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Annual Plant Reviews Online

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https://doi.org/10.1002/9781119312994.apr0774

Annual Plant Reviews (2021) **4**, 767–812
doi: 10.1002/9781119312994.apr0774
http://onlinelibrary.wiley.com

TEN YEARS OF *GYNANDROPSIS GYNANDRA* RESEARCH FOR IMPROVEMENT OF NUTRIENT-RICH LEAF CONSUMPTION: LESSONS LEARNT AND WAY FORWARDS

Enoch G. Achigan-Dako[1], Dêêdi E.O. Sogbohossou[1,2], Carlos A. Houdegbe[1], Mouizz A. Salaou[1], Fernand S. Sohindji[1], Jelila Blalogoe[1], Barthlomew Y. Chataika[3], Herbaud F. Zohoungbogbo[1], Charlotte A.O. Adje[1], Nicodème V. Fassinou Hotegni[1], Rachidi Francisco[1], Mary O. Abukutsa-Onyango[4] and M. Eric Schranz[2]

[1] *Laboratory of Genetics, Biotechnology, and Seed Science (GBioS), Faculty of Agronomic Sciences, University of Abomey-Calavi, Abomey-Calavi, Republic of Benin*
[2] *Biosystematics Group, Wageningen University, Wageningen, The Netherlands*
[3] *Crop Science Department, Faculty of Agriculture and Natural Resources, University of Namibia, Windhoek, Namibia*
[4] *Department of Horticulture, Jomo Kenyatta University of Agriculture and Technology, Nairobi, Kenya*

Abstract: This article reveals progress and gaps in spider plant (*Gynandropsis gynandra* Syn. *Cleome gynandra*) research to date. It synthesises the current knowledge in systematics and botany, geographical distribution, nutrient content, and health values as well as the agronomic practices related to the species. This article further presents the germplasm availability, status, and places of conservation around the world to exploit the extant genetic diversity for genomics-assisted breeding and seed systems development. It describes how various parts of the plant have been used and the potential for economical revamping and further

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industrial valorisation. Nutrient content and phytochemical diversity across cultivation systems and geographical ranges and known health attributes were analysed to identify gaps and bottlenecks for fostering further investigations for industrial food and drug production.

Keywords: cleome, foods and drugs, *Gynandropsis gynandra*, health benefits, leafy vegetable, nutrients, production

1 Introduction

Agricultural diversification is a robust way to increase cropping systems resilience and productivity and also mitigate food and nutrition insecurity in tropical countries in the context of climate change. This pathway is nowadays thoroughly advocated by development agencies to enrich the food basket of resource-poor households. Increased food system diversification is achievable when the wealth of crop plant diversity is thoroughly exploited to generate nutrient-rich products suitable for marginal areas where environmental bottlenecks are more severe.

To date, over 5000 plant species are recorded as food plants in the world. However, less than 20 species provide 60% of the calories and about 56% of the protein that humans consume come directly from plants (Jacobsen et al., 2015). Top species include three cereals (rice, wheat, and maize), and one root crop (potato). The bulk of edible species in the world are therefore non-commodity crops that are mostly overlooked by research and development initiatives. Those species (cultivated or wild) are overall referred to as orphan crops, minor crops, neglected and underutilised species. They include, for instance, cereals such as teff (*Eragrostis tef* (Zucc.) Trotter) and fonio (*Digitaria exilis* (Kippist) Stapf), fruits like bush mango (*Irvingia gabonensis* (Aubry-Lecomte ex O'Rorke) Baill.), baobab (*Adansonia digitata* L.), custard apple (*Annona senegalensis* Pers.), pulses like Kersting's groundnut (*Macrotyloma geocarpum* (Harms) Marechal & Baudet), Bambara groundnut (*Vigna subterranea* (L.) Verdc.), and vegetables such as amaranths (*Amaranthus* spp.), bitter leaf (*Gymnanthemum amygdalinum* (Delile) Sch.Bip. ex Walp.), bitter melon (*Momordica charantia* L.), egusi crops (*Lagenaria siceraria* (Molina) Standl., *Citrullus mucosospermus* (Fursa) Fursa, *Melothria sphaerocarpa* (Cogn.) H. Schaef. & S.S. Renner), and spider plant (*Gynandropsis gynandra* (L.) Briq). Vegetables only represent about 1000 species with a large dominant group of leafy vegetables (Maundu et al., 2009) with widespread consumption.

Leafy vegetables are perceived as nutritionally rich, adapted to marginal and extreme growing conditions, economically affordable with high contribution to the food safety net. They can be produced in home gardens and made available all year round (Ambrose-Oji, 2009). More than 60 plant

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families are used as leafy vegetables in Africa (Maundu et al., 2009; Achigan-Dako et al., 2010, 2011). In the last two decades, leafy vegetables have been promoted by research and development organisations through various interventions. From 1997 to 2020, many interventions and research programmes were involved in the exposure of leafy vegetables for improved nutrition and income generation. Several in-country projects were developed as well in West and East Africa (Batawila et al., 2007; Dansi et al., 2008; Achigan-Dako et al., 2010; Fondo et al., 2005). In Africa, the most prominent programs at the regional level included among others: (i) IndigenoVeg (Networking to promote the sustainable production and marketing of indigenous vegetables through urban and peri-urban agriculture in sub-Saharan Africa) covering fourteen countries in Africa and Europe; (ii) Darwin Initiative (Conservation of Biodiversity in Traditional West African Species) in Benin and Mali; (iii) Cleonomics ('Utilizing the genome of the vegetable species *Cleome gynandra* (spider plant) for the development of improved cultivars for the West and East African markets') in Benin and Kenya; (iv) Recipes for success ('Enhancing productivity and consumption of indigenous horticultural food crops for better nutrition and health through enhanced communication of research results in community-run resource centres') in Benin, Kenya, and Tanzania; (v) Microveg ('Synergizing fertilizer micro-dosing and indigenous vegetable innovations to enhance food and economic security of farmers in the West African sub-region') in Benin and Nigeria. Throughout these programs, leafy vegetable species that were widely researched or promoted included: *Amaranthus* spp., *Solanum* spp., and *G. gynandra*.

Gynandropsis gynandra, a fast-growing leafy vegetable, is widespread in the continent and increasingly valued as a commercial crop in West and Eastern Africa. The crop is well adapted to extreme climatic conditions. Leaves are rich in nutrients including minerals such as iron and zinc, and vitamins A and E (Uusiku et al., 2010; Sogbohossou et al., 2019; Omondi et al., 2017a). The whole plant is used for medicinal purpose. *Gynandropsis gynandra* is considered as a 'famine food' and still harvested in the wild or cultivated in home gardens. The species substantially contributes to food and nutrition for rural communities during food shortage periods (Onyango et al., 2013). Previously harvested in the wild in Kenya, *G. gynandra* is sold in supermarkets and provide income to many stakeholders along its value chains (Onyango et al., 2013). Similar economic dynamics were observed in Lome, Togo by Sogbohossou et al. (2018a).

So far, a large body of research was carried out on *G. gynandra* from 2010 to 2020. These included ethnobotanical research, evaluation, and characterisation of germplasms at country level as well as regional and global levels, the analysis of genetic variation and structure in natural populations, seed germination and seed ecology, nutrients and metabolites analysis, crop physiology, etc. However, many research gaps hinder the utilisation of the full potential of the crop. This article revisits the research achievements in *G. gynandra*

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and propose new areas of endeavours to build a robust pathway for future research and development agenda in spider plant with focus on nutrient content improvement.

2 Origin, Systematics, and Geographical Distribution

Gynandropsis gynandra (syn *Cleome gynnandra* L.) is an erect annual herb up to 150 cm tall, strongly branched, with a long taproot and few secondary roots. The species belongs to the Cleomaceae family, which encompasses eighteen genera and 150–200 species (Patchell et al., 2014). The genus *Cleome* and other genera of the family have been traditionally considered as the subfamily Cleomoïdeae of the family Capparaceae (Inda et al., 2008). In recent phylogenetic studies, Cleomoïdeae were found to be more closely related to the Brassicaceae than Capparoideae (Hall, 2008; Hall et al., 2002; Iltis et al., 2011). Thus, three monophyletic families were delineated: Capparaceae, Cleomaceae, and Brassicaceae (Figure 1). The morphological

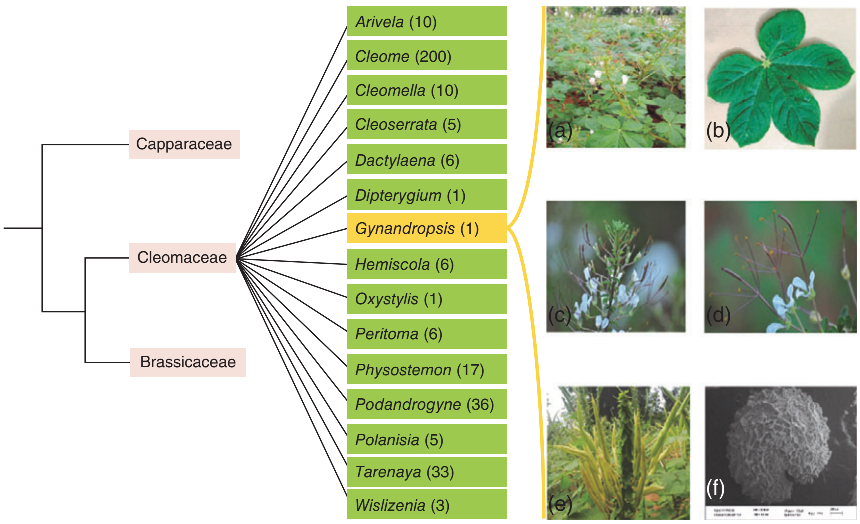

Figure 1 Sister families and genera of Cleomaceae, botanical features of the monotypic genus *Gynandra*. (a) Whole plant at flowering stage; (b) leaf with five leaflets; (c) inflorescence with opened flowers; (d) blooming flowers with petals and bracteates at the base; (e) mature yellowish capsules; (f) subglobose seed with ribbed coat. Genera are ordered alphabetically not phylogenetically. Numbers in brackets represent species diversity. (a–e) Source: Modified from Sogbohossou (2019). Photo credit: Herbaud Zohoungbogbo, Jelila Blalogoe, Mouizz Salaou. (f) Source: Blalogoe, J. S., Odindo, A. O., Sogbohossou, E. O. D., Sibiya, J., & Achigan-Dako, E. G. (2020). Origin-dependence of variation in seed morphology, mineral composition and germination percentage in *Gynandropsis gynandra* (L.) Briq. accessions from Africa and Asia. BMC Plant Biology, 20(1). doi: 10.1186/s12870-020-02364-w.

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characters specific to the Cleomaceae include their mostly herbaceous habit, compound leaves and dry and dehiscent capsules with a replum. Seeds are uniformly strongly curved, reniform or horseshoe-shaped to conduplicate with a deep invagination of the testa, an incurved embryo with always strictly incumbent cotyledons (Iltis et al., 2011). *Gynandropsis gynandra* was also known as *Cleome gynandra* L. (1753), *Cleome pentaphylla* L. (1763), and *G. pentaphylla* (L.) DC. (1824). *Cleome gynandra* was reclassified as the sole member of the monotypic genus *Gynandropsis* based on the presence of a long androgynophore, the characteristic from which its name was derived (Iltis, 1960). However, such a structure has also been observed in *Cleome speciosa* and *Podandrogyne*. Many authors considered, therefore, this character as questionable and the species was renamed *C. gynandra* (Iltis, 1960; Sánchez-Acebo, 2005). Recent molecular studies, however, supported the reestablishment and conservation of *Gynandropsis* as a separate monotypic genus (Feodorova et al., 2010; Hall, 2008; Patchell et al., 2014). Partially because of its wide distribution range and diverse phenotypes, the species has an astounding forty-five synonyms used in literature. This plethora of names desperately calls for a taxonomic revision of the genus *Gynandropsis*.

While its origin and dispersal are still uncertain, Feodorova et al. (2010) suggested that the Cleomaceae family originated from Central Asia with subsequent dispersal to Southern Africa, Australia, and North, Central and South America. The speciation event leading to *G. gynandra* likely occurred in Southern Africa (Feodorova et al., 2010). However, Feodorova et al. (2010) used only a single Internal Transcribed Spacer region and four accessions from Australia and South Africa in their phylogeographic analysis. Further studies integrating more diverse germplasm collections and the use of whole-genome sequences would be helpful to reconstruct the demographic history of the species in the lights of expansion of utilisations (e.g. industrial utilisation of health promoters, establishment of improved seed value chains, leaf processing for consumption) and new scientific endeavours (see Table 2) by Omondi et al. (2017b), Sogbohossou et al. (2020), and Blalogoe et al. (2020).

Closely related species of the *Cleome* genus used as vegetables and medicinal plants in Africa include *Cleome rutidosperma* DC., *Cleome monophylla* L., *Cleome hirta* (Klotzsch) Oliv., and *Cleome viscosa* L. (Bose et al., 2007; Gowele et al., 2019; McNeil et al., 2018; Nguyen et al., 2017; Odhav et al., 2007; Phan et al., 2016; Raju and Rani, 2016; Singh et al., 2018). Recent phylogenetic studies demonstrated that *C. rutidosperma*, *C. monophylla*, and *C. hirta* belonged to the African clade while *C. viscosa* was in the Australian clade. African and Australian clades were clearly separated from the monotypic clade '*Gynandropsis*', another genus to which belongs *G. gynandra* (Feodorova et al., 2010; Patchell et al., 2014). Another famous Cleomaceae species is *Tarenaya hassleriana* (Chodat) Iltis (formerly *Cleome hassleriana*), an ornamental plant native to Southern America and introduced in other regions of the world including

North America, Europe, Australia, and Southern Africa (Bhide et al., 2014; Cheng et al., 2013; Nozzolillo et al., 2010). In Africa, *G. gynandra* is mainly found near human settlements, possibly feral escapes from earlier cultivation. It is often found in cultivated fields or fallows, along roadsides, in fence rows, and along irrigation canals and ditches. *Gynandropsis gynandra* can be found from sea level up to 2400 m altitude and requires warm conditions; its growth is hampered below 15 °C, which is typical of C_4 species. It thrives on a wide range of soils, mostly on sandy to clayey loam, provided they are deep and well-drained with a pH 5.5–7.0. It prefers soils with high organic matter and adequate mineral reserves (Mnzava and Chigumira, 2004).

3 Phytochemistry, Nutritional Value, and Health Benefits

Gynandropsis gynandra is a rich source of nutrients including vitamins, minerals (calcium, zinc, and iron), and protein (Omondi et al., 2017a; Sogbohossou et al., 2019; Yang and Keding, 2009). *Gynandropsis gynandra* leaves, young shoots and occasionally flowers are eaten boiled as potherb, relish, stew, or side dish (Grubben and Denton 2004; Mnzava and Chigumira, 2004). The leaves can also be blanched, made into small balls and sun-dried for preservation (Flyman and Afolayan, 2006). In some countries, the leafy vegetable is particularly sought for during extreme drought or famine periods, and therefore plays a significant role in maintaining household food security (Ekpong, 2009). The consumption of *G. gynandra* leaves can significantly contribute to the Recommended Nutrient Intake (RNI; WHO, 2004) of vitamin A, ascorbic acid, folate, and iron (Abukutsa-Onyango et al., 2010; Schönfeldt and Pretorius, 2011; Steyn et al., 2001; Uusiku et al., 2010; van Jaarsveld et al., 2014). However, variability was high in reported levels of provitamin A, ascorbic acid, riboflavin, iron, calcium, and magnesium across studies. This is potentially due to differences in harvesting and storage conditions, sample preparation, analytical methods, stage of maturity, growing conditions, environment as well as the cultivars/genotypes used. A comparative study between *G. gynandra*, *Brassica oleracea*, and *Beta vulgaris* revealed higher levels of phosphorus, potassium, calcium, iron, zinc, ascorbic acid, total phenolics, and flavonoids in *G. gynandra* than in the two other vegetables (Moyo et al., 2018). Moreover, the species had ratios of phytate:iron and phytate:calcium below the critical thresholds and could therefore be considered as a good source of bioavailable iron and calcium. In contrast, the phytate:zinc ratio was much higher than the critical threshold and thus zinc bioavailability might be compromised (Gowele et al., 2019). The assessment of the levels in provitamin A carotenoids, tocopherols, ascorbic acid, minerals, and phytate in 13 different African leafy vegetables

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revealed that *G. gynandra* had average levels of carotenoids and tocopherols, and high levels of ascorbic acid (Gowele et al., 2019).

Metabolite surveys on *G. gynandra* detected the presence of several health-promoting compounds in the species including unidentified phenolic compounds, flavonoids, glucosinolates, sesquiterpenes, terpenoids, aldehydes, and ketones (Moyo et al., 2018; Neugart et al., 2017; Omondi et al., 2017a; Sogbohossou et al., 2020). Degradation products of glucosinolates (isothiocyanates) have demonstrated anti-cancer properties and also can prevent cardio-vascular diseases (Cartea and Velasco, 2008; Traka and Mithen, 2009). Hydroxycinnamic acid derivatives (e.g. 5-hydroxyferulate, caffeoyl-oxalosuccinate and caffeoyl-hydroxycitric acid), polyphenolic compounds, reportedly possess potent antioxidant, anti-inflammatory properties, and have potential therapeutic benefits for diabetes and hyperlipidaemia prevention (Alam et al., 2016). Terpenoids were reported to have therapeutic properties, including anticancer, antiparasitic, antimicrobial, antiallergenic, antispasmodic, antihyperglycemic, anti-inflammatory, and immunomodulatory properties (Ajikumar et al., 2008).

4 Ethnobotanical Investigations for Increased Nutraceutical Benefits

In the past 10 years, ethnobotanical research has generated rich knowledge on the diversity of uses of spider plant across geographical regions, sociolinguistic groups, gender, age, and according to education status of the users amongst other socioeconomic attributes. The vernacular names of the species are noteworthy as they tell a story about how enslaved Africans migrating to the New World kept generic plant names from their communities of origin (van Andel et al., 2014). For example, *G. gynandra* is called 'Sambo' or 'Somboé' in Ewe and Mina communities of the coastal areas of West Africa while the same name 'Sambo' has been reported by Iltis (1960) in Barbados. Likewise, the vernacular name 'Akaya' in Fon and Mahi communities of Benin is declined by people in Martinique, Suriname, and French Guiana as 'Akaja', 'Akaïa', or 'Caïa'. The name 'Mozambue' or 'Mozembue', used in Angola, have their equivalent in 'Massambee' and 'Mozambe' in Guadeloupe, Barbados, and several other Pacific Islands (Iltis, 1960). While the plant was reported as a popular vegetable in French Guiana and Suriname in the eighteenth century, it is nowadays considered as a weed in those countries (van Andel et al., 2016).

Most studies have shown association amongst socio-demographic and socio-economic factors in the utilisation of the spider plant. For example, authors such as Kiebre et al. (2015), Voster et al. (2007), Sogbohossou et al. (2018a), and Chataika et al. (2020a) reported differences in the utilisation

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of spider plant as a result of cultural belief and influence, tradition and geographical separation, ethnicity, norms, and availability of the species. *Gynandropsis gynandra* is regarded as an efficient medicinal plant in several African and Asian countries. The leaves are used as disinfectants on wounds and taken as medicine for body aches and pains, eye infections, malaria, typhoid fever, anaemia, and skin conditions (Sogbohossou et al., 2018a; Yetein et al., 2013). In Kenya, the spider plant is consumed in recuperating individuals such as pregnant and lactating mothers, circumcised boys and invalids, and regular consumption of the leaves by expectant mothers has been reported to relieve childbirth complications as well as reduce the length of the labour period (Onyango et al., 2013). In India, *G. gynandra* has been used for several years as an anthelmintic and antimicrobial agent and in the treatment of diabetes mellitus (Ajaiyeoba, 2000). Medicinal uses of spider plant have been identified amongst different sociolinguistic groups including the use for curing eyesight, marasmus and scurvy in northern Namibia (Chataika et al., 2020b), for boosting immunity and blood production, treating diarrhoea, anaemia, rheumatism, chest pains, digestive disorders, inflammation, epilepsy, and malaria (Mnzava and Chigumira, 2004; Iwu, 2014; Sogbohossou et al., 2018a) and ulcers (Chinsembu, 2016). In South Sudan, Issa et al. (2018) reported the use of leaves of *G. gynandra* as herb to improve eyesight, cure spleen problems, expel worms, relieve headache and rheumatic pain. The species is also believed to possess antibacterial, antifungal, antiviral, analgesic, anticarcinogenic, anti-inflammatory, and acaricidal properties (Yang and Keding, 2009; Ghogare et al., 2009; Moyo et al., 2013; Abugre et al., 2011). The high levels of flavonoids, tannins, glucosinolates, and iridoids amongst other phytochemicals might be responsible for the medicinal and insecticidal properties. This implies that the species has a pharmaceutical potential that can be exploited through further research for the development of spider plant extracts and drugs.

Consumers' preferences varied depending on the countries and regions. The bitter leaves were preferred by the west African people who consider the bitterness of the leaves as an indicator of healing properties of the species. In contrast, East and Southern African communities prefer 'sweeter' varieties and use various methods to attenuate the bitterness of the leaves, for instance, by cooking them in milk (Sogbohossou, 2019; Flyman and Afolayan, 2006). This variation in consumers' preferences is therefore taken into account in breeding programs today. This has prompted extensive research into the secondary metabolites influencing the taste and aroma of leaves as well as their health-beneficial properties.

The economic potential of spider plant production was investigated in several African countries. In Namibia, the vegetable is sold in open markets (Chataika et al., 2020b) and was reported to generate income, in Namibian dollars, of N$1131.36 (USD71.37) per season per household (Kakujaha-Matundu, 1996), while in Kenya and South Africa, the vegetable was sold in open markets and supermarkets (Shackleton et al., 1998), generating an income, in South African rand, of R413 per month (USD26.05). Culturally, the vegetable has been used to serve chiefs and important people in the society (Onyango et al., 2013), while Kisii and Luo communities of Kenya serve the vegetable to high profile visitors to signify respect. Spider plant leaves are sometimes cooked with other species, such as *Amaranthus* spp., to improve the taste. Sometimes, cooked leaves are dried and flattened into cakes, locally known as 'omavanda' in Namibia, for off-season use or to sell at the open markets (Chataika et al., 2020a).

5 Reproductive Biology, Cytogenetics, and Hybridisation

Early in 1990, it was reported that plants of the genus *Cleome* can be both self- and cross-pollinating. Uniformity between populations for most traits (days to flowering, plant height, number of primary leaves, leaf length, leaf breadth, fresh leaf weight and dry leaf weight) was also observed (Omondi, 1990). Such uniformity can only arise from a predominantly self-pollinating species although this needs to be quantified. This uniformity raises the question of self-compatibility in *G. gynandra* and this can be determined following the classification used by Lloyd and Schoen (1992), Kalin Arroyo and Uslar (1993) based on hand pollination for self and cross-pollination. This was done by Omondi et al. (2017b) under greenhouse conditions and results showed a possibility of seed set after selfing, and average seed numbers per fruit were balanced in self- and cross-pollinations. Omondi et al. (2017b) then concluded that *G. gynandra* is self-compatible or at least partially self-compatible. One important remark was that the floral structure in *G. gynandra*, with its open flowers exposing the anthers and stigmas, colourful petals for pollinator attraction, sticky pollen, and elongated stigma may favour cross-pollination more than self-pollination in open fields. From there, Zohoungbogbo et al. (2018) initiated their study to clarify the preferential mating system in *G. gynandra* especially under open field conditions. They observed that open-pollinated flowers of *G. gynandra* produced more fruits and seeds than hand-pollinated flowers. Natural selfing was also possible but resulted in low fruit and seed set. In addition, hand selfing gave high fruit set suggesting that *G. gynandra* is self-compatible as previously observed by Omondi et al. (2017b). It was concluded that *G. gynandra* is a self-compatible and predominantly outcrossing species. The high outcrossing rate can be due to the floral structure of *G. gynandra*, which also attracts pollinators. *Gynandropsis gynandra* vegetative growth, flowering, and fruiting events were concomitant and very prominent during the period of three to six weeks after sowing. Raju and Rani (2016) reported that *G. gynandra* is polygamodioecious, consisting of andromonoecious individuals

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producing both staminate and fertile hermaphrodite floral types and fertile hermaphrodite individuals. The fertile hermaphrodite individuals have either medium gynoecium short stamen floral type, or medium gynoecium sessile stamen floral type.

Zohoungbogbo et al. (2018) did not observe the hermaphrodite individuals with either medium gynoecium short stamen floral type, or medium gynoecium sessile stamen floral type during their study and concluded that *G. gynandra* was an andromonoecious plant with three categories of flowers: functional staminate with short gynoecium, functional hermaphrodite with medium gynoecium, and functional hermaphrodite with long gynoecium. These different categories of flowers contributed to increasing the pollen availability and viability rate and presence of pollinators.

Cross-pollination in *G. gynandra* is expected to increase with insect activities. Raju and Rani (2016) observed that 69% of total foraging visits of insects for *G. gynandra* were made during dusk hours and the remaining percentage during the morning hours of the following day. Common visitors are bees (90%), flies (7%), and butterflies (3%). The insects recorded by Raju and Rani (2016) were bees (*Apis cerana*, *Trigona iridipennis*, *Anthophora cingulata*, and *Anthophora*), ants (e.g. *Crematogaster* sp.), and butterfly (*Pachliopta aristolochiae*). For instance, Shilla et al. (2019) confirmed that bees visited the plants in the field at WorldVeg-ESA in Arusha during the less-rainy season, mainly September–January. Zohoungbogbo et al. (2018) observed nocturnal anthesis for *G. gynandra* similarly to *Cleome lutea* Hook. and *Cleome serrulata* Pursh (Cane, 2008). In this study, the flowers attracted no nocturnal visitors in the common gardens, but plentiful bees, wasps, and butterflies during daylight hours, attributes shared with some other desert Cleomaceae. On the other hand, Oronje et al. (2012) in Kenya observed *Hippotion eson*, *Hippotion osiris*, and *Nephele aequivalens* as nocturnal pollinators of *G. gynandra*, with in most cases, pollen presence on their proboscises instead of the head region. More investigations are needed to exhibit the diversity in nocturnal insect visitors and pollinators in regions where *G. gynandra* is distributed to better understand their implications in preferences to the cross-pollination for the species.

Chweya and Mnzava (1997) reported chromosome numbers of $2n = 18$, 20, 22, 32, and 34 for samples of the genus *Cleome* from Asia and South America. Specifically, Inda et al. (2008) reported that *G. gynandra* has a basic chromosome number ranging from 16 ($2n = 32$) to 17 ($2n = 34$). Using the root tip metaphase cells of *G. gynandra*, Omondi et al. (2017b) revealed that the species is diploid with a chromosome number of $2n = 34$. Different genome sizes of *G. gynandra* have been documented, including an approximate size of 1 Gb (van den Bergh et al., 2014) confirmed by Omondi et al. (2017b) who found that the genome size is of 2.31–2.45 pg/2C with an average genome size of 2.38 pg/2C.

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Intraspecific hybridisation in *G. gynandra* resulted in a high fruit set and good seed viability (Zohoungbogbo et al., 2018). Intraspecific hybridisation opened the door to the development of inbred lines and hybrids of *G. gynandra* based on the market requirements. Interspecific crosses between *G. gynandra* and its relatives may be possible (Chweya and Mnzava, 1997; Wang et al., 2004) and this was also attempted in the screen house at WorldVeg-ESA in 2014 (Shilla et al., 2019). Interspecific hybridisation is very useful in the transfer of desired functional genes from wild relatives. In this regard, the choice of the prospective relative species considering the chromosome number and other reproductive features contributes to overcoming potential bottlenecks associated with such practices.

6 Production and Husbandry

Statistics about production, yield, and cultivated area of spider plant across Africa are scanty. Spider plant, cowpea, leaf amaranth, and African nightshade represented 86% of the total horticultural production in Kenya in 2014 (Matui et al., 2016). More importantly, the production of spider plant increased from 19 428 metric tons in 2012 to 21 507 metric tons in 2013 with associated increases in acreage from 5634 acres to 8249 acres in the same country (HCDA, 2014). More statistics might exist at the local level but are not accessible globally. Efforts are needed to document the production statistics of the species as well as other important traditional crops.

The cultivation systems of *G. gynandra* has been extensively investigated with the ultimate goal to develop best agricultural practices for high leaf yield and nutritional value. Agronomic practices included planting techniques (direct seeding or transplanting), sowing depth, net cover colour, planting density, harvest techniques, planting date, pests, deflowering, and fertilisation (Ayua et al., 2016; Garjila et al., 2017; Gonye et al., 2017; Maniaji, 2018; Masinde and Agong, 2011; Mauyo et al., 2008; Mavengahama, 2013; Mutua et al., 2015; Obel et al., 2019; Seeiso and Materechera, 2012; Wangolo et al., 2015).

In some areas (e.g. northern Togo, north-eastern Benin), the plant appears with the first rains and harvest quickly to bridge the shortage gap between two production seasons. However, *G. gynandra* can equally become invasive and treated as weed (Figure 2) and removed accordingly during land clearing for major crops or it can be abandoned till senescence.

6.1 Quality Seed Availability and Management

Seed quality plays a crucial role in determining yield and quality of crop production (Wimalasekera, 2015). However, limited information and research to

Figure 2 Invasive spider plants in a waste area along road side in Kara (northern Togo).

understand seed behaviour and improve seed quality are available for most African Leafy vegetable including spider plant.

Spider plant was traditionally harvested in the wild and not cultivated by farmers. Low germination capacity, delay, and non-uniformity in germination are major constraints in the species, mainly propagated by seeds recognised as orthodox (Kamotho et al., 2014). As a result, farmers have difficulties to get access to quality seeds, which are essential to achieve high productivity. Once the seed is harvested and dried, it must be stored in a dry area for better germination. *Gynandropsis gynandra* seeds were shown to be negatively photoblastic when exposed to continuous light beyond 12 hours (Ochuodho and Modi, 2005; Sowunmi and Afolayan, 2015). Therefore, the optimum conditions for germination of the seed would be continuous dark and alternating dark and light for mostly 8 hours of light per day. Because of the tropical origin of *G. gynandra*, warm temperatures would be ideal for its germination and development. The favourable temperature for germination percentage higher than 50% ranged from 25 to 40 °C (Ochuodho and Modi, 2005; K'Opondo et al., 2011; Zharare, 2012; Sowunmi and Afolayan, 2015). The optimum temperature of germination varied from one study to another but was always within this range. However, Zharare (2012) found alternating 4/27°C for 16/8 hours improved seed germination, contradicting the tropical origin of the species, in which low temperatures typically do not promote the germination capacity.

6.2 Planting Techniques and Density

Planting techniques in *G. gynandra* include direct seeding or transplanting as the species is propagated through seeds. Seeds are small and for direct

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seeding, they are mixed with dry sand at a ratio 1 : 10 or 1 : 4 before broadcasting or drilling in rows spaced at 20–60 cm depending on the cultivation system (Chweya and Mnzava, 1997; Mnzava and Chigumira, 2004). Thinning is done three weeks after emergence, to leave 10–15 cm between plants. A deep sowing must be avoided to favour emergence of seedlings and have homogenous field. Therefore, shallow sowing at depths less than 1 cm is recommended. In the case of transplanting, seeds are sown in seedling trays filled up with compost, sand, or growth medium and grown for two to three weeks (Houdegbe et al., 2018). Transplanting offered a higher yield than direct sowing (Orchard and Ngwerume, 2009), while seed drilling in rows allowed better plant growth than broadcasting (Maniaji, 2018). The recommended spacing is 30–50 cm between rows and 15–20 cm within row for direct sowing (Oluoch et al., 2009), while 15–20 cm between and within rows was recommended for transplanting (Houdegbe et al., 2018). It is essential to highlight that seeds must be pre-treated to improve the uneven germination in the species. To this end, the grower can either go through the application of Gibberellin acid (GA3) for 6–12 hours or heating at 40 °C for three days (Ekpong, 2009; Muasya et al., 2009).

6.3 Fertilisation

Fertilisation exhibits a significant effect on the leaf yield and nutritional quality of the species. The dose depends on the type of fertiliser (organic or inorganic type). The recommended doses were 300 kg ha^{-1} of NPK, 300 kg ha^{-1} of lime ammonium nitrate (28% N) and 120 kg ha^{-1} of urea (40% N) for higher leaf yield (AVRDC, 2004; Mavengahama, 2013; Mutua et al., 2015). Gonye et al. (2017) found that 10 t ha^{-1} poultry manure, 30 t ha^{-1} cattle manure and 300 kg ha^{-1} NPK + 150 kg ha^{-1} ammonium nitrate improved leaf biomass, iron and vitamin C, vitamin A, and crude protein content when planting occurred at the beginning of the growing season. A dose of 20 t ha^{-1} farmyard manure and 11.5 t ha^{-1} of composted farmyard manure were recommended for farmers growing spider plant (Abukutsa-Onyango et al., 2005; Ng'etich et al., 2012). Kiebre et al. (2019) observed that the dose of 6 t ha^{-1} compost enhanced biomass yield as well as β-carotene and mineral content. The authors also pointed out the genotype effect on the response to compost. The wide range of recommended fertilisers might be attributed to the diversity of the environment (i.e. soil type, climatic conditions) where the studies were conducted as well as genotype and the type of fertiliser. Consequently, investigations should continue to identify the optimal dose in the target environment taking into account the locally available fertiliser. Also, the period of the fertiliser application during the crop growth cycle needs to be investigated.

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6.4 Deflowering

Early flowering represents a major constraint for *G. gynandra* farmers. The continuous flower/inflorescence removal as soon as they appear during production increases leaf yield and fresh shoot yield in comparison to shoot tip removal and to natural growth (Chweya and Mnzava, 1997; Mavengahama, 2013; Wangolo et al., 2015). Topping also extended the leaf production period in the species. However, these practices might imply additional costs for farmers, especially when commercial production is envisaged. Therefore, selection for late flowering remains the best option and should be of priority for breeding programs. In this vein, Zorde et al. (2020) identified the cultivar SP7-1 as promising with delayed flowering.

6.5 Harvesting Techniques

Harvesting practices include cutting (using a sharp-edged object for incision of the stem 15 cm above ground), topping (picking individual leaves or young shoots at defined intervals and harvesting tender stems, leaves, and flowers), and single harvesting by uprooting whole plants at 15 cm height or four to five weeks after sowing (Matro 2015; Oluoch et al., 2009). A comparison of some of those techniques revealed that harvesting tender stems, leaves, and flowers induced the highest economic leaf yield per plant and harvesting the whole plant at the base (above the first four nodes) gave overall significantly higher economic yield (Oluoch et al., 2009). In addition, the evaluation of the effects of different cutting techniques revealed that the highest leaf yield was obtained when all edible leaves were cut continuously weekly (Seeiso and Materechera, 2012). Weekly harvest increased leaf yield from first to fifth cutting before it started decreasing (Seeiso and Materechera, 2012). Chweya and Mnzava (1997) reported that under weekly harvest, leaf yields increased with plant age until about the seventh week of growth and then started declining. By the tenth week of growth, leaf yield decreased by about 90%. The same authors reported that biweekly removal of tender leaves allows regeneration of branches. It appears that harvest can be done at one or two weeks' interval. A comparison of the cutting frequency in the species suggested two-week intervals as the best practice for high leaf yield (Houdegbe et al., 2018). Another key component of cutting is the height; cutting at least 15 cm above ground allows adequate regrowth and higher biomass yield (Houdegbe et al., 2018). On the other hand, Mnzava (1986) observed that response to cutting in the species is genotype-dependent and further investigations should be carried out to select the best harvesting techniques for the cultivars taking into account farmers' best practices.

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6.6 Pest and Disease Management

Pests found in *G. gynandra* included stem borers, leaf miners, webbers, and defoliators (caterpillars, beetles) (Sithanantham et al., 2004). About 17% yield loss due to insects was estimated on a station in Kenya by Sithanantham et al. (2004). Cotton bollworm (*Helicoverpa armigera* Hübner) and greenflies attacked leaves of the species (Figure 3a). Cabbage aphid (*Brevicoryne brassicae* L.) is one of the serious pests, causing stunted growth

Figure 3 Pests associated with *Gynandropsis gynandra*. (a) *Helicoverpa armigera*. (b) *Brevicoryne brassicae*.

and wrinkling of the leaves and growing tips and caused total crop failure (Figure 3b) (Mnzava and Chigumira, 2004). Others insects include flea beetles (*Phyllotreta* spp.), green vegetable bugs (*Nezara* spp.), cabbage sawfly (*Athalia* spp.), cotton jassids (*Empoasca* spp.), and hurricane bugs (*Bagrada* spp.). *Phyllotreta* spp. attacks leaves by devouring leaves and making them not suitable for consumption (Schippers, 2004). Fungal diseases such as powdery mildew (*Sphaerotheca fuliginea* (Schltdl.) U. Braun et S. Takam., *Oidiopsis taurica* (Léveillé) E.S. Salmon), and leaf spot (*Cercospora* spp.) were also reported. *Gynandropsis gynandra* is also sensitive to root-knot nematodes (*Meloidogyne* spp.). While application of insecticides and biopesticides help control those pests, the development of pest and disease resistant cultivars remains non-investigated is needed.

7 Genetic Resources: Characterisation and Evaluation

Germplasm resources for *G. gynandra* are available in local, regional, and international genebanks. For example, a total of 295 accessions are currently maintained at World Vegetable (AVRDC), including 112 from East and Southern Africa and 183 from Asia, and thirty-one accessions from Southern Africa were recorded at the United States Department of Agriculture (USDA). Germplasm collections are maintained in Botswana, Kenya, Namibia, Tanzania, Zambia, and Zimbabwe (Mnzava and Chigumira, 2004). Germplasm collection missions were recently conducted in Benin, Togo, Ghana, Niger, Burkina Faso, and 164 accessions from these countries are maintained at the Laboratory of Genetics, Biotechnology, and Seed Sciences (GBioS) at the Faculty of Agronomic Sciences, University of Abomey-Calavi (UAC) in Benin. Germplasm collections represent global resources to develop and sustain a breeding programme for the species and characterisation and evaluation investigations are underway.

Omondi et al. (2017a) characterised 30 spider plant entries from six East and Southern African countries, including farmers' cultivars, gene bank accessions and advanced lines. The authors identified five morphotypes based on the stem and petiole colourations. All the morphological traits considered (germination percentage, days to 50% flowering, plant height, number of primary branches, number of seeds per silique, total shoot fresh and dry mass, leaf fresh and dry mass) exhibited significant genotypic variation except for 100 seed weight and silique weight. The morphological characterisation of a larger collection of 242 accessions of *G. gynandra* from East/Southern Africa and Asia revealed striking differences between accessions of the two regions (Wu et al., 2018). The gynophore and filament played a key role in taxonomical identification. The most variable traits between accessions were plant height, silique length, leaf size, flower colour,

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and flowering earliness. Distinct morphological differentiation was detected between Asian and African accessions. On average, African accessions were larger, less uniform and flowered later than the Asian ones. The results were used to establish a core collection of 49 *Gynandropsis* accessions (Wu et al., 2018). Sogbohossou et al. (2019) worked with a more comprehensive collection of accessions from East/Southern Africa, West Africa and Asia and found that the morphology of *Gynandropsis* accessions was location specific.

Gynandropsis gynandra exhibits significant genetic variation at the molecular level, which was revealed by random amplified polymorphic DNA (RAPD), inter simple sequence repeat (ISSR), simple sequence repeat (SSR), and single nucleotide polymorphism (SNP) markers. The first reported markers in the species were RAPD by K'Opondo et al. (2009), who generated 31 polymorphic bands from 10 primers to differentiate four Kenyan morphotypes (identified based on stem and petiole colours) of cultivated and wild plants. Kiebre et al. (2017) successfully assessed the diversity in Burkina-Faso's accessions using 10 polymorphic ISSR markers and pointed out that climatic factors drove the observed genetic differentiation among populations. Omondi et al. (2017b) developed 11 amplified fragment length polymorphism (AFLP) and nine SSR markers, which revealed high variation among studied accessions. The SSR markers revealed heterozygosity values between 0.18 and 0.78. The polymorphic information content (PIC) varied between 0.17 and 0.74. The average pairwise genetic distance among genotypes was 0.47 (0.13–0.77). With these markers, the authors were also able to differentiate farmers' cultivars from the genebank's accessions and advanced lines. A better understanding of the genetic diversity, differentiation, and population structure in the species was provided by Sogbohossou (2019) through the genome sequencing of 53 Asian and African accessions using SNP markers. The author revealed a positive association between the genome variation and the geographic provenance with Asian, West African and East/South African populations. Asian populations were closer to West African ones and both distant from Eastern/Southern populations, with the later the probable centre of origin of the species. Also, efforts are underway to assemble the genome of the species to provide a strong resource to speed up improved cultivar development.

8 Quantitative Variations and Breeding Value

Quantitative genetic parameters of target traits are prerequisite for designing an appropriate breeding program for new cultivar development and include analysis of variance components, heritability, breeding values, and combining ability. This information is still lacking for many African leafy vegetables,

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including *G. gynandra*. This situation results from the fact that many actions towards the promotion of African leafy vegetables over the last decades focused on assessing morphological and genetic diversity and agronomy, while overlooking the development of suitable breeding programs. Also, a poor understanding of the reproductive biology of the species contributed to this, as the species was believed to be self-pollinated (Chweya and Mnzava, 1997), while it is self- and cross-compatible with predominantly out-crossing (Omondi et al., 2017b; Raju and Rani 2016; Zohoungbogbo et al., 2018).

Based on the reported farmers' constraints and the participatory evaluation of some accessions, leaf yield, flowering time, leaf traits, plant height, storability, regrowth ability as well as leaf bitterness are candidate traits for the exploration of gene actions (Matro, 2015; Onyango et al., 2013). In addition, nutrients such as vitamin, mineral, and secondary metabolite contents are key areas of investigation for breeding values (Sogbohossou, 2019). To the best of our knowledge, limited information on genetic parameters of these traits is available. Understanding the variation components requires the development of breeding populations using different mating designs such as diallel, North Carolina, bi-parental, F2 populations, recombinants inbred lines as well as immortalised populations. Variance component analysis revealed that the genetic variance has both additive and dominance components using progenies generated from North Carolina Design (Salaou, 2020) and diallel (Akita, 2020). The predominance of additive or dominance components is trait and environment-specific. This implies that cultivar development in the species should target a specific environment. More investigations are still underway to decipher the environmental influence on the inheritance of functional traits in the species as well the genetic mechanism controlling each trait to better address farmers' and consumers' preferences.

Combining ability estimates are very important in the selection of parents and progenies for breeding population development. The species displayed high significant general and specific combining ability effects (Akita, 2020; Salaou, 2020). Consequently, some parents exhibited high general combining ability effects as well as some crosses with high specific combining ability effects. Moreover, several F1 progenies outperformed the parents, suggesting the existence of hybrid vigour in the species. Heterosis displayed by the species was both negative and positive and trait-specific. Investigations are needed to assess the heterosis by environment interaction as well as maternal effects in the species.

Heritability is an important parameter and helps assess the response to selection and include narrow- and broad-sense heritability. Using F_2 populations, Sogbohossou (2019) observed high broad-sense heritability for some agronomic traits and essential vitamins in the species. Moreover, Kangai Munene et al. (2018) and Kiebre et al. (2017) reported high broad-sense heritability for leaf biomass, fruit traits, plant height, stem diameter, primary branches number, and days to 50% flowering in *G. gynandra* (Table 1).

Table 1 Broad-sense heritability and genetic gain for leaf biomass and related traits in *Gynandropsis gynandra* (Kiebre et al., 2017; Munene, 2017).

Functional traits	Broad-sense heritability (H^2)	Genetic gain ($i = 5\%$) over mean (%)
Stem diameter	0.72	33.09
Plant height	0.82–0.97	36.10–90
Number of primary branches	0.69–0.94	27.87–56.67
Leaflet width	0.68	24.38
Leaflet length	0.78–0.89	28.99–43.57
Leaf area	0.86–0.87	36.10
Days to 50% flowering	0.78–0.82	13.73–15.30
Leaf biomass	0.81	57.63

Source: Kiebre, Z., Bationo-Kando, P., Barro, A. et al. (2017). Estimates of genetic parameters of spider plant (*Cleome gynandra* L.) of Burkina Faso. International Journal of Agricultural Policy and Research, 5(9): 138–144; Munene, A. K. (2017). Genetic Characterization and nutritional analysis of Eastern and South African Cleome gynandra (spider plant) accessions. University of Nairobi, Kenya.

More importantly, the genetic variance was higher than the environmental variance (Kangai Munene et al., 2018; Kiebre et al., 2017). On the other hand, narrow-sense heritability of leaf yield and related traits ranged from low to high and trait-specific (Akita, 2020; Salaou, 2020). With the high broad-sense heritability, significant genetic gain ranging from 13% to 58% with the highest for biomass (Kiebre et al., 2017). Therefore, significant genetic improvement can be achieved in *G. gynandra*.

8.1 Conventional Breeding, Genomics, and Marker-Assisted Selection

Sogbohossou et al. (2018b) proposed the pathways for conventional breeding and genomics or markers assisted selection in *G. gynandra* for cultivar development. Known sources of variations and diversity are nowadays well characterised and included so far accessions from Asia, West Africa, and East Africa. West African accessions are short plants with small leaves, with high tocopherol contents, and relatively low carotenoid contents; Asian accessions are short plants with broad leaves and with relatively low carotenoid and high tocopherol contents; while East-Southern African plants were tall with high contents of both carotenoids and chlorophylls, and low tocopherol contents according to Sogbohossou et al. (2019). Also, accessions differed significantly with respect to seed size (area, perimeter, length, width), 10-seed weight, mean germination time, and germination percentage. Asian accessions exhibited smaller seed size and recorded higher values in terms of germination percentage. West African accessions had bigger seed size but with lower germination percentage (Blalogoe et al., 2020). Those sources of variation can be potentially exploited for accelerated cultivar development. In *G. gynandra*, preferred traits by local communities include leaf size, late flowering, number of branches. According to Sogbohossou et al. (2018a), retailers and consumers seek good appearance, long shelf-life, superior taste and aroma, high nutritional value, and affordability. Besides, phytochemical studies indicated that *G. gynandra* is rich in vitamin C, provitamin A, and high concentrations of glucosinolates, flavonoids, tannins, iridoids, and other phytochemicals in the leaves. To improve *G. gynandra* and assemble preferred traits in higher-yielding cultivars, Sogbohossou et al. (2018b) indicated that the ideotype can take the form of a pure line variety, an open-pollinated variety, a hybrid or, in some cases, a clonally propagated cultivar. With our current knowledge of *G. gynandra*, selection of lines for conventional breeding are underway and this will be reinforced with genomic tools.

Like many African leafy vegetables, no genomic resources were reported in *G. gynandra* before 2015. Luckily, the increasing awareness of the potential of species in combating hidden hunger leads to implementation of many projects with the focus on generating genomic resources. For instance, the species is among the 101 selected species for which a reference genome will be generated by the African Orphan Crops Consortium. The reference genome of the species is already assembled and will be made available for researchers soon (http://africanorphancrops.org/ongoing-projects/). To date, there are no reports on genome-wide association studies (GWAS) nor genomic selection (GS) in the species. However, efforts are underway to investigate GWAS and GS in *G. gynandra* using African and Asian accessions. More germplasm from the distribution area of the species is required to enhance the knowledge on the genomic regions controlling the morphological and agronomic, nutritional and metabolic elements in the species.

9 Industrial Development Pathways and New Research Avenues

Recent development in *G. gynandra* research witnessed a lot of interesting findings that can be valuable for the industry if they are promoted. Main thematic areas investigated so far include genetic resources and phytochemistry, genetic diversity, reproductive biology and ecology, cytology, crop physiology, pre-breeding and selection, seed system, crop husbandry (Table 2).

Phytochemical investigations revealed for instance a large variation in 936 semi-polar compounds including flavonoids, terpene glycosides, glucosinolates, and various phenolic compounds (Sogbohossou et al., 2020). In addition, the levels of carotenoids and tocopherols in the leaves varied

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Table 2 Main thematic areas for improving Cleome utilisations for development.

Main thematic areas	Authors	Research focus	Research highlights	Industrial opportunity/ research gaps
Genetic resources, phytochemistry	Sogbohossou et al. (2020)	Secondary metabolites variation in 48 African and Asian accessions	Large variation in 936 semi-polar compounds including flavonoids, terpene glycosides, glucosinolates, and various phenolic compounds	Specialised pharmacological production of compounds for healthcare systems
			The variation in levels of the semi-polar metabolites was mainly driven by geography, with accessions from both West Africa and Asia forming a group clearly separated from East African accessions	Conservation and utilisation of genetic resources based on geographical origin; further investigation of gene actions involved in semi-polar metabolites synthesis
			Detected volatile metabolites included various sesquiterpenes, aldehydes, ketones, and sulphur-containing isothiocyanates with no geographic signature	Further plant-herbivore interaction studies required to understand resistance/tolerance mechanisms in *G. gynandra*
			The relative abundance in glucosinolates and isothiocyanates in the leaves allowed the clustering of accessions into two main groups	Core collection development for further utilisation in metabolites synthesis in healthcare systems

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Table 2 *(continued)*

Main thematic areas	Authors	Research focus	Research highlights	Industrial opportunity/ research gaps
Genetic resources, phytochemistry	Sogbohossou et al. (2019)	Association between vitamin content, plant morphology, and geographical origin	Levels of carotenoids and tocopherols in the leaves varied significantly across accessions and were linked with the geographical origin and morphological variation	Fine mapping QTLs/identifying genes involved in biosynthesis pathways of carotenoids and tocopherols in *Gynandropsis gynandra*
				Assessment of variation in metabolic profiles across plant developmental stages
				Effect of cooking in nutrient bioavailability
				Selection of parental accessions with interesting metabolic profiles for good by good crosses
			Accessions grouped into 3 clusters based on variation in nutrient content and morphology	Participatory field evaluation of accessions with promising morphological traits/nutritional profiles – QTL analysis and elucidation of gene actions underlying specific traits (e.g. flowering time, plant height, leaf size, branching patterns, etc.)

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Genetic resources, phytochemistry	Mamboleo et al. (2018)	Vitamin C, iron and zinc levels at different stages of maturation	Decreased zinc content from 21 days to 35 days after planting with an increased iron content during the period	Evaluation of genotype × environment interaction of mineral content using a large number of accessions
Genetic resources, phytochemistry	Makokha et al. (2019)	Assessment of levels of minerals at different harvesting stages and locations of production in Western Kenya	Variation in minerals content among locations and harvesting stages	Optimised harvesting time for the exploitation of high mineral content; evaluation of genotype × environment interaction of mineral content using a large number of accessions
Genetic resources, phytochemistry	Omondi et al. (2017a)	Mineral content, glucosinolates and flavonoids and morphological variation in 30 entries of spider plant from Eastern and Southern African countries	High variation among entries in mineral concentration and mainly in potassium, calcium, magnesium, phosphorus, iron, manganese and zinc	Selection of accessions with interesting levels of mineral content; evaluation of breeding populations for phenotypic variance partitioning
			The main glucosinolate was aliphatic 3-hydroxypropyl glucosinolate while glycosides of quercetin, kaempferol and isorhamnetin were the main flavonoids with their highest concentration was plant organ specific	Aliphatic 3-hydroxypropyl glucosinolate, quercetin, kaempferol derived drugs for healthcare systems; Fine mapping QTLs/identifying genes involved in biosynthesis pathways of specific glucosinolates or flavonoids interesting for human nutrition and health

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Table 2 *(continued)*

Main thematic areas	Authors	Research focus	Research highlights	Industrial opportunity/ research gaps
			Morphological characterisation revealed five morphotypes the stem and petiole colourations	Participatory field evaluation of accessions with promising morphological/agronomic traits – QTL analysis and elucidation of gene actions underlying specific traits (e.g. flowering time, plant height, leaf size, branching patterns, etc.)
Genetic resources, phytochemistry	Somers et al. (2020)	Evaluation of five selected genotypes for elemental minerals, anti-nutrients, antioxidant activity, total polyphenol and total flavonoid content grown in Eastern Africa and the Eastern United States	Significant variation was observed between genotypes grown under different conditions	Further identification of environmental drivers in nutritional values changes
Genetic resources, phytochemistry	Jinazali et al. (2017)	Nutrient composition of spider plant collected from different agro-ecological zones in Malawi	Significant variation in calcium and zinc was observed between samples collected from different conditions	Utilisation of spider plant for supplement drugs

Genetic resources, phytochemistry	Nyalala et al. (2011)	Acetonitrile (methyl cyanide) emitted by the African spider plant (*Gynandropsis gynandra* L. (Briq)): Bioactivity against spider mite (*Tetranychus urticae* Koch) on roses	This study provides a very strong indication that foliar emissions of acetonitrile by *G. gynandra* are responsible, to a significant degree, for the spider mite repellent activity of the plant when used as an intercrop with roses	This research opens doors to the use of quantification and use of secondary metabolites in Spider plant to fight against pests/diseases. Possible use in agroecology
Genetic Diversity, Reproductive biology and cytology	Omondi et al. (2017b)	Mating biology, nuclear DNA content and genetic diversity in 30 entries of spider plant from Eastern and Southern African countries	Hand pollination study revealed that the species is self- and cross-compatible	Utilisation of both reproductive system to develop several types of improved cultivars through several breeding pipelines
			All 30 entries were diploid with genome sizes ranging from 2.31 to 2.45 pg/2C. The chromosome numbers of $2n = 34$ in root tip metaphase was reported	Clear knowledge on the chromosome number for possible genetic map establishment for any target traits. Further investigation of genome variation in a large collection from different geographical regions of the world. Genome sequencing and annotation to facilitate omics-assisted breeding

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Table 2 *(continued)*

Main thematic areas	Authors	Research focus	Research highlights	Industrial opportunity/ research gaps
			Genetic diversity among the 30 studies entries was revealed by 11 amplified fragment length polymorphism (AFLP) and nine SSR markers to differentiate farmers cultivars from the genebank's accessions and advanced lines	Further utilisation of the identified AFLP and SSR markers to assess large collection of the species germplasm at a relative low cost. Re-sequencing of several accessions or breeding population for genome-wide marker development (SNPs) to accelerate breeding efforts
Reproductive biology and ecology	Zohoungbogbo et al. 2018	Understanding the reproductive biology and floral morphology in African and Asian accessions	*Gynandropsis gynandra* benefits from both self and cross-pollination to ensure reproductive success	Further development of Open Pollinated Varieties (OPVs) and Hybrids Varieties by seed companies
			The andromonoecy reproductive mode offers a range of possibilities to future breeding programs in *G. gynandra*	Different possibility to accelerate the seeds production and varieties development in *G. gynandra*
			Seeds viability or seedling vigour were almost similar for the different types of pollinations with low germination rate	Further seeds dormancy breaking studies required to understand dormancy mechanisms of *G. gynandra*

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Reproductive biology and ecology	Raju and Rani (2016)	Understanding the functionality of sexual system in the floral types of *G. gynandra*	Polygamodioecious sexual system supported by highest fruit and seed set rates in hermaphrodite	Different possibility to accelerate the seeds production and varieties development in *G. gynandra*
			The flower-opening occurs during dusk hours and it is pollinated principally by bees during dusk hours and again during the forenoon period of the next day	Facilitate crossing for hybrids development in *G. gynandra*
			The pollen production rate is very high and it is almost similar in all three floral types	Further investigation in pollen viability and characteristics required to understand their impact on the crossing success rate in *G. gynandra*
			The ability of the plant to use both bees or insects and wind is indicative of ambophily	Identification of the bees attracted by *G. gynandra* and the importance of nectar production of the species
Reproductive biology and ecology	Cane (2008)	Seed production and species-rich bee guilds of *Cleome*	Flowering patches of *Cleome* attract and feed diverse floral generalists from local bee communities	Potential value of the plant for native bee communities
Crop physiology	Mavengahama (2013)	Yield response of bolted spider plant (*G. gynandra*) to deflowering and application of nitrogen topdressing	The removal of flowers and nitrogen application resulted in significant increases in the fresh and dry weight of spider plant leaves. The removal of flowers resulted in a 46% increase fresh weight of leaves	Further investigation about the trade-off mechanism could be useful to understand the process of leaf yield accumulation

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Table 2 *(continued)*

Main thematic areas	Authors	Research focus	Research highlights	Industrial opportunity/ research gaps
Crop physiology	Aubry et al. (2016)	A specific transcriptome signature for guard cells from the C4 Plant *Gynandropsis gynandra*	Genes associated with C4 photosynthesis were more highly expressed in guard cells of C4 compared with C3 leaves. In the first, genes previously associated with preferential expression in the bundle sheath showed continually decreasing expression from bundle sheath to mesophyll to guard cells. In the second, expression was maximal in the mesophyll compared with both guard cells and bundle sheath. These data imply that at least two gene regulatory networks act to coordinate gene expression across the bundle sheath, mesophyll, and guard cells in the C4 leaf	Understand the structure of C3 and C4 cleome species based on their origin
Crop physiology	Reeves et al. (2018)	Natural variation within a species for traits underpinning C4 photosynthesis	Accessions of *G. gynandra* collected from locations across Africa and Asia exhibit natural variation in key characteristics of C4 photosynthesis. Variable traits include bundle sheath size and vein density, gas-exchange parameters, and carbon isotope discrimination associated with the C4 state	Need to extend research on how some *Cleome* species evolved from C3 to C4. This will help in the current development of C4 species from C3 species (case of C4 rice project)

Breeding/ Selection	Zorde et al. (2020)	Screening of 4536 spider plants derived from nine different advanced lines of spider plant accessions for delayed flowering time	The cultivar SP7-1 showed a longer vegetative duration than other accessions and flowering time was heritable	Potential development of delayed flowering cultivars for longer vegetative growth and multiple harvests
Breeding/ Selection	Mosenda et al. (2020)	Evaluation of 14 selected Kenyan spider plant accessions under drought stress and non-drought stress conditions with drought stress conditions included (40%, 60%, and 80% field capacity)	Reduction in leaf yield and growth ranged from 25.7% to 74.2%	Necessity to develop drought-tolerant cultivars for local communities. Further investigation of drought-tolerant accessions using a worldwide accessions
			Differential response to drought among genotypes with accessions GBK-032210, Baringo, Kuria, Homabay, Kakamega and GBK040449 were identified as promising candidate genotypes for drought breeding in spider plant	Further exploitation of these cultivars in breeding programs and investigating gene action underlying drought tolerance in the species for implementing sound drought-tolerant cultivars

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Table 2 *(continued)*

Main thematic areas	Authors	Research focus	Research highlights	Industrial opportunity/ research gaps
Seed system	Ekpon (2009)	Seed maturity, seed storage and germination pre-treatments on seed germination in *G. gynandra*	The species exhibited various forms of seed dormancy	Deeper understanding of seed dormancy in *G. gynandra* seeds
			Seed dormancy was broken after three months at 15 °C and room temperature	Validation of seed storage effect with large accessions
			Water trapped in the tissue between the embryo and seed coat has created an oxygen barrier	
			Pre-heating at 40 °C for period of 1–5 days was the most effective method in breaking dormancy in *G. gynandra*	Development of commercial varieties
Seed system	K'opondo et al. (2011)	Temperature and light optima for seed germination and seedling development of morphotypes from western Kenya	Temperature optimum for seed germination is 35 and 40 °C, and light had no influence on seed germination	Development of seed testing protocol

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			Seedling development was normal at 30 °C, and white light was required for seedling development	
Seed system	Seeiso and Materechera (2012)	Effects of seed sowing depth on emergence and early seedling development of two African indigenous leafy vegetables	Seeds of *Cleome gynandra* should be sown at shallower depths (1–5 mm) in order to ensure rapid emergence and early establishment of seedlings if sown directly into the soil	Good agronomic practices for better seed germination plant development
Seed system	Kamotho et al. (2014)	Management practices and seed maturity stages for seed quality and yield production	Nip the first flower heads and harvest at yellow pod maturity	Development of strategies for seed companies and farmers in seed quality production
Seed system	Kamotho et al. (2014)	Seed maturity stage, desiccation and storage period for quality of *G. gynandra* seed	Spider plant seed has been depicted as orthodox seed	Long period of seed conservation
			Spider plant seed germination increased when harvested at yellow pod maturity stage, dried to 5% moisture content and stored for six months	Study of storage period required for each accession to reach high germination rate

(*continued overleaf*)

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Table 2 *(continued)*

Main thematic areas	Authors	Research focus	Research highlights	Industrial opportunity/ research gaps
Seed system	Motsa et al. (2015)	Effect of light and temperature on seed germination of selected African leafy vegetables	Optimum temperatures for seedling emergence ranged from 25 to 31 °C	Possibility to accelerate production in tropical regions
			Light has no effect on cleome seed germination	Validate the effect of light on cleome seed germination using accessions from various origins
Seed system	Zharare (2012)	Variation in seed dormancy breaking for two biotypes from Zimbabwe and South Africa	Evidence of habitat-specific driven selection in *G. gynandra* biotypes	Core collection development for further analysis of seed germination variation
			Differences in seed dormancy expression between the biotypes of *G. gynandra*	Assessment of the natural variation of seed dormancy in *G. gynandra* at phenotypic and genotypic levels
			The biotypes differed in environmental requirements for breaking seed dormancy	Interaction between breaking methods and seed provenance

Seed system	Blalogoe et al. (2020)	Seed morphology, mineral composition and germination percentage in 29 accessions from West-Africa, east-southern Africa and Asia	Asian accessions exhibited lower seeds with high germination	Selection of accessions for production. Seeds traits can be considered in breeding programs for better seed germination
			West Africa exhibited bigger seeds with lower germination	Development of hybrids with high germination for farmers
			Variation in minerals such as potassium, carbon, and calcium content according to the geographical origin	Accessions with extreme values can be used to develop mapping populations for seed related traits, including fatty acid, protein, and gibberellic acid content
Crop husbandry	Houdegbe et al. (2018)	Effect of seedling age, plant density, cutting height and frequency on growth and leaf yield	Survival of two and three weeks old seedlings	Transplanting for better crop standing and higher leaf yield
			Spacing of 15 cm × 15 cm, cutting height greater than 15 cm and harvesting at two weeks' interval induced better regrowth and high leaf yield	Better agronomic practices for a large species cultivation in market gardening system. Further evaluation of different genotypes under the identified genotypes

significantly across accessions and were linked with the geographical origin and morphological variation (Sogbohossou et al., 2019). Other research revealed that zinc content can decrease from 21 days to 35 days after planting while iron content increases during the same period (Mamboleo et al., 2018). Significant variation in calcium and zinc was observed between samples collected from different environment (Jinazali et al., 2017). With increased consumer awareness of the nutraceutical importance of the species and the introduction of the species into vegetable production systems, seed companies would be interested in providing farmers with high-quality seeds. As indicated above, scientific evidence of the presence of a wide range of health-promoting compounds in the species coupled with the utilisation of the species in local pharmacopoeia can strengthen campaigns to raise consumer awareness on the importance of consuming spider plant and other local leafy vegetables. A bio-based economy could be developed around spider plant. For instance, specialised pharmacological production of compounds for healthcare systems is expected. Spider plant can be selected and abundantly cultivated for supplement drug production. Findings also revealed that foliar emissions of acetonitrile by *G. gynandra* are responsible, to a significant degree, for the spider mite repellent activity of the plant, when used as an intercrop with roses. This knowledge opens doors to the quantification and use of secondary metabolites in spider plant to fight against pests/diseases in agroecological production systems. Knowledge on targeted genotypes is available and those genotypes are currently well conserved in renown genbanks. With the progress in phytochemical research new questions arise and are related to (i) the degree of heritability of genes involved in semi-polar metabolite synthesis; (ii) plant-herbivore interactions to understand resistance/tolerance mechanisms in *G. gynandra*; (iii) genes involved in biosynthesis pathways of carotenoids and tocopherols in *G. gynandra* for fine mapping of QTLs; (iv) metabolic profiles across plant developmental stages; (v) nutrient bioavailability after cooking; (vi) gene actions underlying specific traits (e.g. flowering time, plant height, leaf size, branching patterns); (vii) harvesting time for exploiting high mineral content; (viii) genotype × environment interaction of mineral content based on a large number of accessions.

Gynandropsis gynandra seeds are rich in oleic, linoleic, and hexadecanoic acids (Aparadh and Karadge, 2010; Mnzava, 1990). The seed oil composition is comparable to that of leguminous seeds. As such, the oil can be used as cooking oil. High yielding seed cultivars can therefore be developed for that purpose. However, there is a need to advance our knowledge of the variation of oil content and fatty acid composition among genotypes to develop improved oily cultivars.

Cytological analysis and reproductive biology shed light onto the possibility for intra and interspecific mating (Omondi et al., 2017b; Zohoungbogbo et al., 2018; Raju and Rani, 2016). Clear knowledge on the chromosome number offers the possibility for genetic mapping for any target traits. Further investigation of genome variation in a large collection from different geographical regions of the world may increase our knowledge of genome size variation in the species. With the knowledge of the chromosome number, genome sequencing and annotation to facilitate omics-assisted breeding are foreseeable.

Gynandropsis gynandra benefits from both self and cross-pollination to ensure reproductive success. This is an opportunity for the utilisation of both reproductive systems to develop several types of improved cultivars with several breeding pipelines. The ability of the plant to use both bees or insects and wind is indicative of ambophily. Further development of Open Pollinated Varieties (OPVs) and Hybrids Varieties by seed companies is now within reach. Further investigations can focus on pollen viability and characteristics required to understand their impact on the crossing success rate in *G. gynandra*.

In *G. gynandra*, the removal of flowers and nitrogen application resulted in significant increases in the fresh and dry weight of leaves. The removal of flowers resulted in a 46% increase fresh weight of leaves (Mavengahama, 2013). This calls for further investigations about the trade-off mechanisms that could be useful to understand the process of leaf yield accumulation. Aubry et al. (2016) reported differences in the expression of genes associated with photosynthesis pattern of *G. gynandra* with genes associated with C_4 photosynthesis more highly expressed in guard cells of C_4 compared with C_3 leaves. The same authors also reported that genes previously associated with preferential expression in the bundle sheath showed continually decreasing expression from bundle sheath to mesophyll to guard cells in *G. gynandra*. Also, it was observed that genes expression was maximal in the mesophyll compared with both guard cells and bundle sheath. These data imply that at least two genes regulatory networks act to coordinate gene expression across the bundle sheath, mesophyll, and guard cells in the C_4 leaf (Aubry et al., 2016). Here the type of gene functions needs to be further investigated because accessions of *G. gynandra* collected from locations across Africa and Asia exhibit natural variation in key characteristics of C_4 photosynthesis (Reeves et al., 2018). Variable traits include bundle sheath size and vein density, gas-exchange parameters, and carbon isotope discrimination associated with the C_4 state. There is a need to extend research on how a number of *Cleome* species evolved from C_3 to C_4. This will help in the current development of C_4 species from C_3 species (case of C_4 rice project) by including functional components of C_4 photosynthesis pathway to C_3 photosynthesis pathway. This will call for a manipulation of both anatomical and biochemical traits of C_3 species. Overall, future research should explore variation across genotypes taking also the photosynthetic pattern into account to depict variation in water uptake, photosynthetic efficiency, and

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water use efficiency traits like leaf conductance, photosynthetic assimilation rate, chlorophyll content, leaf thickness, initial nitrogen use efficiency.

So far breeding efforts in *G. gynandra* has focused on flowering time and drought tolerance in a limited number of accessions. For instance, Zorde et al. (2020) screened 4536 spider plants derived from nine different advanced lines of spider plant accessions for delayed flowering time. These authors revealed that the cultivar SP7-1 showed a longer vegetative duration than other accessions and flowering time was heritable. This is a very interesting result for the development of delayed flowering cultivars with longer vegetative growth and multiple harvests options. Mosenda et al. (2020) evaluated 14 selected Kenyan spider plant accessions under drought stress (drought stress conditions included 40%, 60%, and 80% of field capacity) and non-drought stress conditions and observed a reduction in leaf yield and growth range from 25.7% to 74.2%. In consequence, exploring a wider range of genotypes from diverse sources may bring new insights into drought-tolerant cultivars.

For further horticultural development, a stronger seed system needs to be established for *G. gynandra*. Currently, seeds are mostly purchased informally and saved from the previous season with a lot of incertitude about germination percentage and purity. Moreover, seed dormancy should be more well understood and a simple innovative dormancy breaking approach developed. Zharare (2012) observed differences in seed dormancy expression between the biotypes of *G. gynandra*. This was further confirmed by Blalogoe et al. (2020) who found that Asian accessions exhibited small seeds with high germination. A possible way to solve the low germination in some accessions would be to select out the genes limiting that trait.

Finally, our knowledge of crop husbandry is still limited (Houdegbe et al., 2018). More specifically, little is known about fertilisation modes and nutrients required during growth and development. Also, several pests and diseases limit *G. gynandra*'s production, but this remains insufficiently documented.

10 Conclusion

Gynandropsis gynandra is nowadays known to be highly promising as a leafy vegetable but also as a source of secondary metabolites and mineral elements such as provitamin A, vitamin C, iron, and zinc. Other important metabolites include flavonoids, terpene glycosides, glucosinolates, and various phenolic compounds. In many areas, knowledge of *G. gynandra* as a model orphan plant has improved. For instance, we know a bit more about the structure of the genetic diversity and how this diversity is distributed in the world. We also have a better understanding of seed dormancy types and possibility for higher production and genetic improvement of cultivars. However, there

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are important areas of investigation that can be propelled with advances in genomic and physiological data. To accelerate such investigation, more awareness should be raised among consumers and end-users about the nutraceutical benefits of this plant.

Supporting Information

Additional supporting information may be found online in the Supporting Information section in the HTML rendition of this article.

Related Articles

Genetics, Genomics and Metabolomics
Quantitative Genetics and Genomics of Plant Resistance to Insects
Advances in Plant Metabolomics
Sustainable Crop Production for Environmental and Human Health – The Future of Agriculture

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