Sesame response to nitrogen management under contrasting water availabilities

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ABSTRACT

Sesame is mainly cultivated under traditional, low-input agro-systems. Recent breeding developments promoted the modernization and mechanization of sesame cultivation. However, only a few articles have been published concerning fertilization requirements for both modern and traditional agro-systems. In field trials at two locations, we determined the response of irrigated sesame to nitrogen (N). Three promising sesame lines were tested combining two irrigation levels with four N levels. At a high irrigation level, N had a significant effect on growth, branching, and consequently, seed yield exceeding two-ton ha^{-1}. A high N doze was accompanied by a decrease in the photosynthetic rate and leaf water potential. The δ^{13}C confirmed lower stomatal conductance under high N treatments. Under deficit irrigation, the N level had a minor effect on the monitored parameters, indicating N fertilization was not efficient. Seed oil content was negatively correlated with seed N concentration. Our results question the necessity of N application when water is limited, as N fertilization promotes vigorous development that rapidly depletes soil water. Thus, water availability should be considered when developing an N management strategy. For high-yielding agro-systems, roughly 80–120 kg ha^{-1} N is required for optimal yield, bearing in mind the negative association between seed-N and oil content.

1. Introduction

Sesame (*Sesamum indicum* L.; genome $2n = 2x = 26$) is an important oilseed crop, being used for a wide range of products in the food industry, such as cooking oil, paste (tahini), baking, and pharmaceutical (Mushtaq et al., 2020). Sesame seeds contain a considerable amount of essential mineral nutrients, with high bio-accessibility (Teboul et al., 2020). Its health properties are attributed to various nutritional quality characteristics, including its high protein and high mineral contents (Lu et al., 2019), as well as to several nutraceutical phytochemicals. In recent years, the demand for sesame seeds (and secondary products) has been increasing as part of the global trends toward healthier plant-based food products.

Recent breeding efforts have introduced new sesame varieties adapted for mechanical harvest (Langham et al., 2010; Couch et al., 2017; Teboul et al., 2022), which enables modern sesame cultivation techniques, including irrigation and fertigation. Under an intensive agro-system, sesame yields exceeded 2 t ha^{-1}, nearly four times higher than the reported global average for traditional agro-systems (Myint et al., 2020). The low-input sesame agro-systems are not supported by

adequate research and breeding efforts, making sesame an 'orphan crop' in modern cultivation techniques and breeding (Varshney et al., 2012; Wei et al., 2013; Zhang et al., 2013; Zhang et al., 2013; Sabag et al., 2021). Thus, it is necessary to bridge the knowledge gap between production and market demand and develop fertilization management strategies for intensive agriculture practices.

Acquisition of N by plant's roots is largely dependent on water availability that facilitates the movement of minerals into and across the root (Barber 1995). Most of the world's sesame cultivation is rainfed, relying on summer rains or residual soil moisture. Mass flow of N to the root relays on the transpiration rates, therefore, N acquisition is enhanced by high water availability (Oyewole et al., 2014), while the opposite is true in the case of water deficiency (Alam 1999; Stamatiadis et al., 2016). Furthermore, N nutrition may affect plant response to drought to the two extremes: synergy (Meng et al., 2016) or antagonism (Albornoz 2016). In forests, drought stress was alleviated by N supply through the promotion of root development and activation of antioxidative activities (Guo et al., 2010). On the contrary, in the rainfed wheat cropping system, high N levels led to severe water stress through vigorous shoot development and limited water supply (Van Herwaarden

et al., 1998; Wang et al., 2019).

The common paradigm is that sesame is well adapted to low soil fertility and thus, in practice, fertilization is sporadic, applying either manure or mineral fertilizers (Bedigian 2010). The literature lacks solid fertilization recommendations or guidelines, yet a handful of evidence illustrates a positive yield response to N under field conditions and traditional cultivation (Ahmad et al., 2001; Shehu et al., 2010; Nandan et al., 2015; Zenawi and Mizan 2019). In a classic controlled study, Mitchell et al. (1974) investigated sesame yield and biomass response to N concentrations in potted sand culture. The authors drew N response curves and found that the highest seed yield was in response to N concentrations of 4.0–8.0 mmol/L N (56–112 mg L^{-1}). Despite being thorough and comprehensive, these results were not validated under field conditions. Various sporadic field tests generated a wide range of N recommendations from 45 kg ha^{-1} (El Mahdi 2008; Bellaloui et al., 2018) up to 205 kg ha^{-1} (Noorka et al., 2011), applied mostly as base fertilizer, while water availability and expected yields are generally ignored. Split N application that follows plant demand is considered critical to obtaining high N use efficiency (NUE) (Zenawi and Mizan 2019). Couch et al. (2017a,b) illustrated the pattern of N accumulation in modern sesame cultivars and suggested that N fertilizer should be adjusted to plant developmental stages.

Fertigation is a modern fertilization method in which liquid fertilizers are applied through the irrigation system. Fertigation is considered a superior and precise technology, as it enables controlling the time and place of fertilizer application throughout the season (Bar-Yosef 1999; Wang and Zhang 2010). Fertigation enables the optimization of fertilizer doze according to plant development, following established accumulation schemes (Couch et al., 2017). Continuous supply of low N doze by fertigation is also expected to reduce N leaching in sandy soils, therefore, minimizing environmental contamination (Zenawi and Mizan 2019). Despite its acknowledged benefits, we could not find any large-scale experiments testing the effect of fertigation levels on sesame developmental and reproductive traits. Nonetheless, this technology is expected to gain popularity as a result of successful breeding efforts for high-yielding varieties suitable for mechanical harvest (Langham et al., 2010; Couch et al., 2017; Teboul et al., 2022). The objective of the present study was to develop guidelines for sesame fertilization with N under modern fertigated agro-systems and to determine the impact of water availability on sesame N requirements.

2. Materials and methods

2.1. Plant material

Three outstanding sesame genotypes from the Hebrew University of Jerusalem sesame collection (SCHUJI; Sabag et al., 2021) were selected based on their high yield potential under intensive cultivation. These varieties represent a wide array of plant architecture characteristics and geographical origin: S-1034 originated from Egypt, characterized by low branching tall growth habit, and large light brown seed color. S-3 originated from Ethiopia (also known as "Humera") and is mainly grown for sesame paste (Tahini) production, characterized by high branching, early blooming, and white seed color. S-8 is a traditional Israeli variety used for sesame paste and sweets and is characterized by a slow growth rate, late-blooming, moderate branching, and brown seeds. Representing pictures illustrating morphological differences between the three varieties used in the field experiments are presented in Fig. 1. Principal components analysis adapted from Sabag et al. (2021) reveals pronounced genetic variability among these varieties (Fig. S1).

2.2. Experimental sites and design

From spring to summer of 2017, two field experiments were conducted at two locations: (1) the Experimental Farm at the Gilat Research Center (31.340, 34.671) and (2): the Experimental Farm of the Faculty of Agriculture, Food and Environment in Rehovot (31.906, 34.800). Soil texture and mineral concentrations are presented in Table S1. Generally, Gilat is located in a semi-arid environment with higher potential ET (Fig. S2) and lower precipitation (216 mm year^{-1}) compared to the Mediterranean climate in Rehovot (528 mm year^{-1}). The accumulative potential ET from the 1st of May to the end of August was 926 and 868 mm in Gilat and Rehovot, respectively. No rain events occurred during both experiments.

The experimental setup included two irrigation levels (high and low) that essentially each represent an independent trial. At each irrigation level, three sesame varieties were tested against four N concentrations at four repetitions. In total, 4 N levels × 2 irrigation levels × 4 repetitions = 32 experimental plots. Each experimental plot was composed of three varieties that were sown in three neighboring rows for each variety (S-3, S-8, and S-1034), summing up to 96 sub-plots. Plot sizes were 16.2 m^2 in
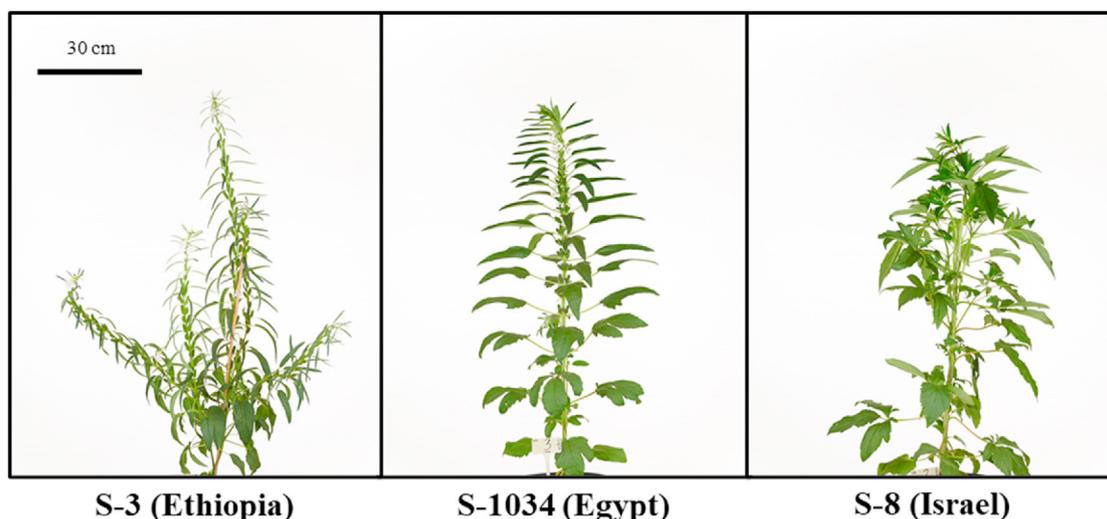

Fig. 1. A representative photo of the three sesame varieties tested in the current study. Pictures were taken 68 days after germination at the Gilat research center.

Gilat and 13.5 m² in Rehovot- 1.8 m width, 9 m length in Gilat and 7.5 m length in Rehovot. Plant density was six plants per meter and 60 cm between the rows (10 plants ·m⁻²). Irrigation was applied by an integral, pressure-compensated drip-line (UniRam™, Netafim, Israel) connected to a controller (SAS-control, Israel) that operated the valves and fertigation pump for each treatment separately (MixRite 2.5, Tefen, Israel). Water and liquid fertilizer volume were operated by the controller according to the water meter (Model-M, Arad, Israel) and fertilizer meter (SF, Arad, Israel) output. The irrigation level and plant density were set following previous studies in our lab (Gadri et al., 2020). Immediately after sowing, several irrigation events were applied for uniform and high germination rates (Fig. S2). Following germination, plots were irrigated according to the measured ET_0 multiplied by the Pennman-Monthith crop coefficient (Kc). At the early stage, Kc was 0.8 until flowering. During capsules development, Kc was set to 1.0 and later reduced to 0.5 during capsules ripening. The low irrigation level was set to ~**45%** of the high irrigation level. Actual irrigation levels in the two sites are presented in Fig. S2. The actual irrigation volume was 338 and 152 mm for the high and low irrigation levels in Rehovot and 396 and 178 mm for the high and low irrigation levels in Gilat. After germination, fertigation was supplied continuously in each irrigation event by injecting tailor-made liquid fertilizer. Target N concentrations were: 0, 15, 55 and 100 mg l⁻¹ for the two irrigation levels, e.g., fixed concentrations (mg·L⁻¹) rather than fixed N doses (kg· ha⁻¹). Therefore, per given N concentration, the low irrigation experiment received a lower N dose (Table S2). Average measured concentrations are presented in Table S2. The remaining nutrients were similar for all treatments: **2.3**, 34, 40 and 12 mg L⁻¹ P, K, Ca and Mg, respectively. When capsules turn yellowish, fertilizer was stopped.

2.3. Growth and yield characteristics

We marked three representative plants from each plot × variety, located in the middle of the central row. Throughout the trial, these plants were used for the measurement of leaf area index (LAI), gas exchange, and yield components. LAI was determined weekly by LAI Ceptometer (LP-80, Decagon Devices, USA). Physiological measures were determined at mid-day when plans were at the peak of the reproductive stage (July 27 Gilat and 31 Rehovot). Gas exchange measurements were carried out by CIRAS-III device (PP Systems, USA) for S-1034 only on two dates (66 and 71 DAP (days after planting) in Rehovot and 66 and 97 DAP in Gilat). Simultaneously, stem water potential was determined on the same plants by pressure chamber (ARIMAD 3000, MRC, Israel).

Plants were harvested manually when the first capsule started to dehisce. The monitored plants were cut from the base of the stem and left to sun-dried until all capsules were dehisced. Following harvest, growth characteristics were recorded: number of branches, number of capsules, and total fresh weight. After drying, yield characteristics were recorded: number of seeds per plant, seed weight per plant, 1000 seeds weight (TSW), and the number of seeds per capsule. Simultaneously, 15 m² per plot were manually harvested into bags. Samples were threshed using a laboratory thresher (Wintersteiger AG LD 350, Austria) and after sifting, the seeds were weighed to obtain seed yield.

2.4. Laboratorial analysis

Oil content was measured only in S-1034 seeds using soxhlet apparatus. Briefly, 3 g of seeds were ground and extracted by hexane circulated for 6 h by boiling and cooling. The seeds were weighted before and after oil extraction to determine their oil content. Seed N concentration was tested using the Dumas method (Rapid N exceeded, Elementar, Germany). N concentration in irrigation water and in soil (saturated paste) were colorimetric analyzed using Gallery Discrete Analyzer, Thermo-Fisher, USA). The carbon isotope ratio (δ^{13}C) was tested at S-1034 seeds at the Institute of Earth Sciences, the Hebrew University of

Jerusalem. Seeds were taken from plants fed in the high N treatment (N100) and from the no N treatment (N0) in both irrigation levels. A representative sample of seeds was weighed (0.3–0.8 mg), inserted into aluminum capsules and burned at a temperature of 1050 °C. The CO_2 gas released during the combustion was injected with helium gas into Mass Spectrometer (Multiskan SkyHigh- ThermoFisher Scientific, Germany). The $C/^{12}C^{13}$ ratio was measured and expressed in differential notation as δ^{13}C relative to the international standard fossil V-PDB (Vienna Pee Dee Belemite). δ^{13}C = (R_{sample} - $R_{standard}$)/$R_{standard}$ × 1000, where R_{sample} and $R_{standard}$ are the isotope ratios of the sample and standard, respectively. The precision of the isotopic analysis was better than ±0.1‰

2.5. Data analyses

Agronomic N use efficiency was also calculated by the N contribution to the yield:

$$\frac{\text{N input (soil N + fertilization)} \left(\frac{\text{kg}}{\text{ha}}\right)}{\text{N removed from the field (seeds N \% × total seed weight)}}$$

All data analyses were conducted in JMP version 15 (SAS Institute Inc., Cary, NC). Similar growing practices and field conditions led to comparative homogeneity between treatments, therefore, analysis of variance was performed in random blocks in one or two -way ANOVA. Data of growth and yield components were tested in two-way ANOVA considering N levels, genotypes (G) and their interaction. When the interaction was insignificant, the data were combined and averaged across genotypes. In the case of branching, G × N level was significant, and therefore each line was tested individually (Table S1).

3. Results

3.1. Effect of N and irrigation levels on growth characteristics

Generally, in both trials, N application had a significant effect on vegetative biomass under control irrigation treatment, but not under the low irrigation levels at the Gilat site (Fig. 2). Under high irrigation level in the Gilat field experiment biomass increased from 93 g·plant⁻¹ at
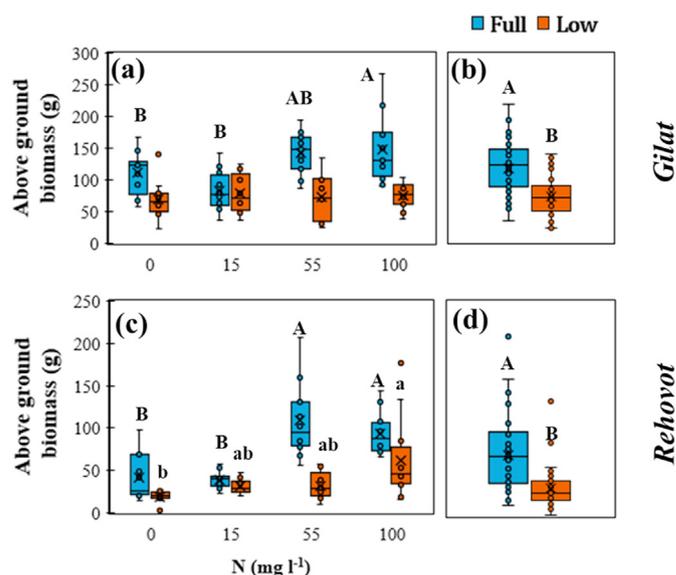
Fig. 2. Box plots of above-ground biomass at harvest in response to N concentration and irrigation levels in the Gilat (a,b) and Rehovot (c,d) field experiments. Blue boxes refer to full irrigation and red to water-limited treatment. The effect of irrigation levels (**b**) and (**d**) represents scaled averages of all lines and N levels. Different letters indicate significant differences between treatments using the Tukey-HSD test ($P \leq 0.05$) ($n = 36$).

treatment N0 to 148 g· plant^{-1} at treatment N100. At the low irrigation plots, N levels did not affect shoot weight. At the Rehovot field experiment, shoot weight increased with N levels from 25 g·plant^{-1} at treatment N0 to 108 g·plant^{-1} at treatment N55 of the full irrigated plots and from 18 g at N0 to 61 g at treatment N100 at the low irrigation level (Fig. 2c). Comparable results were obtained for the LAI measured in July during the vegetative growth (Fig. S3). The LAI was positively related to N level at the high irrigation level but had a minor effect when water availability was lower. Water availability had a very pronounced effect on growth elements such as LAI and plant biomass which at low irrigation level was approximately half of the high irrigation level regardless of the N level (Fig. 2b and d), 132 g·plant^{-1} at the high irrigation and 72 g·plant^{-1} at the low irrigation in Gilat and 79 g·plant^{-1} in the high irrigation and 37 g·plant^{-1} at the low irrigation in Rehovot.

3.2. Effect of N and irrigation levels on branching

The three sesame lines differed greatly in their tendency to branch (Figs. 1 and 3b). Branching response to N showed a line-specific increase in branching with N level. At the Rehovot field experiment, branching increased from 1 to 2 to 4–5 in S-3 and S-8 but not in S-1034 which hardly branched at all (Fig. 3c, Table S3). Interestingly, irrigation level did not affect branching (Table S3) despite an increase in total above-ground biomass (Fig. 2b and d).

3.3. Effect of irrigation level on yield components

The seed yield of an individual plant is composed of the following yield components: number of capsules per plant, number of seeds per capsule, and 1000 seed weight (TSW). Regardless of N availability, low water availability affected yield components of the three sesame lines. Water stress was significantly associated with a sharp decrease in the number of capsules per plant in the two field experiments. 196 capsules plant^{-1} at high irrigation and 104 capsules plant^{-1} at low irrigation in Gilat and 104 capsules plant^{-1} at high irrigation and 59 capsules plant^{-1} at low irrigation in Rehovot (Fig. 4 a,b). Similarly, the number of seeds per capsule and TSW was 20% lower under the water-limited treatment.

TSW was decreased from 2.8 g to 2.3 g in Gilat and from 2.8 g to 2.2 g in Rehovot and seed per capsule was decreased from 40 to 35 in Gilat and from 48 to 37 in Rehovot (Fig. 4). Consequently, total seed weight was more than doubled at the fully irrigated plots and increased from an average of 680 kg ha^{-1} to 1570 kg ha^{-1} in Rehovot and from 810 kg ha^{-1} to 2410 kg ha^{-1} in Gilat (Fig. 5b, d).

3.4. Effect of N level on yield components

The response of measured yield components to N level varied among traits, irrigation level, and location. In the Gilat field experiment, the number of capsules increased from 148 capsules·plant^{-1} at treatment N0 to 210 at N100 observed at the high irrigation plots, while at the low irrigation treatments it was statistically similar at 100–120 capsules·plant^{-1} for all N levels (Fig. 4a). In the Rehovot field experiment, high irrigation and low N treatments (N0, N15) yielded 53 capsules ·plant^{-1} compared to 130 at high N treatments (N55, N100, Fig. 4d). At low irrigation plots, the number of capsules increased from 33 to 70 when N increased from 0 to 100 mg L^{-1}.
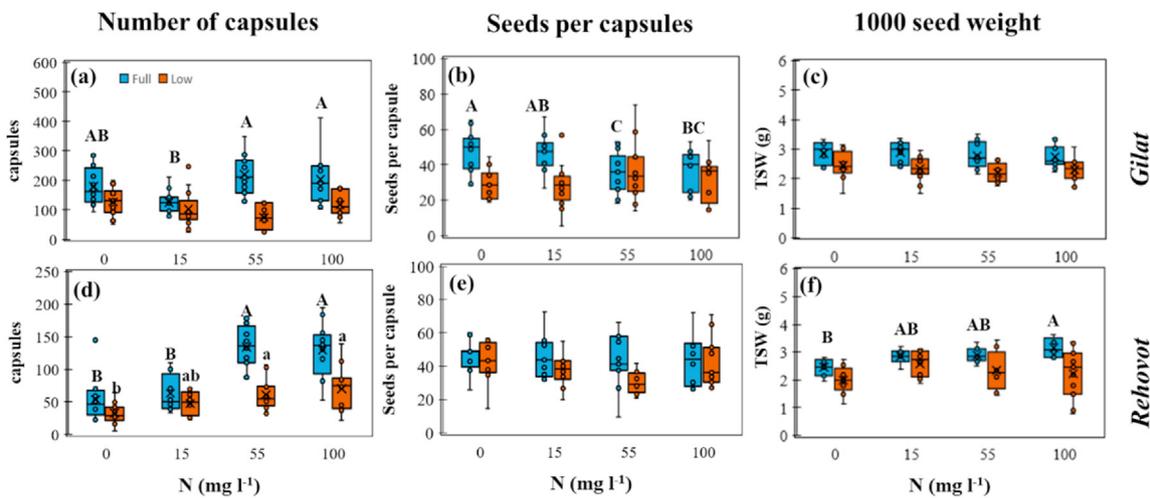
The number of seeds per capsule was not affected by N levels except for the high irrigation plots in Gilat, which showed a 26% decrease in seeds per capsule from N0 to N100 (Fig. 4b). In both trials, under low irrigation levels, TSW was not affected by N levels. TSW only increased with N application in Rehovot under full irrigation (Fig. 4c, f).

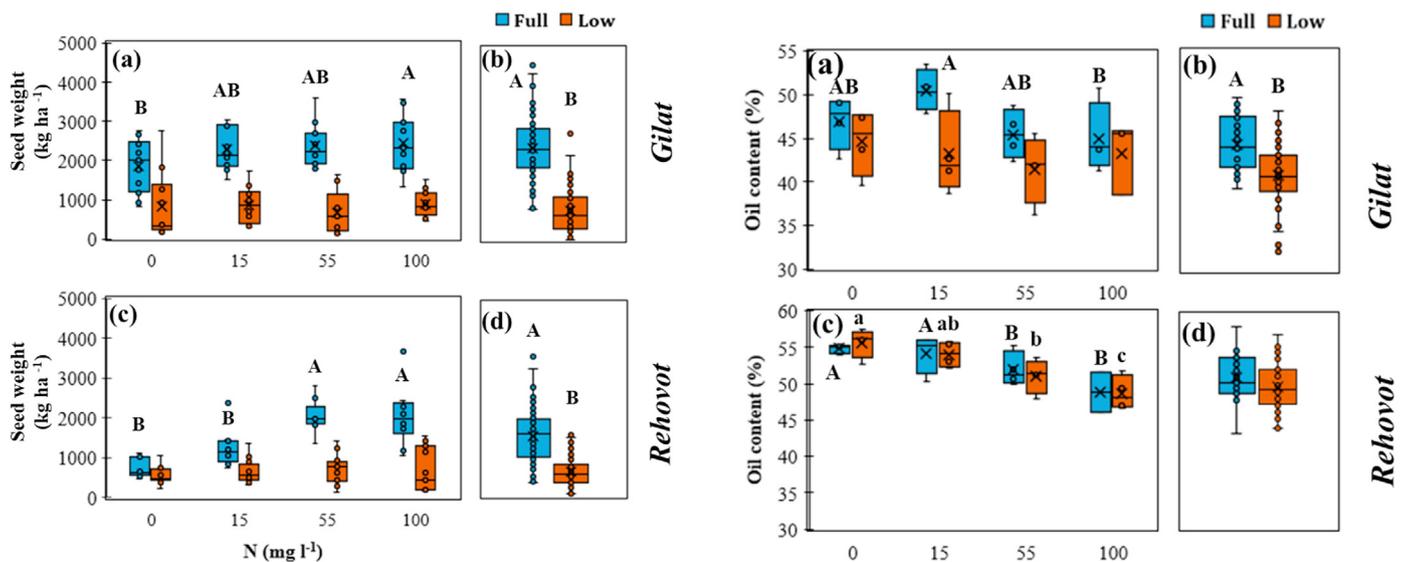### 3.5. Effect of N and irrigation levels on net seed yield

In both field trials, N did not affect seed yield at the low irrigation plots (Fig. 5) and yield was significantly lower than at the high irrigation level. At the Gilat field trial (high irrigation), yield increased from 1807 kg ha^{-1} at treatment N0 to 2832 kg at treatment N55 (Fig. 5a). In the Rehovot trial, under high irrigation, yield increased from 702 kg ha^{-1} at N0, to 2107 kg at N100. Results were consistent when the whole sub-plot was measured (Fig. 5) or three selected representative plants in the center of the sub-plot (Fig. S4).
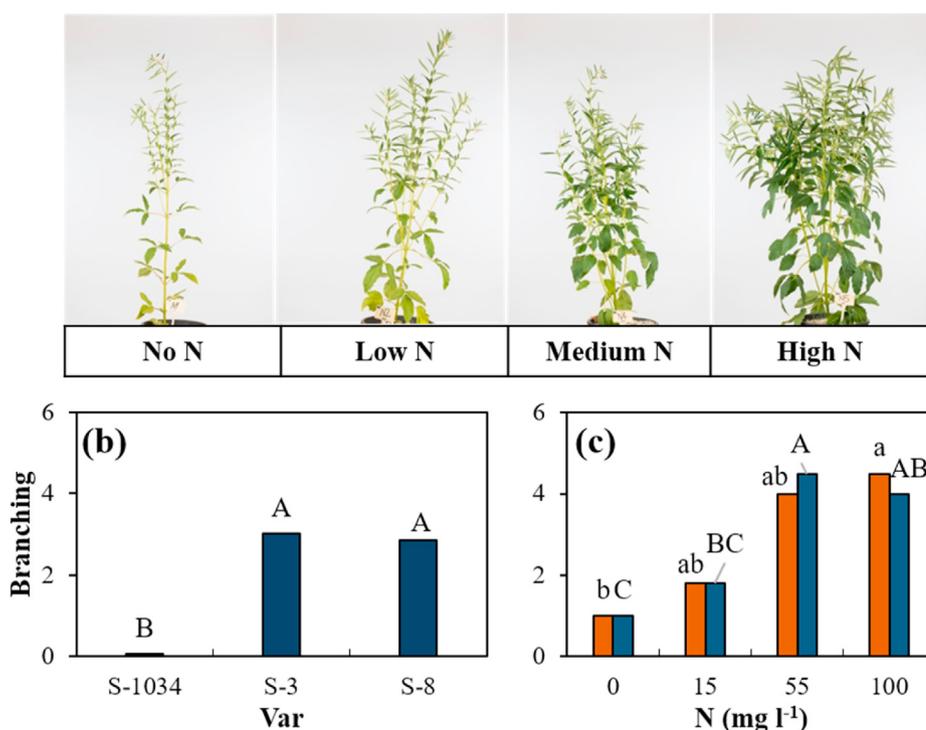
Fig. 3. The number of branches as affected by genotypes and N levels. (**a**) Representative images of var S-3 in response to N levels. (**b**) The average number of branches among the three sesame lines in the Rehovot field experiment (high and low irrigation). (**c**) Branching in response to N levels in line S-3 grown in the Rehovot field. Blue boxes refer to full irrigation and red to low irrigation. Different letters indicate a significant difference between lines and treatments using the Tukey-HSD test ($n = 5$).

Fig. 4. Yield components. Box plots of the number of capsules per plant (**a,d**), number of seeds per capsule (**b,e**), and 1000 seed weight (TSW) (**c,f**) as affected by N concentration and irrigation level in the Gilat field experiment (**a,b,c**) and Rehovot (**d,e,f**). Blue boxes refer to full irrigation and red to low irrigation. Different letters indicate a significant difference between treatments using the Tukey-HSD test ($n = 12$).
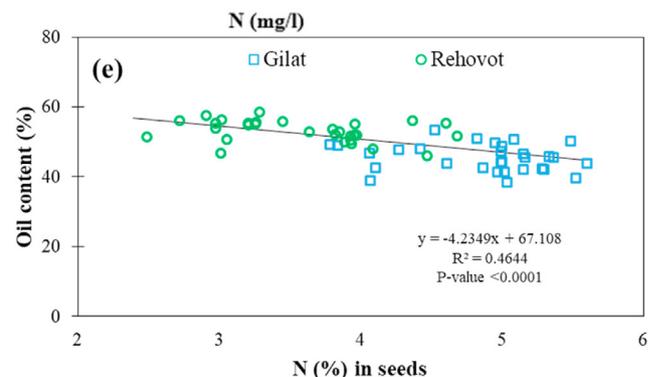

Fig. 5. Net seed yield. Box plots of yield in response to N concentration and irrigation level in Gilat (**a,b**), and Rehovot (**c,d**). Blue boxes refer to full irrigation and red to low irrigation. The effect of irrigation levels (**b**) and (**d**) represents scaled averages of all lines and N levels. Different letters indicate a significant difference between treatments using the Tukey-HSD test ($n = 12$).

3.6. Effect of N and irrigation levels on seed oil content

Oil content was only measured for S1034 and it fluctuated between 40 and 55% depending on the site, N, and irrigation level. In Gilat, oil content decreased with N level and significantly increased with irrigation level from 42.8% at the low irrigation level to 47.2% at the high irrigation level (Fig. 6b). Combining the two trials showed a significant and negative correlation between seed oil content and N concentration (Fig. 6e).

3.7. Interaction between irrigation and N levels

Full irrigation plots showed higher stem water potential (SWP), stomatal-conductance and lower δ^{13}C (indirect measure for stomatal conductance). High N levels were associated with lower stem water potential (SWP), stomatal conductance, and higher δ^{13}C, indicating that

Fig. 6. Seed oil content. Box plots of oil content depending on N concentrations and irrigation levels in the field experiments Gilat (**a,b**) and Rehovot (**c,d**). Blue boxes refer to full irrigation and red to low irrigation. Different letters indicate a significant difference in Tukey-HSD test. (**e**) Linear regression of seed oil content and N (%) in seeds.

high N elevated water stress and diminished transpiration. In the Gilat field, the phenomenon of lower SWP and stomatal conductance occurred

only in fully irrigated plots, while at the low irrigation level N did not affect plant water relations. In Rehovot, both irrigation levels showed a negative correlation between N level and water stress indicators. Similar results were measured earlier in the season (Fig. S5).

3.8. Nitrogen balance and NUE

Net N balance negative values indicated that plant offtake (in yield only) exceeded the N applied through fertilization while positive values indicated N surpluses (Fig. 8). When no N was applied, Gilat soil provided substantially more N than the sandy soil of Rehovot; N offtake was 68 kg ha^{-1} compared to merely 21 in Rehovot (Table 1). Nonetheless, on both sites, zero net N balance was reached between N15 and N55. The NUE under the N55 treatment at the irrigated was fair, 49–68% while the highest N levels were associated with declined NUE to 33–38% and minimal impact on yield or N offtake. Since we used constant concentration rather than constant doze, at the low irrigation plots, the amount of N was lower at the low irrigation plots and therefore, N surpluses were lower than at the high irrigation. Yet, NUE tends to be lower, especially at the highest N dose (Table 1). Overall, N requirements of sesame (for yield only) are estimated at 80–120 kg ha^{-1} if water is highly available and 30–40 kg ha^{-1} when water is limited.

4. Discussion

Understanding the physiological response of sesame plants to N fertilization under changing water availabilities will set the basis for future intensive sesame cropping system development. Here, we developed an N fertilization strategy for irrigated agro-systems considering the sesame N requirements for a high-yielding system. We tested the sesame responsiveness to increasing levels of N application under contrasting water availabilities using three representative lines and found a strong interaction between water availability and sesame response to N.

Plants response to N is strongly affected by irrigation level. Back in the 19th century, Justus von Liebig defined the "Sprengel-Liebing law of minimum" specifying that plant production is proportional to the most limiting factor. Despite its simplifying nature (Paris 1992), it rationally holds in our study. Sesame response to N was negligible when water was the most limiting factor, whereas, under high water availability, plants responded tremendously to N (Fig. 2 biomass and Fig. 5 seed yield). For example, in Rehovot under high irrigation, yield increased by ~300% when N increased from 0 to 100 mg l^{-1}. Similarly, lower N demand was reported to be related to water availability shortage in irrigated maize (*Zea mays*) (Derby et al., 2005) and sunflower (*Helianthus annuus*) (Kiani et al., 2016). These authors concluded that N doze should be adjusted to follow the expected water availability. In oilseed, Ma and Herath (2016) reported a lack of response of canola (*Brassica napus*) to N only on dry years. Our results showed that under limited water availability, soil N mineralization supplied the sesame demand for N in the loamy soil of Gilat but not in the sandy soil of Rehovot. Indeed, soil tests indicated higher fertility in Gilat compared to Rehovot (Table S1). When water is limited, sesame demand for N is situated around 20–40 kg ha^{-1} and the need for N fertilization is questionable. One of the reasons for the lack of response to N is the negative impact of N on sesame response to water stress (Fig. 7).

In the current study, we choose to design the experiment on fixed concentration rather than fixed dose. The question of how to best apply nutrients when evaluating water supply levels, without introducing an unintentional response-driving factor is particularly important when water and nutrients are supplied together via fertigation at very high frequencies. As crops respond to concentrations of minerals in their root zone soil environment, giving equal doses of nutrients to treatments receiving deficit irrigation would be expected to drive the concentrations exposed to by roots to very high, causing negative effects of reduced osmotic potential and excess, possibly toxic mineral concentrations. Additionally, in our experimental environment (hot and dry) water and

Table 1

Nitrogen use efficiency (NUE) in Gilat and Rehovot field experiments. Each value represents an average of four plots from each line ($n = 12$).

Treat	Irrigation	N (kg·ha^{-1})	Yield (kg·ha^{-1})	N in seeds (%)	N removed (kg·ha^{-1})	NUE
Rehovot						
N0	Full	4	702 ± 247.1	3.0 ± 0.4	21 ± 2.2	1
N15		32	1097 ± 242.5	3.2 ± 0.7	35 ± 5.3	0.71
N55		120	2035 ± 422.5	3.3 ± 0.6	67 ± 10.3	0.49
N100		222	2107 ± 467.8	3.8 ± 0.8	80 ± 8.8	0.33
N0	Low	2	559 ± 308.9	3.0 ± 0.4	17 ± 1.8	1
N15		14	637 ± 242.5	3.4 ± 0.7	21 ± 5.3	0.72
N55		52	721 ± 422.5	3.7 ± 0.6	27 ± 10.3	0.40
N100		97	645 ± 563.8	3.7 ± 0.5	24 ± 5.6	0.21
Gilat						
N0	Full	7	1807 ± 829.8	3.8 ± 0.5	68 ± 27.4	1
N15		45	2288 ± 548.0	4.0 ± 0.6	92 ± 31.8	0.87
N55		130	2832 ± 545.9	4.6 ± 0.4	129 ± 35.2	0.68
N100		226	2437 ± 718.8	4.4 ± 0.4	108 ± 26.4	0.38
N0	Low	3	857 ± 580.9	4.5 ± 0.5	39 ± 24.7	1
N15		20	903 ± 478.9	4.5 ± 0.4	41 ± 25.9	0.74
N55		27	710 ± 558.4	4.6 ± 0.5	33 ± 28.4	0.36
N100		98	914 ± 340.1	4.6 ± 0.5	42 ± 19.1	0.31

carbon assimilation are expected to be closely related (Ben-Gal et al., 2003; Grunzweig et al., 2003). Since the C/N ratio in plants has been shown to have a narrow range (Gifford et al., 2000) there is a strong association between irrigation, C assimilation, and N demand. Therefore theoretically, higher irrigation volumes will lead to higher C assimilation and greater demand for N and vice-versa. Indeed, even when N allocation was proportionally reduced in the low irrigation treatment, plant response was minimal. We speculate that if N dose of the low and high irrigation plots was similar (i.e., 220 kg ha^{-1} for the high N level), N would have had a more pronounced negative impact on the water-stressed plants. A posteriori, matching N dose to irrigation level was justified and confirms previous studies (Sadras 2002). Balanced N nutrition is specifically important in a rainfed agro-system where the farmer has little control over water availability. Both excessive and deficient N application can lead to elevated water stress due to unbalanced root or foliage development (Bonfil et al., 2004). The response of sesame to high N levels in the field reported here demonstrates that under water stress conditions, N nutrition is leading to a vigorous growth that rapidly depletes the limited soil water and, consequently, decreased LWP and photosynthesis (Fig. 7). Furthermore, δ^{13}C indicates that the stomatal conductance of plants supplied with ample N was consistently lower in Rehovot (Fig. 7), leading to lower carbon (C) assimilation (per given leaf area). In agreement, rainfed wheat supplied with high N levels during years with low precipitation elevated water stress indicators due to vigorous vegetative growth and depletion of soil water at early growth stages (Van Herwaarden et al., 1998; Bonfil et al., 2004). We, therefore, conclude that under conditions of water scarcity, N should be applied mildly to avoid fast consumption of the sub-soil water resource to prevent severe stress during the seed filling stage. N over-fertilization has
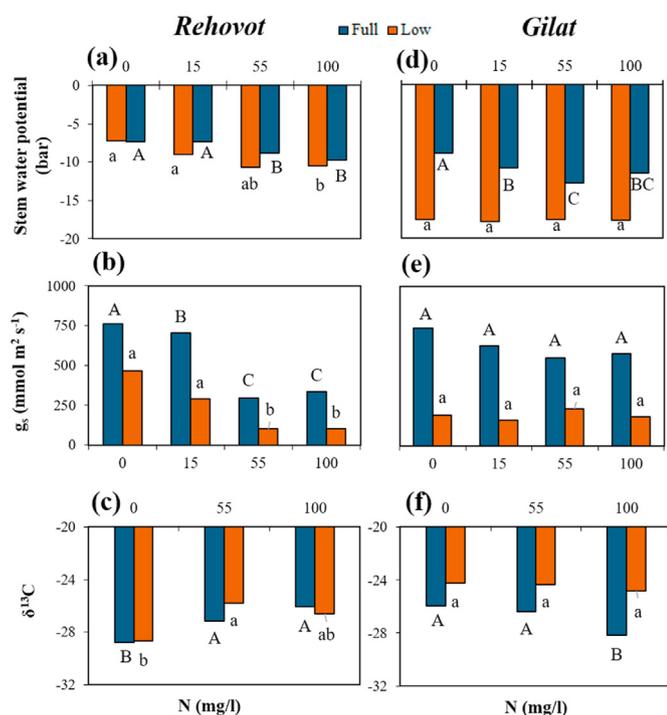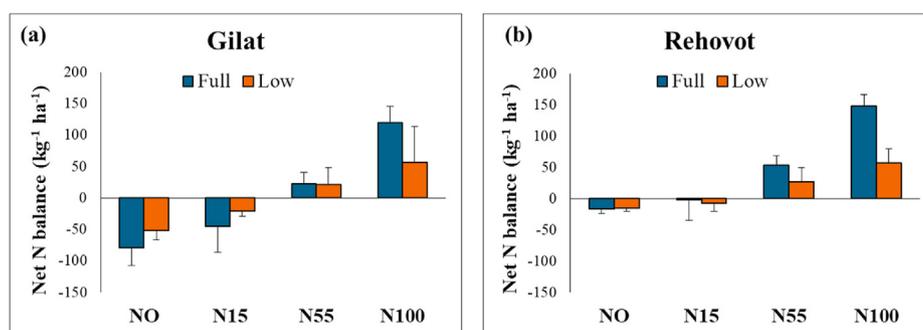
Fig. 7. Stem water potential, stomatal conductance and δ ^{13}C as affected by N and irrigation levels. Water potential and gas exchange were measured simultaneously at mid-day in late July ($n = 12$). The blue bars refer to the control irrigation (full) and the orange bars refer to the deficient irrigation level (low). δ^{13}C was measured in the seeds at the end of the experiment ($n = 4$). Different letters indicate a significant difference between treatments using the Tukey-HSD test.

correlation between seed N and oil content in our study supports this paradigm. Furthermore, N over-fertilization is expected to have a negative impact on the oil fatty-acids composition (Bates et al., 2013; Erel et al., 2013; Khan et al., 2018). This postulation requires further investigation. Interestingly, a high irrigation level resulted in higher oil content (significant in the Gilat field, Fig. 6).The typical NUE of the major field crops is as low as 20–40% depending on the agro-system tested (Cassman et al., 2002). Specifically, drip irrigation is considered to be an efficient tool to increase NUE (Ullah et al., 2019). In our field trials, N was applied proportionally to the irrigation (fixed concentration rather than fixed dose). In the fully irrigated plots, NUE varied from 33 to 87% depending on the site and N levels. In the sandy soil in Rehovot, NUE was generally lower than in the loamy soil in Gilat (Table 1). Increasing N concentration from 55 to 100 mg L^{-1} led to a dramatic decrease in NUE from 49-68% to 33–38% while having a marginal effect on yield. We, therefore, suggest that optimal N application of irrigated sesame with high yield potential should be higher than 50 and lower than 150 kg ha^{-1}, depending on the expected yields and soil N mineralization potential. These N rates are expected to lead to a reasonable NUE of over 50%. In line with our study, Couch et al. (2017a,b) reported the N removal of modern-irrigated sesame cultivars was 70–99 kg ha^{-1}. Under low-input agro-systems, when expected yield is low (i.e.,>1000 kg ha^{-1}), N requirements are low (20–40 kg ha^{-1}) and fertilization should be considered only if natural soil fertility is low and can't supply plant's demand.

5. Conclusion

Novel sesame lines promoted the expansion of sesame cultivation into modern-irrigated cropping systems that have the potential to boost grain yield (Dossa et al., 2017). While global sesame grain yield is around 500 kg ha^{-1} (Couch et al., 2017; Myint et al., 2020), we found that the yield potential can exceed 2000 kg ha^{-1} under a fertigated agro-system. This drastic shift from traditional to modern cropping systems requires adjusted N fertilization management. This work lays the foundation for fertilization management under modern irrigated agro-systems. Our results reveal that both N excess and deficiency may lead to significant yield losses. At modern agro-systems (yield ~ two ton·ha^{-1}), plant requires 120-80 kg ha^{-1} of N for optimal yield. In low-input agro-systems where yield is mainly limited by water (~700 kg ha^{-1}), N fertilization should be mildly supplied with caution, to prevent excessive leaf area, which later results in a severe water stress. Furthermore, N is negatively associated with seed oil content and therefore excessive N application may reduce oil yield. This study emphasizes the need for balanced N fertilization considering environmental factors and yield potential. For complete understanding of N management, further research is desired to investigate the effects of irrigation and fertilization on sesame oil composition and quality parameters.

multiple adverse effects on plants, the environment, and quality parameters of agro-products and consequently, the net income (Albornoz 2016). Furthermore, N over-fertilization has a negative impact on the productivity of a given agro-system (Weinbaum et al., 1992; Albornoz 2016) as we reported for olives under control (Erel et al., 2013) and field conditions (Haberman et al., 2019). In accordance, we found that the seed oil content significantly and continuously declined as the seed N level increased (Fig. 6). Reduction in oil content is specifically important for growers in Asia where sesame is cultivated mostly for its oil (Myint et al., 2020). Reduction in oil content in response to accumulation of N was reported previously for canola (Zhao et al., 1993; Brennan et al., 2000; Ma and Herath 2016) and sesame (Bellaloui et al., 2018). The antagonism between N and oil accumulation was suggested to be a result of the protein-oil competition (Bates et al., 2013). The negative

Fig. 8. Nitrogen balance as affected by N and irrigation levels in the field experiments, Gilat (**a**) and Rehovot (**b**). Blue boxes refer to full irrigation and red to low irrigation.

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.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ocsci.2022.11.003.

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