

Spodoptera frugiperda

(Fall Armyworm)

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Background Information

Common Names:

Fall armyworm, whorl worm

Scientific Name:

Spodoptera frugiperda (J.E. Smith)

Taxonomy:

Kingdom: Animalia; Phylum: Arthropoda; Class: Insecta; Order: Lepidoptera; Family: Noctuidae

Crop Hosts:

Cotton (*Gossypium* sp.), maize (*Zea mays*), rice (*Oryza sativa*), sorghum (*Sorghum* spp.), sugarcane (*Saccharum* sp.), Poaceae



Figure 1. Typical damage from *Spodoptera frugiperda* on maize.

Introduction

Spodoptera frugiperda, perhaps best known as the Fall armyworm, is an important lepidopteran pest in the

Americas. It became important during the mid-19th Century when it was reported attacking maize, sugarcane, rice and grasses in the southern USA (Hinds and Dew 1915). The colloquial name Fall armyworm derives from its annual rapid range expansion northwards into North America where it lays eggs, and the larvae develop throughout the Fall (Autumn).

Two distinct genotypes of *S. frugiperda*, each with its host preferences and some minor differences in biology have been reported (Pashley 1986; Pashley et al. 1992; Nagoshi et al. 2017a). These genotypes have since been characterised as comprising sister species (Otim et al., 2018). The “maize/corn” species prefers to attack maize and sorghum, while the “rice” species prefers to attack rice and certain forage grasses (Meagher et al. 2004; Nagoshi et al. 2007).

Since its invasion of West Africa during 2016 (Goergen et al. 2016; Cock et al. 2017) and subsequent rapid spread to many countries in sub-Saharan Africa (ACAPS 2017), *S. frugiperda* has become a threat to grain production on the African continent (Abrahams et al. 2017). Both the corn and rice species have been introduced into Togo in Africa (Nagoshi et al. 2017a); either concurrently, or within a very short time window.

Spodoptera frugiperda is likely to become more damaging to maize than other species of the same genus occurring in Africa (Goergen et al. 2016). Adult females of *S. frugiperda* prefer maize and sorghum and also oviposit directly on these plants, whereas congeneric Afrotropical armyworms first build up dense populations on wild grasses before spilling-over onto cultivated grasses (Rose et al. 2000). As shown in several countries in the tropical Americas where climatic conditions allow a constant reproduction of the pest, the damage inflicted to maize is particularly severe.

We do not yet have any evidence that the corn and rice species of *S. frugiperda* have any significant differences in their climatic niche, and most existing distribution records are confused as to the identity of the moths in relation to the corn/rice distinction. Hence, for the modelling in this report, all records have been treated as part of the species complex, *S. frugiperda*

sensu lato. As more information becomes available on the distribution of the corn and rice species, it may be prudent to revisit this pest geography.

Known Distribution

The fall armyworm is native to the tropical regions of the western hemisphere from the United States to Brazil and Argentina (Sarmiento et al. 2002; Ferreira et al. 2010). Survival of Fall army worm populations during winter months in the United States is usually only observed in southern Florida and southern Texas (Pair et al. 1986; 1991; Nagoshi et al. 2017b). *Spodoptera frugiperda* has a remarkable dispersal capacity (Johnson 1987), a feature that is understood to have evolved as part of its life history strategy (Nagoshi and Meagher 2008). During annual migrations, it is able to migrate northwards from its overwintering area in the warmer parts of central and South America over more than 2 000 km across the US and up into Canada; and southwards, reaching the northern parts of Argentina and Chile (Pair et al. 1986; Johnson 1987; Nagoshi et al. 2017a).

With its recent introduction into Africa, *S. frugiperda* extended its distribution to regions outside the tropics of the Americas and the Caribbean (Pogue 2002). In 2016 it was reported for the first time from the African continent, in Nigeria, Sao Tomé, Benin and Togo (IITA 2016; IPPC 2016), and it has subsequently been recorded in most sub-Saharan countries (ACAPS 2017).

Description and Biology

Since the spatial distribution of larvae on plants is a product of plant growth stage, damage on maize may be observed on all plant parts depending on plant development stage (Morris and Greene 1973). The most characteristic symptom of *S. frugiperda* damage is the presence of skeletonized leaves (Figure 1) (Davis et al. 1992). Early in the season, severe feeding damage to young plants can kill the growing point, causing dead heart symptoms. Larvae usually feed on host plant foliage until the final instar and pupate in the soil (Sparks 1979). The whorl (funnel) may be a mass of holes, with the edges ragged and larval frass inside (CABI 2017a;b). During the maize vegetative phase, constant larval feeding results in skeletonized leaves and heavily windowed whorls (Davis et al. 1992). However, if seedlings are attacked, larger larvae can cut the base of the plant. Mature plants suffer attack on ears.

Temperature has a significant influence on the duration of *S. frugiperda*'s lifecycle. Capinera (2007) reported that *S. frugiperda* completes its lifecycle in about 30 days during the summer, 60 days in spring and autumn, and 80 to 90 days during the winter. The number of generations occurring in an area varies with

the appearance of the dispersing adults. Up to eight generations per year can, however, occur in maize fields in tropical areas (Busato et al. 2005). *Spodoptera frugiperda* is a tropical pest that does not have the ability to diapause when temperatures decrease (Luginbill 1928; Johnson 1987). It has, however, been reported that this species may survive mild winters (Johnson 1987).

The wing span of moths is approximately 3.7 cm while the length of the body is approximately 1.6 cm. The colour patterns on the fore wings of males and females differ. Fore wings of males are mottled (light brown, grey, straw coloured) with a straw coloured discal cell on three quarters of the area. The forewings of female moths are mottled and do not have the straw coloured distal cell (CABI 2017b).

Eggs are spherical (0.75 mm diameter) and have a green colour at the time of oviposition. Eggs become light brown prior to eclosion and take between 2 and 3 days to become mature (20-30°C). Egg masses of approximately 150-200 eggs are laid on the surface of the leaf. The egg mass is usually covered with a protective, felt-like layer of scales (setae) from the female abdomen. Up to 1000 eggs may be laid by a female (CABI 2017b).

Larvae are light green to dark brown with longitudinal stripes. In the sixth instar, larvae are 3-4 cm long (CABI 2017b). Neonate larvae are green with black lines and spots. Large larvae are characterized by an inverted Y-shape in yellow on the head, and four black spots arranged in a square on the second-to-last abdominal segment. There are usually six larval instars, occasionally five. A full description of the larvae is provided by Passoa (1991) and colour plates are provided by King and Saunders (1984).

Larvae are cannibalistic and have the ability to dominate interspecific competitors and reduce intraspecific rivals (Chapman et al. 1999). Due to this high level of cannibalism, which commences already during the early instars, only between one and three fully grown larvae remain per plant, in spite of very high initial numbers of neonates per plant (Chapman et al. 1999).

Although pupation may occur in plant tissues such as leaf bases or ears, final instar larvae usually move to the soil where they pupate underneath the soil surface (2 – 6 cm) (Sparks 1979). Male and female pupae are 1.3-1.5 cm and 1.6-1.7 cm long respectively. The length of the pupal period may range between seven and 45 days, depending on temperature (Sparks 1979; Johnson 1987).

Host Crops and Other Plants

Although commonly reported to be highly polyphagous with a host range of almost 100 recorded plant

species in 27 families (Pogue 2002; CABI 2017a;b), the primary, and by far the most important hosts are maize (*Zea mays*), sorghum (*Sorghum* spp.) (Luginbill 1928; Sparks 1979; Meagher et al. 2004) and certain grass and pasture species (Chang et al. 1985; Flanders et al. 2017; Meagher et al. 2004). Other grain crops that are attacked are millet, rice, wheat and sugar cane. Luginbill (1928) reported that *S. frugiperda* would probably confine its feeding to maize, sorghum and grasses if these were always available. Apart from isolated reports of *S. frugiperda* attack on cowpea and groundnut in Ghana (West Africa), attacks have been limited to poaceous crops (Cock et al. 2017). Secondary host plants reported in the Americas include alfalfa (*Medicago sativa*), sugarcane (*Saccharum* sp.), wheat (*Triticum* sp.), groundnut (*Arachis hypogaea*), various grass species, vegetable crops and cotton (*Gossypium* sp.) (Ashley 1986).

Potential Distribution

CLIMEX (Sutherst and Maywald 1985; Kriticos et al. 2015) was used to model the potential distribution of *S. frugiperda* using the “Wet Tropical” species template as a starting point. Where appropriate, parameter values were informed by knowledge of the species biology. The remaining parameters were adjusted iteratively until the projected potential distribution (area where the Ecoclimatic Index > 0) was in accord with the known distribution of overwintering sites in the Americas. The CliMond 1975H historical climate dataset was used throughout the modelling (Kriticos et al. 2012). The model parameters (Table 1) were fitted using a natural rainfall scenario. Subsequently, an irrigation scenario (2.5 mm day⁻¹ applied as top-up) was run and the results compared with xeric areas where cropping is conducted under irrigated conditions. A composite climate suitability map was created by combining the natural rainfall and irrigation scenario results using the data from Portmann et al. (2010).

In framing the modelling of the niche of *S. frugiperda*, consideration was given to the significant effect of migration in the life history of the moth, and how this affects the pest risk area. We also gave consideration to the effects of irrigation in extending the area of habitat suitability into otherwise inhospitable regions. The irrigation areas were taken from Portmann et al. (2010).

Soil moisture parameters were set to biologically reasonable values. The soil moisture limit for growth was set to approximate permanent wilting point (Kriticos et al. 2003). The upper limit for optimal growth (SM2) was set to 2.5, acknowledging that *S. frugiperda* can tolerate conditions with substantial water-logging. The lower limit for optimal growth (SM1) was adjusted to provide appropriate suitability in marginally dry areas.

Table 1 CLIMEX Parameter Values for *Spodoptera frugiperda*

| Parameter | Description | Value |
|---|--|---------------------------|
| Moisture | | |
| SM0 | Lower soil moisture threshold | 0.15 |
| SM1 | Lower optimal soil moisture | 0.8 |
| SM2 | Upper optimal soil moisture | 1.5 |
| SM3 | Upper soil moisture threshold | 2.5 |
| Temperature | | |
| DV0 | Lower temperature threshold | 12 °C |
| DV1 | Lower optimal temperature | 25 °C |
| DV2 | Upper optimal temperature | 30 °C |
| DV3 | Upper temperature threshold | 39 °C |
| Cold stress | | |
| TTCS | Cold stress temperature threshold | 12 °C |
| THCS | Cold stress accumulation rate | 0.001week ⁻¹ |
| Heat stress | | |
| TTHS | Heat stress temperature threshold | 39 °C |
| THHS | Heat stress accumulation rate | 0.005week ⁻¹ |
| Dry stress | | |
| SMDS | Soil moisture dry stress threshold | 0.1 |
| HDS | Dry stress accumulation rate | -0.005 week ⁻¹ |
| Wet Stress | | |
| SMWS | Soil moisture wet stress threshold | 2.5 |
| HWS | Wet stress accumulation rate | 0.002 week ⁻¹ |
| Threshold Annual Heat sum | | |
| PDD | Minimum degree day sum needed to complete a generation | 600 °C days |
| Irrigation Scenario | | |
| 2.5mm day ⁻¹ as top-up throughout the year | | |

The lower temperature threshold for growth was set to 12 °C, taking into account the variation in estimated lower temperature limits reported in literature, which reflect the tropical distribution of *S. frugiperda*. Available estimates include: 16.95 °C (Barfield et al. 1978), 13.4 °C (Hogg et al. 1982), 12.69 °C (Ali et al. 1990), 10.9 °C (Ramirez-Garcia et al. 1987) and 8.7 °C (Valdez-Torres et al. 2012). The lower temperature for optimal growth was set to 25 °C as suggested by Valdez-Torres et al. (2012). The upper optimal temperature for growth was set to 30 °C (Simmons 1993), and the maximum temperature was set at 39 °C, near the threshold of 39.8°C reported by Valdez-Torres et al. (2012).

Fall armyworm does not diapause and cannot survive the winters in temperate areas (Luginbill 1928; Johnson 1987). Diapause was therefore not included in this model.

A temperature threshold model of Cold Stress was used, with a 12 °C threshold and a stress accumulation rate of -0.001 week⁻¹. With these settings cold stress limits the potential range in the USA to the areas where *S. frugiperda* has been reported to survive winter months, in south-western Texas and in southern Florida (Luginbill 1928; Sparks 1979; Johnson 1987).

Heat Stress parameters were set to allow persistence in all of the known locations from which it has been observed. The threshold of 39 °C is the same as the upper temperature limit for development.

Dry Stress was fitted by using the lower soil moisture growth threshold and adjusting the rate to limit the distribution to tropical and subtropical regions where it has been reported.

The Wet Stress threshold was set to the upper level of soil moisture for growth and the accumulation rate was set to 0.002 week⁻¹ to allow persistence throughout the known distribution in the southern parts of North America.

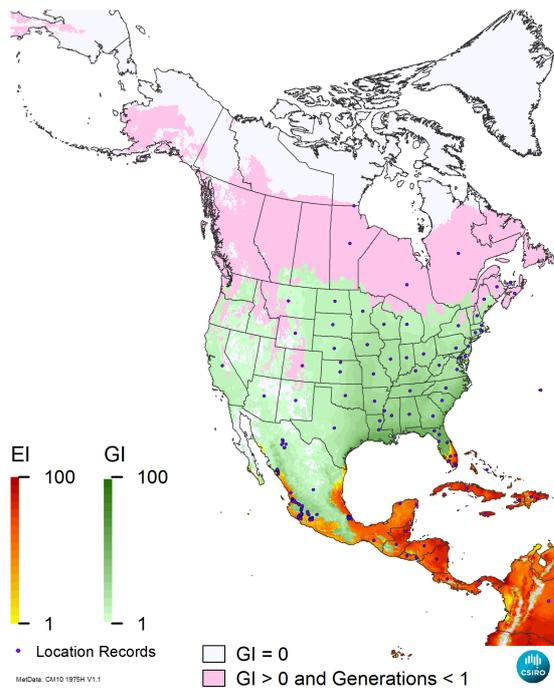


Figure 2. Climate suitability for *Spodoptera frugiperda* in North and Central America modelled using CLIMEX, including the spatially-explicit effects of irrigation. The Ecoclimatic Index (EI) describes the potential suitability for persistence, while the Growth index (GI) describes suitability for population growth. Distribution points in the USA and Canada are centroids of states or provinces respectively.

The threshold annual heat sum required for population persistence (PDD) was set to 600 degree days above 12 °C, the lower temperature limit for development.

The CLIMEX Ecoclimatic Index accords well with the known overwintering sites in the southern USA (Figure 2). Elsewhere, we must be more circumspect regarding the limits of establishment of permanent populations, because reports do not distinguish clearly between seasonal and permanent populations. The Annual Growth Index (GI_A) illustrates areas that are climatically suitable for at least one generation (Figure 2). The extent of the areas at risk from chronic infestations of *S. frugiperda* are tropical and sub-tropical regions, while its pest status will most likely be reduced to that of an annual or sporadic pest that re-invades areas outside of regions where populations are sustained on crops throughout the year. Analyses of climatic data (Figure 3) show that the *S. frugiperda*

could establish permanent and significant populations in West, Central and southern Africa, from where it may spread to other regions when weather or temperatures are favourable for pest development (Abrahams et al. 2017). Jeger et al. (2017) considered the possibility that *S. frugiperda* may invade Europe in the future. The CLIMEX model estimates permanent establishment as described above with seasonal invasions into temperate regions where low winter temperatures do not allow *S. frugiperda* to overwinter. The CLIMEX model results offer a refinement to the preliminary modelling presented in Abrahams et al. (2017), defining the regions where persistent and ephemeral populations may impact production, and also including explicit treatment of irrigation effects on the potential distribution of this pest.

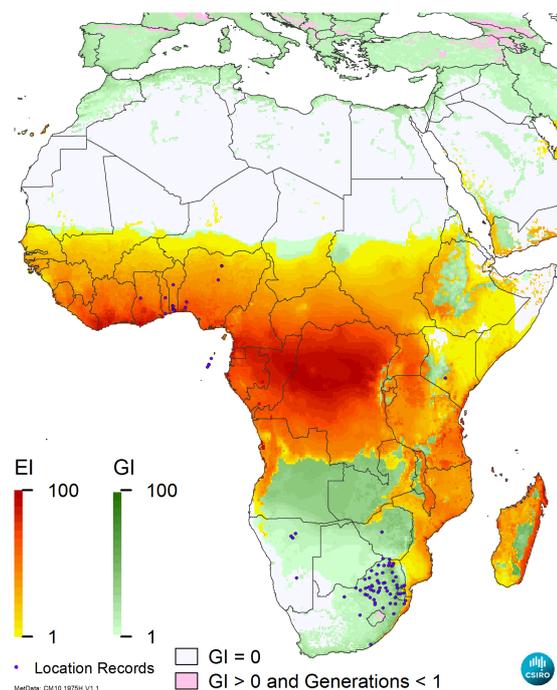


Figure 3. Climate suitability for *Spodoptera frugiperda* in Africa modelled using CLIMEX, including the spatially-explicit effects of irrigation. The Ecoclimatic Index (EI) describes the potential suitability for persistence, while the Growth index (GI) describes suitability for population growth.

Although *S. frugiperda* has already expanded its range throughout the African continent, it has most likely not yet reached its geographical limits there. Its high dispersal ability (Johnson 1987; Cock et al. 2017; Nagoshi et al. 2017b; Europhyt 2017), large reproductive capacity (Muru'a and Virla 2004), absence of diapause (Johnson 1987), and host plant range which includes many tropical and temperate grasses such as *Sorghum* spp. will most likely facilitate its colonization of most of sub-Saharan Africa.

While its biological and ecological adaptation to conditions on the African continent is still unknown, indications are that it has spread across much of sub-

Saharan Africa since the first report during 2016 (CABI 2017a). Pathways of the introduction of fall armyworm into West and Central Africa are unknown. However, the presence of at least two distinct haplotypes reported by Goergen et al. (2016) and Nagoshi et al. (2017a) suggests that the present incursion originated from at least two sources.

Since *S. frugiperda* has spread from the Americas, there may be little stopping its spread eastwards into Asia and Australasia (Figure 4). Huesing et al. (2018) observes that this spread could have serious impacts on regional and international trade. The irrigated areas of the Nile Valley in Egypt and the highlands of Ethiopia may provide important seasonal stepping-stones into southern Europe and the Middle-East (Figures 3 and 4).

The irrigated agriculture on the southern and eastern fringes of the Arabian Peninsula appear climatically suitable for *S. frugiperda* to establish (Figures 3 and 4) posing a seasonal threat to countries to the north, and eastwards into south-east Asia.

The pest status of *S. frugiperda* in the United States, where it is mostly a seasonal migratory pest may be a good indication of the potential threats posed to Europe and the Middle-East. However, the lack of a proximal source for a persistent population equivalent to the Caribbean and Southern Florida may significantly reduce the threat to Europe where *S. frugiperda* may have to migrate significant distances over deserts in order to re-invade Europe each Spring. Global warming may provide marginally-suitable conditions for establishment in the far South of Europe and small pockets of coastal North Africa (data not shown).

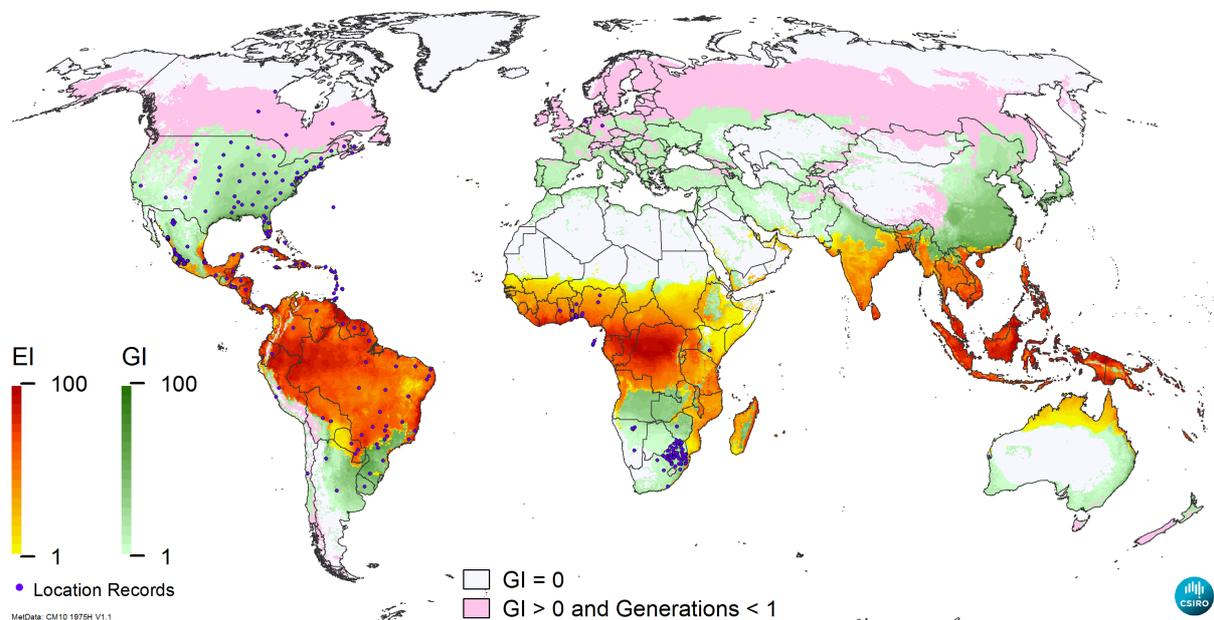


Figure 4. Climate suitability for *Spodoptera frugiperda* globally modelled using CLIMEX, including the spatially-explicit effects of irrigation. The Ecoclimatic Index (EI) describes the potential suitability for persistence, while the Growth index (GI) describes suitability for population growth.

References

Abrahams, P., Beale, T., Cock, M., Corniani, N., Day, R., Gdwin, J., Murphy, S., Richards, G. and Vos, J. (2017). Fall Armyworm Status. Impacts and control options in Africa: Preliminary Evidence Note. <http://www.invasivespecies.org/Uploads/InvasiveSpecies/FAW-inception-report.pdf>

ACAPS. 2017. ACAPS Thematic Report: Armyworm outbreak in Africa. <http://reliefweb.int/sites/reliefweb.int/files/resources/>

Ali, A., Luttrell, R.G. and Schneider, J.C. 1990. Effects of temperature and larval diet on development of the Fall armyworm (Lepidoptera: Noctuidae). *Annals of the Entomological Society of America*. 88(4):725-733.

Ashley, T.R. (1986). Geographical distributions and parasitization levels for parasitoids of the Fall armyworm, *Spodoptera frugiperda*. *Florida Entomologist*. 69:516-524.

Barfield, C.S., Mitchell, E.R. and Poe, S.L. 1978. A temperature-dependent model for fall armyworm development. *Annals of the Entomological Society of America*. 71:70-74.

Busato, G.R., Grützmacher, A.D., Garcia, M.S., Giolo, F.P., Zotti, M.J. and Bandeira, J.M. 2005. Exigências térmicas e estimativa do número de gerações dos biótipos “milho” e “arroz” de *Spodoptera frugiperda*. *Pesquisa Agropecuária Brasileira*. 40(4):329-335.

CABI. 2017a. Invasive species compendium. *Spodoptera frugiperda* (fall armyworm). <http://www.cabi.org/isc/datasheet/29810>. Accessed 4 May 2017.

- CABI. 2017b. How to identify Fall armyworm. Available from: <http://www.plantwise.org/KnowledgeBank/Datasheet.aspx?dsid=29810>. Accessed 11 July 2017.
- Capinera, J.L. 2007. Fall Armyworm, *Spodoptera frugiperda* (J.E. Smith) (Insecta: Lepidoptera: Noctuidae). Document nr. EENY098. Department of Entomology and Nematology, UF/IFAS Extension. <http://edis.ifas.ufl.edu>.
- Chang, N.T., Wiseman, B.R., Lynch, R.E. and Habeck, D.H. 1985. Fall armyworm: expressions of antibiosis in selected grasses. *Journal of Entomological Science*. 20:179-188.
- Chapman, J.W., William, T., Escribano, A., Caballero, P., Cave, R.D. and Goulson, D. 1999. Fitness consequences of cannibalism in the fall armyworm, *Spodoptera frugiperda*. *Behavioral Ecology*. 10:298-303.
- Cock, M.J.W., Beseh, B.K., Buddie, A.G., Cafa, G. and Crozier, J. 2017. Molecular methods to detect *Spodoptera frugiperda* in Ghana, and implications for monitoring the spread of invasive species in developing countries. *Scientific Reports*. 7:4103.
- Davis, F.M., NG, S.S. and Williams, W.P. 1992. Visual rating scales for screening whorl-stage corn for resistance to fall armyworm. Mississippi Agricultural and Forestry Experiment Station. Technical Bulletin 186. Mississippi, USA.
- EUROPHYT [Internet]. Interceptions of harmful organisms in imported plants and other objects, annual Interception. [cited 2016 Jun 18] Available from: http://ec.europa.eu/food/plant/plant_health_biosecurity/europhyt/interceptions/index_en.htm
- Ferreira Filho, J.B.S., Alves, L., Gottardo, L. and Georgino, M. 2010. Dimensionamento do custo economico representado por *Spodoptera frugiperda* na cultura do milho no Brasil. 48 Congresso Sociedade Brasileira de Economia, Administração e Sociologia Rural, 21 pp.
- Flanders, K.L., Ball, D.M. and Cobb, P.P. 2017. Management of Fall armyworm in pastures and hayfields. Alabma Cooperative Extension System. ANR-1019. www.aces.edu.
- Goergen, G., Kumar, P.L., Sankung, S.B., Togola, A. and Tamò, M. 2016. First report of outbreaks of the Fall Armyworm *Spodoptera frugiperda* (J E Smith) (Lepidoptera, Noctuidae), a New Alien Invasive Pest in West and Central Africa. *PLoS ONE* 11(10):e0165632. [doi:10.1371/journal.pone.0165632](https://doi.org/10.1371/journal.pone.0165632)
- Hinds, W. E. and Dew, J.A. (1915). The grass worm or fall army worm. *Alabama Agricultural and Experiment Station Bulletin*. 186:61-92.
- Hogg, D.B., Pitre, H.N. and Anderson, R.E. 1982. Assessment of early-season phenology of the fall armyworm (Lepidoptera: Noctuidae) in Mississippi. *Environmental Entomology*. 11:705-710.
- Huesing, J.E., Prasanna, B.M., McGrath, D., Chinwada, P., Jepson, P. and Capinera, J.L. Integrated Pest Management of Fall Armyworm in Africa: An Introduction. In: B.M. Prasanna, Joseph E. Huesing, Regina Eddy, Virginia. M. Peschke (eds). 2018. Fall Armyworm in Africa: A Guide for Integrated Pest Management, First Edition. Mexico, CDMX: CIMMYT.
- IITA, 2016. First report of outbreaks of the "Fall Armyworm" on the African continent. *IITA Bulletin*, No. 2330. <http://bulletin.iita.org/index.php/2016/06/18/first-report-of-outbreaks-of-the-fall-armyworm-on-the-africancontinent/>
- IPPC, 2016. Les dégâts causés par *Spodoptera frugiperda*. (The damage caused by *Spodoptera frugiperda*). IPPC Official Pest Report. Rome, Italy: FAO. <https://www.ippc.int/>
- Jeger, M., Bragard, C., Caffier, D., Candresse, T., Chatzivassiliou, E., Dehnen-Schmutz, K., Gilioli, G., Gregoire, J.-C., Jaques Miret, J.A., Navarro, M.N., Niere, B., Parnell, S., Potting, R., Rafoss, T., Rossi, V., Urek, G., Van Bruggen, A., Van der Werf, W., West, J., Winter, S., Gardi, C., Aukhojee, M. and MacLeod, A. 2017. Pest categorization of *Spodoptera frugiperda*. *EFSA Journal*. 15(7):4972, 37pp. <https://doi.org/10.2903/j.efsa.2017.4927>.
- Johnson, S.J. 1987. Migration and the life history strategy of the fall armyworm, *Spodoptera frugiperda* in the Western Hemisphere. *Insect Science and its Application*. 8:543-549. [doi: 10.1017/S1742758400022591](https://doi.org/10.1017/S1742758400022591)
- King, A.B.S and Saunders, J.L. 1984. The invertebrate pests of annual food crops in central America. Tropical Development and Research Institute. London, United Kingdom (E-book).
- Kriticos, D.J., Sutherst, R.W., Brown, J.R., Adkins, S.A. and Maywald, G.F. 2003. Climate change and the potential distribution of an invasive alien plant: *Acacia nilotica* ssp. *indica* in Australia. *Journal of Applied Ecology*. 40: 111-124.
- Kriticos, D.J., Webber, B.L., Leriche, A., Ota, N., Macadam, I., Bathols, J. and Scott, J.K. 2012. CliMond: global high resolution historical and future scenario climate surfaces for bioclimatic modelling. *Methods in Ecology and Evolution*. 3:53-64.
- Kriticos, D.J., Maywald, G.F., Yonow, T., Zurcher, E.J., Herrmann, N.I. and Sutherst, R.W. 2015. CLIMEX *Version 4: Exploring the effects of climate on plants, animals and diseases*. Canberra: CSIRO.
- Luginbill, P. 1928. The Fall army worm. Technical bulletin No. 34. United States Department of Agriculture Washington, D.C., 91pp. (E-book).
- Meagher, R.L., Nagoshi, R.N., Stuhl, C. and Mitchell, E.R. 2004. Larval development of Fall armyworm (Lepidoptera: Noctuidae) on different cover crop plants. *Florida Entomologist*. 87:454-460.
- Morril, L.W. and Greene, G.L. 1973. Distribution of Fall armyworm larvae. 1. Regions of field corn plants infested by larvae. *Environmental Entomology*. 2:195-198.
- Muru'a, G. and Virla, E. 2004. Population parameters of *Spodoptera frugiperda* (Smith) (Lep.: Noctuidae) fed on corn and two predominant grasses in Tucuman (Argentina). *Acta Zoologica Mexico*. 20:199-210.
- Nagoshi, R.N., Fleischer, S., Meagher, R.L., Hay-Roe, M., Khan, A., Muru'a, M.G., Silvie, P., Vergara, C. and Westbrook, J. 2017b. Fall armyworm migration across the Lesser Antilles and the potential for genetic exchanges between North and South American populations. *PLoS ONE* 12(2):e01717. <https://doi.org/10.1371/journal.pone.0171717>.
- Nagoshi, R.N., Koffi, D., Agboka, K., Tounou, K.A., Banerjee, R., Jurat-Fuentes, J.L. and Meagher, R.L. 2017a. Comparative molecular analyses of invasive fall armyworm in Togo reveal strong similarities to populations from the eastern United States and the Greater Antilles. *PLoS ONE* 12(7): e0181982. <https://doi.org/10.1371/journal.pone.0181982>
- Nagoshi, R.N. and Meagher, R.L. 2008. Review of fall armyworm (Lepidoptera: Noctuidae) genetic complexity and migration. *Florida Entomologist*. 91(4):546-554.
- Nagoshi, R.N., Silvie, P., Meagher, R.L., Lopez, J. and Machado, V. 2007. Identification and comparison of Fall armyworm (Lepidoptera: Noctuidae) host strains in Brazil, Texas, and Florida. *Annals of the Entomological Society of America*. 100:394-402.
- Otim, M.H., Tay, W.T., Walsh, T.K., Kanyesigye, D., Adumo, S., Abongosi, J., Stephen Ochen, S., Julius Sserumaga, J., Alibu, S., Grace Abalo, G., Asea, G. and Agona, A. 2018. Detection of sis-

ter-species in invasive populations of the fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) from Uganda. *PLoS One* 13, e0194571. doi:10.1371/journal.pone.0194571.

Pair, S.D., Raulston, J.R., Sparks, A.N., Westbrook, J.K. and Douce, G.K. 1986. Fall armyworm distribution and population dynamics in the southeastern states. *Florida Entomologist*. 69:468-487.

Pair, S.D., Raulston, J.R., Westbrook, J.K., Wolf, W.W., Adams, S.D. 1991. Fall armyworm (Lepidoptera: Noctuidae) outbreak originating in the lower Rio-Grande Valley, 1989. *Florida Entomologist*. 74(2):200-13.

Pashley, D.P. 1986. Host-associated genetic differentiation in fall armyworm (Lepidoptera, Noctuidae): a sibling species complex? *Annals of the Entomological Society of America*. 79(6):898-904.

Pashley, D.P., Hammond, A.M., Hardy, T.N. 1992. Reproductive isolating mechanisms in fall armyworm host strains (Lepidoptera, Noctuidae). *Annals of the Entomological Society of America*. 85(4):400-405.

Passoa, S. 1991. Color identification of economically important *Spodoptera* larvae in Honduras (Lepidoptera: Noctuidae). *Insecta Mundi*. 5:185-196.

Pogue, M. 2002. A world revision of the genus *Spodoptera* Guene'e (Lepidoptera: Noctuidae). *Memoirs of the American Entomological Society*. 43:1-202.

Portmann, F.T., Siebert, S. and Doll, P. 2010. *MIRCA2000-Global monthly irrigated and rainfed crop areas around the year 2000: A new high-resolution data set for agricultural and hydrological modeling*. *Global Biogeochemical Cycles*. 24: p. Gb1011.

Ramirez Garcia, L., Bravo Mojica, H., Llanderal Cazares, C. 1987. Development of *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) under different conditions of temperature and humidity. *Agrociencia, Mexico*. 67: 161-171.

Rose, D.J.W., Dewhurst, C.F. and Page, W.W. 2000. *The African armyworm handbook*. 2nd ed. Chatham: Natural Resources Institute, University of Greenwich; 2000.

OTIM MH, TAY WT, WALSH TK et al. (2018) Detection of sister-species in invasive populations of the fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) from Uganda. *PLoS One* 13, e0194571. doi:10.1371/journal.pone.0194571.

PORTMANN FT, SIEBERT S & DOLL P (2010) MIRCA2000-Global monthly irrigated and rainfed crop areas around the year 2000: A new high-resolution data set for agricultural and hydrological modeling. *Global Biogeochemical Cycles* 24, Gb1011. doi:10.1029/2008gb003435.

Sarmiento, R.A., Aguiar, R.W.S., Aguiar, R.A.S.S., Vieira S.M.J., Oliveira, H.G. and Holtz, A.M. 2002. Revisão da biologia, ocorrência e controle de *Spodoptera frugiperda* (Lepidoptera, Noctuidae) em milho no Brasil. *Bioscience Journal*. 18:41-48.

Simmons, A. 1993. Effects of constant and fluctuating temperatures and humidities on the survival of *Spodoptera frugiperda* pupae (Lepidoptera: Noctuidae). *Florida Entomologist*. 76(2):333-340.

Sparks, A.N. 1979. A review of the biology of the Fall armyworm. *Florida Entomologist*. 62: 82-87.

Sutherst, R.W. and Maywald, G.F. 1985. A computerised system for matching climates in ecology. *Agriculture, Ecosystems and Environment*. 13:281-299.

You, L., Wood-Sichra, U., Fritz, S., Guo, Z., See, L. and Koo, J. (2014) Spatial Production Allocation Model (SPAM) 2005 Version 1. International Food Policy Research Institute.

Valdez-Torres, J.B., Soto-Landeros, F., Osuna-Enciso, T. and Báez-Sañudo, M.A. 2012. Phenological prediction models for white corn (*Zea mays* L.) and Fall armyworm (*Spodoptera frugiperda* J.E. Smith). *Artículo en Agrociencia*. 46:399410.

