

Review

# South Africa: An Important Soybean Producer in Sub-Saharan Africa and the Quest for Managing Nematode Pests of the Crop

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Received: 28 May 2020; Accepted: 13 June 2020; Published: 22 June 2020



**Abstract:** With an increase in the global population, a protein-rich crop like soybean can help manage food insecurity in sub-Saharan Africa (SSA). The expansion of soybean production in recent years lead to increased land requirements for growing the crop and the increased risk of exposing this valuable crop to various pests and diseases. Of these pests, plant-parasitic nematodes (PPN), especially *Meloidogyne* and *Pratylenchus* spp., are of great concern. The increase in the population densities of these nematodes can cause significant damage to soybean. Furthermore, the use of crop rotation and cultivars (cvs.) with genetic resistance traits might not be effective for *Meloidogyne* and *Pratylenchus* control. This review builds on a previous study and focuses on the current nematode threat facing local soybean production, while probing into possible biological control options that still need to be studied in more detail. As soybean is produced on a global scale, the information generated by local and international researchers is needed. This will address the problem of the current global food demand, which is a matter of pressing importance for developing countries, such as those in sub-Saharan Africa.

**Keywords:** Africa; soybean; *Meloidogyne*; *Pratylenchus*; management

## 1. The Potential of Soybean to Manage Food Insecurity

United Nations (UN) estimates indicated that the world population increased from 6,145,007 to 7,795,482 during 2000–2020, while the sub-Saharan Africa (SSA) population almost doubled (645,007 to 1,106,573) in the same period [1]. This increase in population density can result in severe food insecurity especially in SSA, where food demand can increase by more than 300% by 2050. Cereals, such as maize (*Zea mays*), millet (*Panicum* spp.), rice (*Oryza sativa*), sorghum (*Sorghum bicolor*), and wheat (*Triticum*) are the most important crops with regards to calorie intake in SSA, although large yield gaps still exist for crops like maize [2,3].

Recent estimates indicate that there are over 475 million farms worldwide that can be defined as smallholder entities, producing at least half of the world's food [4]. However, the situation is different in South Africa, where most farms are commercial and from which the bulk of food is produced while smallholder farms are more predominant in poor rural areas [5]. In SSA, smallholder farms face various challenges, including low productivity, and high levels of poverty and food insecurity, resulting in low agricultural growth that cannot match the rapid population increase [6]. To help manage the food demand in SSA, alternative crops, such as soybean (*Glycine max* (L.) Merr.), can be used. It is one of the most important summer legume crops worldwide that serves as an important dietary protein and oil source for animal and human consumption. Soybean seeds consist of about 18% oil and 38% protein

while providing protein equal in quality to that of animal sources and has the possibility to nourish people in SSA. Global soybean production has already increased since the 1960s and future increases can also be expected due to larger areas being cultivated and higher yields obtained [7]. However, as with the other important food crops grown in SSA, soybean is also parasitized by a variety of pests and diseases, of which plant-parasitic nematodes (PPN) represent an important constraint [8,9]. Other than PPN, various insect pests damage soybean in SSA of which stem feeding pests are of great concern. Similarly, a range of pathogenic bacterial and fungal diseases of soybean have been listed in association with soybean crops in SSA countries of which the most important are most likely bacteria that cause bacterial blight (*Pseudomonas savastanoi* pv. *glycinea*) and fungi (*Phakopsora pachyrhizi* and/or *P. meibomia*) causing soybean rust.

## 2. Soybean Production in South Africa and Sub-Saharan Africa

Soybean production in countries, such as Argentina, Brazil, China, Paraguay, and the United States of America (USA), are significantly higher when compared to those of SSA. During the past few years, the USA and Brazil were the world's biggest soybean producing countries (Table 1) [10], producing over 120 and 117 million metric tons (MT), respectively, in 2018/19. However, projections for 2019/20 places Brazil's soybean production at 126 million MT [10]. Although SSA has an estimated total land area of 21.2 million square kilometers with 600 million hectare (ha) of arable land, less than 10% is cultivated. Therefore, SSA can be considered as the most underutilized land reserve in the world [11]. The agro-ecological regions in SSA have a high potential for growing soybean [12]. The importance of soybean in SSA is evident in its increased production. In the early 1970s, SSA produced 13,000 MT of soybean, while 2019/20 estimates for soybean production are at 2.55 million MT when combining the top two soybean producing countries in this region, namely South Africa and Nigeria [10,11]. In 2018/19, South Africa was the largest soybean producer in SSA (1.17 million MT) followed by Nigeria and Zambia (Table 1). However, Zambia had very similar yield figures per ha compared to that of South Africa for 2018/19, indicating a steep increase in the production of soybean. Outside of these three countries, there is very little soybean production in the rest of SSA [10].

**Table 1.** Data regarding soybean production in the top sub-Saharan Africa countries and selected international countries from 2018/19 to projected data for 2019/20 [10].

Area	Country	Area Harvested (Million ha)	2018/19		Area Harvested (Million ha)	2019/20	
			Yield (Metric Tons Per ha)	Production (Million MT)		Yield (Metric Tons Per ha)	Production (Million Metric Tons)
International	Argentina	16.60	3.33	55.3	17.00	3.18	54.00
	Brazil	35.90	3.26	117.00	36.90	3.41	126.00
	Bolivia	1.40	1.93	2.70	1.40	2.00	2.80
	Canada	2.54	2.86	7.27	2.30	2.61	7.27
	India	11.33	0.96	10.93	11.25	0.83	9.30
	Indonesia	0.41	1.27	0.52	0.40	1.28	0.51
	Japan	0.15	1.45	0.21	0.15	1.69	0.25
	Paraguay	3.70	2.39	8.85	3.54	2.80	9.90
	Turkey	0.03	3.80	0.10	0.03	3.89	0.11
	USA	35.45	3.40	120.52	30.36	3.19	96.84
Sub-Saharan Africa	Nigeria	1.00	1.05	1.05	1.00	1.10	1.10
	South Africa	0.73	1.60	1.17	0.80	1.81	1.45
	Uganda	0.05	0.60	0.03	0.05	0.60	0.03
	Zambia	0.19	1.58	0.30	0.20	1.43	0.28

In South Africa, soybean, maize, and sunflower (*Helianthus annuus* L.) are the top grain crops produced in terms of area planted and production. The socioeconomic value of soybean in South Africa is of such importance that this crop is produced in each of the country's nine provinces. Numerous commercially available cultivars that are adapted to different climatic regions contribute to the crop being grown widely throughout the different climatic zones in South Africa [13]. The growing need for the proteins and oils provided by soybean is evident in the increased amount of land dedicated to its

production during the past three decades [7,13]. In the early 1990s, fields in South Africa that were used for soybean cultivation made up as little as 87,000 ha. However, the area dedicated to soybean production increased to an astonishing 730,500 ha during 2018/19, which was slightly less than the record figure of 787,200 ha recorded during 2017/18 [14].

The Department of Agriculture, Forestry, and Fisheries (DAFF) estimated that in 2010, soybean production in South Africa ranged from 450,000 to 500,000 MT per annum [15]. However, in the 2016/2017 and 2017/2018 seasons, annual production was at a record high of 1.3 and 1.5 million MT per annum, respectively [14]. The Free State, Mpumalanga, and Kwa-Zulu Natal are the three provinces with the highest soybean production, with environmental conditions (particularly drought as experienced during 2018/19) being a main constraint that limit production under local conditions. In the past few decades, the average soybean yield in SSA was reported at  $1.1 \text{ t ha}^{-1}$ , while the world average was more than double ( $2.4 \text{ t ha}^{-1}$ ) [11]. However, sporadic reports exist of extraordinary high and healthy pod formation and yield of soybean in South Africa; for example, a farmer in the Highveld region of the Mpumalanga province recorded a record 1893 pods per plant cultivated under conservation agriculture tillage practices during the 2020 growing season [16]. This is due to the benefit of increased use of conservation agriculture practices in SSA countries, such as South Africa, Ghana, and Zambia. This type of production practice can increase yields and reduce labor requirements while also improving soil fertility [17]. Yet, as with any crop, soybean production is threatened by abiotic (e.g., temperature) [7] and biotic (pests and diseases) [18,19] factors. The low soybean yields in SSA are most likely due to a combination of these factors since the cultivars used nowadays are genetically improved to deliver optimal growth and yield [20].

### 3. Value of Soybean in South Africa and Sub-Saharan Africa

The increase in demand of soybean and its products in SSA led to an annual soybean import of 6.8 million MT from 2013–2016 at a cost of 4.4 billion USD [14]. Botswana, Kenya, Nigeria, Seychelles, South Africa, Zambia, and Zimbabwe are among the top soybean importers in SSA [21]. Yet, it has been reported that SSA achieved 4.6% inflation-adjusted annual mean increases in agricultural growth from 2000–2016 [6]. More people in SSA countries realize the potential of this protein-rich crop, resulting in its use in several food products, such as dawadawa (fermented dried seeds of the African locust bean *Parkia biglobosa*), mahewu (non-alcoholic home-brewed drink made of thin slightly fermented maize-meal porridge), and nshima (a dish made from ground maize flour), consumed by local people in many SSA countries. Furthermore, some SSA countries use soymilk and soup as daily meals for malnourished children and patients infected with HIV/AIDS. Nigeria is also an SSA country that took advantage of soybean consumption and this resulted in the development of processing technologies for soy-based food [11]. In other countries, such as Rwanda, more than half of the smallholder farmers consume their entire soybean harvest as an unprocessed food source, while Zambia exports large amounts of their soybean to Botswana and Zimbabwe [21].

South Africa has seen a dramatic increase in the demand for protein sources, such as soybean, as feed for the growing livestock sectors. This led to significant investment in soybean production since the early 2000s [14,22]. In a 2016 report released by Meyer and co-authors [22], the gross value of agricultural output for field crops contributed 23% to the gross domestic product (GDP) of South Africa, compared to 29% from horticulture and 47% from livestock. Soybean contributed 8% to the total value of field crop output [22,23]. Moreover, the production of soybean increased to 1.55 million MT in 2017/2018, with a gross value of approximately ZAR7 139 million compared to approximately ZAR4 598 million for 2015/2016. The estimated gross value for soybean in 2018/2019 was approximately ZAR6 023 million, although the price per MT (ZAR/MT) decreased from 2015/2016 (ZAR6 197) to 2018/2019 (ZAR4 719) [24].

Besides socioeconomic benefits, soybean and associated *Rhizobium* and *Bradyrhizobium* microbes contribute to nitrogen fixation in soils. Nitrogen fertilization is tremendously expensive and poses ecological risks, such as water eutrophication and the emission of greenhouse gases, that contribute

to global warming [24,25]. In South Africa, the expense of applying synthetically derived nitrogen to crop fields as part of fertilization programs is one of the biggest financial outputs that farmers undertake to obtain target or expected yields [26]. Therefore, biological nitrogen fixation is a valuable and ecologically safe alternative that warrants further utilization as an added value factor when growing a legume crop, such as soybean. The increasing development and release of *Rhizobium* and/or *Bradyrhizobium* products, such as RhizoFlo® and HiStick® (BASF South Africa (Pty) Ltd., Port Elizabeth, South Africa) [27], to optimize nitrogen fixation additionally contributes towards increasing biodiversity in agricultural soils [28].

#### 4. Pests and Diseases of Soybean

Soybean crops are susceptible hosts to various pests and diseases. The threat of fungal diseases, such as frog-eye leaf spot (caused by *Cercospora sojina*), red leaf blotch (caused by *Coniothyrium glycines*), rust (caused by *P. pachyrhizi* and/or *P. meibomia*), and sudden death syndrome (caused by various pathogenic species of *Fusarium*), are common to soybean production in Africa [29]. Red leaf blotch appears to be endemic to SSA and is of major concern; there is little information about this disease with regards to its occurrence, as it has only been documented in Africa [30]. Soybean rust has, however, already been reported in Argentina, Brazil, and some of the top SSA soybean producing countries, such as South Africa, Nigeria, and Zambia [21].

Diseases caused by bacteria, such as bacterial blight (*Pseudomonas savastanoi* pv. *glycinea*), bacterial pustule (*Xanthomonas axanapodis* pv. *glycines*), and wildfire (*Pseudomonas syringae*), are also known to occur worldwide on soybean and limit production of the crop [21]. Insect and nematode pests of soybean are also of major concern [19]. Stem feeding pests of soybean in Africa are the soybean stem flies (*Melanagromyza sojae* and *Ophiomyia phaseoli*). Soybean foliar pests include the American serpentine leafminer (*Liriomyza trifolii*), the bean leafroller (*Omiodes diemenalis*), and the soybean looper (*Thysanoplusia orichalcea*). Other insects, including the legume pod borer (*Maruca vitrata*) and the southern green stink bug (*Nezara viridula*), feed on soybean pods [19,31].

Although there are also various foliar pests on soybean, the damage caused by these organisms often results in little yield loss [31]. Along with the diseases and insect pests that were mentioned previously, PPN are also known to be major pests of soybean and various other crops [19,32,33]. Of the known PPN that cause damage to soybean globally [32], soybean cyst (*Heterodera glycines*), root-knot nematode (*Meloidogyne*), and lesion (*Pratylenchus*) nematode are the most important pests [18]. However, in South Africa, the soybean cyst nematode *H. glycines* has not yet been found [26]. The soybean cyst nematode causes severe infections and yield losses in various countries in Asia as well as North and South America [9]. Root-knot nematodes, together with *Heterodera* and *Globodera* (the cyst nematodes) are generally seen as economically important nematode pests of various crops worldwide [34,35]. Concerning root-knot nematodes, *Meloidogyne arenaria* was reported in soybean fields of South Africa as early as 1959 [36], with the list of root-knot nematode species associated with soybean expanding over the years (Table 2) [33]. Root-knot nematodes are obligate biotrophic sedentary endoparasites, have a global distribution, and can cause major damage to almost all vascular plants. Inevitably, their parasitism results in substantial damage to various economically important crops, such as fruit, grain, industrial, potato, and soybean crops [35–37]. Lesion nematodes are also considered as one of the most economically important nematode pests of several crops, including banana (*Musa* spp.), cereals, coffee (*Coffea arabica* L.), maize, and soybean (Table 2) [18,38]. The first lesion nematode found to be associated with soybean in South Africa was *P. brachyurus* in 1984 [39], with reports thereafter highlighting the presence of this nematode species in soybean fields [40,41].

As soybean production in South Africa and SSA increases, the risk of exposing this crop to various pests and diseases also increases. This is evident in the number of root-knot and lesion nematodes already reported to be associated with soybean in South Africa (Table 2). Although soybean production in SSA is on the rise, the extent of research on the root-knot and lesion nematodes associated with soybean in SSA remains insufficient. The research done in South Africa [33] with regards to

predominant nematode pests associated with soybean could greatly benefit soybean production in the rest of SSA. Thus, there is a need to understand the potential impact of the two predominant nematode pest genera, *Meloidogyne* and *Pratylenchus*, can have on soybean production, as well as a discussion of the current and future management strategies to ensure sufficient yields.

**Table 2.** Countries where *Meloidogyne* and *Pratylenchus* spp. have been found to be associated with soybean.

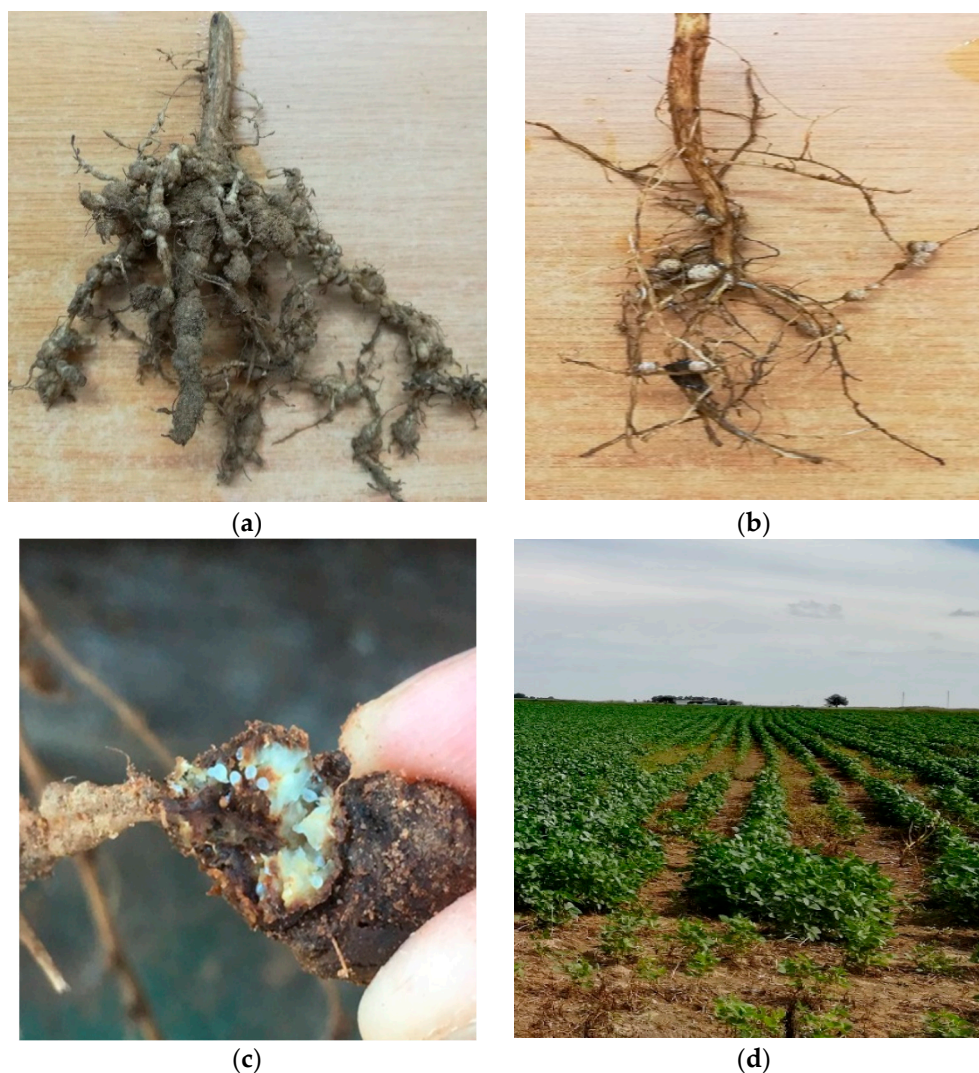
Genus	Species	Countries
<i>Meloidogyne</i>	<i>M. arenaria</i>	South Africa [36], USA [42]
	<i>M. ethiopica</i>	South Africa [40]
	<i>M. enterolobii</i>	USA [43]
	<i>M. hapla</i>	China [44], South Africa [40]
	<i>M. incognita</i>	Brazil [45], China [44], South Africa [41,46], Pakistan [47], USA [42]
	<i>M. javanica</i>	Brazil [45], Greece [48], Nigeria [49], South Africa [41,46], Pakistan [47], USA [42]
	<i>Meloidogyne</i> spp.	Germany [18], South Africa [39]
<i>Pratylenchus</i>	<i>P. brachyurus</i>	Brazil [50], South Africa [39,41]
	<i>P. crenatus</i>	Germany [18], South Africa [40,41]
	<i>P. flakkensis</i>	South Africa [41]
	<i>P. neglectus</i>	Germany [18], South Africa [41]
	<i>P. scribneri</i>	South Africa [41]
	<i>P. penetrans</i>	Germany [18], South Africa [51]
	<i>P. teres</i>	South Africa [40,41]
	<i>P. thornei</i>	Australia [52], South Africa [40,41]
	<i>P. zae</i>	South Africa [41]
	<i>P. vulnus</i>	South Africa [41]
	<i>Pratylenchus</i> spp.	South Africa [53], USA [54]

## 5. Impact of *Meloidogyne* and *Pratylenchus* on Soybean

### 5.1. *Meloidogyne*

When plant roots are infected by root-knot nematode second-stage juveniles (J2), this specific life stage as well as feeding females usually cause the formation of characteristic galls, making their presence in the roots of soybean and other crops easy to identify and study [33]. Symptoms caused by root-knot nematode infection can be divided into above- and belowground symptoms. The formation of galls on soybean roots interferes with the anatomical and physiological functioning of the roots, since infected roots cannot optimally take up and translocate water and nutrients to the aerial plant parts. Although gall formation caused by root-knot nematodes varies with the population density and or species [9], it is not advisable to attempt species identification of this genus using the extent of galling, or the size and shape of galls. However, a clear difference exists between galls caused by root-knot nematodes (Figure 1a), and the nodules formed by *Bradyrhizobium* or *Rhizobium* species (Figure 1b) [13]. These nitrogen-fixing nodules are easy to remove from the root system, as compared to the root-knot nematode galls, which form part of the root system. Although nodules can easily be removed, Bridge and Starr [55] indicated that these structures might also be infected with root-knot nematodes, with the same being found in South Africa (Figure 1c). Additionally, depending on the stage of development and infection, the color of the tissue inside the nodules will differ. In soybean, the nodules are usually pink when they are healthy as opposed to the greenish color when infected [36], but in cowpea, for example, nodules that have a pink color are healthy while infected nodules can be soft and dark brown-black in color [55]. Aboveground symptoms resulting from root-knot nematode infection generally represent stunting, wilting, yellowing, and, in severe cases, the death of plants (Figure 1d) [9,36]. However, these symptoms do not provide a conclusive diagnosis for root-knot nematode infection since it may be represented by other abiotic and/or biotic constraints, such as drought, lack of nitrogen-fixing ability of *Bradyrhizobium*/*Rhizobium*, water logging, and others. It is therefore recommended that plants are uprooted to see if the galling is present on the roots.





**Figure 1.** (a) Heavily infected and galled root, (b) healthy soybean root with no root-knot nematode galls visible and with nitrogen-fixing nodules, (c) *Meloidogyne* females found in nitrogen-fixing nodules, and (d) stunted growth of soybean plants infected with root-knot nematodes. Photos by: (a,b,d) G. Engelbrecht, North-West University, Potchefstroom and (c) by Suria Bekker, Econemaria, Potchefstroom.

## 5.2. *Pratylenchus*

Individuals of this genus are obligate biotrophic migratory endoparasites. The belowground symptoms caused by lesion nematodes to soybean roots are characterized by the formation of necrotic tissue (inside the roots) being visible as discolored (greyish, brownish, or blackish) areas (as seen in Figure 2a) on the surface of infected roots [37]. Infections can occur along the entire length of the root, with damage done to the epidermis, cortex, and root endodermis [32]. Necrotic root tissue caused by feeding lesion nematodes can, however, also be confused with damage caused by other pest and/or diseases and therefore it is not an easy task to exclusively link it to the infection of lesion nematodes [37]. Aboveground symptoms of lesion nematode infection usually resemble that caused by plant-parasitic nematodes in general but can also include patches of stunted (Figure 2b) and chlorotic (yellowish) plants, and a reduction in leaf size and the number of leaves produced on heavily infected plants for which yields can be substantially reduced. It is also possible for symptoms of *Pratylenchus* infection to mimic those of soil-borne diseases and insect damage [37]. One of the most notable symptoms of *Pratylenchus* infection is the stubby and discolored roots (lesions caused by necrosis seen in Figure 2a).



**Figure 2.** (a) Necrotic soybean roots infected with lesion nematodes, and (b) a stunted plant with a reduced and necrotic root system (green circle) compared to a noninfected plant (Photos: (a) Suria Bekker and (b) Driekie Fourie, North-West University, Potchefstroom, South Africa).

### 5.3. Interactions between *Meloidogyne* and/or *Pratylenchus* and Other Soilborne Pathogens

Root-knot and lesion nematodes can form associations with various pathogenic bacteria and fungi, leading to the development of disease complexes. This is a result of the wounds caused by the nematodes when parasitizing on the plant roots, which then act as an entry point for other soilborne pathogens. The resulting symptoms of the host plant can then be different as compared to when the host is infected by only one of these pathogens [56]. For example, wounds made by *M. incognita* have been found to result in a disease complex with *Ralstonia solanacearum* (causing bacterial wilt) [57] and *M. hapla* to *Agrobacterium tumefaciens* [56]. These two nematode genera are amongst the most commonly reported to be involved in disease complexes with fungal pathogens [58]. *Meloidogyne incognita* has been known to form disease complexes with the fungal pathogen *Rhizoctonia solani* (seedling blight), which is of great concern for soybean production in Canada [58,59]. A synergistic co-infection of these pests can result in plant damage that exceeds the sum of individual damage caused by the pest and pathogen ( $1 + 1 > 2$ ) [58]. It has also been reported that *M. incognita* can form synergistic disease complexes with *Fusarium graminearum* and *F. equiseti* (wilt fungus) in soybean [60]. High populations of *Pratylenchus* spp. were found in soybean plants infected with *R. solani* in the USA [61]. Although there is limited research regarding *Fusarium* pathogens of soybean in SSA, and the disease complex it can form with nematodes [62], Hartman and co-authors [62] found *F. incarnatum-equiseti* and *F. sambucinum* isolates from infected soybean roots in Ethiopia and Ghana. In South Africa, the increased root-knot and lesion nematode densities in soybean fields [40,41] can also lead to increased disease complexes with other soilborne pathogens, such as *Fusarium brasiliense* (soybean sudden death syndrome) [63].

### 5.4. Potential Yield Losses

Root-knot and lesion nematodes are known to cause substantial yield loss of soybean on a global scale. The damage caused to the host crop by these two nematode genera depends on the susceptibility of the infected crop genotype and the population density of the nematode [9]. However, other factors, such as the pathogenicity of the nematode population, environmental conditions, soil type, and others [7,18,19,52], can also contribute towards the damage caused to soybean crops by these genera. It is estimated that plant-parasitic nematodes, including root-knot and lesion nematodes, are responsible for yield losses of up to 80% in fields that are heavily infested [64]. Some reports suggest that the soybean yield reduction of 73,600 MT in Argentina, 313,600 MT in Brazil, and 16,600 MT in China in 1998 was caused by PPN parasitism [45].

Soybean losses in Florida, USA, due to *M. incognita* were estimated at 90%, while other root-knot species contributed to 93 000 MT of the annual yield losses in Canada and the USA from 1999–2002 [65,66].

With regards to lesion nematode infections, a soybean yield loss of 30% to 50% was reported in Brazil [67], while the lesion nematode, *P. brachyurus*, was able to result in a 31% yield loss of ‘Lee’ soybean [68]. For SSA and South Africa, yield loss figures for lesion nematodes infecting soybean crops are not available [26]. However, early reports found that the damage caused by PPN to soybean in South Africa contributed about 9% of the annual yield losses prior to and/or in the 1980s [39]. In some cases, such as that reported by Smit and De Beer [69], severe infection of PPN assemblages, consisting predominantly of root-knot nematodes, caused a total loss of soybean in the Mpumalanga province of South Africa. More recent reports suggested that *M. incognita* caused up to a 41% yield loss on the soybean cultivar Prima2000 [56]. Along with the direct effect of root-knot and lesion nematodes on soybean yield, feeding of these genera also disturbs the nitrogen fixation process, which can lead to reduced N fixation, resulting in reduced yield [18].

The main reasons why root-knot and lesion nematodes continue to be problematic pests in soybean production are their wide host ranges, the fact that several species can be present in one field [70,71], and the lack of adequate nematicides, whether chemical or biological, being registered on soybean [72]. Yet, the main strategies used to manage root-knot nematode pests in soybean fields worldwide are nematicides (chemical and biological), crop rotation, and genetic host plant resistance [55]. Although chemical control is the preferred choice for nematode management, the application of a combination of management strategies, like those mentioned above, represents an integrated pest management (IPM) strategy. Such a strategy will be the best way to limit the impact of PPN on soybean.

## 6. Nematode Management Strategies

### 6.1. Chemical Control

Chemical control refers to the usage of products containing chemical compounds, either synthetically or naturally derived, that are either lethal to nematodes or cause disruption of their behavior, with the latter generally referred to as ‘nematostatic’ [73]. The effective use of chemical nematicides against PPN has been in practice since the 1950s [74,75]. Chemically derived nematicides, such as carbofuran, furfural, oxamyl, organophosphates, and halogenated compounds, are used on a large scale across the world to combat PPN [76,77]. However, the development of new synthetically derived nematicides has decreased over the past few decades mainly due to the withdrawal of many chemical products from international markets (as they have elevated levels of toxicity detrimental to environmental, animal, and human safety). As a result, there is an increase in the research and use of environmentally friendly nematicides and approaches. Specifically, seed-coat products are seen to have a more targeted effect of the chemical compounds applied, limiting the potential negative effects of these products [78,79].

Despite the downscaling in the development and registration of synthetically derived nematicides, research is still ongoing with regards to these chemicals. Field studies in the USA reported that the synthetically derived nematicides Bolster 15G (aldicarb) and Counter 20G (turfufos) were able to significantly decrease nematode pests of soybean, which included *Pratylenchus* [80,81]. Although a pre-planting fumigant Telone® II is also registered for use on various crops (including soybean) against both root-knot and lesion nematodes [82], the active ingredient of this product (1,3-dichloropropene) is a methyl bromide alternative, which faces increased regulatory restraints [83]. A greenhouse study also identified methyl pelargonate as being effective in the management of *M. incognita* in soybean [84].

The use of seed treatments is, however, gaining more attention, especially in Brazil where products, such as Ecolife®, Cruiser®, Maxim Advanced®, Avicta®, and other abamectin-containing products, have been found to reduce population densities of target species, such as *M. javanica* and *P. brachyurus*, in glasshouse and in vitro studies [85–87]. Another seed treatment product ILeVO® (Bayer CropScience) that uses fluopyram as an active ingredient was registered in 2014 against sudden death syndrome and p nematode pests of soybean [88]. The use of chemical nematicides on soybean, especially in South Africa, has seldom been found to be cost-effective [89]. Of the granular and fumigant nematicides



tested, only EDB<sup>®</sup> (AL; 1800 g<sup>-1</sup>) was found to consistently reduce root-knot nematode populations. However, the use of aldicarb and terbufos treatments did not always differ significantly ( $p \leq 0.05$ ) from the control [89].

There is currently only one nematicide, the seed treatment Avicta<sup>®</sup> (contains abamectin as its active ingredient), that is in the process of being registered for use on soybean in South Africa [26,90] with limited or no other chemically derived products predicted to be registered in the foreseeable future [37]. Avicta<sup>®</sup> Complete Beans is also a registered nematicide for soybean in the USA, Argentina, and Brazil [26,90]. Although products, such as ALVURAN<sup>®</sup> 100 G and CROP GUARD 80, are known nematicides, they remain unregistered for use on soybean in South Africa but can be used on maize and sunflower (usually used in rotation with soybean) [26]. Although chemicals remain one of the most common methods for root-knot nematode management [91], the safety concerns that these chemicals pose [79] calls for the urgent development of more environmentally friendly PPN control methods.

Biochemicals or semiochemicals are natural compounds that can be used instead of synthetic nematicides [92] and are products derived from biological organisms, such as microorganisms, plants, and/or by-products of animals and plants. The pyrethroids produced by *Chrysanthemum cinerariaefolium*, citronella oil, and garlic extract are only a few examples of natural compounds that have nematocidal activity [93–95]. Semiochemicals, on the other hand, are compounds that can influence the behavior patterns of pests [93]. Sordidin, a male pheromone produced by *Cosmopolites sordidus*, has been used as a trapping mechanism of various pests [96].

## 6.2. Crop Rotation

The use of crop rotation as a management strategy for root-knot and lesion nematodes is difficult since species of both genera have wide host ranges [9,71]. When using crop rotation as a management strategy, it is important to use the rotation of susceptible crops with non-host or resistant crops [9]. Before any crop/cultivar is planted to form part of a rotation management strategy, it is also important to test the susceptibility of that host against the target nematode pest, as the population density [52] and species present [97] can impact that decision. In the USA, a maize genotype (Pioneer 3223), pearl millet (*Pennisetum glaucum* L.) cultivar (Tifgrain 102), and Bahia grass (*Paspalum notatum*) have been known to reduce *M. arenaria* densities [98,99]. In Australia, certain maize genotypes have also been found to cause reduced *M. hapla* densities [100], while growing the barley (*Hordeum vulgare*) genotype Clipper reduced *Pratylenchus* spp. densities [101]. In Brazil, the rotation of soybean with forage crops (*Andropogon gayanus* genotype Planaltina, *Cajanus cajan* genotype Caqui, and *Macrotyloma axillare* genotype Java), *Crotalaria* species, and oilseed radish reduced *P. brachyurus* densities [102,103]. Concerning the African continent, African marigold (*Tagetes erecta*) and sunn hemp (*Crotalaria juncea*) have been found to reduce *M. incognita* densities in soybean fields of Nigeria [104]. It is evident that crop rotation as a strategy to reduce root-knot and lesion nematode populations is not an effective control strategy in soybean-based cropping systems across South Africa [37,105]. A significant increase in RKN densities was detected when soybean was included once in four years in a maize-based cropping system [105]. Crops that are usually rotated with soybean in South Africa, such as dry bean (*Phaseolus vulgaris* L.), maize, potato (*Solanum tuberosum* L.), sunflower, and various vegetable crops, are susceptible to root-knot and lesion nematode infections [106]. If crop rotation is considered as a control strategy, it is recommended that poor host or root-knot nematode-resistant cultivars (cvs.) of rotation crops be used [37]. Yet, the use of such cvs. in rotation might cause an increase in the population density of other non-target PPN, such as a lesion nematode species for which no cultivar evaluation has been done in South Africa [26]. Coupled with this shortcoming is the lack of screening of newly released commercial cultivars of rotation crops on an annual or ongoing basis. The possibility also exists that the use of non-host or resistant crop cvs. have low or even no local interest or value to farmers [107].

### 6.3. Host Plant Resistance

Genetic host plant resistance translates to the inhibition/limitation of the penetration, feeding, development, and reproduction of target PPN species as a result of gene expression. Plants usually have none, low, moderate, or high levels of resistance to a target nematode species [37]. The use of genetic resistance against PPN, such as root-knot and lesion nematodes, have been identified as one of the most cost-effective and environmentally friendly management strategies of these pests in soybean [55]. There are soybean cvs. that are either resistant or tolerant towards a few root-knot nematode species [9]. The USA soybean genotype PI 567516C was identified as being an excellent source of resistance as it displays resistance against not only *M. incognita* but also soybean cyst nematode and reniform (*Rotylenchulus reniformis*) nematodes [108]. An early study also identified three soybean cultivars, Centennial, Forrest, and Hartwig, that were resistant against both the soybean cyst nematode (race 3) and *M. incognita* (race 3) [109]. Out of 29 soybean cultivars tested in Brazil for their resistance against *M. javanica*, none were found to be resistant, with only two (TMG 1288 RR and NS 8270) having moderate levels of resistance [110]. In Pakistan, local soybean varieties/lines viz. (Ajmeri and NARC-4) were found to be resistant to *M. incognita* in a greenhouse trial when they were inoculated with 1000 J2 per plant. However, the same cultivars were susceptible to *M. incognita* at  $Pi = 2000$  J2 per plant [47], demonstrating the ability of resistance to be rendered ineffective at high population levels. In the USA, some of the Edamame soybean breeding lines have also been identified as having resistance towards *M. incognita* and these traits can be introduced into commercial cultivars [111]. Certain USA soybean genotypes, like Henderson, have moderate levels of resistance towards *M. incognita* but are again susceptible to *M. arenaria* and *H. glycines* races 2, 3, and 14 [78,112].

A substantial amount of research has been done in Africa assessing the host status of soybean genotypes to root-knot nematodes [33,113]. Fourie and Mbatyoti [113,114] found that a few soybean cvs. had different levels of resistance to different root-knot nematode species and races, while Mbatyoti [113] performed a similar work but only for *M. incognita*. Further research focused on introgression of *M. incognita* and *M. javanica* resistance into conventional high-yielding commercial cultivars [33]. However, such research is dated since new cvs. enter the market on an annual basis. In addition, introgression of resistance traits should be done for Roundup Ready® cvs. as they dominate the local market [41]. In South Africa, more than 90% of soybean cultivation used glyphosate-tolerant cultivars during the 2017 growing season [11]. Another major drawback in terms of the potential use of host plant resistance in SSA countries is the lack of information about the host status of soybean cultivars to infection by lesion nematode species. The same situation applies to Brazil, where soybean crops are adversely affected by *P. brachyurus* without any resistant sources being identified to date [113,115,116]. However, some soybean genotypes (BRSGO Chapadões, BRSGO Paraíso, M-Soy 7211 RR, M-Soy 8008 RR, Emgopa 313 RR, M-Soy 8411, BRSGO Juliana RR, Emgopa 316 RR, BRSGO Luziânia RR, and TMG 103 RR) were found to reduce *P. brachyurus* densities [117]. Ultimately, due to the impact that population density, species, and the race of nematode pests have on resistance levels, it is recommended that screening for resistance should be done with different populations and races [37,118].

With the impact of climate change also being evident on pest abundance, distribution, and diversity [119], evaluation of cultivars should also be done at different temperature regimes so that those with superior levels of resistance can be identified. Mbatyoti [113] demonstrated that the superior *M. incognita* resistance exhibited by 'LS5995' and some of its progeny (into which the trait has been introgressed) was not compromised by an increase in the temperature regime of between 3 and 4 °C. However, the same study also showed that the *M. incognita* densities in the roots of susceptible cvs. increased under the same increased temperature regimes at which soybean crops are likely to be exposed. Besides the valuable information to be generated at increased temperature regimes, there is a need to evaluate soybean cultivars for their reaction to drought. Most soybean production in South Africa occurs under rain-fed conditions, with severe drought conditions being experienced from time to time [11]. Although this may not be the case for some SSA countries that are situated in the tropics or subtropics, climate change is foreseen to be coupled with periods of severe droughts [11,120].

#### 6.4. Biological Control

Biological control is a management strategy to combat PPN and refers to the use of live microbial agents to reduce population densities of target nematode pests [89]. The use of bacterial and fungal strains is an alternative management strategy for root-knot and lesion nematode infections [121,122] and can reduce the damage done to economically important crops like soybean (Table 3). Bacteria known to exhibit nematocidal activity against *Meloidogyne* and *Pratylenchus* populations include several species of *Bacillus* as well as *Pseudomonas* and *Pasteuria*, including: *B. megaterium*, *B. cereus*, *B. nematocida*, *B. subtilis*, *B. thuringiensis*, *B. pumilus*, *B. firmus*, *B. amyloliquefaciens*, *Pseudomonas fluorescens*, and *Pasteuria thornei* [115,123–126]. *Bacillus* spp. have various distinctive attributes that emphasize their potential use as bionematicides, including the production of biologically active molecules [127], such as antimicrobial compounds (antibiotics) [128], enzymes, exotoxins, and metabolites with reported nematocidal activity [129]. They are ubiquitous within the rhizosphere [128], can colonize plant roots [124], and are plant growth-promoting rhizobacteria [125,130]. Ultimately, *Bacillus* and *Pseudomonas* spp. used as biological control agents are safe to the environment and non-target organisms (animals, humans, and other soil-dwelling organisms) [131]. Some fungal species, such as the novel *Polyphilus sieberi* and *P. frankenii* [132], can penetrate and colonize nematode eggs. These two species can directly kill the eggs and thus reduce the parasite load on host plants. Kath [133] also found that some *Trichoderma* spp. can produce various enzymes, such as chitinase, lipase, and protease, which have nematocidal effects on *P. brachyurus* [133,134].

**Table 3.** Bacteria and fungi used in biocontrol of *Meloidogyne* and *Pratylenchus* spp. on soybean.

Microorganism	Species	Results	Country
Bacteria	<i>B. subtilis</i> [135]	Reduced egg and second-stage juvenile densities of <i>M. incognita</i> and <i>M. javanica</i> on susceptible genotypes by more than 70%	Brazil
	<i>Pasteuria thornei</i> [85]	Reduced <i>P. brachyurus</i> densities by up to 50%	Brazil
	<i>Lactobacillus plantarum</i> + <i>B. subtilis</i> + <i>Enterococcus faecium</i> , and <i>B. licheniformis</i> + <i>B. subtilis</i> + <i>Trichoderma longibrachiatum</i> [136]	Substantially reduced densities of <i>M. javanica</i> and <i>P. brachyurus</i>	Brazil
	<i>T. harzianum</i> T22 [137]	Reduced egg, second-stage juvenile and female densities of <i>M. incognita</i>	Nigeria
	Mixture of <i>Bacillus</i> isolates [138]	<i>In vitro</i> studies showed larval mortality of >80%. Greenhouse studies showed reduced gall formation and egg densities of <i>M. javanica</i>	South Africa
Fungi	<i>Pochonia chlamydosporia</i> var. <i>chlamydosporia</i> [139]	Reduced egg densities of <i>M. incognita</i>	Brazil
	<i>Pleurotus ostreatus</i> , <i>P. tuberregium</i> [140]	Reduced gall formation and second-stage juvenile densities	Nigeria

The use of bacteria and fungi as a biocontrol management strategy has led to the development of commercial products, such as Compost-Aid™, Nem-Out™ [136], and Rhizotec® [139]. Although it is evident that research is now focused on the identification of microorganisms with anti-nematode properties, the use of such products is still limited [78]. Biocontrol products are not necessarily limited to the use of bacteria and fungi as some algae also have nematocidal characteristics [141]. *Botryocladia cabillaceae* have been reported to reduce *M. incognita* gall and egg mass numbers significantly on soybean roots in Egypt [141].

Of fundamental importance for effective biocontrol is that endemic microbial agents are exploited and that these are adapted to the environmental conditions of a country/climatic zone to enable optimal adaptation and proliferation in the rhizospheres of soybean crops [142]. Such an approach will also prevent a potential ‘biological contamination’ scenario resulting from the use of exotic microbes that are imported and released within soils, where they may outcompete their native microbe counterparts and negatively affect the preservation of endemic biodiversity and soil health [142,143].

## 7. Conclusions

This review emphasizes the important economic and socioeconomic impacts of soybean in South Africa and the wider SSA, while identifying the major risks posed by *Meloidogyne* and *Pratylenchus* infections. Soybean is a crop that is grown globally and is of great importance to human and animals as a high-protein-content food source. Although, only as little as 2% of the yearly soybean production is used for direct human consumption [7], the high protein content of this crop has excellent potential for undernourished people worldwide, especially SSA. A recent study showed that 40–65% of people in SSA countries are employed in the agriculture sector, which contributes on average to 25% of the GDP [6]. With the steep increase in the SSA human population, the importance of food security also intensifies, thus contributing to the need for the production of food crops with high protein contents, such as soybean. However, it is evident that the PPN problem faced by soybean production in Brazil has caused major yield losses. It is also known that species of *Meloidogyne* and *Pratylenchus* are co-occurring in soybean fields in South Africa (and other SSA countries) and that such pests might lead to soybean yield losses similar to those experienced in Brazil. The current nematode management practices used in South Africa (highest soybean producer in SSA) might not be sufficient or sustainable enough to deal with the rising PPN threat. An IPM approach for the management of root-knot and lesion nematodes on soybean on a worldwide basis is suggested as a viable option to protect the crop and other crops grown in rotation. A major concern that still faces soybean producers on a local and global scale is the availability of registered environmentally friendly biocontrol products for soybean. It is therefore crucial that both governments and the private sectors of SSA countries invest adequate resources into the research, development, registration, and production of biocontrol products, thereby contributing to food security and preserving the environment. More research is also needed on a local and SSA scale to truly understand the interaction of *Meloidogyne* and *Pratylenchus* communities as well as their associated microbe populations play in soybean rhizospheres, and how the co-occurrence might impact soybean yield losses.

**Author Contributions:** G.E. initiated the writing of this review article and compiled the initial manuscript. The promotor H.F. and co-promoters S.C. and C.M.S.M. of G.E.'s PhD studies, respectively, edited and provided valuable inputs to the manuscript. All authors have read and agreed to the published version of the manuscript.

**Funding:** We acknowledge the funding support of the National Research Foundation (NRF) (Grant numbers: 106783 and 115233), the Maize Trust (providing a bursary to G. Engelbrecht) and the Protein Research Foundation (for funding most of the research up to 2015). Any opinions, findings, conclusions or recommendations expressed in this material is that of the authors alone and the NRF does not accept any liability in this regard.

**Conflicts of Interest:** The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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