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Effects of day length on flowering and yield production of *Salicornia* and *Sarcocornia* species

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ABSTRACT

Salicornia is a new vegetable crop that can be irrigated with highly saline water, even at salt concentrations equivalent to full-strength seawater. During leafy vegetable cultivation, the onset of the reproductive phase is an undesired phenomenon that reduces yield and quality and prevents year-round cultivation. Knowledge about the regulation of floral induction in the members of the tribe Salicornieae, however, is lacking. To establish year-round cultivation, we studied the flower induction of five *Salicornia* and two *Sarcocornia* varieties. Plants were grown under two day lengths, 13.5 h and 18 h, and harvested by a repetitive harvest regime. A 13.5-h day length prevented flower induction in the Israeli *Salicornia* varieties, but a longer day length was required to prevent flower induction in two species originating from more northern latitudes. The onset of the reproductive phase under suboptimal short day length conditions severely reduced vegetative growth and yields in *Salicornia*. In *Sarcocornia*, the repetitive harvest regime prevented flowering, making it a promising candidate for year-round cultivation. Irrigating the plants with full-strength seawater (electrical conductivity 48 dS m^{-1}) vs. water with moderate salinity (electrical conductivity 10 dS m^{-1}) did not change the general flowering pattern of the studied Salicornieae members.

1. Introduction

Salicornia has long been consumed by humans as a fresh or pickled vegetable (Chevalier, 1922; Davy et al., 2001). It has recently generated considerable interest as a new vegetable crop that can be irrigated with highly saline water and seawater (Ventura et al., 2010, 2011). The almost identical *Sarcocornia* is distinguished from the annual *Salicornia* by its distinct perennial growth habit (Davy et al., 2006) and by differences in flower arrangement (Kadereit et al., 2007). Both genera produce succulent shoots suitable for leafy vegetable production, but they differ in terms of yield and nutritional value (Ventura et al., 2010, 2011).

In light of the increasing interest in *Salicornia* for its versatile commercial products, such as seed oil, protein meal, and fresh salad greens, the flowering pattern of *Salicornia bigelovii* was investigated (York et al., 2000). This species was found to be sensitive to photoperiod, and as such, shortening the number of hours of day light (day length) resulted in flowering (Fu and Zhao, 2003; Lu et al., 2001; Zerai et al., 2010). Flower induction reduces vegetative growth in leafy vegetables (Chweya, 1997), and therefore, it presents an important productivity parameter. At the onset of the reproductive phase, *Salicornia* terminal fruiting spikes are produced at the shoot tips and vegetative development is retarded, which ultimately may negatively impact yield performance. Moreover, flowering is undesired during *Salicornia* vegetable production as only young, fibreless vegetative shoots have market value.

The use of photoperiodic light is a well known agro-technique to regulate flowering in horticultural crop production (Demers et al., 1998). Preventing *Salicornia* from entering its natural, early flowering mode may enable year-round market supplies to the benefit of consumers and farmers alike. Toward the development of a practice that will enable the farmer to control and regulate the vegetative to reproductive relationship, we investigated the effect of day length as a means of controlling the flowering of Salicornieae tribe members.

Salinity stress, which may also affect a plant's flowering pattern, was shown to delay flowering in *Arthrocnemum fruticosum*, a halophyte plant belonging to the tribe Salicornieae (Saad Eddin and

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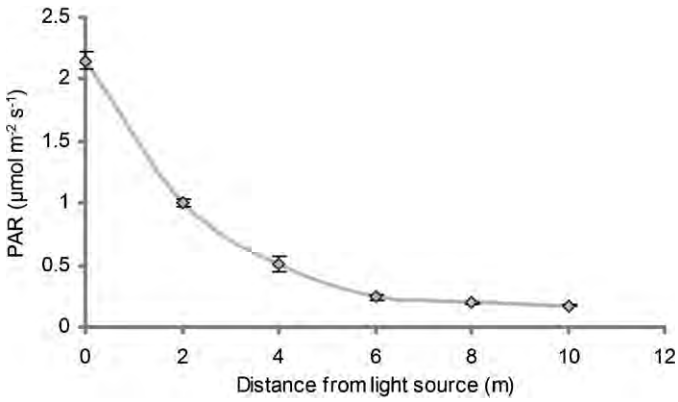

Fig. 1. Photosynthetically active photon flux density created by 3 incandescent bulbs as a function of the distance from the light source. Measurements were performed horizontal at plant height during the time of artificial light addition. Each value represents the mean of 3 measurements (±SE).

Doddema, 1986). Because information about the effects of salinity on the flowering behaviors of Salicornieae members is virtually non-existent, this study also examined whether salinity had an effect on plant flowering patterns.

The current research indicates that the control of day length regime, but not salinity, together with the selection of suitable species or varieties with different day length requirements, should result in sustainable, year-round *Salicornia* vegetable production.

2. Materials and methods

2.1. Plant material

We evaluated a selection of *Salicornia* and *Sarcocornia* samples from different regions of Europe and Asia. *Salicornia* types RN (31°N) and DS (31°N) were collected in the Dead Sea area, and *Sarcocornia* EL (32°N) and *Salicornia* N (32°N) originated from the northern Mediterranean coastline of Israel. *Sarcocornia* type VM (31°N) was found in an inland salt pan in the Ramat HaNegev district. *Salicornia* type FR originated from the coast of Brittany (France, ~48°N) and KZ from a highly saline area near the shore of the Aral Sea (Kazakhstan, ~46°N).

2.2. Experimental layout

All experiments were carried out in the south of Israel, either in the city of Beer Sheva (31°14′N 34°47′E) or at the Ramat HaNegev research station (30°52′N 34°47′E).

To simulate differences in the amount of time plants were exposed to daylight (i.e., to shorten day length) we tested light gradients. We used a fixed light source (three 100-W incandescent bulbs in a row), perpendicular to which the plants were positioned at increasingly larger distances, either incrementally (2-m intervals) or continuously (i.e., plants arranged in rows of cultivation sleeves). Natural daylight was extended by turning the lights on earlier in the morning and by turning them off later in the evening to create a total day length of either 13.5 h or 18 h. The resulting light flux during the artificial light supplement was measured on a horizontal surface in plant height and presented in photosynthetically active radiation (PAR), which reached maximum values of 2.15 μmol m^2 s^{-1} directly below the light source. The light flux decreased rapidly to 0.24 μmol m^2 s^{-1} at a distance of 6 m from the light source with a subsequent minor reduction to 0.17 μmol m^2 s^{-1} at a distance of 10 m (Fig. 1). Midday photosynthetic photon flux density in the greenhouse was 300–500 μmol m^{-2} s^{-1}.

Seeds were germinated in cultivation sleeves filled with perlite (Agrekal Habonim Industries Ltd., Moshav Habonim, Israel; www.agrekal.co.il) or on sand dune soil and irrigated daily with tap water [Electroconductivity (EC) 0.7 dS m^{-1}] supplemented with 90 mM NaCl (EC 10 dS m^{-1}) and commercial fertilizer N-P-K (5-3-8; Haifa Chemicals Ltd., Haifa, Israel) to supply the plants with approximately 80 ppm nitrogen.

To investigate the effects of sowing date on reproductive stage onset, we sowed RN genotype seeds four times during the shorter days of fall and winter at one-month intervals from October (natural day length: 11 h 20 min, shortening days), to January (natural day length: 10 h 6 min, lengthening days). Plants were grown under natural light conditions in a greenhouse approaching ambient temperatures (Ramat HaNegev area, Israel).

We studied the effect of a 13.5-h day length with plants germinated in the beginning of October, at decreasing day length condition, and arranged at continuous distances (0–20 m) from the light source. An identical greenhouse without extended daylight was used as a control.

To study the effect of natural flower initiation on yield production, plants were sown at the beginning of March at increasing day length condition and grown without artificially extended daylight in sand-dune soil. Shoots were harvested, as described below, during a one-year growing season or until the natural occurrence of flowers stopped plant growth.

To examine the effect of seawater salinity (EC 48 dS m^{-1}) on flower induction, plants were cultivated in a hydroponic system as previously described (Ventura et al., 2011). Briefly, seeds were germinated at the end of August in 14-cm plastic pots filled with perlite. Pots were placed in 18-L boxes (dimensions 37 cm × 31 cm × 16 cm) that were then filled with equal amounts of 50% seawater supplemented with 200 ppm commercial N-P-K fertilizer (20-20-20 + microelements, Haifa Chemicals Ltd.). The seawater solution (RSW) was prepared by dissolving 33 g Red Sea Salt® in 1 L water (Red Sea Fish Pharm Ltd., Eilat, Israel; www.redseafish.com) according to the manufacturer's instructions. Irrigation water salinity was gradually increased – over the course of one month – until it reached full-strength seawater concentration. This experiment investigated the 18-h light regime with plants positioned at 2-m intervals from 0 m (directly below the light source) to 10 m from the light source.

2.3. Evaluation of reproductive and vegetative parameters

The flowering index was determined by the visual observation of a plant population of at least 20 plants before every harvest. The index was defined by the following values: 0-vegetative nodes; 1-emergence of short, fertile segments; 2-beginning of pistil appearance from the fertile segments; 3-beginning of stamen appearance from the fertile segments; 4-completely flowering cones and beginning of seed development (Supplementary Fig. A).

Plant height and the number of reproductive and vegetative nodes were determined two months after sowing in the end of November (natural day length: 10 h 17 min) before the first harvest.

2.4. Harvest regime and biomass accumulation

In all experiments, plants were harvested under a repetitive harvest regime. Harvesting started approximately two months after sowing when a shoot size of approximately 10–15 cm was reached, by cutting the plants about 5 cm above ground level, resulting in a "cutting-table". After about one month, when the majority of the shoots had re-grown 10 cm or more above cutting-table height, they were again harvested by cutting them back to the height of

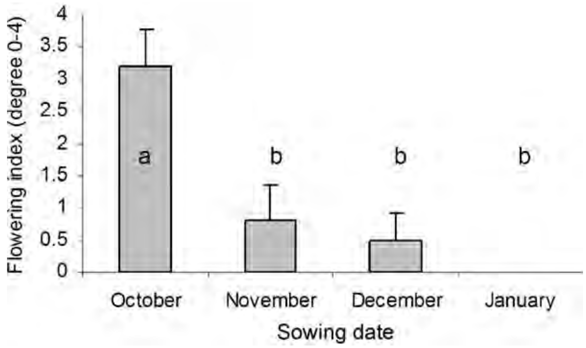

Fig. 2. Effect of sowing date (October, November, December, January and the respective natural day lengths: 11 h 20 min, 10 h 31 min, 10 h 4 min, 10 h 6 min) on the appearance of flowers on *Salicornia* type RN grown under natural light conditions in Ramat HaNegev. The index was evaluated in April (day length: 13 h 25 min) at the end of the experiment. Values represent means ± SE ($n = 3$). Values followed by different letters are significant different, $p < 0.006$.

the cutting-table. Total yields were calculated as the cumulative biomass of the harvest period.

2.5. Statistical analysis

Significant differences between treatments were analyzed by a one-factorial analysis of variance (ANOVA) using the JumpIn 5.0.1a software package (SAS Campus Drive, Building S, Cary, NC) (SAS Institute Inc., 2002). When ANOVA indicated significance, we compared treatment means according to the Tukey–Kramer HSD. Correlation coefficients were calculated to determine the degree of association between the characters.

3. Results

3.1. Effect of sowing date during shortening days on flower induction

Salicornia plants from seeds of genotype RN sown in October (day length: 11 h 20 min) during the shortening days of fall and irrigated with water containing salts at an EC level of 10 dS m^{-1} flowered completely at the end of the experiment in April (day length: 13 h 25 min). Planting seeds later in the year, such as November and December (day length: 10 h 31 min and 10 h 4 min, respectively), repressed the onset of the reproductive stage. Finally, when seeds were sown in January (day length: 10 h 6 min, lengthening days), onset of the reproductive stage was completely inhibited under conditions of increasing day length (Fig. 2).

3.2. Effect of 13.5 h day length on flower induction

Extending natural daylight during the Israeli short-day season (October–April) to 13.5 h using incandescent bulbs turned on in the morning before sunrise and turned off in the evening after sunset, prevented flowering in all, but one, genotypes in plants irrigated with water at an EC of 10 dS m^{-1} (Fig. 3). Three months after sowing, the FR plants (origin in the northern latitudes), situated below the light source, started to enter the reproductive stage by showing the emergence of short nodes (flowering index degree 1.5). Once flowering was initiated in the FR plants, the process progressed with time until April when all the plants were completely flowering (flowering index degree 4). All other *Salicornia* (RN, DS, N) and *Sarcocornia* (EL, VM) types did not enter the reproductive stage when grown directly below the light, which was set to the 13.5-h day length (Fig. 3).

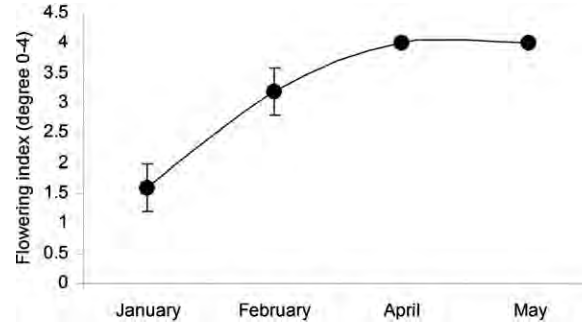

Fig. 3. Flowering index evaluated monthly for *Salicornia* type FR located directly below the light source applying a day length of 13.5 h. All other types (RN, DS, VM, EL, N) received indices of 0. Values are evaluation points representing mean values (±SE) of at least 20 examined plants.

3.3. Light gradient as a means of shortening day length

To test whether plant distance from the light source could provide an experimental means of shortening day length to mimic the natural environmental conditions of the different *Salicornia* types, we determined flower induction for all types as a function of the distance from the light source in January (day length: 10 h 6 min) three months after sowing and in May (day length: 13 h 26 min) seven months after initiation of the experiment (Fig. 4). In January, FR plants that were situated 5 m from the light source completely flowered, but onset of the reproductive stage among the other plant types at the same distance was prevented by the light (Fig. 4a). Flowering was gradually induced for types RN and

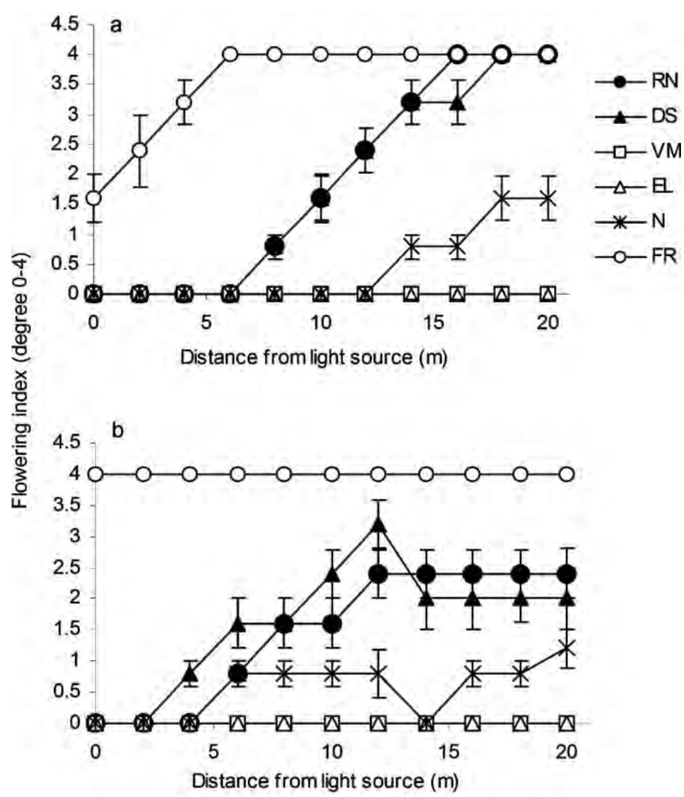

Fig. 4. Effect of distance from the light source (13.5 h day length) on the flower induction of seven Salicornieae types evaluated (a) in January (natural day length: 10 h 12 min): three months after sowing at short day conditions and (b) in May (natural day length: 13 h 26 min): seven months after sowing during lengthening days. Values are evaluation points representing mean values (±SE) of at least 20 examined plants.

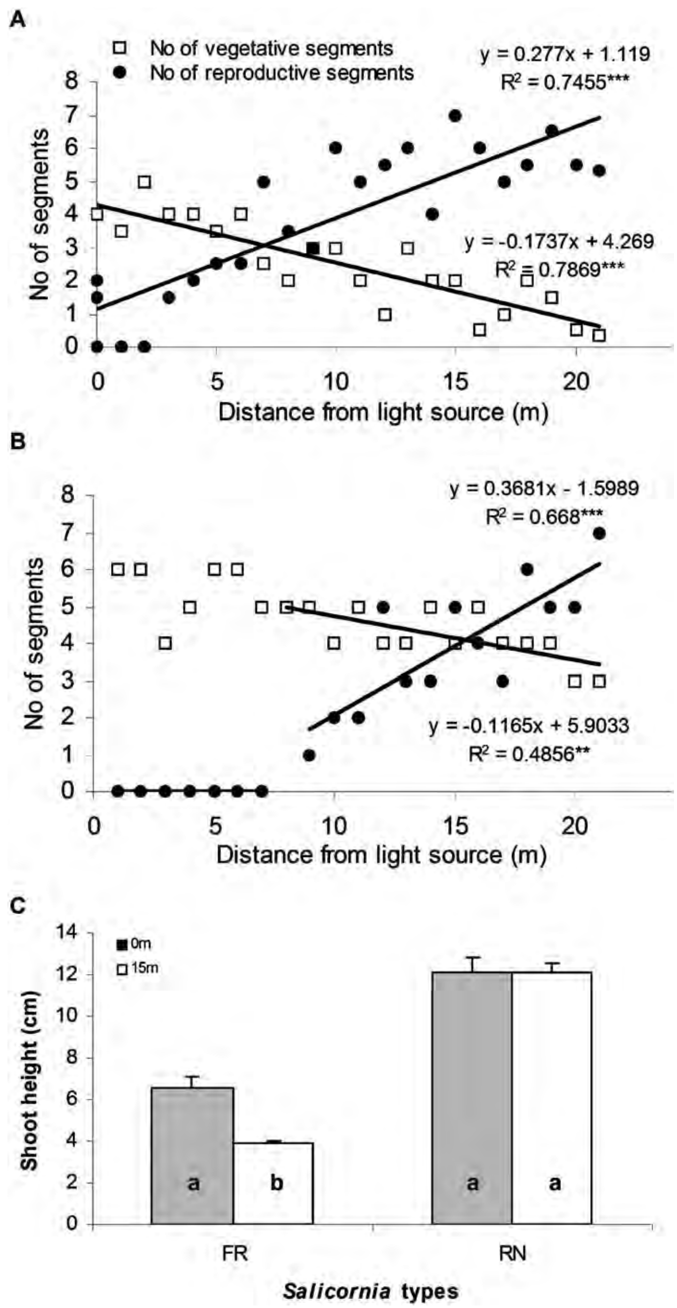

Fig. 5. Effect of distance from light source (13.5 h day length) on the appearance of vegetative and reproductive segments in two *Salicornia* types evaluated two months after sowing. Correlations between the number of vegetative and reproductive segments and the distance from the light source are shown for type FR (A) and RN (B), (n = 24), $^{**}p < 0.005$ and $^{***}p < 0.001$, respectively. Plant height is given for both *Salicornia* types, directly below the light source (0 m) and in a distance of 15 m from the light source (C). Values represent means ± SE (n = 5). Values followed by different letters within the *Salicornia* types are significant different, $p < 0.001$.

DS situated more than 8 m from the light (Fig. 4a). Plants of type N, less influenced by the light, exhibited their first signs of reproduction 12 m from the light source and onwards, but no type N plants, even those at the furthest distance of 20 m, reached full bloom (Fig. 4a). In May, when natural day length reached 13.5 h and after three shoot harvests, evaluations of reproductive activity showed that type FR flowered completely at all distances from the light source (Fig. 4b), indicating that this native of the northern latitudes requires a day length longer than 13.5 h to prevent the onset of reproduction. For types DS, RN and N, the distance from the light source at which flowering was prevented was determined to be 2, 4, and 4 m, respectively. Nevertheless, in plants located beyond these distances, the reproductive stage was still induced in new shoots similar to plants during the short day conditions, suggesting "partial hysteresis", since none of these plants reached full bloom. *Sarcocornia* types VM and EL, regardless of plant distance from the light, showed no inclination to enter the reproductive stage (Fig. 4a and b), indicating the existence of alternative regulatory mechanisms to day length. Plant distance from the light source, therefore, provided a reliable means of shortening day length at least for the annual *Salicornia*, the different types of which were shown to flower as the strength of the light decreased with increasing plant distance from the light source according to the plants native flowering conditions.

To investigate how day length affected flower induction and plant growth, the switch from vegetative growth to reproductive development was monitored in two plant types that differed in their day length responses and geographic origins (Supplementary Fig. B). FR was chosen to represent plants from northern latitudes (longest day: >16 h), and RN corresponded to the Israeli types (longest day: 14 h 15 min). Two months after sowing FR seeds, the number of vegetative segments correlated negatively with plant distance from the light source (R^2 = 0.787), causing a marked decrease in plant height (Fig. 5A). Moreover, at the same time the number of reproductive segments observed on FR plants increased, a change that was correlated with plant distance from the light source (R^2 = 0.746). In the most extreme cases, either 55 days old plants germinated at the furthest distance from the light source (20 m), or 47 old plants transferred from 14 h to 10 h 30 min day length at the age of 14 days, exhibited only reproductive segments, indicating that flowering can be induced relatively short time after germination (Fig. 5A, Supplementary Figs. B and C).

Plants of type RN, however, no reproductive segments were found on plants up to 7 m from the light source. Beyond this distance, the number of reproductive segments increased rapidly, an observation supported by a good correlation (R^2 = 0.668) and a steep slope (Fig. 5A and B), while the number of vegetative segments was only slightly reduced (R^2 = 0.486), compared to plants situated up to 7 m from the light source. The heights of type FR plants decreased by 40.5% in plants grown at a distance of 15 m from the light source compared to the plants situated below (i.e., 0 m from) the light while no change in plant height was found for RN plants (Fig. 5C).

3.4. Yield accumulation without day length manipulations

Yield accumulation was evaluated at a salinity level of EC 10 dS m^{-1} on sand dune soil and under natural light conditions, starting in March (day length: 11 h 30 min) when the day length was

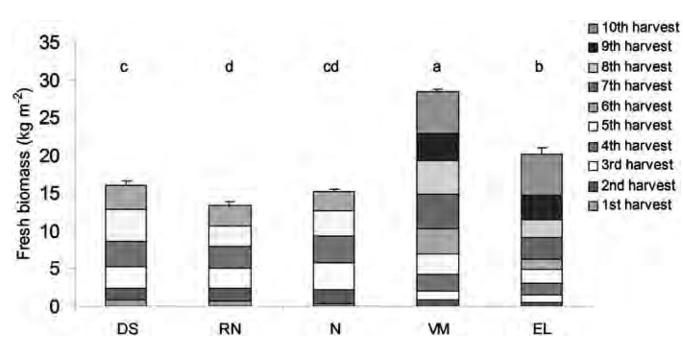

Fig. 6. Cumulative biomasses of the *Salicornia* and *Sarcocornia* types after a one-year growing cycle starting in March (day length: 11 h 30 min), when day length was increasing. Values are means ± SE (n = 4). Values followed by different letters are significantly different, $p < 0.001$.

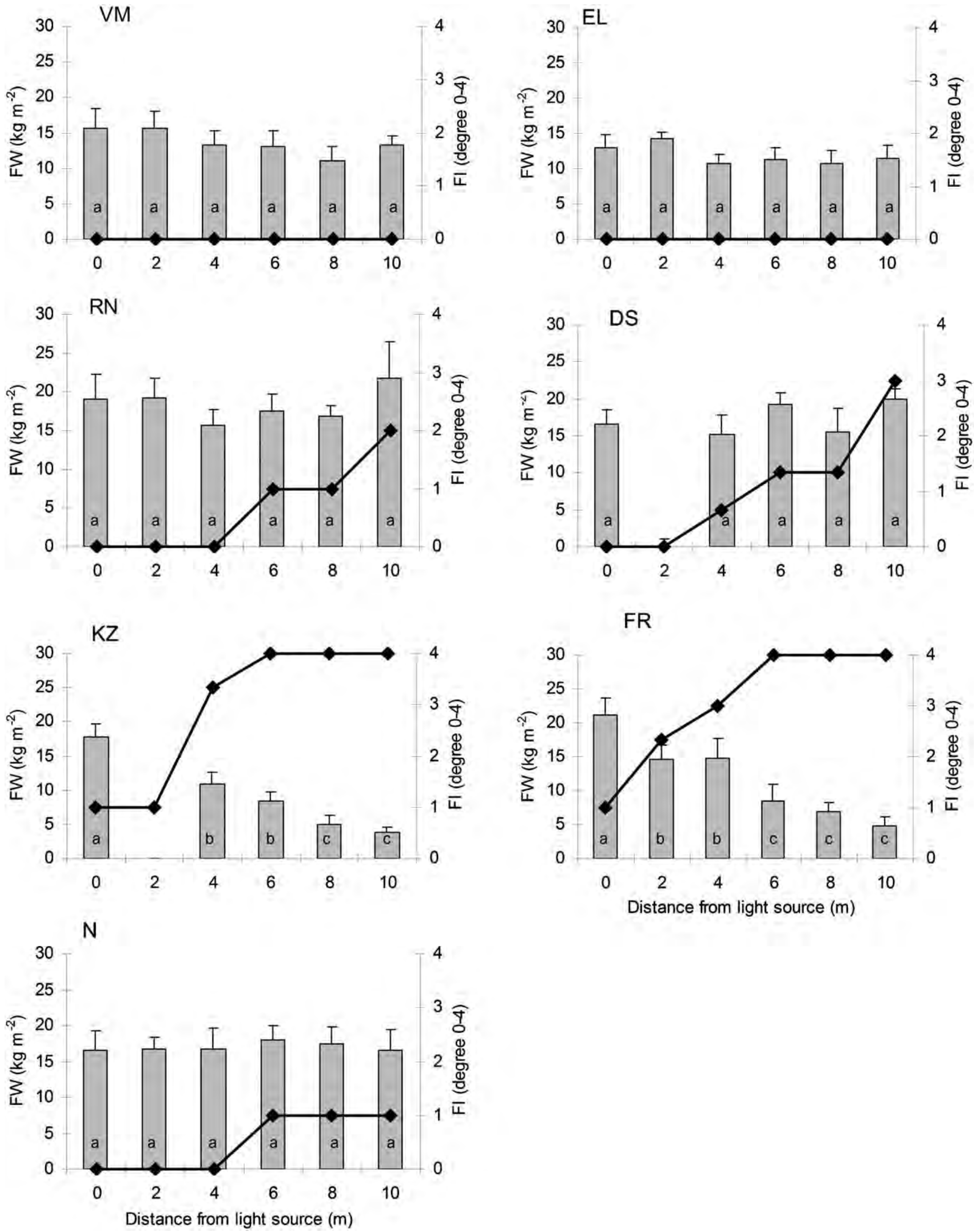

Fig. 7. Cumulative yields of seven harvests and the flowering index determined in June (day length: 14 h 15 min), 10 months after sowing for *Salicornia* and *Sarcocornia* types grown on an 18-h day length. Biomass for types DS and KZ located 2 m from the light source was not determined. Fresh biomass is presented in columns and the flowering index in lines. Values are means ± SE ($n = 3$). Values followed by different letters are significantly different, $p < 0.001$.

increasing. The cumulative biomasses of six harvests were significantly different ($p < 0.001$) for *Salicornia* types DS, N and RN (16.04, 15.19 and 13.40 kg m^{-2}, respectively) until plants started flowering six months after initiation of the experiment during the shortening days in September (Fig. 6). At that time, harvests were stopped for the annual *Salicornia*, but the *Sarcocornia* types VM and EL skipped the reproductive stage and continued to accumulate an additional 18.06 and 13.81 kg m^{-2}, respectively, during four additional harvests for total yields of 28.43 and 20.04 kg m^{-2}, respectively, during a one year cultivation cycle (Fig. 6). In comparison, non-harvested *Sarcocornia* plants that grew during the same time period began to flower in the beginning of September (Supplementary Fig. D), indicating that it was the periodic cutting regime that most likely prevented the *Sarcocornia* plants from flowering.

3.5. Effect of day length and irrigation with seawater on flower appearance and biomass production

Since both *Salicornia* and *Sarcocornia* can be irrigated with seawater, we tested whether the extremely high salinity affects the plants' reproductive phases. A longer day length of 18 h (to completely avoid flower induction) was evaluated and we concurrently determined the yield performances by periodically harvesting all plant types from August (day length: 12 h 53 min) until June (day length: 14 h 15 min).

Salicornia cultivation by irrigation with full-strength seawater (EC 48 dS m^{-1}) vs. irrigation with saline water (EC 10 dS m^{-1}) had no effect on the general flowering pattern of the different *Salicornia* and *Sarcocornia* types. As expected, *Sarcocornia* types VM and EL did not flower throughout the experiment (Fig. 7) under the repetitive harvest regime, as shown before in plants grown on EC 10 dS m^{-1}. At the end of March (day length: 12 h 25 min), eight months after sowing, plants of types RN and DS situated 6 and 4 m, respectively, from the light source, entered the reproductive stage, and their flowering indices increased with plant distance from the light source (Fig. 7). Flowering was induced in type N plants located 6 m from the light source, and the lowest flowering index was continuously observed for the plants farthest from the light source. Of significance to this study, the longer day length only temporarily prevented flowering in FR type plants situated directly below the light; eight months after sowing, however, plants from 0 m onwards started to produce short segments, and the highest flowering index was observed at 6 m. Similar results were recorded for KZ, an additional northern latitude species (Fig. 7).

The onset of the reproductive phase resulted in reduced growth and ultimately in a reduction in the harvested shoot biomass of both northern species FR and KZ, while the distance from the light source had no significant effect on the yield accumulations of the non-flowering *Sarcocornia* types VM and EL and on the Israeli *Salicornia* types RN, DS, and N (Fig. 7).

4. Discussion and conclusions

Genotypes from the tribe Salicornieae flower naturally in Great Britain from mid August until mid September (Davy et al., 2001, 2006). Fu and Zhao (2003) showed that short days promoted flowering in *S. bigelovii*, and they proposed 15 h as its critical day length. In the current investigation, all *Salicornia* species were found to be sensitive to changes in day length. Shortened day lengths, expressed in our study by light flux reduction from the light source, resulted in a switch in *Salicornia* species from vegetative growth to the development of reproductive organs (Figs. 4 and 5 and Supplementary Fig. B), emphasizing the appropriateness of the light source gradient, used in our current study, as a suitable tool for investigating day length effects on flowering pattern.

However, the critical day length differed markedly between the *Salicornia* types from different geographic regions. Species originating from northern latitudes, such as *Salicornia type* FR (∼48°N) and type KZ (∼46°N), needed longer days (18 h) to temporarily prevent flowering, while for *Salicornia* types, which originated farther south in Israel, a continuous 13.5-h day length completely inhibited the onset of reproductive growth (Figs. 4 and 7). In support of this notion, York et al. (2000) reported that flower induction of *S. bigelovii* populations from northern latitudes (∼38°N) was more sensitive to short-day treatments than their southern *Salicornia* counterparts (∼28°N). Given that the northern latitude species started flowering after eight months of cultivation directly below (i.e., 0 m from) the light source regardless of its exposure to the 18-h day length (Fig. 7), factors other than day length are likely to be involved in triggering the onset of reproduction in these *Salicornia*.

As an annual, *Salicornia's* performance in nature is constrained to the length of the growing season, and its determinate growth habit limits vegetative plant development after floral induction (Davy et al., 2001). In cultivation, a similar effect, observed after the onset of the reproductive stage in *Salicornia*, was particularly evident in the northern species FR and KZ. Vegetative growth declined (Fig. 5), ultimately leading to a reduction, based on low yields, in the biomass produced (Figs. 6 and 7).

When flowering was induced by shortening day length in all annual *Salicornia* types, the new, post-harvest shoots, in a sort of "partial hysteresis", "remembered" the previously received trigger and entered the reproductive stage, although at that point the plants were growing during a period of increasing day length (Fig. 4b). These findings highlight the importance of preventing flower induction during commercial cultivation of the annual *Salicornia* for vegetable production.

As long as plants were harvested frequently, the perennial *Sarcocornia* did not enter the reproductive phase during a complete, yearly cultivation cycle, during which plants were grown under either adjusted day length or natural light conditions (Figs. 4, 6 and 7). In contrast, non-harvested plants flowered in September under natural light conditions (Supplementary Fig. D). Therefore, we conclude that the repetitive harvest regime prevented *Sarcocornia* plants from flowering, which extended the harvest period and led to ultimately higher yields (Fig. 6). Moreover, the absence of an effect from additional light due to the repetitive harvest regime confers commercial appeal on the *Sarcocornia* genotypes for year-round vegetable cultivation.

Despite the reported critical value of 15 h light for *S. bigelovii* (Fu and Zhao, 2003), a substantially shorter day length of 13.5 h was sufficient to prevent flowering in annual *Salicornia* types collected in Israel (Fig. 4). In addition, for seeds germinated as early as January, even though total day length was still short (day length: 10 h 6 min), but lengthening, no light supplement was necessary until the natural photoperiod decreased below the critical value of 13.5 h in autumn for the Israeli ecotypes (Fig. 2).

First flower inductions for *Salicornia* types DS, RN, and N were noticed on plants placed between 2 m and 4 m from the light source at both the tested day lengths of 13.5 h and 18 h (Figs. 4 and 7). Therefore, for year-round *Salicornia* production in controlled, commercial operations, we suggest spacing light sources 4 m from each other to provide sufficient light intensity to prevent flower induction in the Israeli types. On the other hand, for *Salicornia* species from northern latitudes, adjusting day length to 18 h was not sufficient to completely prevent flowering (Fig. 7), making this species less attractive for commercial production.

Salicornieae are arguably one of the most salt tolerant terrestrial plants, as they can be irrigated with full-strength seawater without suffering any reduction in biomass for *S. bigelovii* (Grattan et al., 2008) and only minor declines for the annual *Salicornia* and the perennial *Sarcocornia* types (Ventura et al., 2011). Correspondingly, cultivation based on seawater (EC 48 dS m^{-1}) compared to saline irrigation (EC 10 dS m^{-1}) had no effect on the general flowering pattern of the different Salicornieae types (Figs. 4 and 7). We thus conclude that genetic background, plant origin, suboptimal day length, and the repetitive harvest regime more substantially affect reproductive development in *Salicornia* and *Sarcocornia* than salinity.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.scienta.2011.08.008.

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