SEED DORMANCY, VIABILITY AND GERMINATION OF CLEOME GYNANDRA (L.) BRIQ.: A REVIEW

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Abstract

***Cleome gynandra* L. (Brig.) like many other indigenous vegetables is grown by subsistence farmers in many areas in sub-Saharan Africa. Farmers use their own saved seeds from volunteers, neighbours and from local markets for propagation, although of recent some seed companies have started selling seeds, such as Simlaw in Kenya. In literature, there have been claims that *C. gynandra* seed has low germination tendency especially for the freshly harvested seeds and this was assigned to endogenous, non-deep physiological dormancy. In addition, different seed lots have shown different germination rates which was assumed to be influenced by the provenance and habitat from where it was collected. The low germination phenomenon is reported to decrease with increasing time of storage and is realised at the three months of storage and beyond. However, this contradicts to a preliminary study on seed germination test of spider plant which was carried out at AVRDC – The World Vegetable Centre, Eastern and Southern Africa in 2013 in Arusha, Tanzania. The test employed freshly harvested seeds from pods with three different maturity status, namely mature green, yellow and brown pods. From the test, seeds from all pods were germinated although those from brown pods had the highest germination rate followed by yellow and finally green pods. It is hereby recommended that further studies on, but more diverse and large number of accessions taken from different storage periods is done to explain the narrow scientific information available with regards to low *C. gynandra* seed germination.**

Introduction

Cleome gynandra L. (Briq.) is a nutritive herbaceous leafy vegetable, indigenous to many parts of sub-Saharan Africa (K'Opondo *et al.,* 2009; Zharare, 2012) and mainly cultivated by subsistence farmers or semi-domesticated (Muasya *et al.,* 2009). *C. gynandra* is commonly known as cat's whiskers, spider flower, spider plant or African cabbage. *C. gynandra* shares the common name "spider plant" with *Chlorophytum comosum*, a well-known ornamental plant in Europe and America. Like many other indigenous leafy vegetables, its seed used to be collected by farmers from volunteer plants, propagated for home consumption and in some cases for sale in local markets (Chweya and Eyzaguirre, 1999). Moreover, other sources of seeds were farmers' saved seeds, local markets, borrowed from neighbours and relatives, or collected from wild plants (Maundu *et al.,* 1993; Simiyu *et al.,* 2003). Today some seed companies, stockists and agro-vets for instance in Kenya have started selling *C. gynadra* and other Traditional African Vegetable seed (Muasya *et al.,* 2009; Shango, 2015). Similarly, some companies in Tanzania are also handling the seed of Traditional African vegetables. In South Africa seeds can be obtained from the Vegetable and Ornamental Plant Institute of the Agricultural Research Council at Roodeplaat (VOPI, Motsa *et al.,* 2015). AVRDC makes some seed available through seed kits supported by various projects.

Besides being a nutritious vegetable, it is as well said to encompass several medicinal properties (Chweya and Mnzava, 1997; Aparadh and Karage, 2010). Regardless of its benefits, lack of improved cultivars with

quality seed is one of the major constraints in cultivation of the crop (Chweya and Ezyaguirre, 1999; Abukutsa-Onyago, 2007). Quality seed is a key element for a successful crop production (Ochuodho, 2005). Seed quality is determined by several internal and external factors that influence seed development and maturation. The quality of seed is enhanced at physiological maturity when the maximum of the seeds sown germinate, and produce normal and vigorous seedlings (Hilhorst and Toorop, 1997). The minimum acceptable germination percentage of a seed lot of a particular crop is 85% (Abukutsa-Onyango, 2003). Seed samples from most African indigenous vegetables, including *C. gynandra*, collected from farmers' stores and other sources had a germination percentage range of 15 – 92% (Abukutsa-Onyango, 2003). It was supposed that the variability observed in germination might have been the result of poor seed processing and inherent dormancy. Contrary to this, a high germination percentage (about 95%) was reported for seeds obtained from research institutions (Kamotho, 2004; Kamotho *et al.,* 2014).

The dormancy characteristics and optimum conditions for *C. gynandra* (L.) seed germination and the genus *Cleome* in general have not been clearly explained (Ochuodho and Modi, 2005; de Castro *et al*., 2014). While several publications show that *C. gynandra* has very low seed germination, a preliminary seed germination test at AVRDC – The World Vegetable Center, Eastern and Southern Africa, that used seeds from mature green (i.e. with black mature seeds), yellow and brown pods, had good germination percentage (Dinssa and Shilla, pers. comm.). Seed development and germination are separated by a period of low metabolic activity referred to as dormancy or quiescence in majority of plant species. In weedy species, seed dormancy secures long-term survival by allowing the seeds to germinate over a long period (Shango, 2015). However, in commercial seed production, seed dormancy lowers the quality of seed by decreasing crop stand (Ochuodho and Modi, 2005). Caboche *et al*. (1998) observed that dormancy is a complex quantitative character controlled by several genes some of which are in turn controlled by environmental factors. This review article gives insights into seed dormancy, viability and germination of *C. gynandra* L.

Seed viability, dormancy and germination

Seed viability

A seed is said to be viable when dormancy is broken and the seed germinates and develops into a plant under favourable conditions (Gomez-Campo, 2007). Kamotho *et al* (2014) indicated that seed viability has a direct relation and is actually represented by the percent germination of seeds. The viability of seed is very critical for better production of crops derived from seed. Ngoze and Okoko (2003) showed that good seed namely high viability and vigour, can contribute about 30 per cent to the total crop production. Monitoring the viability of germplasm collections is one of the most important routine programmes for all gene bank managers. It enables managers to plan for regeneration before viability has fallen to a level where important genotypes might be lost (Gold *et al*., 2008). Despite the fact that there are other methods to test seed viability such as the tetrazolium test, the germination test remains the most reliable and effective method for assessing the viability and vigour of seed (Geneve, 1998; Gold *et al*., 2008).

Seed dormancy in general

Yongqing (1996), Mashingaidze (2000) and Bradford and Nonogaki (2007) defined seed dormancy as the disability of viable seeds to germinate even when the favourable environmental conditions are provided. Usually it is a pre-requisite that dormancy factors must be relieved for the germination to occur. Commonly there are two major types of seed dormancies. These are primary and secondary dormancies.

***Primary dormancy*:** This describes dormancy that has been induced during seed

maturation on the mother plant. This type of dormancy is said to either result from hard or thick seed coat, immature embryo or suppression of vigorous germination, mainly regulated by the plant growth hormone abscisic acid shortly called ABA (Bewley and Black, 1994). It is caused by conditions within the seed that prevent germination even in favourable germination conditions (Tibugari *et al.*, 2012). There are three recognized groups within the primary dormancy, the exogenous, endogenous and combinational dormancy (Hartmann *et al*., 1997).

Exogenous dormancy is imposed by factors outside the embryo. The factors include maternal tissues (seed coat or pericarp) or mechanical resistance on the radicle from the endosperm (Geneve, 1998). It impacts germination through the tissues enclosing the embryo hence, inhibiting water uptake, creates mechanical restraint to embryo expansion and radicle emergence, limits oxygen diffusion to the embryo, prevents leaching of inhibitors from the embryo as well as supplies inhibitors to the embryo (Bewley and Black, 1994). The most common form of exogenous dormancy often arise as a result of "hard" seed coats in which seed coat is normally suberized and become impervious to water. Even so, this dormancy type allows dry seed to be successfully stored for many years, even at warm storage temperatures. Germination in hard seeds can be increased by any method that can soften or "scarify" the seed covering (Hartmann *et al.*, 1997). Exogenous dormancy can be further divided into physical, mechanical and chemical dormancies which are not discussed here.

Endogenous dormancy is another type of primary dormancy that is caused by factors within the embryo (Geneve, 1998). Two categories of endogenous dormancies are recognised*; viz.* morphological and physiological. Morphological dormancy is exhibited when the embryo has not completed development at the time the seed is shed from the plant (Geneve, 1998). It is always a must for the embryo to complete development prior to germination. In some cases, seed with morphological dormancy can have either rudimentary or undeveloped embryos (Atwater, 1980). Species with rudimentary embryos have little more than a proembryo embedded in a massive endosperm like those found in Ranunculaceae (*Anemone*, *Ranunculus*), Papaveraceae (*Papaver*, *Romneya),* and Araliaceae (*Aralia*, *Fatsia*). Effective methods for inducing germination in a crop include: exposure to temperatures of more than 15°C, exposure to alternating temperatures, and chemical treatment such as potassium nitrate or gibberellic acid (GA_3). Physiological dormancy on the other hand occurs due to physiological changes within the embryo leading to change in growth potential or seed metabolic rates (Baskin and Baskin, 1971) not allowing the radicle to escape the restraint of the seed coverings. Such seed changes are regulated by endogenous growth promoters and inhibitors such as phenolics, cyanogenic compounds, ABA, GA's and cytokinins. These endogenous promoters and inhibitors in turn, interact with environmental factors such as light and temperature. Physiological dormancy is further categorised into non-deep, intermediate and deep dormancies. Non-deep endogenous physiological dormancy is the most common form in seed (Baskin and Baskin, 1998). This type of dormancy includes species that require light or darkness to germinate and must undergo an "after-ripening" period of dry storage to lose dormancy.

Combinational dormancy is the type that includes a combination of two or more types of primary dormancy (Geneve, 1998; Baskin and Baskin, 2004). Examples include exo-endodormancy (seed coat dormancy and intermediate physiological dormancy), epicotyl dormancy or morphophysiological (rudimentary embryo with physiological) dormancy. The most common form of combinational dormancy in flower and

vegetable crops is morphophysiological (Geneve, 1998). Morphophysiological dormancy may simply require warm (> 15^{o}C) or cold (1-10^{o}C) conditions during embryo development to break physiological dormancy. However, more complex forms of morphophysiological dormancy may require extended cycles of warmness and coldness (Baskin and Baskin, 1998). In seeds with epicotyl dormancy, separate dormancy conditions for the radicle and epicotyl are required (Baskin and Baskin, 1998).

Secondary Dormancy: is the dormancy induced in certain non-dormant seeds when the environment is not favourable for germination. It refers to imposition of a new dormancy mechanism in seed that have overcome primary dormancy (Geneve, 1998). Induced or secondary dormancy occurs when seed or vegetative part is exposed to non-germinative conditions after release from the parent. In nature, primary dormancy is an adaptation to control the time and conditions for seed germination and secondary dormancy is a further adaptation to prevent germination of an imbibed seed when environmental conditions are not favourable for seedling growth (Geneve, 1998). Conditions that prevent germination can be one or more of the unfavourable temperatures, prolonged light or darkness, water stress, or absence of oxygen supply (anoxia). These are factors involved in conditional dormancy and prolonged survival of weed seeds in soil banks (Baskin and Baskin, 1998).

Seed dormancy on *Cleome gynandra* seeds

Spider plant and genus *Cleome* have been grouped among the vegetable and flower genera that have primary non-deep endogenous physiological seeds dormancy (Geneve, 1998). Within this category Geneve (1998) specifically, has placed *Cleome* species under the group that require light as one of the important factor for the seeds to germinate.

Yepes (1978), Ochuodho (2005) and Zharare (2012) determined that seed of *C. gynandra* have an after harvest rest period (latency), especially for the fresh harvest, that extends to the 5th month after collection and active germination starts 6 months after harvest, and increases to 88% in 3 months. In another study, Ochuodo and Modi (2005) reported that poor seed germination in *Cleome* could be due to the hard seed coat, immature embryos or induced secondary dormancy. Neverthless, Ekpong (2009) indicated that seed dormancy of *C. gynandra* might not be attributed to the seed coat as a physical barrier to water absorption. In his study, seeds permeable to water could still not germinate until after 12 hours of soaking. Moreover, slight decrease in germination was observed when longer soaking time was practised, and the reason might be water trapped in the tissue between the embryo and seed coat has created an oxygen barrier, a situation also reported in *Datura ferox* and *D. stramonium* seeds (Reisman-Berman *et al*., 1989). Norton (1986) as well reported that anoxia caused by prolonged soaking of seed may result in irreversible injury due to accumulation of toxic metabolites.

So far, studies that have reported that *C. gynandra* seed exhibit dormancy leading to low seed germination are contrary to results from preliminary seed germination test carried out at AVRDC – The World Vegetable Center, Eastern and Southern Africa, Arusha, Tanzania. In the preliminary test, fresh seeds from mature green pods (with black seeds indicating physiological maturity), yellow and brown pods were harvested and immediately sowed in soil trays in a screen house. Seeds from all the three different categories of pods germinated. The only difference noticed was that seeds from brown pods germinated fast within first three days after sowing, followed by seeds from yellow pods and lastly green pods about nine days after sowing. Seeds from all pods had germinated within nine to ten days after harvest and sowing, without any prior treatment. The difference in

germination time was assumed to be associated with differences in final maturity attained, where brown (dry) pod seeds were supposed to have reached final maturity, followed by yellow pods and finally mature green pods that contained seeds with lowest maturity.

Ekpong (2009) noticed that an increase in germination of *C. gynandra* seeds to about 72% was achieved after pre-washing seeds in running water for 60 minutes indicating that this treatment was able to overcome the dormancy in *C. gynandra*, which is supposed to arisen from presence of inhibitors on the seed coat. In addition, pre-heating at 40ºC for only 1 day was able to break dormancy of seeds. This latter case is supported by Bewley and Black (1982) who noted that at high temperature degradation of the seed tissues is enhanced. As a result, the energy supply to embryonic axis may increase and diffusion in and out of the seeds by such substances as water, oxygen, inhibitors and carbon dioxide, may be easier, and hence, promotes germination. As well Ekpong (2009) reported a pre-chilling test on seeds of spider plant for 1 day that was able to break dormancy and increased germination to about 66%. Khan (1997) reported that duration of moist chilling to release embryo dormancy is influenced by factors such as covering structures and inhibitors. It was hypothesized that pre-chilling released dormancy as a result of various metabolisms that occur during these treatments, such as increasing the level and responsiveness of endogenous gibberellins (Hilhorst and Karssen, 1992), but substantially decreasing ABA level (Bewley and Black, 1982).

Despite some studies indicating that seeds of spider plant exhibit dormancy that need to be attended prior to sowing, authors of this manuscript recommend a more detailed study to be taken to clarify few contradictions existing. Future research should take into account a larger number and diverse accessions, different times of storage from harvest, light requirement and necessary treatments as highlighted in different studies in order to explain the nature and mechanism of seed dormancy in spider plant.

Seed germination

Little information is available on seed germination of *Cleome* (de Castro *et al.*, 2014). Some studies have reported low and non-uniform germination, presence of seed dormancy and a significant variation in germination rates depending on the seed lot used (Ochuodho and Modi, 2007; Raboteaux and Anderson, 2010; K'Opondo, *et al.*, 2011). Moreover, Chweya and Mnzava (1997) reported that poor and delayed seed germination is among the problems that make *C. gynandra* propagation difficult. Maximum seed quality is attained at different times during seed maturation in different plant species. In addition, the condition under which the mother plant (seed crop) is grown (Ochuodho, 2005) and the differences in times of male and female flower production (Tibugari *et al*., 2012) have great influence on the quality of seeds produced hence affect germination of seeds. *C. gynandra* seeds might not be exempted from factors explained and might lead to low seed germination in the field as a result of developed seed dormancy (Simiyu *et al.*, 2003; Kamotho, 2004). Almekinders and Louwaars (2000) and Ndinya (2003) recorded *C. gynandra* seed germination as low as 37 and 46%, respectively. This might force farmers to plant more seeds per hill to obtain optimal plant stands (Muasya *et al.*, 2009).

Seeds germinate when appropriate conditions are met. Generally, for seeds to germinate, optimum temperature, soil moisture, air and light must be provided as basic conditions based on the crop species. However, there are specific requirements depending on the nature of the crop. With regards to spider plant some studies have been carried out on seed germination. Of these, some came up with the recommendation that spider plant seed has

very low germination rate that increases with time of storage and maximum germination is achieved after six months (Kamotho, 2004; Ekpong, 2009; Kamotho *et al.*, 2014).

Viability of seed is said to be positively correlated to percent germination, while high seedling vigour is positively correlated to mean germination time. Kamotho *et al.* (2007) found that seed dried to 5% moisture content and stored at -20^{o}C recorded the highest viability as observed from its percent germination, and the highest vigour as indicated by its mean germination time. In this study Kamotho *et al.* (2007) also observed higher results as storage time increased from fresh harvest (14.5%) to three months (78%) and maximum after six months (95%).

However, to farmers it is unusual practice to store *C. gynandra* seed, as well as other traditional African vegetables for such a long storage period; normally seeds are stored for not more than three months (Muasya *et al.*, 2009). With regards to erratic seed germination, various pre-treatments have been reported that may help farmers rise the level of germination. Ochuodho *et al* (2004) indicated that among the different methods of breaking seed dormancy in *C. gynandra*, such as chemical and physical treatments, only scarification at the radicle end improved seed germination. In general, seed dormancy not only causes problem in actual agricultural production but also complicates assessment of seed quality by seed analyst who requires prompt germination during evaluation of seed lots and to genebank curators who have to carry multiplication and monitor the viability of stored seeds (Geneve, 1998).

In addition, both a 15 days pre-heating of (1 and 2 years stored) seed lots at 40.8^{0}C and scarification effectively broke seed dormancy in *C. gynandra* (L.) (Ochuodo *et al.*, 2004; Ochuodo and Modi, 2005) and recovered germination ability. Despite the above success a significant difference in germination between seed lots tested has been reported. Ochuodo and Modi (2005) noticed that seed lot from South Africa (Agricultural Research Council, ARC) showed slow rate of germination and low final germination percentage than lots from Kenya (Kenya Seed Company, KSC) seed lots. Although it is not very clear on the cause of such a difference, it is hypothesized that the environmental conditions during seed development in the two locations could have influenced the germination rates of seed lots since the two seed lots were obtained from very different locations. Bohringer *et al* (1999) obtained maximum germination of only 25% at 31°C in darkness, six months after harvest. Raboteaux and Anderson (2010) as well found that most of *Cleome* seed lots attained high germination when sowed in the dark following cold stratification whereas de Castro et *al*, (2014) in another study found that optimal conditions for the germination were observed to be different for each of *C. spinosa*, *C. dendroides* and *C. rosea* species. Moreover, *C. spinosa* has physiological dormancy, while *C. dendroides* and *C. rosea* do not exhibit dormancy under in vivo conditions. This also stresses another key information that even within the genus germination differences between species do occur.

In a seed germination experiment Ochuodho and Modi (2005) found that seed of *C. gynandra* responded negatively to continuous white light when exposed beyond 12 hours at 20^{o}C by a reduced germination rate. This photo-inhibition was more evident in seeds harvested after maximum physiological maturity (i.e. dry brown pods) as compared to seeds harvested earlier (mature green pods) where it was much less or no effect. The photo-inhibition was so severe such that un-germinated seeds did not completely recover their germination ability when transferred to optimum germination conditions, except after treatment with GA_3. Ochuodho and Modi (2005) recommended that germination of *Cleome* seed should be

performed under conditions of darkness and either alternating 20-30°C or continuously at 30°C. This is in agreement with the study by Kamotho *et al.* (2007) who found *C. gynandra* seed to germinate well under dark condition that increased with storage time of seeds from three to six months at -20^{o}C and seed moisture content of 5%. Another study by Raboteaux and Anderson (2010) on *Cleome* species indicated germination of *C. droserifolia* Del. ranged between 44.3 (control) to 0.2% when incubated at 30^{0}C during the day and 15^{0}C at night in petri dishes due to differences in seed lots. In line to this Bohringer *et al.* (1999) indicated a minimum and a maximum temperature of 13^{0}C and 37^{0}C respectively for *C. gynandra* seeds below and above which there is very poor germination.

Zharare (2012) indicated that seed germination in *C. gynandra* and *Amaranthus* species is not only influenced by factors explained above but also was strongly biotype dependant where, differences in seed germination in *C. gynandra* biotypes that originated from different environments, were assumed to reflect habitat specific selection. More so, the biotypes as well differed in environmental requirements for breaking seed dormancy such as differences in the extent to which darkness and postharvest storage period promoted germination between the two biotypes, one having been collected from Harare (17°44" 33″ S; 30° 57′ 12.66″ E: Altitude, 1477 m) in Zimbabwe and the other near Neslpruit (25°26′ 25″S; 30°58′ 57″ E; altitude of 640 m) in the Mpumalanga province of South Africa. With regards to the data mining information on seed germination of *C. gynandra*, several pieces of information have been offered but still there is a gap as to what are the optimum required conditions to achieve an optimum *C. gynandra* seed germination. This once more pave way to further investigation on the area of seed germination.

Determination of seed storage periods

Ekpong (2009) showed that storage of seed has a significant role in overcoming seed dormancy. From his study, he reported a germination of more than 90% when freshly harvested seeds of Cleome were stored at 15 ^{0}C and room temperature for 5 months. He recommended that seed dormancy in *C. gynandra* could be overcome within 3 months under the two storage conditions. Similar results were observed by Ochuodho (2005) where *C. gynandra* seeds stored at 15.8 ^{0}C and temperature of 30-38^{0}C were found to break the dormancy after three months of storage. However, Kamotho *et al.* (2007) showed that for long storage it may be worth to store seeds at -20^{0}C with the seed moisture content ranging from 2 to 5%. This latter situation poses a challenge to farmers as there is no way of achieving these temperature conditions and moisture level.

Chweya and Mnzava (1997), Geneve (1998) and Kamotho *et al.* (2007) stressed that *C. gynandra*, as it is the case for many freshly harvested seeds of herbaceous plants, needs postharvest ripening period before dormancy is broken. Such results have also been found in *Arabidopsis thaliana* which is a close sister clade of spider plant (Ali-Rachedi *et al*., 2004). Our preliminary observation on germination test, mentioned earlier, does not support the results of these studies. It might be that seeds enter into dormancy not immediately after harvest or threshing but after some period of postharvest, the time of which needs further investigation.

As one of the strategies to avoid dormancy period, in most cases farmers collect seeds and keep them for the next season planting. This is done by collecting the yellow capsules before they are ripe and dry them in controlled way so that seeds can be retained. However, storage of seeds is challenging to commercial seed companies and farmers due to inevitable deterioration of seeds in storage which leads to low vigour and reduced number of viable seeds (Mutegi, 1999), which supports a more extensive study be

undertaken to determine proper seed storage conditions. Ngoze and Okoko (2003) and Kamotho *et al.* (2007) also reported that despite seed dormancy, other factors which may deny seeds to farmers to be not readily available for propagation is the production practices, harvesting, processing, packaging and storage of *C. gynandra*, contributing to poor quality of seeds. Traditionally seeds are kept in guards and pots. Kamotho *et al.* (2014) indicated that to achieve high seed quality, *Cleome* seed should presumably be harvested at yellow pod maturity stage, dried under the sun to 5% moisture content and stored for up to six months.

Conclusion

Based on the information extracted from different studies, it can be summarised that *Cleome* seeds has been reported to exhibit seed dormancy, which could be overcome as early as from 3 months under room temperature storage, sometimes accompanied with some kinds of seed treatments such as scarification, pre-washing seeds in running water for 60 minutes, pre-heating at 40^{o}C for only 1 day and pre-chilling of seeds for 1 day (Ekpong, 2009). Several authors have also reported low and non-uniform germination and a significant variation in germination rates depending on the seed lot used (Ochuodho and Modi, 2007; Raboteaux and Anderson, 2010; K'Opondo, *et al.*, 2011). In addition, data mining indicated that dormant seeds of *C. gynandra* may prevent an all year round production by the majority of farmers who do not have access to certified seed, and rely on own saved and seed collection.

Based on the observation we had at AVRDC – The World Vegetable Center, Eastern and Southern Africa as explained in this review, we hypothesize that *C. gynandra* seed may enter a state of dormancy sometimes after harvest, the time that need to be determined. Authors at the time of review of this manuscript concur with the study by Zharare (2012) that seed germination in *C. gynandra* is biotype specific and environmentally adapted or habitat dependant, although that also need strong scientific support. In this regards, and in the light of the literature mining, as per time of development of this manuscript, further studies are worth to explain the contradictions in various studies on spider plant seed dormancy, germination and storage period and conditions. Since seed dormancy must be broken prior to planting, a proper method of overcoming seed dormancy must be identified and recommend to farmers who in most cases use seeds from their harvest not buying from stockists or seed dealers.

Moreover, storage time and conditions of farmers' seed harvest is worth to be evaluated because to date there are still no improved cultivars of spider plant, as a result of which farmers mostly depend on their own collections and few cultivars sold by some seed companies. As well, since seed companies usually keep large stock of seeds of some improved cultivars of traditional vegetables, further studies on storability of pre-treated seeds are necessary, especially for commercial cultivars taking into account the recommendation by Kamotho *et al* (2007) and K'Opondo *et al* (2011) that *C. gynandra* seed is in the orthodox group and, for long storage it may be worth to store at -20 ^{0}C with the seed moisture content as low as 2-5%.

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