

## ***Prostephanus truncatus* IN AFRICA: A REVIEW OF BIOLOGICAL TRENDS AND PERSPECTIVES ON FUTURE PEST MANAGEMENT STRATEGIES**

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### **ABSTRACT**

The pest status of the Larger grain borer, *Prostephanus truncatus* (Coleoptera: Bostrichidae), is higher in African countries than in Latin America, its region of origin. This pest reduces the storage period of maize grain and cassava chips in granaries of small scale farmers. This reduced storage period results from larval and adult feeding, with consequent shortening of the period these commodities are available for food and income generating sources. Depending on storage time, yield losses of up to 45 and 100% have been recorded for maize and cassava chips, respectively, in West Africa; while 62% yield losses have been reported in Mozambique. Since *P. truncatus* invaded Africa from approximately 1970, research mostly addressed its biology, ecology, dispersal and control methods. This review paper aims at evaluating *P. truncatus* pest status in Africa as a basis for designing pragmatic strategies for its control. *Prostephanus truncatus* pest status in Africa is high and the degree of infestation and damage vary between regions. The variation in pest status is due to climatic conditions, food sources, and degree of storage infra-structure development and efficacy of control methods. *Prostephanus truncatus* has established in 20 African countries. Its temporal and spatial dispersion is unpredictable and depends on ecological factors, maize and dry cassava trade routes, and availability of forest host plants. Development of sustainable integrated management strategies is a key to future successful management of this pest. Area-wide management strategies using the predator, *Teretrius nigrescens*, parasitoids, plant derived products and environmentally friendly insecticides is needed. Integrated management practices must be based on improved knowledge of *P. truncatus* population dynamics and its determining factors.

**Key Words:** Integrated pest management, maize, Mozambique

### **RÉSUMÉ**

Le statut de la peste de dévoreur des grains, *Prostephanus truncatus* (Coleoptera: Bostrichidae), est plus élevé dans les pays africains que dans ceux d'Amérique Latine, sa région d'origine. Cette peste réduit la période de stockage des grains de maïs et de manioc dans des grainiers des petits exploitants. Ceci est dû à l'alimentation des larves et adultes, avec pour conséquence, l'écourtement de la période dont de ces produits devraient être disponibles pour nourriture et sources de génération des revenus. Dépendamment du temps de stockage, les pertes de rendement d'environ 45 et 100% ont été observées pour le maïs et le manioc, respectivement en Afrique de l'ouest; pendant que 62% de pertes de rendement ont été reportées au Mozambique. Depuis l'invasion de l'Afrique par *P. truncatus* aux environ de 1970, la recherche s'est en grande partie attablée sur sa biologie, écologie, propagation et méthodes de contrôle. Cette revue évalue le statut de la peste *P. truncatus* en Afrique pour comme base de conception des stratégies pragmatiques pour son contrôle. Le statut de la peste de *Prostephanus truncatus* est élevé en Afrique et les degrés d'infestation et dommage varient entre les régions. La variation du

statut de cette peste est due aux conditions climatiques, sources d'aliments et, degré de développement des infrastructures de stockage et l'efficacité des méthodes de contrôle. Le *Prostephanus truncatus* s'est établi dans 20 pays africains. Sa propagation temporelle et spatiale est imprédictible et dépend des facteurs écologiques, les voies de commercialisation du maïs et manioc sec, et disponibilité des plantes hôtes dans des forêts. Le développement durable des stratégies de gestion intégrée est une clé pour un succès futur de gestion de cette peste. Des stratégies de gestion utilisant le prédateur, *Teretriusnigrescens*, les parasitoïdes, les produits dérivés des plantes et des insecticides environnementalement viables sont nécessaires. Des pratiques de gestion intégrée doivent être basées sur l'amélioration des connaissances sur la dynamique des populations de *P. truncatus* et ses facteurs déterminants.

*Mots Clés:* Gestion intégrée de la peste, maïs, Mozambique

## INTRODUCTION

The Larger grain borer, *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) was first recorded in Africa in the Tabora region of Tanzania in 1981 (Dunstan and Magazini, 1981) and afterwards in Togo (Harnisch and Krall, 1984). Since then, the Larger grain borer became a serious pest of stored maize and dry cassava; reducing the storage period of these commodities in granaries of small scale farmers. This reduction results from larval and adult feeding, with consequent shortening of the period these commodities are available for food and income generating sources. This pest can also infest and cause damage to stored timber and timber products (Wright, 1984).

Several papers have been published about the pest status of Larger grain borer in Africa prior to 2002; however, no assessment has been done in this with reference to East Africa and Mozambique (Hodges *et al.*, 1983; Hodges, 1986; Markham *et al.*, 1991; Helbig *et al.*, 1992; Hodges, 1994; Birkinshaw *et al.*, 2002). So, the question can rightfully be asked: What is the current pest status of *P. truncatus* in Africa? Infestation and resulting damage by *P. truncatus* is preceded by spatial and temporal habitat invasion and colonisation by the pest. Dispersal of this pest is influenced by its capability to survive on dry wood of several forest plant species (Helbig *et al.*, 1992; Nang'ayo *et al.*, 1993; Nansen *et al.*, 2002), predation by *Teretrius nigrescens* (Coleoptera: Histeridae), as well as climatic conditions and availability of food sources (Helbig, 1995; Hill *et al.*, 2002; Hodges *et al.*, 2003).

Efforts to control the Larger grain borer largely involved the use of synthetic insecticides (Bekele

*et al.*, 1997; Cugala *et al.*, 2007; Chintzoglou *et al.*, 2008), plant derived products (Tapondjou *et al.*, 2002; Smith *et al.*, 2006) and biological control by means of the exotic predator, *T. nigrescens* (Richter *et al.*, 1997; Holst and Meikle, 2003; Hell *et al.*, 2006; Mahumane *et al.*, 2009).

Pest management strategies have been developed and include the use of several inert dusts (Golob, 1997), synthetic insecticides in combination with diatomaceous earth (Chintzoglou *et al.*, 2008), and wood ash and entomopathogenic fungi (Smith *et al.*, 2006). Despite the development of these control practices, this pest continuously disperses and causes severe damage to maize grain and dry cassava chips in granaries of small scale farmers in Africa. This paper reviews and discusses information on the pest status of *P. truncatus*, its dispersal since its introduction in Africa and perspectives on future pest management strategies.

**Pest status.** *Prostephanus truncatus* has become a serious pest of farm-stored maize and cassava in Africa (Borgemeister *et al.*, 1994; Borgemeister *et al.*, 1998). The seriousness of *P. truncatus* damage to stored maize grain and cassava chips varies considerably among countries. Infested commodities are physically destroyed and become unsuitable for human consumption and trade (Richter *et al.*, 1997) due to adults and larvae boring and damaging maize grain and dry cassava chips. High infestation levels result in accumulation of starch from insect metabolic excrements, fungal growth on stored produce and build-up of detritus in storage facilities.

The Larger grain borer was reported to cause losses in maize of nine percent over a five month

period in western Tanzania (Golob, 1988). Pantennius (1988) reported dry weight loss of up to 45% of maize grain after eight months of storage in Togo. Gnonlonfin *et al.* (2008), also in Benin, investigated infestation and population dynamics of insects on stored cassava and yam chips, and found that *P. truncatus* was more prevalent with up to 90.9% of individuals and 100% infestation in the Northern Guinea Savannah. Hodges *et al.* (1985) reported losses up to 52.3% for fermented and 73.6% for unfermented cassava chips in Tanzania. This high level of damage was observed after a storage period of only four months. In Ghana, this beetle reduced storability of cassava chips from a previously acceptable period of one year or more, to between four and five months, with losses amounting to between 39 and 57% (Stumpf, 1998). In Mozambique, Cugala *et al.* (2007) found that *P. truncatus* infestations in maize granaries resulted in losses of up to 59 and 62% in Manica and Tete Provinces, respectively. Maize grain storage periods in Tete were reduced from 10-12 to 6-8 months. These authors argued that this reduction resulted from invasion of *P. truncatus* during the early 1980's in the Mutarara district, Tete Province. Borgemeister *et al.* (1997) reported increased losses of stored cassava chips since *P. truncatus* was first reported in West Africa. Gueye *et al.* (2008) reported up to 35% of stored maize grain loss caused by mixed infestations of *P. truncatus* and *Sitophilus zeamais* Motscholsky (Coleoptera: Curculionidae), *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) and *Rizopertha dominica* (Fabricius) (Coleoptera: Bostrichidae) in Senegal.

Information on the exact quantities of maize and cassava chips stored by farmers is scarce; however, Helbig and Schulz (1996) estimated that 70% of the 120,000 to 150,000 metric tonnes of cassava produced annually in Togo was stored. This information, as well as the market prices of commodities is needed to enable a scientific estimate of the economic importance of the Larger grain borer in Africa. Apart from the lack of sufficient appropriate storage infrastructure, the lack of sustainable and low-cost control methods contribute significantly to high levels of damage by *P. truncatus* to important commodities such as maize and cassava.

#### **Alternative food sources and forest plant species.**

The Larger grain borer also infests and damages commodities other than maize and dry cassava chips. Wheat (*Triticum aestivum* Poaceae), rice (*Oryzae sativa* Poaceae), chickpea (*Cicer arietinum* Fabaceae), sweet potatoes (*Solanum tuberosum* Solanaceae), sorghum (*Sorghum bicolor* Poaceae) and several leguminous crops are some commodities that can host *P. truncatus* larvae and adults (Roux, 1999).

Information on infestation and survival of *P. truncatus* on commodities, other than maize and cassava, in Africa is scarce. The beetle damages stored timber and timber-derived products and forest plant species. Infestation and survival of *P. truncatus* in several host plant species has been reported by Makundi (1987) and Nang'ayo *et al.* (1993) (Table 1). Jia *et al.* (2008) reported that different grass, forbs and shrubs as well as forest tree species were hosts that facilitated survival of the lesser grain borer, *Ryzopertha dominica* F. (Coleoptera: Bostrichidae). Since members of the Bostrichidae are evolutionary, typically wood borers, the latter authors hypothesized that *P. truncatus* had the potential to survive in several non-crop host plant species, similar to that of *R. dominica*.

A survey done in the Herbaria of the Department of Biological Sciences, at Eduardo Mondlane University showed that the plant species listed in Table 1 occur widely in Mozambique. Herbarium records show that it has been collected in Manica, Barue and Guro districts of Manica Province, Chibabava in Sofala Province, Massingir district in Gaza Province, Mocuba district in Zambezia Province as well as in different forests and human settlements (Senkoro *et al.*, unpubl.). This finding suggests that *P. truncatus* breeding and survival, particularly in the natural forests of Mozambique, are possible. However, no study has been done to test this hypothesis.

Studies are needed to assess the role that wild host plant species play in the ecology of this pest. Therefore, more research on distribution, abundance, diversity and potential of local forest plant species in hosting *P. truncatus* is needed. This information can be used to predict temporal and spatial colonisation and establishment of *P. truncatus* in different regions in Africa. Maize,

TABLE 1. List of host plant species utilised by *Prostephanus truncatus* (modified from Makundi (1987) and Nang'ayo *et al.* (1993))

Forest plant species	Family	Plant part attacked	Source
<i>Acacia</i> spp.	Fabaceae	Seed and wood	Roux (1999)
<i>Commiphora africana</i>	Burseraceae	Seed and wood	Borgemeister <i>et al.</i> (1998), Roux (1999)
<i>Delonix regia</i>	Fabaceae	Seed	Helbig <i>et al.</i> (1992), Borgemeister <i>et al.</i> (1998)
<i>Leucaena</i> spp.	Fabaceae	Seed	Roux (1999)
<i>Prosopis</i> spp.	Fabaceae	Seed	Roux (1999)
<i>Spondias purpurea</i>	Anacardiaceae	Seed and wood	Ramirez-Martinez <i>et al.</i> (1994)
<i>Ficus exasperate</i>	Moraceae	Seed	Nang'ayo <i>et al.</i> (1993), Helbig and Schulz (1996), Kega and Warui (1983)
<i>Ceiba pentandra</i>	Bombacaceae	Seed	Hill <i>et al.</i> (2002)
<i>Lannea nigritana</i>	Anacardiaceae	Seed and wood	Nansen <i>et al.</i> (2002)
<i>Bursera fagaroides</i>	Burseraceae	Seed	Ramirez-Martinez <i>et al.</i> (1994), Helbig and Schulz (1996)
<i>Tectona grantis</i>	Verbenaceae	Seed	Borgemeister <i>et al.</i> (1998) Nansen <i>et al.</i> (2004)
<i>Sterculia tragacantha</i>	Sterculiaceae	Seed and wood	Helbig and Schulz (1996)

cassava, wheat, sorghum, other commodities and forest host plants can play a role as food for *P. truncatus* colonisation and establishment on the African continent.

***Prostephanus truncatus* dispersal trends.** The term dispersal as used here denotes population redistribution, which results in a time and spatial spread of a population as a consequence of individual movements (Tuchin and Omland, 1999). Dispersal is a crucial and functional variable of population dynamics, since it is determined by climatic factors such as temperature and humidity, wind speed, altitude and latitude. Dispersal is affected by environmental heterogeneity, for example food quantity and quality, its distribution in time and space, disturbed and undisturbed fields or habitats, and variations in topography, soil and biota within each field (Price, 1997; Huffaker and Gutierrez, 1999; Wellington *et al.*, 1999). Dispersal of insect individuals and species can result from tritrophic metapopulation interactions, inter- and intra-specific competition for food, feeding and breeding habitats (Gutierrez, 1999). Broadly, dispersal of insects is based on ecosystem dynamics and processes (Price, 1997), trophic complexity of insect communities (Thompson and Althoff, 1999) and on insect-plant population and community interactions (Nowierski *et al.*, 1999).

The dependence of dispersal on multiple factors has arisen from the assumption that insect

individual variation is a key in dispersal ecology, linking movement behaviour and dispersal and population processes (Hawkes, 2009). From this approach some conceptual knowledge is generated: (i) a quantitative description of dispersal which fit distance data well and incorporates realistic assumptions about the underlying movement is necessary (Okubo and Levin, 2002). This will not only improve the way in which dispersal is described, but will also increase the understanding of movement mechanisms and link dispersal and population dynamics. (ii) Movement between habitat patches and breeding sites must be described as dispersal, quantitatively and qualitatively different from the migration/movement occurring within patches and which is aimed at foraging and finding of mating partners and refuges (Hanski, 1999; Fahrig, 2007). Here we review information on potential factors affecting *P. truncatus* dispersal throughout Africa and discuss potential ways of integrating information and predicting further invasions and damage by this pest.

***Prostephanus truncatus* spatial and temporal dispersal.** *Prostephanus truncatus* long-distance dispersal has been attributed to transport and trade of commodities, particularly maize and dry cassava chips (Tyler and Hodges 2002; Omondi *et al.* 2011). This could, in fact have been the means of transport of this pest from

Mexico and Central America to Africa (Markham *et al.*, 1991), possibly through shipments of infested maize grain (Harnish and Krall, 1984). Inter-country transport and trade of maize grain and dry cassava chips, associated with lack of, or inadequate quarantine regulations, measures and practices have been indicated as factors that lead to *P. truncatus* dispersal around Africa (McFarlane, 1988; Markham *et al.*, 1991; Fadamiro, 1996; Tyler and Hodges, 2002;).

Experiments on short-range flight ability of the Larger grain borer support the observations on long-distance dispersal reported above. For instance, Farrell and Key (1992) used a mark-release-recapture technique and showed that over a 24 hour period, *P. truncatus* could fly in a directed manner to a pheromone source in an upwind direction for 50-100 m from the release point. Distances of 250 to 340 m were the maximum distances of flight reported by Rees (1990) and Farrell and Key (1992) for Larger grain borer flight towards a pheromone source over a 72 hr period. Pike (1993), however, considered *P. truncatus* as a fairly strong flier, after observations that beetles in tethered flight under laboratory conditions could fly 25 km over a period of 45 hours.

These findings demonstrate that the Larger grain borer is capable of dispersing by flight. However, no evidence exists that flight time period in natural environments lasts as long or involves such distances as described above (Farrell, 2000). In addition, individual insect movements and, hence dispersal, can be hindered by physical barriers such patch forest density, mountains, hills and seasonal or permanent flowing rivers. From field and empirical observations in Manica Province in Mozambique, it can be assumed that frequent and seasonal forest fires can kill insects and physically destroy their habitats, and hence inhibit their capability for flight and temporal dispersal at population level. *Prostephanus truncatus* in- and inter-country invasion and dispersal time period and distance is a subject of much discussion since it could provide an estimate of dispersal speed of the pest under different environmental conditions.

Approximately, 20 African countries are affected by *P. truncatus* and estimates based on years of public notification of *P. truncatus* occurrence in the respective countries in Africa

(Table 2) show that the pest took approximately 19 years to disperse and establish in nine countries in West Africa, 16 years in five countries of Eastern and Central Africa, and 15 years in six countries of Southern Africa. These data are rather empirical but biased due to uncertainty of the time of *P. truncatus* invasion in these countries and due to the potential delay that may have occurred in public notification about the occurrence and dispersal of the pest around Africa. Bias can be deducted for example, from countries where information on *P. truncatus* occurrence is still scarce or unknown, while such a country may be located within a region where pest establishment have been confirmed for a long period of time.

The long temporal differences in public notification about *P. truncatus* between, for example two neighbouring countries, can also skew this estimate. However, this overview can contribute to knowledge of the general picture of the total time period of its invasion and establishment on the African continent, and its potential and future negative impacts, if appropriate pest management measures are not taken. Information on the levels of pest infestation, damage, distribution and density in relation to characteristics of the invasion area, could provide improved estimates of *P. truncatus* establishment periods and rate of dispersal on the continent.

**Role of host commodities and forest host plant species.** The role of host commodities in dispersal of this pest has been widely reported (Hodges *et al.*, 1983; Hodges, 1986; Markham *et al.*, 1991; Hodges 1994; Helbig *et al.*, 1995; Borgemeister *et al.*, 1997; Stumpf, 1998; Roux, 1999; Farrell, 2000; Cugala *et al.*, 2007; Gueye *et al.*, 2008). Birkinshaw *et al.* (2002) found a significant correlation between trap catch and infestation of stored maize and other products by *P. truncatus*. These results show that pheromone-baited traps are effective tools for measuring dispersal of *P. truncatus* populations. Fadamiro and Wyatt (1995) indicated that large numbers of pests resulting in significant degradation of food resources could prompt dispersal of *P. truncatus*. Scholz *et al.* (1998) came to similar conclusions when studying *P. truncatus* flight initiation and

TABLE 2. Estimated *Prostephanus truncatus* invasion, dispersal and establishment time periods in Africa. Modified after Schulsen (1996) and Farrell (2000)

Country	Year of first report	Area	Reference	Estimated dispersal and establishment time period between two neighbouring countries (years)	Years
<b>Eastern and Central Africa</b>					
Tanzania	1981	Tabora district	Dunstan and Magazini (1981)	Tanzania and Kenya	2
Kenya	1983	Taveta district	Kega and Warui (1983)		
Burundi	1984	Gisuru market	Schulten (1987)	Kenya and Burundi	1
Rwanda	1993	Kigali	Bonzi and Ntambabazi (1993)	Burundi and Rwanda	9
Uganda	1997	Busia district	Opolot and Odong (1999)	Rwanda and Uganda	4
Total dispersal period in Eastern and Central Africa					16
<b>Southern Africa</b>					
Malawi	1991	Karonga district	Munthali (1992)	Mozambique and Malawi	1
Zambia	1993	Nakonde district	Milimo and Munene (1993)	Malawi and Zambia	2
Namibia	1998	Northern Namibia	Larsen (1998)	Zambia and Namibia	5
Mozambique	1999	Mutarara district	Cugala <i>et al.</i> (unpublished)	Namibia and Mozambique	1
South Africa	1999	Kruger Park	Roux (1999), Giliomee (2011)	Mozambique and South Africa	1
Zimbabwe	2005	Northern Zimbabwe	Nyagwaya <i>et al.</i> (2010)	Zimbabwe and South Africa	5
Total dispersal period in Southern Africa					19
<b>West Africa</b>					
Togo	1984	Lomé area	Harnish and Krall (1984)	Central America and Togo	
Benin	1986	Mono region	Anon. (1986)	Togo and Benin	2
Guinea Conakry	1988	Fouta Djallon region	Kalivogui and Much (1989)	Benin and Guinea Conakry	2
Guinea Bissau	1988	Bissau region	Aman <i>et al.</i> (2007)	Guinea Conakry and Guinea Bissau	1
Ghana	1989	Volta region	Dick and Rees (1989)	Guinea and Ghana	1
Burkina Faso	1991	Togo border	Bosque-Perez <i>et al.</i> (1991)	Togo and Burkina Faso	2
Nigeria	1992	Oyo and Ogun states	Pike <i>et al.</i> (1992)	Burkina Faso and Nigeria	1
Niger	1994	Niamey, Dosso, Gaya	Adda <i>et al.</i> (1996)	Nigeria and Niger	2
Senegal	2007	Vélingara Boydo	Gueye <i>et al.</i> (2008)	Guinea and Senegal	19
Total dispersal period in Western Africa					10

flight activity in Benin. These authors observed that flight initiation depended on changes in the numbers and sizes of beetle populations in a given area, as well as on breeding site availability and suitability.

Reduction in food resources and quality can directly determine initiation of *P. truncatus* dispersal in closed commodity granaries, where the concentration of maize or cassava can be high and become reduced over time. However, in open environments such as forest habitats, the occurrence, distribution and diversity of host-plant species (food), as well as its shortage and quality seem to determine the initiation of Larger grain borer dispersal. Therefore, variation of plant biomass concentration, caused by deforestation and seasonal large-scale forest fires, can hypothetically influence dispersal initiation by *P. truncatus*.

The capacity of the Larger grain borer to utilise forest plant species as a resource for its survival and dispersal has been published by several workers (Makundi, 1987; Nang'ayo *et al.*, 1993; Helbig *et al.*, 1995; Jia *et al.*, 2008). Nang'ayo *et al.* (2002) studied the potential of *P. truncatus* feed and breed on native and agroforestry trees and shrubs, and reported that 27 out of 84 tree species supported the breeding of *P. truncatus* under laboratory conditions. Breeding success varied widely between tree species and showed no trends with regard to systematic position of species or wood hardness. These results suggest that the determining factors, mostly secondary metabolites for forest host plant species exploitation by *P. truncatus*, should be further investigated. In addition, laboratory experiments on insect-host plant interactions should be conducted, particularly on searching, selection, acceptance and preference behaviour, as well as kairomones involved in the process.

Scholz *et al.* (1997) investigated *P. truncatus* host-finding behaviour and concluded that kairomones, specifically those emitted by mature maize ears, and probably by dried cassava functioned as short range attractants. *Prostephanus truncatus* long-range responses and, hence, its primary attraction to stored commodities could not be demonstrated. However, Fadamiro *et al.* (1997) observed the absence of *P. truncatus* upwind flight to food

volatiles or any synergism between pheromones and food volatiles. These authors suggested that the male aggregation pheromone was the only known long-range semiochemical involved in *P. truncatus* dispersal and host selection. Host plant selection, infestation and successful breeding by *P. truncatus* are subjects of research importance since increased knowledge in this field could lead to predicting habitat invasion and colonisation by this beetle in Africa. The use of stable isotope carbon and nitrogen marker methods (Hood-Nowotny and Knols, 2007; Mahrroff and Phillips, 2007) may also be suitable for determining host plant-insect interactions.

Research on forest host plants as well as insect-commodity interactions previously focussed on the role of these substrates as food sources that provide nutritional requirements for growth, development, reproduction and energy flow, rather than insect movements which lead to dispersal.

**Role of host plant resistance.** Varietal resistance of host commodities or host suitability of forest plant species for *P. truncatus* are factors that could also affect *P. truncatus* dispersal. Arnason *et al.* (1992) investigated the role of phenolics in resistance of maize grain to *P. truncatus* and *S. zeamais*, and found that variety-specific phenolic compounds influenced the suitability of grain for the development of the former pest. Kumar (2002) performed a series of infestation, selection and inbreeding experiments over four generations of maize land races and observed that the S<sup>3</sup> maize grain showed a high level of resistance against *P. truncatus*.

This resistance was evident from low powder production caused by pest damage, relative to the susceptible control, as well as the small sizes of individuals developing on the resistant grains. This result suggested that antibiosis could be the mechanism of resistance operating within the S<sup>3</sup> progenies of selected land races. Tefera *et al.* (2011), in Kenya, evaluated 54 hybrids and found eight to be resistant and 40 to be moderately resistant to *P. truncatus* and *S. zeamais*. This finding suggested that resistant hybrids contained genes conferring maize grain to be resistant either through antixenosis or antibiosis, resulting in reduced grain weight loss and powder

production; and subsequently, an overall reduction in the impact of the two pests. However, in laboratory and field experiments, Meikle *et al.* (1998) concluded that maize kernel hardness and physical ear characteristics, such as husk extension and number of leaves might not play a role in plant resistance to *P. truncatus*.

The heterogeneity in chemical and structural composition of plants, together with inter-plant variation prevents herbivorous insects from fully exploiting their host plants (Schoonhoven *et al.*, 1998). Evidence of this is supported by several authors (Berenbaum and Zangerl, 1992; Olckers and Hulley, 1994). It is, therefore, suggested that future research addresses identification and possible use of feeding deterrents in host commodities and in forest host plant species. Such information will contribute to better understanding of the mechanisms of *P. truncatus*-host plant interactions and, hence, identify certain habitat types/host plant communities that are vulnerable to pest invasion and colonisation.

**Role of climate conditions.** Climate conditions which favour abundance, diversity and suitability of food sources have been suggested as driving factors for the continuous dispersal of *P. truncatus* in Africa (Hodges, 1986; Farrell, 2000). Giles *et al.* (1996) in Kenya and Borgemeister *et al.* (1997) in Benin found that the numbers of beetles trapped by means of pheromone traps varied seasonally and annually, signifying weather or climate effects.

At individual level, body temperature is the most basic variable determining rates such as growth, development, feeding, fecundity and insect mortality (Wellington *et al.*, 1999). *Prostephanus truncatus* completes its life cycle in about 25-27 days at the optimum temperature of 32 °C and relative humidity of 70-80% under laboratory conditions on maize grain (Hodges, 1982; Subramanyan and Hagstrum, 1991). Adults live for at least 4 months (Guntrip *et al.*, 1996) excluding the effect of predators or other natural enemies and exogenous factors that can cause unpredicted death. The life-history of the Larger grain borer has been widely studied (Shires, 1980; Howard, 1983; Li, 1988). The capability of insects to disperse mainly by flight is generally determined by the success of their individual

development and life-history trait adaptation to environmental conditions.

Climate directly affects the propensity of insects to disperse through flight. Research on the effect of pheromones as a factor driving *P. truncatus* flight activity and dispersal has been done since Cork *et al.* (1991) identified and synthesized the male beetle aggregation pheromone. This development resulted in the monitoring of flight activity of the Larger grain borer in several countries. Laboratory research has demonstrated the positive response of *P. truncatus* towards synthetic pheromone sources (Fadamiro *et al.*, 1996; Smith *et al.*, 1996). Tigar *et al.* (1993) investigated the period of effective attraction of *P. truncatus* to synthetic pheromones over a 33-day period and observed that the highest number of beetles was caught between 8 and 14 days after traps were put out. These authors also highlighted the possibility of results being influenced by rainfall, temperature, wind and trap positioning.

Nang'ayo (1996) in Kenya, Borgemeister *et al.* (1998) in southern Benin, Birkinshaw (1998) in Ghana, Hodges *et al.* (1998) and Scholz *et al.* (1998) in Togo and Benin, found that the use of pheromone traps for *P. truncatus* dispersal studies skewed surveyed populations by sex, because 60-70% of captured insects were females. In addition, trap captures arrested more young individuals because they were more active fliers (Fadamiro *et al.*, 1996; Scholz *et al.*, 1997). Despite these disadvantages, pheromone-baited traps became the most effective method for studies on *P. truncatus* flight activity and abundance and its relationship with climate and other environmental variables. Birkinshaw *et al.* (2004) and Hodges *et al.* (2004) improved and optimised pheromone lures and trapping methodology to address the skewing of *P. truncatus* trap catches by sex and age.

Scholz *et al.* (1997) showed that commencement of infestation of maize by *P. truncatus* was prompted by releases of the male aggregation-pheromone, late in the storage season. Since the initiation of invasion of granaries is a logical consequence of dispersing beetle populations, it is deductible that pheromone release by males plays an important role in pest dispersal to maize storage facilities. It

is also possible that pheromones may play a role in the dispersal of beetles from granaries into forest environments.

**Modelling and multivariate analysis of flight activity.** Multivariate analysis has been used to design models and to predict *P. truncatus* flight activity, as well as for estimating likely subsequent population outbreaks and infestation of maize and cassava chips in granaries. Meikle *et al.* (1998) in Benin designed a simulation model for *P. truncatus* and concluded that temperature affected development and flight activity more or less linearly; whereas the effect of humidity appeared to be non-linear. Nansen *et al.* (2001) investigated the response of *P. truncatus* flight activity to environmental variables in Benin and concluded that day length, minimum relative humidity, and minimum temperature were the most important variables explaining *P. truncatus* trap catches. This result provided some improvement on early attempts to predict catches.

Hodges *et al.* (2003) in Ghana, examined the relationship between climatic variables, seasonal and annual variations in *P. truncatus* trap catches. These authors then developed a rule-based model, a useful tool to predict years of higher *P. truncatus* flight activity and to estimate the pest status in certain regions.

Current models for *P. truncatus* flight activity are sketchy in some aspects. The day length based-model of Nansen *et al.* (2001), which defined day length as the most important variable for predicting flight activity was able to accurately predict trap catch data between the latitudes of 6 to 9°N, but the model was inaccurate in northern Benin (10°N) (Hodges *et al.*, 2003). This rule-based model, works well under a range of conditions in which *P. truncatus* is likely to be a serious pest. However, it has to be tested under more extreme conditions and in different environments. It was also found to be difficult to set the scale (calibrate) for trap catches in areas where previous data were scarce or unknown. In addition, the scale of the rule-based model was seen to wrongly estimate host-plant suitability and the impact of predators and parasitoids on *P. truncatus* populations.

A model based on climatic factors, designed by Omondi *et al.* (2011), accurately predicted

seasonal trends of larger grain borer flight behaviour in Kakamega in western Kenya and Mombasa in coastal lowlands of the same country, but it was inaccurate in highland regions. Besides the availability of stored grain, the influence of climate factors, altitude, latitude and solar radiation on accuracy of prediction models should be considered.

The question can, therefore, be asked: “Will models that accurately predict *P. truncatus* flight activity and, hence, spatial and temporal dispersal become a reality in future, and will it be possible to use these on a large scale?” The positive answer to this question is more theoretical than practical, because variations in climate patterns and environmental variables such as habitat patches, topography, solar radiation, wind speed and host-plant species, host commodities and habitat connectivity vary significantly at local and regional level. These factors complicate the development of a model for which development relies on large investment in resources, as well as time consuming. Simultaneous, large-scale spatial and temporal surveys needed to collect data for use in model development. It, therefore, seems more appropriate that models be developed at country or regional level.

**Predators and parasitoids.** Several studies on the impact of *Teretrius nigrescens* on *P. truncatus* have been conducted. These studies mostly highlighted the importance of the predator to suppress pest population density in granaries or forests (Helbig and Schulz, 1996; Richter *et al.*, 1997; Holst *et al.*, 2003; Schneider *et al.*, 2004; Hell *et al.*, 2006). The subject of *P. truncatus* biological control is of our further concern.

The direct effect of the predator on pest population dynamics, specifically on flight activity patterns and dispersal is mostly unexplored. Borgemeister *et al.* (1997) observed that peaks of *T. nigrescens* flight activity were correlated with precipitation; whereas those of *P. truncatus* were only weakly related to precipitation. The latter study on the influence of seasonal and weather factors on annual flight patterns of *P. truncatus* and *T. nigrescens* did not show clear direct cause-effect relationships between the predator-prey population fluctuations. Omondi *et al.* (2011) monitored *P.*

*truncatus* and *T. nigrescens* flight activity in Kenya and observed that the prediction model they used did not allow for assessment of the impact of the pests density because it relied on direct effect of temperature, humidity and precipitation and also excluded availability of stored maize grain. Some research on monitoring *P. truncatus* trap catches, after *T. nigrescens* releases have been made, showed no or only small numerical differences in pest density and flight activity compared with periods prior to establishment of the predator (Giles *et al.*, 1996; Hill *et al.*, 2003). It was also observed that *T. nigrescens* did not reduce the abundance of pest populations in Guinea and Sudan savannas in West Africa (Nansen *et al.*, 2001; Schneider *et al.*, 2004).

A decrease in numbers and eventual total absence of predator populations was observed a few months after their release in the western highlands of Kenya was also observed (Omondi *et al.*, 2011). The theory of stable equilibrium (Hoddle, 2003) may explain the variation observed in insect population densities as observed for *T. nigrescens* and *P. truncatus*. Hypothetically, the large-scale and periodical use of pheromone sticky traps that attract and kill both the Larger grain borer and the predator can gradually reduce the numbers of *T. nigrescens*. The aim of pest management is to reduce pest numbers. However, reduction of *T. nigrescens* populations in the process reduces the effectiveness of the predator and hence, its dispersal. Berryman and Gutierrez (1999) reported that predators can indirectly limit or regulate dispersal of their prey through regulation of population density.

#### CURRENT STATUS OF MANAGEMENT IN AFRICA

Integrated Pest Management (IPM), as defined by Kogan (1998) is the combined use of host plant resistance, biological control, cultural control and chemical control in order to keep pest populations below economic injury levels. This approach to pest management is discussed below with reference to *P. truncatus*.

**Chemical control.** Based on the use of fumigants such as phosphine and methyl-bromide has been

applied since the pest invaded Africa (Golob and Hanks, 1990; Meikle *et al.*, 1999; OEPP/EPPO Bulletin, 2012). Ritcher *et al.* (1998) investigated the efficacy of dust-formulated insecticides in traditional maize granaries, and found that pyrethroids, particularly deltamethrin, effectively controlled the Larger grain borer in West Africa.

The use of inert dusts, particularly diatomaceous earths, has widely been tested and applied against *P. truncatus* in Africa. Barbosa *et al.* (1994) reported that precipitated and fumed silicas were effective in causing mortality of adult *P. truncatus*. Stather *et al.* (2004) evaluated two commercially enhanced diatomaceous earth products (DE), admixed with grain commodities and concluded that these could be effective and persistent for the control of storage pests, especially of the larger grain borer. The use of inert dust by small scale farmers can be a sustainable alternative to conventional chemical insecticides. However, cost-effectiveness of processing DE products from raw material is a matter of high concern, and the development of such products remains a challenge.

The efficacy of plant derived products for control of *P. truncatus* has been widely investigated. Locally available plant materials have been traditionally used by rural farmers in Nigeria (Poswal and Aka, 1991), Botswana (Jackai and Daust, 1986; Bila, 1996), Zambia and Tanzania (Berger 1994), and in Mozambique (Mapilele *et al.*, 1996; Segeren, 1993; Muatinte unpubl.). Bekele *et al.* (1997) found dry ground leaves and oils of *Ocimum kenyense* (Lamiaceae) to be repellent and toxic against *S. zeamais* and *R. dominica* in Kenya. Tapondjou *et al.* (2002) in Cameroon tested leaf powder and essential oils of *Chenopodium ambrosioides* L. (Chenopodiaceae) against the Bruchidae, *Callosobruchus chinensis*, *C. maculatus* and *Acanthoscelides obtectus*, the curculionids, *S. zeamais* and *S. granarius*, and *P. truncatus*. These researchers found *C. ambrosioides* products to provide effective protection of stored products. However, further research is needed to determine seasonal variability of the active ingredient, effective dosages and appropriateness for use by rural small scale farmers.

The use of plant derived products, especially essential oils and powders with repellent, toxicant

or antifeedant properties, represents a possible way forward in development of IPM strategies against *P. truncatus*. The use of these products against storage pests is increasingly being investigated in Africa and worldwide (Bouda *et al.*, 2001; Tapondjou *et al.*, 2005; Rajendran and Sriranjini, 2008; Nukenine *et al.*, 2010; Silva *et al.*, 2012).

**Biological control - use of predators.** Biological control with the use of the predator, *T. nigrescens* has become one of most promising alternatives for the control of *P. truncatus* in Africa. The effectiveness of *T. nigrescens* in suppressing population numbers of *P. truncatus* has been demonstrated under laboratory conditions. Helbig (1995) in Togo investigated maize grain damage under near-traditional storage conditions and reported that damage was reduced by approximately 23% in the presence of the predator after nine months of storage. Holst *et al.* (2003) in Benin developed a simulation model based on life-table data and found that *T. nigrescens* significantly reduced population growth of *P. truncatus* and the non-target, *S. zeamais*.

In field experiments, Richter *et al.* (1997) observed that infestation by *P. truncatus* in granaries decreased after introduction of *T. nigrescens* in Benin. The number of *P. truncatus* individuals was reduced by 93%, while damage to grains was reduced by approximately 40% in the presence of the predator. Schneider *et al.* (2004) in Benin and Togo, found that *P. truncatus* numbers caught in traps decreased steadily after introduction of *T. nigrescens* during 1992.

Augmented releases of *T. nigrescens* done by Hell *et al.* (2006) for Larger grain borer control in cassava chips in Benin, resulted in reduction of cassava chip losses by 5 and 11% after one and five months of storage, respectively. Contrastingly, Mahumane *et al.* (2009) in Manica Province, Mozambique, reported that *T. nigrescens* had no impact on *P. truncatus* numbers two years after it was released. However, the predator had established and dispersed to new localities. Generally, the studies mentioned above indicate that *T. nigrescens* can impact on *P. truncatus* numbers, indicating its usefulness for control of this pest.

The use of sticky pheromone traps in monitoring programmes of *P. truncatus* flight activity can hypothetically lower the predator density in areas where populations are newly established, or when the numbers are still low, since they can stick and kill *T. nigrescens* together with the pest. Inundated and augmented releases of the predator can increase its abundance, followed by increased efficacy in controlling *P. truncatus* in natural environments. Bucket funnel traps, which are suitable for capturing both *P. truncatus* and the predator without causing mortalities, have the advantage that individuals of the latter can be released back into granaries of the wild.

Hymenopteran parasitoids have been suggested for control of *P. truncatus*. Helbig (1998) in Benin found that *Anisopteromalus calandrae* (Howard) (Hymenoptera: Pteromalidae) was more effective in controlling *P. truncatus* under laboratory conditions than *Teocolax elegans* (Westwood) (Hymenoptera: Pteromalidae). The latter species showed more promise than *Cerchysiella* sp. (Hymenoptera: Encyrtidae), *Pediobius furvus* (Gahan) (Hymenoptera: Eulopidae) and species of Bethyilidae family. Helbig (1999) reported that the predatory bug, *Xylocoris flavipes* (Reuter) (Heteroptera: Anthocoridae), was not effective in controlling *P. truncatus* in traditional maize granaries in Southern Togo.

Although the above studies do not show large scale impact of *T. nigrescens* on *P. truncatus*, biological control holds potential and is most likely the only strategy that could have sustainable impact on the African continent, if predator populations adapt and establish. Investigations into parasitoid-pest interactions in both natural and granary environments must be intensified. In addition to this, the potential synergism between the predator and parasitoids, as well as other biological interactions are subjects for further research to better understand and exploit the role that natural enemies could play in management of *P. truncatus*.

The use of entomopathogenic fungi (EPF) and fungus-derived products constitutes another tool for use in biological control of stored product pests. Odour *et al.* (2000) reported the presence

of the entomopathogenic fungus, *Beauveria bassiana* (Balsamo) Vuillemin (Hyphomycetes) on pests of stored maize in Kenya and highlighted it as a potential control agent. Hertlein *et al.* (2011) reviewed the use of Spinosad against storage pests, including *P. truncatus* and reported to be effective against *R. dominica*, *T. castaneum*, *T. confusum* and *Oryzaephilus surinamensis* (L.) (Coleoptera: Silvanidae). This insecticide is reduced-risk derived by fermentation of the soil actinomycete, *Saccharopolyspora spinosa* Mertz & Yao (Bacteria: Actinobacteridae) (Chintzoglou *et al.*, 2008; Hertlein *et al.*, 2011). However, its large scale use under small scale grain storage conditions requires further investigation.

**Use of semiochemicals.** Information on the economic impact of using semiochemicals to protect stored products from insect pest infestation, especially whether these provide effective, control is scarce. However, mass trapping using sex pheromones is potentially useful despite the fact that their efficacy depends on trap design and possible saturation of traps, particularly under conditions of high pest densities. Another disadvantage is single sex attraction and the possible effects of inappropriate positioning of traps, maintenance of traps in the field, and possible immigration of individuals towards traps from outside the study areas (Cox, 2004).

Moreover, feeding or oviposition stimulants have been used, especially to improve the efficacy of insecticides and biocontrol agents. Laboratory research results of Steward-Jones *et al.* (2004; 2007) showed strong evidence of the existence of a high concentration of compounds in *P. truncatus* dust that acts as a contact kairomone for the predator *T. nigrescens*.

The results from the above studies explained the predator-prey arrestment mechanism between *T. nigrescens* and *P. truncatus* that occurs at close range such as in granaries and conventional maize storage facilities. Additionally, these findings complement the known attraction of *T. nigrescens* to by *P. truncatus* male aggregation pheromone. This attraction towards *P. truncatus* aggregation pheromone, results in *T. nigrescens* flight from significant long distances in open environments

such as forests and agro-ecosystems (Scholz *et al.*, 1998). However, attraction of *T. nigrescens* using synthetic pheromone of *P. truncatus* was not observed by Hodges and Dobson (1998) in laboratory experiments. This fact is contrary to the finding that *T. nigrescens* can fly or walk (Rees *et al.* 1990) into traps baited with synthetic pheromones of *P. truncatus*, but stresses the hypothesis from Steward-Jones *et al.* (2004) that there may be other compound cues involved in this predator-prey interaction.

**Integrated pest management (IPM).** The combined use of several control methods for *P. truncatus* in granaries of small scale farmers in Africa has been widely investigated. Tyler and Hodges (2002) recommended implementation of phytosanitary measures, particularly quarantine inspection of large-scale traded maize, cassava and other *P. truncatus* host commodity products. However, these authors considered that stopping *P. truncatus* long-term dispersal around Africa was unrealistic.

Some of the promising approaches towards effective IPM for *P. truncatus* comprises of the application of Spinosad combined with diatomaceous earth (Chintzoglou *et al.*, 2008; Vayias *et al.*, 2009; Kavallieratos *et al.*, 2010), insect-resistant maize and biological control using *T. nigrescens* (Bergvinson *et al.*, 2011). The application of wood ash, combined with conidia of the fungus *B. bassiana*, as suggested by Smith *et al.* (2006), as well as the use of hermetic bags (Groote *et al.*, 2013) hold potential for the control of the larger grain borer.

Research on integration of several methods for the control of the Larger grain borer in Africa has, to a large extent, been done. Integrating effective technologies and getting farmers involved in evaluating them under real conditions in order to develop sustainable IPM strategies remains a challenge.

## CONCLUSION

The pest status of the Larger grain borer in Africa is high. Continuous monitoring should be done at local and national level to determine pest presence. This pest continues to disperse within and between African countries. Research on

factors influencing its population dynamics should be done and monitoring programmes implemented at international, regional, national and local levels. Modelling of *P. truncatus* population dynamics should be done to predict its dispersal and movements and for its application in pest management. The use of entomopathogenic fungi in combination with diatomaceous earth and plant derived products should be further investigated.

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