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REVIEW ARTICLE

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The use of plant extracts to control tilapia reproduction: Current status and future perspectives

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Abstract

Control of prolific reproduction is vital for a profitable tilapia aquaculture enterprise. All-male tilapia culture is a popular method used to control prolific breeding, because the male individuals grow faster than female and mixed-sex populations. Presently, most farmers use 17α-methyl testosterone (MT) to produce all-male tilapia individuals, although synthetic hormones are linked to human health and environmental risks. Recently, considerable attention has focused on plant-based products as alternatives to MT, because they are affordable, safe, and eco-friendly. Despite the growing interest in using plant extracts to prevent frequent spawning in tilapia production, the available information is not collated to standardize application guidelines. Accordingly, this review article consolidates existing knowledge on the use of plant extracts to control prolific breeding in tilapia culture systems. In addition, limitations to commercial application of the extracts are identified. To date, seed, root, and leaf extracts of 20 plant species, most notably, *Tribulus terrestris*, *Mucuna pruriens*, and *Carica papaya*, exhibit potential for controlling unwanted breeding in tilapia production systems. The extracts are mainly administered orally, incorporated in fish feeds. Saponins and flavanoids are the main bioactive compounds in the phytoextracts,

which induce sex inversion and fertility impairment in tilapia. The commercialization of plant extracts is, however, hampered by lack of standardized information on extract preparation, optimal dosages, and mechanism of action. Thus, future studies should address these technical limitations and highlight economic incentives for commercial use of plant extracts in tilapia aquaculture.

KEYWORDS
all-male tilapia, aquaculture, phytochemicals, synthetic hormones, 17α-methyl testosterone

1 | INTRODUCTION

Tilapia is the second most farmed food fish after carps globally. According to the Food and Agriculture Organization of the United Nations (FAO), the global production of tilapia has continued to grow, rising from 3.1 million tonnes in 2010 to 5.6 million tonnes in 2018 (FAO, 2020). This has highlighted the significant contribution of the tilapia industry to the global economy as one of the world's primary sources of proteins for human consumption (FAO, 2020). The exponential increase in tilapia production is related to the suitable aquacultural attributes: (a) ease to breed in captivity; (b) having a short production cycle because of fast growth rate; (c) acceptability of artificial feeds after yolk-sac absorption; and (d) marketability (El-Sayed, 2006; Mair, 2001). Technology advancements, including control of early maturity and prolific breeding, have also contributed to the expansion of tilapia's global production (Beardmore, Mair, & Lewis, 2001; FAO, 2017; Toguyeni, Fauconncau, Fostier, & Abucay, 2002). Prolific breeding results in excessive fingerling recruitment in grow-out systems causing overpopulation, and competition for resources, and consequently stunted and small-sized fish, which fail to attract good market prices (Teichert-Coddington, Manning, Eya, & Brock, 2000). Therefore, periodic harvesting of fry and fingerlings, high-density culture, cage culture, polyculture with predator fish, sterilization by application of heat shock, and all-male culture, are applied to minimize unwanted reproduction in tilapia production systems (Fortes, 2005; Guerrero, 1982; Mair & Little, 1991). Currently, the culture of all-male tilapia individuals is commonly practiced because, in addition to control of prolific spawning, males grow faster and larger than females, resulting in a shortened production cycle (Baroiller & D'Cotta, ; Beardmore et al., 2001; El-Greisy & El-Gamal, 2012; Megbowon & Mojekwu, 2014).

All-male tilapia populations are achieved through: (a) sex-sorting by hand; (b) hormonal sex inversion using androgens; (c) environmental manipulation (such as temperature treatment); and (d) genetic/chromosomal manipulation (Angienda, Aketch, & Waindi, 2010; Beardmore et al., 2001; Dauda, Yakubu, & Oke, 2014; Desprez et al., 2003; Green, Veverica, & Fitzpatrick, 1997; Olufeagba & Okomoda, 2015). Among these methods, hormonal sex reversal using exogenous steroids, mainly 17α-methyl testosterone (MT), yields high success of masculinization (Gale, Fitzpatrick, Lucero, Contreras-Sanchez, & Schreck, 1999; Homklin, Ong, & Limpiyakorn, 2011; Phelps, 2006; Phelps & Popma, 2000). The high sex inversion potency of MT is associated with the hormone's ability to inhibit aromatase activity, thereby obstructing estrogen biosynthesis while promoting androgenesis in the differentiating gonads (Golan & Levavi-Sivan, 2014). Consequently, MT is the most widely used method for the production of all-male individuals in tilapia culture. However, the carcinogenicity of MT and the associated adverse effects on human health and aquatic ecosystems continue to raise public concerns (Baroiller & D'Cotta, ; Biswas, Morita, Yoshizaki, Maita, & Takeuchi, 2005; Dabrowski, Rodriquez, Abiado, Sanchez, & de Jesus, 2005; Haitham, 2018; Jegede, 2010; Leet, Gall, & Sepulveda, 2011; Mlalila, Mahika, Kalombo, Swai, & Hilonga, 2015). Prolonged exposure to MT during

the application process can cause hepatotoxicity and fetotoxicity (Hartleb & Nowak, 1990; Schardein, 1980; Velazquez & Alter, 2004; Vick & Hayton, 2001; Wilkins, 1960). As such, MT poses a health risk to hatchery personnel involved in tilapia seed production (Megbowon & Mojekwu, 2014). Besides, 30% of the administered hormone-treated diet is unavailable to the fish during feeding (Ramirez-Godinez et al., 2013; Vick & Hayton, 2001). Meanwhile, only 10% of the hormone in the consumed diet is utilized for sex inversion (de Ziegler & Fanchin, 2000; Ong, Chotisukarn, & Limpiyakorn, 2012). As a result, hormone residues build-up in the closed environments as either active metabolites excreted by the treated fish or leachates from uneaten food. The accumulation of hormonal residues is facilitated by the hydrophobic nature of MT that allows it to rapidly adsorb onto sediments (Mlalila et al., 2015). The leakages of MT and its metabolites into the aquatic environment from uneaten or un-metabolized food have the potential to disrupt endocrine and reproductive systems of nontarget aquatic organisms (Abucay & Mair, 1997; Gomelsky, Cherfas, Peretz, Ben-Don, & Hulata, 1994; Hulak et al., 2008; Nian, Tumbokon, & Serrano-Jr, 2017; Ramirez-Godinez et al., 2013; Rivero-Wendt, Miranda-Vilela, Ferreira, Borges, & Grisolia, 2013). Further, fish treated with synthetic chemicals are not readily accepted by consumers because of safety concerns (Biswas et al., 2005; Reverter, Bontemps, Lecchini, Banaigs, & Sasal, 2014). In view of the above negative consequences, several countries prohibit use of synthetic hormones for fish food production (Chakraborty, Horn, & Hancz, 2013). As such, there is need for research efforts to identify and develop environmentally friendly, economically viable, and socially acceptable alternatives to the synthetic steroids.

Various interventions have demonstrated the possibility of utilizing plant extracts as possible options to synthetic steroids in aquaculture in response to the increasing consumer demand for organically produced agricultural products, including fish (Leet et al., 2011). The acceptance of plants for use in aquaculture is linked to ease of access and being relatively safer for the environment and humans, than synthetic hormones (Chakraborty et al., 2013; Logambal, Venkatalakshmi, & Michael, 2000; Olusola, Emikpe, & Olaifa, 2013; Reverter et al., 2014). To date, several plant extracts are predominantly used to improve fish growth, enhance innate immune responses, and control disease in aquaculture, as compared to reproduction control (Baluran, Quiazon, Garcia, Fernando, & Velasco, 2018; Logambal et al., 2000; Olusola et al., 2013; Reverter et al., 2014). Nevertheless, the androgenic compounds present in some plant extracts could be used to control unwanted reproduction in tilapia production systems (Chakraborty et al., 2013; Gabriel et al., 2017; Ghosal, Mukherjee, & Chakraborty, 2021). The phytoandrogens, for example, testosterone, androstenedione, and dehydroepiandrosterone, have been implicated in sex reversal of fish (Godwin, Luckenbach, & Borski, 2003).

In this review, an account of the current state of knowledge on the plant extracts used to control unwanted reproduction in tilapia culture is provided. The literature review strategy involved searching from Web of Science, Science Direct, Google Scholar, and Scopus using "tilapia reproduction control" and "plant extracts" as keywords. Conference proceedings and doctoral theses were also collected from various libraries using the online catalogue. The search results were screened and selected by title relevance to the present review, concerning plant extracts for tilapia reproduction control. This search strategy yielded 47 scientific publications, whose findings are reported in this review. The effectiveness of extracts from different plants and the corresponding dosages inducing sex change are documented. Further, the information gaps and the future research directions are highlighted. The review contributes to a better understanding of plant extracts' application in controlling unwanted spawning in tilapia aquaculture, as an alternative to the currently, most used synthetic hormones.

2 | PLANT EXTRACTS USED IN THE CONTROL OF TILAPIA REPRODUCTION

Plant extracts are becoming an integral part of fish culture, as alternatives to chemicals, drugs, and hormones, in response to the increasing pressure to reduce adverse impacts associated with aquaculture on human and environmental health. The organic plant products are relatively safe, inexpensive and easy to prepare, and are thus viewed as a means to achieving sustainable fish production (Chakraborty et al., 2013; Hoseini, Mirghaed, & Yousef, 2019;

Makkar, Francis, & Becker, 2007; Reverter et al., 2014). Moreover, consumers are increasingly demanding good quality and safe fish products, which are free of pollutants (Chakraborty et al., 2013). Therefore, adopting safe and environmentally clean fish production practices will promote tilapia to meet new market requirements. Accordingly, efforts are required to identify and develop novel plant-based products for tilapia production to replace synthetic hormones and chemicals (Ahmed, Fathy, Fayek, & Mohamed, 2019; Citarasu, 2010; Turan & Akyurt, 2005).

Natural compounds found in plants such as; flavonoids, tannins, terpenoids, alkaloids, and steroids promote androgenic and anabolic processes as well as stimulation of digestion, appetite, and immunity (Chakraborty et al., 2013; Chakraborty & Hancz, 2011; Citarasu, 2010; Gabriel, Qiang, Kpundeh, & Xu, 2015; Ugoala, Ndukwe, Ayo, & Mustapha, 2014). The phytochemicals, including steroidal saponins (Golan et al., 2008) and flavonoids (Miyahara et al., 2003; Tarigan, Nasution, & Widjaja, 2016), attenuate estrogen production by inhibiting the action of aromatase. Phytochemicals may also compete with endogenous estrogens for binding sites to the estrogen receptor, thereby suppressing estrogen biosynthesis (Eng et al., 2001; Golan et al., 2008; Miyahara et al., 2003). Consequently, the phytochemicals act as "phytoandrogens" that exert functional effects similar to testosterone in animals, elevating male reproductive characteristics (Turan & Akyurt, 2005). The potential of phytochemicals in plant extracts to induce either masculinization or fertility impairment in fish has been harnessed to control prolific breeding in tilapia, with positive results (Ampofo-Yeboah, 2013; Gabriel et al., 2017; Ghosal et al., 2021; Jegede, 2010; Mukherjee, Ghosal, & Chakraborty, 2015a; Nian et al., 2017; Omitoyin, Ajani, & Sadiq, 2013; Stadtlander et al., 2008). The section that follows describes plant species, the respective phyto-constituents utilized to overcome unwanted tilapia reproduction and subsequently present results from previous studies.

2.1 | Plants with androgenic and fertility impairment effects on tilapia

Extracts from 20 plant species, belonging to 17 families are reported to control reproduction in tilapia culture systems. The geographical distribution, usable parts phytochemical composition, androgenic and fertility impairment attributes of these plants are described below:

2.1.1 | Aspilia plant, *Aspilia mossambicensis*

A. mossambicensis, also known as "wild sunflower," belongs to the order Asterales and family Compositae (Musyimi, Ogur, & Muema, 2007). The plant is widespread in central and eastern tropical Africa (Norton, Huang, & Rodriguez, 1993). Aspilia is widely used as an uterotonic agent to induce uterine contraction and labor in pregnant women (Gruber & O'Brien, 2011; Musyimi, Ogur, & Muema, 2008). The leaves and roots extract of aspilia plants contain flavonoids, alkaloids, saponin, and steroids (Kapinga, Limbu, Madalla, Kimaro, & Tamatamah, 2019; Musyimi et al., 2008). The anti-fertility effect of *A. mossambicensis* is linked to the presence of saponins, and flavonoids (Musyimi et al., 2007). The feeding of Nile tilapia (*Oreochromis niloticus*) on diets containing 2–8 g of *A. mossambicensis* leaf extract kg^{-1} of diet degenerated seminiferous tubules, thereby reducing the number of hatchlings in the experimental fish (Kapinga et al., 2019; Kapinga, Limbu, Madalla, Kimaro, & Tamatamah, 2018). The extracts from *A. mossambicensis* are thus potent in the control of prolific breeding of Nile tilapia.

2.1.2 | Bitter kola, *Garcinia kola*

G. kola is a flowering plant, indigenous to the tropical rain forests of West and Central Africa (Manourova et al., 2019), belonging to order Malpighiales and family Clusiaceae. The plant is commonly referred to as bitter kola, male kola, or wonder plant (Ekene & Erhirhie, 2014). Bitter kola contains flavonoids, mainly apigenin, which inhibits

the enzyme aromatase (Iwu & Igboko, 1982; Jeong, Shin, Kim, & Pezzuto, 1999). The enzyme aromatase catalyzes the conversion of androgens to estrogens, in the final step of the biosynthesis of the gonadal steroids, subsequently increasing testosterone (Elbrecht & Smith, 1992; Sanderson, 2006). The blockage of estrogen synthesis causes anti-fertility effects, which can be harnessed to control animal reproduction (Abu, Amuta, Buba, & Inusa, 2013; Akinloye, Igharna, Olaniyi, Alaka, & Oke, 1999). In aquaculture, the inclusion of 1, 3, and 6% of bitter kola seed powder in the diet of female Nile tilapia for 70 days diets mixed resulted in the impairment of gonadal development (Nyadjeu, Angoun, Ndasi, & Tabi-Tomedi, 2019). Besides, significant reduction (83.45%) in the number of eggs spawned by Nile tilapia, maintained on a diet constituting of 6% bitter kola seed powder for 44 days (Sulem-Yong et al., 2018) was linked to the presence of flavanoids.

2.1.3 | Cotton, *Gossypium herbaceum*

G. herbaceum is native to semi-arid regions of Sub-Saharan Africa and Arabia. Cotton is classified under order Malvales and family Malvaceae, and grows to approximately three meters tall (Al-Snafi, 2018). The plant contains a naturally occurring polyphenolic compound known as gossypol, which forms part of the self-defense system of the cotton plant against predators (Jodi & Gabriela, 2008). However, Gossypol, present in the stem, seeds, and roots also inhibit reproduction in fish, rats, and humans (El-Sharaky, Newairy, Elguindy, & Elwafa, 2010; Qian & Wang, 1984; Tope-Jegede, Fagbenro, & Olufayo, 2019). Inclusion of *G. herbaceum* root bark extracts in the diet of Nile tilapia at 20 g kg^{-1} of diet, for 70 days, eroded the connective tissue of the testes and disintegrated the seminiferous lobule, causing a reduction in the volume of milt (Akin-Obasola & Jegede, 2016). Similarly, the substitution of 25, 50, 75, and 100% of soybean meal protein with cottonseed meal for 90 days destroyed spermatocytes and distorted vitellogenic stages of Nile tilapia (Tope-Jegede et al., 2019). However, gossypol is a known anti-nutritional factor (Mbahinzireki, Dabrowski, Lee, El-Saidy, & Wisner, 2001) and could, therefore, result in undesirable effects on the growth performance of fish. Therefore, the dose of cottonseed meal recommended for control of unwanted spawning in tilapia should not inhibit growth performance of the fish.

2.1.4 | Fenugreek, *Trigonella foenum graecum*

T. foenum-graecum is a leguminous plant mainly grown in Europe, Africa, and Asia (Petropoulos, 2002). It belongs to the order: Fabales, family: Fabaceae, and grows up to a height of 30–60 cm (Ghosh, Chandra, & Chatterjee, 2015). The seeds of fenugreek contain rich steroidal saponins, especially Diosgenin (Marker et al., 1947; Murakami, Hishi, Matsuda, & Yoshikawa, 2000; Petropoulos, 2002). Diosgenin functions as a phytoandrogen (Raju, Patlolla, Swamy, & Rao, 2004), and hence masculinizes Nile tilapia (Stadtlander et al., 2008; Table 1).

2.1.5 | Guava, *Psidium guajava*

P. guajava is a member of the order Myrtales and family Myrtaceae (Shruthi, Timilsina, & Sunita, 2013). It is grown in tropical and sub-tropical countries, mainly to provide of fruit for human consumption (Gutierrez, Mitchell, & Solis, 2008). The extract from *P. guajava* leaves contains alkaloids, saponins, tannins, and flavanoids (Tarigan et al., 2016; Uboh, Okon, & Ekong, 2010). These extracts, especially saponins and flavanoids, have antifertility effects in rats (Nayaka, Londonkar, & Umesh, 2014) and fish (Obaroh, Nzeh, & Oguntoye, 2012). For example, anti-implantation and sterility was observed in rats treated with *P. guajava* extracts (Sri Retno, Endang, Elfi, & Setiyani, 2008). Dietary inclusion of *P. guajava* extracts *guajava* at 4.0 and 8.0 g kg^{-1} for 56 days, induced atrophy

TABLE 1 Use of plant extracts at different concentrations to sex inverse tilapia

Botanical name	Treatment (parts/products used)	Dosage	Exposure period (days)	Treatment method	Tilapia species	Best dosage	Masculinization success (%)	Reference
Mucuna pruriens	Seed methanol extract	0.1, 0.15, & 0.2 g kg^{-1} of feed	30	Oral	*Oreochromis niloticus*	0.2 g kg^{-1} of feed	93.79 ± 0.95	Mukherjee, Ghosal, Hancz, and Chakraborty (2018)
	Seed powder	0.0, 2.0, 3.5, & 5.0 g kg^{1} of feed	30	Oral	*O. niloticus*	5.0 g kg^{-1} of feed	73.33 ± 0.67	Mukherjee, Ghosal, and Chakraborty (2015b)
	Seed aqueous extract	0.02, 0.035, & 0.05 g L^{-1}	30	Immersion	*O. niloticus*	0.05 g L^{-1}	74.67 ± 0.33	Mukherjee et al. (2015b)
Asparagus racemosus	Root methanol extract	0.1, 0.15, & 0.2 g kg^{-1} of feed	30	Oral	*O. niloticus*	0.2 g kg^{-1} of feed	92.24 ± 0.13	Mukherjee et al. (2018)
	Root aqueous extract	0.01, 0.015, & 0.02 g L^{-1}	30	Immersion	*O. niloticus*	0.015 g L^{-1}	90.60 ± 1.56	Mukherjee et al. (2015a)
Carica papaya	Seed powder	15 g kg^{-1} of feed	30	Oral	*Oreochromis mossambicus*	15 g kg^{-1} of feed	65	Ampofo-Yeboah (2013)
	Seed powder	10, 15, 20, 25, & 30 g kg^{1} of feed	120	Oral	*O. mossambicus*	20 g kg^{-1} of feed	77.8	Omeje (2016); Omeje, Lambrechts, and Brink (2018)
	Seed powder	6 g kg^{1} of feed	45	Oral	*O. niloticus*	6 g kg^{-1} of feed	68	Ahmed et al. (2019)
Moringa oleifera	Seed powder	15 g kg^{-1} of feed	30	Oral	*O. mossambicus*	15 g kg^{-1} of feed	65.5	Ampofo-Yeboah (2013)
Tribulus terrestris	Seed powder aqueous, methanol, ethanol, dichloromethane, hexane & successive methanol extracts	0.5, 1.0, & 1.5 g kg^{-1} of feed	30	Oral	*O. niloticus*	1.5 g of ethanol extract kg^{-1} of feed	88.9 ± 1.1	Ghosal, Mukherjee, Hancz, and Chakraborty (2015); Ghosal and Chakraborty (2020).
	Trib 60 extract (Tonvara premium natural supplements, UK).	0.0, 1.0, 1.5, 2.0 & 2.5 g kg^{-1} of feed	42	Oral	*O. niloticus*	2.5 g kg^{-1} of feed	83.67 ± 4.04	Omitoyin et al. (2013)
	Seed powder	0.0, 5.0, 10.0, & 15.0 g kg^{-1} of feed	30	Oral	*O. niloticus*	15.0 g kg^{-1} of feed	76.6 ± 0.5	Ghosal, Mukherjee, Hancz, and Chakraborty (2016)

TABLE 1 (Continued)

Botanical name	Treatment (parts/products used)	Dosage	Exposure period (days)	Treatment method	Tilapia species	Best dosage	Masculinization success (%)	Reference
	Seed aqueous extract	0.05, 0.1, & 0.15 g L^{-1}	30	Immersion	*O. niloticus*	0.15 g L^{-1}	81.4 ± 0.5	Ghosal et al. (2016)
	Seed aqueous extract	0.00, 0.05, 0.10, & 0.15 g L^{-1}	30	Immersion	*O. niloticus*	0.15 g L^{-1}	81.4 ± 0.5	Ghosal and Chakraborty (2014a)
	Seed powder ethanol extract	0.0, 2.0, 2.5, & 3.0 g kg^{-1} of feed	30	Oral	*O. niloticus*	2.0 g kg^{-1} of feed	91.53 ± 0.38	Ghosal and Chakraborty (2020).
	N/S	1.0 & 2.0 g kg^{-1} of feed	28	Oral	*Oreochromis sp.* (red tilapia)	2.0 g kg^{-1} feed	84.4	Zaki, Said, Tahoun, and Amer (2021)
Basella alba	Leaf powder of aqueous, methanol, ethanol, dichloromethane, hexane & successive methanol extracts	0.5, 1.0, & 1.5 g kg^{-1} of feed	30	Oral	*O. niloticus*	1.0 g of ethanol extract kg^{-1} of feed	83.2 ± 0.7	Ghosal et al. (2015); Ghosal and Chakraborty (2020).
	Leaf aqueous extract	0.00, 0.05, 0.10, & 0.15 g L^{-1}	30	Immersion	*O. niloticus*	0.1 g L^{-1}	70.3 ± 1.9	Ghosal and Chakraborty (2014b)
	Leaf powder	0.0, 5.0, 10.0, & 15.0 g kg^{-1} of feed	30	Oral	*O. niloticus*	10.0 g kg^{-1} of feed	70.3 ± 1.2	Ghosal et al. (2016)
	Leaf aqueous extract	0.05, 0.10, & 0.15 g L^{-1}	30	Immersion	*O. niloticus*	0.1 g L^{-1}	71.9 ± 1.9	Ghosal et al. (2016)
Trigonella foenum-graecum	Saponin methanol extract	0.15 & 0.30 g kg^{-1} of feed	30	Oral	*O. niloticus*	0.30 g kg^{-1} of feed	56 ± 12.6	Stadtlander et al. (2013)
	Saponin methanol extract	40, 60, & 80% TS (0.15 and 1.00 g kg^{-1} of feed)	120	Oral	*O. niloticus*	80% TS (0.15 g kg^{-1} of feed)	73	Stadtlander et al. (2008)
Quillaja saponaria	Saponin (QS; Sigma, St. Louis, MO)	0.05, 0.15, 0.30, 0.50, & 0.70 g kg^{-1} of feed	60	Oral	*O. niloticus*	0.70 g kg^{-1} of feed	69	Francis, Levavi-Sivan, Avitan, and Becker (2002)
	Saponin methanol extract	40, 60, & 80% QS (0.15 & 1.00 g kg^{-1} of feed)	120	Oral	*O. niloticus*	80% QS (0.15 g kg^{-1} of feed)	73	Stadtlander et al. (2008)

(Continues)

TABLE 1 (Continued)

Botanical name	Treatment (parts/products used)	Dosage	Exposure period (days)	Treatment method	Tilapia species	Best dosage	Masculinization success (%)	Reference
Pinus tabulaeformis	Pollen powder	0.00, 0.08, 0.16, 0.32, & 0.64 g kg^{-1} of feed	60	Oral	*O. niloticus*	0.32 g kg^{-1} of feed	89.1 ± 3.6	Nian et al. (2017)
Pinus kesiya	Pollen powder	(0.5 g of pine pollen + 0.5 g MT) kg^{-1} of feed & 1.0 g of pine pollen kg^{-1} of feed	28	Oral	*O. niloticus*	1.0 g of pine pollen kg^{-1} of feed	88	Nieves (2017)
Aloe vera	Crude powder extract	0, 1.0, 2.0, & 4.0% of feed	30	Oral	*O. niloticus*	4.0% of feed	67.62 ± 4.37	Gabriel et al. (2017)
Hibiscus rosa-sinensis	Flower extract	0.16, 0.50, 1.00, 3.00, & 4.00 g kg^{-1} of feed	28	Oral	*O. niloticus*	4.00 g kg^{-1} of feed	73.13 ± 6.38	Abella et al. (2015)
Butea superba	Root powder	100, 200, & 300 g kg^{-1} of feed	30	Oral	*O. niloticus*	200 g kg^{-1} of feed	72.2 ± 25.5	Mengumphan, Samitasiri, and Carandang (2006)
	Root powder ethanol extract	0.00, 0.04, 0.08, 0.12, 0.16, & 0.20 g kg^{-1} of feed	21	Oral	*O. niloticus*	0.20 g kg^{-1} of feed	100	Kiriyakit (2014)
Eurycoma longifolia	Root methanol extract	0.00, 0.03, 0.06, & 0.09 g kg^{-1} of feed	30	Oral	*O. niloticus*	0.06 g kg^{-1} of feed	82.10	Yusuf, Andayani, Risjani, & Faqih, 2019
	Root powder ethanol extract	0.00, 0.02, 0.04, & 0.06 g L^{-1}	60	Immersion	*O. niloticus*	0.06 g L^{-1}	67.44	Rinaldi, Zairin-Jr, Soelistyowati, and Imron (2017)
Garcinia kola	Seed powder	0, 10, 20, & 30 g kg^{-1} of feed	28	Oral	*O. niloticus*	30 g kg^{-1} of feed	65.75 ± 4.19	Tigoli et al. (2018)

Abbreviations: MT, 17α-methyl testosterone; N/S, Not specified; QS, *Quillaja saponaria* saponin; TS, *Trigonella foenum-graecum* saponin.

and necrosis of the testicular tissues and ovaries of Nile tilapia (Obaroh et al., 2018). This distortion of Nile tilapia gonads reduces the number of hatchlings (Obaroh & Achionye-Nzeh, 2013), thus impairing breeding in this fish.

2.1.6 | Indian spinach, *Basella alba*

The Indian spinach is a leafy fast-growing vegetable, belonging to order Caryophyllales and family Basellaceae (Adhikari, Naveen, & Shruthi, 2012; Kumar, Prasad, Iyer, & Vaidya, 2013). *B. alba* is native to tropical Asia but was introduced in tropical Africa and South America (Deshmukh & Gaikwad, 2014; Roy, Gangopadhyay, & Mukherjee, 2010). The leaves of *B. alba* contain flavanoids, tannin, steroid, and saponin phyto-compounds (Ghosal et al., 2015). It is postulated that the presence of steroids increases testosterone levels in animals treated with *B. alba* extracts (Moundipa et al., 1999, 2005, 2006; Nantia et al., 2011). The incorporation of 1.0 g of *B. alba* methanol extract kg^{-1} of diet masculinized *Poecilia reticulate* (Chakraborty, Molnar, & Hancz, 2012), which was linked to the ability to stimulate testosterone production. Similarly, treatment of Nile tilapia fry with *B. alba* extracts yielded up to 83.2% male individuals (Table 1).

2.1.7 | Jack plant, *Eurycoma longifolia*

Jack plant (*E. longifolia*), also known as Tongkat Ali, is a medium size slender tree (reaching a height of 18 m) belonging to order Sapindales and family Simaroubaceae (Bhat & Karim, 2010). *E. longifolia* is distributed in South East Asian countries, mainly: Malaysia, Indonesia, Vietnam, and Thailand (Arifah & Nurkhasanah, 2014; Bhat & Karim, 2010). The aphrodisiac properties of the root extracts of Jack plant increase sexual quality and libido in animals (Ang & Lee, 2002; Ang, Lee, & Kiyoshi, 2003, 2004). The *E. longifolia* extracts contain saponin, phytosterol, isoprenoid, alkaloid, and minerals (Fe, Co, Mg, Zn), which stimulate proliferation of spermatogenic, sertoli, and leydig cells in rats (Bogar, Tendean, & Turalaki, 2016; Rosida, 2003) and subsequently augment production of testosterone (Nainggolan & Simanjuntak, 2005). Notably, phytosterol (i.e., stigmasterol) in *E. longifolia* stimulated androgen hormone production in Nile tilapia, thus favoring masculinization (Rinaldi et al., 2017; Syarifuddin, Sri, Yenny, & Rahem, 2019; Yusuf et al., 2019; Table 1).

2.1.8 | Mango, *Mangifera indica*

Mangoes are native to tropical Asia (Nwinuka, Monanu, & Nwiloh, 2008), but introduced to most tropical countries. *M. indica* belongs to order Sapindales and family Anacardiaceae (Shah, Patel, Patel, & Parmar, 2010), and is utilized as a medicinal herb (Ojewole, 2005). The leaf extracts of *M. indica* have a high concentration of alkaloids, saponins, steroids, tannins, and alkaloids (Aiyelaagbe & Osamudiamen, 2009; Biu, Yusuf, & Rabo, 2009). Saponins occur in higher concentration compared to the other bioactive compounds, hence believed to be responsible for the antifertility effects of *M. indica* extracts (Obaroh et al., 2012). Inclusion of *M. indica* leaf powder in Nile tilapia diets at dosages of 0.5–8.0 g kg^{-1} for 56 days reduced the number of spawned hatchlings, with complete inhibition of spawning observed at ≥2.0 g kg^{-1} of diet (Obaroh & Achionye-Nzeh, 2013). The saponins in *M. indica* extract disintegrate sperm cells and rupture follicles of Nile tilapia, thus inhibiting reproduction (Obaroh et al., 2012).

2.1.9 | Moringa, *Moringa oleifera*

This species is a perennial tree, belonging to order Brassicales and family Moringaceae (Raja et al., 2016). It is indigenous to India, Pakistan, Bangladesh, and Afghanistan and is well adapted to tropical areas, growing to a height ranging

from 10 or 12 m (Ampofo-Yeboah, 2013). The leaves, roots, and bark of moringa plant contain flavonoids, steroids, and triterpenoids (oleanolic acid-3-glucoside and β-sitosterol; Bamishaiye, Olayemi, Awagu, & Bamshaiye, 2011; Kasole, Bimenya, Ojok, Ochieng, & Ogwal-Okeng, 2010; Kawo et al., 2009; Kumar, Mishra, Ghosh, & Pand, 2010; Lambole & Kumar, 2011). Oleanolic acid-3-glucoside and β-sitosterol bioactive compounds in *M. oleifera* extracts are potential anti-fertility agents in animals (Ampofo-Yeboah, 2013; Das, 1980; Kumar et al., 2010). In fish, *M. oleifera* extracts caused skewness in sex ratios to mainly male gender (Table 1). Similarly, *M. oleifera* seed powder mixed in the diet of sexually immature and mature Mozambique tilapia (*Oreochromis mossambicus*) at 2.0 and 5.0 g kg^{-1} fed for 60 days, expressed anti-fertility effect and prevented fish reproduction (Ampofo-Yeboah, 2013). Notably, prolonged treatment of Nile tilapia on diets with *M. oleifera* leaf extracts at 5% of total dietary protein, for 90 days, severely degenerated the oocyte cytoplasm (Nwankpa, 2017). The previous experimental studies suggest that *M. oleifera* extracts can be exploited to prevent unwanted breeding in tilapia culture facilities.

2.1.10 | Neem tree, *Azadirachta indica*

A. indica is commonly known as "Neem tree" belongs to order Rutales, and is a member of mahogany family known as Meliaceae (Hashmat, Azad, & Ahmed, 2012). It is a broad-leaved plant that grows up to 30 m tall and with a girth of 2.5 m (Ndodo et al., 2013). The tree is native to the tropical and semi-tropical regions (Silayo & Kiwango, 2010). The extracts of various parts of neem tree have antimicrobial, anti-inflammatory, and spermicidal effects, as well as antifertility activity and abortifacient properties (Biswas, Chattopadhyay, Banerjee, & Bandyopadhyay, 2002; Jegede & Fagbenro, 2007; Priya, Saravanan, & Renuka, 2012). This is attributed to the high concentration of fertility-regulating-saponins and tannins in neem extracts (Atangwho et al., 2009; Biu et al., 2009; Kapinga et al., 2018), in addition to sodium nimbinate, "a spermicide" (National Research Council, 1992). Consequently, the neem tree's anti-fertility activity has been harnessed to control prolific breeding in tilapia in culture systems. The inclusion of 2.0 g kg^{-1} of *A. indica* leaf powder rendered the testes and ovaries of *Tilapia zilli* devoid of spermatids and oocytes after 60 days of treatment (Jegede & Fagbenro, 2008b). Likewise, Nile tilapia, fed on diet containing 1.0–8 g kg^{-1} of crude *A. indica* ethanol-based leaf extracts reduced the number of hatchings, with no spawning by the fifth week (Obaroh & Achionye-Nzeh, 2011; Obaroh & Achionye-Nzeh, 2013; Obaroh et al., 2012). However, *A. indica* only lowered the spawning of Nile tilapia by 76% at the highest inclusion of 8.0 g of the leaf powder kg^{-1} diet for 90 days (Kapinga et al., 2018). This inconsistency in performance of *A. indica* extracts could be attributed to differences in extraction media and seasons (Isah, 2019). These discrepancies hamper wide-scale utilization of neem extracts to control tilapia reproduction.

2.1.11 | Pawpaw, *Carica papaya*

C. papaya, commonly known as "Pawpaw," is an herbaceous succulent plant that belongs to Brassicales order and Caricaceae family (Yogiraj, Goyal, Chauhan, Goyal, & Vyas, 2014), growing mostly in tropical and subtropical countries (Krishna, Paridhavi, & Patel, 2008). The plant grows to the height between 5 and 10 m, with leaves confined to the top of the trunk (Bamisaye, Ajani, & Minari, 2013). The fruit contains micronutrients such as vitamins A and C, carotene, and minerals (Krishna et al., 2008). Pawpaw seeds contain alkaloids, steroids, flavonoids, saponins, and tannins (Ezike, Akah, Okoli, Ezeuchenne, & Ezeugwu, 2009; Krishna et al., 2008; Oloyede, 2005). The saponin, oleanolic acid 3-glucoside, is the main bioactive compound in pawpaw seeds with anti-fertility or sterility potential (Das, 1980; Lohiya et al., 2005; Mansura, Ameh, Ibrahim, Ayo, & Ambali, 2009; Udoh & Kehinde, 1999; Verma, Nambiar, & Chinoy, 2006). The glucosides in pawpaw seed meal can also disintegrate gonadal cells in testes and ovaries of tilapia (Abbas & Abbas, 2011; Ekanem & Okoronkwo, 2003; Jegede & Fagbenro, 2008a; Waweru, Raburu, & Elizabeth, 2019). As a result, pawpaw seed meal has been utilized to prevent prolific spawning in tilapia culture

systems. The inclusion of pawpaw seed powder in tilapia diets for 28–60 days, at dosages of 2.0 g–5.0 g kg^{-1} of the diet, rendered the testes and ovaries of Nile tilapia and Mozambique tilapia, devoid of spermatids and oocytes (Ampofo-Yeboah, 2013; Jegede & Fagbenro, 2008a; Solomon, Ugonna, Olufeagba, & Okomoda, 2017). Dosage increment of pawpaw seed powder to at least 8.0 g kg^{-1} of feed for 60 days resulted in atretic follicles of ovaries and degenerates spermatozoa in testes of sterility in Nile tilapia (Abbas & Abbas, 2011; Ekanem & Okoronkwo, 2003; Waweru et al., 2019). The dosage of 120 g kg^{-1} led to permanent sterility in Nile tilapia (Abdelhak et al., 2013). Likewise, the inclusion of pawpaw seed powder in the diets of Nile tilapia and Mozambique tilapia fry (Table 1) shifted fish sex to all-male (Ahmed et al., 2019; Ampofo-Yeboah, 2013; Omeje et al., 2018). The masculinization of tilapia could be linked to the androgens in pawpaw seed meal that lower 17β-estradiol levels in the female fish, while favoring production of testosterone (Ampofo-Yeboah, 2013).

2.1.12 | Pine trees, *Pinus* spp.

Taxonomically, pine trees belong to the Pinales order and Pinaceae family (Christenhusz et al., 2011). The trees are mainly distributed in North America, China, South-East Asia, North Africa, and Europe (Keeley, 2012). The purplish male cones of pine trees are a source of "pollen," containing high quantities of testosterone, epitestosterone, and androstenedione (Jones & Roddick, 1988; Velasco, Drexel, Lexter, & Tereso, 2018). For example, pollen from *Pinus silvestris* contains 80 ng g^{-1} of testosterone, 110 ng g^{-1} epitestosterone, and 590 ng g^{-1} androstenedione (Saden-Krehula, Tajic, & Kolbah, 1971; Zhong-han, Yin, Zong-xun, & Tsao, 1994). In *Pinus bungeana* and *Pinus tabulaeformis*, the testosterone concentrations range from 11 to 27 ng g^{-1} dry weight of pollen (Zhong-han et al., 1994). Pine pollen can be considered a store of testosterone (Adenigba, Tumbokon, & Serrano-Jr, 2017; Jones & Roddick, 1988; Saden-Krehula et al., 1971; Saden-Krehula, Tajic, & Kolbah, 1979; Velasco et al., 2018; Zhong-han et al., 1994). The utilization of pollen from *Pinus tabulaeformis* and *Pinus kesiya* to produce all-male individuals of Nile tilapia resulted in considerable increase in the rate of masculinization (Nian et al., 2017; Nieves, 2017; Table 1).

2.1.13 | Puncture vine, *Tribulus terrestris*

T. terrestris is an herbaceous perennial plant growing to a height of 10–60 cm. It belongs to order Zygophyllales and family Zygophyllaceae (Yanala, Sathyanarayana, & Kannan, 2016), occurring abundantly in Asia, Europe, and Africa (Yilmaz, Cek, & Mazlum, 2013). The seeds of *T. terrestris* contain alkaloids, steroidal saponins, tannins, flavonoids, and flavonol glycosides, as bioactive compounds (Chhatre, Nesari, Somani, Kanchan, & Sathaye, 2014; Ghosal et al., 2015). The androgenic activity of *T. terrestris* is linked to the presence of protodioscin, a steroidal saponin (Dinchev et al., 2008; Ganzera, Bedir, & Khan, 2001), which induces production of testosterone phyto-dehydroepiandrosterone, dihydrotestosterone, and dehydroepiandros-teronesulfate in men (Adimoelja, Sartono, & Soedjono, 2005), rabbits and rats (Gauthaman, Adaikan, & Prasad, 2002; Gauthaman & Ganesan, 2008). Therefore, puncture vine extracts are used to treat sexual infertility, improve libido and spermatogenesis in humans (Adaikan, Gauthaman, Ng, & Prasad, 2000; Adaikan, Gauthaman, & Prasad, 2001; Adimoelja, 2000; Adimoelja & Adaikan, 1997; Bucci, 2000; Neychev & Mitev, 2005). In fish production, treatment of *Clarias gariepinus*, *Cichlasoma nigrofasciatum*, *Poecilia reticulate*, and *Oncorhynchus mykiss* with *T. terrestris* resulted in successful sex reversal, spermatogenesis, and better growth rates (Cek, Turan, & Atik, 2007a, 2007b; Kavitha & Subramanian, 2011; Turan & Cek, 2007; Yilmaz et al., 2013). The potential of *T. terrestris* extracts to trigger testosterone and 11-ketotetestosterone (11-KT) production, which transforms fish sex to males (Gharaei, Ebrahimi, Mirdar, & Kolangi, 2020; Ghosal et al., 2021), can be harnessed to control prolific spawning in tilapia production. Studies achieved up to 91.5% masculinization success of Nile tilapia, through oral administration of 2.0 g of *T. terrestris* seed powder of kg^{-1} feed for 30 days (Table 1).

2.1.14 | Red hibiscus, *Hibiscus rosa-sinensis*

H. rosa-sinensis is an ornamental herb, commonly known as red hibiscus, belonging to order Malvales and family Malvaceae (Pekamwar, Kalyankar, & Jadhav, 2013). The herb is native to China; but was widely introduced in tropics and sub-tropics (Hou, Tong, Terahara, Lou, & Fujii, 2005; Khristi & Patel, 2016). The phytochemical analysis of flowers, leaves, and roots revealed the presence of saponins, steroids, tannins, and flavonoids (Pekamwar et al., 2013). The flavonoids in *H. rosa-sinensis* extracts are reported to induce anti-implantation and anti-spermatogenic effects in animals (Jiang, 1998; Murthy, Reddy, & Patil, 1997; Tan, 1983; Zhou, 1998). The treatment of Nile tilapia with *H. rosa-sinensis* leaf powder at 3.0 and 4.0 g kg^{-1} of feed ruptured testes and ovary tissues after 60 days of treatment, thereby inducing sterility (Jegede, 2010). The inclusion of *H. rosa-sinensis* flower extracts also induced masculinization of Nile tilapia fry, producing up to 73.13% male individuals (Abella et al., 2015; Table 1). Therefore, more studies are required to clarify the specific effect of *H. rosa-sinensis* extracts on reproductive organs of fish, before recommendation for commercial adoption as population control agents in tilapia culture systems.

2.1.15 | Red kwao krua, *Butea superba*

B. superba belongs to order Fabales, and family Leguminosae (Cherdshewasart, Bhuntaku, Panriansaen, Dahlan, & Malaivijitnond, 2008). This indigenous Thai herb is used to increase men's sexual performance (Kiriyakit, 2014). The roots of *B. superba* contain flavonoids, tannins, alkaloids, glycosides, and phenols (Vijayan, Seethalakshmi, Jayanthi, & Ragunathan, 2016). These phytochemicals, especially flavonol and flavonoid glycoside, isolated from Red kwao krua function as phytoandrogens, with similar effects as testosterone (Cherdshewasart & Nimsakul, 2003; Manosroi & Manosroi, 2005). The presence of flavonoid glycoside stimulates testosterone production, which augments sex shift to male individuals. Attempts to use *B. superb* extracts for controlling prolific spawning in tilapia through all-male production yielded up to 100% male tilapia individuals (Mengumphan et al., 2006; Kiriyakit, 2014; Table 1).

2.1.16 | Shatavari, *Asparagus racemosus*

A. racemosus is a woody climber that belongs to the Asparagales order and Asparagaceae family (Alok et al., 2013; Hasan, Ahmad, Zohrameena, Khalid, & Akhtar, 2016). It is native to India, but is distributed in the tropical and subtropical regions, growing to a height of one to two meters, mainly in low altitudes (Hasan et al., 2016; Tripathi, Pandey, Bhushan, Sahu, & Dubey, 2017). The root extracts of *A. racemosus* contain saponins, steroids, tannins, and flavonoids (Mukherjee et al., 2015a; Mukherjee et al., 2018). These bio-compounds, mainly the steroidal saponins, have therapeutic, aphrodisiac, and androgenic effects in animals (Alok et al., 2013; Mishra, Sheikh, Agnihotri, & Chourey, 2010; Thakur, Chauhan, Bhargava, & Dixit, 2009). The steroids in the root extracts of *A. racemosus* enhance production of 11-keto testosterone (11-KT) in testis of Nile tilapia, favoring sex change to all-male (Ghosal et al., 2021). As such, *A. racemosus* root extract inversed Nile tilapia sex resulting in significant masculinization (Table 1). This suggests that *A. racemosus* contains potential organic products that could be utilized for reproduction control in tilapia production systems.

2.1.17 | Soapbark tree, *Quillaja saponaria*

The soap bark tree belongs to the order Fabales and family Quillajaceae (Guerra & Sepulveda, 2020). This tree is native to China, Peru, and Chile (Angeles Jr., Gallego, Navarro, & Chien, 2017; Francis et al., 2002). The bark of *Q. saponaria* contains triterpenoidal saponins, mainly triterpene glycoside, which can inhibit fish reproduction and

increase growth performance (Bankefors, Nord, & Kenne, 2008; Francis, Makkar, & Becker, 2005; Stadtlander et al., 2008). The feeding of sexually mature female Nile tilapia on *Q. saponaria* extract at 300 mg kg^{-1} of diet inhibited spawning (Francis et al., 2005; Francis, Makkar, & Becker, 2001), in addition to inducing masculinization of the female Nile tilapia fry (Table 1). A dose of 700 mg of *Q. saponaria* saponin kg^{-1} of diet shifted the sex of Nile tilapia to mostly males (Francis et al., 2002). Similarly, *Q. saponaria* saponin extracts incorporated in Nile tilapia diets resulted in a significant increase in the number of male individuals (Stadtlander et al., 2008). As such, triterpenoid saponins in *Q. saponaria* need to be harnessed for production all-male populations in tilapia culture.

2.1.18 | True aloe, *Aloe vera*

A. vera is a stemless or very short-stemmed perennial succulent plant that belongs to order Liliales, and family Asphodelaceae (Sanchez-Machado, Lopez-Cervantes, Sendon, & Sanches-Silva, 2017). It is widely distributed in tropical and semitropical regions. *A. vera* contains saponins, flavonoids, tannins, anthraquinones, and alkaloids (Langmead, Makins, & Rampton, 2004; Patel, Patel, & Dhanabal, 2012). Among the bioactive constituents, saponin and flavonoids were implicated in the control of reproduction in animals (Francis et al., 2002; Omitoyin et al., 2013; Patel et al., 2012). The inclusion of *A. vera* extracts, as low as 2.0 ml kg^{-1} in Nile tilapia diets, caused disintegration of spermatids and follicles thus inhibiting gonadal development and functioning (Jegede, 2011; Kushwaha, 2013). The saponins in *A. vera* extracts (Kumar, Chandana, Preethi, & Chauhan, 2012) elevate testosterone production in animals such as rats (Gauthaman & Ganesan, 2008) and fish (Table 1), which favors development of male sex organs.

2.1.19 | Velvet bean, *Mucuna pruriens*

M. pruriens is a widespread tropical and sub-tropical legume belonging to the order Fabales, family Leguminosae, and subfamily Fabaceae. The plant grows to a height of 3–18 m in bushes, hedges, and forests (Lampariello, Cortelazzo, Guerranti, Sticozzi, & Valacchi, 2012; Sathiyanarayanan & Arulmozhi, 2007). The seeds of *M. pruriens* contain tannin, saponin, alkaloid, glycoside, flavonoid, and steroid phytochemicals (Mukherjee et al., 2015b; Mukherjee et al., 2018). In particular, the steroids in *M. pruriens* extracts increased the serum testosterone in animals (Ahmad, Rahma, Akhtar, & Ali, 2012), stimulating androgenic effects, as was observed in rats (Muthu & Krishnamoorthy, 2011) and fish (Mukherjee et al., 2018). Accordingly, the phytoandrogens in *M. pruriens* seed extracts produced up to 93% all-male Nile tilapia (Table 1). However, the action of the plant extracts on gonadal function and spawning of tilapia has not been elucidated. Nonetheless, experimental treatment of rats with *M. pruriens* extract triggered increment in spermatozoa, together with the sexual and androgenic activities (Suresh & Prakash, 2012; Suresh, Prithiviraj, & Prakash, 2009).

3 | ROUTE OF ADMINISTRATION OF PLANT EXTRACTS

During fish culture operations, plant extracts are administered either through incorporation in fish feeds (oral method), immersion, or injection (Bulfon, Volpatti, & Galeotti, 2015). The oral and immersion techniques are considered noninvasive, hence commonly used methods during reproduction control in tilapia (Table 1). Overall, oral administration is the predominant method because of the low cost of application, potential of treatment of large numbers of fish at the same time, causes no stress or reduced stress (Bulfon et al., 2015; Sakai, 1999; Yoshida, Kruger, & Inglis, 1995) and yields at least 95% sex masculinization (El-Greisy & El-Gamal, 2012; Phelps & Popma, 2000). Nonetheless, the effectiveness of oral method is reduced by differences in the amount of the sex steroids available to the fish, linked to non-uniform distribution of the extracts in the diets during mixing.

The immersion technique is crucial in fish species whose gonadal labile period occurs before first feeding, such as in yolk sac larvae or during embryogenesis (Devlin & Nagahama, 2002). In tilapia, the labile period of sex differentiation occurs during the first 30 days post-hatch, the period within which fry can ingest exogenous diets (Mateen & Ahmed, 2007). Immersion of tilapia in plant extracts during post-hatching stages has yielded up to 90% masculinization (Table 1). However,fish immersion method requires mixing the extracts with culture water at each exposure time , which results in wastages of the masculinization agent, and high rate of release into the environment.

Intra-peritoneal injection of fish is efficient and rapid, necessitated by quick absorption of the extracts (Reverter et al., 2014). However, the process of injecting fish is expensive, laborious, stressful to fish, and impractical for small fish, that is, less than 15 g fish^{-1} (Anderson, 1992; Beardmore et al., 2001; Blazer, 1992; Reverter et al., 2014; Sakai, 1999). Besides, the method requires technical skills to avoid inflicting damage onto the fish (Hoga, Almeida, & Reyes, 2018). As such, the injection method is rarely utilized to administer sex inversion reversal agents in tilapia culture systems.

4 | MECHANISM OF ACTION OF PLANT EXTRACTS AS CONTROL AGENTS OF REPRODUCTION IN TILAPIA

The precise mechanisms by which plant bioactive compounds manipulate reproduction in tilapia are not yet elucidated. Nevertheless, two pathways, that is, endocrine system modulation and induction of gonadal histological changes are postulated as plausible functional mechanisms responsible for changes on the reproductive physiology of fish.

4.1 | Endocrine system modulation

Phyto-compounds modulate the endocrine system of fish, hence referred to as endocrine disrupting compounds (EDCs). The phyto-compounds can disrupt the biosynthesis, distribution, and functions of steroid hormones subsequently interfering with the reproductive physiology of fish (Omeje, 2016). The EDCs interrupt gonadal differentiation in fish by interfering with the biosynthesis of sex steroids through: (a) inhibiting aromatase enzyme; and (b) antagonizing estrogen nuclear receptors (Cek et al., 2007a, 2007b; Chakraborty et al., 2013; Cheshenko, Pakdel, Segner, Kah, & Eggen, 2008; Francis et al., 2002; Rempel & Schlenk, 2008).

The phyto-compounds are hypothesized to inhibit aromatase enzyme Cytochrome P450 aromatase enzyme, which catalyzes the conversion of androgens to estrogens, thus favoring development of female characteristics (Eng et al., 2001). The enzyme is inhibited through either competitive inhibition of natural substrates for the enzyme, decreasing the expression of cyclic adenosine monophosphate (cAMP) responsive element binding (CREB) protein or inhibiting the generation of cAMP. Consequently, the pathway regulating aromatase expression is altered, which in turn augments production of androgens, modifying sex ratio in favor of male individuals (Cheshenko et al., 2008). Phyto-compounds such as flavonoids and steroidal saponins, are reported to inhibit aromatase enzyme activity (Golan et al., 2008) increasing the production of testosterone, a process towards induction fish masculinization (Gauthaman & Ganesan, 2008).

The phyto-compounds may also antagonize endogenous estrogens by interacting with estrogen nuclear receptors. The antagonicity of phyto-compounds is facilitated by similarity in structures to estrogens and high affinity for estrogen receptors. Besides, the phytochemicals have stable structures and low molecular weights, which permit passage although the cell membranes (Ososki & Kenelly, 2003). Within the cytoplasm, the phyto-compounds compete with endogenous estrogens for binding sites of estrogen receptors, hence acting as estrogen antagonists (anti-estrogens). The anti-estrogens block or alter estrogen receptors, preventing estrogenic activity and consequently reversing the estrogenic effects (Matozzo, Gagne, Marin, Ricciardi, & Blaise, 2008; Ososki & Kenelly, 2003). Anti-

estrogenic compounds such as flavonoids have structures that mimic estrogens, enhancing the affinity for estrogen receptors (Bennetau-Pelissero et al., 2001; Chen & Chang, 2007; Green & Kelly, 2009; Miyahara et al., 2003; Tarigan et al., 2016). Therefore, the anti-estrogenic compounds can easily bind onto the estrogen receptors, subsequently disrupting the effect of estrogens.

4.2 | Induction of gonadal histological changes

The phyto-compounds may impair fertility by inducing histological changes in the gonads of fish: (a) delay gonadal maturation and (b) obstruct reproductive functions. The histological changes in fish testes and ovaries include disintegration of gonad cells, rupture of seminiferous lobule and follicles as well as gonadal necrosis. As a consequence of gonadal damage, testes and ovaries become devoid of spermatids and oocytes, respectively (Abdelhak et al., 2013; Ampofo-Yeboah, 2013; Jegede, 2010; Jegede & Fagbenro, 2008a, 2008b). For example, the saponins in *C. papaya* seed powder rendered the testes and ovaries of *O. niloticus* and *O. mossambicus* devoid of spermatids and oocytes (Ampofo-Yeboah, 2013; Jegede & Fagbenro, 2008a, 2008b; Solomon et al., 2017).

5 | LIMITATIONS TO THE UTILIZATION OF PLANT EXTRACTS AND FUTURE PERSPECTIVES

The use of plant extracts to control prolific spawning in tilapia culture systems is an emerging innovation. As such, a number of drawbacks continue to constrain commercial application of phytoextracts. Generally, technical and economic limitations continue to hinder the progress in application of plant extracts from experimental to field levels (Chakraborty et al., 2013; Ghosal & Chakraborty, 2020; Kapinga et al., 2019; Mukherjee et al., 2018).

5.1 | Technical limitations

The existing knowledge lack reliable information on the: (a) ideal extraction methods of phytochemicals, (b) effective bioactive compounds in plants, (c) effect of seasons, environmental parameters and stage of plant growth on the yield and biological activity of extracts, (d) optimal dose requirements, (e) precise mechanism of action, and (f) long-term effects of plant extracts on quality of fish's flesh and physiological processes such as growth and immunity (Chakraborty et al., 2013; Gabriel et al., 2017; Ghosal et al., 2021; Mukherjee et al., 2015b; Stadtlander et al., 2008).

The present review observed discrepancies in extraction methods of plant extracts, especially extraction solvents used, yet the yield and functional properties of phytochemicals are dependent on the extraction techniques (Dhanani, Shah, Gajbhiye, & Kumar, 2017; Tiwari, Kumar, Kaur, Kaur, & Kaur, 2011). A variety of bioactive compounds from different plant extracts have varying solubility properties in different solvents such as aqueous, ethanol and methanol (Truong et al., 2019). It is therefore necessary to select an ideal extraction solvent especially, of appropriate polarity, to maximize the yield of the target bioactive compounds without disrupting their functional activities (Dhanani et al., 2017). Further, little is known on the effect of the plant's growth stage (Akula & Ravishankar, 2011), seasons and environmental parameters (Isah, 2019) and geographical origin (Dinchev et al., 2008), on the concentration and composition of phytochemicals believed to control reproduction in tilapia. With regard to the effectiveness of plant extracts, variable optimal doses are reported by different studies, even for extracts from the same plant (Table 1). Similarly, the effects of specific bioactive compounds from the same plant are not defined. The reviewed studies, therefore, attribute the observed effects of plant extracts to various phytochemicals present in the plant. In addition, the precise mechanism modulating tilapia sex inversion or fertility impairment is not understood, further hampering the harmonization of the optimal dosages and treatment regimen.

Given the technical information gaps in utilizing plant extracts in tilapia culture, low reproducibility of results is reported, a concern that needs to be addressed before commercialization of the technology. Research on developing efficient methods for isolating and quantifying bioactive compounds in plant extracts, including determining ideal extraction solvents for target phytochemicals that induce sex manipulation in tilapia is vital. Further, the hypothesized mechanisms of action necessitate comprehensive analysis either by searching for sex gene expression profiles at the transcriptomic level or changes in the sex steroid levels (Capel & Tanaka, 2013; Ross & Capel, 2005), to validate the specific role/s of plant extracts on the tilapia sex differentiation pathway. This would facilitate the designing of a standard utilization protocol including: extraction procedure for bioactive ingredients of interest, extraction solvents that result in highly purified concentrations, administration approaches, and subsequently optimal doses levels of plant extracts (Dhanani et al., 2017; Mukherjee, Ghosal, Moniruzzaman, De, & Chakraborty, 2019).

The commercial application of plant extracts in masculinization of tilapia is also limited by inadequate information regarding the long-term effects of the extracts on the quality of fish's flesh and other physiological processes. Plant extracts may either positively or negatively modulate the physiological functioning of fish, depending on plant type and the administered dose. Besides reproduction control, plant extracts such as saponins also enhance the immune system and subsequently growth performance of fish. However, a specific dosage of the extracts that is effective in controlling unwanted breeding may trigger negative growth response in the same fish. Some plant extracts also contain antinutritional factors such as gossypol in cotton, which interfere with feed utilization, hence adversely affecting health and growth of fish. (Ayotunde & Ofem, 2008; Chakraborty et al., 2013; Gabriel et al., 2015; Kapinga et al., 2018; Prasad & Mukthiraj, 2011). Thus, in-depth explorations focusing on determining optimal doses of plant extracts for sex manipulation that do not cause undesirable effects to the fish's flesh and physiological processes are needed.

5.2 | Economic limitations

Although viewed as relatively cheap and readily available alternative to synthetic hormones, no study has sufficiently described the economic viability of utilizing plant extracts in aquaculture. As such, information on the cost effectiveness of plant-based products for commercial application in tilapia culture is lacking. Therefore, research to determine the benefit–cost ratio of utilizing plant extracts is needed to guide recommendations for an economically feasible alternative to synthetic hormones.

6 | CONCLUSION

This review underpins the potential of plant extracts as alternatives to synthetic steroids in controlling unwanted reproduction in tilapia culture. However, addressing the technical limitations and generating information on economic incentives are key to fostering adoption of plant extracts as effective, environmentally sustainable, and socially acceptable approach to masculinization of tilapia.

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CONFLICT OF INTEREST

The authors of this study declare no conflict of interest.

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