 mM NaCl. Data represent means of three replications ± SD between treatments.

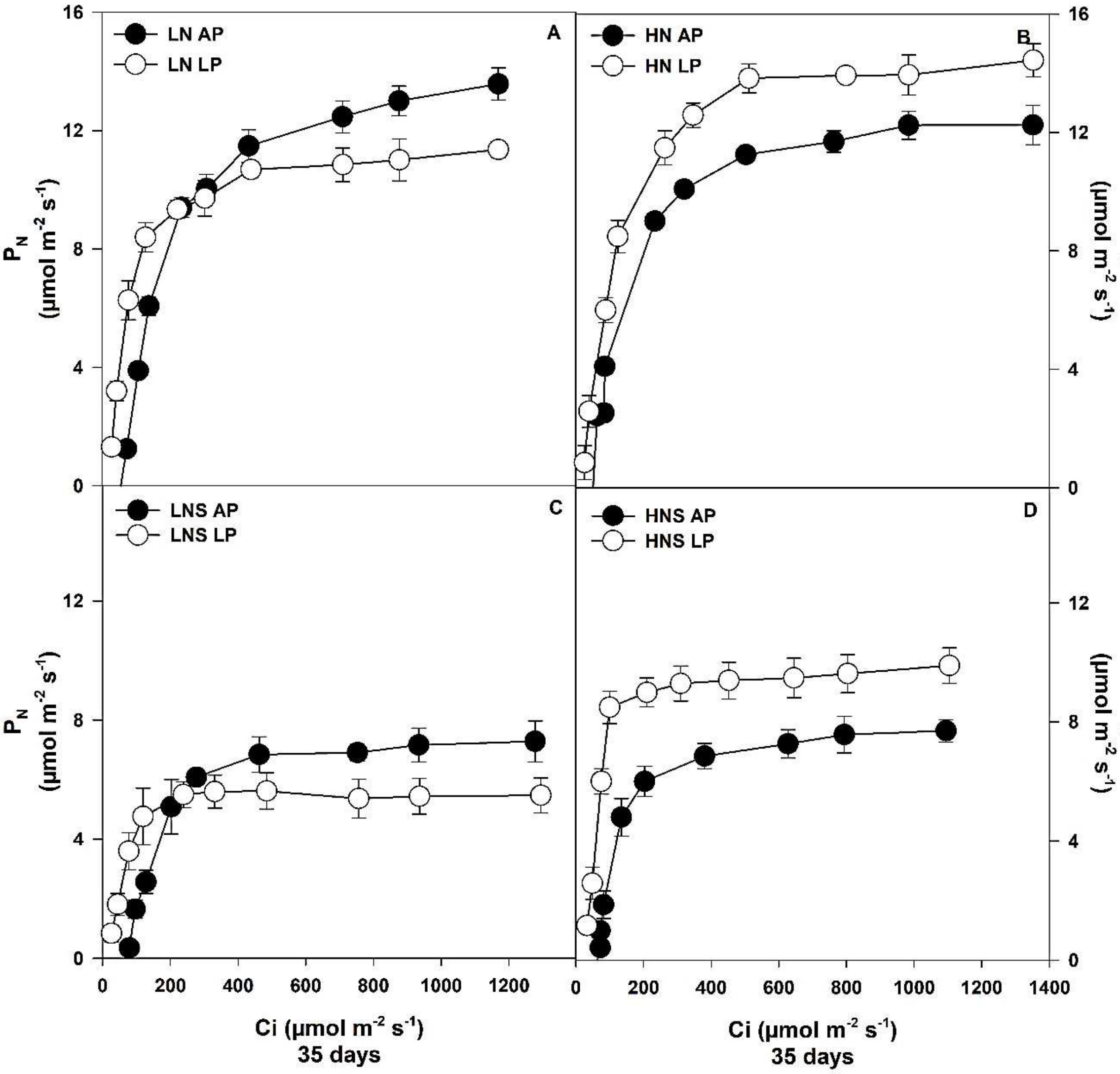


Figure 2 – Response of conductance stomatal as a function of CO_2 concentration (AP – ambient photorespiration and LP – low photorespiration) of cashew seedlings exposed to high salinity under two contrasting nitrate levels, low (0.1 mM NO_3^- – LN) and high nitrate (10 mM NO_3^- – HN) after 34 days of treatments (DAT) and 49 days after plant emergence (DAE). (A) 0.1 mM NO_3^- + 0 mM NaCl, (B) 10 mM NO_3^- + 0 mM NaCl, (C) 0.1 mM NO_3^- + 100 mM NaCl and (D) 10 mM NO_3^- + 100 mM NaCl. Data represent means of three replications ± SD between treatments.

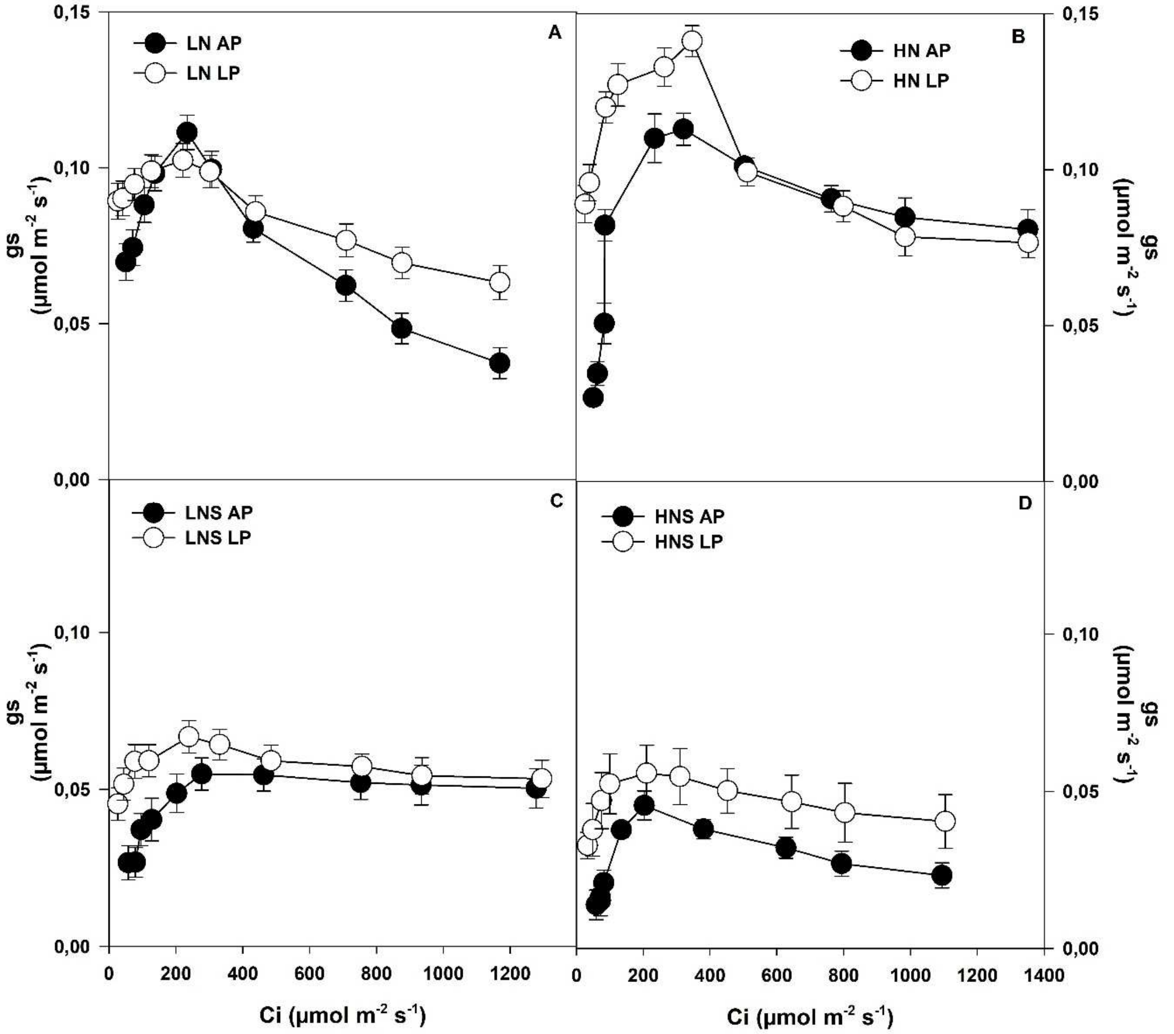


Figure 3 - Characterization photosynthetic. Response of assimilation CO2 (A, B), stomatal conductance (C, D) and transpiration (E, F) in cashew seedlings after 14 (A, C and E) and 22 (B, D and F) days of high salinity treatment (100 mM) under two contrasting nitrate levels (0.1 mM NO_3^- – LN and 10 mM NO_3^- – HN). The treatments were applied 15 days after seedling emergency (DAE). Data represent means of three replications ± SD and different letters represent significant differences between treatments using the Tukey test ($p<0.05$).

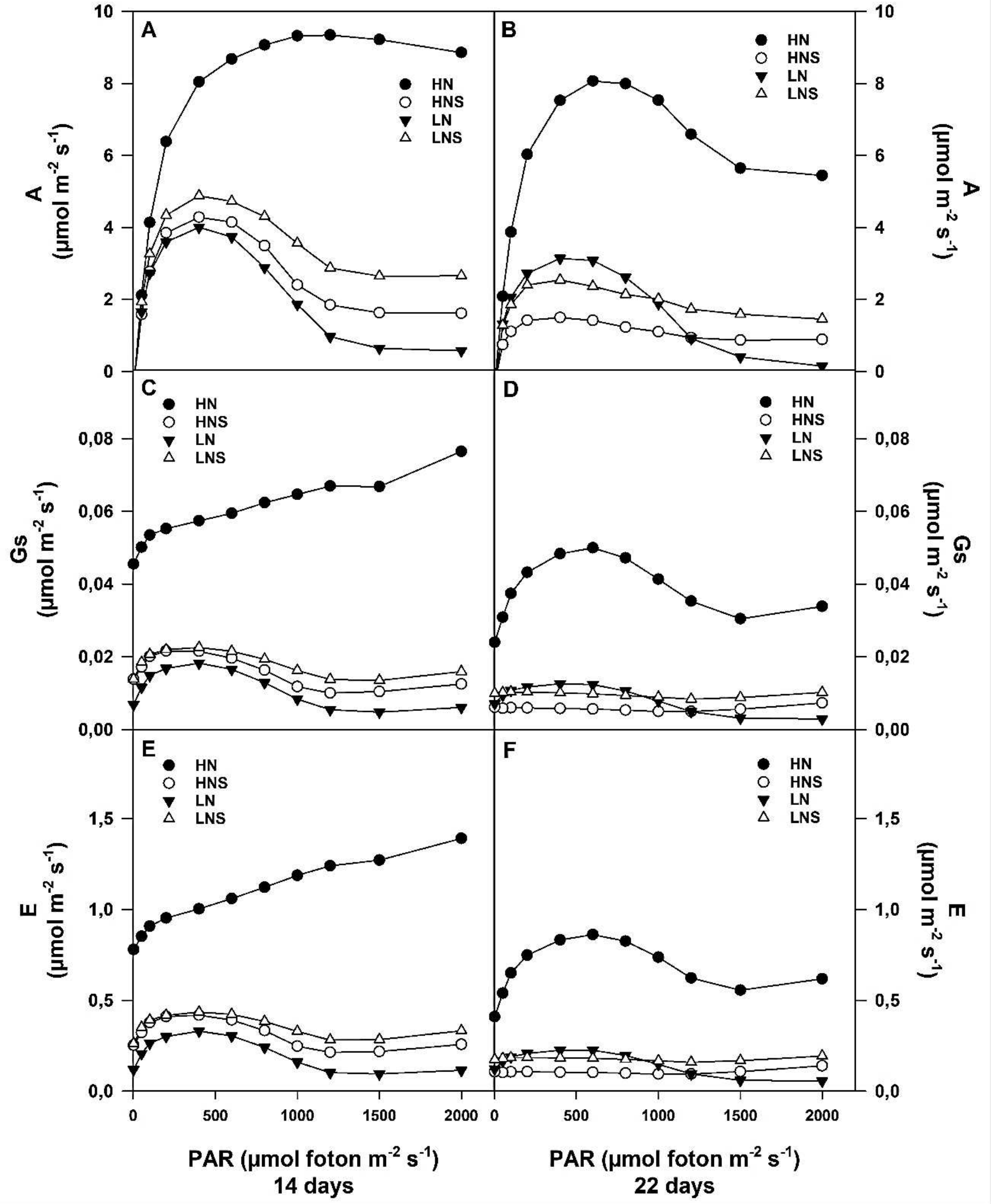


Figure 4 – Characterization photosynthetic. Assimilation CO_2 (A, B) and photorespiratory evolution CO_2 (C, D) in cashew seedlings after 14 (A, C) and 22 (B, D) days of high salinity treatment (100 mM) under two contrasting nitrate levels (0.1 mM NO_3^- – LN and 10 mM NO_3^- – HN). The treatments were applied 15 days after seedling emergency (DAE). Treatments and statistic comparisons are described in figure 1.

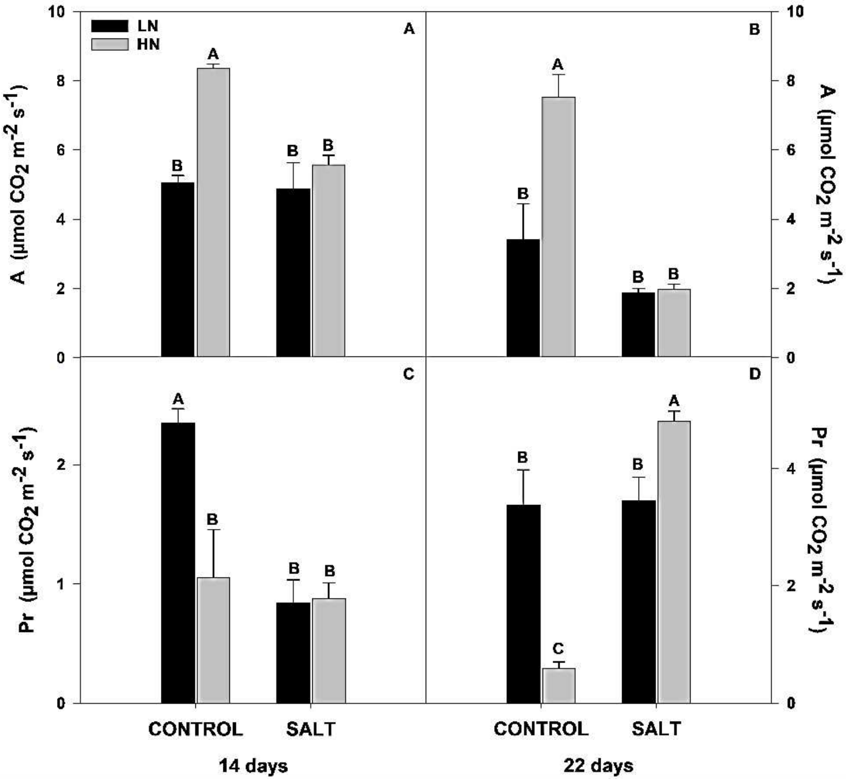


Figure 5 – Characterization photosynthetic. Electron flux to rubisco carboxylation (A, B), electron flux to rubisco oxygenation (C, D) and Jo/Jc ration (E, F) in cashew seedlings after 14 (A, C and E) and 22 (B, D and F) days of high salinity treatment (100 mM) under two contrasting nitrate levels (0.1 mM NO_3^- – LN and 10 mM NO_3^- – HN). The treatments were applied 15 days after seedling emergency (DAE). Treatments and statistic comparisons are described in figure 1.

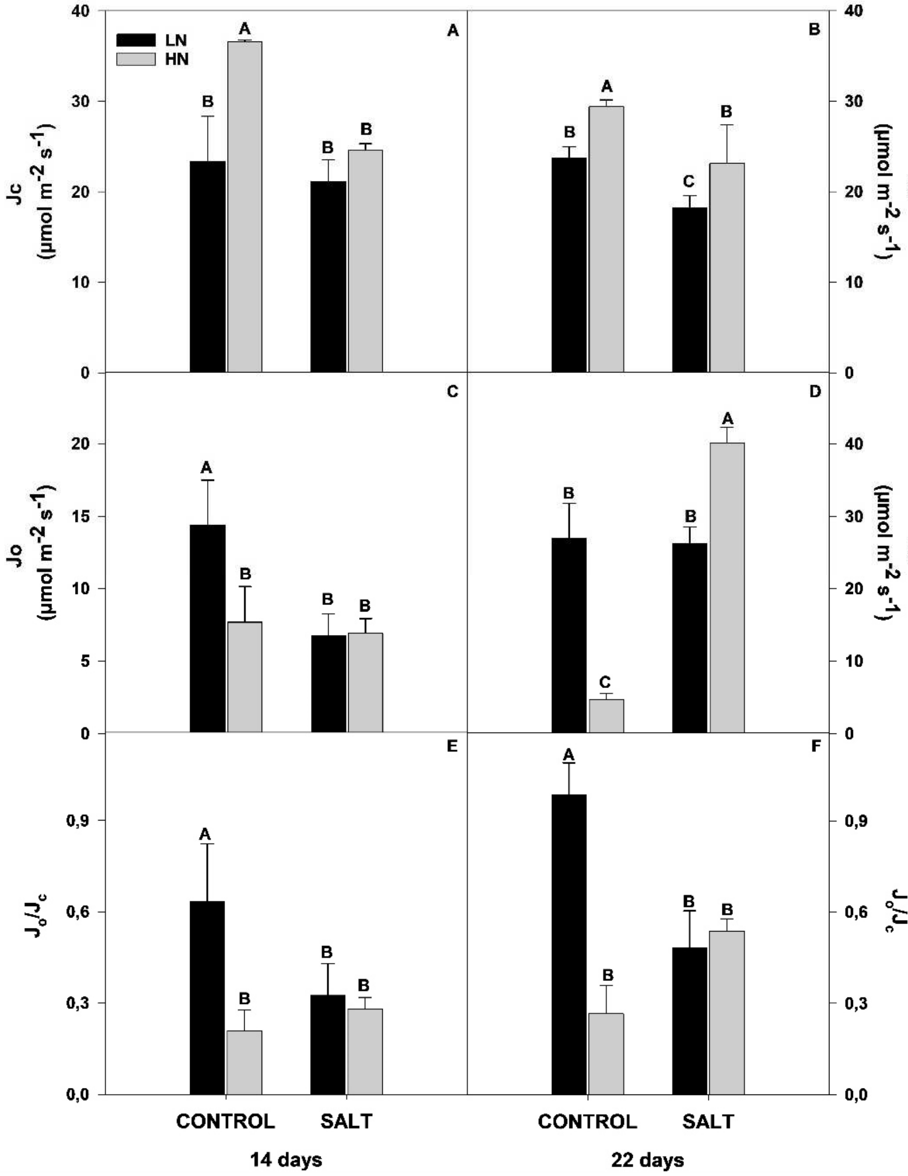


Figure 6 – Characterization photosynthetic. Rubisco maximum carboxylation rate (A, B), maximum electron transport rate for RuBP regeneration (C, D) and breathing in the dark (E, F) in cashew seedlings after 14 (A, C and E) and 22 (B, D and F) days of high salinity treatment (100 mM) under two contrasting nitrate levels (0.1 mM NO_3^- – LN and 10 mM NO_3^- – HN). The treatments were applied 15 days after seedling emergency (DAE). Treatments and statistic comparisons are described in figure 1

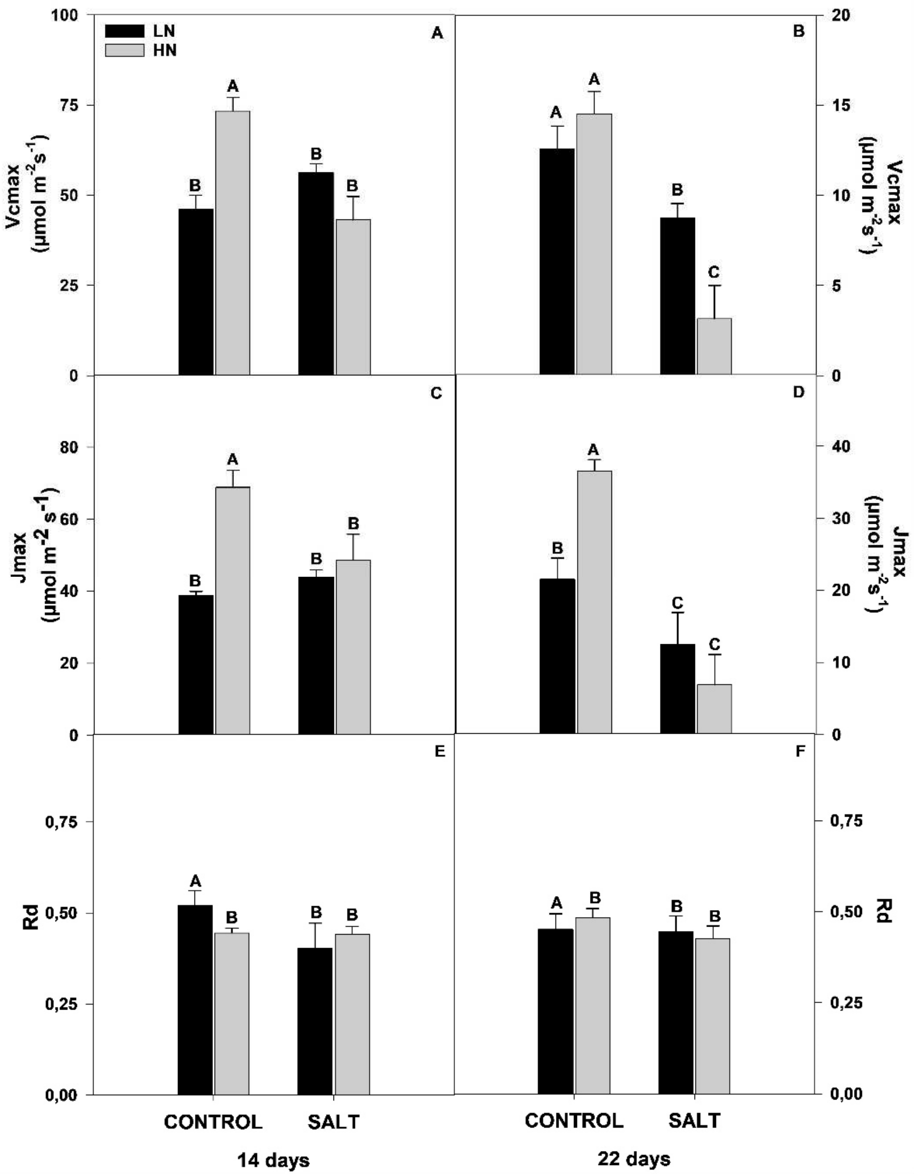


Figure 7 – Characterization photosynthetic. Effective quantum yield of PSI (A), effective quantum yield of PSII (B), electron transport rate of PSI (C) and electron transport rate of PSII (D) in cashew seedlings after 14 days of high salinity treatment (100 mM) under two contrasting nitrate levels (0.1 mM NO_3^- – LN and 10 mM NO_3^- – HN). The treatments were applied 15 days after seedling emergency (DAE). Treatments and statistic comparisons are described in figure 1.

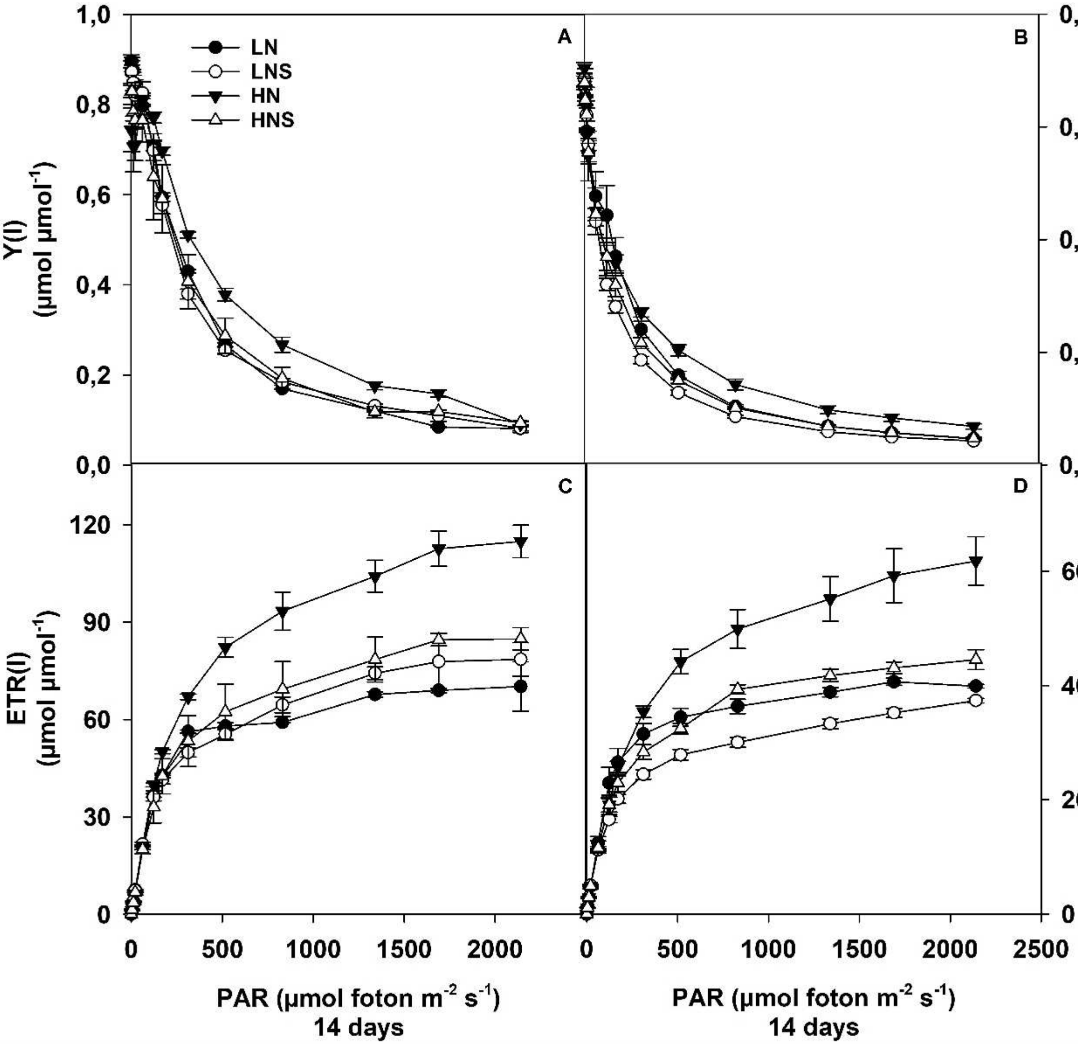


Figure 8 – Characterization photosynthetic. Effective quantum yield of PSI (A), effective quantum yield of PSII (B), electron transport rate of PSI (C) and electron transport rate of PSII (D) in cashew seedlings after 22 days of high salinity treatment (100 mM) under two contrasting nitrate levels (0.1 mM NO_3^- – LN and 10 mM NO_3^- – HN). The treatments were applied 15 days after seedling emergency (DAE). Treatments and statistic comparisons are described in figure 1.

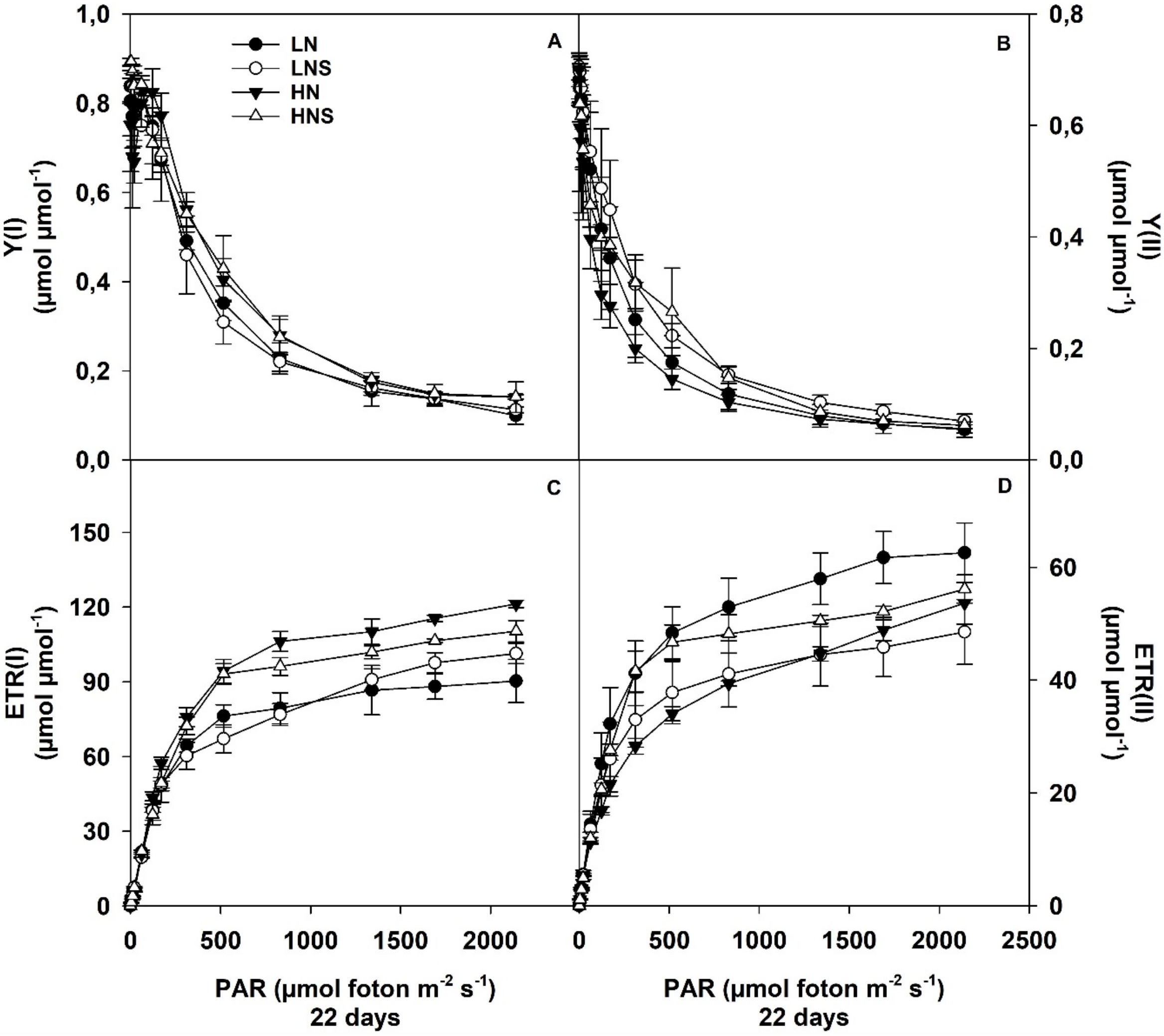


Figure 9 – Characterization photosynthetic. Effective quantum yield of PSI (A), effective quantum yield of PSII (B), electron transport rate of PSI (C) and electron transport rate of PSII (D) in cashew seedlings after 34 days of high salinity treatment (100 mM) under two contrasting nitrate levels (0.1 mM NO_3^- – LN and 10 mM NO_3^- – HN). The treatments were applied 15 days after seedling emergency (DAE). Treatments and statistic comparisons are described in figure 1.

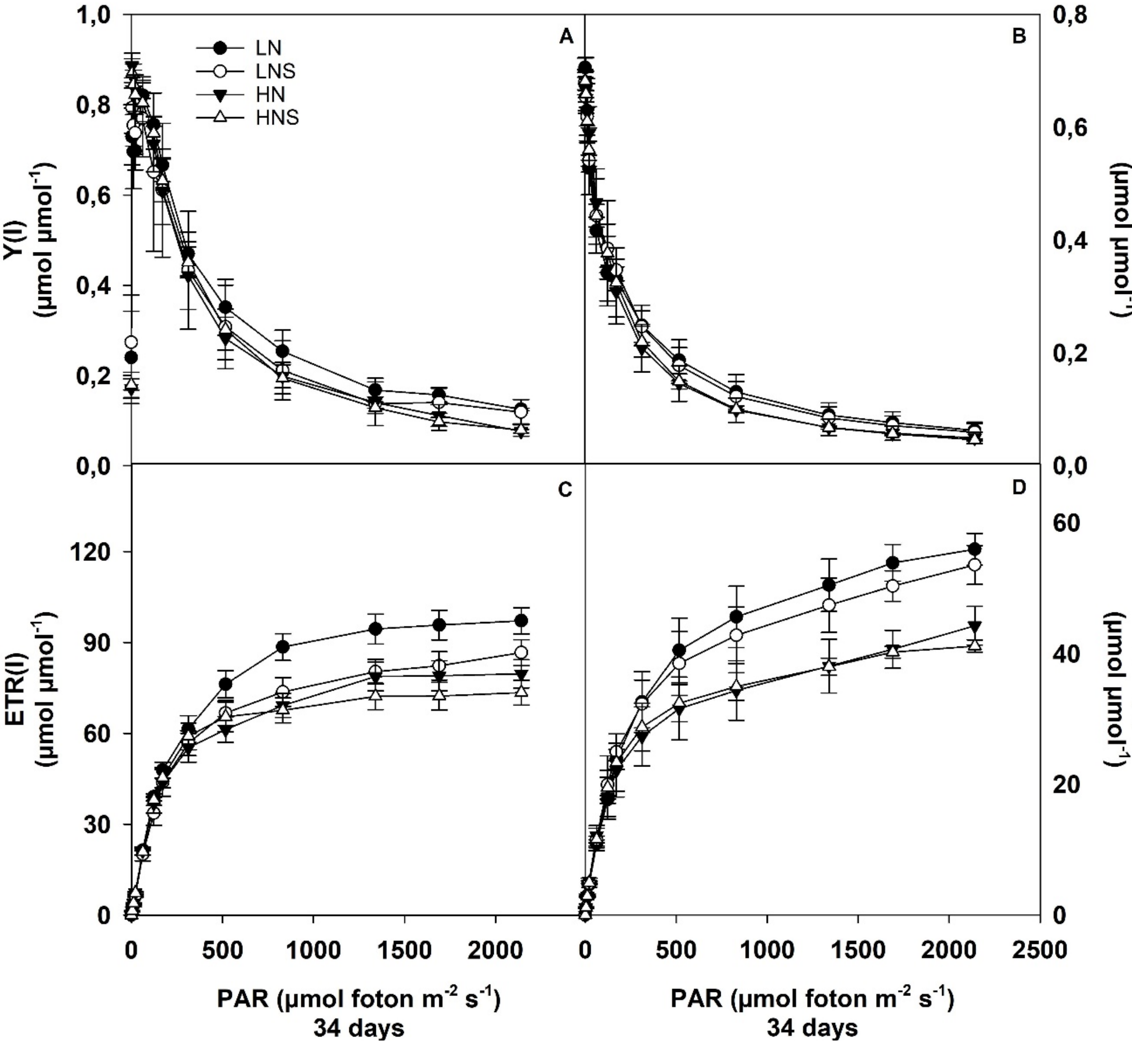


Figure 10 – Physiological stress indicators. Total chlorophyll content (A, B), chlorophyll a content (C, D) and chlorophyll b content (E, F) in cashew seedlings after 15 (A, C and E) and 30 (B, D and F) days of high salinity treatment (100 mM) under two contrasting nitrate levels (0.1 mM NO_3^- – LN and 10 mM NO_3^- – HN). The treatments were applied 15 days after seedling emergency (DAE). Data represent means of four replications ± SD and different letters represent significant differences between treatments using the Tukey test (p<0.05).

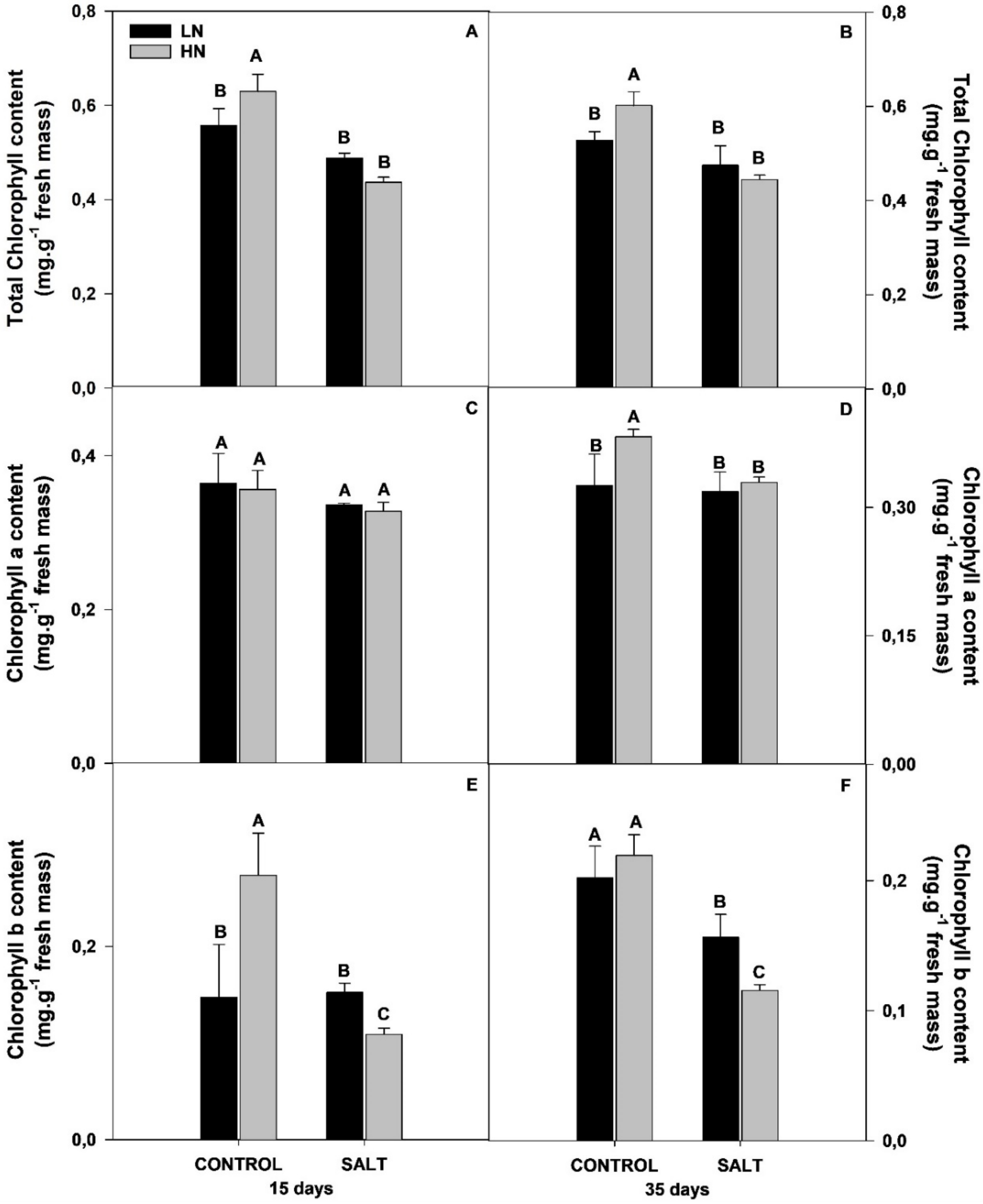


Figure 11 – Physiological stress indicators. Relative water content (A, B) and relative humidity (C, D) in cashew seedlings after 15 (A, C) and 30 (B, D) days of high salinity treatment (100 mM) under two contrasting nitrate levels (0.1 mM NO_3^- – LN and 10 mM NO_3^- – HN). The treatments were applied 15 days after seedling emergency (DAE). Treatments and statistic comparisons are described in figure 1.

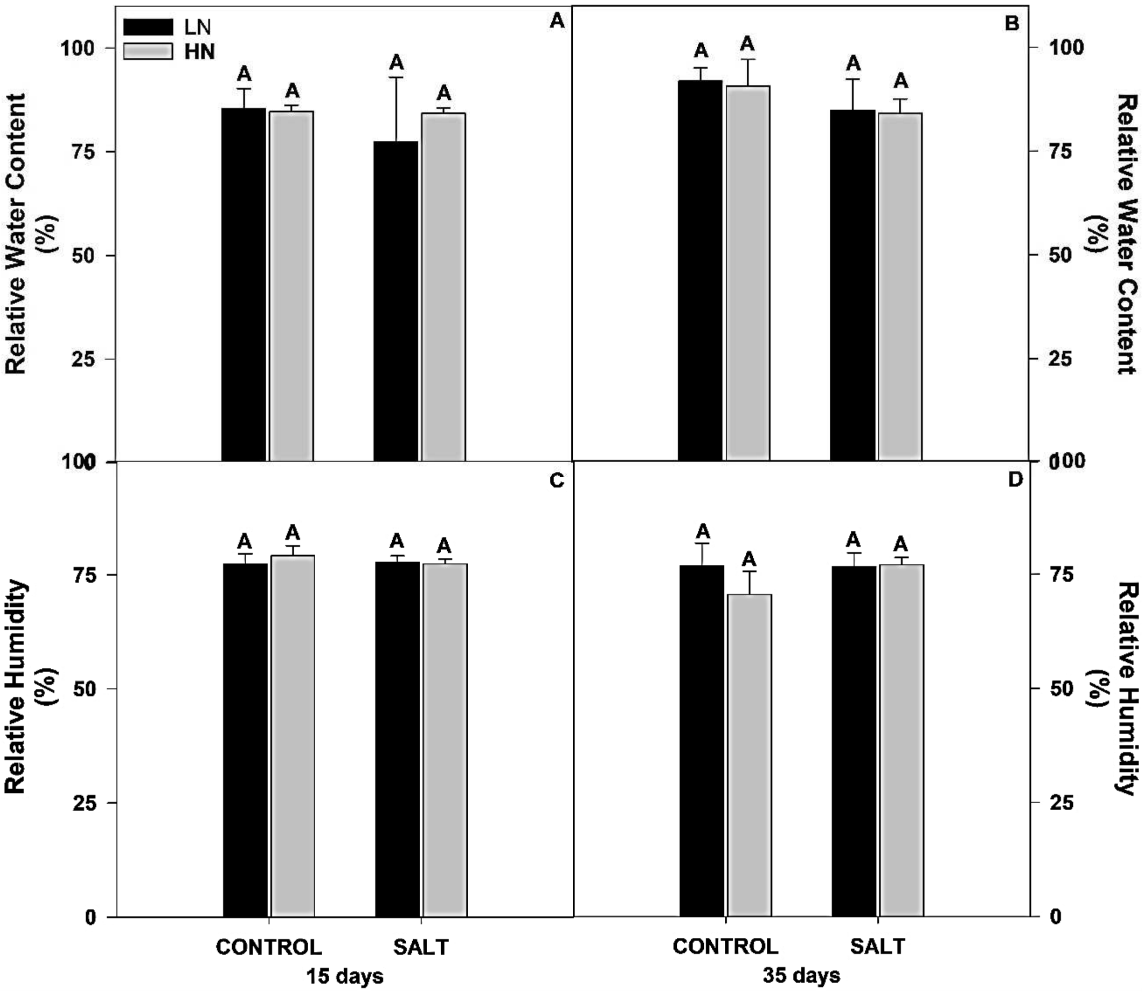
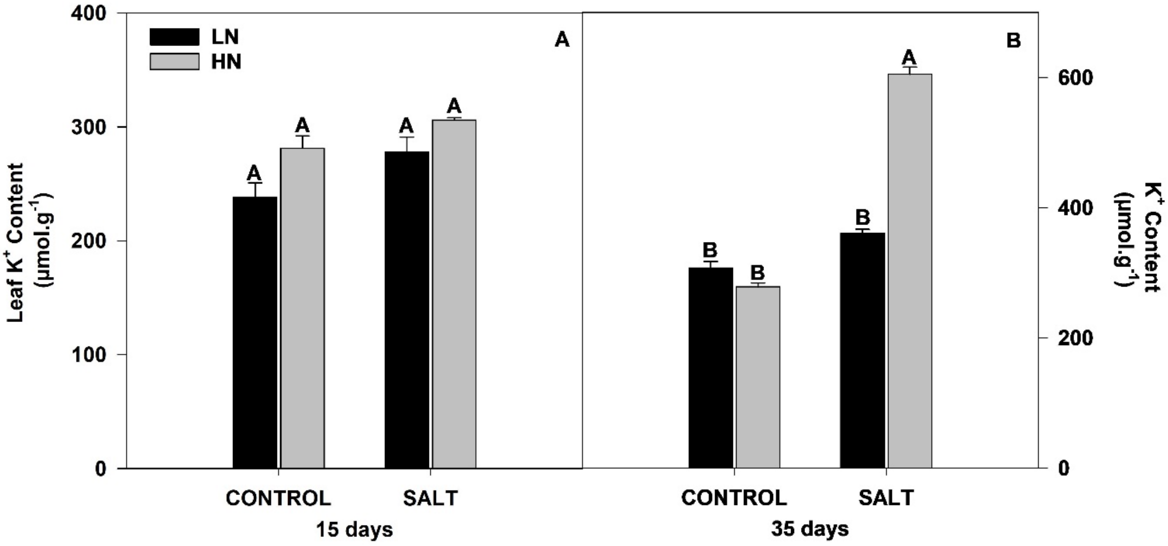


Figure 12 – Ionic stress indicators. Leaf K+ content (A), and leaf K+ content (B) in cashew seedlings after 15 (A) and 30 (B) days of high salinity treatment (100 mM) under two contrasting nitrate levels (0.1 mM NO_3^- – LN and 10 mM NO_3^- – HN). The treatments were applied 15 days after seedling emergency (DAE). Treatments and statistic comparisons are described in figure 1.



APÊNDICE C - FOTOS ORIGINAIS DO EXPERIMENTO

Figure 1 – Schematic experimental design of cashew trees exposed to high salinity (0 and 100 mM NaCl) in the presence of two contrasting levels of NO3-, 0.1 mM (low) and 10.0 mM (high), for 35 days at home of vegetation. The timeline of the experimental design (A) and the indication of the leaves used in the different measurements (B) are shown.

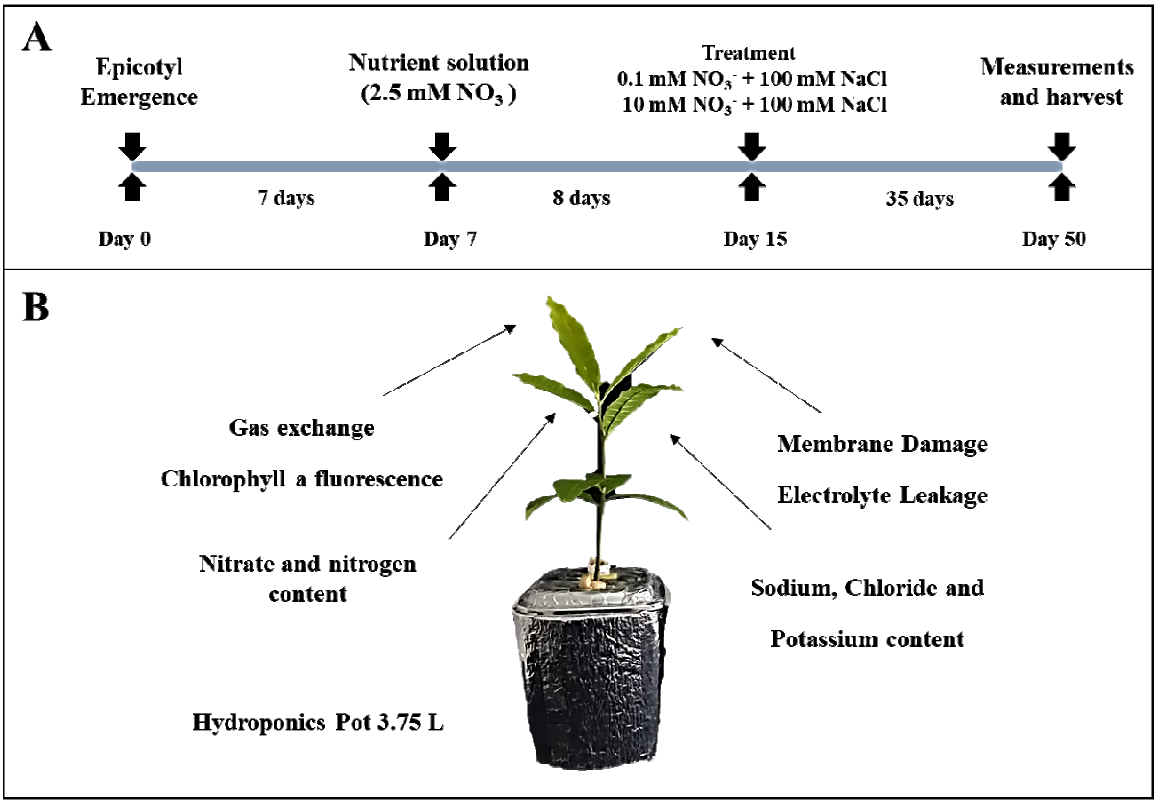
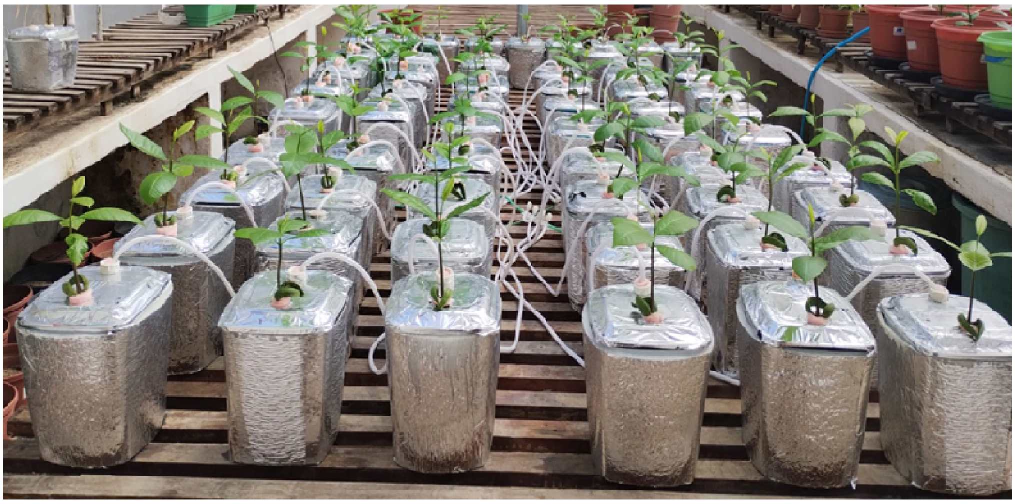


Figure 2 – Conducting the experiment. (A) emergence of the epicotyl and expansion of the four primary folios, (B) period of transplantation and acclimatization of seedlings to the hydroponic system (C) beginning of treatments.

A – Emergence of the epicotyl and expansion of the four primary folios

B – Period of transplantation and acclimatization (2.5 mM NO_3^-)



C – Treatments 0.1 mM NO_3^- + 100 mM NaCl - 10 mM NO_3^- + 100 mM NaCl

Figure 3 – Morphological aspects. (A) 10 mM NO3-, (B) 0.1 mM NO3-, (C) 10 mM NO3- + 100 mM NaCl (D) 0.1 mM NO3- + 100 mM NaCl in cashew seedlings after 7 days of treatment. The treatments were applied 15 days after seedling emergency (DAE).

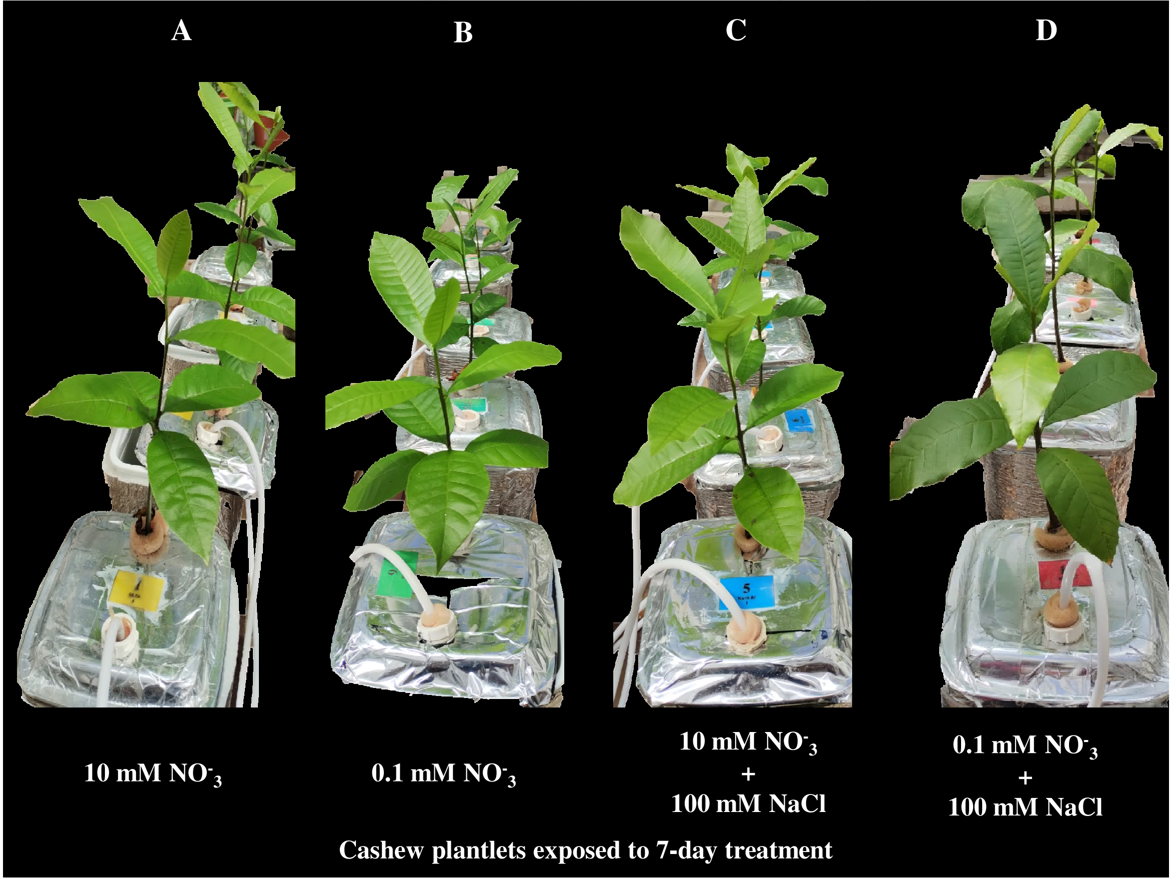


Figure 4 – Morphological aspects. (A) 10 mM NO3-, (B) 0.1 mM NO3-, (C) 10 mM NO3- + 100 mM NaCl (D) 0.1 mM NO3- + 100 mM NaCl in cashew seedlings after 20 days of treatment. The treatments were applied 15 days after seedling emergency (DAE).

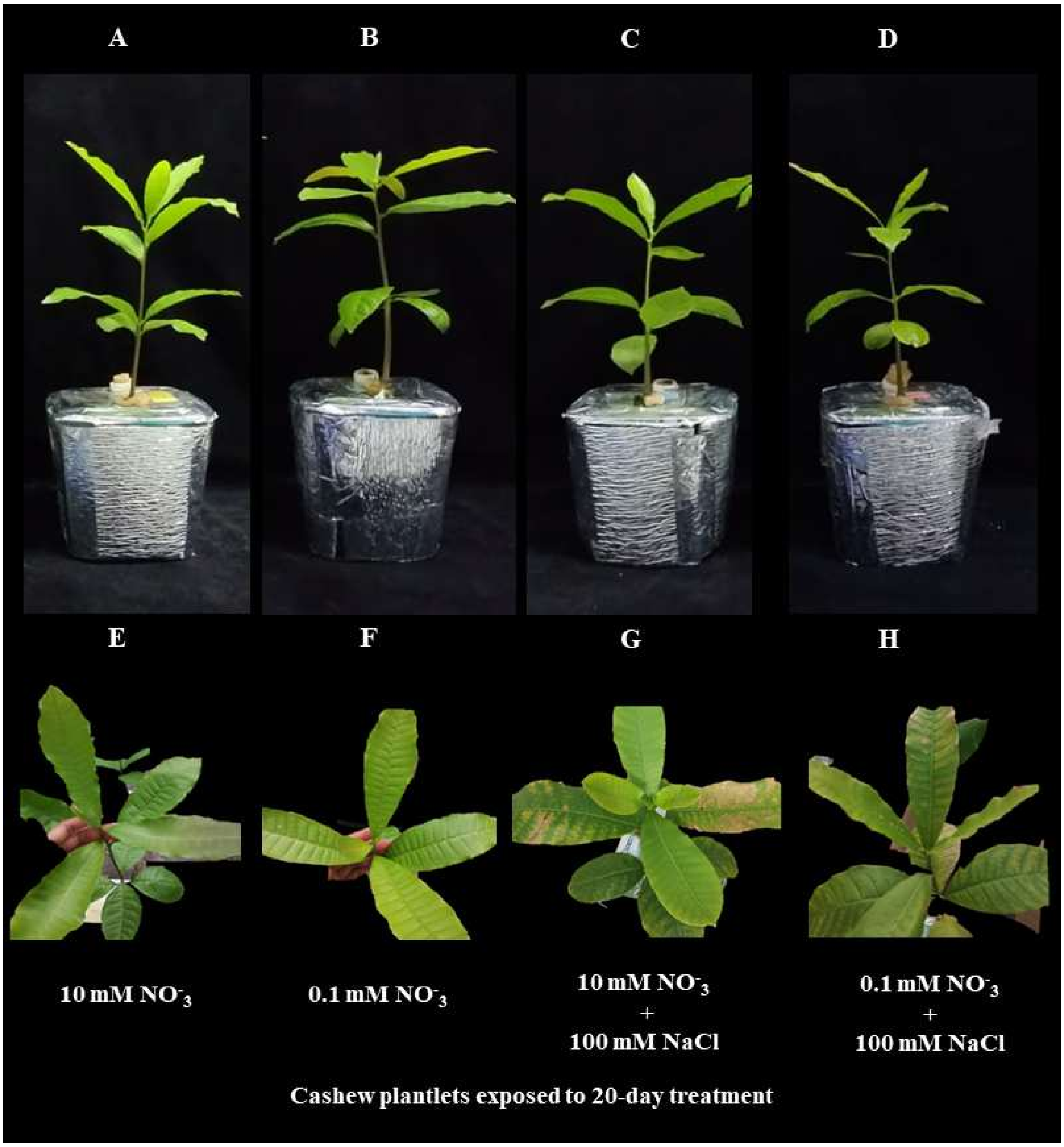


Figure 5 – Morphological aspects. (A) 10 mM NO3-, (B) 0.1 mM NO3-, (C) 10 mM NO3- + 100 mM NaCl (D) 0.1 mM NO3- + 100 mM NaCl in cashew seedlings after 35 days of treatment. The treatments were applied 15 days after seedling emergency (DAE).

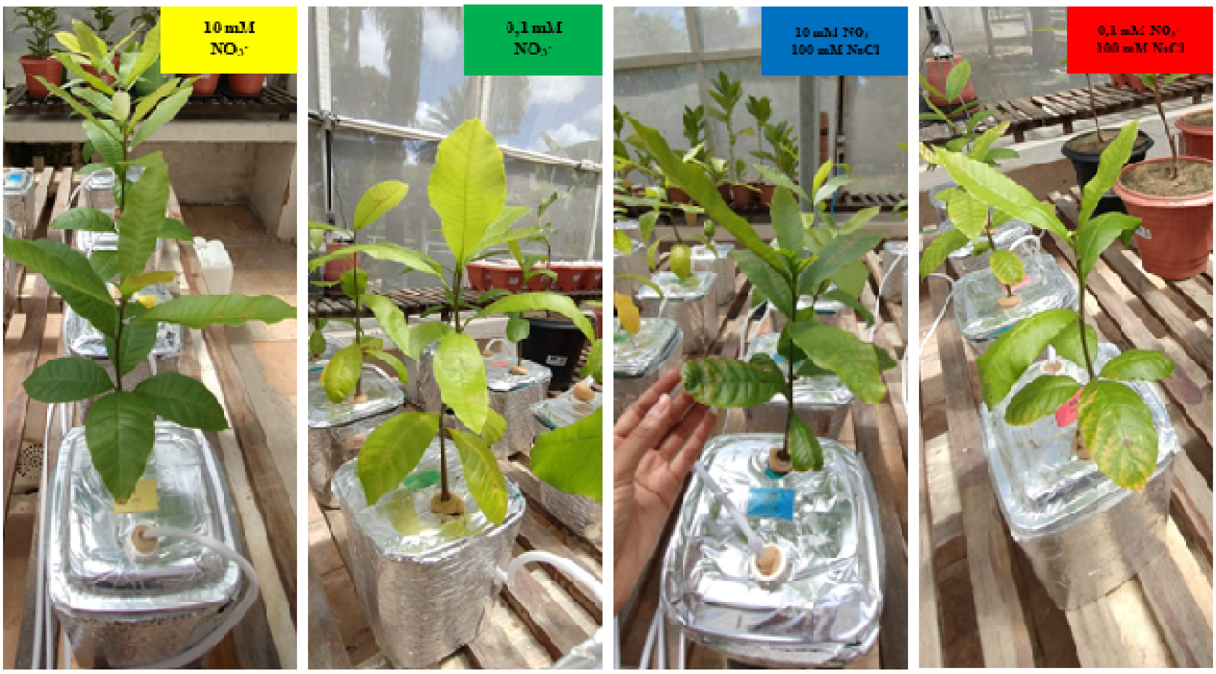
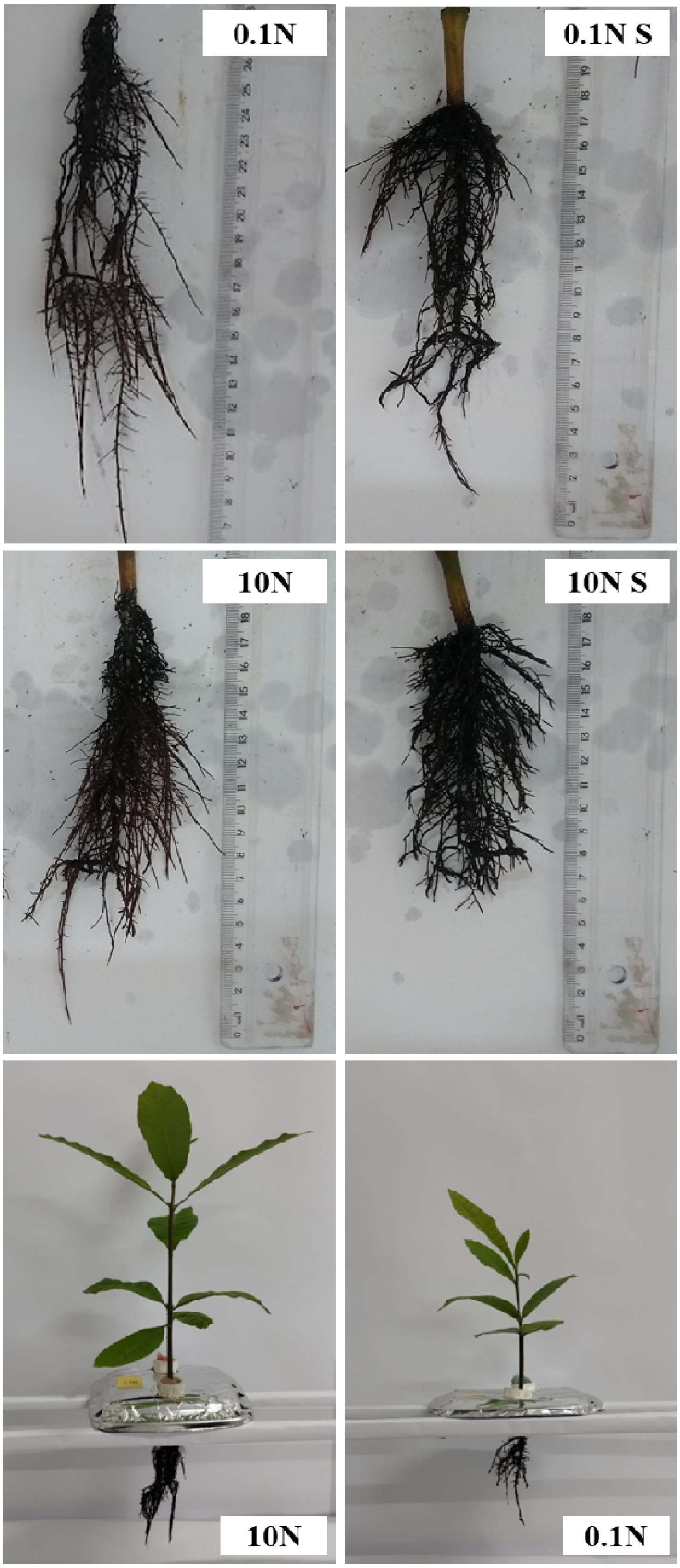
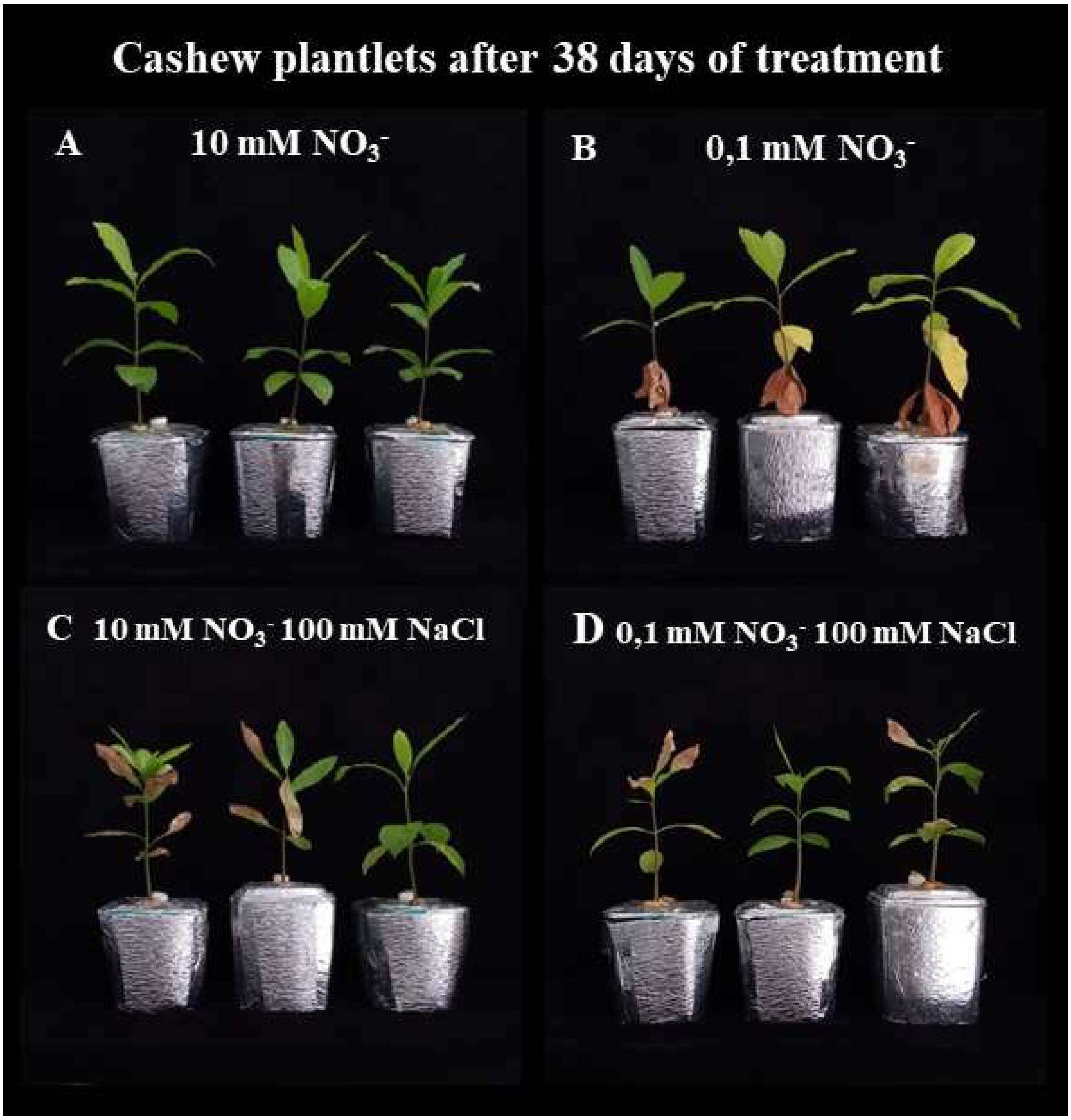


Figure 6 – Morphological aspects. (A) 10 mM NO3-, (B) 0.1 mM NO3-, (C) 10 mM NO3- + 100 mM NaCl (D) 0.1 mM NO3- + 100 mM NaCl in cashew seedlings after 35 days of treatment. The treatments were applied 15 days after seedling emergency (DAE).




Cashew plantlets after 38 days of treatment
A 10 mM NO3-
B 0,1 mM NO3-
C 10 mM NO3- 100 mM NaCl
D 0,1 mM NO3- 100 mM NaCl