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Review

Cultivation Practices, Adaptability and Phytochemical Composition of Jerusalem Artichoke (*Helianthus tuberosus* L.): A Weed with Economic Value

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Abstract: The Jerusalem artichoke (*Helianthus tuberosus* L.) is a perennial weed that is cultivated for bioethanol production or pharmaceutical purposes, as its aerial parts and tubers contain several chemical compounds. This review summarizes important data on the effects of the main cultivation practices (e.g., the planting density and pattern, weed management, fertilization, irrigation, genotypes and harvest) on tuber yield and quality. The most widespread method for the propagation of the Jerusalem artichoke is planting the tubers directly in the field, with a plant density of about 33,000–47,000 plants ha^{-1}. Weed management is based on herbicide application, mechanical cultivation and hand hoeing, while the nutrient requirements are low, and irrigation relies on weather conditions. For instance, under Mediterranean semi-arid conditions, the crops are irrigated from June to September. In addition, the harvest time depends on the genotype and the purpose of cultivation, which is an important consideration for obtaining a high-quality product. In conclusion, Jerusalem artichoke yield and quality depend on several factors, and this plant, due to its high productivity, constitutes a promising crop with numerous uses.

Keywords: drought; harvest time; inulin; tolerance; weed management

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1. General Characteristics and Importance of *Helianthus tuberosus*

The Jerusalem artichoke (*Helianthus tuberosus* L.; family Asteraceae) is an invasive, perennial weed species native to North America [1,2] and has been introduced in Europe and Asia (Figure 1) as a cultivated plant [3,4]. This species is grown in Europe, Asia and many other regions of the world [5–7]. The Jerusalem artichoke can reach 300 cm in height [8] and has a light-green or green-violet branched stem [9] with lanceolate, lanceolate-ovate [9,10] or, rarely, ovate leaves [10]. The root system develops rhizomes that form fleshy tubers [2]. The tubers can be white, red [8], light brown, brown [9,10], violet-brown [9] or dark brown [10], and the shape is mainly oval but can also be rounded [8,10], oblong [8,9] or pear-shaped/slender [9].

The Jerusalem artichoke has many uses [11–14], as both above- and underground parts of the plant contain various chemical constituents such as proteins, glucose, fructose, sucrose and inulin [11,15–19]. The aerial parts and tubers can be used for bioethanol production and in the food industry [11,12,14]. According to Matías et al. [20], Jerusalem artichoke is an emerging energy crop for bioethanol production due to its high biomass yield. The leaves and stems can be used as forage in animal production [21], while the tubers, which are a rich source of inulin, can be used for pharmaceutical purposes as well as for food or fodder production [22–26].

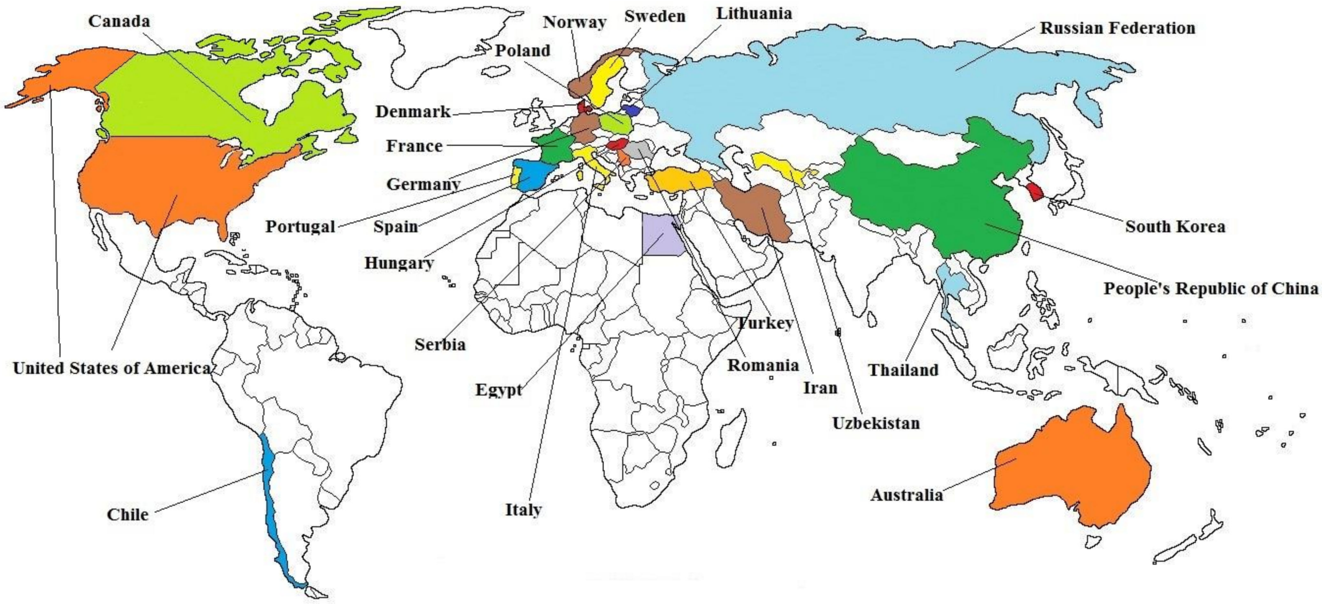

Figure 1. Selected countries where Jerusalem artichoke is grown.

Studies have shown that the Jerusalem artichoke has many positive effects on health because of its anti-obesity, antidiabetic, antifibrotic and anti-inflammatory properties [27]. Kang et al. [28] reported the potential use of *H. tuberosus* tuber extract as a topical treatment for atopic dermatitis and inflammatory skin diseases. The mineral contents of the tubers are also valuable for human health since these elements are significant for cation balance (potassium and magnesium) and bone stability (calcium and phosphorus) [15].

A study in rats revealed that Jerusalem artichoke tubers might be a potential prebiotic additive, since inulin and fructo-oligosaccharides alter the intestinal morphometry and ameliorate blood metabolites [29]. Kleessen et al. [30] observed that the addition of Jerusalem artichokes to bakery products enhances the growth of fecal bifidobacteria after one week of consumption.

The above studies show the usefulness of products derived from Jerusalem artichoke. Thus, increasing the yield and quality of the plant is considered important. Several studies have shown that cultivation practices, such as plant density [31], weed competition [32], nitrogen fertilization [33,34], irrigation [31,33], genotypes [8,11,19,35] and harvest date [20], affect the tuber or aboveground biomass yield and quality (e.g., inulin content) of this plant.

For the above-mentioned reasons, this review aims to summarize important data on the chemical constitution of the Jerusalem artichoke's parts, possible uses and adaptability to abiotic stresses. The emphasis is on thoroughly describing the main cultivation practices (e.g., the planting density and pattern, weed management, fertilization, irrigation, genotypes, and harvest) implemented, as well as their effects on tuber yield and quality.

2. Climate and Soil Requirements

The Jerusalem artichoke grows in soils with different textures, such as sand [36], loamy sand [19,37], sandy loam, loam [20], sandy clay loam [38] and clay [39]. It also grows in soils with a pH of 5.1–8.2 [20,38,40–42]. The Jerusalem artichoke is tolerant to both low and high temperatures [36].

The plant is adaptable to different growing conditions and is cultivated in areas with various climate types, such as Mediterranean, tropical and temperate monsoon [31,36,41]. In regions with a tropical climate, seasonal variations in temperature and precipitation play an important role in plant growth [36]. In a study conducted in Southeast Asia, Puangbut et al. [36] observed that the conditions that prevailed during the early rainy season (e.g., high temperature (mean minimum temperature: 23 °C in 2011 and 2012; mean maximum temperature: 32.0 and 32.4 °C in 2011 and 2012, respectively)) were favorable for vegetative growth, and thus, the aboveground biomass (stems and leaves) increased. However, in the post-rain season, the conditions (low temperature (mean minimum temperature: 20.2 and 21.7 °C in 2011 and 2012, respectively; mean maximum temperature: 30.4 and 31.0 °C in 2011 and 2012, respectively) and short photoperiod (11 h)) favored tuber development, and consequently, the tuber yield increased [36].

3. Adaptability of Jerusalem Artichoke to Abiotic Stresses

3.1. Drought

The Jerusalem artichoke is tolerant to several abiotic stresses, including drought [21]. This plant has been studied widely under water stress, as there is evidence of its use in drought-prone areas. Despite its tolerance to drought, Jerusalem artichoke's growth, physiological parameters and yield can be severely reduced. Namwongsa et al. [43] observed decreased tuber yield, shoot biomass and height under water stress, while Puangbut et al. [23] reported that full irrigation favors aboveground growth compared to drought conditions. In another study, Puangbut et al. [44] observed that drought reduced the leaf area, biomass, stomatal conductance and photosynthetic rate by 57%, 46%, 64% and 62%, respectively.

Jerusalem artichoke genotypes differ in their tolerance to drought conditions. According to Ruttanaprasert et al. [45], the highest values of several root traits (e.g., diameter, surface area and biomass) of certain Jerusalem artichoke genotypes were observed under field capacity conditions. The same authors also reported that some genotypes produced tubers with a high dry weight under water stress, due to alterations in the root growth pattern and the ability of the plants to absorb more water from dry soils. Zhang et al. [46] reported that the drought-tolerant variety 'Xiuyan' has a higher proline content in its leaves compared with the variety 'Yuli'. Recently, Nacoon et al. [42] reported that the arbuscular mycorrhizal fungi *Rhizophagus irregularis* (strain BM-2 g1) and *Glomus etunicatum* (strain UDCN52867 g5) improve the drought tolerance of Jerusalem artichoke.

Water stress also affects the chemical compound content in tubers or the aerial parts of Jerusalem artichoke. Puangbut et al. [23] observed enhanced and reduced inulin content under moderate and severe drought stress. In another study, Aduldecha et al. [19] examined the effects of three different water regimes (field capacity, 50% and 25% available water) on the inulin concentration and yield and found a reduction in the inulin yield in the 50% and 25% available water treatments, while drought had a small impact on the inulin concentration, which differed among the examined genotypes. The reduction in inulin yield is due to a decrease in tuber yield, since the inulin yield shows a positive and significant correlation with tuber dry weight.

In addition to drought, high temperatures can also affect the physiological mechanisms in the Jerusalem artichoke. Yan et al. [47] observed that heat stress (40 to 48 °C) decreases the photosynthetic rate and negatively affects photosystem II function, while photosystem I is not as susceptible to high-temperature induced stress as photosystem II. Moreover, the same authors reported an increase in relative variable chlorophyll a fluorescence at high temperatures (>40 °C) compared to 25 °C.

3.2. Salinity

The Jerusalem artichoke shows moderate tolerance to salinity [48], and different genotypes have different levels of salinity tolerance [48,49]. The varieties 'Stampede' and 'White Fuseau' are moderately tolerant to salinity [4,50]. In another study, Long et al. [49] reported that the salt-tolerant variety 'N1' has a higher tuber yield and inulin content compared to the 'N7' variety with lower tolerance to salinity.

In general, salinity affects the growth and yield of Jerusalem artichoke. Dias et al. [4] reported that the tuber yield at moderate salinity (6.6 dS m^{-1}) was 83 t ha^{-1}, while that after control treatment (1.2 dS m^{-1}) was 92 t ha^{-1}. In a recent study, Bhagia et al. [50]

showed that irrigation with high-salinity water (electrical conductivity (EC) 12 dS m^{-1}) reduces the tuber yield.

At a salinity of 6.6 dS m^{-1}, Dias et al. [4] reported that the tuber yield and shoot biomass decrease by 11% and 37%, respectively. This reduction is due to high chloride (Cl^-) levels in the leaves and roots [4]. Chloride accumulation in the leaves, stems and roots under saline conditions was also reported by Newton et al. [51], who observed that the sodium concentrations in plant leaves were low, except under high salinity (1.2 dS m^{-1}). In addition, Shao et al. [52] observed the lowest tuber and aboveground biomass in highest-salinity soil (2.7 g NaCl/kg).

Xue et al. [53] reported that salt stress reduces the photosynthetic rate and chlorophyll content of the Jerusalem artichoke and causes high lipid peroxidation. They also showed that salt stress reduces the activity of antioxidant enzymes (e.g., catalase, superoxide dismutase and peroxidase). The addition of Ca^{2+} could have a protective and restorative role against salt stress. According to Xue et al. [53], the addition of Ca^{2+} enhanced the activity of antioxidant enzymes, protecting the plants from both oxidative damage and loss of membrane permeability, and also reduced the leaf malondialdehyde content. Long et al. [49] reported that the salt-tolerant variety 'N1' has higher soluble sugar and proline contents in the leaves. In addition, the salt-tolerant cultivar had a higher K^+/Na^+ ratio and a lower Na^+/Ca^{2+} ratio compared with the non-tolerant variety 'N7', indicating the importance of the K^+/Na^+ and Na^+/Ca^{2+} ratios as mechanisms to adjust to osmotic stress [49].

3.3. Waterlogging

Jerusalem artichoke is non-tolerant to waterlogging [54]. According to Yan et al. [54], moderate and severe waterlogging decreased the tuber yield by 71.5% to 100%. Waterlogging can also affect several physiological and biochemical parameters. Under waterlogging conditions, the malondialdehyde and H_2O_2 contents in the leaves of Jerusalem artichoke plants increase, while the photosynthetic rate and stomatal conductance decrease [54]. The magnitude of these changes directly depends on the level of waterlogging stress. In another study conducted in Germany, Ruf et al. [55] reported that Jerusalem artichoke adapts to waterlogging conditions and thus can be cultivated in fields with periodic waterlogging during winter.

4. Cultivation Practices

4.1. Soil Preparation

Usually, in autumn or winter, the soil is plowed with a moldboard plow at a depth of 0.30–0.40 m [5,20,34,56], while in spring, the soil is harrowed twice before planting Jerusalem artichoke [20,34,39,52,57]. For secondary tillage, different types of tools, such as a disc harrow, tine harrow or rotary hoe, can be used. Soil compaction should be avoided during tillage, since this results in a lower tuber yield [20]. Conditions that contribute to this problem are (a) high precipitation during winter and (b) low plant residues incorporated into the soil from the preceding crop [20].

4.2. Rotation

Limited studies have examined the impact of the rotation system on Jerusalem artichoke yield. In Italy, cotton, artichoke, wheat and sunflower are reported as preceding crops of Jerusalem artichoke [5]. Jerusalem artichoke monocropping should be avoided. In a recent study, Zhou et al. [58] reported that continuous monocropping of Jerusalem artichoke for 3 successive years altered the composition of the soil bacterial community, while rotation with wheat had beneficial effects on the soil bacteria. Chi et al. [59] found that monocropping of Jerusalem artichoke for 4–5 years negatively affected plant growth and tuber quality by reducing their sugar content.

4.3. Planting

Jerusalem artichoke is propagated using its fleshy tubers and seeds. The most widespread propagation method is the use of tubers, since the use of seeds slows plant growth and decreases the tuber yield [31]. However, seeds of Jerusalem artichoke that are primed with gibberellic acid, pre-chilled at 5 °C for 2 weeks and then placed in a chamber at 15–25 °C for 2 weeks show a high germination (85.3%) [60]. Tubers are cut into fragments consisting of three to five buds [9], which are planted directly in the field at a depth of 0.05–0.10 m [56,61,62].

In some cases, to expedite tuber sprouting, tuber segments are incubated under moist conditions for 3 to 7 days in plastic bags that contain charred rice husks [63,64]. After incubation, the tubers are planted in plastic trays until the stems have two to six leaves, and then the transplants are planted in the field [36,63,64].

In Europe, planting occurs in spring, from middle March to middle May [11,20,56,57,61], while in regions of Northern America and the Southern Hemisphere, Rossini et al. [13] reported that Jerusalem artichoke planting in the field takes place from February to March and during the period of September-October, respectively.

Tubers or transplants are planted in the field in rows with a spacing of 0.35–0.75 m apart and plant spacing in the row of 0.30–0.67 m [22,33,36,39,52,56,57]. In most cases, the row spacing is 0.70–0.75 m, while the spacing between plants in the row is 0.30–0.40 m [11,20,22,39,56]. This planting pattern corresponds to a density of 33,000–47,000 plants ha^{-1}. Planting density can affect plant growth and the tuber yield of Jerusalem artichoke crops. Low plant population leads to an increase in the tuber weight, however, the tuber yield per hectare is reduced [31]. Early planting should be avoided since low temperatures (10–17 °C) during the first growth stages of plants were shown to affect the germination of tubers [65].

4.4. Fertilization

The nutrient requirements of Jerusalem artichoke are low [66], and the application of fertilizers should be based on soil analysis results [41]. A synthetic fertilizer that contains nitrogen, phosphorus and potassium can be incorporated into the soil prior to planting [20]. The application of nitrogen, phosphorus and potassium can lead to an increase in the total sugar content in the tubers by 19.1% [67]. Matías et al. [20] reported that NPK fertilization (9-18-27) at a rate of 600 kg ha^{-1} (N-P-K: 54–108–162 kg ha^{-1}) is sufficient to achieve high aboveground dry biomass (22.7 t ha^{-1}), while they found no significant differences in this parameter at a high rate of 1200 kg ha^{-1} (N-P-K: 108-216-324 kg ha^{-1}). In another study, Gao et al. [41] applied 80 kg ha^{-1} of N, 20 kg ha^{-1} of P and 40 kg ha^{-1} of K, based on both soil analysis results and nutrient requirements of Jerusalem artichoke.

A nitrogen fertilizer (e.g., urea) can be applied after crop emergence [34]. Gao et al. [33] observed that nitrogen fertilization (25 or 50 kg ha^{-1}) increases the tuber and aboveground biomass yield, particularly when combined with irrigation. In their study, urea was applied at two equal rates at seedling and bud stages. In another study, Niu et al. [34] reported that the application of 80 kg ha^{-1} of urea (36.8 kg ha^{-1} of N) at the seedling stage increases the dry matter of tubers in comparison to the control treatment. In contrast, in a study conducted in Finland, nitrogen fertilization (30, 60 and 90 kg ha^{-1}) had no impact on the aboveground biomass yield [66].

4.5. Irrigation

The irrigation requirements of Jerusalem artichoke depend on the climatic conditions. In the Mediterranean region, drip irrigation is used from June to September to prevent water stress [35]. The irrigation frequency during summer depends on the air temperature. In Spain, Matías et al. [20] reported that in June and September, irrigation is used on planted fields once or twice per week, while the irrigation frequency during the hottest summer months (July and August) increases to three times per week.

Irrigation increases the Jerusalem artichoke underground biomass and tuber yield in comparison to no irrigation [31,33,68]. According to Monti et al. [61], irrigation favors growth, while rain-fed conditions and water stress cause the plant to develop a deeper root system.

4.6. Weed Management

Jerusalem artichoke shows high competitiveness against weeds. According to Schittenhelm [32], the Jerusalem artichoke yield loss due to weed competition was only 8%. The highly competitive ability of Jerusalem artichoke [14] may be due to its rapid growth [68], large size [32], and allelopathic ability [69,70]. Typically, weed management is based on herbicide application, mechanical cultivation and hand hoeing.

The herbicide linuron is effective against several broad-leaved and grass weeds [71] and can be applied pre-emergence [20,35]. Both mechanical weeding and hand hoeing are performed after crop establishment at different crop stages during the growing period [5,57,72]. Hand hoeing is first performed at the seedling stage and then again when necessary [9,19,39,66].

4.7. Genetic Material

The primary goal of Jerusalem artichoke breeding is high yield. Selecting an appropriate variety for a specific region with specific environmental and soil conditions is crucial in order to obtain high tuber and aboveground biomass yields. Table 1 presents certain genotypes of Jerusalem artichoke that are cultivated in different regions around the world.

The genotypes have different productivity values. In Spain, Curt et al. [35] noted that middle-season/late clones of Jerusalem artichoke had higher stem, leaf and tuber weights compared to early clones. In addition, early clones had higher sugar productivity compared to middle-season/late clones, and consequently, middle-season/late clones appeared more appropriate for bioethanol production [35]. In contrast, in Norway, under different environmental conditions, Slimestad et al. [8] observed that late varieties had a lower tuber yield and number of tubers per plant compared with early varieties.

The varieties differ not only in the yield and harvest time but also in the content of various components. In Denmark, Bach et al. [73] studied the varieties 'Mari', 'Rema' and 'Draga', which are early, middle-late and late varieties, respectively. 'Rema' had both higher dry matter (21.4 to 22.8 g/100 fresh weight) and inulin (11.3 to 12 g/100 g fresh weight) content compared with 'Mari' and 'Draga', independent of the harvest time (30, 38 and 46 weeks after planting) [73].

Table 1. Selected Jerusalem artichoke genotypes (e.g., clones and varieties) cultivated or evaluated in different countries.

Genotypes	Countries	References
Draga, Mari, Rema	Denmark	[73]
UKR 1/82, UKR 2/82, UKR 3/82	Serbia	[74]
Gute Gelbe	Poland	[75]
LZJ119, Nanyu No. 1	China	[76,77]
Violet de Rennes	Italy, Poland	[56,78]
Reka, Fredonia Nova	Germany	[32]
Tápió korai, Tápió sima, Ceglédi, Gyöngyvér	Hungary	[15]
Albik, Rubik, Sauliai	Lithuania	[18,79]
Sireniki-1, Skorospelka	Russian	[80,81]
Bragança	Portugal	[31]
Elverum, Gram, Hvaler, Saturn, Slaagedal, Suitestad, Tysnes	Norway	[8]
Columbia, Early White, Huertos de Moya, Salmantina, Violet de Rennes	Spain	[35]
JA5, JA89, JA125, HEL65	Thailand	[19]
Stampede	USA	[4]
Faiz Baraka	Uzbekistan	[82]

5. Main Diseases and Pests

5.1. Diseases

Jerusalem artichoke is infected by several pathogens (Table 2). Stem rot disease is caused by the fungus *Sclerotium rolfsii* Sacc., which is one of the most important pathogens causing tuber and stem rot and up to 60% loss in Jerusalem artichoke yield [64,83–85]. Growing resistant varieties is an important method of controlling *S. rolfsii* [85]. According to Junsopa et al. [85], Jerusalem artichoke varieties differ in their resistance to *S. rolfsii*, with JA98', 'HEL278' and 'HEL29' being considered resistant.

Table 2. Main diseases and pests that infest Jerusalem artichoke.

Diseases	**References**
Stem rot (*Sclerotium rolfsii*)	[64,83–85]
White mold (*Sclerotinia sclerotiorum*)	[86]
Sclerotinia blight (*Sclerotinia minor*)	[86]
Powdery mildew (*Erysiphe cichoracearum*)	[83,86]
Rust (*Puccinia helianthi*)	[83,86]
Alternaria blight (*Alternaria helianthi*)	[87]
Pseudomonas syringe pv. *tagetis*	[88,89]
Pests	
Tobacco cutworm (*Spodoptera litura*)	[90]
Banded sunflower moth (*Cochylis hospes*)	[91]

In a greenhouse experiment, Sennoi et al. [84] assessed 91 genotypes of Jerusalem artichoke for *S. rolfsii* resistance. The genotypes HEL 280, HEL 278, HEL 293 and JA 98 were resistant (29 days until permanent wilting), while JA 13, JA 49 and JA 126 were susceptible (1 day until permanent wilting).

Junsopa et al. [85] observed high disease severity in adult Jerusalem artichoke compared to seedlings. Except for resistant genotypes, soil solarization and biocontrol could be useful in the case of *S. rolfsii*. In a study conducted in Thailand, Charirak et al. [92] reported that a combination of solarization with the application of *Trichoderma harzianum* T9 and the arbuscular mycorrhizal fungus *Glomus clarum* minimizes disease incidence and improves the tuber yield, while without solarization, carboxin application with *T. harzianum* T9 was the most effective treatment.

Other diseases/pathogens infecting Jerusalem artichoke are white mold (*Sclerotinia sclerotiorum* (Lib.) de Bary (1884)), powdery mildew (*Erysiphe cichoracearum* (DC.) (1805), synonym *Golovinomyces cichoracearum* (DC.) V.P. Heluta), rust (*Puccinia helianthi* Schwein. (1822)), Alternaria blight (*Alternaria helianthi* (Hansf.) Tubaki & Nishih., (1969)) and *Pseudomonas syringe* pv. *tagetis* [83,86–89].

5.2. Pests

The Jerusalem artichoke is also prone to insects (Table 2), and infestations by the banded sunflower moth (*Cochylis hospes* (Walsingham, 1884); Lepidoptera: Tortricidae) and the tobacco cutworm (*Spodoptera litura* F.; Lepidoptera: Noctuidae) have been reported [90,91]. Several accessions of *H. tuberosus* show different resistance to *S. litura*: four accessions (TUB 07, TUB 08, TUB 15 and TUB 2729) are susceptible to infestation, while TUB 1705 is resistant [90]. In the TUB 1705 accession, the mortality of 4-day-old larvae reached 97.7% [90]. This accession can be exploited in breeding programs to induce resistance in the plant against this pest. In South Korea, the pest *Aphelenchoides fragariae* (Ritzema Bos, 1891) Christie, 1932 (Nematoda: Aphelenchoididae), a foliar nematode, infested the leaves of Jerusalem artichoke [93]. To the best of our knowledge, there are no studies on the chemical control of these pests in Jerusalem artichoke.

6. Harvest and Yield or Quality

The harvest time for Jerusalem artichokes depends on several factors, such as the genotype, cultivation purpose and environmental conditions. The growing period ranges from 110 to 240 days and depends on the cultivated genotype and region [36,74,94]. If Jerusalem artichoke is cultivated for tuber production, the harvest should be done after stem drying, while if the main product is the aerial part, harvest can occur during tuber bulking [95]. For bioethanol production, the stems should be harvested between the flower bud and dry head stages in early clones and at the flower bud stage in middle-season/late clones, since the sugar content in the stem reduces after these stages [35].

Tuber yield ranges between 1.85 and 16.7 t ha^{-1} (Table 3), while the aboveground biomass yield varies between 3.05 to 30.7 t ha^{-1} [20,31–33,36,41,96]. With regard to the effects of the harvest time on crop yield, in Spain, Matías et al. [20] observed increased aboveground biomass yield (18.7 t dw ha^{-1}), tuber yield (10.9 t dw ha^{-1}) and total sugar yield (7.9 t ha^{-1}) in the autumn harvest compared with the winter harvest. In a study conducted in Sweden, Gunnarsson et al. [11] reported that harvesting in September led to higher fresh biomass yield (62 t ha^{-1}) compared to harvesting in December, while conversely, the highest fresh tuber yield (44 t ha^{-1}) was obtained in December. In China, Gao et al. [33] observed that the harvest time affected the fresh tuber yield, with the highest yield (21.25–50.45 t ha^{-1}) being recorded after frost exposure.

Crop harvesting at an inappropriate time deteriorates the quality of the harvested product. Gunnarsson et al. [11], in Sweden, observed significantly higher inulin content in tubers harvested in September compared to those harvested in October and December. In contrast, Danilcenko et al. [79], in Lithuania, noted the highest inulin content in October and November. In Hungary, Barta and Patkai [15] observed that over-wintering of tubers in the soil and delayed harvest in April increased sucrose and reducing sugar contents, followed by a decrease in inulin and fructose/glucose contents compared to tubers harvested in December. Over-wintering could reduce the inulin chain length [97]. Tubers harvested in autumn contain inulin with a higher degree of polymerization that can be used for dietary fiber and other prebiotic effects, whereas with winter or spring harvesting after over-wintering in the soil, the tubers are at full maturity and contain low-molecular-weight inulin; thus, they are suitable for fermentation, the isolation of fructo-oligosaccharides [11,98,99] and ethanol production [18].

Table 3. Aboveground biomass and tuber yield in selected locations where Jerusalem artichoke is cultivated.

Locations	Tuber Yield (t dw ha^{-1})	Aboveground Biomass Yield (t dw ha^{-1})	References
Inner Mongolia, China	2.87–11.20 1.85–2.79	8.22–17.6 -	[33] [41]
Gansu, China	3.6–10.3	9.4–30.7	[96]
Braunschweig, Germany	8.4–12.9	3.05–5.84	[32]
Tomaszkowo, Poland	7.57–16.66	18.15-28.65	[68]
Bragança, Portugal	7.1–15	-	[31]
Guadiana River Basin, Spain	6.1–15.8	10.0–22.1	[20]
Khon Kaen, Thailand	3.24–5.09	6.25–9.77	[36]

The tubers harvested in spring after over-wintering can be used as dry products (e.g., flour and chips), as they have a high content of phenolic compounds, carbohydrates and dry matter [79]. However, they cannot be used for diabetic products, since they have a high sucrose content; therefore, tubers should be harvested in autumn [18].

7. Storage

Harvested tubers can be stored at low temperatures (0–2 °C) and high relative humidity (90–95%) for several months; nevertheless, tuber storage for long periods can cause inulin degradation, freezing, sprouting and desiccation, impairing their quality [16,100]. Modler et al. [101] reported that the optimum quality of tubers is observed at 2 °C after a 12-month storage period, while at higher temperatures (5 °C), sprouting occurs after 6 months.

Cabezas et al. [100] studied the inulin and sugar contents in tubers under different storage temperatures (−18, 4 and 18 °C). Regardless of the storage temperature, the inulin content in the tubers decreased, with the highest reduction recorded at 4 and 18 °C. In addition, the sucrose content increased between days 10 and 12, especially at 4 and 18 °C, and then decreased. By contrast, the glucose content increased at 4 and 18 °C and decreased at −18 °C [100].

Mu et al. [76] reported that tuber storage at low temperatures (−18 and 0 °C) enhances the antioxidant capacity of the tubers due to a higher degree of polymerization and inulin content. Maicaurkaew et al. [102] reported that at −18 °C, the inulin depolymerization in tubers decreases. The degradation of tuber quality during storage is affected by the storage method. Danilcenko et al. [16] examined the effects of storage methods (polyethylene net bags and bulks covered with sand or peat) on the tuber quality over time. Their results revealed that polyethylene bags lead to the highest weight and soluble solid losses.

8. Chemical Composition

8.1. Carbohydrates: Inulin

Jerusalem artichoke tubers contain several chemical compounds (Table 4). Carbohydrates are the main chemical components: monosaccharides (e.g., glucose and fructose), oligosaccharides (e.g., sucrose) and polysaccharides (e.g., inulin) [15–19]. According to Barta and Patkai [15], tubers contain 80–90% inulin, 7–14% sucrose and 3–6% reducing sugars. The reducing sugars include fructose and glucose [16]. The enzyme fructan exohydrolase causes inulin degradation in tubers over time and affects the fructo-oligosaccharide content [99]. Moreover, the transfructosylation reaction of sucrose leads to the production of fructo-oligosaccharides [103].

Inulin is the most abundant carbohydrate in the tubers and stems of the Jerusalem artichoke [16,104]. The degree of polymerization (number of units) of this compound typically ranges from 2 to 60 [103,105], while its content in tubers (Table 5) varies among different genotypes [11,19,106]. Gunnarson et al. [11] examined the inulin content in the tubers of 11 clones and found that the inulin content ranged from 79.1% to 82.9%.

Aduldecha et al. [19] reported that the inulin content in the tubers of several genotypes ranged from 61% to 85%, which was slightly affected by the irrigation level. Harvest time is also an important factor that significantly affects the inulin content of tubers [102]. Thus, tuber harvesting must be performed at the appropriate stage of maturity. In addition, the degree of polymerization of inulin significantly affects inulin's functionality and could be affected by the harvest time and weather conditions during the growing period [11,97].

According to Matías et al. [20], the degree of polymerization of inulin was greater (6.6) in an autumn harvest compared to a winter harvest (5.4). As mentioned above, Jerusalem artichoke leaves and stem also contain carbohydrates. According to Slimestad et al. [8], the stem contains greater amounts of fructo-oligosaccharides (sucrose, fructose and glucose) compared with the leaves and thus can be used as biofuel or fodder. However, the tubers have a higher total soluble sugar content compared with the aboveground parts [96].

Jirayucharoensak et al. [107] reported that the fructose, sucrose and glucose content in the powder of tubers was 7.81, 4.91 and 0.16 g/100 g of powder. In addition, the 1-kestose, nystose and 1^F-β-fructofuranosyl nystose content was 3.81, 3.90 and 3.41 g/100 g of powder. In another study, Slimestad et al. [8] observed that the most abundant fructo-oligosaccharide in the tubers is sucrose, reaching 23.6% of the total fructo-oligosaccharide content.

Other carbohydrates found in the tubers and aboveground parts of the Jerusalem artichoke are hemicellulose and cellulose [11,96]. According to Liu et al. [96], the aerial parts (stem and leaves) contain more cellulose than the tubers, while Gunnarsson et al. [11] reported that the cellulose and hemicellulose content in the aerial parts of the plant were 15.1–24.8% and 10.8–13.5%, respectively.

Table 4. Main chemical constituents in the tubers and aboveground parts of Jerusalem artichoke.

Chemical Constituents	References
Carbohydrates (monosaccharides, oligosaccharides and polysaccharides)	
Monosaccharides Glucose, fructose, arabinose and galactose	[11,15,18,19,104,107]
Oligosaccharides Sucrose, 1-kestose, nystose and 1^F-β-fructofuranosyl nystose	
Polysaccharides Inulin, hemicellulose and cellulose	
Amino acids	
Arginine, aspartic acid, histidine, glycine, isoleucine, leucine, lysine, phenylalanine, valine, methionine, cystine, threonine, threonine, serine, glutamic acid, proline, alanine, tyrosine and lysine	[82,108]
Carotenoids	
α-carotene, β-carotene, γ-carotene, lutein, lycopene and zeaxanthin	[109]
Volatile compounds	
α-Pinene, β-bisabolene, kauran-16-ol, undecanal, pentylfuran, a-copaene, sabinene, hexanal, linalool, 1-butanol, 2-methyl-1-butanol, calarene, verbenone, squalene and β-sesquiphellandrene	[6,73,110]
Other organic compounds	
Caffeic acid, 3,5-dicaffeoyquinic acid, 1,5-dicaffeoylquinic acid, 4,5-dicaffeoyquinic acid, 3,5-dicaffeoyquinic acid methyl ether, 3-O-caffeoyquinic acid, 3,5-O-dicaffeoyl, 3,4-O-dicaffeoyl, 4,5-O-dicaffeoyl, crypto-chlorogenic acid, neo-chlorogenic acid and chlorogenic acid	[111,112]
Nutrient elements	
Potassium, magnesium, zinc, calcium, sodium, copper, iron and phosphorus	[22,113]

Table 5. Inulin content and degree of polymerization in tubers at the harvest stage in selected locations where various Jerusalem artichoke varieties are cultivated.

Locations	Inulin Content (%)	Inulin Degree of Polymerization (%)	References
Guadiana River Basin, Spain	-	4.8–7.7	[20]
Alnarp, Sweden	76.0–85.0 (DW)	up to 14.0	[11]
Khon Kaen, Thailand	60.0–85.0 (DW) 55–78.3 (DW)	- -	[19] [23]
Riverside, USA	49.1–61.2 (DW)	6.0–8.0	[4]

8.2. Proteins

Tubers have high nutritional value since they contain proteins [11,113,114]. The protein content of tubers varies among Jerusalem artichoke genotypes. Gunnarson et al. [11] examined the chemical composition of 11 clones and found that the protein content of the tubers ranged from 6.6% to 8.8%. The harvest time also affected the protein content, since the highest protein content was recorded in tubers harvested in September. In another study, Radovanovic et al. [114] recorded a higher protein content (10.15–13.31%). The aboveground parts also contain proteins but to a lesser amount [11]. According to Gunnarsson et al. [11], the protein content in the aerial parts of the Jerusalem artichoke range between 1.1% and 5.8%. Rakhimov et al. [82] and Lindberg et al. [108] reported that the Jerusalem artichoke contains several amino acids such as arginine, aspartic acid, glycine, glutamic acid, leucine, serine, proline and alanine (Table 4). In addition, Rakhimov et al. [82] observed that the most abundant amino acid is glutamic acid (3.6%), followed by aspartic acid, leucine and arginine in descending order. Bogucka and

Jankowski [56] examined the content of amino acids in the tubers of three varieties and found that the most abundant amino acid is arginine (17.68–22.07 g/100 g of protein), followed by glutamic acid (7.31–9.84 g/100 g of protein), aspartic acid (7.34–8.92 g/100 g of protein) and phenylalanine (4.79–5.36 g/100 g of protein).

8.3. Nutrient Elements

Jerusalem artichoke tubers contain various nutrient elements, such as potassium, magnesium, zinc, calcium, sodium, copper, iron and phosphorus [22,113]. According to Judprasong et al. [113], the highest content in fresh tubers was recorded for potassium (339 mg/100 g fresh weight (FW)), followed by phosphorus (74 mg/100 g FW).

The aerial parts of the plant contain nitrogen, phosphorus, potassium, calcium, magnesium, sulfur and sodium [25,115]. Sawicka et al. [25] observed that the highest amount was recorded for potassium (24.14–42.52 g/kg dry weight (DW)), followed by nitrogen (22.61–31.52 g/kg DW). The nutrient element content in Jerusalem artichoke is affected by climatic conditions, harvest date, fertilization and genotype [22,25,39,115].

8.4. Other Bioactive Compounds

The aerial parts and tubers of Jerusalem artichoke contain several carotenoids such as α-carotene, β-carotene, γ-carotene, lutein, lycopene and zeaxanthin [56,109]. According to Ersahince and Kara [109], at the full flowering stage, the most abundant carotenoid in the aerial parts is lutein (120.14 mg kg^{-1} DW), followed by β-carotene, zeaxanthin, α-carotene and lycopene in descending order. Bogucka and Jankowski [56] examined the β-carotene content in the tubers of three varieties and found that it ranged from 0.82 to 0.97 mg kg^{-1} DW.

The aboveground parts and tubers of the Jerusalem artichoke also contain small amounts of essential oils [6,110]. Radulović and Đorđević [6] studied wild and cultivated populations of *H. tuberosus* and identified 192 essential oil compounds from tubers. The main constituents were β-bisabolene, α-pinene, kauran-16-ol, undecanal and pentylfuran, while β-bisabolene was the dominant constituent (22.9–30.5%). Bach et al. [73], observed that after β-bisabolene, the monoterpene α-pinene was the most abundant constituent. In addition, Helmi et al. [110] reported that the essential oil from leaves had a higher concentration of β-bisabolene compared to that from tubers.

9. Jerusalem Artichoke and Possible Risks for the Natural Ecosystem

Jerusalem artichoke spread in the natural ecosystem should be recorded [116] since it is an invasive species [117] that is attractive to several insect pollinators (e.g., *Apis melifera* and *Bombus* spp.) [116] and can affect the biodiversity in the ecosystem [2]. According to Filep et al. [1], the spread of this species into new regions is linked with its allelopathic activity against several other weed species, such as *Gallium mollugo* and *Elymus repens*. Salicylic acid, 2-OH-cinnamic acid and 4-OH-benzaldehyde are the main allelochemicals found in Jerusalem artichoke leaves and roots [1]. The management of this invasive species in non-cultivated areas should be based on herbicide application and mowing [118,119]. Janikova et al. [119] reported that the application of the herbicide clopyralid+fluroxypyr+MCPA in combination with manual and mechanical mowing provided the best control of Jerusalem artichoke.

10. Conclusions

The Jerusalem artichoke can be used in the food industry, as its tubers contain carbohydrates, proteins and nutrient elements. Inulin constitutes the most abundant carbohydrate and is important both in bioethanol production and in the food industry. The Jerusalem artichoke grows successfully in different soil types and for crop establishment, tubers are planted directly in the soil. In general, the Jerusalem artichoke is a low-input crop and is tolerant to various environmental conditions and abiotic stresses, including drought stress. However, despite its tolerance to drought, irrigation enhances plant growth and increases both the tuber and the inulin yield. In the future, more experiments should be conducted to evaluate the impact of agronomic techniques (e.g., irrigation, fertilization and weed control) on tuber quality. Jerusalem artichoke genotypes vary in their agronomic performance and the selection of high-yielding varieties is also extremely important.

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