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REVIEW

Grass pea (*Lathyrus sativus* L.): orphan crop, nutraceutical or just plain food?

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Abstract

Main conclusion **Although grass pea is an environmentally successful robust legume with major traits of interest for food and nutrition security, the genetic potential of this orphan crop has long been neglected.**

Grass pea (*Lathyrus sativus* L.) is a Neolithic plant that has survived millennia of cultivation and has spread over three continents. It is a robust legume crop that is considered one of the most resilient to climate changes and to be survival food during drought-triggered famines. The hardy penetrating root system allows the cultivation of grass pea in various soil types, including marginal ones. As an efficient nitrogen fixer, it meets its own nitrogen requirements and positively benefits subsequent crops. However, already in ancient India and Greece, overconsumption of the seeds and a crippling neurological disorder, later coined neurolathyrism, had been linked. Overemphasis of their suspected toxic properties has led to disregard the plant's exceptionally positive agronomic properties and dietary advantages. In normal socio-economic and environmental situations, in which grass pea is part of a balanced diet, neurolathyrism is virtually non-existent. The etiology of neurolathyrism has been oversimplified and the deficiency in methionine in the diet has been overlooked. In view of the global climate change, this very adaptable and nutritious orphan crop deserves more attention. Grass pea can become a wonder crop if the double stigma on its reputation as a toxic plant and as food of the poor can be disregarded. Additionally, recent research has exposed the potential of grass pea as a health-promoting nutraceutical. Development of varieties with an improved balance in essential amino acids and diet may be relevant to enhance the nutritional value without jeopardizing the multiple stress tolerance of this promising crop.

Keywords Neglected legume · Drought tolerance · Nutrition · Socio-economic disease · Health

Importance of grass pea (*Lathyrus sativus* L.)

History of the crop

Grass pea (*Lathyrus sativus* L.) is one of the oldest cultivated crops with a long history of domestication. In archaeological excavations in Turkey and Iraq, seeds of *Lathyrus* species had been found as collected or cultivated items. Similarly, seeds from 2500 BC were identified in the oldest excavations in India (Kislev 1989) and already in the Balkan in 8000 BC. According to the legend, grass pea was brought to Ethiopia (Abyssinia) by the queen of Sheba after visiting King Salomon in the tenth century BC (Budge 1928).

The origin of the name *Lathyrus* is from the Greek word "la thyros" that hints at something exciting, referring to the aphrodisiacal qualities ascribed to grass pea (Loudon et al. 1855). Although the term "lathyrism" used to designate a disease caused by overconsumption of grass pea was coined by Cantani of Naples only in 1873, the history of lathyrism dates back to ancient times (Barrow et al. 1974). In the funeral offerings found in the Egyptian pyramids, various legume seeds were present, including grass pea. Apparently, grass pea was considered a special food to be offered to kings, in contrast to the present-day reputation of being the

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survival food of the poorest of the poor. Ancient civilizations in the Middle East and the Americas included grain legumes and cereals in diets with well-balanced composition in essential amino acids.

Foods prepared from grass pea seeds are very tasty. They have been and are still popular in many European countries (e.g., Spain, France, Portugal, Italy, and Poland), in Africa (for instance, Ethiopia), and in South Asia (e.g., India, Bangladesh, and Nepal). In Ethiopia, grass pea dishes include boiled whole seeds (*nifro*), roasted whole seeds (*kollo*), the traditional sauce (*shiro wott* and *kik wott*), the local drink (*areke*), and the green unripe seeds eaten as snack by young boys on their way from school to home (*eshet*) (Fikre et al. 2011a). Moreover, many European languages have also their own local names for *Lathyrus* (Gry et al. 1998). For example, a gastronomic festival of *chícharo* (grass pea) in Alvaiázere, a small village in the central region of Portugal, is organised yearly for one whole week since 2001. The purpose of the festival is to promote the local knowledge on this forgotten crop and its associated traditions. Moreover, it provides opportunities for local farmers to sell their products outside the conventional commercial systems. With the support of many local restaurants, a great diversity of grass pea menus is offered during the festival days (Vaz Patto 2009). In different parts of Spain, *titos*, *almortas*, *muelas*, or *guijas* are some of the names used for grass pea. During the Spanish Civil War and World War II in the Greek maquis, this presently neglected species was an important crop (Lambein 2015). It was used for different purposes, from animal feed, as supplement to cereals, to human consumption. In these regions, one of the most "healthy" and amazing custom for almost all village children until the 1960s was "*corer los titos*" ("running for grass peas"). The aim of the game was to slip into the neighbours' grass pea fields and to eat the immature green seeds with the hope not to be caught by the owners. Today, in these same countries, grass pea is an almost forgotten crop, just sown in a few small plots to be consumed mainly during some religious festivities (Caminero Saldaña and Grajal Martín 2009).

Grass pea, a geographically successful crop

Grass pea is an important annual legume crop cultivated in several drought-prone areas of the world, including Eurasia, North America, temperate South America, and East Africa (Vaz Patto et al. 2006a; Yan et al. 2006; Dixit et al. 2016). Whereas in India, it is cultivated up to 1300 m above sea level (Duke 1981), in some parts of Ethiopia, it can be grown at a height of 2500–3000 m with annual rainfall averaging 1000 mm (Fikre et al. 2011b). Grass pea is farmed as a summer crop in the high altitudes of Kashmir and Nepal and as a winter crop at low altitudes, for instance, in Bangladesh (Girma and Korbu 2012). Unlike most orphan crops often adapted to local environments and with a limited geographical distribution, grass pea has spread over three continents and has adapted well to various harsh environments, from the highland volcanic soils of Ethiopia to heavy clay in the paddy rice (*Oryza sativa*) fields of Bangladesh (Fig. 1).

The total acreage of grass pea is estimated at 1.50 million ha with an annual production of 1.20 million tons, mainly in South Asia and in East Africa (Sammour 2014). In Ethiopia, the production of the crop has increased both in area coverage and production volume, from 185,490 tons in 2005 to 287,674 tons in 2015. The productivity per hectare has also

Fig. 1 Grass pea cultivation in Ethiopia: **a** grass pea in the greenhouse, **b** grass pea in the field, **c** grass pea on Ethiopian volcanic soil

risen from 1260 kg to 1808 kg in the same period (Central Statistical Authority 1990–2009). In Bangladesh, grass pea (*Khesari*) is cultivated on 239,343 ha with a mean yield of 728 kg/ha both in dry areas and in flooded rice fields and it is often used as intercrop in wheat (*Triticum* sp.) or rice fields (Malek et al. 2000).

The genus *Lathyrus*, which belongs to Fabaceae (Leguminosae), is represented by more than 160 species worldwide (Allkin et al. 1986), some of which are economically important as food (pulse), fodder, forage, ornamental crops, and even in traditional medicine (mainly *L. sativus*, *L. cicera*, and *L. odoratus*) (Vaz Patto and Rubiales 2014). In Europe, the interest in grass pea was revived because of the urgent need to recover marginal land and to provide an efficient alternative to land overexploited by cereal cultivation (Granati et al. 2003). A list of the species known to be historically or currently cultivated for agriculture or horticulture is presented (Table 1).

Grass pea is a typical orphan legume crop, such as cowpea (*Vigna unguiculata*), groundnut (*Arachis hypogaea*), and bambara groundnut (*Vigna subterranea*) (Cullis and Kunert 2017). Orphan or underutilized crops, including orphan legume crops, play a significant role in many developing countries, because they provide food and nutrition security to consumers, as well as an income to resource-poor farmers. They are so-called orphan crops, because they have largely been neglected and their cultivation and use are poorly documented by the international scientific community, the research networks, and the industry, when compared to cash crops, such as rice, corn (*Zea mays*), and wheat (Foyer et al. 2016). This is mainly due to their limited economic importance in the global market and the weak or lack of formal seed supply systems (Cullis and Kunert 2017).

Orphan legumes are primarily grown by resource-poor farmers, predominantly women, who use their own seeds on small landholdings in specific agro-ecological niches and on marginal and sub-marginal lands to provide families with high nutritional value food (Diane 2016). In particular, the vital importance of grass pea in many low-input farming systems (Vaz Patto et al. 2006a) originates from its tolerance to abiotic stresses, such as drought, salinity, flood, and waterlogged conditions (Kumar et al. 2011; Jiang et al. 2013; Piwowarczyk et al. 2016; Zhou et al. 2016). In years of severe flooding or drought, grass pea is the only crop that survives in the field. Interestingly, in Eastern Poland, cultivation of grass pea (*Podlaska lentil*) was stimulated after several crop failures due to drought in the 1990s (Milczak et al. 1997). Grass pea has a hardy and penetrating root system suited to a wide range of soil types, from low fertility soils to heavy clays (Girma and Korbu 2012). Grass pea also responds positively to a favorable environment, giving yields as high as 5 tons/ha under good agro-climatic and management conditions (Briggs et al. 1983).

The robustness of grass pea along with its intrinsic capacity to fix biologically atmospheric nitrogen through its rhizobia-containing roots, a feature shared with other legumes, makes it an attractive crop to grow under adverse agricultural conditions (Campbell et al. 1993). As an efficient nitrogen fixer, grass pea is a good green manure that improves soil fertility by supplementing approximately 67 kg/ha of nitrogen in a single season. This specific ability confers yield and protein benefits for the subsequent non-legume crop

Table 1 Historic or currently cultivated *Lathyrus* species. Source: Adapted from Rizvi et al. (2016) and Llorent-Martínez et al. (2017)

Species	Use	Usage	Location
L. annuus	Pulse, fodder	Rare	Europe, North America
L. aphaca	Fodder	Rare	India
L. blepharicarpus	Pulse	Historic	Near East
L. cicera	Pulse, fodder, medicine	Rare	South Europe, North Africa
L. clymenum	Pulse	Rare	Greece
L. czeczottianus	Medicine	Rare	Turkey
L. gorgoni	Fodder	Historic	Middle East
L. hirsutus	Pulse, forage	Common	USA
L. latifolius	Horticulture	Common	Europe
L. nissolia	Medicine	Rare	Turkey
L. ochrus	Pulse, fodder	Rare	Greece, Middle East
L. odoratus	Horticulture	Common	Widespread
L. pratensis	Forage	Rare	South Europe, North Africa
L. rotundifolius	Horticulture, medicine	Common	Widespread
L. sativus	Pulse, forage, medicine	Common	Widespread
L. sylvestris	Forage	Rare	South Europe, North Africa
L. tingitanus	Fodder	Rare	North Africa
L. tuberosus	Tubers	Rare	West Asia

(Kumar et al. 2013). In India, most of the grass pea acreage (~70%) lies in a rice-growing region where additional irrigation is available only for rice and, consequently, not for subsequent winter crops. Hence, grass pea is the only alternative crop that can be cultivated after rice (Yadav and Mehta 1995), because it efficiently uses moisture retained in the soil and has beneficial effects on soil fertility and soil health. Similarly, in the Eastern Indo-Gangetic plains, a sizeable area is mono-cropped with rice. The lack of irrigation water and the delay in harvesting the rice fields do not normally permit double cropping. Under such conditions, relay cropping of *Lathyrus* could transform these mono-cropped areas into double-cropping areas, increasing the productivity and sustainability of the agricultural system (Dixit et al. 2016).

Grass pea, boon or bane?

Nutritional, nutraceutical, and pharmaceutical properties of grass pea

Grass pea can serve a variety of purposes, such as animal feed and fodder, but also as human food, thanks to 18–34% and 17% of protein content in seeds and mature leaves, respectively (Rizvi et al. 2016). These values are higher than those of field pea (*Pisum sativum* subsp. *arvense* (L.) Asch) (23%), faba bean (*Vicia faba*) (24%), or lupine (*Lupinus albus*) (32%) (Petterson et al. 1997), but lower than those of soybean (*Glycine max*) (42%) (Ravindran and Blair 1992). The *L. sativus* seed protein is composed of albumins (14%), globulins (66%), glutelins (15%), and prolamins (5%) (Chandna and Matta 1994). Whereas animal feed from grass pea usually consists of ground or split grain or flour and is used primarily to feed lactating cattle or other draft animals, human diets include *Lathyrus* as grains that are boiled and then either consumed whole or processed for split dal (Enneking 2011). Moreover, grass pea is highly suitable for human consumption because 58% of the fatty acids are polyunsaturated (Grela et al. 2010). As a nutrient-dense food/feed crop and its high drought tolerance with minimal input requirements for its cultivation, grass pea provides food and nutrition security to many low-income communities.

Grass pea, like other orphan legumes, is still an untouched treasure for compounds that can contribute to human health. For instance, it is the only known dietary source of L-homoarginine. Therefore, as nutraceutical, grass pea is an excellent example of a potential "functional food" (Singh and Rao 2013; Llorent-Martínez et al. 2017). The amino acid L-homoarginine provides benefits in cardiovascular disease treatments (Rao 2011; Singh and Rao 2013; van Wyk et al. 2016) and in overcoming the consequences of hypoxia, i.e., the inadequate oxygen supply at the tissue level, associated with cancer tumor development (Ke and Costa 2006; Jammulamadaka et al. 2011). Thus, a daily dietary intake of L-homoarginine through small quantities of grass pea may be valuable for human health and deserves to be studied further (Rao 2011).

Furthermore, as most grain legumes, grass pea is deficient in the essential sulfur-containing amino acids, methionine and cysteine, but is rich in lysine that is low in cereals (Gatel 1994; Ravindran and Blair 1992; Mahler-Slasky and Kislev 2010). The amino acid profiles of *L. sativus* are similar to those reported for many grain legumes (Hanbury et al. 2000). The deficiency of essential sulfur-containing amino acids, such as methionine that plays a vital role in the central nervous system (Amara et al. 1995), may be overcome with a balanced diet containing cereals (Lambein and Kuo 2004).

However, grass pea suffers from a reputation of being toxic, because under certain circumstances its overconsumption has caused neurolathyrism, a neurodegenerative disease in humans and domestic animals (Lambein and Kuo 2009), due to its content of the neuroexcitatory β-*N*-oxalyl-L-α,β-diaminopropionic acid (β-ODAP) (Vaz Patto and Rubiales 2014). This crippling, but not lethal, disease is more pronounced when grass pea is the dominant component of the diet and accounts for at least 30% of the caloric intake for a period of at least 3–4 months (Kumar 1998). Despite this stigma, β-ODAP in grass pea has also been described as a multifunctional plant metabolite. One of the physiological functions with possible therapeutic potentials is the activation of protein kinase C, which adds a new dimension to explore its potential in the treatment of Alzheimer's disease, hypoxia, and long-term potentiation of neurons essential for memory (Singh and Rao 2013). Recently, the biological properties (antioxidant, enzyme inhibitory, and cytotoxic effects) and phytochemical profiles of selected *Lathyrus* species (*L. czeczottianus* and *L. nissolia*) (Llorent-Martínez et al. 2017) have been studied for the first time. Whereas *L. czeczottianus* exhibited remarkable antioxidant abilities with the highest concentration of phenolics, *L. nissolia* had promising enzymatic inhibitory effects against cholinesterase, amylase, and glucosidase. Thus, these species could be utilized to design new phytopharmaceutical and nutraceutical formulations.

To further challenge the bad reputation of grass pea and its metabolite β-ODAP, a Chinese group has obtained a patent for the use of β-ODAP as a hemostatic agent during surgery (Lan et al. 2013). β-ODAP is also present in the longevity-promoting *Panax ginseng* root (Kuo et al. 2003) that under the name Dencichin is known for its hemorrhage-stopping property and thrombopoiesis treatment (Ding et al. 2018). In China, it is even added in some toothpaste brands and used as an herbal medicine to avoid bleeding. Recent investigations have revealed that β-ODAP induces wound healing and can be considered as a natural wound-curative agent (Sharma et al. 2018). An increasing number of therapeutic applications derived from *Lathyrus* may be developed in the coming years.

Neurolathyrism

The symptoms of both neurolathyrism and konzo are sudden onset of non-progressive symmetric spastic paraparesis. Intriguingly, these two diseases with identical clinical symptoms are linked to the consumption of totally different plant foodstuffs. The occurrence of konzo (meaning tied legs in the Yaka language) is associated with ingestion of the carbohydrate-rich roots of *Manihot esculenta* (cassava) that contain residual cyanogens, whereas neurolathyrism (guaya beshita in Amharic, meaning broken legs) is correlated with the consumption of the protein-rich seeds of *L. sativus* that contain a neuro-excitatory amino acid. The distinction between konzo and neurolathyrism can only be made by the historical consumption of cassava roots and grass pea seeds, respectively (World Health Organization 1996). The etiology of both diseases involves oxidative stress that has many contributing factors, such as imbalance of micronutrients, depletion of reducing power and of glutathione by the lack of sulfur-containing amino acids and antioxidants in the diet.

The epidemiology and the socio-economic background of the two diseases that occur in different geographical areas are also very similar, because both diseases happen mainly among very poor rural people, living as subsistence farmers on drought-prone and marginal lands. Epidemics of konzo in Mozambique and Tanzania (1980s and 1990s), epidemics of neurolathyrism in Bangladesh (1980s), India (1980s), and Ethiopia (1980s and 1990s) had all spread during or after drought periods (Bradbury and Lambein 2011). The question arises whether konzo and neurolathyrism are caused by intoxication, by an essential nutrient deficiency, or a combination thereof. Very plausibly, a nutrient deficiency together with toxic insults could cause a common syndrome (Bradbury and Lambein 2011). Both conditions can be considered socio-economic famine diseases.

From epidemiological surveys in Ethiopia and Bangladesh, neurolathyrism occurs seemingly only when three conditions are present: extreme poverty of the grass pea farmers, illiteracy of the consumers, and availability of grass pea as the cheapest food during drought-triggered famines, because, as mentioned, it is the only crop that can survive in the field, with prolonged overconsumption as a consequence. In Bangladesh, during the last neurolathyrism epidemic, the price of grass pea was the lowest of all foodstuffs. Even, although the grass pea production has increased in Bangladesh, no new cases of neurolathyrism have been reported. The price of grass pea is now equal or higher than that of rice and, hence, overconsumption as the cheapest food is no longer a risk for the poor (Haque et al. 1997).

Recently, stress has been identified as a risk factor for neurolathyrism. Experiments with new-born rats that received daily injections of β-ODAP revealed a 4.5-fold higher incidence of neurological symptoms when put under stress (Kusama-Eguchi et al. 2010). The impact of stress may be the reason for the extremely high incidence of neurolathyrism among the inmates in a World War II labor camp in Vapniarca (Ukraine) (Lambein et al. 2001). Stress may also have played a role during the civil war in Spain or in the maquis in Greece during World War II, when cases of neurolathyrism were reported. It may also affect the integrity of the blood/brain barrier that in a healthy person protects the central nervous system from toxic metabolites in the bloodstream, including β-ODAP after grass pea consumption (Kusama-Eguchi et al. 2010).

The incidence of neurolathyrism can be reduced by simple dietary measures. The occurrence of the disease can be prevented by addition of sufficient cereals to improve the amino acid score of the diet and of antioxidant-containing nutrients (fruits and vegetables) (Getahun et al. 2003). Moreover, seeds can be partly detoxified by various food processing methods (such as soaking in water or boiling) and the grains can be roasted at 150 °C (Kumar et al. 2011). Furthermore, fermentation has been found to reduce β-ODAP by 80–90% (Kuo et al. 1995), although an attempt to use fermentation with *Bacillus* species might not become useful due to practical difficulties. Chemical compounds, such as lime water, sodium chloride, sodium bicarbonate, ascorbic acid, etc., can easily be used in households to reduce the β-ODAP content in grass pea seeds without any effect on the quality parameters, namely content of protein, carbohydrates, and sugar (Geda et al. 1995).

Importantly, both konzo and neurolathyrism are restricted to rural areas, in contrast to urban areas, where the availability of other foodstuffs is higher. Contrary to many infectious diseases, konzo and neurolathyrism are not reportable diseases. However, these socio-economic diseases can be considered as alarming signals of extreme poverty and food insufficiency. Regarding toxicity, it is good to go back to Paracelsus (1493–1541) who mentioned that “everything is toxic and nothing is free of toxicity, only the dose determines toxicity”. Indeed, for instance, 500 g of kitchen salt or sodium chloride in a minimal volume of water is lethal, but kitchen salt is never labeled with toxicity symbols. After β-ODAP had been discovered as a neuroactive non-protein amino acid in grass pea seeds in 1964 (Rao et al. 1964), it was believed to be the cause of neurolathyrism. Neurotoxicologists considered neurolathyrism as a special case of neurodegeneration for which the origin was known, in contrast to other neurodegenerations, such as Alzheimer’s disease and amyotrophic lateral sclerosis (ALS). Although numerous studies were published on the “toxicity” of this unusual amino acid and the plant producing it, the presence of β-ODAP could not explain all the results. Neither the threshold toxicity level, nor the 50% effect level of the neuroexcitant could ever be established. In contrast to the unprocessed roots of bitter cassava and high amounts of kitchen salt, ingestion of grass pea is not fatal. An intake of at least 50 kg during a limited, uninterrupted period and without mixing with cereals or antioxidant-rich condiments would be necessary to obtain a 5% chance of irreversible crippling, without impact on longevity or cognitive functions.

In India and Nepal, a ban on the sale and storage of grass pea that had been imposed in 1961 after an epidemic of neurolathyrism has been the main reason behind a drastic reduction in grass pea cultivation (Kumar et al. 2011). The epidemic was in part triggered by the local tradition to pay poor labourers in kind with cheap food, sometimes exclusively with grass pea (Rutter and Percy 1984), a practice that was later prohibited. Nevertheless, the production area decreased from 1.30 million ha to approximately 850,000 ha in recent decades. Proposals and discussions to lift this ban are ongoing in the Indian media, even though a research panel headed by the Indian Council of Medical Research (ICMR) has cleared the consumption of *khesari* dal—considered the poor man's dal due to its low cost (Utkarsh 2016). Similarly, before the 1960s, grass pea was widely planted in North-West China (in Gansu province, more than 20,000 ha), but in the 1970s, a severe drought caused a terrible famine in this area and a severe neurolathyrism epidemic. Grass pea was then forbidden and the remaining seeds were confiscated (Yang and Zhang 2005).

The biochemistry behind neurolathyrism

The etiology of neurolathyrism is complex. As mentioned, the cause has been suggested to be the neuroexcitatory amino acid β-*N*-oxalyl-L-α,β-diaminopropionic acid (β-ODAP), present in the *Lathyrus* species (Bell 1964). This small molecule has many physiological and biochemical activities and its level in the seeds is affected by genetic and environmental factors (Lambein et al. 2007). β-ODAP is biosynthesized from a heterocyclic amino acid β-isoxazolin-5-on-2-yl-alanine (BIA) that is only abundantly present at the seedling stage of grass pea. BIA is also found in seedlings of the garden pea (*Pisum sativum*) and lentil (*Lens culinaris*), where, in contrast with grass pea, it is not further metabolized into β-ODAP (Kuo et al. 1998). Drought, zinc depletion, and excess iron or cadmium in the soil can stimulate the plant to increase its production of β-ODAP. Recently, the biosynthesis pathway of β-ODAP has been studied in grass pea by means of metabolomics and has clearly been linked with the primary metabolism (Liu et al. 2017). The β-ODAP biosynthesis was found to be co-regulated with the nitrogen and sulfur metabolisms, more specifically with serine and cysteine that were inversely proportional to the β-ODAP accumulation, and β-cyanoalanine synthase was identified to be the key enzyme (Liu et al. 2017). However, the crucial metabolic step from BIA to β-ODAP remained unexplored. This is the fundamental difference with lentil and garden pea, in which the similarly abundant BIA is not further metabolized into β-ODAP. Nevertheless, the enzymatic step leading from BIA to β-ODAP had been studied previously (Ikegami et al. 1999). More recently, a novel *cysteine synthase* (*LsCSase*) gene from grass pea has been identified and characterized through bioinformatics approaches (Chakraborty et al. 2018). The *LsCSase* gene was up-regulated in young seedling tissues as well as in young seeds with an increased expression level under zinc-iron stress conditions and polyethylene glycol-induced osmotic stress. Hence, this preliminary investigation implies a correlation between the *LsCSase* gene and the β-ODAP biosynthesis pathway (Chakraborty et al. 2018). Further studies are needed, for example through the development of genetically engineered grass pea lines in terms of the *CSase* gene to explore its exact activity during the β-ODAP biosynthesis.

The best known and most studied property of β-ODAP is the excitation of a subgroup of glutamate receptors, the α-amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid (AMPA) receptors (Pearson and Nunn 1981) that trigger a cascade of neurophysiological reactions, including Ca^{2+} transport and NO production (Van Moorhem et al. 2010). β-ODAP inhibits not only the transport of the natural neuroexcitant glutamate, increasing and extending the excitation (Kusama et al. 2000), but also the enzymes involved in amino acid metabolism (Shasi Vardhan et al. 1997) and the mitochondrial activity (Ravindranath 2002). Besides the excitation of glutamate receptors, β-ODAP has many additional physiological and biochemical effects (Lambein et al. 2007). Recent sophisticated experiments, in which a human glioma cell line was treated with β-ODAP (Tan et al. 2017), confirmed the decrease in mitochondrial membrane potential, leading to the Ca^{2+} release from the mitochondria into the cellular matrix. The increased Ca^{2+} in the cellular matrix activated a new pathway and brought about the overexpression of specific proteins on the cell membrane surface. This new pathway led to cytoskeleton polymerization inhibition, cell microfilaments distortion, and, ultimately, cytoskeleton collapse. New-born chicks with an immature blood/brain barrier are susceptible to β-ODAP that generates transient neurological symptoms different from those of neurolathyrism (Anil Kumar et al. 2018). Proteomic analyses of chick brains revealed that several proteins involved in cytoskeletal structure, signalling, cellular metabolism, free radical scavenging, oxidative stress, and neurodegenerative disorders were initially up-regulated 2 h after treatment and reverted to normal levels by 4 h (Anil Kumar et al. 2018). Research on the effect of low concentrations of β-ODAP on human neuroblastoma cell lines indicated that β-ODAP can be explored as a stimulator of various reactive oxygen species (ROS)-mediated cell signalling pathways that are not detrimental to cells (Anil Kumar et al. 2018). Unravelling the fundamental steps and regulation of the β-ODAP biosynthesis in grass pea will be important for the development of improved varieties of this orphan legume.

Research areas and achievements in grass pea improvement

Grass pea, a climate-resilient crop

Grass pea is cultivated worldwide and is one of the cheapest sources of dietary protein in the developing world (Enneking 2011). It is an excellent example of an orphan crop adapted to drought and salinity and with a high water use efficiency (Kumar et al. 2011; Jiang et al. 2013; Piwowarczyk et al. 2016; Zhou et al. 2016). Under the prevailing climate change and the serious concerns about sustainability of agricultural production and food security worldwide, investigation of the basis of this high tolerance to drought, heat, and salinity is of great interest taking full advantage of grass pea as an elite germplasm resource (Boukecha et al. 2017). Grass pea is among the priority crops in the Kew's Millennium Seed Bank and the Global Crop Diversity Trust project "Adapting Agriculture to Climate Change". A primary objective of the Kew's project is to collect and protect the genetic diversity of plants harboring traits that could be used for adaptation of the world's most important food crops to new climatic conditions. Such adaptation is considered a key component in securing the world's future food production (Dempewolf et al. 2014). Grass pea is largely considered as an "insurance crop" in areas that are prone to abiotic stresses, because it can produce reliable yields when all other crops fail due to drought (Yan et al. 2006; Vaz Patto and Rubiales 2014).

Water shortages negatively influence plant growth and development, consequently heavily limiting plant productivity. Cell turgor is lost by the reduced water availability and, subsequently, cell elongation and plant growth are hampered (Taiz and Zeiger 2010). Although the exact physiological and molecular mechanisms behind grass pea tolerance to abiotic stresses are still unknown, reports hint at a high ability to adjust the plant's osmotic potential (Jiang et al. 2013; Piwowarczyk et al. 2014) and at the accumulation of polyamines and β-ODAP (Xing et al. 2001; Xiong et al. 2006). Furthermore, the mechanism of salinity tolerance in grass pea was found to result probably from the elevated activity of antioxidant enzymes in the root cells, manifested by the increased accumulation of phenolic compounds and peroxidase activity (Jiang et al. 2013; Piwowarczyk et al. 2016) that might provide a better adaptation to emerging stresses (Hura et al. 2009). Additionally, the defense responses of grass pea were stronger than those of garden pea when subjected to drought stress, including the up-regulated expression of genes encoding antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione peroxidase (GPX), an enhanced antioxidant defense system, and a high content of two osmoprotectants, proline and soluble sugars (Jiang et al. 2013).

Compared to other legumes, grass pea has developed several morphological drought tolerance traits as adaptive mechanisms, including narrow leaves, winged stems, and a deep and extensive root system. Therefore, under drought stress, the grass pea performance is closely related to the root system development and root system distribution (Bultynck et al. 2004; Franks 2013; Koevoets et al. 2016). Indeed, the greater the root depth and root biomass, the more efficiently any available soil moisture is extracted (Blum 2011; Fenta et al. 2014). Moreover, to avoid drought, the plant matures early, a characteristic that can prevent any terminal desiccation. To forestall dehydration, both the green leaf area can be reduced, keeping a higher water status for photosynthesis maintenance, and the stomatal openings can be diminished to minimize the transpiration rate (Cullis and Kunert 2017). Under stress, grass pea also decreases its flower and pod production and concentrates its resources in a small number of surviving pods (Gusmao et al. 2012). Noteworthy, transpiration and other physiological processes in drying soil do not begin to decrease immediately after water is withheld, but only after a threshold soil water content has been reached (Kong et al. 2015). Grass pea, unlike garden pea, curls or rolls its leaves to diminish water loss through transpiration, which is an evolutionary adaptation (Jiang et al. 2013) identified as one of the most common responses to water deficit stress in some plant species (Turgut and Kadioglu 1998). Moderate leaf curling or rolling helps to improve photosynthetic efficiency, accelerates dry-matter accumulation, increases yield, reduces the solar radiation on leaves, and decreases leaf transpiration under drought stress (Lang et al. 2004).

Variety amelioration research

Grass pea has a tremendous potential as a source of multiple stress-tolerant genes for general crop improvement with suitable breeding strategies (Hao et al. 2017; Wang et al. 2015). For example, donor germplasm with the desirable phenotypes can be used to form new breeding materials and available genomic tools can be applied to speed up the breeding process. However, when compared to other legume crops, the genomic resources for grass pea are still scarce because of its big complex 8.2-Gb genome (Bennett and Leitch 2012). In addition, biotechnological investments remain limited. Hence, to date, very limited research efforts have been devoted to genetic improvement of the crop. Grass pea is a diploid with a chromosome number of $2n = 14$. Moreover, it has a very slow breeding process (Hao et al. 2017), possibly due to a very narrow range of genetic variations, resulting from self-pollination and interspecific incompatibility (Nerkar 1976). Increasing the genetic erosion presents a challenge to sustain its genetic diversity, which provides the basis for all plant improvements.

Therefore, there is still a pressing need to collect, conserve, and characterize the genetic variation of grass pea present across diverse geographical regions by means of both ex situ (for instance, seed storage in gene banks) and in situ (i.e., within the natural habitats) techniques (Vaz Patto and Rubiales 2014). For instance, the International Center for Agricultural Research in Dry Areas (ICARDA) in Syria has collected and conserved nearly 3600 accessions, representing 45 wild *Lathyrus* species from more than 40 countries (Dixit et al. 2016). Since 2016, 2720 *Lathyrus* accessions are conserved in collections of the National Bureau of Plant Genetic Resources (NBPGR) in New Delhi (Dixit et al. 2016). For details on other important ex situ *Lathyrus* collections, the reader is referred to Vaz Patto and Rubiales (2014). In addition to ex situ collections, in situ preservation is recommended, because this method safeguards both the population and the evolutionary processes that enable the population to adapt to changing environments by management of the organisms in their natural state or within their normal range. The potential for a high-level improvement exists within these materials, because high variability found in the primary gene pool within *L. sativus* accessions (Vaz Patto and Rubiales 2014; Abate et al. 2018; Khillari et al. 2018) allows the enhancement of yield, quality, and adaptability. In the different collections, the *Lathyrus* accessions have been identified for agronomically/economically important traits, including earliness (< 100 days), number of pods (> 50 per plant), grain yield (> 10 g/plant), seed size (> 12 g/100 seed), and β-ODAP content (< 0.2%) (Dixit et al. 2016). In particular, biotic and abiotic stress tolerances and nutritional and technological qualities are also important target traits to be characterized in the *Lathyrus* germplasm (Vaz Patto and Rubiales 2014). Broadly, the grass pea germplasms can be divided into two groups: the Asian and Mediterranean groups with small and large seeds and on average a high and low β-ODAP content, respectively (Fig. 2).

Moreover, the results of interspecific hybridization in grass pea offer many opportunities for improvement through the identification and transfer of desirable traits from exotic and wild germplasm (Yunus and Jackson 1991). Taxonomic relationship studies have shown that only two species, *L. amphicarpos* and *L. cicera*, produce viable hybrids when crossed with *L. sativus* (Yunus and Jackson 1991). Yet, to overcome strong reproductive barriers among different species, biotechnological tools,

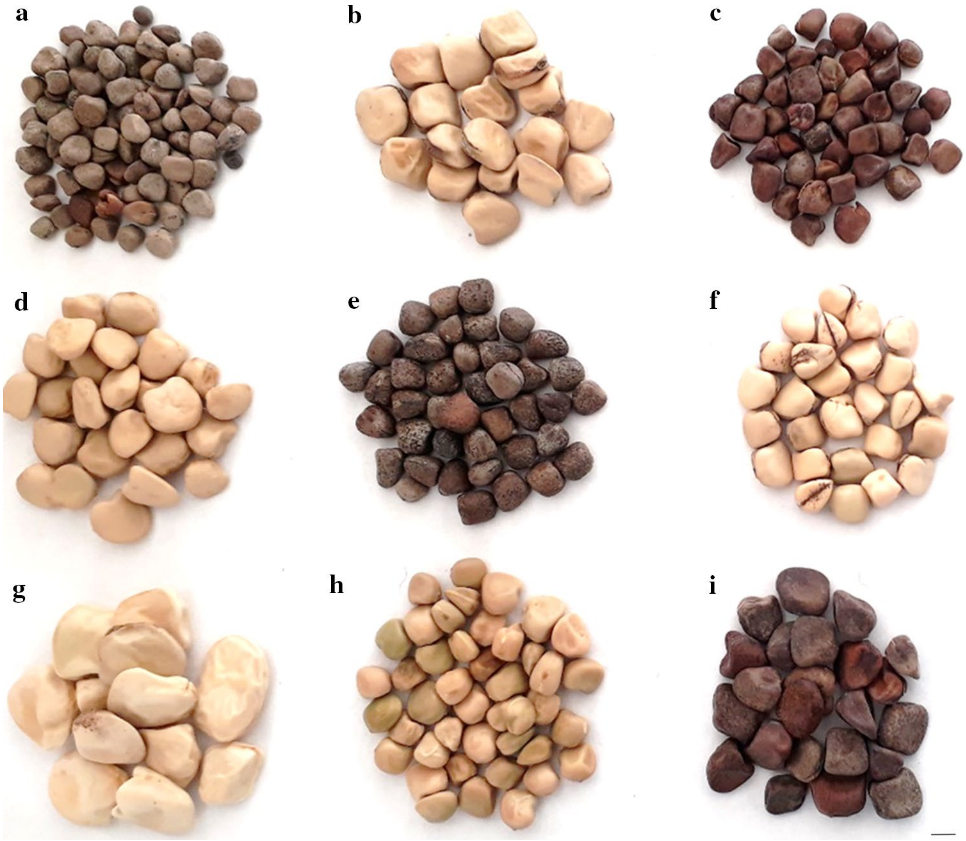

Fig. 2 Diversity of *Lathyrus sativus* seed varieties. Broadly, grass pea germplasms can be divided into two groups: the Asian and Mediterranean groups with small and large seeds and on average a high and low β-ODAP content, respectively, **a** Bangladesh, **b** China, **c** Ethiopia, **d** Canada, **e** India, **f** Nepal, **g** Portugal, **h** Poland, **i** China (scale: 5 mm)

including tissue culture, somaclonal variation, and protoplast fusion techniques may also be utilized (Ochatt et al. 2001; Piwowarczyk and Pindel 2015; Tripathy et al. 2016).

Historically, the crop improvement of grass pea followed three phases. A first phase lasted for almost 20 years (1940–1960) and focused on yield improvement (Gautam et al. 1998) with the development of several cultivars recommended for cultivation. A second phase (1974–1990s) involved the development of improved varieties with low β-ODAP content. Evaluation of grass pea collections worldwide has revealed a considerable variation in β-ODAP content of the seeds, ranging from 0.02 to 2.59% (Kumar et al. 2011), but no β-ODAP-free plants have ever been identified in either germplasm or wild species (Emmrich 2017; Xu et al. 2017). Whereas the highest β-ODAP concentrations are measured in some of the Indian germplasm (Nagarajan and Gopalan 1968), the lowest level of β-ODAP (0.02%) has been reported in Australian germplasm from ICARDA (Hanbury et al. 1999). Several improved grass pea cultivars, all with a β-ODAP content $< 0.1\%$, have been released as the result of various national and international breeding initiatives (Ali-Bar in Kazakhstan; Ceora and Chalus in Australia; Gurbuz 1 in Turkey; Wasie in Ethiopia; Prateek, Mahateora, Ratan, and Pusa 24 in India; Bari Khesari 1, Bari Khesari 2, and Bina Khesari 1 in Bangladesh) (Abd El Moneim et al. 2001; Kumar et al. 2011). In a third phase (1990s onwards), several varieties and lines were developed that combined low β-ODAP ($< 0.1\%$) with high-yield potential (up to 1.5 tons/ha) and resistance to a variety of biotic and abiotic stresses (Kumar et al. 2013).

Although a number of cultivars with a low β-ODAP have been released, the long-term results of these efforts are often questioned. The β-ODAP content is highly influenced by climatic and edaphic conditions and has a strong genotype × environment effect (Tadesse 2003; Fikre et al. 2011b; Jiao et al. 2011; Girma and Korbu 2012). For instance, the β-ODAP content of the Ethiopian variety Wasie has increased from < 0.08 to $> 0.2\%$ from the laboratory to field tests (Fikre et al. 2011b). Various factors that affect β-ODAP accumulation in grass pea include the plant growth stage, nutrients, and abiotic stresses, such as drought, salinity, water, and heavy metals (Jiao et al. 2011). Indeed, water stress can double the β-ODAP content in the plant (Hanbury et al. 1999; Xing et al. 2001) and application of zinc sulphate to the soils has been suggested to reduce the β-ODAP content by 10–40% (Lambein et al. 1994; Kumar et al. 2011), but the mechanism is still unknown. Grass pea tends to synthesize more of this neuroexcitatory amino acid when stressed than when it grows under optimal conditions (Abd El Moneim et al. 2001).

Pest and disease resistance

One of the advantages of grass pea is that it does not suffer much from pests and diseases (Campbell 1997). In fact, the *Lathyrus* gene pool offers a source of resistance to important legume diseases caused by fungi, such as Ascochyta blight (*Mycosphaerella* or *Didymella pinodes*) (Robertson and Abd El Moneim 1996; Gurung et al. 2002), downy mildew (*Peronospora lathyri-palustris*), and powdery mildew (*Erysiphe* spp.) (Vaz Patto et al. 2006b). Only in South Asia is downy mildew an important disease of grass pea and in parts of Ethiopia are rust diseases (*Uromyces* spp.) problematic (Campbell 1997). There are many more reports on the biotic than on the abiotic stress resistance evaluation of *Lathyrus* germplasm collections. Studies under natural infection conditions identified promising lines without visible symptoms of downy mildew (Narsinghani and Kumar 1979; Asthana and Dixit 1998; Pandey et al. 1998) and lines with a moderate resistance to powdery mildew (Lal et al. 1985; Gautam et al. 1998; Vaz Patto et al. 2006b). Lines with an exceptional resistance or immunity to leaf spot *Cercospora pisi sativae* were also characterized (Mishra et al. 1986). Screenings of a set of 50 *Lathyrus* accessions for rust disease established the presence of high resistance in all accessions against *Uromyces viciae-fabae* and *Uromyces ciceris arietini*, and a partial resistance to *Uromyces pisi* (Vaz Patto and Rubiales 2014). Besides, *Sclerotinia sclerotiorum*, a necrotrophic fungal pathogen, instigates white mould on more than 400 plant species, including important crops, such as cotton (*Gossypium hirsutum*), tomato (*Solanum esculentum*), sunflower (*Helianthus annuus*), soybean, and grass pea (Heller and Witt-Geiges 2013). Oxalic acid (OA) is considered as a pathogenesis factor for this devastating phytopathogenic fungus that synthesizes and secretes OA during host colonization (Malenčić et al. 2010; Kabbage et al. 2015; Uloth et al. 2015).

Wild *Lathyrus* species, including *L. ochrus*, *L. clymenum* (Sillero et al. 2005), and *L. cicera* (Fernández-Aparicio et al. 2009; Fernández-Aparicio and Rubiales 2010) are resistant to broomrape (*Orobanche crenata*), a common parasitic weed to the faba bean, a trait that is absent in the cultivated gene pool. In addition to its reduced β-ODAP content (varying between 0.07 and 0.51% across 142 accessions), *L. cicera* may be a promising source of other important agronomic traits, including earliness and cold tolerance (Robertson and Abd El Moneim 1996).

Moreover, the root knot nematode (*Meloidogyne artiella*) and cyst nematode (*Heterodera ciceri*) can attack grass pea, but resistance to both has been identified at ICARDA (Campbell 1997). Thrips (*Caliothrips indicus*) are a pest of high economic concern for grass pea cultivation, in particular in India (Dixit et al. 2016). Screening of 56 accessions against thrips at Raipur revealed two lines with moderate resistance (Asthana and Dixit 1998; Pandey et al. 1998). Resistant *Lathyrus* genotypes may serve as a source of new and useful genetic traits in the breeding of related major legume crops, such as peas, lentils, and vetches.

Molecular toolbox for variety amelioration

The genetic potential of grass pea could be exploited to enhance food and nutrition security, to provide feed for livestock, and to improve soil fertility as green manure in harsh drought-prone environments. Regardless of the availability of low toxin lines, listing grass pea as a toxic plant and banning seed sales in some countries have considerably limited funding for genetic improvement of grass pea through modern breeding techniques as well as genetics and omics tools. As a consequence, sparse genomic resources exist today for this orphan legume, hampering its potential exploitation in crop breeding (Hao et al. 2017).

Mutagenesis Improvement strategies focusing on mutation breeding have been explored as a valuable addition to conventional breeding. As a mutation is defined as a change in the heritable constitution of an organism, mutation breeding increases the genetic variability, thus widening the scope on the isolation and characterization of novel genetic variants (Girma and Korbu 2012). Mutation breeding in grass pea has generated several viable diploid mutants with altered plant characters, such as growth habit, branching, stem and internodes, leaflets, stipules, flower colour, pod features, and seed traits (Talukdar 2009). For instance, mutants were generated with erect, determinate, and semi-dwarf characteristics, with also an increased number of primary and secondary branches, along with a high grain yield and low seed β-ODAP content (Talukdar and Biswas 2006). These mutants have been used to identify and map the desirable morphological markers on specific grass pea chromosomes (Talukdar 2009). Through induced mutagenesis, a robust cytological stock was developed as well, comprising trisomics, tetrasomics, double trisomics, various reciprocal translocations, and autotetraploid lines (Talukdar 2012a). Similarly to morphological changes, marked biochemical changes have been introduced into grass pea by mutagenic treatments. Most mutations have been reported to contribute directly or indirectly to the plant antioxidant defense systems. A glutathione (GSH)-deficient mutant (*gshl-1*) revealed a greater sensitivity to cadmium than its mother plants (Talukdar 2012a). By contrast, grass pea mutants were developed with an enhanced tolerance to salt and arsenic toxicity (Talukdar 2011, 2013). In grass pea, arsenic exposure significantly reduces seed germination, inhibits photosynthetic activities and plant growth, but significantly enhances the level of the seed neuroexcitatory β-ODAP (Talukdar 2012b, 2013).

Molecular markers development Breeder-friendly genomic tools become more and more available to improve the efficiency of breeding protocols in grass pea (Bohra et al. 2014). Unlike morphological descriptors, tools, such as molecular markers, detect diversity and variation among and within species directly at the DNA level and independently of environmental factors. They can be used to determine number, position, and individual effects of genes/quantitative trait loci (QTLs) that control interesting traits, such as disease or pest resistance, reduced β-ODAP concentration, increased protein content, and other characteristics of agronomic importance, via, for instance, genetic mapping and QTL analysis (Campbell et al. 1993).

Genetic diversity in the *Lathyrus* genus can be detected by means of diverse molecular markers, including, among others, restriction fragment length polymorphism (RFLP), random amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP), and sequence-related amplified polymorphism (SRAP) (Chtourou-Ghorbel et al. 2001; Marghali et al. 2016; Nosrati et al. 2012; Tavoletti and Iommarini 2007). Another widely used class of molecular markers are simple sequence repeat (SSR) or microsatellite markers that can be obtained by searching in the expressed sequence tags (ESTs) available at the National Center for Biotechnology Information (NCBI) GenBank for *Lathyrus* (http://www.ncbi.nlm.nih.gov/genbank/dbest/dbest_summary/) (Lioi et al. 2011; Ponnaiah et al. 2011; Shiferaw et al. 2012; Sun et al. 2012; Lioi and Galasso 2013; Soren et al. 2015; Gupta et al. 2018). Today, whereas the number of ESTs is limited for *L. sativus* and *L. cicera* (178 and 126, respectively) at the NCBI GenBank, many more ESTs (8702) are available from *L. odoratus*. This EST-SSR marker system generally has a high degree of conservation and can be transferred among species. Thus, cross-species and cross-genus amplification of molecular markers facilitate comparative genomic mapping, providing an alternative for the development of new molecular markers for orphan species (Gutierrez et al. 2005). Hence, they have allowed the use of *Lathyrus* as a source of interesting traits for other related species and, vice versa, the increase in the number of molecular markers available for *Lathyrus* species, in particular for *L. cicera* and *L. sativus* (Chandra 2011; Lioi et al. 2011; Shiferaw et al. 2012; Almeida et al. 2014a). For instance, a large number of molecular markers from *Medicago truncatula* (barrel medic), garden pea, lentil, lupine, and faba bean were shown to be transferable to *L. cicera* and *L. sativus* for their future applications in mapping and diversity studies (Almeida et al. 2014a).

Thus far, two linkage maps have been developed for *L. sativus* by means of molecular markers (Chowdhury and Slinkard 1999; Skiba et al. 2004). One of these maps was used to locate two QTLs, that explained the relatively small percentage of observed variation in the resistance against

Ascochyta blight (Skiba et al. 2004), but no candidate genes were identified at that time for these resistance QTLs, hampering their use in precision breeding. Moreover, these two linkage maps were not adequately saturated with markers and presented many gaps and short linkage groups, so that they could not be aligned and compared with linkage maps of other legume species (Almeida et al. 2015).

Recently, the application of next-generation sequencing (NGS) to grass pea has provided a means to exploit the repertoire of genomic resources for the orphan legume *Lathyrus*. NGS platforms were used to generate large-scale SSR-enriched sequence data and develop SSR markers that will facilitate the construction of high-resolution maps for positional cloning and QTL mapping (Yang et al. 2014; Wang et al. 2015). Thanks to the sensitive and quantitative high-throughput transcriptome analysis, referred to as RNA-sequencing technology, new genetic markers could be identified for some orphan legumes, such as *Bituminaria bituminosa* (Arabian pea or pitch trefoil) (Pazos-Navarro et al. 2011). The availability of new tools for both the de novo assembly of transcriptomes and their alignment to newly assembled genomes may help identify differential gene expression in response to stress, for instance. In 2014, by the RNA-sequencing technology, the first high-throughput transcriptome assemblies were generated from control and with rust (*Uromyces pisi*)-inoculated leaves of susceptible and rust-resistant grass pea genotypes (Almeida et al. 2014b). The study generated a large number of new gene-based molecular tools, e.g., ESTs, EST-SSRs, and single nucleotide polymorphism (SNP)-based markers. These markers will be instrumental for future work on high-throughput mapping of the genetic basis of disease resistance in *L. sativus* and, eventually, comparative mapping with other legume species. Meanwhile, this transcriptome analysis provided a comprehensive insight into the molecular mechanisms underlying rust resistance in *L. sativus*. The differences in rust resistance between the two (resistant and susceptible) genotypes seemed to be mainly due to the activation of several pathogenesis-related genes, including the “mildew resistance locus O (MLO)-like protein” involved in signalling in response to biotic stresses. The MLO-encoding gene, first identified in barley (*Hordeum vulgare*), conferred resistance to powdery mildew (Jørgensen 1992). Later, by coupling high-throughput sequencing (Illumina) technology with serial analysis of gene expression (SAGE) analyses, a set of differentially expressed genes was identified in the leaves of *L. sativus* in response to *Ascochyta lathyri* inoculation (Almeida et al. 2015). Functional categorization associated these genes with processes involved in biotic/abiotic stress, cell wall metabolism, and hormone signalling (Almeida et al. 2015). Very recently, the *L. cicera* transcriptome was investigated in response to rust (*Uromyces pisi*) and different types of molecular markers were developed to construct the first *L. cicera* linkage map with potential for genetic mapping of resistance in this robust species and its most closely related species *L. sativus* (Santos et al. 2018).

Regeneration and genetic transformation To exploit the potential of grass pea as a source of multiple stress-tolerant genes for general crop improvement through modern approaches, such as genetic transformation, good in vitro culture and regeneration protocols are a first prerequisite. Legumes, and grass pea in particular, are very challenging to regenerate and transform, because of the problematic somatic embryogenesis or organogenesis (Iantcheva et al. 2013). After many attempts, a regeneration protocol of fertile plants from meristematic tissues was established for *L. sativus* in 2002 (Zambre et al. 2002). Using this regeneration protocol, Ethiopian grass pea could be transiently and genetically transformed for the first time using *Agrobacterium*-mediated transformation (Girma 2010). Here, in an effort to boost the seed protein quality, the genetic transformation was conducted with a common bean (*Phaseolus vulgaris* L.) gene coding for additional amounts of methionine, but without further analyses (Girma 2010). In contrast, a genetic transformation procedure was designed with epicotyl segments of Indian *L. sativus* varieties co-cultivated with *Agrobacterium* and expressing both a reporter gene (*β-glucuronidase*) and a selectable marker gene (*neomycin phosphotransferase II*) (Barik et al. 2005). Unfortunately, only one event could be stably transformed in the progenies. Similarly, currently, only one broadly applicable virus-induced gene silencing (VIGS) reverse genetics approach has been reported for *L. odoratus* that resulted in a bleaching phenotype, hinting at a down-regulation of the *phytoene desaturase* (PDS) gene expression (Grønlund et al. 2008).

Recently, in vitro direct multiple shoot induction was obtained from mature seed embryo with two cotyledons as explants. This protocol has been shown to be a time-saving approach for regenerating whole plants from this type of explant. It by-passes the callus induction phase and thus decreases somaclonal variations usually seen in plants produced by tissue culture (Barpete et al. 2017). It can be helpful in future genetic transformation and biotechnology-based breeding of grass pea. Meanwhile, soybean and grass pea genetically engineered by *Agrobacterium*-mediated transformation had an improved nutritional quality and an enhanced tolerance to fungal pathogens, without any adverse impact on plant growth, development, and seed protein quality (Kumar et al. 2016). The reduced level of the antinutritional metabolite oxalic acid (OA) in transgenic seeds of soybean (up to 73%) and grass pea (up to 75%) was observed by the constitutive and/or seed-specific expression of an oxalate-degrading enzyme, oxalate decarboxylase (FvOXDC) of the fungus *Flammulina velutipes*. In addition, the β-ODAP level of grass pea seeds had also decreased up to 73%. In transgenic grass pea lines, the reduced OA content was interrelated with the associated increase in seed micronutrients, such as calcium, iron and zinc, manganese, and magnesium. Moreover, the constitutive expression of FvOXDC led to an improved tolerance against the fungal pathogen *Sclerotinia sclerotiorum* that requires OA during host colonization (Kumar et al. 2016). Although the genotype used was not mentioned in the study, this recent genetic transformation protocol for grass pea, if successfully reproducible, may help future proof-of-function studies of putative *Lathyrus* genes via overexpression, deletion, or silencing.

Conclusions

Grass pea is a plant with a combination of exceptional agronomic properties, such as tolerance to drought, flooding, salinity, a high nitrogen fixation capacity that increases the yield of subsequent crops, easy cultivation with minimal inputs, and adaptability to different climates and soils. As a legume, it is also a highly nutritious food and fodder crop. Considered one of the most climate-resilient crops, grass pea is the only crop that survives in the field during severely dry years, providing no alternative to many low-income communities but to overconsume the seeds as the only dietary component. Uncounted thousands of people have survived famines thanks to grass pea, hence deemed a life-saver crop. However, overconsumption of grass pea has caused the crippling disease neurolathyrism in many European countries in historical times and more recently in Asia and Africa. The forced overuse of grass pea in diets during severe famines has given it its present undeserved reputation of being a toxic plant. Due to this stigma, investments to improve *Lathyrus* varieties are considerably limited and, consequently, sparse genomic resources exist, hampering its potential exploitation in crop breeding (Hao et al. 2017).

Although drought-caused famine has not happened in the last few years, climate change and, particularly, global warming are a serious source of concern for the sustainability of the agricultural production and the food security worldwide, thus, calling for the development of climate-smart crops. Grass pea holds a tremendous potential as a source of multiple stress-tolerant genes for general crop improvement (Hao et al. 2017). The basis of the high tolerance to drought and salinity should be further investigated and the crop could be used as an elite germplasm resource for traits to adapt the world's most important crops to new climatic conditions (Boukecha et al. 2017). Moreover, the high variability found in the primary gene pool within the *Lathyrus* accessions allows the improvement of yield, nutritional quality, and adaptability of grass pea itself. Modern approaches and, especially the Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR) or CRISPR-associated protein 9 (CRISPR/Cas9) system will enable genome editing in grass pea, both as a research tool for the engineering of signalling pathways or regulatory mechanisms involved in the protection of grass pea against drought and as a mean to accelerate crop improvement (Emmrich 2017).

For more than 3 decades no new cases of neurolathyrism have been reported (Singh and Rao 2013). Importantly, when neurolathyrism occurred, it was restricted to rural areas among very poor people, living as subsistence farmers on marginal lands. This socio-economic disease can be considered as alarming signals of extreme poverty and food insufficiency. The low incidence of clinical symptoms caused by neurolathyrism among grass pea consumers and in experimental animals was first explained by the individual variability, without considering the total diet. Only afterwards, deficiency in the essential amino acids methionine and cysteine was taken into account. These sulfur-containing amino acids play important roles in the redox homeostasis of the cell and protect against oxidative stress. Addition of methionine to grass pea as chicken feed shielded against neurological symptoms (Fikre et al. 2010), whereas sufficient cereals supplemented to a grass pea diet is a protective factor in the neurolathyrism epidemiology (Getahun et al. 2003). An old experiment by Justus von Liebig (reported by Pasero 2017), in which a soldier ate solely garden peas for several months, resulted in neurological symptoms described as "*erbsenwahn*" or pea madness. Although this ancient experiment on a single subject needs confirmation, it implies that legumes considered wholesome should not be used as exclusive diet.

In view of the climatic change pressure, this plant could be made into a wonder crop for drought-prone and marginal lands. To this end, grass pea should be used properly in a well-balanced diet and research investments should be increased to improve the nutritional quality of seeds with focus on the essential amino acid balance. The past attempts to strive for zero or low β-ODAP content in grass pea caused researchers to look for other improvement options (Girma and Korbu 2012). Advances in genomics and genetic engineering could help boost the seed protein quality and enhance the content of essential amino acids. In the near future, exploitation of the non-neurotoxic potentials of β-ODAP as nutraceutical and development of economically important traits in grass pea, such as tolerance to biotic and abiotic stresses, for general crop improvement will presumably take the stage. Moreover, instead of focusing on the reduction of β-ODAP content, research efforts to develop grass pea varieties with increased methionine and cysteine contents may be more relevant to improve the nutritional value without loss of its hardy nature. Additionally, other aspects should be considered, such as the very high nitrogen-fixing capacity and the potential role played by β-ODAP. The presence of homoarginine in grass pea seeds is hardly mentioned in the literature, albeit its positive effect on cardiovascular health (Rao 2011). The impact of a regular and moderate consumption of grass pea on longevity and strong cardiovascularity should be a priority in epidemiological research.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Abate A, Mekbib F, Fikre A, Ahmed S (2018) Genetic variability and heritability in Ethiopian grass pea (*Lathyrus sativus* L.) accessions. Ethiop J Crop Sci 6(Spec issue):79–94

Abd El Moneim AM, van Dorrestein B, Baum M, Ryan J, Bejiga G (2001) Role of ICARDA in improving the nutritional quality and yield potential of grass pea (*Lathyrus sativus* L.) for subsistence farmers in dry areas. Lathyrus Lathyrism Newsl 2:55–58

Allkin R, Goyder DJ, Bisby FA, White RJ (1986) Names and synonyms of species and subspecies in the *Vicieae*: issue 3. *Vicieae* Database Project, Experimental Taxonomic Information Products, Publication 7. Southampton University, Southampton

Almeida NF, Leitão ST, Caminero C, Torres AM, Rubiales D, Vaz Patto MC (2014a) Transferability of molecular markers from major legumes to *Lathyrus* spp. for their application in mapping and diversity studies. Mol Biol Rep 41:269–283. https://doi.org/10.1007/s11033-013-2860-4

Almeida NF, Leitão ST, Krezdorn N, Rotter B, Winter P, Rubiales D, Vaz Patto MC (2014b) Allelic diversity in the transcriptomes of contrasting rust-infected genotypes of *Lathyrus sativus*, a lasting resource for smart breeding. BMC Plant Biol 14:376. https://doi.org/10.1186/s12870-014-0376-2

Almeida NF, Krezdorn N, Rotter B, Winter P, Rubiales D, Vaz Patto MC (2015) *Lathyrus sativus* transcriptome resistance response to *Ascochyta lathyri* investigated by deepSuperSAGE analysis. Front Plant Sci 6:178. https://doi.org/10.3389/fpls.2015.00178

Amara A, Coussemacq M, Geffard M (1995) Molecular detection of methionine in rat brain using specific antibodies. Neurosci Lett 185:147–150

Anil Kumar D, Natarajan S, Bin Omar NAM, Singh P, Bhimani R, Singh SS (2018) Proteomic changes in chick brain proteome post treatment with *Lathyrus sativus* neurotoxin, β-*N*-oxalyl-L-α,β-diaminopropionic acid (L-ODAP): a better insight to transient neurolathyrism. Toxicol Res 34:267–279. https://doi.org/10.5487/TR.2018.34.3.267

Asthana AN, Dixit GP (1998) Utilization of genetic resources in *Lathyrus*. In: Mathur PN, Ramanatha Rao V, Arora RK (eds) Lathyrus genetic resources network. (Proceedings of the IPGRI-ICARDA-ICAR regional working group meeting, 8–10 December 1997, New Delhi, India). International Plant Genetic Resources Institute-Office for South Asia, New Delhi, pp 64–70

Barik DP, Mohapatra U, Chand PK (2005) Transgenic grass pea (*Lathyrus sativus* L.): factors influencing *Agrobacterium*-mediated transformation and regeneration. Plant Cell Rep 24:523–531. https://doi.org/10.1007/s00299-005-0957-5

Barpete S, Aasim M, Ozcan SF, Khawar KM, Ozcan S (2017) High frequency axillary shoots induction in grass pea (*Lathyrus sativus* L.). Bangladesh J Bot 46:119–124

Barrow MV, Simpson CF, Miller EJ (1974) Lathyrism: a review. Q Rev Biol 49:101–128

Bell EA (1964) Relevance of biochemical taxonomy to the problem of lathyrism. Nature 203:378–380

Bennett MD, Leitch IJ (2012) Angiosperm DNA *C*-values database (release 8.0, Dec. 2012). http://data.kew.org/cvalues/CvalServlet?querytype=2

Blum A (2011) Drought resistance—is it really a complex trait? Funct Plant Biol 38:753–757. https://doi.org/10.1071/Fp11101

Bohra A, Jha UC, Kishor PBK, Pandey S, Singh NP (2014) Genomics and molecular breeding in lesser explored pulse crops: current trends and future opportunities. Biotechnol Adv 32:1410–1428. https://doi.org/10.1016/j.biotechadv.2014.09.001

Boukecha D, Laouar M, Mekliche-Hanifi L, Harek D (2017) Drought tolerance in some populations of grass pea (*Lathyrus sativus* L.). Legum Res 41:12–19. https://doi.org/10.18805/LR-346

Bradbury JH, Lambein F (2011) Konzo and neurolathyrism: similarities and dissimilarities between these crippling neurodegenerative diseases of the poor. Food Chem Toxicol 49:537–538. https://doi.org/10.1016/j.fct.2010.11.001

Briggs CJ, Parreno N, Campbell CG (1983) Phytochemical assessment of Lathyrus species for the neurotoxic agent, β-*N*-oxalyl-L-α,β-diaminopropionic acid. Planta Med 47(3):188–190. https://doi.org/10.1055/s-2007-969982

Budge EAW (1928) A history of Ethiopia, Nubia and Abyssinia (according to the hieroglyphic inscriptions of Egypt and Nubia, and the Ethiopian chronicles), vol II. Methuen, London

Bultynck L, Ter Steege MW, Schortemeyer M, Poot P, Lambers H (2004) From individual leaf elongation to whole shoot leaf area expansion: a comparison of three *Aegilops* and two *Triticum* species. Ann Bot 94:99–108. https://doi.org/10.1093/aob/mch110

Caminero Saldaña C, Grajal Martín I (2009) From a survival food of the poor to a festivity main dish: "titos" (grass pea, *Latyrus sativus*) in La Gamonal and in Papilla de Abajo (Burgos, Spain). Grain Legum 54:40–41

Campbell CG (1997) Grass pea. *Lathyrus sativus* L. Promoting the conservation and use of underutilized and neglected crops, vol 18. Institute of Plant Genetics and Crop Plant Research, Gatersleben/International Plant Genetic Resources Institute, Rome. https://www.bioversityinternational.org/e-library/publications/detail/grass-pea-lathyrus-sativus-l/

Campbell CG, Mehra RB, Agrawal SK, Chen YZ, Abd El Moneim AM, Khawaja HIT, Yadov CR, Tay JU, Araya WA (1993) Current status and future strategy in breeding grass pea (*Lathyrus sativus*). Euphytica 73:167–175. https://doi.org/10.1007/bf00027192

Central Statistical Authority (1990–2009) Crop production and area statistics. Addis Ababa, Ethiopia

Chakraborty S, Mitra J, Samanta MK, Sikdar N, Bhattacharyya J, Manna A, Pradhan S, Chakraborty A, Pati BR (2018) Tissue specific expression and in silico characterization of a putative *cysteine synthase* gene from *Lathyrus sativus* L. Gene Expr Patterns 27:128–134. https://doi.org/10.1016/j.gep.2017.12.001

Chandna M, Matta NK (1994) Studies on changing protein levels in developing and germinating seeds of *Lathyrus sativus* L. J Plant Biochem Biotechnol 3:59–61. https://doi.org/10.1007/bf03321950

Chandra A (2011) Use of EST database markers from *M. truncatula* in the transferability to other forage legumes. J Environ Biol 32:347–354

Chowdhury MA, Slinkard AE (1999) Linkage of random amplified polymorphic DNA, isozyme and morphological markers in grass pea (*Lathyrus sativus*). J Agric Sci 133:389–395

Chtourou-Ghorbel N, Lauga B, Combes D, Marrakchi M (2001) Comparative genetic diversity studies in the genus *Lathyrus* using RFLP and RAPD markers. Lathyrus Lathyrism Newsl 2:62–68

Cullis C, Kunert KJ (2017) Unlocking the potential of orphan legumes. J Exp Bot 68:1895–1903. https://doi.org/10.1093/jxb/erw437

Dempewolf H, Eastwood RJ, Guarino L, Khoury CK, Müller JV, Toll J (2014) Adapting agriculture to climate change: a global initiative to collect, conserve, and use crop wild relatives. Agroecol Sustain Food Syst 38:369–377. https://doi.org/10.1080/21683565.2013.870629

Diane N (2016) Forgotten crops may hold key to nutritional security. https://www.ucdavis.edu/news/forgotten-crops-may-hold-key-nutritional-security

Ding S, Wang M, Fang S, Xu H, Fan H, Tian Y, Zhai Y, Lu S, Qi X, Wei F, Sun G, Sun X (2018) D-dencichine regulates thrombopoiesis by promoting megakaryocyte adhesion, migration and proplatelet formation. Front Pharmacol 9:297. https://doi.org/10.3389/fphar.2018.00297

Dixit GP, Parihar AK, Bohra A, Singh NP (2016) Achievements and prospects of grass pea (*Lathyrus sativus* L.) improvement for sustainable food production. Crop J 4:407–416. https://doi.org/10.1016/j.cj.2016.06.008

Duke JA (1981) A handbook of legumes of world economic importance. Plenum Press, New York. https://doi.org/10.1007/978-1-4684-8151-8

Emmrich PMF (2017) Genetic improvement of grass pea (*Lathyrus sativus*) for low β-L-ODAP content. Ph.D. Thesis, University of East Anglia. https://ueaeprints.uea.ac.uk/63944/1/PMF_Emmrich_PhD_thesis.pdf

Enneking D (2011) The nutritive value of grass pea (*Lathyrus sativus*) and allied species, their toxicity to animals and the role of malnutrition in neurolathyrism. Food Chem Toxicol 49:694–709

Fenta BA, Beebe SE, Kunert KJ, Burridge JD, Barlow KM, Lynch JP, Foyer CH (2014) Field phenotyping of soybean roots for drought stress tolerance. Agronomy 4:418–435

Fernández-Aparicio M, Rubiales D (2010) Characterisation of resistance to crenate broomrape (*Orobanche crenata* Forsk.) in *Lathyrus cicera* L. Euphytica 173:77–84

Fernández-Aparicio M, Flores F, Rubiales D (2009) Field response of *Lathyrus cicera* germplasm to crenate broomrape (*Orobanche crenata*). Field Crops Res 113:321–327

Fikre A, Yami A, Kuo Y-H, Ahmed S, Gheysen G, Lambein F (2010) Effect of methionine supplement on physical responses and neurological symptoms in broiler chicks fed grass pea (*Lathyrus sativus*)-based starter ration. Food Chem Toxicol 48:11–17

Fikre A, Van Moorhem M, Ahmed S, Lambein F, Gheysen G (2011a) Studies on neurolathyrism in Ethiopia: dietary habits, perception of risks and prevention. Food Chem Toxicol 49:678–684

Fikre A, Negwo T, Kuo Y-H, Lambein F, Ahmed S (2011b) Climatic, edaphic and altitudinal factors affecting yield and toxicity of *Lathyrus sativus* grown at five locations in Ethiopia. Food Chem Toxicol 49:623–630

Foyer CH, Lam H-M, Nguyen HT, Siddique KHM, Varshney RK, Colmer TD, Cowling W, Bramley H, Mori TA, Hodgson JM, Cooper JW, Miller AJ, Kunert K, Vorster J, Cullis C et al (2016) Neglecting legumes has compromised human health and sustainable food production. Nat Plants 2:16112

Franks PJ (2013) Passive and active stomatal control: either or both? New Phytol 198:325–327. https://doi.org/10.1111/nph.12228

Gatel F (1994) Protein quality of legume seeds for non-ruminant animals: a literature review. Anim Feed Sci Technol 45:317–348. https://doi.org/10.1016/0377-8401(94)90036-1

Gautam PL, Singh IP, Karihaloo JL (1998) Need for a crop network on *Lathyrus* genetic resources for conservation and use. In: Mathur PN, Ramanatha Rao V, Arora RK (eds) Lathyrus genetic resources network. (Proceedings of the IPGRI-ICARDA-ICAR regional working group meeting, 8–10 December 1997, New Delhi, India). International Plant Genetic Resources Institute-Office for South Asia, New Delhi, pp 15–21

Geda AK, Rastogi N, Pandey RL (1995) New processing approaches of detoxification for low toxin *Lathyrus*. In: Tekle-Haimanot R, Lambein F (eds) *Lathyrus sativus* and human lathyrism: a decade of progress. Ghent University, Ghent, pp 117–120

Getahun H, Lambein F, Vanhoorne M, Van der Stuyft P (2003) Food-aid cereals to reduce neurolathyrism related to grass-pea preparations during famine. Lancet 362:1808–1810. https://doi.org/10.1016/s0140-6736(03)14902-1

Girma D (2010) Ethiopian grass pea (*Lathyrus sativus* L.) started the genomics era: transient genetic transformation of grass pea. LAP Lambert Academic Publishing, Köln

Girma D, Korbu L (2012) Genetic improvement of grass pea (*Lathyrus sativus*) in Ethiopia: an unfulfilled promise. Plant Breed 131:231–236. https://doi.org/10.1111/j.1439-0523.2011.01935.x

Granati E, Bisignano V, Chiaretti D, Crinò P, Polignano GB (2003) Characterization of Italian and exotic *Lathyrus* germplasm for quality traits. Genet Resour Crop Evol 50:273–280. https://doi.org/10.1023/a:1023562532753

Grela ER, Rybiński W, Klebaniuk R, Matras J (2010) Morphological characteristics of some accessions of grass pea (*Lathyrus sativus* L.) grown in Europe and nutritional traits of their seeds. Genet Resour Crop Evol 57:693–701. https://doi.org/10.1007/s10722-009-9505-4

Grønlund M, Constantin G, Piednoir E, Kovacev J, Johansen IE, Lund OS (2008) Virus-induced gene silencing in *Medicago truncatula* and *Lathyrus odorata*. Virus Res 135:345–349. https://doi.org/10.1016/j.virusres.2008.04.005

Gry J, Rosa E, Rosner H, Andrade I, Gevers E, Hallikainen A, Hedley C, Holm S, Lambein F, Laursen P, Strigl A, Sørensen H, Vidal-Valverde C (1998) NETTOX list of food plants. Danish Veterinary and Food Administration, Søborg

Gupta P, Udupa SM, Sen Gupta DS, Kumar J, Kumar S (2018) Population structure analysis and determination of neurotoxin content in a set of grass pea (*Lathyrus sativus* L.) accessions of Bangladesh origin. Crop J 6:435–442. https://doi.org/10.1016/j.cj.2018.03.004

Gurung AM, Pang ECK, Taylor PWJ (2002) Examination of *Pisum* and *Lathyrus* species as sources of ascochyta blight resistance for field pea (*Pisum sativum*). Australas Plant Pathol 31:41–45. https://doi.org/10.1071/ap01069

Gusmao M, Siddique KHM, Flower K, Nesbitt H, Veneklaas EJ (2012) Water deficit during the reproductive period of grass pea (*Lathyrus sativus* L.) reduced grain yield but maintained seed size. J Agron Crop Sci 198:430–441. https://doi.org/10.1111/j.1439-037X.2012.00513.x

Gutierrez MV, Vaz Patto MC, Huguet T, Cubero JI, Moreno MT, Torres AM (2005) Cross-species amplification of *Medicago truncatula* microsatellites across three major pulse crops. Theor Appl Genet 110:1210–1217. https://doi.org/10.1007/s00122-005-1951-6

Hanbury CD, Siddique KHM, Galwey NW, Cocks PS (1999) Genotype-environment interaction for seed yield and ODAP concentration of *Lathyrus sativus* L. and *L. cicera* L. in Mediterranean-type environments. Euphytica 110:45–60. https://doi.org/10.1023/a:1003770216955

Hanbury CD, White CL, Mullan BP, Siddique KHM (2000) A review of the potential of *Lathyrus sativus* L. and *L. cicera* L. grain for use as animal feed. Anim Feed Sci Technol 87:1–27. https://doi.org/10.1016/S0377-8401(00)00186-3

Hao X, Yang T, Liu R, Hu J, Yao Y, Burlyaeva M, Wang Y, Ren G, Zhang H, Wang D, Chang J, Zong X (2017) An RNA sequencing transcriptome analysis of grass pea (*Lathyrus sativus* L.) and development of SSR and KASP markers. Front Plant Sci 8:1873. https://doi.org/10.3389/fpls.2017.01873

Haque A, Hossain M, Lambein F, Bell EA (1997) Evidence of osteolathyrism among patients suffering from neurolathyrism in Bangladesh. Nat Toxins 5:43–46. https://doi.org/10.1002/(SICI)(1997)5:1%3c43:AID-NT7%3e3.0.CO;2-M

Heller A, Witt-Geiges T (2013) Oxalic acid has an additional, detoxifying function in *Sclerotinia sclerotiorum* pathogenesis. PLoS ONE 8:e72292. https://doi.org/10.1371/journal.pone.0072292

Hura T, Hura K, Grzesiak S (2009) Leaf dehydration induces different content of phenolics and ferulic acid in drought-resistant and -sensitive genotypes of spring triticale. Z Naturforsch 64c:85–95

Iantcheva A, Mysore KS, Ratet P (2013) Transformation of leguminous plants to study symbiotic interactions. Int J Dev Biol 57:577–586. https://doi.org/10.1387/ijdb.130239pr

Ikegami F, Yamamoto A, Kuo Y-H, Lambein F (1999) Enzymatic formation of 2,3-diaminopropionic acid, the direct precursor of the neurotoxin β-ODAP, in *Lathyrus sativus*. Biol Pharm Bull 22:770–771. https://doi.org/10.1248/bpb.22.770

Jammulamadaka N, Burgula S, Medisetty R, Ilavazhagan G, Rao SLN, Singh SS (2011) β-*N*-oxalyl-L-α,β-diaminopropionic acid regulates mitogen-activated protein kinase signaling by down-regulation of phosphatidylethanolamine-binding protein 1. J Neurochem 118:176–186. https://doi.org/10.1111/j.1471-4159.2011.07299.x

Jiang J, Su M, Chen Y, Gao N, Jiao C, Sun Z, Li F, Wang C (2013) Correlation of drought resistance in grass pea (*Lathyrus sativus*) with reactive oxygen species scavenging and osmotic adjustment. Biologia 68:231–240. https://doi.org/10.2478/s11756-013-0003-y

Jiao C-J, Jiang J-L, Ke L-M, Cheng W, Li F-M, Li Z-X, Wang C-Y (2011) Factors affecting β-ODAP content in *Lathyrus sativus* and their possible physiological mechanisms. Food Chem Toxicol 49:543–549. https://doi.org/10.1016/j.fct.2010.04.050

Jørgensen JH (1992) Discovery, characterization and exploitation of *Mlo* powdery mildew resistance in barley. Euphytica 63:141–152. https://doi.org/10.1007/bf00023919

Kabbage M, Yarden O, Dickman MB (2015) Pathogenic attributes of *Sclerotinia sclerotiorum*: switching from a biotrophic to necrotrophic lifestyle. Plant Sci 233:53–60. https://doi.org/10.1016/j.plantsci.2014.12.018

Ke Q, Costa M (2006) Hypoxia-inducible factor-1 (HIF-1). Mol Pharmacol 70:1469–1480. https://doi.org/10.1124/mol.106.027029

Khillari AV, Patil AE, Puttawar MR, Jayde VS (2018) Studies on genetic divergence among explored germplasm from Eastern Vidarbha and selected varieties in Lathyrus (*Lathyrus sativus* L.). Int J Curr Microbiol Appl Sci (Special Issue-6):2208–2217

Kislev ME (1989) Origins of the cultivation of *Lathyrus sativus* and *L. cicera* (Fabaceae). Econ Bot 43:262–270. https://doi.org/10.1007/bf02859868

Koevoets IT, Venema JH, Elzenga JTM, Testerink C (2016) Roots withstanding their environment: exploiting root system architecture responses to abiotic stress to improve crop tolerance. Front Plant Sci 7:1335. https://doi.org/10.3389/fpls.2016.01335

Kong H, Palta JA, Siddique KHM, Stefanova K, Xiong Y-C, Turner NC (2015) Photosynthesis is reduced, and seeds fail to set and fill at similar soil water contents in grass pea (*Lathyrus sativus* L.) subjected to terminal drought. J Agron Crop Sci 201:241–252. https://doi.org/10.1111/jac.12102

Kumar J (1998) Utilization of *Lathyrus*. In: Mathur PN, Ramanatha Rao V, Arora RK (eds) Lathyrus genetic resources network. (Proceedings of the IPGRI-ICARDA-ICAR regional working group meeting, 8–10 December 1997, New Delhi, India). International Plant Genetic Resources Institute-Office for South Asia, New Delhi, pp 57–59

Kumar S, Bejiga G, Ahmed S, Nakkoul H, Sarker A (2011) Genetic improvement of grass pea for low neurotoxin (β-ODAP) content. Food Chem Toxicol 49:589–600. https://doi.org/10.1016/j.fct.2010.06.051

Kumar S, Gupta P, Barpete S, Sarker A, Amri A, Mathur PN, Baum M (2013) Grass pea. In: Singh M, Upadhyaya HD, Bisht IS (eds) Genetic and genomic resources of grain legume improvement. Elsevier, Amsterdam, pp 269–292. https://doi.org/10.1016/B978-0-12-397935-3.00011-6

Kumar V, Chattopadhyay A, Ghosh S, Irfan M, Chakraborty N, Chakraborty S, Datta A (2016) Improving nutritional quality and fungal tolerance in soya bean and grass pea by expressing an oxalate decarboxylase. Plant Biotechnol J 14:1394–1405. https://doi.org/10.1111/pbi.12503

Kuo Y-H, Bau H-M, Quemener B, Khan JK, Lambein F (1995) Solid-state fermentation of *Lathyrus sativus* seeds using *Aspergillus oryzae* and *Rhizopus oligosporus* sp T-3 to eliminate the neurotoxin β-ODAP without loss of nutritional value. J Sci Food Agric 69:81–89. https://doi.org/10.1002/jsfa.2740690113

Kuo Y-H, Ikegami F, Lambein F (1998) Metabolic routes of β-(isoxazolin-5-on-2-yl)-l-alanine (BIA), the precursor of the neurotoxin ODAP (β-*N*-oxalyl-L-α,β-diaminopropionic acid), in different legume seedlings. Phytochemistry 49:43–48. https://doi.org/10.1016/s0031-9422(97)01001-7

Kuo Y-H, Ikegami F, Lambein F (2003) Neuroactive and other free amino acids in seed and young plants of *Panax ginseng*. Phytochemistry 62:1087–1091. https://doi.org/10.1016/S0031-9422(02)00658-1

Kusama T, Kusama-Eguchi K, Ikegami F, Yamamoto A, Kuo Y-H, Lambein F, Watanabe K (2000) Effects of β-ODAP, the *Lathyrus sativus* neurotoxin, and related natural compounds on cloned glutamate receptors and transporters expressed in *Xenopus* oocytes. Res Commun Pharmacol Toxicol 5:37–55

Kusama-Eguchi K, Yamazaki Y, Ueda T, Suda A, Hirayama Y, Ikegami F, Watanabe K, May M, Lambein F, Kusama T (2010) Hind-limb paraparesis in a rat model for neurolathyrism associated with apoptosis and an impaired vascular endothelial growth factor system in the spinal cord. J Comp Neurol 518:928–942. https://doi.org/10.1002/cne.22257

Lal MS, Agrawal I, Chitale MV (1985) Genetic improvement of chickling vetch (*Lathyrus sativus* L.) in Madhya Pradesh, India. In: Kaul AK, Combes D (eds) Lathyrus and Lathyrism, proceedings of the international symposium, held in Pau, France. Third World Medical Research Foundation, New York, pp 146–160

Lambein F (2015) *Lathyrus sativus* L. (grass pea) toxic plant or nutraceutical? CCDN News 25:1–2

Lambein F, Kuo Y-H (2004) Prevention of neurolathyrism during drought. Lancet 363:657. https://doi.org/10.1016/S0140-6736(04)15601-8

Lambein F, Kuo Y-H (2009) Lathyrism. Grain Legum 54:8–9

Lambein F, Haque R, Khan JK, Kebede N, Kuo Y-H (1994) From soil to brain: zinc deficiency increases the neurotoxicity of *Lathyrus sativus* and may affect the susceptibility for the motorneurone disease neurolathyrism. Toxicon 32:461–466

Lambein F, Ngudi DD, Kuo Y-H (2001) Vapniarca revisited: lessons from an inhuman human experience. Lathyrus Lathyrism Newsl 2:5–7

Lambein F, Kuo Y-H, Kusama-Eguchi K, Ikegami F (2007) β-*N*-oxalyl-L-α,β-diaminopropionic acid, a multifunctional plant metabolite of toxic reputation. Arkivoc Part ix:45–52

Lan G, Chen P, Sun Q, Fang S (2013) Methods for treating hemorrhagic conditions. United States Patent, No. US 8,362,081 B2. http://www.freepatentsonline.com/8362081.html

Lang Y, Zhang Z, Gu X, Yang J, Zhu Q (2004) Physiological and ecological effects of crimpy leaf character in rice (*Oryza sativa* L.). I. Leaf orientation, canopy structure and light distribution. Acta Agron Sin 30:806–810

Lioi L, Galasso I (2013) Development of genomic simple sequence repeat markers from an enriched genomic library of grass pea (*Lathyrus sativus* L.). Plant Breed 132:649–653. https://doi.org/10.1111/pbr.12093

Lioi L, Sparvoli F, Sonnante G, Laghetti G, Lupo F, Zaccardelli M (2011) Characterization of Italian grass pea (*Lathyrus sativus* L.) germplasm using agronomic traits, biochemical and molecular markers. Genet Resour Crop Evol 58:425–437. https://doi.org/10.1007/s10722-010-9589-x

Liu F, Jiao C, Bi C, Xu Q, Chen P, Heuberger AL, Krishnan HB (2017) Metabolomics approach to understand mechanisms of β-*N*-oxalyl-L-α,β-diaminopropionic acid (β-ODAP) biosynthesis in grass pea (*Lathyrus sativus* L.). J Agric Food Chem 65:10206–10213. https://doi.org/10.1021/acs.jafc.7b04037

Llorent-Martínez EJ, Zengin G, Fernández-de Córdova ML, Bender O, Atalay A, Ceylan R, Mollica A, Mocan A, Uysal S, Guler GO, Aktumsek A (2017) Traditionally used *Lathyrus* species: phytochemical composition, antioxidant activity, enzyme inhibitory properties, cytotoxic effects, and in silico studies of *L. czeczottianus* and *L. nissolia*. Front Pharmacol 8:83. https://doi.org/10.3389/fphar.2017.00083

Loudon JC, Don G, Wooster D (1855) Loudon's encyclopædia of plants. Longman, Brown, Green and Longmans, London

Mahler-Slasky Y, Kislev ME (2010) *Lathyrus* consumption in late bronze and iron age sites in Israel: an Aegean affinity. J Archaeol Sci 37:2477–2485. https://doi.org/10.1016/j.jas.2010.05.008

Malek MA, Afzal A, Rahman MM, Salahuddin ABM (2000) *Lathyrus sativus*: a crop for harsh environments. In: Knight R (ed) Linking research and marketing opportunities for pulses in the 21st century, proceedings of the third international food legumes research conference, held in Adelaide, 22–26 September 1997. Current plant science and biotechnology series, vol 34. Springer, Dordrecht, pp 369–373. ISSN:978-94-010-5884-1. https://doi.org/10.1007/978-94-011-4385-1_33

Malenčić D, Kiprovski B, Popović M, Prvulović D, Miladinović J, Djordjević V (2010) Changes in antioxidant systems in soybean as affected by *Sclerotinia sclerotiorum* (*Lib.*) *de Bary*. Plant Physiol Biochem 48:903–908. https://doi.org/10.1016/j.plaphy.2010.08.003

Marghali S, Touati A, Gharbi M, Sdouga D, Trifi-Farah N (2016) Molecular phylogeny of *Lathyrus* species: insights from sequence-related amplified polymorphism markers. Genet Mol Res. https://doi.org/10.4238/gmr.15017198

Milczak M, Pedzinski M, Mnichowska H, SzwedUrbas K (1997). Hodowla twórcza ledzwianu siewnego (*Lathyrus sativus* L.) - podsumowanie pierwszego etapu (in Polish). In: Proceedings of the international conference "*Lathyrus sativus*—cultivation and nutritional value in animals and human" Poland, Lublin, Radom, 9–10 June 1997, pp 13–22

Mishra RP, Kotasthane SR, Khare MN, Gupta OM, Tiwari SP (1986) Screening of germplasm collections of *Lathyrus* spp. against *Cercospora pisi sativae* f. sp. *lathyri sativae*. Indian J Mycol Plant Pathol 16:302

Nagarajan V, Gopalan C (1968) Variation in the neurotoxin β-(N)-oxalylamino-alanine content in *Lathyrus sativus* samples from Madhya Pradesh. Indian J Med Res 56:95–99

Narsinghani VG, Kumar SM (1979) Field reaction of powdery and downy mildew in *Lathyrus* genetic stock. J Mycol Plant Pathol 9:252–253

Nerkar YS (1976) Mutation studies in *Lathyrus sativus*. Indian J Genet 76:223–229

Nosrati H, Hosseinpour-Feizi M-A, Nikniazi M, Razban-Haghighi A (2012) Genetic variation among different accessions of *Lathyrus sativus* (Fabaceae) revealed by RAPDs. Bot Serbica 36:41–47

Ochatt S, Durieu P, Jacas L, Pontécaille C (2001) Protoplast, cell and tissue cultures for the biotechnological breeding of grass pea (*Lathyrus sativus* L.). Lathyrus Lathyrism Newsl 2:35–38

Pandey RL, Sharma RN, Chitale MW (1998) Status of *Lathyrus* genetic resources in India. In: Mathur PN, Ramanatha Rao V, Arora RK (eds) Lathyrus genetic resources network. (Proceedings of the IPGRI-ICARDA-ICAR regional working group meeting, 8–10 December 1997, New Delhi, India). International Plant Genetic Resources Institute-Office for South Asia, New Delhi, pp 7–14

Pasero N (2017) Madness and peas: a connection and two works. Strum Crit 3:305–320. https://doi.org/10.1419/87891

Pazos-Navarro M, Dabauza M, Correal E, Hanson K, Teakle N, Real D, Nelson MN (2011) Next generation DNA sequencing technology delivers valuable genetic markers for the genomic orphan legume species, *Bituminaria bituminosa*. BMC Genet 12:104. https://doi.org/10.1186/1471-2156-12-104

Pearson S, Nunn PB (1981) The neurolathyrogen, β-*N*-oxalyl-L-α,β-diaminopropionic acid, is a potent agonist at 'glutamate preferring' receptors in the frog spinal-cord. Brain Res 206:178–182. https://doi.org/10.1016/0006-8993(81)90112-8

Petterson DS, Sipsas S, Mackintosh JB (1997) The chemical composition and nutritive value of Australian pulses, 2nd edn. Grains Research and Development Corporation, Canberra

Piwowarczyk B, Pindel A (2015) Determination of an optimal isolation and culture conditions of grass pea protoplasts. BioTechnologia 96:192–202. https://doi.org/10.5114/bta.2015.54205

Piwowarczyk B, Kamińska I, Rybiński W (2014) Influence of PEG generated osmotic stress on shoot regeneration and some biochemical parameters in *Lathyrus* culture. Czech J Genet Plant Breed 50:77–83

Piwowarczyk B, Tokarz K, Kamińska I (2016) Responses of grass pea seedlings to salinity stress in in vitro culture conditions. Plant Cell Tissue Organ Cult 124:227–240. https://doi.org/10.1007/s11240-015-0887-z

Ponnaiah M, Shiferaw E, Pè ME, Porceddu E (2011) Development and application of EST-SSRs for diversity analysis in Ethiopian grass pea. Plant Genet Resour 9:276–280. https://doi.org/10.1017/S1479262111000426

Rao SLN (2011) A look at the brighter facets of β-*N*-oxalyl-L-α,β-diaminopropionic acid, homoarginine and the grass pea. Food Chem Toxicol 49:620–622. https://doi.org/10.1016/j.fct.2010.06.054

Rao SLN, Adiga PR, Sarma PS (1964) The isolation and characterization of β-*N*-oxalyl-L-α,β-diaminopropionic acid: a neurotoxin from the seeds of *Lathyrus sativus*. Biochemistry 3:432–436. https://doi.org/10.1021/bi00891a022

Ravindran V, Blair R (1992) Feed resources for poultry production in Asia and the Pacific. II. Plant protein sources. Worlds Poult Sci J 48:205–231. https://doi.org/10.1079/WPS19920017

Ravindranath V (2002) Neurolathyrism: mitochondrial dysfunction in excitotoxicity mediated by L-β-oxalyl aminoalanine. Neurochem Int 40:505–509. https://doi.org/10.1016/S0197-0186(01)00121-8

Rizvi AH, Sarker A, Dogra A (2016) Enhancing grass pea (*Lathyrus sativus* L.) production in problematic soils of South Asia for nutritional security. Indian J Genet Plant Breed 76:583–592. https://doi.org/10.5958/0975-6906.2016.00074.2

Robertson LD, Abd El Moneim A (1996) *Lathyrus* germplasm collection, conservation and utilization for crop improvement at ICARDA. In: Arora RK, Mathur PN, Riley KW, Adham Y (eds) Lathyrus genetic resources in Asia, proceedings of a regional workshop, 27–29 December 1995, Raipur, India. International Plant Genetic Resources Institute Office for South Asia, New Delhi, pp 97–111

Rutter J, Percy S (1984) The pulse that maims. New Sci 103(1418):22–23

Sammour RH (2014) Genetic diversity in *Lathyrus sativus* L. germplasm. Res Rev BioSci 8:325–336

Santos C, Almeida NF, Alves ML, Horres R, Krezdorn N, Leitão ST, Aznar-Fernández T, Rotter B, Winter P, Rubiales D, Vaz Patto MC (2018) First genetic linkage map of *Lathyrus cicera* based on RNA sequencing-derived markers: key tool for genetic mapping of disease resistance. Hortic Res 5:45. https://doi.org/10.1038/s41438-018-0047-9

Sharma D, Singh P, Singh SS (2018) β-*N*-oxalyl-L-α,β-Diaminopropionic acid induces wound healing by stabilizing HIF-1α and modulating associated protein expression. Phytomedicine 44:9–19. https://doi.org/10.1016/j.phymed.2018.04.024

Shasi Vardhan K, Pratap Rudra MP, Rao SLN (1997) Inhibition of tyrosine aminotransferase by β-*N*-oxalyl-L-α,β-diaminopropionic acid, the *Lathyrus sativus* neurotoxin. J Neurochem 68:2477–2484

Shiferaw E, Pè ME, Porceddu E, Ponnaiah M (2012) Exploring the genetic diversity of Ethiopian grass pea (*Lathyrus sativus* L.) using EST-SSR markers. Mol Breed 30:789–797. https://doi.org/10.1007/s11032-011-9662-y

Sillero JC, Cubero JI, Fernández-Aparicio M, Rubiales D (2005) Search for resistance to crenate broomrape (*Orobanche crenata*) in *Lathyrus*. Lathyrus Lathyrism Newsl 4:7–9

Singh SS, Rao SLN (2013) Lessons from neurolathyrism: a disease of the past & the future of *Lathyrus sativus* (*Khesari dal*). Indian J Med Res 138:32–37

Skiba B, Ford R, Pang ECK (2004) Construction of a linkage map based on a *Lathyrus sativus* backcross population and preliminary investigation of QTLs associated with resistance to ascochyta blight. Theor Appl Genet 109:1726–1735. https://doi.org/10.1007/s00122-004-1812-8

Soren KR, Yadav A, Pandey G, Gangwar P, Parihar AK, Bohra A, Dixit GP, Datta S, Singh NP (2015) EST-SSR analysis provides insights about genetic relatedness, population structure and gene flow in grass pea (*Lathyrus sativus*). Plant Breed 134:338–344. https://doi.org/10.1111/pbr.12268

Sun X-L, Yang T, Guan J-P, Ma Y, Jiang J-Y, Cao R, Burlyaeva M, Vishnyakova M, Semenova E, Bulyntsev S, Zong X-X (2012) Development of 161 novel EST-SSR markers from *Lathyrus sativus* (Fabaceae). Am J Bot 99:e379–390. https://doi.org/10.3732/ajb.1100346

Tadesse W (2003) Stability of grass pea (*Lathyrus sativus* L.) varieties for ODAP content and grain yield in Ethiopia. Lathyrus Lathyrism Newsl 3:32–34

Taiz L, Zeiger E (2010) Plant physiology, 5th edn. Sinauer Associates Inc., Sunderland

Talukdar D (2009) Recent progress on genetic analysis of novel mutants and aneuploid research in grass pea (*Lathyrus sativus* L.). Afr J Agric Res 4:1549–1559

Talukdar D (2011) Isolation and characterization of NaCl-tolerant mutations in two important legumes, *Clitoria ternatea* L. and *Lathyrus sativus* L.: induced mutagenesis and selection by salt stress. J Med Plants Res 5:3619–3628

Talukdar D (2012a) An induced glutathione-deficient mutant in grass pea (*Lathyrus sativus* L.): modifications in plant morphology, alteration in antioxidant activities and increased sensitivity to cadmium. Bioremediat Biodivers Bioavailab 6:75–86

Talukdar D (2012b) Changes in neurotoxin, β-*N*-oxalyl-L-α,β-diaminopropionic acid (β-ODAP), level in grass pea (*Lathyrus sativus* L.) genotypes under arsenic treatments. J Appl Biosci 38:148–153

Talukdar D (2013) Arsenic exposure modifies *Fusarium* wilt tolerance in grass pea (*Lathyrus sativus* L.) genotypes through modulation of antioxidant defense response. J Plant Sci Mol Breed 2:4. https://doi.org/10.7243/2050-2389-2-4

Talukdar D, Biswas AK (2006) An induced internode mutant in grass pea. In: Das RK, Chatterjee S, Sadhukhan GC (eds) Proceedings of the all india congress of cytology and genetics, perspectives in cytology and genetics, vol 12. Hindasia Publishers, New Delhi, pp 267–271

Tan R-Y, Xing G-Y, Zhou G-M, Li F-M, Hu W-T, Lambein F, Xiong J-L, Zhang S-X, Kong H-Y, Zhu H, Li Z-X, Xiong Y-C (2017) Plant toxin β-ODAP activates integrin β1 and focal adhesion: a critical pathway to cause neurolathyrism. Sci Rep 7:40677. https://doi.org/10.1038/srep40677

Tavoletti S, Iommarini L (2007) Molecular marker analysis of genetic variation characterizing a grass pea (*Lathyrus sativus*) collection from central Italy. Plant Breed 126:607–611. https://doi.org/10.1111/j.1439-0523.2007.01407.x

Tripathy SK, Panda A, Nayak PK, Dash S, Lenka D, Mishra DR, Kar RK, Senapati N, Dash GB (2016) Somaclonal variation for genetic improvement in grass pea (*Lathyrus sativus* L.). Legum Res 39:329–335. https://doi.org/10.18805/1r.v0iOF.6853

Turgut R, Kadioglu A (1998) The effect of drought, temperature and irradiation on leaf rolling in *Ctenanthe setosa*. Biol Plant 41:629–633. https://doi.org/10.1023/A:1001817105685

Uloth MB, Clode PL, You MP, Barbetti MJ (2015) Calcium oxalate crystals: an integral component of the *Sclerotinia sclerotiorum*/*Brassica carinata* pathosystem. PLoS ONE 10:e0122362. https://doi.org/10.1371/journal.pone.0122362

Utkarsh A (2016) ICMR panel clears 'unsafe' khesari dal banned in 1961. The Indian Express, January 17, 2016. https://indianexpress.com/article/india/india-news-india/icmr-panel-clears-unsafe-khesari-dal-banned-in-61/

Van Moorhem M, Decrock E, Coussee E, Faes L, De Vuyst E, Vranckx K, De Bock M, Wang N, D'Herde K, Lambein F, Callewaert G, Leybaert L (2010) L-β-ODAP alters mitochondrial Ca^{2+} handling as an early event in excitotoxicity. Cell Calcium 47:287–296. https://doi.org/10.1016/j.ceca.2010.01.001

van Wyk SG, Kunert KJ, Cullis CA, Pillay P, Makgopa ME, Schlüter U, Vorster BJ (2016) Review: the future of cystatin engineering. Plant Sci 246:119–127. https://doi.org/10.1016/j.plantsci.2016.02.016

Vaz Patto MC (2009) Alvaiázere, grass pea capital: a taste on patrimony. Grain Legum 54:38–39

Vaz Patto MC, Rubiales D (2014) *Lathyrus* diversity: available resources with relevance to crop improvement—*L. sativus* and *L. cicera* as case studies. Ann Bot 113:895–908. https://doi.org/10.1093/aob/mcu024

Vaz Patto MC, Skiba B, Pang ECK, Ochatt SJ, Lambein F, Rubiales D (2006a) *Lathyrus* improvement for resistance against biotic and abiotic stresses: from classical breeding to marker assisted selection. Euphytica 147:133–147. https://doi.org/10.1007/s10681-006-3607-2

Vaz Patto MC, Fernández-Aparicio M, Moral A, Rubiales D (2006b) Characterization of resistance to powdery mildew (*Erysiphe pisi*) in a germplasm collection of *Lathyrus sativus*. Plant Breed 125:308–310. https://doi.org/10.1111/j.1439-0523.2006.01220.x

Wang F, Yang T, Burlyaeva M, Li L, Jiang J, Fang L, Redden R, Zong X (2015) Genetic diversity of grass pea and its relative species revealed by SSR markers. PLoS ONE 10:e0118542. https://doi.org/10.1371/journal.pone.0118542

World Health Organization (1996) Konzo—a distinct type of upper motoneuron disease. Wkly Epidemiol Rec 71:225–228

Xing G, Cui K, Li J, Wang Y, Li Z (2001) Water stress and accumulation of β-*N*-oxalyl-L-α,β-diaminopropionic acid in grass pea (*Lathyrus sativus*). J Agric Food Chem 49:216–220. https://doi.org/10.1021/jf000912k

Xiong Y-C, Xing G-M, Li F-M, Wang S-M, Fan X-W, Li Z-X, Wang Y-F (2006) Abscisic acid promotes accumulation of toxin ODAP in relation to free spermine level in grass pea seedlings (*Lathyrus sativus* L.). Plant Physiol Biochem 44:161–169. https://doi.org/10.1016/j.plaphy.2006.03.002

Xu Q, Liu F, Chen P, Jez JM, Krishnan HB (2017) β-*N*-oxalyl-L-α,β-Diaminopropionic acid (β-ODAP) content in *Lathyrus sativus*: the integration of nitrogen and sulfur metabolism through β-cyanoalanine synthase. Int J Mol Sci 18:526. https://doi.org/10.3390/ijms18030526

Yadav VK, Mehta SL (1995) *Lathyrus sativus*: a future pulse crop free of neurotoxin. Curr Sci 68:288–292

Yan Z-Y, Spencer PS, Li Z-X, Liang Y-M, Wang Y-F, Wang C-Y, Li F-M (2006) *Lathyrus sativus* (grass pea) and its neurotoxin ODAP. Phytochemistry 67:107–121. https://doi.org/10.1016/j.phytochem.2005.10.022

Yang H, Zhang X-Y (2005) Considerations on the reintroduction of grass pea in China. Lathyrus Lathyrism Newsl 4:22–26

Yang T, Jiang J, Burlyaeva M, Hu J, Coyne CJ, Kumar S, Redden R, Sun X, Wang F, Chang J, Hao X, Guan J, Zong X (2014) Large-scale microsatellite development in grass pea (*Lathyrus sativus* L.), an orphan legume of the arid areas. BMC Plant Biol 14:65. https://doi.org/10.1186/1471-2229-14-65

Yunus AG, Jackson MT (1991) The gene pools of the grass pea (*Lathyrus sativus* L.). Plant Breed 106:319–328. https://doi.org/10.1111/j.1439-0523.1991.tb00517.x

Zambre M, Chowdhury B, Kuo Y-H, Van Montagu M, Angenon G, Lambein F (2002) Prolific regeneration of fertile plants from green nodular callus induced from meristematic tissues in *Lathyrus sativus* L. (grass pea). Plant Sci 163:1107–1112. https://doi.org/10.1016/S0168-9452(02)00319-9

Zhou L, Cheng W, Hou H, Peng R, Hai N, Bian Z, Jiao C, Wang C (2016) Antioxidative responses and morpho-anatomical alterations for coping with flood-induced hypoxic stress in grass pea (*Lathyrus sativus* L.) in comparison with pea (*Pisum sativum*). J Plant Growth Regul 35:690–700. https://doi.org/10.1007/s00344-016-9572-7