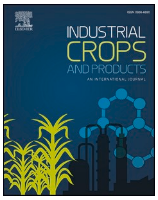
Industrial Crops & Products 234 (2025) 121528

Contents lists available at ScienceDirect

Industrial Crops & Products

journal homepage: www.elsevier.com/locate/indcrop



Assessing different physiological, seed yield and quality responses of camelina lines to drought

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ARTICLE INFO

Keywords:
Oilseed crops
morphology
seed yield
oil content
fatty acid composition

ABSTRACT

Camelina sativa (L.) Crantz is recognized as one of the most drought-tolerant Brassica oilseed species, yet variability in the response to stress among different genotypes remains underexplored. With the aim of investigating the response of four different camelina lines (UNT4, UNT18, UNT21 and UNT46) to drought, they were tested in twenty-four lysimeters under favorable (21 % volumetric water content, VWC) and drought (9 % VWC) conditions, imposed from the start of flowering. Physiological parameters were measured to identify possible different response mechanisms at early stage. All the surveyed parameters were significantly affected by the imposition of water stress and lines, but only some variables (i.e., A, g_s, and iWUE) were affected by the interaction "line × stress", revealing differences in their stress response behavior to drought. Indeed, although UNT18 was the line showing the lowest reduction of physiological parameters under drought, it was one of the less productive lines considering seed yield, reporting 0.25 g/plant in control conditions and 0.16 g/plant in drought. Otherwise, UNT46 showed a higher tolerance to drought with surprisingly significantly higher seed yield under drought (0.44 g/plant) than in well-watered conditions (0.26 g/plant), and this was detectable at earlier stage by an increased intrinsic water use efficiency. A complex and diverse response mechanism to drought in the studied lines emerged. UNT46 and UNT21 showed a trade-off between seed size and weight, whilst UNT4 showed a restricted response to drought stress at physiological level, despite being severely impacted in terms of yield. Interestingly, among physiological parameters surveyed early after stress imposition only leaf fluorescence (Fv/Fm) resulted significantly and negatively correlated with final seed yield ($r = -0.59$), while seed oil content resulted highly correlated with many of them, particularly with silique walls g_s ($r = 0.65$). In conclusion, UNT46 and UNT21 had the best performance under drought being able to keep stable their seed yield, presumably in relation to the capacity to produce a higher number of siliques, which were actively contributing to photosynthesis.

1. Introduction

Bioeconomy is rapidly expanding and the demand for sustainable industrial crops not competing with food crops is dramatically increasing (Zanetti et al., 2024). These crops can also provide an opportunity for farmers to diversify their agricultural systems, sustain additional income and possibly fulfill ecosystem services (Johnson et al., 2017). *Camelina sativa* (L.) Crantz (camelina) is an annual oilseed species of the *Brassicaceae* family, undergoing a rediscovery by academics and growers undoubtedly because of its favorable characteristics (Zanetti et al., 2021). These include its capacity to reach acceptable yields under low input agricultural systems, which allows rainfed cultivation, and the reduction in the use of fertilizers and plant protection products (Avola et al., 2021). Camelina can be included in a variety of agricultural systems thanks to its short growth cycle, the availability of spring and winter biotypes (Wittenberg et al., 2019) and wide environmental adaptability. Camelina reportedly tolerates a range of biotic (Séguin-Swartz et al., 2009) and abiotic stresses, including drought

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Abbreviations: A, net photosynthesis; C18:1, oleic acid; C18:2, linoleic acid; C18:3, α-linolenic acid; GDD, growing degree days; g_s, stomatal conductance; iWUE, intrinsic water use efficiency; RWC, relative water content; TGW, thousand grain weight; VWC, volumetric water content.

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https://doi.org/10.1016/j.indcrop.2025.121528
Received 31 January 2025; Received in revised form 10 July 2025; Accepted 14 July 2025

(Campbell et al., 2013, Čanak et al., 2020), low temperature (Fang et al., 2023) and frost (Berti et al., 2011). Lastly, camelina's characteristic seed oil content and composition makes it a suitable candidate for food, feed and industrial applications (Mondor and Hernández-Álvarez, 2022). Camelina seeds contain between 28 % and 49 % of oil, which is highly unsaturated with a prevalence of α-linolenic acid (omega-3) and linoleic acid (omega-6; Sydor et al., 2022). Among its numerous uses, the cultivation of camelina as an intermediate crop or on marginal land to produce biofuels and sustainable aviation fuels is now of high interest (Bansal and Durrett, 2016).

Abiotic stress is defined as any environmental factor e.g., temperature, light, nutrient supply, that can hinder crop productivity (Vernieri et al., 2006), any deviation from the *optimum* environment can constitute a source of stress. The more relevant abiotic stresses are often considered to be drought, salinity, temperature and nutritional stress (Koyro et al., 2012). Water scarcity is recognized as a serious problem for agriculture, particularly in the Mediterranean region, and especially during spring and summer. This period is often characterized by limited precipitation and high temperatures, which can result in dry spells with a detrimental impact on crop production. Moreover, the severity and frequency of drought episodes is increasing because of global warming and associated climate change effects (Tramblay et al., 2020).

Drought stress can occur when the rate of water loss, through transpiration from the plant aerial tissues, exceeds the rate of water absorption by the root system. Periods of reduced or absent precipitation and the presence of high temperatures and low relative humidity combine to impact crop performance (Seleiman et al., 2021). For the growers, this can translate into yield losses and undesirable modifications in the quality of the harvestable product (Yang et al., 2021). Plant response to drought can vary based on different factors, including genotype, phenology, and intensity and duration of the stress (Pinheiro and Chaves, 2011). These responses, often categorized as escape, tolerance, or avoidance strategies, include a wide range of modifications on a morphological, physiological and biochemical level (Marín-de la Rosa et al., 2019). In camelina, drought stress can negatively impact the development of the plant, limiting growth and resulting in shorter plants with reduced branching (Ahmed et al., 2019). Furthermore, water shortage can disrupt photosynthesis in camelina in different ways. When subjected to mild stress, a decline in the rate of photosynthesis is attributed to stomatal closure limiting gas exchanges. As the stress intensifies, non-stomatal factors come into play; mainly, the excessive production of ROS that can damage chloroplast structure (Ahmed et al., 2020). Moreover, drought impacts productivity in camelina. The stunted development and eventual shortening of the growth cycle to escape the stress leads to seed yield reduction and impacts seed quality. Several studies identify a decrease in yield components such as number of branches per plant, number of pods per plant, seed yield and thousand seed weight (Ahmad et al., 2021; Haghaninia et al., 2023; Waraich et al., 2017a, 2017b). Water deficit also causes a reduction in seed oil content, due to the limited amount of carbohydrate available for triacylglycerol synthesis coupled with an increase in lipid oxidation (Rad et al., 2024). Oil composition is influenced by genotype and environment factors (Berti et al., 2016). Drought stress seems to determine a greater accumulation of saturated fatty acids and oleic acid, with reduced accumulation of polyunsaturated fatty acids probably linked to the inhibition of desaturases enzymatic activity (Ahmed et al., 2019).

The period between flowering and seed filling has been identified as the most sensitive to drought stress in camelina, leading to reduced fertility, flower abortion and consequent reduction of many yield components (Borzoo et al., 2021). Therefore, cultivating camelina in regions with a dry and hot spring-summer season could expose the crop to the risk of drought stress in a period of sensitivity. Camelina could be an optimal candidate to help diversify European agriculture and the transition towards a green economy, thanks to its adaptability and low input requirements. However, to guarantee acceptable yields, particularly when cultivated with a spring/summer cycle, the availability of drought tolerant genotypes with resilience during sensitive phenological phases e.g., flowering and seed filling, is fundamental. Moreover, it might be economically advantageous knowing any possible yield losses caused by drought before harvesting. For these reasons, a lysimeter experiment was undertaken with the aim of comparing the response of four different camelina lines to limited water availability throughout the reproductive to ripening period. During water stress, physiological traits were measured to assess possible relationships between these parameters and production data at harvest, as well as to possibly highlight different response behaviors in the tested camelina lines. The use of one cubic meter lysimeters proved to be a good compromise between the necessity of controlling the water intake of the plants and the need to subject them to an environment representative of field conditions.

2. Materials and methods

2.1. Seed material

Four camelina lines (UNT4, UNT18, UNT21, and UNT46) selected from the UNTWIST (EU H2020 project) core collection were used in this trial. UNT4 originated from the Camelina Company (CCE, Spain) breeding program, UNT18 is the commercial variety Celine, UNT21 originated from the National Research Institute for Agriculture, Food and Environment (INRAE, France), and UNT46 (name CUOO5 or Omskij, public accession, geographical region of Russia). The lines were previously characterized based on their distinct genetic and epigenetic backgrounds.

2.2. Lysimeter experiment set-up

The trial was conducted in 1-m^3 lysimeters at the experimental farm of the University of Bologna in Cadriano (44° 33' N, 11° 23' E, 33 m a.s. l.) in spring 2022, in a completely randomized experimental design with three replicates. Twenty-four lysimeters were placed under a prefabricated structure covered with transparent polyethylene film (90 % PAR transmission). This setup allowed a semi-controlled environment with regulated irrigation. Before sowing, lysimeters were filled with silty-clay-loam soil (45 % sand, 15 % clay, 40 % silt, 1.60 % organic matter, pH = 8.13, N = 0.78 g/kg, P = 17 mg/kg, K = 134 mg/kg) and equipped with a micro-irrigation system. Two Frequency Domain Reflectometry (FDR) probes were placed horizontally into each lysimeter, one at one third and the second at two thirds of total depth to continuously monitor soil moisture. Each camelina line was sown on 7 March 2022 in six lysimeters at a density of 500 seeds m^{-2} 0.10 -mrow spaced. Each row was provided with a micro-irrigation line. Nitrogen fertilization (as urea) was manually applied at a rate of 50 kg N ha^{-1} at the beginning of stem elongation. Irrigation occurred twice a week, with water requirements calculated using the Volumetric Water Content (VWC) method (water volume/soil volume). The field capacity for this specific soil type was set at 21 %, and the difference between the VWC, detected by the probes, and the theoretical field capacity determined the irrigation need for each lysimeter. The structure was equipped with a portable meteorological station (T-monitor/ZT, μ-METOS, PESSL Instruments, Austria) able to collect hourly and daily data on minimum (T_{min}) and maximum (T_{max}) air temperatures. Growing Degree Days (GDD) were calculated as $\Sigma[T_{max}+T_{min})/2]$, using a T_{base} of 4°C as suggested by (Gesch and Cermak, 2011).

2.2.1. Imposition of water stress

When the plants reached the first open flower stage (BBCH 600–01, according to Martinelli and Galasso, 2011), water limitation was applied until full maturity (BBCH 809). Three lysimeters per line were randomly assigned to the drought (Dr) treatment, while the remaining three were maintained under well-watered (Ct) conditions. Lysimeters in the D treatment were irrigated to maintain 9 % VWC, while those in the C treatment were kept at 21 % VWC.

2.2.2. *Surveys during the growth cycle*

Number of physiological traits were measured fourteen days (d) after the onset of water stress and at the final stage of silique development (BBCH 709). Chlorophyll content was estimated using a SPAD-502 by Minolta Co., Ltd. (Japan). RWC was determined by collecting one leaf from 3 different plants per lysimeter. Leaf fresh weight (FW) was recorded, then the leaf was placed in an Eppendorf tube with distilled water for 6 h to measure turgid weight (TW), and the leaf was dried in an oven at 105°C until a constant dry weight (DW) was achieved. RWC was calculated as RWC (%) = [(FW - DW)/(TW - DW)] x 100 (Bukhari et al., 2022). PSII efficiency was determined by Handy PEA+ (Hansatech Instruments, UK) as F_v/F_m where F_v is the variable fluorescence and F_m is the maximum fluorescence value. Gas exchange was measured through the portable gas analyzer CIRAS-3 (PP Systems, Amesbury, MA, USA). For leaf measurements, a PLC3 Universal Leaf Cuvette (PP Systems, Amesbury, MA, USA) was used, while a PLC3 conifer & narrow cuvette with an LED light unit (PP Systems, Amesbury, MA, USA) was used for silique measurements. Parameters assessed included net photosynthesis (A) and stomatal conductance (g_s). The intrinsic water use efficiency (iWUE) of leaves, at 14 DOS, and of silicles, at 18 DOS, were calculated as the ratio A/g_s. Specifically, after fourteen d of stress (DOS), chlorophyll content, relative water content (RWC), photosystem II (PSII) efficiency, and gas exchange (net photosynthesis, A; stomatal conductance, g_s; and intrinsic water use efficiency, iWUE) were assessed on the seventh fully developed leaf of the main stem. At the final green silique dimension, gas exchange parameters were measured on the silicles of the main raceme of three plants for each lysimeter.

2.2.3. *Measurements of selected yield parameters*

Plants were harvested at full maturity (BBCH 809). Four plants from each lysimeter were randomly selected for final measurements. The number of silicles on the plant and on lateral branches were counted, and plant height was recorded. Plants were then manually cut at soil level and weighed to determine fresh biomass. Seeds were separated from the straw and weighed, then placed in an oven at 60°C until a constant weight was achieved. After drying, the seeds were weighed again to determine residual moisture. Seed production data are presented on a dry matter (DM) basis.

2.3. *Seed quality analyses*

2.3.1. *Analysis of seed fatty acids*

Samples of three replicates per plot with twenty seeds each were weighted and placed in glass vials mixed with 2.0 mL of 1 mM L^{-1} of heptadecanoic acid (internal standard C17:0, Sigma-Aldrich®) methylation mix. The methylation mix was composed of 66 % methanol, 28 % toluene, 4 % 2,2-Dimethoxypropane and 2 % sulfuric acid. The capped vials were heated to 85°C for 4 h (pilot experiments were undertaken to ensure one hour was sufficient to ensure full methylation), allowed to cool to room temperature, and 1 mL of 1 % sodium chloride was added. The samples were mixed, and lipids extracted into 0.5 mL 100 % hexane. Following methylation, the hexane fraction was dried under continuous nitrogen flow and re-suspended in 1 mL of hexane. Methyl ester derivatives of total fatty acids (FAMEs) were analyzed by Gas Chromatography (GC) (Agilent 7890 A, Agilent Technologies, USA) using an Agilent J&W 122–2332 column (30 m×250 µm×0.25 µm, Agilent Technologies). Inlet and detector temperature were set to 250°C and 1 µL of each sample was analyzed using 15:1 split ratio injection and a constant flow rate of 1.5 mL min^{-1}. The oven temperature cycle as start temperature of 150°C held for 2 min to allow vaporized samples and the solvent (hexane) to condensate at the front of the column. Oven temperature was then increased to 240°C at 10°C min^{-1}. The final temperature of 240°C was held for one minute and 50 s giving a total run time of 12 min and 50 s per sample. FAMEs were detected using a Flame Ionisation Detector (FID). Chromatograms were analyzed using the offline session of the Agilent ChemStation software (Agilent Technologies, USA). The peak area of each FAME was normalized to the internal standard and further normalized to the weight of the initial sample. The retention time and identity of each peak was calibrated using the Supelco® 37 Component FAME Mix (certified reference material TraceCERT®, Sigma-Aldrich®).

2.3.2. *Measurement of seed oil content*

Camelina seed oil contents were measured by low-resolution time domain NMR spectroscopy using a Minispec MQ20 (Bruker) fitted with a robotic sample-handling system (Rohasys). The oil and moisture calibration were constructed according to the manufacturer's instructions using nine (∼ 0.5 g) oilseed seed samples ranging between approximately 5 % and 10 % moisture content and between approximately 30 % and 55 % oil content ($r^2 > 0.99$). Seed percentage oil content values were adjusted to the water content. Approximately 1 g of seed was used for each measurement. Representative samples from the lysimeters were analyzed at Rothamsted Research (UK). All seed were stored in the room alongside the instrument for 24 h prior to analysis to ensure equilibration with room temperature and humidity.

2.3.3. *TGW determination*

Thousand grain weight (TGW) was assessed by mass balance and thousand seed counted (TGW determination) using a Seed Counter ELMOR C1 (Elmor Ltd., Switzerland). Once TGW was determined, also the seed production per plant was surveyed by multiplying the seed yield by the seed weight.

2.3.4. *Measurements of total nitrogen, carbon, and ^{13}C stable isotope content in seeds and straw*

At harvest, straw and seed samples from each lysimeter were grinded and then analyzed for C and N content, and ^{13}C abundance by Continuous Flow-Isotope Ratio Mass Spectrometry (CF-IRMS) with an elemental analyzer (Flash 2000, Thermo Fisher Scientific) coupled with an isotopic ratio mass spectrometer (Delta V Advantage Thermo Fisher Scientific). The N content of seeds was multiplied by 6.25 to obtain the seed protein content.

The isotopic composition of C and N were expressed as delta values, $\delta^{13}C$ ‰ calculated as follow: $\delta^{13}C$ (‰) = [(RsampleRstd)-1]× 1000, where Rsample is the isotope ratio $^{13}C/^{12}C$ of the sample and Rstd is the $^{13}C/^{12}C$ ratio of the international standard (Vienna PeeDee Belemnite).

Seed protein content was then calculated with the formula: N content× 6.25.

2.4. *Statistical analysis*

Prior to ANOVA, the homoscedasticity of variance was verified with Bartlett's Test for $P \leq 0.05$. Considering that the experimental design was a completely randomized with three replicates, a two-way ANOVA was adopted to test the effect of the main effects: stress (drought vs. control) and line, on the surveyed physiological, morphological, and agronomic parameters and quality seed traits. When ANOVA revealed statistically different means, the LSD Fisher's test was used to separate means ($P \leq 0.05$). A correlation study was carried out to evaluate the relationships among physiological traits surveyed after stress imposition (SPAD, PSII efficiency, RWC, iWUE, A and g_s) and biometric and agronomic traits surveyed at harvest (plant height, number of branches, number of siliques, plant biomass, lateral branch biomass, seed yield, and TGW). When the correlations were found significant for $P \leq 0.05$, the Pearson's correlation coefficient (r) was reported. All the statistical analyses were carried using the Statgraphics Centurion 18 software (ver. 18.1.13, Statgraphics Technologies Inc., Virginia, USA).

3. Results

3.1. Meteorological data during the lysimeter trial

The mean temperature during the lysimeter experiment was 14.9°C, fluctuating from −1.8°C on March 19, twelve days after sowing, up to 25–26°C from May 25 until harvest, which occurred on June 13. The total GDD accumulated from sowing to harvest was 1108. This value is in line with available literature for spring camelina (Zanetti et al., 2021). Drought imposition did not affect camelina cycle length. Moreover, line UNT21 was characterized by about seven days delay in flowering start compared to the other lines, while maturity was contemporaneous with the others.

3.2. Physiologic responses during crop cycle

The physiological traits surveyed during the study included: SPAD, PSII efficiency, RWC, iWUE, A and g_s. Measurements were made at 14 DOS on leaves, while at 18 DOS iWUE, A, and g_s were surveyed on silicles, whereas the other parameters were assessed on leaves. The ANOVA results on leaf traits at 14 DOS are reported in Table 1. The SPAD index was significantly affected by the line: UNT46 reported the lowest value (34.5), UNT18 and UNT21 the highest ones (40.9 and 39.4, respectively), and UNT4 an intermediate, and not significantly different value between these two groups (37.9). Leaf PSII efficiency was not significantly affected by line and water level, nor by their interaction, while leaf RWC was affected by both line and water stress (Fig. 1). UNT21 showed 17 % higher RWC values compared with the mean of all the other lines. Regarding water level effect, well-watered plants had 73 % higher leaf RWC compared to stressed plants ($P \leq 0.05$). Net photosynthesis (A) and stomatal conductance (g_s) were significantly affected by the main factors line and stress, and by their interaction (Table 2). Control plants had five-fold higher g_s compared to plants under drought (Table 2). When analysing the “line × stress” interaction, significant differences emerged (Fig. 2). In well-watered conditions, UNT46, 18 and 21 reported significantly higher g_s values than UNT4 (Fig. 2A). Under drought conditions, all the g_s values were significantly reduced, with differences found in response to line. The stomatal conductance of UNT46, which reported the highest value in control conditions, was drastically reduced under drought. UNT18 had the highest value in drought condition compared to all the other lines. Similar trends were found for A, with significant differences in response to the main factors, line and stress, and their interaction (Table 1). UNT18 showed the highest A values, followed by UNT46, which were significantly different from UNT4 and UNT21 (Table 2). Again, under control condition A was approximately triple that of plants under drought (Table 2). The interaction “line × stress” also showed significant differences (Fig. 2B). UNT46 and UNT18 had the highest and similar values under well-watered, although under drought UNT46 was one of the worst lines, while UNT18 had a better response. The results for the intrinsic water use efficiency (iWUE) at 14 DOS revealed significant differences in response to line, stress and their interaction (Table 1). Among the camelina lines, UNT21 had the lowest iWUE compared to all the others (0.07 vs. ~0.10 μmol mmol^{-1}, $P \leq 0.05$, Table 2). As expected, plants under drought stress had a significantly high iWUE, almost double that of control plants (0.12 vs. 0.07 μmol mmol^{-1}, $P \leq 0.05$, Table 2). The line × stress interaction showed significant differences (Fig. 2C). UNT46 under drought had the highest iWUE, while UNT21 showed the lowest values under drought, which were not different from the iWUE in control conditions. Interestingly, UNT21 also had the lowest value of iWUE in the control, which was significantly different to the other camelina lines in the same condition, confirming that the regulation of iWUE in UNT21 was different to the other lines in the study.

Table 1
ANOVA results (F-values) for the physiological parameters surveyed at 14 DOS, leaf chlorophyll (SPAD index), leaf PSII maximum quantum efficiency (F_v/F_m), relative water content (RWC), stomatal conductance (g_s), net photosynthesis (A), intrinsic water use efficiency (iWUE).

Source of variation	SPAD index	F_v/F_m	RWC (%)	Leaf g_s (mmol m^{-2} s^{-1})	Leaf A (μmol CO$_2$ m^{-2} s^{-1})	Leaf iWUE (μmol CO$_2$ mol^{-1} H$_2$O)
Line (A)	3.52**	0.76 ns	6.09**	11.0**	16.3**	11.7**
Stress (B)	2.06**	0.09 ns	218.5**	277.4**	238.9**	139.5**
A x B	0.78 ns	1.73 ns	2.08 ns	7.39**	7.31**	3.15**

** significant for $P \leq 0.05$; ns = not significant

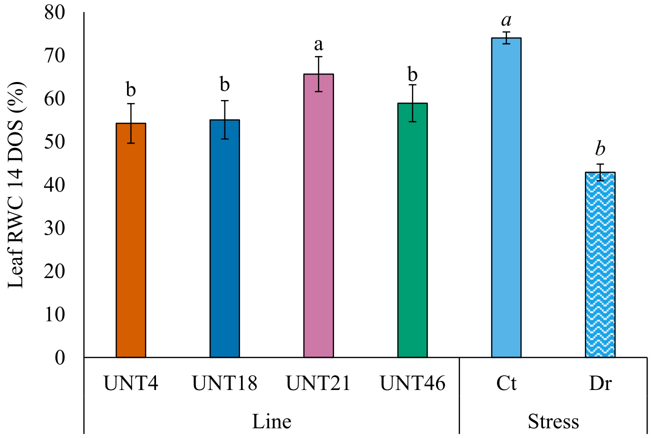


Fig. 1. Mean leaf relative water content (RWC, %) in response to the main factors line and stress, surveyed at 14 DOS. Ct=control, Dr=drought. Vertical bars: standard error. Different letters, within the main factor line, refer to statistically different means for $P \leq 0.05$, LSD Fisher’s Test. Different italic letters, within the main factor stress, refer to statistically different means for $P \leq 0.05$, LSD Fisher’s Test.

Examining the drought response in older plants, the ANOVA results for the parameters surveyed at 18 DOS on leaves or silicles are reported in Table 3. Results for SPAD on leaves were comparable to those surveyed at 14 DOS, with significant differences observed only in response to line, but their ranking was slightly different than in the earlier survey. In fact, UNT18 which had the highest value at 14 DOS, displayed the lowest at 18 DOS (26.2), lines UNT4 and UNT21 had the highest values (35.5 and 35.2, respectively), while UNT46 reported an intermediate value (32.4) between these two groups. Results for leaf PSII efficiency at 18 DOS reported significant differences in response to the main factors: line and stress (Fig. 3). All the camelina lines had similar F_v/F_m values, except UNT21 which showed a value about 20 % lower compared to the others. In response to drought, F_v/F_m values significantly decreased of about 11 % compared to control plants. As compared to earlier measurements at 14 DOS, RWC surveyed on leaves at 18 DOS was not significantly affected by any of the main factors under study in the experiment. Measurements on photosynthesis at 18 DOS were carried out on silicles, since in *Brassicaceae* species the contribution of leaves to photosynthesis tends to decrease in favor of silicles, which are green organs during the majority of seed maturation and supply CO$_2$ for assimilation (Aschan and Pfanz, 2003; Hua et al., 2012). Silique wall stomatal conductance (g_s) was significantly affected only by stress, with plants under drought reporting a significant lower value compared to those under control conditions (441 vs. 3075 mmol m^{-2} s^{-1}, drought vs. control, respectively, $P \leq 0.05$, Table 2). Silique net photosynthesis (A) surveyed at 18 DOS was significantly affected by the two main factors (line and stress) and by their interaction (Table 2). Examining the individual camelina lines, UNT46 had the highest silique net photosynthesis, followed by UNT21, while UNT4 and UNT18 had similar and

Table 2
Camelina stomatal conductance (g_s), net photosynthesis (A), and intrinsic water use efficiency (iWUE) surveyed at 14 DOS on leaves, and at 18 DOS on silique wall, in response to the main factors line and stress. Mean values ± standard error. Different letters, within the same parameter and factor, refer to statistically different means for $P \leq 0.05$, LSD Fisher's Test.

Factor	Leaf g_s (mmol m^{-2} s^{-1}) at 14 DOS	Leaf A (μmol CO_2 m^{-2} s^{-1}) at 14 DOS	Leaf iWUE (μmol CO_2 mol^{-1} H_2O) at 14 DOS	Silique wall g_s (mmol m^{-2} s^{-1})	Silique wall A (μmol CO_2 m^{-2} s^{-1})	Silique wall iWUE (μmol CO_2 mol^{-1} H_2O) at 18 DOS
Camelina lines						
UNT4	58.0 ± 7.01 b	5.09 ± 0.47c	0.100 ± 0.005 a	2698.5 ± 891.9 a	9.35 ± 1.67c	0.012 ± 0.002 bc
UNT18	111.0 ± 11.9 a	8.23 ± 0.53 a	0.097 ± 0.008 a	1665.3 ± 288.7 a	10.0 ± 1.37c	0.009 ± 0.001c
UNT21	111.6 ± 12.9 a	5.74 ± 0.48c	0.069 ± 0.005 b	1122.8 ± 260.9 a	13.6 ± 1.38 b	0.023 ± 0.002 a
UNT46	100.4 ± 17.2 a	7.16 ± 0.84 b	0.108 ± 0.008 a	2069.7 ± 351.9 a	21.5 ± 1.82 a	0.018 ± 0.003 ab
Stress						
Control	155.5 ± 7.99 a	9.22 ± 0.36 a	0.122 ± 0.005 a	3075.3 ± 406.2 a	19.2 ± 1.05 b	0.020 ± 0.002 a
Drought	33.2 ± 2.21 b	3.75 ± 0.23 b	0.065 ± 0.002 b	442.1 ± 50.9 b	6.72 ± 0.63 a	0.013 ± 0.002 b

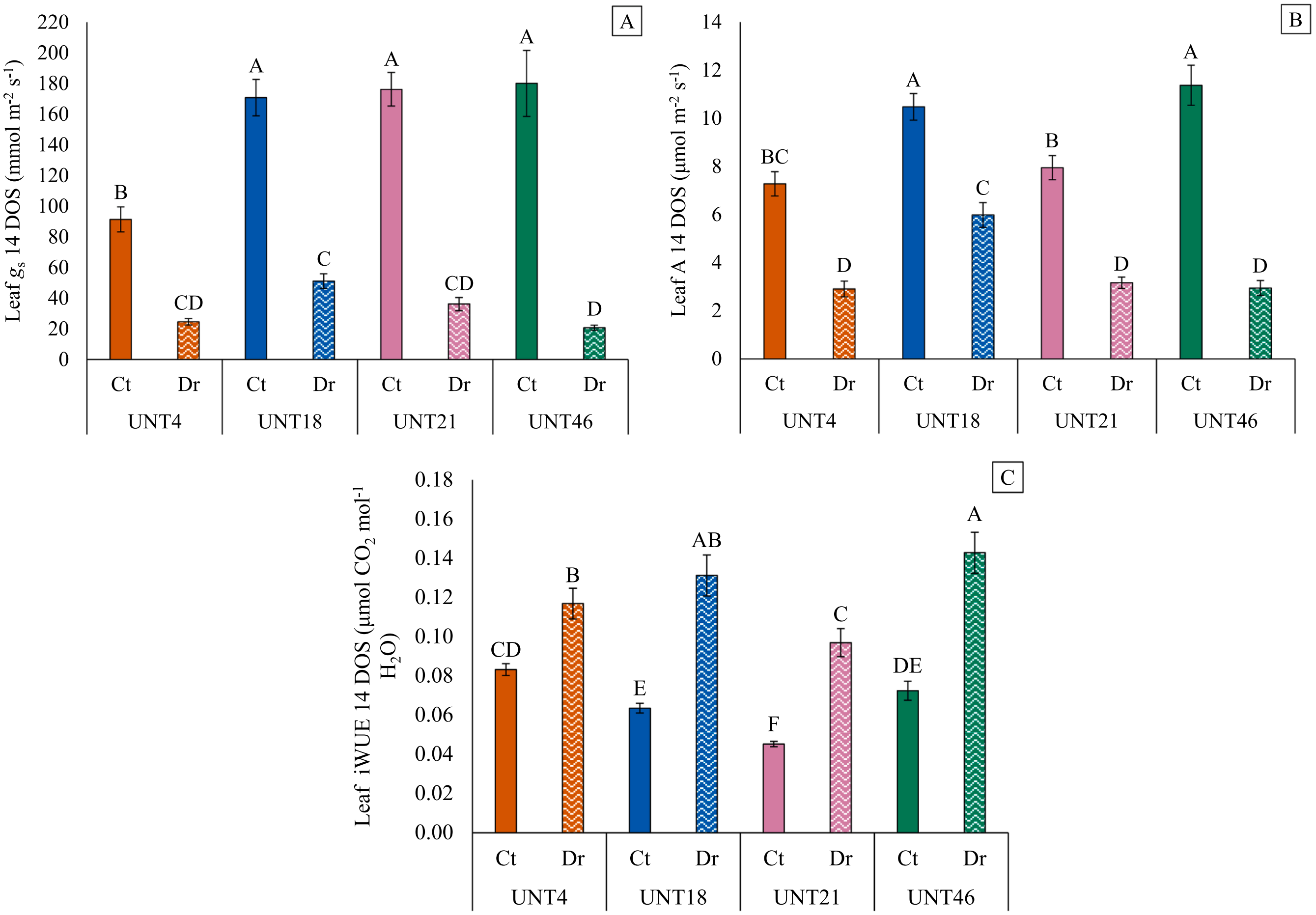


Fig. 2. Mean values of: A) leaf stomatal conductance (g_s) surveyed on leaves at 14 DOS, B) net photosynthesis (A) surveyed on leaves at 14 DOS, and C) intrinsic water use efficiency (iWUE) surveyed on leaves at 14 DOS, in response to the interaction "line × stress". Vertical bars: standard error. In each image (A, B and C), different letters refer to statistically different means for $P \leq 0.05$, LSD Fisher's Test.

Table 3
ANOVA results (F-values) of the physiological parameters surveyed at 18 DOS on camelina leaves and silicles in the lysimeter experiment.

Source of variation	Leaf chlorophyll content (SPAD index)	Leaf PSII efficiency (F_v/F_m)	Leaf RWC (%)	Silicle wall g_s (mmol m^{-2} s^{-1})	Silicle wall A (μmol CO_2 m^{-2} s^{-1})	Silicle wall intrinsic water-use efficiency (μmol CO_2 mol^{-1} H_2O)
Line (A)	3.27**	4.52**	1.75 ns	1.52 ns	27.4**	11.2**
Stress (B)	0.00 ns	4.74**	0.41 ns	38.7**	166.0**	11.6**
A x B	1.08 ns	0.55 ns	2.31 ns	1.11 ns	3.45**	0.70 ns

** significant for $P \leq 0.05$; ns = not significant

lower values (Table 2). As expected, plants under control conditions had significantly higher photosynthesis than those under drought with (approximately triple that of stress; Table 2). The interaction between line and stress revealed significantly different behaviors amongst the camelina lines in response to drought (Fig. 4). Interestingly, UNT46 had the highest value of assimilation under control conditions, and under

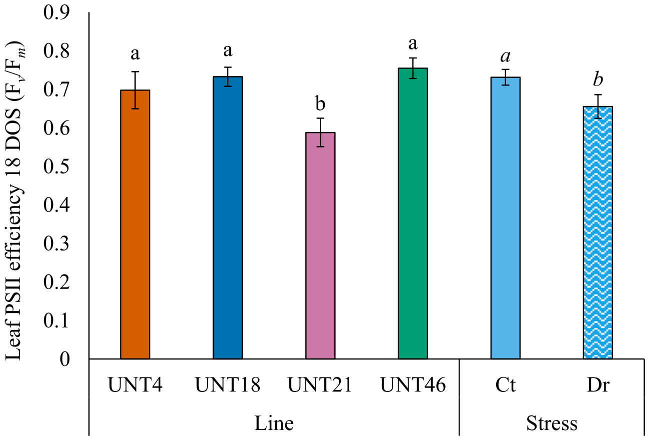


Fig. 3. Mean leaf PSII efficiency (F_v/F_m) in response to the main factors, line and stress, surveyed at 18 DOS in the camelina lysimeter experiment. Ct=control, Dr=drought. Vertical bars: standard error. Different letters, within the main factor line, refer to statistically different means for $P \leq 0.05$, LSD Fisher's Test. Different italic letters, within the main factor stress, refer to statistically different means for $P \leq 0.05$, LSD Fisher's Test.

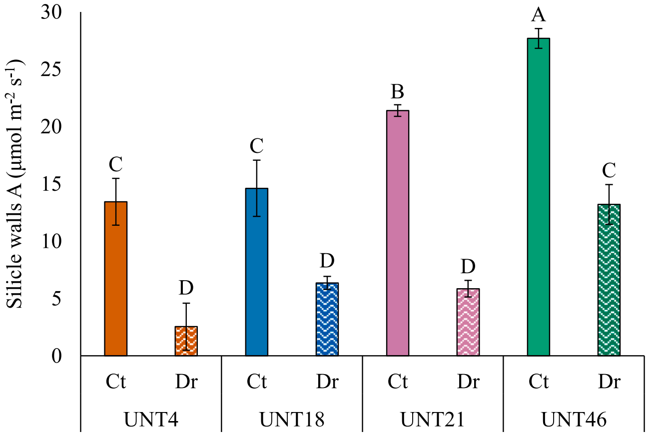


Fig. 4. Mean net photosynthesis (A) surveyed on silique walls at 18 DOS in response to the interaction "line × stress". Ct=control, Dr=drought. Vertical bars: standard error. Different letters refer to statistically different means for $P \leq 0.05$, LSD Fisher's Test.

drought, its net photosynthesis was similar to those of UNT18 and UNT4 under control conditions, with values approximately double that of all the other camelina lines under drought (Fig. 4), indicating a lower impact of drought stress on silique net photosynthesis compared to the other lines. The iWUE surveyed at 18 DOS on the silicles showed significant differences in response to the line and the stress (Table 1). Interestingly, UNT21 which had the lowest iWUE at 14 DOS presented the highest value at a later stage, but it was not different than UNT46, which kept remaining characterized by the highest iWUE. At this later stage, UNT18 had the lowest iWUE. As in the earlier survey, the iWUE of camelina plants under drought was significantly higher than in the control condition, but the difference was slightly less marked than at 14 DOS (Table 2).

3.3. Agronomic performance: biometric, productive and quality results at harvest

The performances of the camelina lines in control and subject to drought treatment were evaluated using several agronomic parameters. The ANOVA results for the parameters surveyed at harvest are reported in Table 4. The final plant height was significantly affected by the two

Table 4
ANOVA results (F-values) of the main morphological parameters (final plant height, number of silicles and number of lateral branches), productive (main stem biomass, total lateral branch biomass, seed yield, seed production, straw C/N, and seed C/N), and quality (TGW, seed oil content, seed protein content, oleic (C18:1), linoleic (C18:2), and linolenic (C18:3) acid contents), surveyed in camelina at harvest in the lysimeter experiment.

Source of variation	Final plant height (m)	Silicle count	Lateral branch count	Main stem biomass (g DM)	Total lateral branch biomass (g DM)	Seed yield (g DM $plant^{-1}$)	Seed production (seeds $plant^{-1}$)	Seed C/N	Straw C/N	TGW (g)	Seed oil content (% DM)	Seed protein content (% DM)	C18:1 (% DM)	C18:2 (% DM)	C18:3 (% DM)	$\delta^{13}C$ (‰ DM)
Line (A)	3.84**	1.19 ns	2.12 ns	1.57 ns	1.85 ns	1.95 ns	4.14**	3.99**	1.22 ns	216.9**	14.7**	3.16 ns	52.6**	169.4**	69.6**	0.55 ns
Stress (B)	114.1**	16.8**	3.00 ns	13.6**	35.8**	0.17 ns	0.28 ns	7.19**	2.84 ns	18.9**	76.0**	5.57**	16.4**	4.54**	14.5**	97.8**
A x B	8.98**	0.64 ns	1.26 ns	1.78 ns	2.94**	4.83**	3.78**	3.21 ns	2.23 ns	2.44 ns	5.16**	4.62**	3.65**	2.60 ns	4.78**	1.30 ns

** significant for $P \leq 0.05$; ns = not significant main factors and by their interaction. Amongst the lines, UNT4 had the tallest plants, while UNT21 and UNT46 were shorter (Table 5), but in general any differences in height were moderate. Drought stress reduced plant height by approximately 15 % compared to the control (Table 5). Interestingly, when analyzing the interaction between line and stress (Fig. 5), it emerged that UNT46 maintained constant plant height in the two water conditions, while all the other lines significantly reduced their final height when subjected to drought stress. Concerning all the productive parameters surveyed at harvest, most of the significant differences were caused by drought stress, with substantial reductions in total number of silicles, main stem biomass, and lateral branches biomass (Tables 4 and 5), while the number of lateral branches resulted in no effect by any of the studied factors. Amongst the described parameters, the reduction between drought and control conditions was in the range of 20–27 %, excluding lateral branches biomass which decreased almost 50 % under drought compared to control conditions, even though number of branches remained stable in the two conditions (Table 5). Differences in the surveyed morphological and productive parameters were never significant in response to line choice. Interestingly, significant interactions "line × stress" were surveyed for both lateral branches biomass and plant seed yield (Table 4). Focusing on the lateral branch biomass (Fig. 6), UNT4 maintained stable values under drought compared to control conditions, while all the other lines had a significant decrease of lateral branch weight under drought. UNT18 recorded the highest impact of drought, with a marked decrease in weight of about 75 % compared to UNT46 and UNT21 which reported only 45 % lower lateral branches biomass under drought. Final seed yield was significantly affected by the "line × stress" interaction (Table 4). Notably, distinct response behaviors were surveyed, with UNT46 under drought achieving significantly higher seed yield than in the control, UNT18 and UNT4 were the opposite, significantly reducing their seed yield under drought, and finally UNT21 was able to maintain a stable seed yield within the conditions (Fig. 7).

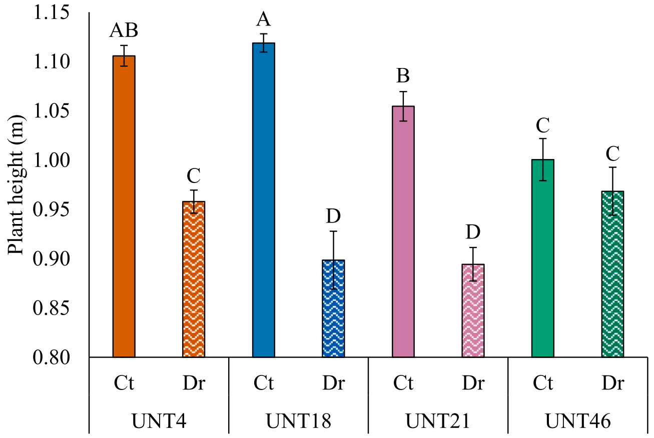


Fig. 5. Mean final plant height at harvest in response to the interaction "line × stress". Ct=control, Dr=drought. Vertical bars: standard error. Different letters refer to statistically different means for $P \leq 0.05$, LSD Fisher's Test.

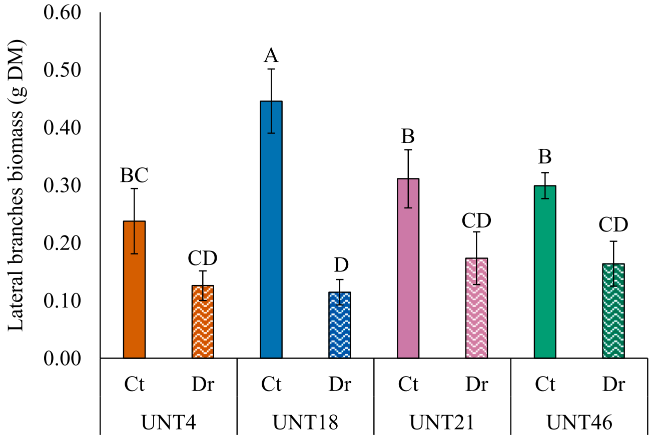


Fig. 6. Mean total lateral branches biomass at harvest in response to the interaction "line × stress". Ct=control, Dr=drought. Vertical bars: standard error. Different letters refer to statistically different means for $P \leq 0.05$, LSD Fisher's Test.

Of interest were the results for the ^{13}C isotope discrimination carried out at harvest in both straw and seed (Table 4). For seed δ^{13}C, it was possible to significantly discriminate between drought and control (-27.6 vs. −30.3 $\delta\ ^{13}$C drought vs. control, respectively, $P \leq 0.05$), but not amongst lines. On the other hand, when analyzing the results for $\delta\ ^{13}$C in straw, significant differences emerged in response to line and stress (Table 4). Again, $\delta\ ^{13}$C in straw was significantly increased under drought compared to control condition (-28.8 vs. −30.4 $\delta\ ^{13}$C, drought vs. control, respectively, $P \leq 0.05$, Fig. 8). Interestingly, among varieties UNT21 was characterized by a lower capacity to discriminate ^{13}C compared to UNT4 and UNT18, while UNT46 showed intermediate values among these two groups (Fig. 8). The ANOVA results for the surveyed quality parameters are reported in Table 4. In general, camelina seed quality appeared more influenced by stress than the morphological and productive parameters. All the surveyed seed quality parameters (TGW, seed oil content, oleic, linoleic and linolenic contents) were significantly affected by the main factors line and stress, and for seed oil content, seed protein content, oleic and linolenic contents also the interaction "line × stress" was significant (Table 4.). Concerning TGW, UNT18 was characterized by the heaviest seeds, while UNT21 had the lightest ones (Table 6). Drought stress significantly increased TGW, but the change was almost negligible (+5 %, Table 6). After the determination of TGW, it was also possible to determine the seed production per plant. This trait was significantly influenced by line and by the interaction line × stress (Table 4). Among tested camelina lines, UNT46 and UNT21 were characterized by the ability to produce a significantly higher number of seeds per plant (+70 % on average) compared to UNT4 and UNT18 ($P \leq 0.05$, Table 5). The significant interaction "line × stress" demonstrated that UNT46 and UNT21 were able to maintain stable seed production levels under drought, whilst drought impacted UNT4 and resulted in impaired seed set (Fig. 9). Conversely, compared

Table 5
Morphological (final plant height, number of silicles and number of lateral branches) and productive (main stem biomass, total lateral branch biomass, seed yield, seed production, and seed C/N) results surveyed at harvest in response to stress. Mean values ± standard error. Different letters within the same parameter refer to statistically different means for $P \leq 0.05$, LSD Fisher's Test.

Stress	Final plant height (m)	Number of silicles (silicles plant^{-1})	Number of lateral branches (branches plant^{-1})	Main stem biomass (g DM)	Total biomass lateral branches (g DM)	Seed yield (g DM plant^{-1})	Seed production (seeds plant^{-1})	Seed C/N
Control	1.07 ± 0.01 a	103.2 ± 4.90 a	4.71 ± 0.19 a	1.14 ± 0.05 b	0.59 ± 0.05 a	0.28 ± 0.03 a	319.7 ± 41.2 a	11.2 ± 0.29 a
Drought	0.93 ± 0.01 b	75.9 ± 4.47 b	4.25 ± 0.19 a	1.42 ± 0.05 a	0.29 ± 0.04 b	0.26 ± 0.03 a	296.4 ± 31.0 a	10.4 ± 0.25 b

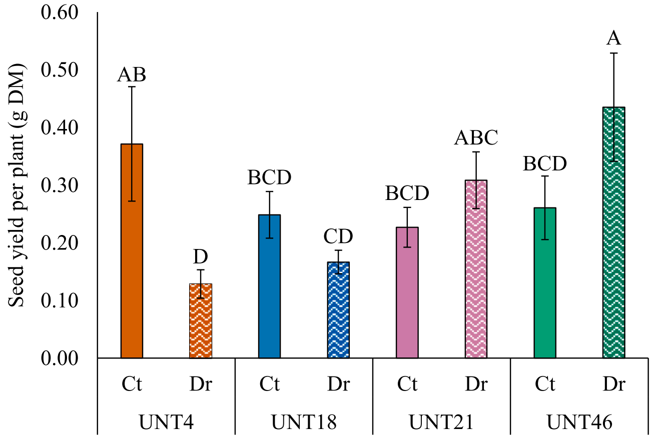


Fig. 7. Mean final seed yield in response to the interaction "line × stress". Ct=control, Dr=drought. Vertical bars: standard error. Different letters refer to statistically different means for $P \leq 0.05$, LSD Fisher's Test.

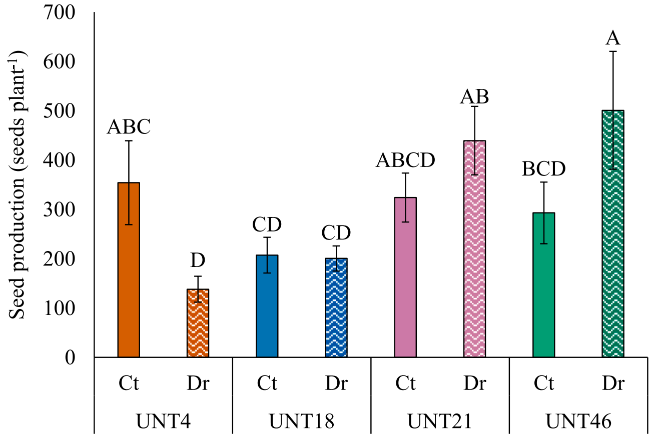


Fig. 9. Mean seed production in response to the interaction "line × stress". Ct=control, Dr=drought. Vertical bars: standard error. Different letters refer to statistically different means for $P \leq 0.05$, LSD Fisher's Test.

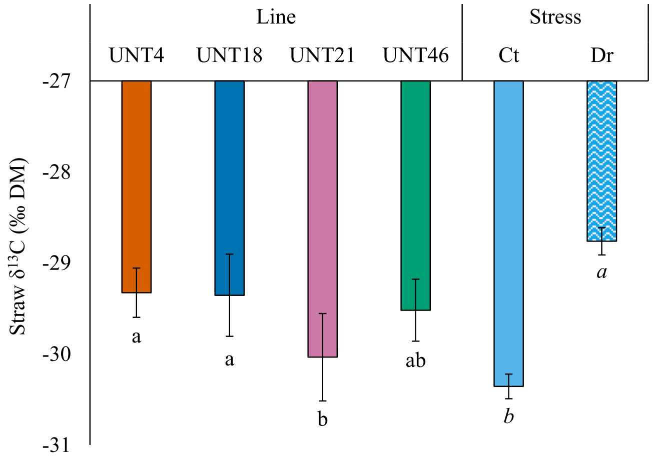


Fig. 8. Mean straw δ^{13}C in response to the interaction "line × stress". Ct=control, Dr=drought. Vertical bars: standard error. Different letters, within the main factor line, refer to statistically different means for $P \leq 0.05$, LSD Fisher's Test. Different italic letters, within the main factor stress, refer to statistically different means for $P \leq 0.05$, LSD Fisher's Test.

to the other camelina lines UNT18 was characterized by a lower ability to form seed in both conditions, this trait having a negative impact on its productivity (Fig. 9). The straw C/N ratio was not affected by any of the factors under study, while that of seed was significantly affected by the line and the stress (Table 4). Amongst the lines, UNT21 had significantly lower C/N than UNT18 and UNT4, but not different than that of UNT46 (Table 5), confirming some shared responses between these two lines. In general, drought stress caused a significant decrease of C/N (10.4 vs. 11.2 C/N, drought vs. control, respectively, $P \leq 0.05$, Table 5). Concerning seed oil content, UNT4 and UNT18 had similar values which were the highest compared to the other lines, while UNT21 was characterized by the lowest oil content (Table 6). Drought stress negatively affected seed oil content, causing a reduction of about 7 % ($P \leq 0.05$, Table 6). Interestingly, a significant interaction line × stress emerged for seed oil content. As evident in Fig. 10A, as earlier shown for seed yield, UNT46 was not negatively affected by drought keeping the seed oil content in the two water regimes, while all the other camelina lines showed significant decreases in this parameter, with UNT4 showing the highest reduction (-11 %). Also, seed protein content was affected by the imposition of drought stress (Table 4), causing a significant increase on the protein content under drought, confirming how the production patterns of protein and oil in the seeds are concurrent (Table 6). Remarkably, also for seed protein a significant interaction line × stress was surveyed (Fig. 10B). In detail, UNT46 had a lower seed protein content under drought compared to control, while all the other lines increased protein content in drought, although this increase was significant only in UNT21. The contents of oleic, linoleic and linolenic acids were significantly affected by the line, UNT46 and UNT21 were the richest in oleic and linolenic acid, while UNT18 had the highest content of linoleic acid and lowest values for oleic and linolenic acid, and UNT4 had intermediate values of all the main fatty acids (Table 6). Concerning the effect of drought stress on the main fatty acids, it significantly reduced both oleic and linoleic acid content, but it promoted linolenic acid content (C18:3). Significant effect of the interaction "line × stress" emerged for oleic and linolenic acid. Oleic acid content in UNT4 and UNT46 was maintained at a similar level in stressful conditions. Notably, UNT46 had the higher oleic acid amount under drought, whilst in UNT4 it was higher under control conditions. For both UNT18 and UNT21 significant decreases in oleic acid content were surveyed under drought (Fig. 11A). Concerning linolenic acid content, in all camelina lines

Table 6
Seed quality parameters [TGW, seed oil content, seed protein content, oleic (C18:1), linoleic (C18:2), and linolenic (C18:3) acid contents] in response to the main factors: line and stress. Mean values ± standard error. Different letters, within the same parameter and factor, refer to statistically different means for $P \leq 0.05$, LSD Fisher's Test.

Main factor Camelina line	TGW (g)	Seed oil content (% DM)	Seed protein content (% DM)	C18:1 (% DM)	C18:2 (% DM)	C18:3 (% DM)
UNT4	0.96 ± 0.01 b	36.4 ± 0.58 a	27.2 ± 1.04	15.5 ± 0.19 b	21.9 ± 0.18 b	29.6 ± 0.30 b
UNT18	1.03 ± 0.01 a	36.4 ± 0.37 a	28.0 ± 0.60	14.3 ± 0.12c	23.1 ± 0.05 a	28.7 ± 0.13 c
UNT21	0.72 ± 0.01 d	34.1 ± 0.33c	30.1 ± 1.27	16.5 ± 0.18 a	19.7 ± 0.13 d	32.0 ± 0.27 a
UNT46	0.90 ± 0.01 c	35.3 ± 0.39 b	29.0 ± 0.78	16.2 ± 0.09 a	20.1 ± 0.13c	31.9 ± 0.18 a
Stress						
Control	0.88 ± 0.02 b	36.8 ± 0.31 a	27.7 ± 0.65	15.9 ± 0.17 a	21.3 ± 0.22 a	30.2 ± 0.23 b
Drought	0.92 ± 0.02 a	34.3 ± 0.22 b	29.4 ± 0.71	15.4 ± 0.16 b	21.1 ± 0.27 b	30.9 ± 0.33 a

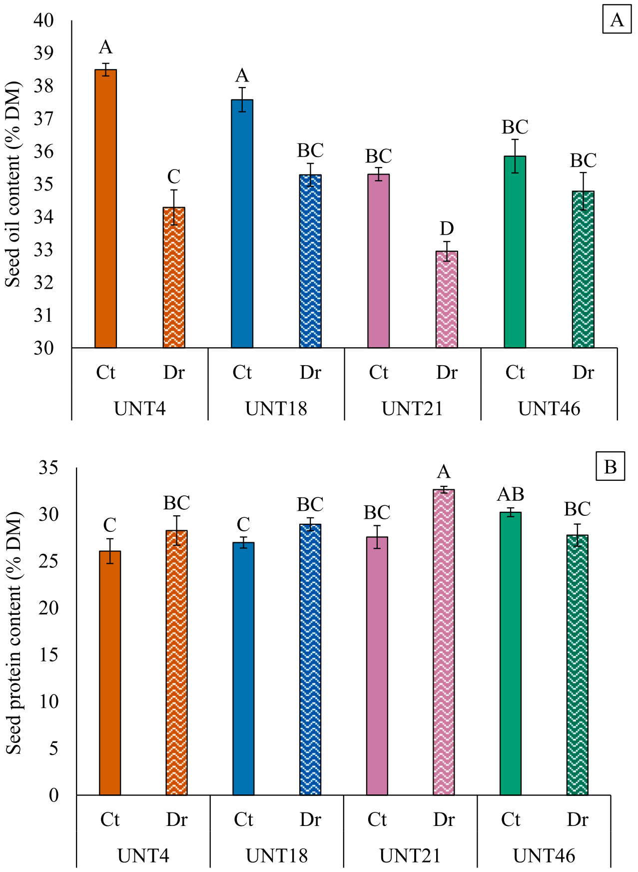


Fig. 10. Mean values of A) seed oil content and B) protein content, in response to the interaction "line × stress". Ct=control, Dr=drought. Vertical bars: standard error. In each image (A, and B), different letters refer to statistically different means for $P \leq 0.05$, LSD Fisher's Test.

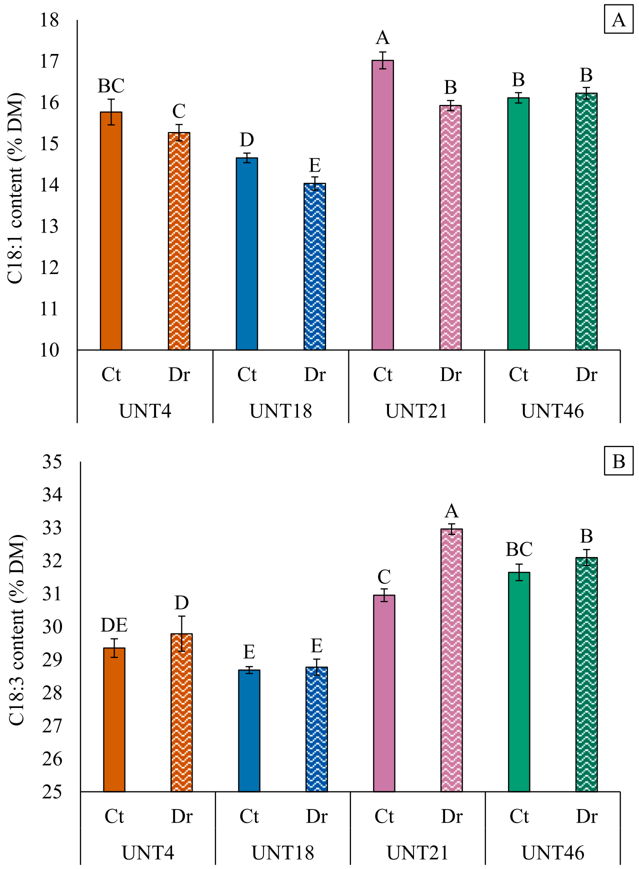


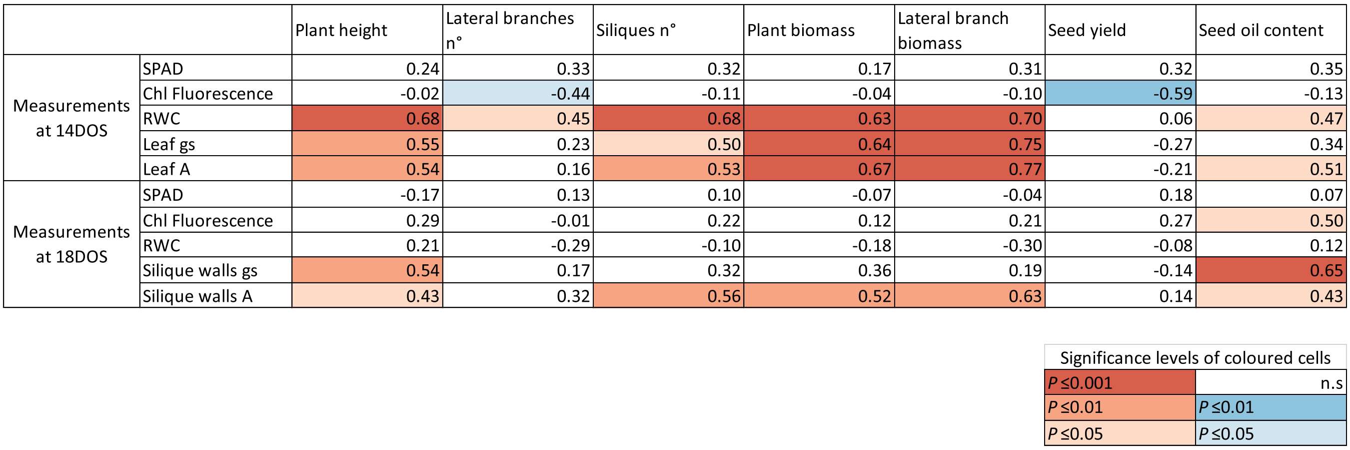
Fig. 11. Mean contents of: A) oleic acid (C18:1) and B) linolenic acid (C18:3), in response to the interaction "line × stress". Ct=control, Dr=drought. Vertical bars: standard error. Different letters, within each parameter, refer to statistically different means for $P \leq 0.05$, LSD Fisher's Test.

higher values were surveyed under drought conditions, but significant differences were evident only for UNT21 (Fig. 11B).

The correlation analysis (Fig. 12) permitted to identify possible significant relationships between physiological traits surveyed after stress imposition and biometric, agronomic and quality traits measured at harvest. Interestingly, plant height, number of siliques, plant biomass and lateral branches biomass were all positively correlated with many of the physiological traits surveyed at 14 DOS, i.e. RWC, leaf A, leaf g_s, while at 18 DOS only silique wall A was still significantly correlated to the same biometric and agronomic traits. Seed yield resulted significantly, but negatively (r = -0.59), correlated only with chlorophyll fluorescence surveyed at 14 DOS, showing that keeping Fv/Fm high was an opposite strategy to seed yield formation. Seed oil content resulted significantly and positively correlated with many of the physiological parameters surveyed either at 14 DOS (i.e., RWC and leaf A) and at 18 DOS (i.e., chlorophyll fluorescence, silique wall A, silique wall g_s). The highest correlation ($r = 0.65$, $P \leq 0.001$) was found for seed oil content and silique wall g_s surveyed at 18 DOS. Camelina plants with higher stomatal conductance at 18 DOS were later able to accumulate higher oil content in their seeds.

4. Discussion

The Mediterranean basin is predicted in many climate models to be highly impacted by decreases in precipitation due to climate-related changes in weather patterns during the warm period between April and September, with reductions up to 10 % by 2030, and increasing to 20 % by 2050 (Woetzel et al., 2020). The predicted period of increased drought overlaps with the reproductive stage of many staple crops. Water shortage occurring during flowering and ripening can be particularly harmful for agricultural production, causing yield losses due to fewer flowers, reduced pollen viability, and poor fruit set (Farooq et al., 2009; Sehgal et al., 2018). Hence, it is important to identify species or varieties that can successfully cope with drought maintaining acceptable seed yields. Many physiological processes in plants (i.e., cell growth and photosynthesis) are influenced by water availability (Waraich et al., 2017b). This implies that water shortage can cause damages to chlorophyll, membranes, and the photosynthetic system (Sehgal et al., 2018). Such effects were identified in the present work, with many physiological parameters (i.e., chlorophyll content, relative water content of leaves, stomatal conductance, and net photosynthesis) lowered by drought; results that agree with previous studies on camelina (Pan et al., 2011; Ahmed et al., 2017, 2020; Gao et al., 2018). Stomatal conductance and net photosynthesis are closely linked in their response to water limitation, as the main challenge for plants in drought conditions is the maintenance of water balance. To this end, plants typically close stomata to reduce water loss (Gao et al., 2018). However, this restricts CO_2 uptake, causing a reduction in net photosynthesis of the plant (Ahmed et al., 2017; Waraich et al., 2017a). In the present work, some camelina morphological traits surveyed at harvest were negatively impacted by drought, i.e., plant height, number of silicles, stem and lateral branches biomass, reflecting previously reported outcomes from other studies on camelina and canola (Elferjani and Soolanayakanahally, 2018; Waraich et al., 2017a, 2017b; Ahmed et al., 2020; Waraich et al., 2020). Moreover, their reductions were significantly correlated with many of the physiological traits surveyed at earlier stages (14 DOS), when camelina



		Plant height	Lateral branches n°	Siliques n°	Plant biomass	Lateral branch biomass	Seed yield	Seed oil content
Measurements at 14DOS	SPAD	0.24	0.33	0.32	0.17	0.31	0.32	0.35
	Chl Fluorescence	-0.02	-0.44	-0.11	-0.04	-0.10	-0.59	-0.13
	RWC	0.68	0.45	0.68	0.63	0.70	0.06	0.47
	Leaf gs	0.55	0.23	0.50	0.64	0.75	-0.27	0.34
	Leaf A	0.54	0.16	0.53	0.67	0.77	-0.21	0.51
Measurements at 18DOS	SPAD	-0.17	0.13	0.10	-0.07	-0.04	0.18	0.07
	Chl Fluorescence	0.29	-0.01	0.22	0.12	0.21	0.27	0.50
	RWC	0.21	-0.29	-0.10	-0.18	-0.30	-0.08	0.12
	Silique walls gs	0.54	0.17	0.32	0.36	0.19	-0.14	0.65
	Silique walls A	0.43	0.32	0.56	0.52	0.63	0.14	0.43

Significance levels of coloured cells	
$P \leq 0.001$	n.s
$P \leq 0.01$	$P \leq 0.01$
$P \leq 0.05$	$P \leq 0.05$

Fig. 12. Correlation matrix for the significant relations between physiological parameters surveyed at 14 DOS and 18 DOS (SPAD, Chl fluorescence, RWC, A and g_s) and biometric, agronomic and quality traits surveyed at harvest (plant height, number of lateral branches, number of siliques, plant biomass, lateral branch biomass, seed yield, and seed oil content) on the four camelina lines under control and drought conditions. In the matrix, the Pearson correlation coefficients are reported as coloured when statistically significant, as defined in the bottom part of the figure. In particular orange cells indicate significant positive correlations, and blue cells indicate significant negative correlations.

plants were at the end of flowering. At this stage, drought negatively impacted all the physiological parameters surveyed. RWC surveyed at 14 DOS showed significant correlations with some of the morphological traits surveyed at harvest (i.e., plant height, stem and lateral branch biomass, number of siliques, etc.). Many of the camelina physiological responses under drought surveyed at 14 and at 18 DOS decreased overall, despite significant differences emerging amongst the lines. Only net photosynthesis, stomatal conductance and WUEi at 14 DOS showed significantly different responses for the interaction of lines with drought stress. Limited photosynthetic activity typically decreases the production of molecules and intermediates available for seed development, leading to significant yield losses (Waraich et al., 2017a; Ahmed et al., 2019, 2020). Furthermore, drought stress lessens the available nutrients and photo-assimilation reserves that are essential for the development of reproductive structures (e.g., pollen tube elongation, Barnabás et al., 2008). Surprisingly, in the present study camelina yield response to water limitation, in terms of seed yield per plant, TGW, and seed production, was not negatively affected by drought, and the response was different depending on the line, confirming the plasticity of stress responses in camelina (Stasnik et al., 2023). Actually, a significant but negative correlation emerged between chlorophyll fluorescence at 14 DOS and seed yield, indicating that plants with higher F*v*/F*m* at earlier stage were more impacted on seed yield, while those characterized by photosynthesis downregulation were able to keep high and stable yield. This behavior results quite in line with mechanisms of stress avoidance, rather than stress tolerance, which might have been put in place by some of the camelina lines tested, as already reported in *Arabidopsis* by Wolfe and Tonsor (2014). With respect to seed production, UNT4 and UNT18 showed yield reduction under drought stress, while UNT21 and UNT46 maintained stable yields, or even increased seed yield (UNT46). Interestingly, at 18 DOS, UNT46 silicles of stressed plants showed the highest net photosynthesis, reporting values like other lines in control conditions. The photosynthetic activity of reproductive organs plays a pivotal role in determining seed yield, supplying carbon and energy useful for seed formation and contributing to the production of seed assimilates which are then remobilized in seeds (Aschan and Pfanz, 2003, Bennett et al., 2011, Hua et al., 2012). Thus, lines characterized by the ability to produce a larger number of siliques and keep their photosynthetic activity as high as possible were identified as the ones suffering less from water shortage, as in the case of UNT21 and UNT46, as previously reported by Habekotté (1993), in rapeseed. It should be noticed that in stressed plants seed yield results had the same trend as silicle photosynthesis, confirming the findings by Wang et al. (2023) where inhibition of silicles photosynthesis in *Brassica napus* caused a dramatic reduction in seed yield. For this reason, improved photosynthetic rate of UNT46 silicles may have boosted its seed production under drought conditions, matched with the ability to keep a high silique number. However, control plants did not show this behavior with UNT4 which was the highest yielding despite having the lowest silicles photosynthesis, while it had the highest WUEi at 14 DOS. It could be possible that in camelina leaf WUEi contribution to seed yield determination still plays an important role in well-watered conditions, where leaves can maintain their photosynthetic activity also during seed filling stage. This is supported by Wang et al. (2016), which reported that final seed yield depends on both photosynthetic production of leaves and silicles. Another factor that may have influenced the yielding performance of UNT46 could be its lower plant height, being stable in the control and drought conditions: indeed, plant height reduction has been reported by Lipiec et al. (2013) to be an adaptative response to stress. Line UNT46 was characterized, together with UNT21, by the lightest seeds, the higher number of siliques per plant, and the lower seed oil content. These traits might have permitted these lines to adjust their capacity to set seeds, maintaining the production high and stable also under drought. On the other hand, UNT18, which was characterized by the heaviest seeds and the highest seed oil content, performed poorly in terms of seed production per plant, with a poor compensatory effect under stress (i.e., seed production remained unchanged in the control and drought condition). The compensatory effect under stressful conditions is frequently reported as an adaptation strategy in rapeseed, which often modulates seed yield by modifying seed weight and seed production per plant (Weymann et al., 2015). In the present study, this compensatory behavior seemed only related to camelina seed formation ability rather than seed weight modulation, which appeared fully under genetic control, but it was evident only in some lines, like UNT21 and UNT46, while in others it was only partly present (UNT4) or not present at all (UNT18). The degree of $\delta\ ^{13}C$ during photosynthesis is closely linked to the conductance of stomata. Open stomata and the free movement of water ensure the free assimilation of CO_2, such that discrimination against ^{13}C is at its maximum. On the contrary, closed stomata, which conserve water, restrict the availability of CO_2 bringing $\delta^{13}C$ at its minimum. The diverse plasticity in the response to abiotic stresses of camelina lines was confirmed by considering the ^{13}C isotope discrimination capacity. Indeed, lines UNT21 and UNT46, which were the more drought-resistant in terms of seed yield, had also the lowest discrimination in straw, this trait might be of interest for future breeding programs. Conversely, $\delta^{13}C$ in seed was not able to distinguish among lines, thus confirming a more complex pattern of responses for seeds, presumably involving numerous metabolic and enzymatic networks (Boutet et al., 2022; Stasnik et al., 2023) rather than only limitation in C assimilation through photosynthesis.

The effects of drought on seed oil content and composition are a primary consideration, given these traits determine the crop value. In the present work, drought lowered seed oil content as previously observed by other studies (Raza et al., 2015; Pavlista et al., 2016; Ahmed et al., 2017, 2019, 2020; Borzoo et al., 2021). Reduction of oil content under drought stress can be ascribed to lowered photosynthetic rate, which determines a limited availability of digestible carbohydrates accessible for triacylglycerol biosynthesis in developing seeds (Sehgal et al., 2018; Ahmed et al., 2019, 2020; Borzoo et al., 2021). This finding was confirmed by the correlation analysis, which highlighted significant and positive correlation with seed oil content and the majority of the physiological traits surveyed, especially at early stage (14 DOS). Furthermore, acyltransferases respond to drought in camelina and impact oil accumulation and composition (Yuan et al., 2017). Moreover, oil content and composition are likely impacted by carbon allocation, changes in enzyme activity, and hormonal signaling. Transcriptional networks respond to drought signals (hormones) and change fatty acid biosynthesis. Fatty acid biosynthesis and the network of oil assembly pathways are thus likely to be sensitive to drought. Maintenance of membrane integrity under drought will result in changes in fatty acid desaturation and transport (Flagella et al., 2002; Ullah et al., 2022; Tan et al., 2024). Indeed, fatty acid composition was impacted by water limitation, with a decrease in oleic and linoleic fatty acid, while linolenic acid increased under drought conditions. These results, although they are negligible as changes, are opposite to what Pavlista et al. (2016) and Ahmed et al. (2019) previously reported. It should be noted that UNT21 and UNT46 had the highest linolenic acid content, which significantly increased in UNT21 under drought conditions. Observed changes in C18:3 can be ascribed to two factors: a) C18:3 is a precursor of jasmonic acid, thus playing a role in plant stress resistance; b) due to its unsaturation degree, C18:3 contributes in maintaining cell membrane fluidity in the optimum range, delaying the detrimental effects of stress (He et al., 2020). In accordance with this, Enjalbert et al. (2013) stated that linolenic acid content is correlated to drought-stress tolerance in camelina, hence this characteristic may be another reason for the improved seed yield of UNT 21 and UNT46 under water shortage conditions.

5. Conclusions

Climate change effects are having a detrimental impact on the typical growing conditions of staple crops. Identifying crops, and genotypes within species, with the capability to quickly adapt and tolerate climate change effects should be one of the main targets of future agriculture. The ancestral oilseed camelina, to which yet little attention has been given by traditional breeding, maintains distinctive traits that could make it a resilient crop for the future. Thus, this species might represent an opportunity for farmers living in areas which are increasingly facing periods of drought, or which soils are marginal and characterized by limited water holding capacity. However, it is important to identify the lines, within this species, which are resilient to drought stress, aiming at possibly developing specific breeding program for dry areas. The present study tried to set a protocol of different physiological measures taken early after the stress imposition to score the resistance of different camelina lines. Drought stress has been confirmed to impact camelina physiological responses at earlier stages of imposition, but an outstanding capacity to overcome drought, coupled with likely trade-off physiological mechanisms has been observed in the present study. Some camelina lines showed negligible or no effects of drought in terms of productive performance. In particular, UNT21 and UNT46 showed to be the best lines in terms of seed production under drought conditions. Moreover, regarding seed oil content, UNT46 was also able to maintain the same oil content in well-watered and in water shortage conditions, thus representing a line that can reach economical yields also in drought areas. Notwithstanding with this, it has to be remarked that an interesting plasticity in terms of physiological, morphological, productive and quality responses have been identified in the camelina lines within this study. Although it was expected that physiological parameters would be linked to yield data, physiological responses related to photosynthesis limitations had significant effects only on some morphological traits (i.e., plant height, stem and lateral branch biomass). On the other hand, most of the seed yield and quality traits highlighted the response variability across camelina lines, quite disconnected with earlier physiological responses. Camelina seed yield formation processes, coupled with oil biosynthesis and fatty acid metabolism, include a complex network of regulation and integration, which so far remains to be fully revealed. In the future, it would be worth to further investigate if in camelina there are any metabolic pathways (i.e., lipidomic, antioxidants, redox status, protein turnover, etc.) able to early predict the response to drought stress in terms of final seed yield formation. Additionally, understanding the response of different camelina lines to multiple and combined stresses, which often occur under field conditions, e.g., heat x drought stress, will probably permit a better understanding of the response behavior of this crop. Additionally, breeding programs might focus on selecting camelina lines able to keep silique formation high also under stress conditions, as this trait might be linked to the capacity to maintain acceptable seed yield under limiting conditions.

CRediT authorship contribution statement

Barbara Alberghini: Writing – original draft, Visualization, Formal analysis, Data curation. **Richard Haslam:** Writing – review & editing, Supervision, Funding acquisition. **Susana Silvestre:** Writing – original draft, Data curation. **Zanetti Federica:** Writing – review & editing, Writing – original draft, Conceptualization. **Miriana Vicino:** Writing – original draft, Data curation. **Walter Zegada-Lizarazu:** Writing – review & editing. **Andrea Monti:** Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This research was supported by the UNTWIST project, which has received funding from the European Union's Horizon 2020 research and innovation program under grant agreement no. 727698.

Data availability

Data will be made available on request.

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