INTERNATIONAL
Agrophysics
www.international-agrophysics.org

Int. Agrophys., 2023, 37, 415-424
doi: 10.31545/intagr/173448

Wild asparagus domestication for food/energy cropping system set up**

Paola A. Deligios[1]†, *Roberta Farci*[2]†, *Marco Cossu*[2]*, *Antonella Sirigu*[3], *Anna Barbara Pisanu*[3], *and Luigi Ledda*[1]

[1]Department of Agricultural, Food and Environmental Sciences, Polytechnic University of Marche,
Via Brecce Bianche 10, Ancona, 60131, Italy
[2]Department of Agriculture, University of Sassari, Viale Italia 39/a, Sassari, 07100, Italy
[3]Agricultural Research Agency of Sardinia (AGRIS), Service of Environmental Studies,
Crop Protection and Production Quality, Cagliari, Italy
†Co-first authors

Received July 3, 2023; accepted October 6, 2023

Abstract. The solar greenhouse sector is currently unbalanced towards energy production. Thus, the introduction of new crop options, such as wild asparagus, could contribute to the promotion of economic and environmental sustainability in these food/energy systems (mixed-systems). We hypothesized that wild asparagus is able to adapt both to sunny and partially shaded environments provided that both nutrient and water supply are guaranteed. Over a three-year experiment, we carried out an intensive examination of within-season phenological, physiological and productive dynamics under a greenhouse with 50% of the roof area covered with photovoltaic panels. Under the photovoltaic roof the net assimilation rate was on average 5 time lower, averaged over the growing seasons (0.6 μmol CO_2 m^{-2} s^{-1}), resulting in negative results for some monitoring dates. However, lower net assimilation rate did not negatively impact spears production in terms of number, length and diameter. The year of establishment affected the length of the spear, which was 4 cm shorter in 2013 than in 2014 and 2015, when no significant difference was observed. The novelty proposed in this study could be a successful option for farmers to promote production diversification and a promising strategy to guarantee the environmental and economic sustainability of the whole mixed system.

Keywords: *Asparagus acutifolius* L., mixed cropping systems, shade-tolerant species, spears, wild edible species

1. INTRODUCTION

Currently, the food challenge does not entail the need to meet an increasing demand only in quantity terms because of the growing importance that quality and healthy and savory characteristics have recently gained. In this regard, the efforts of the agricultural sector aim to enhance the productivity of a small number of crops rather than foster crop diversity. On the other hand, developing new crops and learning to use wild plants makes it possible to diversify global food production and better enable local adaptation to the diverse and changing environments that humans inhabit (Renard and Tilman, 2019). Interest in wild species is primarily linked to their agronomic potential as new crops (Fernie and Yan, 2019), their potential role in the biodiversity protection programs (Ceccanti *et al.*, 2018), and their inclusion in daily diets as potential sources of novel nutraceuticals (Savo *et al.*, 2019). One of these species is wild asparagus (*Asparagus acutifolius* L.) herbaceous perennial species widely distributed in the Mediterranean area commonly gathered from the wild (Schulp *et al.*, 2014) and mainly known for the fine flavour of the spears and for its healthy and high nutritional value (Bilušić *et al.*, 2019). The high price makes it an attractive new crop, especially for marginal areas where its cultivation might fit well within a sustainable agricultural framework of both biodiversity and environmental conservation (Katsenios *et al.*, 2019). To date, research on *Asparagus acutifolius*, as a crop species, has investigated its response to different environmental

---

*Corresponding author e-mail: marcocossu@uniss.it

** The Autonomous Region of Sardinia (Italy) (grant number C04-1). Project RESTART, FSC 2014-2020 (CUP D66C18000260002) of the UniNuoro University Consortium and the Autonomous Region of Sardinia (Italy); Project Innovagreen, FDS2017 of the Banco di Sardegna Foundation (CUP J85F20000360007); Project Atlantide (CUP J88D2000007000202) of the Autonomous Region of Sardinia; Project H2020 Solaqua "Accessible, reliable and affordable solar irrigation for Europe and beyond", funded by the European Commission within Programme Horizon 2020 Framework Programme Call: H2020-LC-SC3-2020-RES-IA-CSA Project: 952879.

factors (*e.g.*, water stress and partial shading conditions) (Mantovani *et al.*, 2019) or its high potential as a new crop, in combination with the olive trees (Pantera *et al.*, 2018). No study has shown the cultivation of wild asparagus under greenhouse conditions with a systematic monitoring of the whole growing cycle. Concomitantly, in the European solar greenhouse sector (mixed systems that combine solar panels and cropping at the same time in the same area) it has become relevant to solve the issues linked to cultivation when light is a constraint, in terms of suitable crops and species, agronomic techniques and management (Kavga *et al.*, 2019). Indeed, the largest part of the solar greenhouses was designed with a high proportion of the roof covered up with photovoltaic panels to achieve the maximum energy production despite crop light needs (Aroca-Delgado *et al.*, 2019). The existing solar greenhouses are characterized by a high photovoltaic cover ratio (from 50 to 100%), which entails a tricky issue related to the lack of agronomic alternatives aimed at finding a balance between energy and food production (Fatnassi *et al.*, 2015). In this context, crop diversification might be effective in affecting profitability since, for instance, the adoption of new high-quality crops might be a successful option to enhance the existing cropping systems (Feliciano, 2019). In the light of the above, it seems necessary to evaluate the potential use and agricultural and environmental sustainability of solar greenhouse systems in order to diversify and intensify crop production through the integration of new crop species such as *Asparagus acutifolius*. Thus, this study has the capacity to provide insight into the potential of introducing a new alternative crop species in the solar greenhouse environment in southern Italy after three growing cycles. Our results might be of relevance for: i) the purposes of adaptive solar greenhouse management planning, ii) long-term sustainability assessments in diversified solar greenhouse production systems, and iii) in the perspective of current agrivoltaic scenarios.

2. MATERIALS AND METHODS

2.1. Greenhouse and experiment description

The experiment was conducted during the 2013, 2014 and 2015 growing cycles in a commercial multi-span iron-plastic greenhouse located at a private farm in southern Italy (Decimomannu, Italy, 39° 19' N, 8° 59' E). The greenhouse had a total area of 2100 m^2 (30 × 10 m per each span), an E-W orientation, a gutter height of 2.5 m, a polyvinyl-chloride (Ondex Bio, Renolit, France) cover on the north-oriented roofs and multicrystalline silicon photovoltaic panels (REC 235PE, REC Solar, USA) on the south-oriented roof of each span, resulting in a percentage of the roof area covered with photovoltaic panels being equal to 50%. The experiment was designed as a strip block design. Three spans, 300 m^2 each, were considered the experimental area to capture the variability in the internal microclimate conditions. Each span was assimilated to a block that included two light conditions (under photovoltaic roof *vs.* under plastic roof) as vertical plots and two plant management systems (pot *vs.* full soil) as horizontal plots. In the full soil treatment, the soil was classified as an Aquic Palexeralf (USDA Soil Taxonomy). Prior to the experiment, the soil properties of the 0-40 cm soil depth layer were pH of 8.2 (H_2O 1:2.5 soil:water suspension), soil organic matter of 13.6 g kg^{-1}, soil bulk density of 1.22 g cm^{-3}, total N of 1.03 g kg^{-1} and available P (Olsen-P) and K (NH_4OAc-extractable-K) of 18.0 and 274 mg kg^{-1}, respectively. The clay, silt and sand contents were 38.9, 20.2 and 40.9% (clay loam texture), respectively, across the 0-60 cm soil depth layer. Full soil plots were prepared before planting by tilling the soil, and laying straw mulch over the planting rows. Plants were placed at a final density of 2.4 plants per m^2 (1.15 m between rows and 0.36 m within rows). In the pot treatment, plants were grown in round 80 plastic pots (30 L each) filled with a 1:1 (v/v) commercial potting soil mix of peat and perlite (Agripan torba-perlite, Perlite Italiana S.r.l., Milan, Italy) with a density of 1 plant per m^2. The pH was 6.5, and the electrical conductivity of the saturated soil extract was 2 mS m^{-1}. The soil surface was covered with a 3 cm layer of fine gravel to reduce evaporation. A single plant was grown in each pot.

2.2. Crop management and monitoring

To ensure the proper establishment of plants, a few months (October 2012) before the beginning of the experiment, in the entire experimental area 3-year-old bare-root plants were transplanted. The plant material used for the experiment was collected from a multiplication field located at the experimental farm 'Mauro Deidda' of the University of Sassari. To ensure optimum water conditions, a drip tape (NetafimTM, Genova, Italy) was laid along the plant rows and pots were equipped with emission outlets and online drippers, respectively, delivering a flow rate of 1 L h^{-1}, and metered by a modular irrigation controller (Mosa Green S.r.l., Pordenone, Italy). The frequency of irrigation ranged between daily, when the water requirements were maximum (vegetative growth, flowering, and fruits ripening), and two times/week, when the water requirements were minimum (harvest of spears). The seasonal supply of water was 240 L m^{-2}. Nitrogen was supplied on a yearly basis by fertigation distributed at approximately 60 kg N ha^{-1} (46% urea form) split into three fractions: a fertigation event before spear emergence and two events during the vegetative phase and before flowering.

2.3. Phenology

Phenological evolution was checked weekly on five tagged plants per subunit, chosen in the central row of each roof, and the details of reproductive phases occurring were documented. The time elapsed between the beginning and the end of flowering (number of days) and the number of cycles of flowering by year (number) were recorded.

2.4. Physiological parameters

Starting from April 2013, at weekly intervals, the physiological status of asparagus (stomatal conductance, internal CO_2 concentration, net photosynthesis, leaf temperature, and transpiration rate) was determined using an infrared gas analyser (CIRAS-2 Portable Photosynthesis System, PP-Systems, Hertfordshire, UK) with a standard 2 × 3 cm chamber (in total 12 measurement dates per growing season). Cuvette conditions during each measurement were maintained at 40% relative humidity, 25°C cuvette temperature, 200 mL min^{-1} flow rate, 350 ppm CO_2, and ambient light. Representative small branches (100 cladodes) were chosen, collected from south-facing orientations and from mid-height. Over each experimental area, plant physiological measurements were carried out along small transects between rows by monitoring four plants per plot, and on each branch, the readings were collected when steady-state was reached.

2.5. Harvesting

Twenty spears were collected from five randomly chosen plants within each plot to assess yield and biometric parameters. At harvest, the following yield parameters were recorded per plant: time of harvest beginning and harvest duration. Only spears taller than 30 cm were harvested when the heads were tight, before they "ferned out", leaving the remaining ones for the next harvest because wild asparagus is harvested for several weeks. Additionally, the spear number, diameter and length were determined.

2.6. Micrometeorological data acquisition

The internal global radiation was measured using six photoradiometers (HD 2012.2, Delta Ohm, Italy), placed at the gutter height. Within each span, there were two photoradiometers: the first one was placed under the plastic roof, while the second one was placed under the photovoltaic roof, in order to be under constant light and shade, respectively. All data were recorded at 10 min intervals. Temperature and humidity were measured at the centre of each experimental area by six thermohygrometers (Mela KPC2-ME, Galtec, Germany), two for each span, placed 1.50 m above the ground level. The external global radiation was measured by a pyranometer (LP Pyra 03, Delta Ohm, Italy), and the external temperature and humidity were measured using a thermohygrometer (HOBO U10-003, Onset, USA).

2.7. Statistical analysis

Statistical data analysis was performed using the MIXED procedure of SAS (Statistical Analysis System, version 9.2, SAS Institute, Cary, NC, USA). Prior to analysis, tests were performed to ensure that normality (Shapiro-Wilk test) and homoscedasticity assumptions (Bartlett's test) were met. Variances not meeting assumptions were transformed appropriately. The data were back-transformed for presentation in figures and tables. The statistical model included year, roof type and plant management, as well as all their interaction terms (two- and threefold) as fixed factors. The block and interactions between block and year, block and light condition, and among block, year and light condition were the random factors. Year was assumed to be fixed, because the effect of treatments could depend on the crop age, especially if the establishment year of a perennial crop is considered. The level of significance was set at 5%, and mean comparisons were conducted according to Tukey's studentized range test.

3. RESULTS

3.1. Microclimate conditions

The daily average temperature changed similarly under plastic and photovoltaic cover (Fig. 1). The difference between temperatures was 1°C on a yearly basis. The maximum temperature during the summer months was between 41°C (under photovoltaic cover) and 43°C (under plastic cover). After August, the temperature decreased according to the trend of the outside temperature. The subunits under plastic cover received an average of three times more radiation on a yearly basis (2 470 MJ m^{-2}) than subunits placed under the photovoltaic cover (707 MJ m^{-2}) (Fig. 1). This difference was higher in summer (up to 82% in June and July) and lower in autumn and winter (5% between October and January), due to the higher amount of diffused radiation in these months.

3.2. Phenological development

Year significantly affected the duration of flowering and the fruit ripening (Table 1), resulting in higher values in 2014. Full flowering, and fruit set phases were significantly affected by a two-way interaction year × management (Table 1; $p<0.0001$ and $p<0.01$, respectively). The latter interactions were mainly because in the first year, plants grown in pots were significantly earlier in reaching the flower bud, full-flowering and fruit-set stages than plants grown in full-soil conditions. In the following years, no significant differences were found between management treatments considering the same phenological phases.

3.3. Physiological parameter monitoring

Over the three growing seasons, photosynthetically active radiation at the plant level (Table 2) showed similar trends between the two types of cover (year × roof interaction significant at the $p<0.0001$ level; Fig. 2a). Indeed, under plastic cover, photosynthetically active radiation was in a range between 297.3 and 457.6 μmol m^{-2} s^{-1}, for 2014 and 2015, respectively. Compared to plastic cover, the

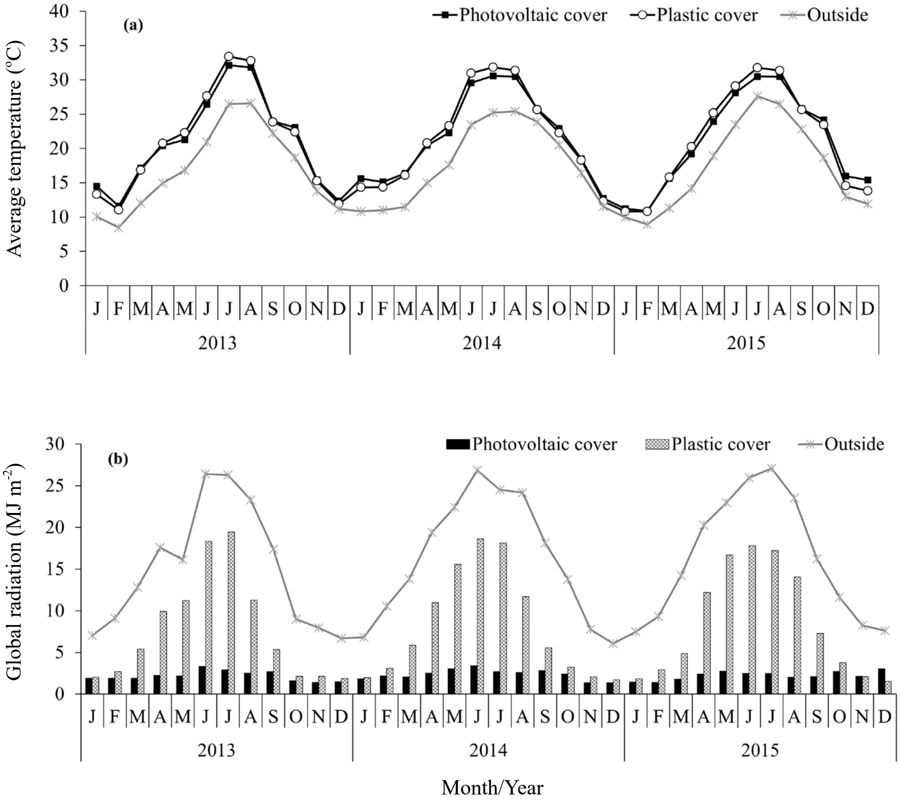

Fig. 1. Daily average temperature (a) and daily average global radiation (b) under the photovoltaic and the plastic roof inside the solar greenhouse during 2013, 2014 and 2015 and comparison with the daily average and global radiation outside the solar greenhouse, and for the same period.

photosynthetically active radiation averages under the photovoltaic cover ranged between 60.7 and 146.0 μmol m^{-2} s^{-1}, for 2015 and 2014, respectively. Under the photovoltaic roof, photosynthetically active radiation peaked to average values of 330 μmol m^{-2} s^{-1} only during winter months because of the declination angle of the sun on the horizon and solar altitude, which were the lowest during mid-autumn. A significant year × roof interaction (Table 2 and Fig. 2b; $p<0.05$) was found for stomatal conductance. In each year, stomatal conductance was slightly higher under plastic roof with significant differences between covers only during the 2014 growing season (Fig. 2b). Although years showed a very similar trend from the micrometeorological point of view, the lowest stomatal conductance was observed in 2015, irrespective of the cover (Fig. 2b). Over the growing seasons, the mean stomatal conductance values were 48.0 and 36.1 mmol m^{-2} s^{-1} for plastic and photovoltaic cover, respectively. The net assimilation rate varied systematically over management treatments and was consistently higher in the pot treatment than in the full-soil treatment under both roofs (Table 2 and Fig. 3a; $p<0.01$), even if, a significant difference was found only under the photovoltaic roof (Fig. 3a). A significant difference in the net assimilation rate between the two covers was observed mostly during the summer and spring months (between April and September), with an average seasonal value under the photovoltaic cover seven times lower than that under plastic cover. From September onwards, the two covers exhibited similar values of net assimilation rates.

3.4. Harvest and spears characteristics

The effect year affected the beginning of the spear harvest period and the spear length (Table 3, $p<0.05$ and $p<0.01$, respectively). The spear emergence period began at the end of January and lasted until June, in conjunction with rising late-spring temperatures. In 2013, a 22-day earlier beginning of the harvesting period compared with 2014 was recorded. However, in the same year the collected spears were significantly shorter (approximately – 4 cm) (Table 3) than the spears collected during 2014 and 2015. A roof × management interaction ($p<0.001$; Table 3) was also found for the spear emergence period. Indeed, on average, plants grown in the full-soil treatment formed spears 28 earlier in the beginning of harvest under both roof conditions. Diameter of spears varied according to a three-way year × roof × management significant interaction ($p<0.05$; Table 3 and Fig. 4). In each year, and within roof condition, full-soil plants provided spears with a significantly higher diameter (3.7 *vs.* 2.6 mm, respectively).

Table 1. Mixed-model analysis of variance containing tests of the fixed effects for year, roof cover, and management type for wild asparagus phenological development

Factor		Flowering			Fruit set (DOY)	Fruit ripening (DOY)
		Duration (no. days)	Cycles by year (no.)	Full flowering (DOY)		
			Year (Y)			
2013		130±7.2 b	3±0.56	139±7.4	173±8.7	238±11.8
2014		207±8.4 a	3±0.57	215±7.7	269±8.7	321±10.7
2015		199±7.8 a	2±0.55	206±7.3	249±8.2	298±11.9
			Roof (R)			
Photovoltaic		181±6.9	2±0.55	186±6.5	229±7.9	295±15.6
Plastic		176±6.3	3±0.62	187±6.2	228±7.6	272±17.7
			Management (M)			
Pot		171±6.4 b	3±0.57	179±6.5	216±7.7	274±11.9
Full-soil		186±6.5 a	2±0.62	194±6.5	239±6.6	293±12.3
Effect	Num DF	Pr > F	Pr > F	Pr > F	Pr > F	Pr > F
Year (Y)	2	*	n.s.	***	***	*
Roof (R)	1	n.s.	n.s.	n.s.	n.s.	n.s.
Management (M)	1	*	n.s.	***	***	n.s.
Y × R	2	n.s.	n.s.	n.s.	n.s.	n.s.
Y × M	2	n.s.	n.s.	***	*	n.s.
R × M	1	n.s.	n.s.	n.s.	n.s.	n.s.
Y × R × M	2	n.s.	n.s.	n.s.	n.s.	n.s.

Within column, different letters indicate statistical difference among years, and between roof type and plant management according to Tukey's test ($p \leq 0.05$). * $p \leq 0.05$, ** $p < 0.01$, *** $p < 0.001$, n.s. – non-significant. Means are followed by standard error values. DOY – day of the year.

4. DISCUSSION

The average thermal requirement for the most common horticultural crops cultivated in greenhouses ranges between 10 and 26°C. Wild asparagus is hypothesized to be quite tolerant to high temperature. In this regard, Mantovani *et al.* (2019), working with potted conditions and under an outside shelter, found that up to 45°C, the photosynthetic activity was almost stable irrespective of light conditions (full light *vs.* partially shaded). In our experimental greenhouse, the "greenhouse effect" was reduced by the limited solar radiation as also suggested by Fatnassi *et al.* (2015). However, the average temperature observed during the coldest months (11°C) of the year was never lower than the minimum threshold of 2°C assessed for cultivated asparagus (Ledda, 2010), avoiding becoming a limiting factor for the following sprouting phase. In Mediterranean climates, solar radiation inside the greenhouse is often high enough (20-22 MJ m^{-2} d^{-1}) around midday to reach values of photosynthetic photon flux density of approximately 1350 μmol m^{-2} s^{-1} (Kittas *et al.*, 2013). The characterization of the amount of light inside the greenhouse, although the availability of radiation is also dependent on the season (solar angle), confirms the results detailed in other trials conducted in similar solar greenhouses (Fatnassi *et al.*, 2015), where 50% coverage with photovoltaic panels arranged in line corresponded to an annual radiation of approximately 400 MJ m^{-2} s^{-1} with negligible differences during the autumn months. The potential of plants to adapt their phenology to limiting light conditions is widely known (Li *et al.*, 2010; Bande *et al.*, 2013); specifically, shading contributes to a prolonged vegetative phase, thus slowing down the reproductive phase (Cai, 2011). Wild asparagus belongs to the *Asparagaceae* family and is a perennial dioecious plant with male and female flowers on separate plants (Kaska *et al.*, 2018); and thus, until ripening only female plants were accounted for. We observed a significant effect of the year factor likely due, rather than to a microclimatic difference among years, to the physiological age of the asparagus plants (being a perennial species) that were well established in 2015 with respect to 2014 and 2013. Based on these results, we can emphasize that photovoltaic coverage had a negligible influence on plant phenological evolution by significantly affecting only the fruit ripening date whereas effects due to management type were more relevant.

Table 2. Mixed-model analysis of variance containing tests of the fixed effects for year, roof cover, and management type for wild asparagus physiological observations

Factor		Photosynthetically active radiation (μmol m^{-2} s^{-1})	Leaf temperature (°C)	Net assimilation rate (μmol CO_2 m^{-2} s^{-1})	Stomatal conductance (mmol H_2O m^{-2} s^{-1})	Internal leaf CO_2 (μmol CO_2 m^{-2} s^{-1})	Transpiration rate (mmol H_2O m^{-2} s^{-1})
				Year			
2013		255.7±25.7	32.0±1.8 a	2.21±0.22 a	53.6±3.3	272.2±13.1 b	2.02±0.11 a
2014		221.6±20.2	32.1±1.9 a	2.15±0.19 a	48.9±3.6	281.2±13.8 b	1.86±0.10 a
2015		259.1±21.4	29.0±1.4 b	0.55±0.10 b	23.8±2.9	322.4±15.2 a	0.69±0.09 b
				Roof			
Photovoltaic		111.7±17.1	31.0±1.9	0.56±0.19	36.1±4.1	334.6±15.2 a	1.30±0.12
Plastic		379.2±22.8	31.0±1.8	2.71±0.22	48.0±4.2	249.3±15.7 b	1.75±0.13
				Management			
Pot		251.2±21.7	31.0±1.7	1.63±0.16	42.4±4.2	307.4±15.7	1.52±0.09
Full-soil		239.7±20.9	31.0±1.9	1.64±0.17	41.8±4.2	276.5±15.2	1.53±0.08
Effect	Num DF	Pr > F	Pr > F	Pr > F	Pr > F	Pr > F	Pr > F
Year (Y)	2	n.s.	*	***	***	*	***
Roof (R)	1	***	n.s.	***	**	***	n.s.
Management (M)	1	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Y × R	2	***	n.s.	n.s.	*	n.s.	n.s.
Y × M	2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
R × M	1	n.s.	n.s.	***	n.s.	n.s.	n.s.
Y × R × M	2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Explanations as in Table 1.

Interestingly, potted plants were highly synchronic in their flowering and fruiting. This suggests that despite strong environmental cues that can trigger plant reproduction outside greenhouses, morphological and physiological intraspecific variability may produce differential responses among individuals because of management conditions. To the best of our knowledge, this study is the first attempt to evaluate both the influence of solar greenhouse conditions on the onset of flowering and fruiting, and whether examined this species differs in its reproductive strategy. This study failed to catch divergent responses to the shading conditions. The development of fruits is important for asparagus breeding and seed production (Lo Porto *et al.*, 2019). Our results might have relevant implications for additional researches aimed to plan seed collection schedules and the subsequent propagation process in nurseries along with further deepening of the use of self-produced seeds for cultivation under solar greenhouse. The lack of a timely and permanent supply of high-quality seed is one of the main difficulty with which the nurseries devoted to propagation of wild plant species have to face (Botha *et al.*, 2005; Lo Porto *et al.*, 2019). Our results provide relevant information on both the inter-annual and inter-specific variation of the phenological pattern, as well as demonstrating that a detailed knowledge of phenological attributes is crucial to develop site-specific gathering seed programs. For the first time, our study pointed out on how wild asparagus plants developmentally acclimate to growth under fluctuating light intensities corroborating the work on Arabidopsis by Vialet-Chabrand *et al.* (2017). Consistent with the photosynthetically active radiation values, our results showed that plastic cover had high rates of net assimilation and transpiration, as observed on previous trials of horticultural crops conducted inside a solar greenhouse with the same design features (Cossu *et al.*, 2021). The pattern of stomatal conductance was slightly different; indeed, the differences between roofs and within years were somewhat insignificant. A previous study suggested that the decrease in photosynthetic capacity under shade conditions was caused by stomatal or nonstomatal limitations (Gong *et al.*, 2015). This research showed the same result, which was the decrease in the net assimilation rate under photovoltaic cover; and thus, in shade conditions, this was not caused by the stomatal effect. In this experiment, light conditions under the plastic roof led to an increase in the photosynthetic rate, while internal carbon

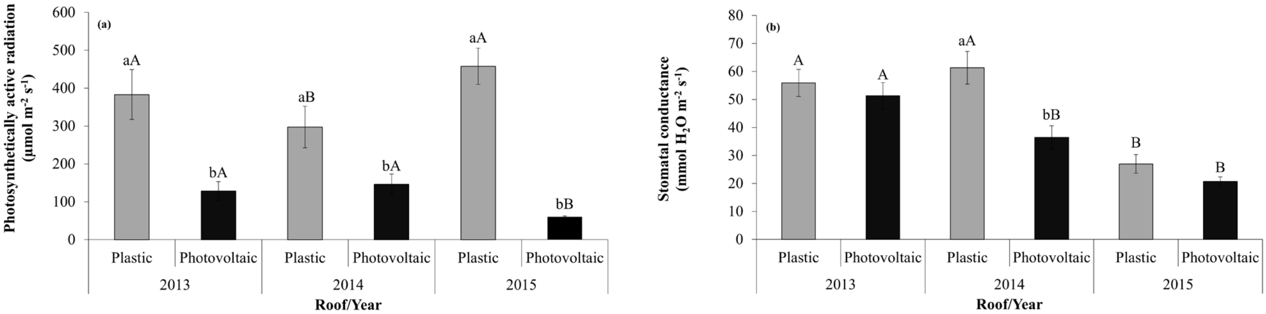

Fig. 2. Photosynthetically active radiation (a) and stomatal conductance (b) affected by year × roof interaction ($p < 0.0001$ and $p < 0.05$, respectively). Different letters indicate significant differences between years (upper-case letters, within roof type) and roof types (lower-case letters, within year) according to Tukey's test (number of replicates = 3).

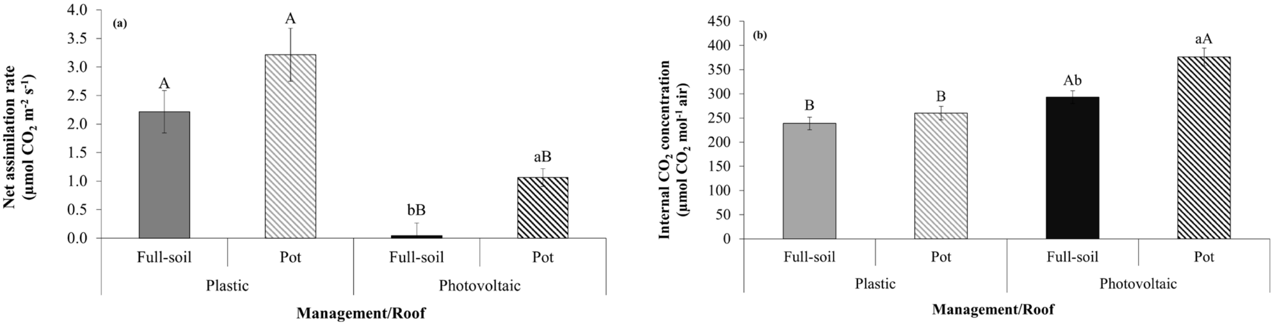

Fig. 3. Net assimilation rate (a) and internal CO_2 concentration (b) affected by roof × management interaction ($p < 0.0001$ and $p < 0.05$, respectively). Different letters indicate significant differences between roof types (upper-case letters, within management) and managements (lower-case letters, within roof) according to Tukey's test (number of replicates = 3).

dioxide levels were lower. This was because sunlight stimulates the plant growth and development, and by photosynthetic processes, plants use sunlight to convert H_2O and CO_2 into carbohydrates (Khalid *et al.*, 2019). In contrast, in shade conditions, sunlight stimulation to photosynthesize is lacking or is attenuated, and as a consequence, CO_2 fills the internal leaf space and it is utilized more slowly by the plant. Under the photovoltaic roof for three dates of monitoring, we recorded negative values, indicating that the plant did not photosynthesize but respired. Conventionally, assimilation leads to negative values in the dark when there is a net release of CO_2 from the leaves due to mitochondrial respiration (Taiz and Zeiger, 2012). However, wild asparagus has shown a great ability to maintain positive CO_2 absorption rates at photosynthetic active radiation over 90 µmol m^{-2} s^{-1}. This is explained by the fact that light saturation levels for shade-adapted plants are substantially lower than those for sun-adapted plants (Taiz and Zeiger, 2012). Phenotypic plasticity (Gratani, 2014) due to variations in physiological features seems to be the main attribute for the adjustment of wild asparagus under different light conditions (Mantovani *et al.*, 2019; Molina *et al.*, 2012). The plant architecture with the greatest influence on light interception and productivity is the amount and distribution of functional leaf area (Gratani, 2014). Indeed, the shoots are usually extremely rich in cladodes that are characterized by a reduced surface area useful for limiting evapotranspiration and reducing water loss. By increasing the number of cladodes the plant strives to compensate for the decreased assimilation that is caused by a reduction in their size (Nakayama *et al.*, 2013). Such traits are the result of ontogenetic and environmental factors, tolerance to shading, shoot and needle structure, branching patterns, crown shape, and the aforementioned penetration of photosynthetic active radiation (Niinemets, 2010). The number of spears per plant and the spear length recorded for wild asparagus were similar to those described for the same species in cultivation experiments or in the natural environment. Previous studies conducted in Italy by Benincasa *et al.* (2007) and Rosati *et al.* (2005) reported on average six number of spears per plant. In contrast, Molina *et al.* (2012) reported a mean number of spears per plant lower than our findings (3-4 spears per plant) in an investigation carried out in a natural environment in order to characterize the gathering pressure on the species. The better growing conditions of the cultivated plants (soil, fertilization, irrigation and weed control) were likely responsible for these considerable differences. Moreover, our results are inconsistent with the findings of Guo (2001), who found that net assimilation rate was positively associated with spear yield in different

Table 3. Mixed-model analysis of variance containing tests of the fixed effects for year, roof cover, and management type for wild asparagus production parameters

Factor		Harvest period		Spear characteristics		
		Begin (DOY)	Duration (days)	Diameter (cm)	Length (cm)	Total number (no. per plant)
			Year (Y)			
2013		78±8.8	50±6.1	0.31±0.01	33.8±3.5	5±1.15
2014		100±9.1	40±5.8	0.29±0.01	38.2±4.2	6±1.05
2015		90±9.0	54±5.7	0.33±0.01	38.3±4.3	6±1.07
			Roof (R)			
Photovoltaic		91±9.1	48±5.0	0.32±0.01	37.0±3.5	6±1.13
Plastic		88±9.0	49±5.1	0.30±0.01	36.5±3.9	6±1.15
			Management (M)			
Pot		103±9.0	50±4.8	0.37±0.01	37.3±4.1	6±1.20
Full-soil		75±9.0	47±4.9	0.26±0.01	36.2±4.1	6±1.17
Effect	Num DF	Pr > F	Pr > F	Pr > F	Pr > F	Pr > F
Year (Y)	2	n.s.	n.s.	***	n.s.	n.s.
Roof (R)	1	n.s.	n.s.	n.s.	n.s.	n.s.
Management (M)	1	***	n.s.	n.s.	n.s.	n.s.
Y × R	2	n.s.	n.s.	n.s.	n.s.	n.s.
Y × M	2	n.s.	n.s.	n.s.	n.s.	n.s.
R × M	1	***	n.s.	n.s.	n.s.	n.s.
Y × R × M	2	n.s.	n.s.	*	n.s.	n.s.

Explanations as in Table 1.

cultivated asparagus genotypes. In our study, the number of spears per plant was independent of net assimilation rate, as no difference was found between covers where the net assimilation rate strongly differed. Lack of differences with respect to net assimilation rate might result from the fact that unlike the cultivated species which is characterized by a winter dormancy period, wild asparagus continues to photosynthesize in autumn-winter months. This gives wild asparagus a great advantage over the cultivated asparagus, which, as a deciduous species, has no green vegetation from autumn to spring and has to regrow all the canopy each year before becoming photosynthetically active. Having photosynthetically active ferns before and during the harvest of the spears, the spring storage depletion reported for the cultivated species (Feller *et al.*, 2018) should be reduced in the wild asparagus, as also hypothesized by Mantovani *et al.* (2019). At the management level, we observed that plants grown in full-soil conditions showed better performance than plants grown in pots. Since wild asparagus is a perennial plant with a root system that in natural conditions can reach 65 cm in depth (Capilleri *et al.*, 2016), we hypothesized that plants in full-soil conditions were probably able to explore and to exploit a greater volume of soil both radially and longitudinally, and this would provide them with an advantage with respect to potted plants under equal microenvironment conditions. Moreover, we noted that potted plants tended to fern-out earlier than full-soil plants with a shift in spear growth from extension to radial growth in the subapical region of the spear; as a consequence, some spears could not be harvested. Guo (2001), during shoot growth measurements in cultivated asparagus, observed a similar growth pattern, but without giving an explanation. Our results can be considered a valuable starting point for further investigation into the interactions at play in solar greenhouse systems, whether for adaptive management purposes and for assessing crop responses in terms of resilience to more restrictive light-limiting conditions.

5. CONCLUSIONS

1. Wild asparagus could be a useful perennial species in challenging contexts such a solar greenhouse is. It proved to have enough developmental plasticity to adapt to a range of light regimes shifting the dynamic of key physiological parameters, including net assimilation rate and phenology, when comparison has been made between photovoltaic and plastic cover.

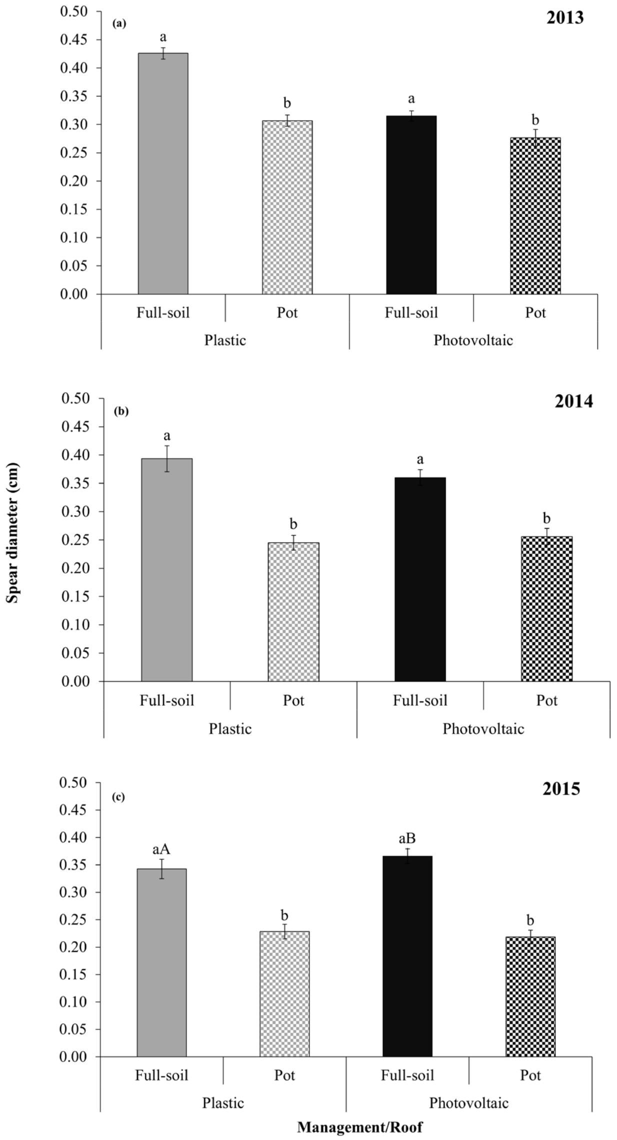

Fig. 4. Spear diameter affected by year × roof × management three-way interaction ($p < 0.05$). For each year, different letters indicate significant differences between roof types (upper-case letters, within management) and managements (lower-case letters, within roof) according to Tukey's test (number of replicates = 3).

2. Our results provide valuable suggestions with regard to the optimization of land use into solar greenhouse avoiding thus leaving unused space. This study provides a comprehensive picture about the potential of a 50% covered solar greenhouse in terms of raising of crop production and an improvement of its quality characteristics, earning capacity, and feasibility. Furthermore, the valorization of solar greenhouse might enable a land saving and a dwindling of environmental footprint by its very nature (*i.e.* renewable energy source).

3. To date, most research and practical efforts in solar greenhouse sector have been devoted to investigating suitability of existing crops, rather than recruiting new local species. Based on our results, to reach an optimal balance between electric energy and crop production in solar greenhouse, native food production should receive more attention in terms of research and use.

ACKNOWLEDGEMENTS

The authors thank Dr. Stefania Solinas for helpful comments on the final draft of the manuscript. We gratefully acknowledge the Murtas family and CIDAM s.s.a. farm staff for their longstanding support, Mr. Tore Pala, Mr. Marco Maxia and Dr. Giulia R. Urracci for their valuable help in collecting data.

Data Availability Statement: The data presented in this study are available on request from the authors.

Conflicts of Interest: The authors declare no conflict of interest.

6. REFERENCES

Aroca-Delgado R., Pérez-Alonso J., Callejón-Ferre Á.-J., and Díaz-Pérez M., 2019. Morphology, yield and quality of greenhouse tomato cultivation with flexible photovoltaic rooftop panels (Almería-Spain). Sci. Hortic., 257, 108768. https://doi.org/10.1016/j.scienta.2019.108768

Bande M.M., Grenz J., Asio V.B., and Sauerborn J., 2013. Fiber yield and quality of abaca (*Musa textilis* var. Laylay) grown under different shade conditions, water and nutrient management. Ind. Crop. Prod., 42, 70-77. https://doi.org/10.1016/j.indcrop.2012.05.009

Benincasa P., Tei F., and Rosati A., 2007. Plant density and genotype effects on wild asparagus (*Asparagus acutifolius* L.) spear yield and quality. Hortscience, 42, 1163-1166. https://doi.org/10.21273/HORTSCI.42.5.1163

Bilušić T., Šola I., Rusak G., Poljuha D., and Čulić V.C., 2019. Antiproliferative and pro-apoptotic activities of wild asparagus (*Asparagus acutifolius* L.), black bryony (*Tamus communis* L.) and butcher's broom (*Ruscus aculeatus* L.) aqueous extracts against T24 and A549 cancer cell lines. J. Food Biochem., 43, e12781. https://doi.org/10.1111/jfbc.12781

Botha J., Witkowski E.T.F., and Cock J., 2005. A review of nurseries as conservation or social forestry outreach tools. Int. J. Biodivers. Sci. Manage., 1, 33-51. https://doi.org/10.1080/17451590509618078

Cai Z.Q., 2011. Shade delayed flowering and decreased photosynthesis, growth and yield of Sacha Inchi (*Plukenetia volubilis*) plants. Ind. Crop. Prod., 34, 1235-1237. https://doi.org/10.1016/j.indcrop.2011.03.021

Capilleri P.P., Motta E., and Raciti E., 2016. Experimental study on native plant root tensile strength for slope stabilization. Procedia Eng., 158, 116-121. https://doi.org/10.1016/j.proeng.2016.08.415

Ceccanti C., Landi M., Benvenuti S., Pardossi A., and Guidi L., 2018. Mediterranean wild edible plants or "new functional crops". Molecules, 23, 2299. https://doi.org/10.3390/molecules23092299

Cossu M., Sirigu A., Deligios P.A., Farci R., Carboni G., Urracci G., and Ledda L., 2021. Yield response and physiological adaptation of green bean to photovoltaic greenhouses. Frontiers in Plant Science, 12, 800. https://doi.org/10.3389/fpls.2021.655851

Fatnassi H., Poncet C., Bazzano M.M., Brun R., and Bertin N., 2015. A numerical simulation of the photovoltaic greenhouse microclimate. Sol. Energy, 120, 575-584. https://doi.org/10.1016/j.solener.2015.07.019

Feliciano D., 2019. A review on the contribution of crop diversification to Sustainable Development Goal 1 "No poverty" in different world regions. Sustainable Development, 27, 795-808. https://doi.org/10.1002/sd.1923

Feller C., and Müller A., 2018. The content of reserve carbohydrates in the crown of asparagus (*Asparagus officinalis* L.) as a function of progressing senescence of fern. Acta Hortic., 1223, 189-194. https://doi.org/10.17660/ActaHortic.2018.1223.26

Fernie R.A., and Yan J., 2019. De novo domestication: an alternative route toward new crops for the future. Mol. Plant., 12, 615-631. https://doi.org/10.1016/j.molp.2019.03.016

Gong W.Z., Jiang C.D., Wu Y.S., Chen H.H., Liu W.Y., and Yang W.Y., 2015. Tolerance vs. avoidance: two strategies of soybean (*Glycine max*) seedlings in response to shade in intercropping. Photosynthetica, 53, 259-268. https://doi.org/10.1007/s11099-015-0103-8

Gratani L., 2014. Plant phenotypic plasticity in response to environmental factors. Adv. Bot., 208747. https://doi.org/10.1155/2014/208747

Guo J., 2001. Physiological characters underpinning cultivar differences in spear yield of field-grown asparagus (*Asparagus officinalis* L.). Dissertation, University of Cantebury.

Katsenios N., Roussis Ie., Efthimiadou A., Kakabouki I., and Bilalis D., 2019. Seed treatment techniques to improve germination of wild asparagus (*Asparagus acutifolius* L.), a potential new crop. Not. Bot. Horti. Agrobo., 47, 995-1000. https://doi.org/10.15835/nbha47311554

Kavga A., Strati I.F., Sinanoglou V.J., Fotakis C., Sotiroudis G., Christodoulou P., and Zoumpoulakis P., 2019. Evaluating the experimental cultivation of peppers in low-energy-demand greenhouses. An interdisciplinary study. J. Sci. Food Agric., 99, 781-789. https://doi.org/10.1002/jsfa.9246

Khalid M.H.B., Raza M.A., Yu H.Q., Sun F.A., Zhang Y.Y., Lu F.Z., Si L., Iqbal N., Khan I., Fu F.L., and Li W.C., 2019. Effect of shade treatments on morphology, photosynthetic and chlorophyll fluorescence characteristics of soybeans (*Glycine max* L. MERR.). Appl. Ecol. Env. Res., 17, 2551-2569. https://doi.org/10.15666/aeer/1702_25512569

Kaska A., Deniz N., and Mammadov R., 2018. Biological activities of wild asparagus (*Asparagus acutifolius* L.). Int. J. Second. Metab., 3, 243-251. https://doi.org/10.21448/ijsm.458827

Kittas C., Katsoulas N., Bartzanas T., and Bakker S., 2013. Greenhouse climate control and energy use. In: Good agricultural practices for greenhouse vegetable crops: principles for Mediterranean climate areas (Eds W. Baudoin, R. Nono-Womdim, N. Lutaladio, A. Hodder *et al.*). Food and Agriculture Organization of the United Nations, Rome, 63-96.

Ledda L., 2010. Vegetable asparagus growing with low input techniques in Sardinia. In: Opportunities and constraints in the evaluation of local productions in Sardinia: asparagus (in Italian). (Eds M. Tedde, F. Nuvoli). Gallizzi Press, Sassari, 23-56.

Lo Porto C., Sergio L., Boari F., Logrieco A.F., and Cantore V., 2019. Cold plasma pretreatment improves the germination of wild asparagus (*Asparagus acutifolius* L.) seeds. Sci. Hortic., 256, 108554. https://doi.org/10.1016/j.scienta.2019.108554

Li H., Jiang D., Wollenweber B., Dai T., and Cao W., 2010. Effects of shading on morphology, physiology and grain yield of winter wheat. Eur. J. Agron., 33, 267-275. https://doi.org/10.1016/j.eja.2010.07.002

Mantovani D., Rosati A., and Perrone D., 2019. Photosynthetic characterization and response to drought and temperature in wild asparagus (*Asparagus acutifolius* L.). Hortscience, 54, 1039-1043. https://doi.org/10.21273/HORTSCI13954-19

Molina M., Pardo-de-Santayana M., García E., Aceituno-Mata L., Morales R., and Tardío J., 2012. Exploring the potential of wild food resources in the Mediterranean region: natural yield and gathering pressure of the wild asparagus (*Asparagus acutifolius* L.). Span. J. Agric. Res., 10, 1090-1100. https://doi.org/10.5424/sjar/2012104-3050

Nakayama H., Yamaguchi T., and Tsukaya H., 2013. Modification and co-option of leaf developmental programs for the acquisition of flat structures in monocots: unifacial leaves in Juncus and cladodes in Asparagus. Front. Plant Sci., 4, 248. https://doi.org/10.3389/fpls.2013.00248

Niinemets Ü., 2010. A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. Ecol. Res., 25, 693-714. https://doi.org/10.1007/s11284-010-0712-4

Pantera A., Burgess P.J., Mosquera Losada R., Moreno G., López-Díaz M.L, Corroyer N., McAdam J., Rosati A., Papadopoulos A.M., Graves A., Rigueiro Rodríguez A., Ferreiro-Domínguez N., Fernández Lorenzo J.L., González-Hernández M.P., Papanastasis V.P., Mantzanas K., Van Lerberghe P., and Malignier, N., 2018. Agroforestry for high value tree systems in Europe. Agroforest. Syst., 92, 945-959. https://doi.org/10.1007/s10457-017-0181-7

Renard D., and Tilman D., 2019. National food production stabilized by crop diversity. Nature, 571, 257-260. https://doi.org/10.1038/s41586-019-1316-y

Rosati A., Pepe R., Senatore A., Perrone D., and Falavigna A., 2005. Productivity of wild asparagus (in Italian). Inf. Agrar., 8, 75-77. https://doi.org/10.17104/0017-1417_2005_2_114

Savo V., Salomone F., Mattoni E., Tofani D., and Caneva G., 2019. Traditional salads and soups with wild plants as a source of antioxidants: a comparative chemical analysis of five species growing in Central Italy. Evid.-Based Complementary Altern. Med., 6782472. https://doi.org/10.1155/2019/6782472

Schulp C.J.E., Thuiller W., and Verburg P.H., 2014. Wild food in Europe: A synthesis of knowledge and data of terrestrial wild food as an ecosystem service. Ecol. Econ., 105, 292-305. https://doi.org/10.1016/j.ecolecon.2014.06.018

Taiz L., and Zeiger E., 2012. Photosynthesis: physiological and ecological considerations. In: Plant physiology (Eds L. Taiz, E. Zeiger). Sunderland: Sinauer, 173-179.

Vialet-Chabrand S., Matthews J.S.A., Simkin A.J., Raines C.A., and Lawson T., 2017. Importance of fluctuations in light on plant photosynthetic acclimation. Plant Physiol., 173, 2163-2179. https://doi.org/10.1104/pp.16.01767