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Review

Jerusalem Artichoke (*Helianthus tuberosus* L.): A Versatile and Sustainable Crop for Renewable Energy Production in Europe

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Abstract: Recently, biofuels have become a strategic focus to reduce vehicle emissions and increase sustainability of the transport sector. However, the sustainability of biofuels production has been questioned owing to its implications for future land footprint. In this respect, the EU Commission has very recently classified as low indirect land-use change (ILUC)–risk biofuels those obtained by crops grown on marginal lands and with low external inputs. Only few crops can reach high yields under both of these conditions across Europe. From this point of view, Jerusalem artichoke (*Helianthus tuberosus* L.) is certainly a species worthy of remark since it has all the attributes to accomplish the aims of the updated EU Renewable Energy Directive (RED II). Starting from physiological aspects, the present review examines and summarizes literature on the ecology, genetic resources, agronomic practices and sustainability of this species. The goal is to point out the recent advances of research in Jerusalem artichoke (JA) potential as alternative biofuel feedstock and to identify what is still needed to better characterize its environmental benefits and agronomic performance.

Keywords: energy crop; Jerusalem artichoke; land-use change; sustainable feedstock; topinambur

1. Introduction

Jerusalem artichoke (*Helianthus tuberosus* L.) is native of North America and it has been introduced in temperate areas where it has become a naturalized plant, within a latitudinal range from 40° N to 55° N [1,2]. Jerusalem artichoke (JA) is widely adapted to diverse and often marginal environments [3]. Its stalks and tubers have high inulin content with potential for producing ethanol to be used as biofuel. While the attention for this species was drawn mainly due to physiological aspects, breeding work and agronomical practices are still not well developed [2,4]. This species is known to be highly polymorphous (Figure 1) and, due to its high adaptability to disparate environments, agronomic practices have been poorly investigated [2,5].

JA is a multi-purpose crop used for human food consumption (directly tubers or to obtain sweeteners), pharmaceutical applications, biomass and bioenergy (bioethanol and biogas) production [2,6,7]. Additionally, similarly to other *Asteraceae* plants such as chicory and safflower, JA has potential also as forage crop [8–10]. Interestingly, due to the rising success of craft the beer industry [11], JA tubers are also used to produce a sweet and fruity-tasting beer [12].

Looking at its potential as an energy crop, JA converts solar energy into plant tissues using few inputs. Biofuels are carbon-based energy sources derived from biological material.

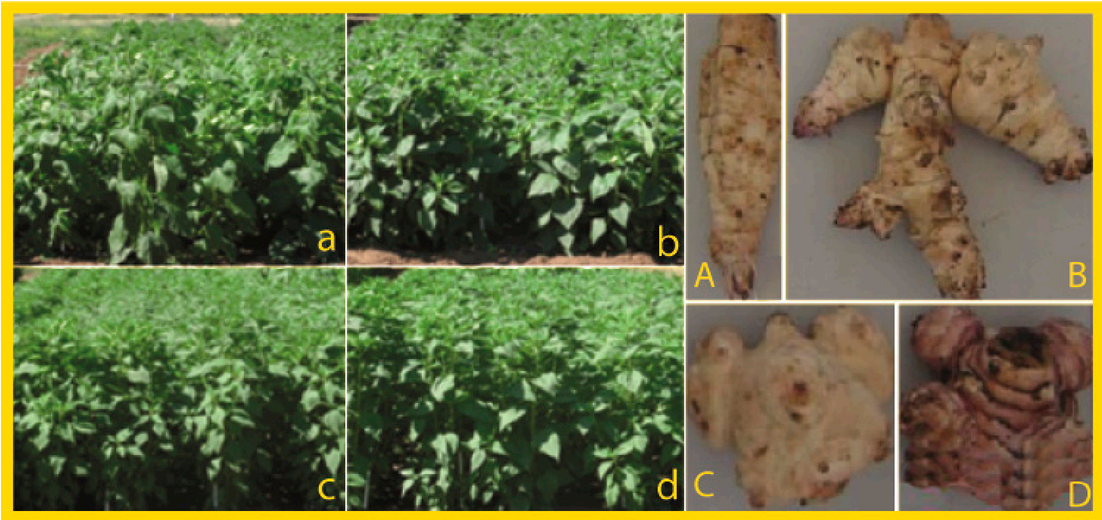

Figure 1. Plants (small letter) and tubers (capital letter) of four Jerusalem artichoke (JA) genotypes grown in Viterbo, central Italy: (**a**,**A**) clone "D19HS2"; (**b**,**B**) clone "K8HS142"; (**c**,**C**) clone "CU3B"; (**d**,**D**) cultivar "Violette de Rennes".

Particularly, organic compounds (such as inulin and cellulose) and sugars are processed to obtain ethanol, through fermentation and distillation. Considerable work has been done in the last 20 years in improving biomass conversion to fuel. However, the first-generation biofuels (bioethanol and biodiesel derived from food crops) have been produced from only few crops with different efficiency of converting solar radiation into chemical energy (biomass). Particularly, biofuel feedstock produced worldwide are mainly rapeseed, palm oil and soybeans for biodiesel and sugar cane, maize, sugar beet and sweet sorghum for bioethanol [13]. Moreover, not all the biomass is harvestable (i.e., the below ground plant biomass is usually left in the soil) so that net carbon capture is reduced and inefficiencies in feedstock processing rise further. For these reasons, plant species for next generation biofuel production systems are expected to overcome some of those limitations, especially if they have harvestable below-ground biomass (i.e., roots or tubers). Furthermore, since agricultural land-use is already intensive in most regions of the world, bioenergy crops should be environmentally sustainable to avoid additional pressures on agricultural biodiversity, soil and water resources.

Research is going in the direction of new generation biofuel energy production systems with lower impact on the environment, greater productivity and greater energy return on investment [14] or reduced land-use competition with food and feed crops [15–17]. Lignocellulosic biomass from dedicated bioenergy crops and agricultural wastes has been considered as a sustainable resource for bioenergy production, but hydrolysis, using cellulolytic enzymes, is a technique more cumbersome to accomplish and expensive than using starch- or molasses-based biomass feedstock. In this respect, among the most attractive next generation biofuel systems there are algae and few additional plant species such as the tuber-producing JA that can be also grown and harvested using the existing infrastructures and machinery used for similar crops (i.e., tuber crops).

The characteristics which make JA a worthy energy crop include: a rapid growth, a high carbohydrates content, a relevant total dry matter per unit land area [18,19], the ability to use nutrient-rich waste water [20], pathogen resistance/tolerance, ability to grow easily with minimal external production costs [18] and in marginal lands [2].

This latter aspect promises to be pivotal for the future of biofuels in Europe. As foreseen by the recast Renewable Energy Directive (RED) adopted by the European Parliament and Council (Directive 2018/2001), the EU Commission has recently adopted a delegated act setting out criteria both for (i) determining the high indirect land-use change (ILUC)-risk feedstock for which a significant indirect expansion of the production area into land with high-carbon stock is observed and (ii) certifying low

ILUC–risk biofuels, bioliquids and biomass fuels. The certification can be granted if fuels meet the following cumulative criteria: (i) compliance with the sustainability criteria set in the recast RED, which entails that feedstock can only be grown on unused land that is not rich in carbon stock; (ii) use of additional feedstock resulting from measures increasing productivity on the already used land, or from cultivating crops on areas which were previously not used for cultivation of crops (unused lands), provided that a financial barrier has been overcome, or the land was abandoned or severely degraded, or the crop has been cultivated by a small farmer; and (iii) robust evidence proving that the two previous criteria are met. Obviously, as required by the Directive, such additional feedstock should qualify for low-ILUC risk fuel production only if it is obtained in a sustainable manner. For this reason, JA is a promising candidate for biofuels production either in southern European environments, where it could easily replace high water demanding crops like sugarbeet and corn, or in European continental climates where lower inputs are required, or marginal lands should be cultivated.

2. Photosynthesis and Assimilate Allocation Strategy

The JA plant fixes carbon dioxide through the Calvin Cycle and thus possesses the metabolic pathway C3 for carbon fixation in photosynthesis. Its photochemical efficiency is higher than that of many C3 species and is comparable to that of some C4 species [2,4]. Leaf life-span of late cultivars is longer, leading to higher photochemical products and higher yields [21]. In general, a decrease of leaf photosynthesis is observed over time. While leaf temperature and photosynthesis are negatively related, leaf photosynthesis is positively affected by leaf nitrogen content as well as chlorophyll content [18].

During the crop cycle, allocation of assimilates sensibly changes between plant organs (Figure 2). At early stages of canopy growth, the vegetative tissues accumulate a high level of nutrients [22]. Conversely, during tuber growth, the rate of biomass accumulation in leaves decreases rapidly as well as in stem and branches; while in tubers, dry matter and carbon content increases until the harvest. Findings have also shown that the reallocation of dry matter coincides with a decline in the plant photosynthetic activity [23]. Leaves and stems act as a temporary sink for assimilates, which are reallocated to the clonal structures afterwards (tubers and stolons). It has been estimated that of the above ground plant parts, stems constitute the primary temporary sink for carbohydrates: they contribute nearly 80% of the carbon content of the mature tubers [22,24].

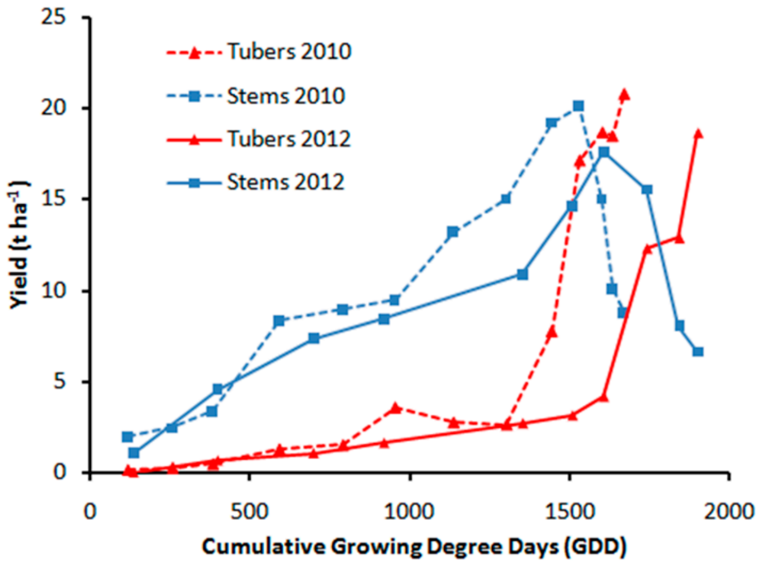

Figure 2. Changes in the yield of tubers and stems (cultivar "Violetto di Rennes") in two growing seasons in Viterbo, central Italy (unpublished data).

Assimilation activities of JA vary during developmental stages and, according to the genotypic earliness, the timing of these activities varies as well [4,25,26]. At higher latitudes, the dry matter distribution between tubers and above ground biomass is more favorable in early- than late-maturing cultivars. In late cultivars, indeed, the translocation of photosynthates from the aerial parts into tubers starts later and, since temperatures below −3 °C stop the transfers from stems to tubers, the translocation is arrested before the plant ends its cycle [4,27].

It has also been observed that environmental conditions influence the biomass allocation to different organs [28]. This highlights the crop ability to change assimilate partitioning strategy. Almost every part of the plant can store reserves, at least temporarily. Stolonization, tubers initiation and filling and aerial structures growth are all processes happening contemporarily. During the first part of the growing season, JA allocates most of photosynthates and nutrients into aboveground organs. In this phase tuber growth is slow since even exceeding assimilates are stored in stems. Shoot and stem dry weight increases progressively until the 18th week after planting to decrease successively and gradually until the 28th week. Between the 18th and 20th week after planting the plant allocation pattern shifts substantially, with the rapid declining of dry matter fixation and the reallocation of the accumulated dry matter from the aboveground parts to the tubers [23]. The second growth phase is thus characterized by tuber growth. During this phase, the rate of dry matter accumulation in tubers reaches its maximum between the 22nd and 30th week after planting.

3. Crop Growth and Yield

3.1. Biomass Distribution and Leaf Growth

The growth kinetics of plant parts indicates the plant strategy and its ability to produce optimum yield in a given environment. From two thirds to three quarters of JA aerial dry matter is represented by stems and branches, while leaves and flowers represent lower percentage. The proportion of the dry weight distribution of JA is highly dependent on many factors: cultivar, time of planting, climatic and growth conditions.

Over 50% of the total plant weight is in the stem and, as Incoll and Neales [24] described, there are two phases of stem growth. During the first five months, a linear increase in stem height and weight is observed. After this period, stem height reaches its maximum and remain unchanged, while its weight decreases. The plant maximum height and weight change depending on the environmental condition and genotype. Zubr and Pedersen [27] reported that early cultivars attain their final height to 140 cm, while in late cultivars the final height is about 280 cm. Consequently, at the end of the growing period, the amount of dry matter in the stalks of late cultivars was about twice than early cultivars. Total biomass of late maturing cultivars is thus higher than early maturing cultivars. Modeling has shown that in late cultivars the longer persistence of optimal leaf area enables a greater assimilation of dry matter [2].

Like most of plants, JA leaves represent the major site of photosynthesis. Leaf growth, leaf area and life-span are strongly correlated with the amount of light intercepted and so with the plant total biomass assimilation and growth. Leaf area index (LAI) reflects the photosynthetically active area of leaves. Meijer and Mathijssen (1996) [29] reported that under no limiting conditions, leaf expansion and canopy longevity are strongly dependent on temperature. Furthermore, leaf extension and thus LAI are more affected by water regime than leaf biomass is [18]. According to several authors, the seasonal maximum LAI, of about 4.2 in early cultivars and 6.2 in late cultivars, is reached in summer at about four months after sowing [4,24,27]. During the subsequent period of growth, the photosynthetically active area of leaves decreases. The initial development of the plant canopy is important in determining LAI. Seed tuber size, pedo-climatic conditions and cultivars are responsible for the plant growth at its beginning. As an example, the number of branches changes among cultivars: late cultivars produce more branches than earlier ones and thus cultivars have different canopy architectures, to which LAI is related.

3.2. Biological Yield and Harvest Index

Biological yield refers to the total biomass of a crop and it is relevant especially when considering an energy crop. The JA total dry matter production ranges from 6 to 9 t ha^{-1} under limiting conditions, and from 20 to 30 t ha^{-1} under favorable ones [2,4]. However, a study indicates that fifteen Chinese clones of JA cultivated in a semiarid region in the northwest China had a biological yield ranging from 25 to 35 t ha^{-1} [30].

Harvest index (HI) is commonly related to tuber yield, although for other application of commercial interest also other components may be quantified. Due to the great dry matter reallocation from stalks to tubers, the JA harvest index is relatively high (from 0.4 to 0.8). This index varies depending on cultivars, since tuber yield depends on the distribution pattern of assimilates, which change between early- and late-maturing cultivars. HI for tubers tends to increase when growing conditions are not favorable to vegetative growth and flowering. Furthermore, high planting densities have shown to increase, within certain limits, tuber yield and thus HI [2]. Since the crop requires a relatively long season for maximum productivity, growing location is critical to obtain high tuber yields. In a study conducted in Italy, Baldini et al. [19] showed a 44% tuber yield increase (from 55.5 to 80 t ha^{-1}, fresh matter) moving from latitude 40° 20′ N to 46° 03′ N. Other studies conducted across Europe, displayed a more than doubled tuber yield in locations ranging from 40° to 45° N than that achieved in locations ranging from 55° to 60° N ([2] and references therein). Despite this, projections of JA distribution as a bioenergy crop in Europe suggested a substantial decline in latitude 45° to 54° N (France and Germany) and a large increase in latitude 65° to 71° N [31].

4. Abiotic Factors Affecting Yield

The analysis of the pedo-climatic conditions is fundamental to grow JA as an agricultural crop. In some cases, the results clearly show the variations in yield-related traits, such as tuber fresh weight, tuber number and size, are affected by environmental factors more than genotypic differences among cultivars [3].

4.1. Soil Type

Thanks to its tolerance to drought and salinity, JA can be cultivated in soils not suitable for other root and tuber crops [6,32]. JA grows well also in soils with pH ranging from 4.4 to 8.6 [32]. Nevertheless, to fully express its yield potential JA requires well-drained, fertile and moist soils [1]. Heavy clayed or hydromorphic soils are not advisable for this crop, because they can make tuber harvesting cumbersome to manage. However, in these conditions JA could be cultivated as a perennial crop, targeting to the high stem storage and early tuberization. Even though JA has shown to be tolerant to waterlogging condition [33], excessive soil moisture content has a different negative effect: it reduces plant emergence, increases stalk development, decreases tuber growth and enhances plant vulnerability to pathogens. Overall, fructan yield, tuber size and shape are affected by soil type. While light-sandy loam soils yield large tubers, heavy-loam soils are reported to produce small tubers [32]. Heavy soils may have an advantage on lighter ones under conditions of low rainfall and no irrigation. In these cases, tuber yields may be higher thanks to the better water retention properties of clayed soils [2].

4.2. Drought

JA is considered a good crop for areas with 500 mm of rainfall per year or higher [31]. Contrasting results on the relation between water availability and sugar yield were found in literature. In southern Italy, some authors suggest water supply negatively affects sugar yield, due to the lower accumulation capacity in the storage organs [34]. Conversely, in northern Italy the higher tuber fructans yield was related to the larger source (tops) favored by the exceptional amount of natural water in the early growth period [18]. Similarly, Puangbut et al. [35], in Thailand, found that a mild water stress favors inulin accumulation in tubers, whereas severe drought reduces it.

Despite JA can well adapt to dry conditions, the plant has low water use efficiency (WUE) due to its poor stomatal regulation. In a recent study, Ruf et al. [33] showed significantly better WUEs in excess soil moisture conditions than in non-excess treatment, for JA plants grown in pots. However, studies conducted in Italy have demonstrated the higher adaptability of this crop to arid environments as compared to other crops such as chicory, kenaf and sweet sorghum [19,21]. Results by Conde et al. [36] have shown that the crop exposure to continuous water stress increases its WUE. Furthermore, the values of WUE recorded under Mediterranean climatic conditions are higher than those recorded in a continental Mediterranean climate, suggesting that WUE increases as the site climatic conditions become more stressful [21,36]. Limited water availability affects more leaves morphology than plant photosynthetic capacity [18]. LAI decreases significantly in stress conditions and aboveground biomass is strongly reduced. However, plant capacity to accumulate photosynthates is not affected by water regime [18,21] but it depends more on stomatal conductance, leaf temperature and leaf nitrogen content [18].

4.3. Salinity

Even though JA was reported as a salt-stable plant, often used in the re-cultivation of saline lands [6], its shoot and tuber yield were recently found to be reduced (−67% and −47%, respectively) by high salinity water (electrical conductivity, ECw = 12 dS m^{-1}) of irrigation water [37]. However, the authors concluded that JA cultivar "Stampede" adapted well to moderate salinity of blended irrigation (ECw = 6.6 dS m^{-1}) since tuber yield decreased only by 11%.

4.4. Radiation

The interception and absorption of solar radiation define the crop capacity to accumulate biomass [21,29]. The crop radiation use efficiency (RUE) is comparable to that reported for others C3 species and has values of 2.7–2.9 g·MJ^{-1} [2,29]. Monti et al. [18] observed that RUE calculated considering the total dry matter is affected by water availability more than RUE calculated for fructan yield.

4.5. Temperature

As for growing temperature, most JA cultivars require a growing season of at least 125 frost-free days [2]. Thermal sum (degree-days) is considered a reliable regression parameter of the crop yield [38]. As this sum increases, tuber yield and sugar content also increase [26]. In general, to obtain optimum yield, growing temperatures in the range of 6–26 °C are required [2]. The optimal thermal sum varies among cultivars and depends on their harvest time. In general, a thermal sum above 3300 °C·d gives the best results in terms of fructan and tuber yield [18,26].

The plant has moderate tolerance to frost. During its early growth the crop tolerates temperature as low as −6 °C, although low temperatures can induce foliar chlorosis. Premature heavy frost in autumn can severely affect the crop, so that late cultivars are often killed. Frost in this season may retard or prevent tuber bulking [4]. Air temperatures of −0.3 °C or lower occurring during the tuber filling are detrimental for tuber yield, since at these temperatures the reallocation of stem reserves to the tubers stops [2,4]. Murai and Yoshida [39] found that a mechanism of cold acclimation of JA tubers exists. Tuber tissues increase their tolerance to frost from −2.8 °C to −8.4 °C, from autumn to winter. Additionally, frost may result in improved tuber flavor, because of the conversion of inulin to fructose [6]. Nevertheless, in dry and cool conditions tubers can show frost sensitivity, since they are susceptible to dehydration at the soil surface [1].

4.6. Photoperiod

Cultivars have different responses to photoperiod [40,41]. JA is considered a short-day plant since most genotypes need long days to complete the vegetative phase and short days for the reproductive initiation [2]. The critical day length of 13–13.5 hours is the photoperiod that must not be exceeded both for flower and tuber induction. Day length sensibly varies with latitude, so that many genotypes do not flower at all in particular geographical conditions. This was verified for late-flowering accessions grown in Norway and clones from northern USA and Canada tested in southern France [41,42].

Tuber initiation is also often induced by short day length. However, treating plants with a short photoperiod results in reduced stem length, stem dry matter and leaf growth, while it favors stolon and tuber growth, increases tuber number and induces senescence. Conversely, long photoperiods promote leaf and stem growth, but stolon and tuber induction is delayed [4,40]. Findings have shown that tuberization occurs under long day length even in photoperiodic sensitive cultivars, nevertheless tubers quality and size are negatively affected [4]. JA tuberization can be induced also by cool night temperatures which seem to be more effective than a short photoperiod [4].

4.7. Wind

It was found that wind combined with high evapotranspiration rates occurring during tuberization affect tuber yield. Moreover, JA plants can be as high as 3 m, thus storm events and high wind speeds may result in damages and lodging [2].

5. Biotic Factors Affecting Yield

In its native environment, several organisms (microorganisms, insects and mammals) interact with JA [1,2,43]. Six different families of bee species have been reported as pollinators of JA, including bumblebees and honeybees which are predominant. Other insects such as wasps, flies, beetles and butterfly seem to have a minor role in pollination. Regardless of pollinators, insect pollination in JA has higher importance in breeding programs than in cultivation [2].

Many phytophagous and microorganisms have been recorded on JA, but very few of them can severely damage the crop. In general, the aerial part of the plant is less affected by diseases, while tubers, during late growth and storage, are more susceptible [4]. The most harmful pathogens for JA are sclerotinia wilt/rot caused by *Sclerotinia sclerotiorum* and southern wilt/blight/collar rot caused by *Sclerotinia rolfsii* as they can totally destroy the plants. The first one is favored by excessive N fertilisation, low soil pH, or hydromorphic soils, while the second one is promoted by moisture combined with high temperatures [4]. Also rust caused by *Puccinia helianthi* and powdery mildew caused by *Erisyphe chicoracearum* are common JA diseases, although their effect is not limiting for the crop [4,43]. Leaf spot caused by *Alternaria helianthi* is an emerging disease of JA in tropical regions. The disease appears as small yellow spots on leaves and then causes severe leaf damage and defoliation of both mature and young leaves [44]. Similar symptoms were found for brown spot caused by *Bipolaris zeae* in China [45]. The importance of each disease depends on the growing conditions and the cultivation site [2]. Tuber diseases may occur also during storage, especially when tubers are damaged during harvesting operation. *Botrytis cinerea*, *Rhizopus nigricans*, *Fusarium* and *Pennicillum* spp. are pathogens affecting tubers during storage. However, freezing treatments effectively control these diseases [32].

Concerning insects, damage by aphis and stem maggot are often reported in JA, but as it is known for other insects their impact is largely negligible [4,43]. *Pseudomonas syringae* pv.*tagetis* can cause apical chlorosis. Spreading and gravity of this bacterium can be controlled using certified or disease-free seed tubers [4,43].

Tobacco mosaic virus and the following nematodes have been found in JA [46]: *Caconema radicicola*, *Ditylenchus dipsaci* (stem nematode), *Aphelenchoides ritzemabosi* (leaf nematode), *Heterodera marioni*, *Het. schachtii* and *Meloidogyne* sp. (root-knot nematode).

Finally, mammalian herbivores (deer, rabbits etc.) and wild boar can cause some yield losses owing to the suitability of both the aerial part and tubers as a good source for animal feeding [1,4,47].

6. Genetic Resources

Valuable biological and biochemical properties of JA are at the basis of its versatile use for food and industry applications, founding the need for genetic improvement of the crop [2]. The main focus of JA breeding is at all times on tuber yield and inulin content for food and feed, and more recently moved also on to biomass for biofuel production and biochemical properties for food supplements [48,49]. Due to traditionally marginal use of JA, a rather poor advancement in breeding was obtained so far with respect to other cultivated species, owing also to discontinuous investments dependent on each country's industry demand [2,48]. The revival of interest for JA in the 1970s and 1980s, attributable to the energy crisis and lack of food, gave hope that more coordinated and intense actions could be made to develop novel cultivars that meet the emerging needs [2,50–52]. Significant expansion of cultivation areas under JA crop was recorded ever since, particularly in the last decade and Asian countries [48]. Considering the current climate changes, need for finding new sustainable sources of energy and decrease in acreage dedicated to food production [49,53], investments in breeding for biomass of fast growing JA seem vastly justified [2,48].

To obtain significant genetic gains in any breeding program, it is essential to have effective means of creating new genetic variability. In the case of JA, there are several biological and cytological characteristics limiting the possibility to increase genetic diversity in short periods. JA is one of the hexaploid species ($2n = 6 \times = 102$) of the *Helianthus* genus with a large genome (14,200 Mbp [54]) implying a complex genetic structure. Meiosis is often irregular, giving origin to gametes with variable chromosome number, which cause severely decreased pollen viability and hybridization rate ([55,56] and references therein). Moreover, by being an allogamous species with high self-incompatibility [48], seed dormancy difficult to brake [56] and a reluctance to flower in the long-day photoperiods [2], the use of sexual means to generate new variability is highly limited, despite being necessary. As a consequence, high genetic similarity is observed among numerous cultivars [30,48,57,58]. JA breeding programs were largely based on the intra-specific hybridization associated with low seed set, resulting in moderate success in creation of new diversity. The inter-specific hybridization of JA with other *Helianthus* species should be preferred instead [48,59]. Strategy of using related species to introgress useful gene variants is commonly used also in other polyploids e.g., wheat [60,61], canola [62] or cotton [63]. In the case of breeding for traits associated with biofuel production (e.g., top and tuber yield, carbohydrate content), both inter- and intra-specific breeding were used, resulting in various superior cultivars. The most significant dedicated programs were established in Canada, Germany, Hungary, France, Sweden and the Netherlands [2].

Germplasm and Diversity

There is a vast number of JA accessions held in world germplasm repositories, totaling to more than 1100 by 2006 (reviewed in [2]) and increasing, as new collections are being gathered (e.g., [30,64]). There is, however, an urgent need for correct clone identification and classification in genetically similar clusters, to enhance conservation and facilitate breeders in choosing cross-compatible parental clones with high probability of giving superior progenies [2]. While many clones have been thoroughly phenotyped for agronomic traits of interest, information on their genetic variability is rarely reported.

Much of research efforts are employed in the evaluation of agronomic traits, revealing that considerable variability is available within the conserved germplasm for any breeding program [2,48]. Targeted studies of genetic diversity for traits strictly related to biofuel productions are not as many [52,53,65,66]. Nonetheless, many of these traits (e.g., top and tuber yield, flowering time, biomass, harvest index, tuber number/plant) are commonly included in more comprehensive analyses under normal [30,41,67,68] and water stressed conditions [69–71]. Inulin and sugar content in tubers and stalks are largely evaluated [50,68,72,73], as well as the tuber, leaf and plant morphology [30,41,51,57,74].

Screening for disease resistance is the most difficult to carry out because of the strong genotype × environment × management interaction in each year. There is a general lack of resistant germplasm for all of important JA diseases [2]. Only a few genotyping surveys are reported so far, two for the Southern stem rot caused by *Sclerotium rolfsii* [75,76] and one for each ring spot viruses, powdery mildew caused by *Oidium neolycopersici* [41] and leaf spot caused by *Alternaria* species [44].

Characterization of genetic diversity was mainly based on the use of molecular markers, including Random amplified polymorphism DNA (RAPD) [58,77], inter simple sequence repeats (ISSR) [77,78], sequence-related amplified polymorphism (SRAP) [77], amplified fragment length polymorphism (AFLP) [79], simple sequence repeat (SSR) [80] and expressed sequence tag (EST)-SSR [81–83]. Limited amount of allelic variability was found in cultivated lines, as well as most of the detected variation could be associated with country of origin [58,79]. The accessions from the USA often showed to have the highest diversity of all [58,75,79]. Substantial genetic variation is expected to be uncovered in future, considering high estimates of population mutation rate and pairwise nucleotide diversity (reviewed in [54]). This is confirmed by recent analysis of the first genomic, transcriptomic and proteomic datasets generated for JA [80,82,84,85]. For an underutilized and genetically poorly described crop such as JA, sequence data produced by the "omics" technologies will promote gene and functional polymorphism discovery, phylogenetic studies, and will speed-up marker-assisted breeding.

7. Agronomic Strategies

JA is a short-day perennial plant cultivated as a warm-season crop with an annual cycle. Even though it can be grown in poor soils with minimum cultivation inputs, the rational use of agronomic practices enhances the crop productivity (Table 1).

7.1. Planting

Planting is done by using seed tubers, as the use of seeds tends to lower the yield [86]. Seed tubers should be disease-free small tubers, or pieces of tubers, and should weigh between 40 and 60 g having at least two or three eye buds [32]. Seed tubers are normally planted in rows, on the level, in small hills, or in ridges, to a depth of 5–15 cm, and are earthed up in the same manner as potatoes when the plants are about 0.3 m tall. Planting distance recommended for silage are 0.5 m between rows and 0.3 m between plants, while tuber yield is favored by low distances within rows (0.3 m) and 1 m row-spacing distance [87].

7.1.1. Planting Date

Planting date and the choice of cultivars are practices which can increase tuber and biomass yield. Furthermore, planting date affects inulin content and yield [88]. Due to the high tuber frost resistance, planting may be undertaken in autumn or early spring. An early planting date ensures a better crop establishment and growth, while delayed planting can sensibly reduce tuber yield by up 50% [2,4]. The planting date depends mostly on the region of cultivation and the climatic conditions. In Northern America planting typically occurs from February to March, while in the southern hemisphere planting occurs in September–October.

Table 1. Tuber yield under a range of agronomic practices across Europe.

Location	Planting Date	Plant Density (plants m^{-2})	Weeding	Fertilization (kg ha^{-1})	Irrigation	Tuber Yield (t ha^{-1})	Reference
Spain (38°51′ N)	Late March	3.8	Chemical	NPK: 0–0–0	Irrigated: 100% ETM	7.1–10.7 DM	[89]
	Late March	3.8	Chemical	NPK: 54–108–162	Irrigated: 100% ETM	8.2–11.7 DM	
	Late March	3.8	Chemical	NPK: 108–216–324	Irrigated: 100% ETM	7.7–13.3 DM	
Portugal (39°55′ N)	April	10.0	n.i.	NPK: 0–0–0	Rainfed	40.0 FM	[90]
Italy (40°20′ N)	Late March-Early April	5.7	Mechanical	NPK: 150–120–0	Irrigated: 100% ETM	80 FM	[19]
Portugal (41°48′ N)	Mid-March	2.0, 3.0, 4.0	Chemical	NPK: 100–20–40	Irrigated: 460 mm	14.9, 12.9, 10.6 DM 29.2, 25.1, 23.9 FM	[86]
	Mid-March	2.0 and 4.0	Mechanical	NPK: 50–15–30	Rainfed	7.4 and 7.1 DM 24.4 and 24.1 FM	
Italy (42°42′ N)	Late March	4.0, 6.0, 8.0	Mechanical	NPK: 120–100–80	Rainfed-Irrigated *	11.7, 15.1, 21.6 DM	[91]
	Late April	8.0, 10.0	Mechanical	NPK: 120–100–80	Rainfed-Irrigated *	16.4, 17.8 DM	
Italy (44°30′ N)	Mid-April	7.0	Mechanical	NPK: 100–100–0	Rainfed	61 FM	[19]
Italy (45°2′ N)	Mid-March	3.6	Mechanical	NPK: 150–100–100	Irrigated: 100% ETM	8–17 DM	[50]
Germany (52°17′ N)	Early to mid-April	4.0	Mechanical	NPK: 0–70–140 + 21MgO	Irrigated	8.4–10.9 DM	[92]
	Early to mid-April	4.0	Mechanical	NPK: 60–70–140 + 21MgO	Irrigated	10.0–12.6 DM	
	Early to mid-April	4.0	Mechanical	NPK: 120–70–140 + 21MgO	Irrigated	10.6–12.9 DM	
Sweden (55°38′ N)	Mid-May	3.3	n.i.	Compost	n.i.	30–80 FM	[93]

* Rainfed until the beginning of tuber formation and then irrigated; FM: fresh matter; DM: dry matter; n.i.: no information provided.

7.1.2. Planting Density

Planting density varies depending on cultivar and climatic conditions. However, there is no clear indication about the best planting density to be adopted for JA. In literature, plant density varies from 2 to 10 plants m^{-2} (Table 1).

Klug-Andersen [38] observed that increasing plant density from 2 to 8 plants m^{-2}, the total number of tubers and the total yield sensibly increased, while the weight of class I tubers was reduced. Swanton et al. [1] indicate as optimal planting density 3 plants m^{-2}. In Mediterranean climatic conditions, Rodrigues et al. [86] observe that low planting densities (2 plant m^{-2}) combined with nitrogen supply are the most effective for increasing the tuber final yield and crop performances. Conversely, Rossini et al. [91], testing four clones and four planting densities (4, 6, 8 and 10 plant m^{-2}) in central Italy, showed that tuber and stalk yield significantly increased up to 8 plants m^{-2}. Pimsaen et al. [3] reported that 4 plant m^{-2} is a suboptimal planting density in tropical areas, but by increasing the planting density the risk of plant lodging and tuber rot might also increase. Very high planting densities reduce and can even suppress tuber growth and initiation. In fact, these conditions sensibly decrease stems growth and size [4], favor diseases and lodging [86], and reduce the time to reach the plant maximum growth rate [1].

7.2. Weeding

JA is a good competitor so that it can become a very competitive weed itself [4,32]. As for other fast-growing species, weed control is necessary only during the crop establishment, until canopy closure [1,92,94]. Both chemical and mechanical (hearting-up, hoeing, etc.) weeding can be applied. It is found that most herbicides tend to decrease tuber yields, while Wall et al. [95] observe a good tolerance of "Columbia" JA to selective preplant incorporated herbicides except for metribuzin used as both preplant and post-emergence herbicide.

Once established, the crop is difficult to eliminate from the soil as tubers or parts of tubers are frequently left in the ground, overwintering very well in the soil [1]. As a result, volunteer JA can be a serious weed problem for the succeeding crop. Several herbicides have been tested for JA control. As early post-emergence treatment Ally (metsulfuron methyl) is found to be the most effective, while as late post-emergence treatments Banvel (dicamba), 2,4-dichlorophenoxyacetic acid (2,4-D), 2-methyl-4-chlorophenoxyacetic acid (MCPA) and blends of Banvel with MCPA or 2,4-D give good results, more than 85% of control [87]. Rotation to a forage crop that has rapid regrowth after cutting can also help to repress volunteer JA. Species requiring multiple cuttings during summer are of interest because they prevent the reallocation of assimilates, and thus tuber formation [2].

7.3. Growth Regulators

Herbicides have been used in JA also as growth regulators. Kosaric et al. [32] report that herbicides applied to the maturing plants can have a positive effect on tuber yield because of the effect of delaying the vegetative growth during the tuber filling. Early treatment with MCPA or 2-methyl-4-chlorophenoxyacetic acid stops earlier stems growth. Similarly, treatment with the herbicide triapenthenol seems to limit the stem growth [4].

It is known that growth inhibitors like triazoles decrease the stem lengths while increase the tuber yield and sugar content. Gibberellins applied to JA favor stem growth while inhibit tuberization and prevent filling of already formed tubers. Conversely, abscisic acid or antiauxin and anti-giberellic growth regulators stop stem elongation, accelerate tuberization and increase sugar yield [4].

7.4. Fertilization

It has been shown that JA benefits from fertilization. Particularly the crop response is highly influenced by nitrogen (N) supply. Gao et al. [28] suggest that 50–75 kg ha^{-1} of N are beneficial for plant aboveground biomass, while just 25 kg ha^{-1} of N for tuber yield in northern China. Rodrigues et al. [86] in Spain found 100 kg ha^{-1} of N significantly increases tuber yield when seed tubers are used as propagation method.

Potassium (K) and phosphorus (P) export is high, although yield responses to these elements are often low. Tubers export 51%–57% of N, 58%–81% of P and 36%–48% of K. Furthermore, JA has high calcium and magnesium demand [4].

7.5. Irrigation

Soil moisture is an important factor affecting JA yield, although in general the crop is defined as highly tolerant to drought and salinity. Several authors observe that drought stress during the early vegetative growth poorly affects the final yield, while the last growth stage is the most critical [18,36]. Denoroy [4] describes three drought sensitive stages for JA: emergence, flowering and late tuber growth. Drought stress during emergence, however, is less damaging for final tuber yield than during the other two stages.

JA shows a certain acclimation to limited water supply. It is found that when subjected to gradual drought stress the crop exhibits high HI, high WUE and yield is reduced by only 20% [36]. In these conditions, roots become longer and deeper to avoid or reduce the effect of drought [28]. Overall, drought stress reduces the plant growth in terms of height, LAI, leaf life-span, tuber weight, number and size [4,18].

Monti et al. [18] showed that favorable water conditions delay the tuber initiation, while they never affect the fructan chains; hence they do not consider irrigation worthwhile in northern Italy. On the other hand, Rodrigues et al. [86] pointed out that in Mediterranean climate conditions JA final yield could be severely reduced by the absence of water supply. In southern Italy, a 50% reduction of the water supply decreases tuber yield by only 17% [96] while, in Germany, Schittenhelm [92] observes that shallow rooting of JA makes it more sensitive than sugarbeet and chicory to a moderate drought stress. Similar results, indicating JA as a non-drought-resistant crop, are also shown in a tropical area [71].

Due to these considerations, a watering regime restoring the crop evapotranspiration from 75% to 100% is not worthwhile for JA grown in temperate areas, while it seems to be more beneficial for a watering schedule to be modified according to the crop water requirements, critical growing stages and local climatic conditions.

Depending on the local conditions (i.e., climate, soil type etc.) irrigation may yield additional economic value or not. It is known that supplemental irrigation is not always favorable for JA, especially when it is cultivated for sugar production [18,97]. Conversely, irrigation can be beneficial in arid and semi-arid areas, where high production costs for the additional watering are justified by significant yield increases. The irrigation method used is dependent on several factors including the portion of the plant to be harvested, the costs and personal preferences.

7.6. Harvesting

Harvesting time is usually related to maturity timelines of cultivars. Since this crop can be grown either for tuber production or aerial plant parts, the harvesting methods and time change accordingly. Harvest time depends not only on yield but also on inulin content and sugar ratio [97,98]. The soluble carbohydrates content is high at harvest time in all early, mid-early and late varieties. Despite the fact that inulin content and polymerization is genetically determined, it tends to decrease with tuber maturity [26,68].

Concerning aboveground plant parts, the optimum time of harvest is at the beginning of tuber bulking [2]. The tops are cut near the soil line and then dried on the ground in the sun. When top moisture content is sufficiently decreased, they are collected and compressed in bales.

For tuber yield, instead, the harvest is undertaken when plant stems are completely dried. It was observed that depending on the harvest date sugar content, concentration and composition sensibly vary. In temperate climates authors report that fructose concentration and composition declines by extending the harvest dates, while the longer period of growth produces maximum yields of both tubers and total sugar [97,99]. In tropical climates, late-harvested tubers showed the optimum maturity regarding tuber and sugar yield. However, the fructose–glucose ratio increased, and inulin composition changed with decreasing fractions characterized by a high degree of polymerization (<10) which are the most valuable from an industrial stand point [98]. In general, it is preferable to harvest the crop before the soil freezes or become excessively wet, since the final product can be damaged or negatively affected. The calorific values of stems and leaves were higher than those of tubers and roots when JA was harvested before freezing, while the opposite trend was obtained for harvest done after freezing [100]. Decreased polymerization, however, results in the production of high-glucose syrups instead of high-fructose syrups [99].

Tubers are commonly harvested with potato harvesters adjusted to reduced sieving web width, because of the smaller tuber size. The use of the simple harvester is very labor intensive since the tubers, lifted out of the soil, are picked up by hand. Once harvested, tubers should be moved as quickly as possible in storage places protected from direct sunlight and high temperatures [2]. Handling of tubers should be done carefully, avoiding rupture of the skin.

7.7. Other Factors

Other agronomic practices can affect JA yield, such as the suppression of organs (i.e., buds, apices, flowers, leaves and roots) and mowing.

Mowing of plant top has not been shown to be advantageous for the crop at any time. In general, the top removal results in delayed harvest and reduced tuber yield [87,101]. Results by Acar et al. [101] show that mowing before flowering gives comparable results with not mowing, while top removal during flowering sensibly reduces tuber yield. Youngen [87] obtains acceptable tuber yield from early cutting, whilst late top-removing occurring after flowering gives higher yields, comparable with that of the uncut plants.

The suppression of sexual reproductive organs, such as floral bud removal, stimulate carbohydrates allocation on asexual organs and thus growth of tubers. Westley [102] observes that JA plants in which floral buds were removed produce more tubers with larger size. Very recently, Gao et al. [103] found that tuber yield increases by removal of the lower one third or one quarter of the leaves, whereas it decreases upon removing an even number or the flank half of the leaves from the plant. Finally, also root-cutting is found to be a feasible method to improve JA tuber yield and calorific value [104].

8. Sustainability of JA as Feedstock for Biofuel Production

In the last twenty years, due to the need to find alternatives to fossil fuels, renewable sources have been considered and consequently, the interest in plant biomass has increased. The organic material produced by a crop can be burnt to produce electricity from the heat or can be transformed and converted into liquid fuels (e.g., ethanol). To date, the most common crops used for ethanol production are corn, sugarcane, sweet sorghum and sugar beet. However, these species depend on fertile farmland and usually need remarkable levels of external inputs (i.e., water, pesticides, fertilizers) to achieve high yields.

Biomass resources should have an ecological perspective regarding the need for water, fertilizers, and other external inputs for their production. Besides the environmental impact, another problem to be faced is the competition for land between food and fuel uses. Concerns related to competition for land include food security and social issues due to the increasing price of many agricultural commodities [13,17,105]. When demand for food and energy rises at the same time, pressure on land conversion rapidly increases, leading to further climate change which, in turn, may affect productivity and availability of land [106], thus originating the "trilemma" described by Tilman et al. [107]. In some countries, alternative crops such as JA are being used as a source for biofuel production. This crop has high potential as an energy crop, mainly because its ability to grow under different climatic conditions with low water/chemicals input is expected to provide good economies and environmental benefits in the long term. Moreover, JA has the advantage that all plant parts can be utilized for biomass production. Furthermore, a recent study reviewed JA as a valuable feedstock to produce different bio-based products (i.e., ethanol, biodiesel, 2,3-butanediol, lactic acid, etc.) using the advances in biorefinery technology [108].

8.1. JA Ethanol Potential in Comparison with Other Energy Crops

Several herbaceous energy crops are widely cultivated as a source of bioethanol. The most important are represented by plants characterized by C4 metabolism: sugarcane, maize and sweet sorghum. Although JA has not the same advantages of a C4 plant, in the last few years it has gained growing interest owing to its high adaptability to several pedo-climatic conditions and its high productivity potential. As well as other energy crops, JA has been evaluated for ethanol production in several countries. For this purpose, both tops and tubers can be used, and depending on the plant part the ethanol production changes. In the same way this happens also for maize from which both ears and stovers can be used.

The United States and Brazil are the world's largest producers of bioethanol fuel (61×10^9 and 30×10^9 L, respectively) accounting for about 84% of global 2018 bioethanol production [109]. Coarse grains and sugarcane are the dominant ethanol feedstock. Ethanol production is expected to use 15% and 18% of global maize and sugarcane production, respectively in 2027 [110]. United States as Europe use mainly starch from maize and wheat for bioethanol production, while Brazil utilizes sugarcane. Overall, sugarcane has an ethanol yield higher than corn and other crops such as JA. Nevertheless, sugarcane is ideal in tropical and subtropical climates but not in temperate climates [111]. Corn and JA are temperate crops and their ethanol production is susceptible to change depending on the cultivation and climatic conditions. JA ethanol production ranges from a minimum of 1500 liters ha^{-1} to a maximum of 11,000 liters ha^{-1} [2], while sugarcane from 3900 to 8764 liters ha^{-1} [111–113] and corn from a minimum of 2000 to 6698 liters ha^{-1} [112,113]. Comparing the available data, a large ethanol yield variability can be observed both within each crop and between crops (Table 2). This is due to the wide diffusion of these crops across countries and continents. Even though all these crops are valuable resources for biofuel conversion, corn ethanol production costs are overall higher than other crops since corn is a high demanding crop [113]. Due to these considerations, JA, by reaching maximum values of ethanol production per hectare, which double that of corn, and being a low-input crop, exhibits its potential as a worthy alternative energy crop in temperate climates.

8.2. Life Cycle Assessment of the Impact of JA Cultivation

Although life cycle assessment (LCA) provides a reliable tool to quantify the potential benefits of biofuels in reducing reliance on petroleum and greenhouse gas (GHG) emission, its use to predict the performance of emerging biofuel crops, such as JA, highlights several issues due to the lack of data.

Table 2. Ethanol yield from different crops and feedstocks.

Crop	Feedstock	Ethanol Yield (L ha^{-1})	References
Jerusalem artichoke	Tubers	1500–11,000	[2] and references therein
	Tops	2835–11,230	[2] and references therein; [65]
Sugarcane	Whole crop	2800–8764	[111–115]
Corn	Grains	2000–6698	[112–114,116]
	Stovers	1258–1767	[117]
Sugar-beet	Roots	5000–6000	[114,118,119]
Sweet sorghum	Juice	532–7619	[116,118,120–123]
	Grains	2370	[120]
	Bagasse	5333–10,365	[120,123]

Information are limited especially when attempting to calculate GHG savings under different JA agronomic options (i.e., with different cultivars, plant densities, irrigation and fertilization strategies and interactions among these factors).

The use of LCA to evaluate the environmental impacts and cost of biofuels have been widely exploited. However, the biofuels considered have been mostly cereal and sugarcane ethanol, biodiesel from residual oils, and from palm, sunflower, soybeans and rapeseed oils [124–126].

Plöchl et al. [127] evaluate the cumulated energy demand necessary for the cultivation of different crops at different fertilization levels as well as the GHG emissions deriving from the production process. Their findings suggest that in northern climates JA can be less productive and less suitable than other crops for biogas production. Although the authors stress the crop high energy demand and the high values of GHG emissions under high-fertilizer input conditions (150 kg ha^{-1} of N), their results confirm at the same time the crop low-input requirements, since fresh and dry matter yield from no fertilization treatment differed just 1.4 t ha^{-1} and 0.4 t ha^{-1}, respectively as compared to high-fertilizer input conditions. Moreover, results on a hectare basis showed the great potential of JA under low fertilizer input treatment, which had the lowest values of cumulated energy demand and GHG emissions. Additionally, in a recent study, Paixão et al. [90] found that, using 100 kg ha^{-1} of N, the land requirements for JA cultivation in Portugal could be reduced by about 50% as compared with no fertilization condition, without much influence on carbon footprint due to N_2O emissions. The same authors, comparing the overall energy consumption and CO_2eq emissions from the JA tuber ethanol process with those from sugarcane/sugar beet and gasoline refinery, interestingly highlighted JA as a promising sustainable alternative feedstock for ethanol fuel gasoline blends. Due to these considerations, the crop has high potential as an energy crop in Europe especially under agronomically well-managed conditions. Finally, studies conducted in central Italy have shown the effectiveness of JA cultivation as biofuel feedstock in reducing GHG emissions as compared to fossil fuel (data unpublished).

9. Conclusions and Future Perspectives

The new Renewable Energy Directive defines an EU-wide renewable energy binding target of at least 32% by 2030, to be achieved collectively by Member States. The Directive limits the production of biofuels from food or feed crops which are identified as having high ILUC-risk, while it promotes feedstocks obtained from crops grown on unused land and with low external inputs (low ILUC-risk feedstocks). Due to its physiological, ecological and agronomic attributes, JA has a great opportunity to be easily certified as low ILUC-risk feedstock across Europe.

This paper provides an overview of the research carried out on JA in the last thirty years, with emphasis on its use as sustainable energy crop. The literature review enabled us to point out what is well known (i.e., crop physiology and ecology) and what will need to be deepened (i.e., agronomic strategies, genetic resources and sustainability). Specifically, in the future, more experiments and multi-year field evaluations should focus on the following topics:

1. yield performance on abandoned or severely degraded lands of Europe using a range of external inputs (e.g., zero, low, medium, high) and a combination of agronomic practices (i.e., planting date and density, cultivar selection, etc.);
2. LCA of JA cultivation using information coming from the above-mentioned field trials;
3. techno-economic assessment of biofuel pathways based on JA in comparison to other low ILUC options;
4. identification and classification of suitable germplasm to enhance breeding efficiency for the traits of interest (i.e., biomass and sugar yield, WUE, RUE, etc.).

In the prospect of being cultivated as a low ILUC-risk crop, the traits of interest could also be those which allow this species to be grown as a perennial (i.e., high stem storage and early tuberization). The recent advances in biorefinery techniques to obtain various bio-based products from JA (including biodiesel) is another aspect worth mentioning here for a better exploitation of this multi-purpose crop. This additional information would greatly help JA to be no longer the underutilized resource as it was until now and would contribute to the sustainable development of Europe defined in the new Renewable Energy Directive.

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