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ORIGINAL ARTICLE

Effect of Water Stress on Morphological and Physiological Traits of some Almond Genotypes

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K E Y W O R D S

Dry matter;
GF677;
Fresh matter;
Irrigation;
Root;
Shoot

A B S T R A C T

A large area of Iran has a dry and semi-arid climate. Therefore, the optimal use of water resources in the agriculture is very important. This research was carried out using split-plot arranged based on randomized complete block design with in four replications. The irrigation as main plots included three levels of 100%, 80% and 60% crop water requirement, and almond genotype as sub-plots included A1, A2, A3, A8, A11, A13, A15, A16, A19, and A22. The results showed that the irrigation level and almond genotype had significant effect on morphological and physiological traits of almond genotypes. Also, the interaction between irrigation and almond genotype significantly affected all morphological and physiological traits of the plant. In irrigations of 80% and 60% crop water requirement, shoot fresh matter was decreased by 14.3% and 35.4%, respectively, and shoot dry matter was decreased by 14.5% and 34.4%, respectively. In irrigation of 60% crop water requirement, the maximum and minimum specific leaf area (SLA) were in the A2 and A1 genotypes, respectively. Also, the maximum and minimum shoot fresh and dry weights were in A2 and A13 genotypes, respectively. However, the maximum and minimum leaf relative water content (RWC) were in the A11 and A3 genotypes, respectively. The morphological and physiological traits of almond genotypes showed that A13, A3, A16, and A19 genotypes had good tolerance to water stress.

Introduction

Water and drought stresses are one of the most common environmental factors affecting the productivity of crops. Plants use different methods to cope with water shortages, and understanding these methods leads to appropriate decisions in irrigation management and the use of capable plant genotypes and cultivars in such conditions (Lotfi *et al.*, 2022). Water stress usually leads to a delay in growth and a significant reduction in the yield of agricultural and horticultural plants by reducing cell division and development, photosynthesis, stomatal conduction, and plant transpiration (Tankari *et al*., 2021; Kapoor *et al*., 2020).

Almond is one of the fruit trees in the temperate regions of the world (Imani *et al*., 2021; Ansari and Gharaghani, 2019). Almond trees usually show morphological and physiological adaptations for survival under water deficit conditions, but the almond

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cultivar's drought tolerance is different. Drought stress tolerance in almonds depends on leaf and root adaptation responses including osmotic adjustment by the production of adaptation materials, reduced stomatal conductance, leaf drop, reduced leaf area, reduced transpiration, increased root density and depth, and root-to-shoot ratio (Razav, 2024; Zokaee-Khosroshahi *et al*., 2014; Yadolahi *et al*., 2011; Isaakidis *et al*., 2004; Torrecillas *et al*., 1996; Ruiz Sanchez *et al*., 1993).

Evaluation of drought tolerance in some rootstocks and cultivars of fruit trees including apricot (Real Fino), peach (Montclar), almond (*P. webbii*) and (Garrigues and GF677) in Spain showed that the two almond species studied were more tolerant than the other species (Martínez-García *et al*., 2020). The evaluation of four irrigation intervals of 3, 5, 10 and 15 days on five grafted almond cultivars (Supernova, Texas, Marcona, Shokofeh and K13-40) on three different rootstocks showed that all cultivars grafted on GF677 rootstock were more tolerant to water stress. Supernova and Shokofeh cultivars grafted on GF677 rootstock were the most tolerant rootstock-graft combinations, but other rootstock-graft combinations were sensitive to water stress (Ranjbar *et al*., 2018).

The effects of water moderate and severe stress (soil water potential =-0.8, -1.6 MPa) were investigated on genotypes/cultivars of K3-3-1, H, 13-40, Sahand and Ferragness grafted on GN15 rootstock. The Sahand and Ferragnes cultivars and H genotype had high and medium tolerance to water stress, respectively, while K3-3-1 and K13-40 were identified as sensitive genotypes (Fathi *et al*., 2017).

The effect of drought stress was studied on some physiological characteristics of five grafted and ungrafted rootstocks including GF677, Garnem, peach seedlings, almond seedlings and a selected local almond× peach hybrid (LAP), with Ferragnes cultivar as a scion in pot plants during four weeks. Three different drought stress levels included moderate (Ψsoil=-0.9 Mpa) severe (Ψsoil=-1.5 Mpa) and a control (Ψsoil=-0.3 Mpa). Physiological traits of photochemical efficiency of photosystem II (Fv/Fm), leaf relative water content (RWC), Chl a, Chl b and total Chl were reduced significantly under drought stress, while proline was increased noticeably. Almond seedlings, GF677 and local LAP almost showed similar responses to drought stress and had more tolerance than Garnem rootstock (Moradi *et al*., 2019).

Investigating mechanisms of drought stress tolerance of GF677 rootstock, peach and almond hybrid, under in vitro conditions showed that the most important mechanisms of drought tolerance of GF677 rootstock are the use of an antioxidant defense system, increasing protein synthesis (enhancing gene expression) and proline accumulation (Mashayekhi *et al*., 2014; Lotfi *et al*., 2010a).

Comparison of the growth response of 13 almond cultivars (grafted on GN rootstock) to different levels of water stress including 70%, 50%, 30% and 10% field capacity showed in all cultivars, with increasing the drought stress intensity, the height, length and width of the seedlings crown, number and length of sub-branches, leaf area and concentration of nitrogen, phosphorus, manganese and zinc in the leaves of almond seedlings was decreased significantly. The GN, Shahrood 8 and Shahrood 12 cultivars in terms of growth characters showed higher tolerance to different levels of drought stress (Safavi *et al*., 2023).

A study of affective factors on drought resistance in one-year-old almond seedlings of Ramillete and Garrigues cultivars in Spain showed that by stopping irrigation for 28 days, the leaf conductance of almond seedlings of the Ramillet and Garrigues cultivars decreased by 79 and 62 percent, respectively (Torcilas *et al*., 1996). In Italy, the response of six cultivars and genotypes of 13-year-old almond trees to water stress was investigated with no irrigation and two irrigations in the summer. The results indicated that water stress significantly reduced parameters such as leaf water potential, crop evapotranspiration, photosynthetic water use efficiency, leaf stomatal conductance coefficient, number, area, weight and density of leaves. Of course, the response of almond cultivars and genotypes was different to water stress (Girona, 1997).

In Spain, the interruption of irrigation of Marcona almond trees at different growth stages showed that periods 15 May-15 June and 15 June-15 August were the most sensitive stages to water deficit (Girona *et al*., 1997). Herald *et al*. (2001) compared fruiting trees and one-year-old almond trees of Masbovera and Lauranne cultivars in Mediterranean climatic conditions (Spain) and found that the adjustment of osmotic pressure and leaf area values, water potential and water use efficiency were greater in Masbovera cultivar and overall this almond cultivar showed better adaptation to dryland conditions in the mentioned climate.

A study comparing five almond cultivars including Francoli, Ferragnes, Glorieta, Lauranne and Masbovera in Portugal assessed their responses to different irrigation conditions. The irrigation was applied three times a week from June 1 to late August, while one group received no irrigation at all. In most of the tested cultivars, leaf water potential, leaf stomatal conductance, leaf photosynthesis, and fruit wet and dry weight were significantly reduced under no-irrigation conditions (Gomes-Laranjo *et al*., 2006).

A study investigating the drought tolerance of six almond seedling genotypes including Shahroud 12, Shahroud 18, Shahroud 21, Talkh, Sefid and Butte was conducted under three different irrigation levels: moderate stress (s = -1.2 MPa), severe stress (s = -1.8 MPa) and a control treatment (s = -0.33 MPa). This investigation, carried out over five weeks, revealed that all genotypes showed an ability to tolerate moderate and severe stresses. Butte and Sefid genotypes had the lowest and highest tolerance to water stress, respectively, while the other genotypes were intermediate (Yadolahy *et al*., 2011).

Water stress on six commercial almond cultivars namely Azar, Sahand, Marcona, Mission, Nonparial and Supernova showed that in most almond cultivars, leaf relative water content (RWC) and net photosynthesis (Pn) significantly decreased. In water stress, soil moisture was maintained at a level of about 10% of soil water capacity. Azar and Supernova cultivars were more tolerant to drought stress, but Sahand and Marcona cultivars were sensitive to drought stress (Barzegar *et al*., 2012). In another study, responses to drought stress in six almond genotypes grafted on GF677 rootstock including Supernova, Ferragnès, Sefid, Mamaei, B-124 and 6-8 were evaluated withholding irrigation for 14 days and a subsequent 10 days rehydration period. The results indicated that leaf relative water content (RWC), photosynthetic intensity, and stomatal conductance of drought-sensitive genotypes significantly decreased by 23, 70, and 97 percent, respectively. Supernova, B-124, and 6-8 genotypes were more tolerant than other genotypes (Karimi *et al*., 2015).

Evaluation of the effects of irrigation with 100%, 75% and 65% water requirement on young five-year-old almond trees (cultivars Guara, Marta, and Lauranne) in Spain showed that although almond is a water-stress tolerant plant, the response of almond cultivars to water stress is different. Based on the results, irrigation at 75% of the water requirement was recommended for the Marta and Lauranne cultivars and at 75% of the water requirement for the Guara cultivar (Gutierrez-Gordillo *et al*., 2020).

This study was conducted to compare the response of different almond genotypes to water stress and selection-tolerant almond genotypes to water stress.

Materials and Methods

This study was conducted in the Temperate Fruit Research Center of Iran (49°35 N, 56°50' E, 1312 m a.s.l.) in Karaj city for two years. The average annual rainfall is 251.8 mm and the region climate is semi-arid and warm semi-arid (BSK) according to the De Martonne and Köppen classifications, respectively. To investigate tolerance of water stress in some almond genotypes, treatments were arranged in a split plot experiment based on RCBD design with 3 replications. The main plots were 10 almond promising genotypes namely A1, A2, A3, A8, A11, A13, A15, A16, A19 and A22 (Imani, 2024) and GF677 rootstock (control), and subplots were three irrigation levels of 100%, 80% and 60% crop water requirement (Table 1).

In May 2021, 150 GN tissue culture rootstocks were planted in pots of 40 cm diameter and depth. The pots were filled by sandy loam soil (Table 2). 10 selected almond genotypes were grafted onto the GN rootstocks in August 2022. The physical and chemical properties of irrigation water are presented in Table 3.

Table 1. Characteristics of the almond promising genotypes.

Genotype	Growth habit	Fruiting habit	Fruit yield	Fruit type	Growth habit	Flowering time
A1	Upright	Mixed	High	papery	Upright	Late-flowering
A2	Upright	Spure	High	Hard	Upright	Late-flowering
A3	Upright	Spure	High	Hard	Upright	Late-flowering
A8	Spread	Mixed	High	Semi papery	Spread	Late-flowering
A11	Spread	Mixed	Medium to high	Papery	Spread	Late-flowering
A13	Semi upright	Spure	High	Hard	Semi upright	Late-flowering
A15	Spread	Mixed	Medium to high	Papery	Spread	Late-flowering
A16	Semi upright	Mixed	Medium to high	Papery	Semi upright	Late-flowering
A19	Spread	Anoual	Medium to high	Hard	Spread	Early-flowering
A22	Semi upright	Spure	Medium to high	Hard	Semi upright	Late-flowering

Table 2. Physical and chemical properties of soil.

Texture	FC (%)	PWP (%)	EC (dS/m)	SAR	pH	Anions (meq lit^{-1})			Cations (meq lit^{-1})		
						CO_3^{--}	HCO_3^-	SO_4^{2-}	Na^+	Ca^{2+}	Mg^{2+}
Sandy Loam	16.5	7.5	2.2	1.7	7.9	0.8	5.4	–	5.2	15.1	4.0

Table 3. Characteristics of irrigation water.

EC (dS/m)	SAR	pH	Anions (meq lit^{-1})			Cations (meq lit^{-1})		
			CO_3^{--}	HCO_3^-	SO_4^{2-}	Na^+	Ca^{2+}	Mg^{2+}
0.44	0.8	7.9	0.1	3.0	–	1.0	2.2	1.0

The irrigation of GF677 rootstock and almond genotypes was carried out in July and August months according to 100%, 80% and 60% crop water requirement. Irrigation time was determined based on a management allowable deficit (MAD=0.4) or water stress conditions in control treatment (GF677 rootstock-100% crop water requirement). The management allowable deficit (MAD) is the average fraction of total available soil water (AW) that can be depleted from the root zone before water stress (reduction in evapotranspiration). The Food and Agriculture Organization (FAO) has recommended 0.4 for almond trees (Allen *et al*., 1998). Therefore, when soil moisture was depleted to 40% AW in control treatment (by daily weighing of pots), the volume of irrigation water (V) in 100% crop water requirement level required irrigation water was determined based on soil moisture deficiency from the field capacity from the following equations:

$$RAW = MAD.AW = MAD\ (FC-PWP) \quad (1)$$

$$D_n = RAW.D_r = MAD\ (FC-PWP)\ D_r \quad (2)$$

$$V = D_n.A$$

where RAW, FC and PWP are readily available water, field capacity and permanent wilting point of the soil, respectively. Also D_n, D_r and A are irrigation depth (cm), crop root depth or pot depth (cm) and pot area (cm^2), respectively.

In September 2023, we measured various morphological and physiological traits of the GF677 rootstock and almond genotypes. The traits assessed included plant height, stem diameter, leaf area, specific leaf area (SLA), leaf relative water content (RWC), levels of chlorophyll a, chlorophyll b, and total chlorophyll, leaf carotenoid content as well as fresh and dry matter for both roots and shoots. To determine the specific leaf area (SLA), four healthy leaves (in the same position) of each plant were separated and the fresh matter (W_f) and area of each leaf (A_{leaf}) were measured. The relative water content (RWC) is a useful indicator of the state of water balance of a plant essentially because it expresses the absolute amount of water, which the plant requires to reach artificial full saturation. Thus there is a relationship between RWC and water potential. This relation varies significantly according to the nature and age of plant material. The leaf RWC was accomplished by excising 1 cm disks of the plant four leaves. The five disks from each pot were weighed immediately, providing a measure of fresh matter (W_f). After weighing, the disks were soaked in deionized water for 24 hours and then weighed again to obtain a fully turgid matter (W_t). Finally, the leaf disks were dried at 85°C and weighed to get a dry matter (W_d). The SLA and leaf RWC are calculated as follows (Schlemmer *et al*., 2005; Dolati-Baneh *et al*., 2019):

$$SLA\ (cm^2\ g^{-1}) = A_{leaf}\ /W_f \quad (3)$$

$$RWC\ (\%) = (W_f-W_d) / (W_t-W_d) \quad (4)$$

The concentrations of leaf chlorophyll a, chlorophyll b, total chlorophyll and carotenoid were calculated using the following equations (Arnon, 1949):

$$\text{Chlorophyll a (mg g}^{-1}) = (12.7\ A663 – 2.69\ A645)\ V / 1000W \quad (5)$$

$$\text{Chlorophyll b (mg g}^{-1}) = (22.9\ A645 – 4.69\ A663)\ V / 1000W \quad (6)$$

$$\text{Total chlorophyll = chlorophyll b+ chlorophyll a (mg g}^{-1}) \quad (7)$$

$$\text{Carotenoid (mg/g)} = 1000\ (A470) - 2.27\ (\text{chl. a}) – 81.4\ (\text{chl. b}) /22 \quad (8)$$

In this context, A represents the light absorption at wavelengths of 663 nm, 645 nm, and 470 nm. V refers to the volume of the extract in milliliters (ml), while W denotes the fresh weight of the leaves in grams (g). Additionally, chl. a and chl. b stand for the chlorophyll a and chlorophyll b content in the leaf, respectively.

All experimental data were analyzed using robust statistical methods to ensure the accuracy and reliability of the findings. Before analysis, all datasets were checked for outliers using box plots and normalized using log transformations when necessary to meet the assumptions of parametric tests. A two-way ANOVA was conducted to assess the effects of irrigation and almond genotype on the measured variables. The significance level was set at 5% and 1%. All the measured traits were analyzed for variance according to the type of experimental design and the means of the tested treatments were compared with Duncan's multiple range test. SPSS and Excel software were used for statistical analysis of the data and drawing graphs.

Results

The results indicated that irrigation treatments significantly affected all morphological and physiological traits of the GF677 rootstock and almond genotypes, except for chlorophyll b and total chlorophyll. In most morphological and physiological traits, irrigation 100% and 60% water requirement had the highest and lowest values, respectively (Table 4). The statistical analysis of morphological and physiological traits showed that there was a significant difference between the almond genotypes (Table 5). The highest shoot fresh and dry matters, chlorophyll a, chlorophyll b, total chlorophyll, carotenoid and leaf relative water content (RWC) were in the GF677 rootstock. The highest stem diameter and specific leaf area (SLA) were in A22 genotype, and the highest leaf area and root fresh and dry matters were in A15 genotype. The A22 genotype had the lowest fresh and dry matter for both shoot and root. The A11 genotype exhibited the lowest levels of chlorophyll a, chlorophyll b, total chlorophyll, carotenoid content, and leaf relative water content (RWC).The lowest leaf area was in A16 genotype, and the lowest stem diameter and specific leaf area (SLA) were in A8 and A1 genotypes, respectively. Also, the interaction effects of irrigation level and almond genotype on all morphological and physiological traits of the tested almond seedlings were significant (Table 6).

Morphological traits

Table 4 shows that the irrigation level significantly affected all morphological traits, including height, stem diameter, leaf area, specific leaf area (SLA), as well as both fresh and dry matter of the shoot and root. Water stress caused a significant decrease in all plant morphological traits, so that irrigations 80% and 60% water requirement caused a decrease of 20.6% and 34.3% in leaf area, 9.8% and 17.9% in SLA, 14.3% and 35.4% in shoot fresh matter and 14.5% and 34.4% in shoot dry matter, respectively (Fig. 1). But, irrigations 80% and 60% water requirement increased almond genotypes root fresh matter to 12.2% and 10.8% and root dry matter to 7.5% and 9.6%, respectively, compared to irrigation with 100% water requirement.

The interaction effects of irrigation and almond genotype (Table 6) showed that in irrigation 80% water requirement, the highest and lowest height reductions were related to A15 (26.7%) and A19 (11.6%) genotypes, respectively, compared to irrigation 100% water requirement. In the case of irrigation at 60% water requirement, the highest and lowest height reductions were observed in A2 (42.2%) and A13 (21.3%) genotypes, respectively, when compared to the 100% water requirement scenario. While GF677 rootstock (control) height reduction was 17.8% and 24.4%, respectively, in irrigations 80% and 60% water requirement. The highest and lowest reduction of stem diameter in irrigation 80% water requirement was related to A2 (25.7%) and A13 (7.1%) genotypes, respectively, compared to irrigation 100% water requirement. In irrigation 60% water requirement, the highest and lowest reduction of stem diameter were related to A2 (43.4%) and A13 (17.5%) genotypes, respectively. The reduction of stem diameter in the GF677 rootstock (control) was 6.3% and 11.9%, respectively, when the irrigation level was reduced to 80% and 60% water requirement.

Table 4. Mean comparison of irrigation level effect on almond genotypes traits.

Irrigation level	Height (cm) **	Stem diameter (mm) **	Leaf Area (cm^2) **	Specific leaf area (cm^2 g^{-1}) **	Shoot fresh matter (g) **	Shoot dry matter (g) **	Root fresh matter (g) **	Root dry matter (g) **	Chlorophyll a (mg.g^{-1}) *	Chlorophyll b (mg.g^{-1}) *	Chlorophyll a+b (mg.g^{-1}) *	Carotenoid (mg.g^{-1}) *	RWC (%)**
100%	4.5 a	3.4 a	20.4 a	110.1 a	46.9 a	24.1 a	235.0 c	104.8 b	0.71 a	0.45 a	1.16 a	7.2 ab	70.3 a
80%	3.7 b	2.8 b	16.2 b	99.2 b	39.9 b	20.3 b	263.7 a	112.7 a	0.66 b	0.43 a	1.09 a	6.8 b	65.4 b
60%	3.1 c	2.4 c	13.4 c	90.4 c	30.3 c	15.8 c	253.7 b	114.9 a	0.68 ab	0.44 a	1.11 a	7.3 a	62.4 c

*, ** significance at 5 and 1%, respectively

Table 5. Mean comparison of genotype effect on almond genotypes traits.

Almond genotype	Height (cm) **	Stem diameter (mm) **	Leaf Area (cm^2) **	Specific leaf area (cm^2 g^{-1}) **	Shoot fresh matter (g) **	Shoot dry matter (g) **	Root fresh matter (g) **	Root dry matter (g) **	Chlorophyll a (mg g^{-1}) *	Chlorophyll b (mg g^{-1}) *	Chlorophyll a+b (mg g^{-1}) *	Carotenoid (mg.g^{-1}) *	RWC (%)**
GF677	3.78 abc	2.98 ab	20.4 a	120.9 a	60.7 a	32.4 a	215.6 d	71.2 f	0.94 a	0.62 a	1.56 a	10.7 a	74.5 a
A1	4.05 ab	2.75 bc	18.7 a	80.8 e	39.1 cd	21.1 bc	286.9 a	131.9 bc	0.70 bcd	0.43 cd	1.13 cd	6.9 cd	64.3 cd
A2	3.62 c	2.69 bc	21.0 a	103.8 b	38.1 cd	19.3 c	237.0 c	110.4 e	0.70 bcd	0.45 cd	1.15 cd	7.1 bcd	67.9 bc
A3	3.62 c	3.10 ab	15.1 b	104.2 b	43.6 b	21.6 b	256.6 b	109.2 e	0.83 ab	0.53 b	1.36 b	8.3 b	66.4 bc
A8	3.88 abc	2.40 c	15.1 b	98.7 bc	39.5 cd	20.3 bc	255.2 b	121.9 cd	0.77 bc	0.50 bc	1.27 bc	7.9 bc	64.2 cd
A11	3.67 bc	2.82 abc	19.2 a	97.7 bc	38.4 cd	20.4 bc	281.7 a	132.9 b	0.40 e	0.27 e	0.67 e	4.4 e	55.1 e
A13	4.12 a	3.09 ab	14.8 b	94.8 cd	37.3 d	20.1 bc	256.8 b	110.3 e	0.67 cd	0.44 cd	1.11 cd	7.0 d	60.7 d
A15	3.61 c	2.44 c	21.2 a	94.6 cd	40.6 bc	20.4 bc	290.6 a	150.0 a	0.61 d	0.39 d	1.00 d	6.5 d	67.2 bc
A16	3.50 c	2.77 bc	10.9 d	90.9 c	30.0 f	14.8 e	240.1 c	108.0 e	0.62 d	0.43 cd	1.05 d	6.5 d	71.0 ab
A19	3.71 abc	3.12 ab	14.9 b	86.7 de	33.9 e	16.9 d	263.6 b	111.8 de	0.62 d	0.37 d	0.99 d	6.2 d	68.4 bc
A22	3.83 abc	3.23 a	12.3 cd	125.5 a	27.8 f	13.4 e	174.9 e	61.3 f	0.62 d	0.41 d	1.03 d	6.0 cd	66.7 bc

*, ** significance at 5 and 1%, respectively

Table 6. Interaction effect of irrigation and almond genotype on morphological and physiological traits

Almond genotype & Irrigation level	Height (cm) **	Stem diameter (mm) **	Leaf Area (cm^2) **	Specific leaf area (cm^2 g^{-1}) **	Shoot fresh matter (g) **	Shoot dry matter (g) **	Root fresh matter (g) **	Root dry matter (g) **	Chlorophyll a (mg g^{-1}) *	Chlorophyll b (mg g^{-1}) *	Chlorophyll a+b (mg g^{-1}) *	Carotenoid (mg.g^{-1}) *	RWC (%)**
GF677-100%	4.5 abc	3.18 c-h	23.8 ab	137.1 a	75.2 a	39.5 a	211.8 klm	66.1 klm	0.91 ab	0.64 a	1.55 abc	10.9 a	76.5 a
GF677-80%	3.7 d-h	2.98 d-k	20.3 a-e	117.2 cde	60.4 b	31.9 b	241.5 hij	81.7 jkl	0.96 a	0.62 ab	1.59 a	10.8 a	74.0 abc
GF677-60%	3.4 e-h	2.80 e-l	17.1 d-i	108.5 c-f	46.4 cde	25.8 c	19.3.6 l-o	65.7 klm	0.96 a	0.60 abc	1.56 ab	10.4 ab	73.2 a-d
A1-100%	4.8 a	3.33 b-f	23.7 ab	81.8 m	45.6 cde	24.4 c	219.0 jkl	84.1 ijk	0.80 a-f	0.48 b-h	1.29 a-f	7.4 c-g	70.8 a-f
A1-80%	3.8 c-g	2.60 h-l	17.8 c-h	80.8 m	42.7 def	23.0 cd	438.7 a	215.7 a	0.66 c-h	0.40 e-i	1.06 d-i	6.9 c-h	63.7 c-i
A1-60%	3.5 e-h	2.33 lm	14.5 g-l	79.9 m	29.1 k-o	15.8 g-k	203.0 k-n	96.0 f-j	0.65 c-h	0.41 e-i	1.06 d-i	6.5 d-i	58.4 hij
A2-100%	4.5 abc	3.50 a-d	24.5 a	119.9 cd	50.7 c	25.7 c	246.0 hij	135.2 c	0.75 a-f	0.50 a-f	1.25 a-f	8.0 c-g	71.9 a-e
A2-80%	3.7 d-h	2.60 h-l	20.4 a-e	102.4 d-j	37.7 f-i	19.1 e-h	220.7 jkl	88.9 g-j	0.63 c-h	0.38 e-i	1.00 e-k	6.2 f-i	66.7 a-h
A2-60%	2.6 i	1.98 m	18.2 c-g	89.1 g-m	25.9 no	13.2 kl	244.3 hij	107.1 efg	0.73 a-g	0.46 c-h	1.19 b-h	7.4 c-g	65.2 b-h
A3-100%	4.2 a-e	3.60 abc	22.4 abc	117.5 cd	48.1 cd	23.7 cd	168.0 op	58.7 mn	0.78 a-f	0.49 a-g	1.27 a-f	7.3 c-g	66.8 a-h
A3-80%	3.5 e-h	3.00 c-j	14.1 g-l	105.2 c-g	46.0 cde	22.5 cde	374.3 b	174.9 b	0.86 abc	0.58 a-d	1.44 a-d	8.8 a-d	66.2 b-h
A3-60%	3.2 ghi	2.73 g-l	8.6 mn	90.0 g-m	36.8 f-i	18.5 e-i	227.3 jk	93.9 f-j	0.84 a-d	0.53 a-e	1.36 a-e	8.8 a-d	66.0 b-h
A8-100%	4.5 abc	2.80 e-l	16.4 d-j	110.1 c-f	48.2 cd	24.2 cd	220.0 jkl	103.8 f-i	0.79 a-f	0.49 a-g	1.28 a-f	7.7 c-g	69.8 a-j
A8-80%	3.8 c-g	2.43 j-m	15.9 e-j	99.4 f-l	43.1 def	22.5 cde	179.3 no	62.5 lm	0.69 b-h	0.47 b-h	1.16 c-h	6.8 c-h	61.5 f-i
A8-60%	3.3 f-i	1.98 m	12.9 i-m	86.7 i-m	27.2 no	14.2 ijk	366.3 b	199.5 a	0.83 a-e	0.53 a-e	1.36 a-e	9.3 abc	61.2 f-i
A11-100%	4.3 a-d	3.40 b-e	20.8 a-d	107.6 c-f	48.4 cd	25.7 c	300.7 de	139.9 c	0.44 hi	0.28 i	0.73 ijk	4.6 hi	76.7 a
A11-80%	3.7 d-h	2.73 g-l	20.4 a-e	100.4 e-k	38.2 f-i	19.8 d-g	266.7 fgh	127.1 cd	0.38 i	0.26 i	0.64 k	4.2 i	60.1g-j
A11-60%	3.0 hi	2.33 lm	15.9 e-j	85.2 klm	28.6 l-o	15.8 g-k	277.7 efg	131.7 cd	0.38 i	0.26 i	0.64 k	4.4 hi	46.5 k
A13-100%	4.7 ab	3.37 b-e	19.6 b-f	104.9 c-h	40.0 e-h	21.7 c-f	224.0 jk	105.3 fgh	0.63 c-h	0.40 e-i	1.02 e-k	6.3 e-i	58.6 hij
A13-80%	4.0 b-f	3.13 c-h	12.7 i-m	93.2 f-m	36.3 f-j	19.8 d-g	289.0 ef	113.7 def	0.63 c-h	0.42 e-i	1.05 d-j	6.4 d-i	54.1 ijk
A13-60%	3.7 d-h	2.78 f-l	12.1 j-m	86.3 j-m	35.5 g-k	18.8 e-i	257.3 gh	111.8 def	0.75 a-f	0.49 a-g	1.24 a-f	8.2 b-f	51.4 jk
A15-100%	4.5 abc	2.98 d-k	22.9 ab	102.9 d-j	50.8 c	26.1 c	326.7 c	173.4 b	0.60 d-i	0.39 e-i	0.99 e-k	6.1 f-i	71.5 a-f
A15-80%	3.3 f-i	2.38 klm	20.9 a-d	94.2 f-m	37.0 f-i	18.6 e-i	247.3 hij	103.6 f-i	0.60 d-i	0.38 e-i	0.98 e-k	6.3 e-i	66.7 a-h
A15-60%	2.9 hi	1.98 m	19.7 b-e	87.7 h-m	33.9 h-m	16.5 g-j	297.7 de	172.9 b	0.63 c-h	0.40 e-i	1.04 e-j	7.2 c-g	63.6 d-i
A16-100%	4.0 b-f	3.10 c-i	13.2 h-l	100.1 f-k	34.2 h-m	17.3 g-j	246.7 hij	113.5 def	0.73 a-g	0.48 b-h	1.20 a-g	7.2 c-g	74.7 ab
A16-80%	3.5 e-h	2.73 g-l	10.4 lm	93.6 f-m	31.5 i-n	15.2 h-k	254.7 ghi	125.7 cde	0.68 b-h	0.46 c-h	1.14 d-h	6.7 d-i	69.2 a-j
A16-60%	3.0 hi	2.50 i-m	9.1 mn	78.9 m	24.4 op	12.0 kl	219.0 jkl	84.9 h-k	0.45 hi	0.35 f-i	0.80 h-k	5.6 ghi	69.2 a-j
A19-100%	4.3 a-d	3.88 ab	16.9 d-i	94.2 f-m	39.4 e-h	20.0 d-g	211.7 klm	93.5 f-j	0.56 f-i	0.33 ghi	0.89 f-k	5.4 ghi	71.0 a-f
A19-80%	3.8 c-g	3.10 c-i	14.0 g-l	83.2 klm	36.2 f-j	17.3 f-j	263.3 fgh	103.6 f-i	0.56 f-i	0.35 f-i	0.91 f-k	5.5 ghi	69.6 a-j
A19-60%	3.0 hi	2.38 klm	13.9 g-l	82.7 lm	26.0 no	13.4 jkl	315.7 cd	138.3 c	0.74 a-f	0.44 d-h	1.18 b-h	7.6 c-g	64.6 b-h
A22-100%	4.7 ab	4.03 a	19.8 b-e	135.4 ab	34.9 h-l	17.1 g-j	211.0 klm	79.0 jkl	0.80 a-f	0.52 a-e	1.32 a-e	8.8 a-d	69.7 a-j
A22-80%	3.8 c-g	3.28 c-f	11.2 klm	121.7 bc	29.4 j-o	13.5 jkl	125.0 p	42.2 n	0.58 e-i	0.39 e-i	0.97 e-k	5.8 f-i	67.7 a-h
A22-60%	3.0 hi	2.40 j-m	5.9 n	119.3 cd	19.0 p	9.6 l	188.7 mno	62.8 lm	0.49 ghi	0.32 hi	0.81 g-k	5.4 ghi	62.6 e-i

*, ** significance at 5 and 1%, respectively

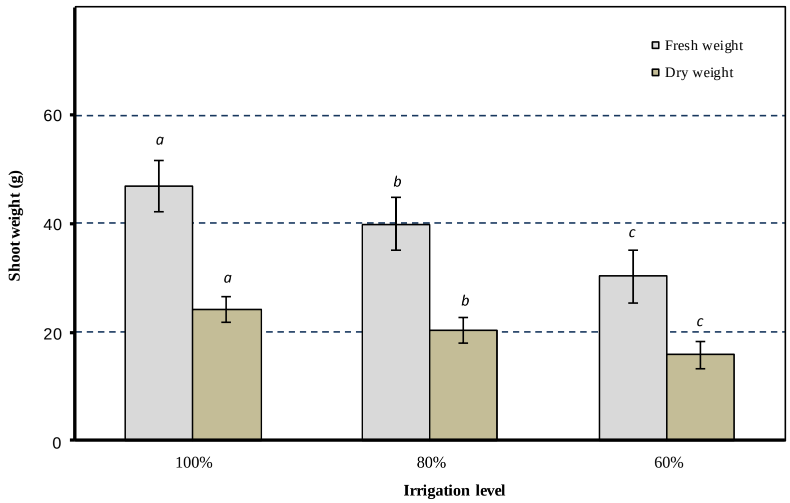

Fig. 1. The effect of irrigation level on shoot fresh and dry matter of almond genotypes

The highest and lowest leaf area reduction in irrigation 80% water requirement were in A22 (43.4%) and A11 (1.9%) genotypes, respectively, compared to irrigation 100% water requirement. However, in irrigation 60% water requirement, the highest and lowest leaf area reduction were in A22 (70.2%) and A15 (14.0%) genotypes, respectively. While the leaf area reduction of GF677 rootstock (control) in irrigations 80% and 60% water requirement were 14.7% and 28.2%, respectively.

The highest and lowest reduction of specific leaf area (SLA), in irrigation 80% water requirement was related to A2 (14.6%) and A1 (1.2%) genotypes, respectively, compared to irrigation 100% water requirement. In irrigation 60% water requirement, the highest and lowest reduction of SLA were related to A2 (25.7%) and A1 (2.3%) genotypes, respectively. However, the SLA reduction of the GF677 rootstock in irrigations 80% and 60% water requirement were equivalent to 14.5% and 20.9%, respectively.

The highest and lowest shoot fresh matter reduction in irrigation 80% water requirement was related to A15 (27.2%) and A3 (4.4%) genotypes, respectively, compared to irrigation 100% water requirement. Also, Genotypes A13, A16 and A19 had 9.3%, 7.9% and 8.1% reduction in shoot fresh matter, respectively. However, in irrigationt 60% water requirement, the highest and lowest shoot fresh matter reduction was related to A2 (48.9%) and A13 (11.3%) genotypes, respectively, compared to irrigation at 100% water requirement. Genotypes A3, A16 and A19 had 23.5%, 28.7% and 34.0% reduction in shoot fresh matter, respectively. In the GF677 rootstock (control), the reduction of shoot fresh matter for the irrigations at 80% and 60% of water requirements was 19.7% and 38.0%, respectively.

The highest and lowest shoot dry matter reduction in irrigation 80% water requirement were related to A15 (28.7%) and A3 (5.1%) genotypes, respectively, compared to irrigation 100% water requirement. However, in irrigation 60% water requirement, the highest and lowest shoot dry matter reduction were related to A2 (48.6%) and A13 (13.4%) genotypes, respectively. The reduction of shoot dry matter of GF677 rootstock (control) in irrigations 80% and 60% water requirement were 19.2% and 44.8%, respectively.

Therefore, the reduction of shoot dry matter of A1, A3, A8, A13, A16, and A19 genotypes in irrigation 80% water requirement and A3, A13, A16, and A19 genotypes in irrigation 60% water requirement were less than the reduction of shoot fresh matter of GF677 rootstock.

The response of different almond genotypes to water stress varied in terms of root fresh and dry matter. For the A1, A3, A13, A16, and A19 genotypes, root fresh matter increased by 3% to 123% under irrigation that provided 80% water requirement. In contrast, the A2, A8, A11, A15, and A22 genotypes experienced a decrease of approximately 41% in root fresh matter under the same irrigation conditions. When the irrigation was reduced to 60% water requirement, genotypes A3, A8, A13, and A19 showed an increase of about 67% in root fresh matter. However, root fresh matter decreased by about 11% for A1, A2, A11, A15, A16 and A22 genotypes under these conditions. While root fresh matter of GF677 rootstock (control) increased by about 14% in irrigation 80% water requirement, it decreased by about 9% in irrigation 60% water requirement.

The root dry matter increased about 11-198% in A1, A3, A13, A16, and A19 genotypes when irrigated by 80% water requirement, while it decreased about 47% in A2, A8, A11, A15, and A22 genotypes. The root dry matter increased by 92% in irrigation 60% water requirement in A1, A3, A8, A13, and A19 genotypes, but it decreased by 25% in A2, A11, A15, A16, and A22 genotypes. The root dry matter of GF677 rootstock (control) increased by 24% in irrigation 80% water requirement, and it decreased slightly (1%) in irrigation 60% water requirement. In general, species and cultivars with greater rooting power are more tolerant to water stress (Sardabi *et al*., 2003).

Physiological traits

The leaf “chlorophyll a” in irrigation 80% water requirement, decreased (non-significant) in most almond genotypes, but in irrigation 60% water requirement, it increased slightly (non-significant) in some tested genotypes (Table 4). The highest and lowest “chlorophyll a” were related to A3 genotype in irrigation 80% water requirement and A11 genotype in irrigation 60% water requirement, respectively. The change of leaf “chlorophyll b” in almond genotypes was similar to “chlorophyll a”, such that the highest and lowest “chlorophyll b” belonged to A3 genotype in irrigation 80% water requirement and A11 genotype in irrigation 60% water requirement, respectively. Also, The leaf total chlorophyll decreased slightly in most almond genotypes in irrigation 80% water requirement and then increased slightly in some tested genotypes in 60% water requirement. The highest and lowest leaf catenoids were in the A8 genotype in irrigation 60% water requirement and genotype A11 in irrigation 80% water requirement, respectively. The decrease in chlorophyll content is due to the destruction of the chloroplast structure and the instability of protein pigment compounds under water stress. The decrease in chlorophyll content can also be due to changes in nitrogen metabolism in relation to the production of compounds such as proline, which are used in osmotic regulation (Lotfi *et al.*, 2010b). Proline synthesis under water stress reduces chlorophyll synthesis (Asadi *et al*., 2020; Sinegh *et al*., 2000; Pavlcic, 2011). However, according to the results of this research, it seems that the process of leaf chlorophyll changes depends on the water stress severity. Some researchers suggest that water stress may increase leaf chlorophyll due to a higher number of cells per unit area or leaf matter (Kardrostami *et al*., 2017; Govan *et al*., 2003). The reduction of leaf chlorophyll content due to water stress has been reported in a large number of fruit trees such as almond, grape and olive (Asadi *et al*., 2020; Arji and Arzani, 2008; Zakai Khosrowshahi *et al*., 2014).

The leaf relative water content (RWC) in almond genotypes showed a significant reduction with increasing water stress, such that irrigation 80% and 60% water requirement have reduced 7.0% and 11.2% RWC compared to irrigation 100% water requirement, respectively (Fig. 2). In irrigations with 80% and 60% water requirement, the highest reduction of RWC was in the A11 genotype (21.6% and 39.4%, respectively) and the lowest reduction of RWC was in A3 genotype (1.0% and 1.2%, respectively) compared to irrigation at 100% water requirement. While RWC reduction of GF677 rootstock (control) in irrigations 80% and 60% water requirement were 3.3% and 4.3%, respectively.

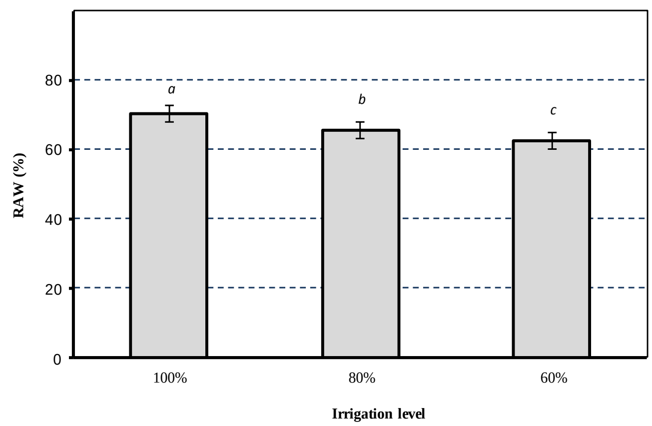

Fig. 2. Effect of irrigation on leaf relative water content (RWC) of almond genotypes.

Discussion

Although almonds are a drought-resistant species, with water stress is becoming one of the main limiting factors for horticultural plant growth. Plants can change their morphological and physiological responses at both organ and cellular levels to reduce the drought severity (Alavipanah *et al*., 2022; 2018; Rousta *et al*., 2022). Nowadays, due to climate problems and the lack of water resources for the cultivation of crops, it is necessary to use cultivars resistant to water stress for economic production (Mansourmoghaddam *et al*., 2022). This research results indicated water stress on morphological characteristics of almond genotypes had negative effect (Table 4). Since growth is one of the most sensitive plant processes to water stress, therefore, growth reduction is the first plant response to irrigation deficit in many plant species, including almonds (Safavi *et al*., 2023; Gupta *et al*., 2020; Gutierrez-Gordillo *et al*., 2020). One important strategy plants use to cope with water stress is to reduce both the area and number of their leaves. The water deficiency can be a negative effect on cell growth and prevents the formation and growth of wood vessels. Water stress reduces cell division due to the effects of water deficiency on activities such as the production of cell wall materials (Martínez-Sancho *et al.,* 2022; Tankari *et al*., 2021; Kapoor *et al*., 2020). The response of plants to water stress is usually observed in leaf and root, and morphological and physiological traits can best reflect the degree of adaptation to environmental stresses. The leaf is the most variable plant organ in long-term adaptation to water stress, responding with symptoms such as twisting, senescence and shedding. Water stress usually leads to a decrease in plant photosynthesis by reducing the leaf number and area and even stopping leaf growth (Wu *et al*., 2022). The effect of water stress on ten almond promising genotypes indicate the significant negative effect of water stress on morphological characteristics such as chlorosis, leaf fall, trunk diameter and plant height (Gohari *et al.,* 2023). Roohi *et al*. (2007) reported that wild almond genotypes lost their leaves during drought stress, but it seems that most of the almond genotypes tested in this research can maintain their leaves under water stress and compensate for the stress with structural and physiological changes (resistance mechanisms).

The A22 genotype had the highest reduction of leaf area in irrigations 80% and 60% water requirement compared to irrigation 100% water requirement (2.95 and 2.49 times the GF677 rootstock, respectively). While A11 and A15 genotypes had the lowest reduction of leaf area, respectively, in irrigations 80% and 60% water requirement (12.9% and 50% the GF677 rootstock, respectively). Most plants have various mechanisms such as reduced leaf area, osmotic regulation, increased storage organs, high water retention and retention capacity, and reduced stomatal conductance to avoid or tolerate water stress and also increase water productivity (Dego *et al*., 2019). Although almond seedlings usually retain their leaf even under severe stress conditions, leaf area decreases to compensate for the effects of stress (Alvarez *et al*., 2020; Yadolahi *et al*., 2011). Water stress on seedlings of five almond species caused a significant reduction in both leaf number and area, with decreases of 36.7% and 51.9%, respectively. (Zakaei-Khosrowshahi *et al*., 2014). Also, an examination of 15 almond cultivars in spring and summer (Italy) indicated a significant decrease in leaf area and stomata number when rainfall decreased under dry-land conditions. The leaf area of the almond species A. webbii significantly decreased by 31%. (Composio *et al*., 2011). A decrease in leaf area due to water stress has also been reported on other crops such as strawberries (Grant *et al*., 2010) and grapes (Dolati-Baneh *et al*., 2019). Fernandez de Oliveira *et al.* (2023) reported that leaf size and roughness may be key characteristics of almond water stress responses and for the efficient endurance of the photosynthetic apparatus, influencing leaf stomatal conductance, transpiration and cell turgor.

The A2 genotype had the highest reduction of specific leaf area (SLA) in irrigations 80% and 60% water requirement compared to irrigation 100% water requirement (1.0 and 1.23 times the GF677 rootstock, respectively). But, A1 genotype had the lowest reduction of specific leaf area in irrigations 80% and 60% water requirement (8.3% and 11.0% the GF677 rootstock, respectively). The SLA is one of the most important plant indicators. This index value depends greatly on environmental conditions and the plant's internal functions.Usually, plants with a high specific leaf area have more nitrogen, and their carbon dioxide absorption ratio per unit leaf matter and nitrogen absorption ratio per unit root area are higher. On the other hand, in plants with a low specific leaf area, the ratio of dry matter to fresh matter is usually higher and the leaves and roots have longer lives (Marshall and Mansrud, 2003; Shipley, 1995). The SLA indicates a plant's tolerance to water stress. Plant rootstocks and cultivars that exhibit minimal changes in SLA during water stress tend to have greater photosynthetic efficiency and are more drought-tolerant. Under water stress, the plant reduces the vegetative growth and biomass production to cope with the water deficit and conserve absorbed water. The plant can tolerate water deficits by reducing aerial growth, which decreases transpiration compared to the water absorbed by the roots, consequently, SLA will decrease naturally.(Yildirim *et al*., 2018; Kennedy, 2008). In addition to leaf thickness, SLA also depends on the leaf tissue density. The density of leaf tissue decreases as leaf relative water content (RWC) increases, making RWC a crucial factor influencing the SLA. Generally, the SLA is lower in plant genotypes or species that are adapted to arid environments.(Yadolahi *et al*., 2011).

The A15 and A2 genotypes had the highest reduction of shoot fresh and dry matters in irrigations

80% and 60% water requirement compared to irrigation 100% water requirement (shoot fresh matter: 1.38 and 1.29 times the GF677 rootstock, respectively, shoot dry matter: 1.49 and 1.08 times the GF677 rootstock, respectively). While A3 and A13 genotypes had the lowest reduction of shoot fresh and dry matters in irrigations 80% and 60% water requirement (shoot fresh matter: 22% and 30% the GF677 rootstock, respectively, shoot dry matter: 27% and 30% the GF677 rootstock, respectively). The access to water and nutrient absorption are reduced under water stress, and therefore the growth and development of leaf cells are limited. Following the reduction in leaf area and the growth of new tissues, the plant's ability to light absorb and the total photosynthetic capacity of the plant is reduced, which leads to a reduction in the plant organs matter (Barshan *et al*., 2016).

The results of our experiment are similar to those of other studies. The water stress with different soil moisture levels on two genotypes of the cultivated almonds (*Prunus dulcis* var. amara) and one ecotype of the natural almond (*Amygdalus scoparia*) showed that water stress reduced significantly the dry matter of leaves and root in all almond seedlings (Sardabi *et al*., 2003). The evaluation of the response of five almond species, including *P. eburnea, P. eleagnifolia, P. haussknechti, Prunus dulcis, and P. scoparia*, to water stress induced by polyethylene glycol (PEG-6000) indicated that water stress reduced significantly the fresh and dry matters of root and shoot, leaf number, total leaf area, and RWC in all almond species. The fresh and dry matters decreased by 6.5-50.9% and 16.9-46.5% percent, respectively, but in *P. eburnea*, the root and stem fresh matters increased 0.2 and 4.7 percent, respectively. *P. eburnea* was more tolerant to water stress than other tested species (Zakaei-Khosrowshahi *et al*., 2014). Also, reducing irrigation to 55% and 35% water requirement in seedlings of 15 grape cultivars reduced significantly fresh and dry matters of root and shoot (Dolati-Baneh *et al*., 2019). In general, various studies indicate that water stress in plants leads to an increase in growth-inhibiting hormones, including abscisic acid (ABA), and a decrease in growth-promoting hormones, and therefore, plant vegetative growth is reduced due to hormonal imbalance and reducing nutrient absorption and transport (Torcilas *et al*., 1996). The evaluation of physiological and biochemical responses of fifteen almond rootstocks to drought stress induced by polyethylene glycol (PEG) showed the number of shoots in all genotypes decreased significantly in response to the increase in the level of drought stress (Yildirim *et al.*, 2021).

The A11 genotype had the highest reduction of leaf relative water content (RWC) in irrigations 80% and 60% water requirement compared to irrigation 100% water requirement (6.54 and 9.16 times the GF677 rootstock, respectively). But, A3 genotype had the lowest reduction of leaf relative water content (RWC) in irrigations 80% and 60% water requirement (30% and 28% the GF677 rootstock, respectively). The RWC is a good indicator of plant water status and it is used to determine plant tolerance to water stress. A reduction RWC due to water deficiency causes stomata to close, leading to a decrease in carbon dioxide absorption. Severe water stress can subsequently alter the physiological state of the photosynthetic apparatus. Assessing the water status of plants is a crucial indicator for identifying their response to water stress. About 1% of total water absorbed by plant roots is consumed by plants, and the rest is lost as vapor. Therefore, increasing the amount of plant water can improve plant growth, especially under water stress (Dolati-Baneh *et al*., 2019; Fathi *et al*., 2017). Higher leaf relative water content (RWC) enables the leaf to retain greater amounts of water under water stress conditions. A positive correlation has been observed between RWC and photosynthesis, chlorophyll and protein concentrations. Due to the role of chlorophyll and protein in maintaining photosynthesis and tolerance to water stress, RWC can be used as an indicator to determine water stress tolerance, such that this indicator decreases with increasing water stress intensity (Gohari *et al.,* 2023; Alvarez *et al*., 2020). The reduction of RWC typically results from decreased available soil water in the plant root zone or lower relative air humidity, which leads to increased plant transpiration. The results of this study showed that with the decrease of irrigation water (an increase of water stress), the average leaf relative water content (RWC) of almond genotypes decreased.

Water stress on seedlings of five almond species decreases RWC by 11.2%, significantly (Zakaei Khosrowshahi *et al*., 2014). Similarly, the occurrence of drought stress caused by polyethylene glycol on five almond cultivars seedlings including Sohtad, Shahroud 21, Supernova, Ferragnes and Tuono reduced significantly RWC (Akbarpour *et al*., 2017). Also, A significant decrease in RWC due to water deficit has been reported in other crops such as grapes (Dolati-Baneh *et al*., 2019). Proper maintenance of RWC under water stress conditions can be due to the decrease in leaf area, deepening of stomata, increased leaf hairiness, increased stomatal density, decreased stomatal size, and thickening of the cuticle (Wu *et al*., 2022). Measuring the RWC in four almond varieties grafted onto rootpac-20 indicated that the almond cultivars studied present a different behaviour with respect to plant water relations (Álvarez *et al.* 2023).

Conclusions

In general, based on changes in morphological and physiological traits of almond genotypes, especially shoot fresh and dry matters, leaf relative water content (RWC), and specific leaf area (SLA) at different irrigation (water stress) levels, and considering the GF677 rootstock (control) as a drought-tolerant rootstock, it seems that A13, A3, A16, and A19 genotypes had good tolerance to water stress, while A1 and A8 genotypes were tolerant to light water stress (irrigation 80% water requirement). Nevertheless, the results of this research must be confirmed under field conditions for assessing the performance of these genotypes.

Conflict of interest

The authors declare no conflicts of interest.

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