Comparison of life history traits and oviposition preferences of *Tuta absoluta* for twelve common tomato varieties in Burkina Faso

Short title: Tomato leafminer life history traits

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Abstract

The South American tomato pinworm, *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae), is an economically important insect pest of tomatoes. Since its discovery in Burkina Faso in 2016, the use of synthetic insecticides was favored, with many cases of treatment failure.

In order to explore alternative control methods, we conducted a screening of the twelve main tomato varieties produced in the country to test two hypotheses: (1) Some tomato varieties are less likely to attract gravid females and be used as oviposition site; (2) Some varieties are unsuitable host plants as they allow slower development and lead to higher mortality. The varieties tested include RomaVF, KanonF1, Cobra 26 F1, FBT1, FBT2, FBT3, RaissaF1, JampacktF1, Mongal, Rio Grande, Tropimech and Petomech.

Tuta absoluta fitness was largely impacted by the tomato variety, especially egg incubation time and larval and pupal stage durations. As a result, the total *T. absoluta* lifecycle was slower on Cobra 26 F1 and Kanon F1 (24.6 ± 1.8 and 25.8 ± 3.3 days, respectively) and faster on FBT1 and Rio grande (22.6 ± 3.0 and 22.8 ± 2.6 days, respectively). None of the variety impacted adult lifespan. All varieties were accepted as hosts by gravid females during multiple choice oviposition assays. The number of eggs laid per females was statistically similar among the varieties.

We conclude that two varieties, Kanon F1 and Cobra 26 F1, have better abilities to slow *T. absoluta* development, limiting the number of generations while increasing the probability that natural enemies find and kill their prey.

Key words: *Solanum tuberosum*, Tomato leafminer, invasive species

Introduction

The South American tomato pinworm, *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) is a voracious miner species that can develop on several plant families with a preference for Solanaceae, and particularly cultivated tomatoes (Bawin et al., 2015, 2016; Caparros Megido et al., 2013; Cherif & Verheggen, 2019). All instars feed on the parenchymal tissues of leaves, tender parts of stems including buds, flowers and developing or ripe fruits (Desneux et al., 2010; Estay, 2000). The result is a considerable reduction in the photosynthetic capacity of the plant in case of heavy attacks, malformation, perforation and then rot of the fruits if they are colonized by secondary pathogens. It can therefore cause yield losses of up to 100% if no effective control methods are used (Desneux et al., 2010).

Thanks to its high dispersal capacity, estimated at 800 km per year, *T. absoluta* has become the most important pest of tomatoes in European, South American and Asian countries (Biondi et al., 2018; Han et al., 2019, Verheggen & Fontus 2019). Since 2008, it has been spreading rapidly over the African continent, particularly in the Maghreb countries, and was first discovered in Burkina Faso (northern region) in 2016 (Son et al., 2017; Mansour et al., 2018). Since then, chemical control has been favored, and most reports produced from the Agricultural Ministry describe cases of treatment failures and abandonment of production plots (Sawadogo et al., 2020a; Sawadogo et al., 2020b). This is probably due to the ability of this insect pest to rapidly develop resistance to the different chemical molecules used (Guedes et al., 2019; Roditakis et al., 2018).

The use of resistant or tolerant varieties could be part of an integrated management strategy (Azevedo et al., 2003). Some varieties can reduce the development capacity of the insect pest while requiring no technical skill on the part of the farmer. Resistance can be the result of the plant phyto-hormonal system, triggered when the plant is attacked by herbivores (Erb et al., 2012; Mouttet et al., 2013). This is followed by the production of defense compounds by glandular trichomes and autonomous epidermal protrusions (McCaskill & Croteau, 1999), such as alkaloids, phenolic compounds and terpenes (Azevedo et al., 2003; Bleeker et al., 2012; Gonçalves et al., 2006). Several of these compounds, including 7-epizingiberene, zingiberene (Azevedo et al., 2003; Bleeker et al., 2012; Lima et al., 2015), acyl sugars (Leckie et al., 2014; Resende et al., 2002) and tridecan-2-one (Leite et al., 2000) increase plant resistance against *T. absoluta*. This resistance is expressed by antixenosis (a deterrent mechanism that prevent colonization by herbivorous insects), antibiosis (the induction of adverse effects on insect survival and development), and tolerance (the ability of the attacked plant to maintain production) (Leite et al., 2000; Vargas, 1970). Thus, commercial tomato varieties with enhanced abilities to produce these defensive compounds may be more tolerant to leafminer, especially during the reproductive stage of the plant, a critical period of attack by this insect pest (Ullé & Nakano, 1994).

It is in this perspective that we conducted a screening of the main commercial tomato varieties available in Burkina Faso to determine their level of vulnerability to *T. absoluta* infestations. We raised two hypotheses: (1) Some of these tomato varieties are less likely to attract gravid females and be used as oviposition site; (2) Some tomato varieties are less suitable hosts than others as they allow slower development and lead to higher mortality.

Materials and methods

Insects **–** About 500 larvae were collected in the village of Goué, located in the Central Plateau region where, as in the whole country, the leafminer is controlled with pesticides (Figure 1). They were reared in a laboratory located in Bobo-Dioulasso, for four generations on tomato plants v. Rossol, in net cages (80 cm long, 40 cm wide and 40 cm high) under a 12: 12 photoperiod before being tested (Hasan &Ansari, 2011). The average temperature and relative humidity of the laboratory were measured daily and maintained at 28 ± 3° C and 50 ± 15%.

Tomato varieties - Twelve tomato varieties were used in this study. They included three varieties developed in the Institute of Environment and Agricultural Research (INERA): FBT 1, FBT2, FBT3, and nine commercially available varieties of which five were hybrids: Cobra 26 F1, Raïssa F1, Kanon F1, Jampakt F1, Mongal, and four were fixed: Petomech, Tropimech, Roma VF, Rio Grande. The major characteristics of these twelve varieties are listed in Table 1.

Evaluation of T. absoluta egg-laying preference - Three weeks after seedlings, plants (10-15 cm high) were transplanted individually into ½ liter pots containing heat-sterilized potting soil and left growing for an additional three weeks in net cages. To evaluate *T. absoluta* oviposition preferences for each variety, one plant of each variety was introduced in a net cage (80×40×40 cm) along with three mated females (less than 5 days old) taken from the mass rearing. Seventy-two hours later, all twelve plants were carefully checked for the number of eggs. This multiple-choice assay was replicated 15 times with new plants.

Evaluation of T. absoluta development - Tomato plants of the twelve varieties were individually placed in net cages with several *T. absoluta* adults (both sexes) overnight. The next morning, eggs were collected. One single egg was deposited on a tomato leaflet (belonging to the same variety it was laid on), placed in a Petri dish (8.9 cm ⌀) containing a piece of moistened blotting paper. The Petri dish was then sealed with parafilm. At least 50 replicates were performed for each variety.

After hatching, the larvae were fed exclusively with the leaves of the tomato variety on which hatching took place. A new leaf was introduced in the Petri dish daily until pupation. After emergence, adults were kept in the same plastic Petri dish with water. Each insect (egg, larvae, pupae and adults) was observed twice a day (at 8 am and 5 pm).

Statistical analysis **-** Normality tests were applied to all measured parameters. The non-parametric test of Kruskal Wallis allowed the comparison of the different varieties. The two-by-two comparison of the rankings of the averages was done using the Dunn method (at 5% significance level). An ascending hierarchical classification (AHC) using the different parameters measured made it possible to classify the different varieties. The graphs and the different analyses were built using R version 3.6.3 and XLSTAT softwares.

Table 1: Characteristics of the twelve tomato varieties used in this study. Precocity: Day After Transplanting

Variety	Precocity	Production period	Main characteristics	Sources
FBT 1	85	Rainy season	Susceptible to fruit bursts	CEDEAO et al., 2016; Some et al., 2014
FBT 2	75	Rainy season	Good resistance to sunburn and fruit bursting	
FBT 3	70	Rainy season	Good resistance to sunburn and fruit bursting	
Petomech	70-80	Cool and hot dry season	Intermediate resistance to *Verticillium* and *Fusarium*, excellent for preservation.	Kimba et al. 2014
Tropimech	65-70	Cool dry season	Resistance to *Fusarium oxysporum* sp. lycopersici race 0 (Fol 0), Tolerance to *Alternaria alternata* f. sp. *Lycopersici* and *Stemphyllium* sp (S). The ideal variety for processing tomatoes with very good firmness for transport, very good shelf life.	
Cobra 26 F1	65	All season	Tolerant to Tomato Yellow Leaf Curled Virus (TYLCV) and bacterial wilt (*Ralstonia solanacearum*); resistance to Fol.0 and 1 and TMV (0)	
Rio Grande	80	Dry and cool season	Resistance to verticilliosis, resistance to fusariosis	
Mongal	60-65	Very hot, cool and winter season	Very high tolerance to bacterial wilt, resistance to Tobacco mosaic virus (0) (TMV), Fol 0 and 1, *Stemphylium* and root-knot nematodes (*Meloidogyne* spp.).	CEDEAO et al., 2016; Kimba et al., 2014
Roma VF	70-80	Cool or winter season	Resistant to Mildew, *Verticilium* and *Fusarium*, Very sensitive to TYLCV.	
Kanon F1	75-80	Dry and cool season	Intermediate resistance to TYLCV and high resistance to Cucumber mosaic virus (CMV), Fol .0 and 1, TMV and *Verticillium.*	Technisem 2016
Jampakt F1	65-70	Dry and cool season	High resistance to *Verticillium dahliae* race 1, Fol: 1 and *Meloidogyne incognita* (Mi) and *Meloidogyne javanica* (Mj).	NTS 2020
Raïssa F1	65-70	Dry and cool season	Resistant to verticilliosis, FOL 1, nematodes, TMV; Good resistance to bursting	

Results

The mean numbers of eggs laid on all tomato varieties were statistically similar among the tested tomato varieties (χ^2 = 10.13 df = 11, *p*-value = 0.518) (Figure 1). We observed an important inter-individual variability, with some laying as few as ten eggs, and others laying as many as 200 eggs.

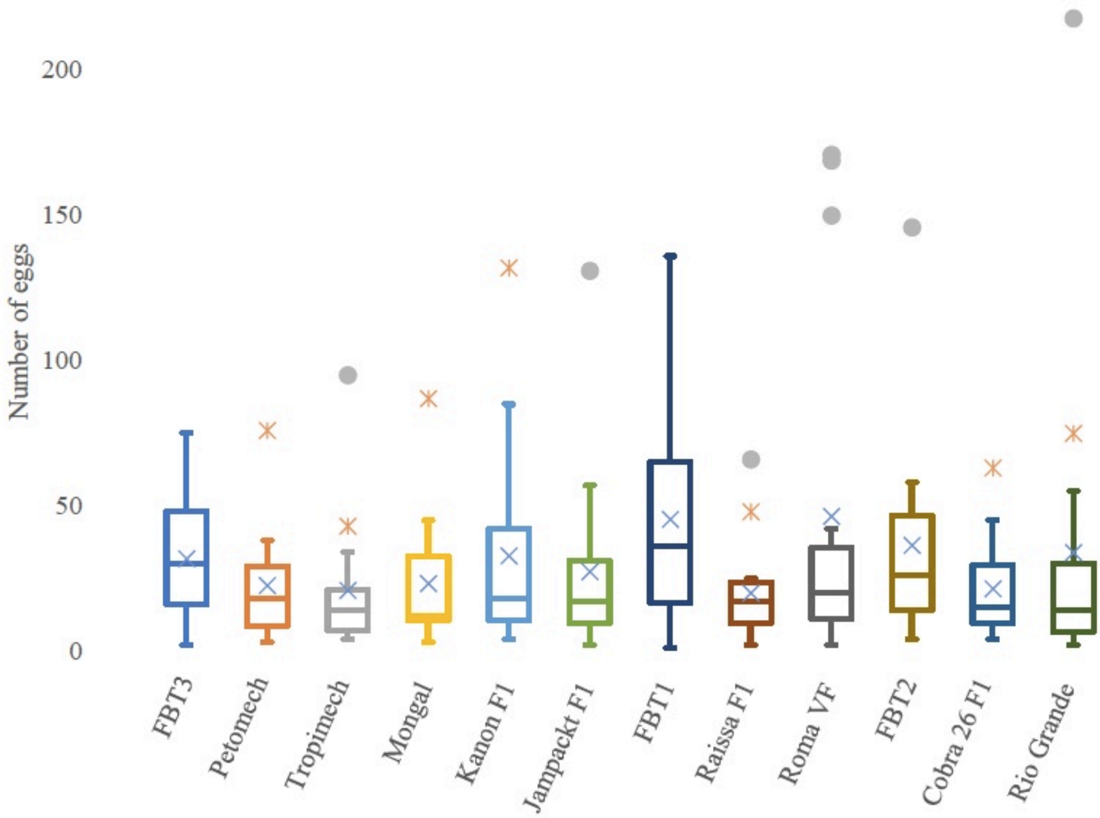

Figure 1: Mean number of eggs laid by *T. absoluta* on twelve tomato varieties

The egg incubation time differed among the varieties (χ^2 = 22.36, df = 11, *p*-value= 0.022) (Table 2), with higher durations observed on Cobra 26 F1, Roma VF and Rio Grande. The average larval development also differed among the tested variety (χ^2= 39. 19, df = 11, *p*-value< 0.001): the longest was recorded on Mongal (12.4 ± 1.5 days), Cobra 26 F1 (12.5 ± 1.1 days) and Kanon F1 (12.7 ± 2.2 days). Similarly, pupal development differed from one variety to another (χ^2= 105.69, df = 11, *p*-value< 0.001). Pupae needed longer period of development on Kanon F1 and Petomech than all the others. Adult lifespan ranged from 9.6 ± 3.6 days on Kanon F1 to 13.2 ± 5.0 days on Rio Grande, but these were not statistically different (χ^2 = 9.51, df = 11, *p*-value=0.575). The average life cycle duration was statistically impacted by the tomato variety (χ^2= 25.32, df = 11, *p*-value=0.008). *T. absoluta* took longer to complete its cycle on the varieties Cobra 26 F1 and Kanon F1 (24.6 ± 1.8 - 25.8 ± 3.3) than on the other varieties.

Table 2: Developmental capacity of *T. absoluta* on 12 tomato commercial varieties in Burkina Faso. Data on the same column sharing the same letter are not significatively different from each other (threshold = 5% according to rankings means of Dunn).

Varieties	Number of insect tested	Survival rate %	Incubation time (days)	Larval development (days)	Pupal development (days)	Adult life span (days)	Life cycle duration (days)
Cobra 26 F1	70	68.57	4.2 ± 0.8 bcd	12.5 ± 1.1 ef	8.0 ± 1.5 d	10.5 ± 3.6	24.6 ± 1.8 c
Kanon F1	52	59.62	4.0 ± 0.7 abc	12.7 ± 2.2 ef	9.1 ± 0.8 e	9.6 ± 3.6	25.8 ± 3.3 c
FBT3	50	82	4.1 ± 1.0 abc	11.8 ± 2.8 cdef	7.8 ± 2.0 cd	9.89 ± 3.41	23.7 ± 4.0 a
Jampakt F1	50	68	4.2 ± 1.1 abcd	11.6 ± 1.1 abc	7.8 ± 1.1 d	10.4 ± 4.8	23.6 ± 1.1 ab
Raïssa F1	50	70	4.1 ± 0.9 abcd	12.1 ± 0.4 bcde	7.4 ± 0.7 bcd	10.1 ± 3.2	23.5 ± 1.3 ab
Roma VF	50	74	4.2 ± 0.7 cd	11.5 ± 3.1 cdef	7.6 ± 0.7 cd	10.9 ± 4.7	23.3 ± 3.3 ab
Petomech	55	76.36	3.9 ± 0.7 abc	10.9 ± 1.9 a	8.8 ± 1.3 e	11.0 ± 3.9	23.6 ± 2.0 ab
Mongal	60	80	3.8 ± 0.9 a	12.4 ± 1.5 f	7.1 ± 1.3 abc	9.8 ± 3.1	23.4 ± 1.9 a
Rio Grande	50	72	4.5 ± 1.0 d	11.8 ± 0.9 abcd	6.6 ± 1.5 ab	13.2 ± 5.0	22.8 ± 2.6 a
FBT2	50	72	3.8 ± 0.6 ab	12.1 ± 1.7 def	7.3 ± 0.7 abcd	10.8 ± 4.2	23.3 ± 2.3 ab
FBT1	50	70	4.0 ± 1.0 abc	12.0 ± 2.7 bcde	6.7 ± 1.1 a	10.2 ± 3.7	22.6 ± 3.0 a
Tropimech	55	80	3.8 ± 0.8 a	11.7 ± 0.7 ab	7.5 ± 1.0 cd	10.2 ± 4.8	23.0 ± 1.3 a
K		11.45	22.36	39.19	105.69	0.855	25.32
p-value		0.407	0.022	< 0.001	< 0.001	0.585	< 0.008

An Ascending Hierarchical Classification (AHC) was performed to compare the 12 tomato varieties using the following variables: survival rate, number of eggs laid, and the durations of egg incubation, larva development, pupa development, entire life cycle (Figure 2). Based on the AHC, three groups of varieties are identified:

(i) The first group includes varieties leading to longer life cycle: Cobra 26 F1, Raïssa F1, Jampakt F1 and Kanon F1 ;

(ii) The varieties of the second group lead to shorter development duration than those of the first group, but faster than those of the third group. It includes Mongal, Tropimech and Petomech.

(iii) The third group includes Rio Grande, FBT2, FBT3, Roma VF and FBT1. These four varieties lead to comparable development durations. Compared to the varieties of the two first groups, they maximize *T. absoluta* fitness.

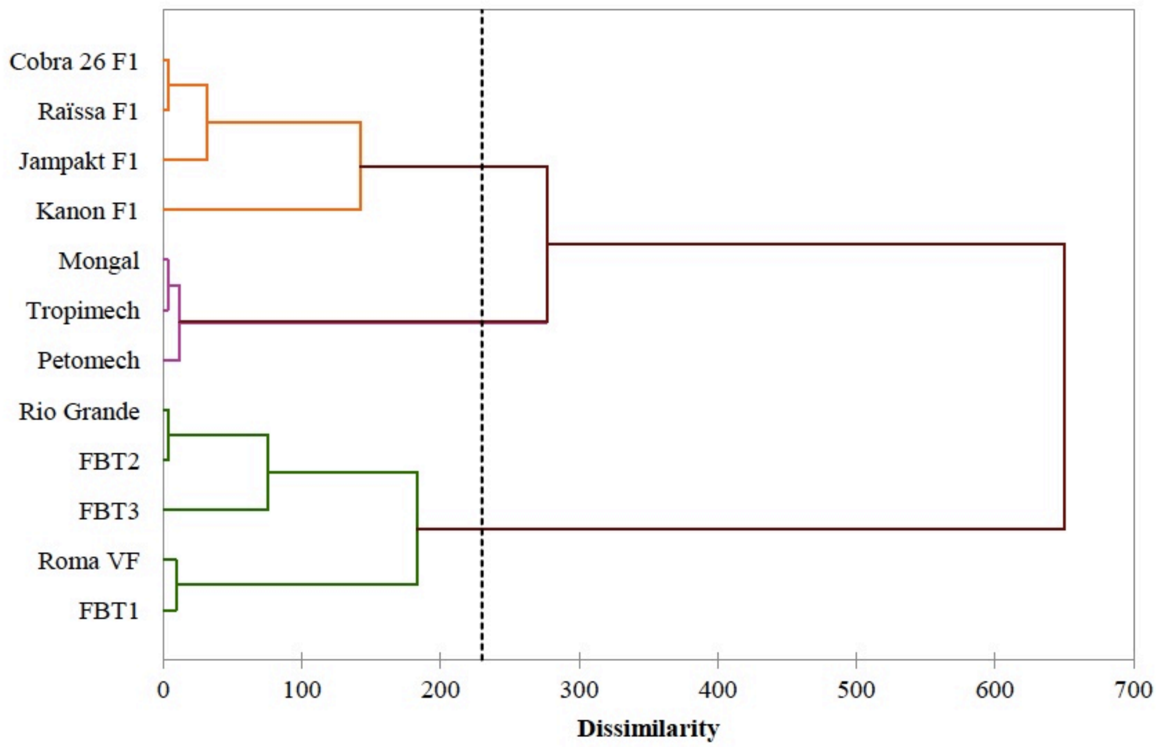

Figure 2: Ascending Hierarchical Classification (AHC) of different varieties.

Discussion

We found no difference in terms of number of eggs on the different tested tomato varieties. According to the basic principles of host plant selection, females select their oviposition site to maximize the survivability of their offspring (Gripenberg et al., 2010). *T. absoluta* females are guided by volatile organic compounds released by their host plants and allowing them to discriminate hosts from non-hosts (Caparros Megido et al., 2014; Proffit et al., 2011). They generally lay their eggs on the underside of the apical leaves because of their low calcium content (Cherif et al., 2013; Proffit et al., 2011). The number of eggs they lay are negatively correlated with the presence of compounds such as α-pinene, β-pinene, myrcene and limonene (Yarou et al., 2017), trichome style I on the leaves (Khederi et al., 2014), heptadecane (Suinaga et al., 1999), and zingiberene (Azevedo et al., 2003; Lima et al., 2015). The density and diversity of glandular and non-glandular trichomes may also impact oviposition site preferences (Khederi et al., 2014). Our results suggest that none of the varieties tested produce repellent compounds. They probably did not differ sufficiently in terms of volatile compounds or trichomes architecture or composition. Bawin et al., (2014) concluded that the oviposition response of *T. absoluta* females is more sophisticated than expected: not just volatile compounds are involved, but also the female previous experience and risk of intraspecific competition. However, field individuals are rarely given the choice among tomato varieties. Our results suggest that any of them is perceived as an adequate oviposition site.

We observed similar survival rates among all 12 varieties suggesting that none of them is genetically armed to counter infestations by the tomato leafminer. The pest has the ability to grow and complete its developmental cycle on all tested varieties. A similar conclusion was drawn by Krechemer & Foerster (2017) with six different tomato varieties (namely Cherry, Cordilheira, Giuliana, Nemoneta, Paron and Santa Clara). However, we found differences in the duration of embryonic development, larval stage duration and pupal stage duration, resulting in a significant difference in the developmental cycle of *T. absoluta* on the different tomato varieties. Embryonic life span can be influenced by poor feeding of females (Boggs, 1992), reduced moisture at the oviposition site (stomatal closure reducing moisture at the leaf surface or necrosis of the tissue at the site) (Bawin et al., 2015; Woods, 2010), as well as volatile and contact chemicals emitted from the leaves (Bawin et al., 2015; Hilker & Meiners, 2011). The third option would be the most plausible in our study, since all females were fed similarly prior to the experiment, and all plants were exposed to similar laboratory conditions. However, one limitation of our experimental setup is that the tomato leaves were excised from the plants before being given as diet to the larvae. By doing so, we might have altered the variety susceptibility and response to the pest feeding activity (e.g. production of plant metabolites), which could be different by whole plants compared to excised leaves.

Three varieties led to longer larval developmental (Mongal, Cobra 26 F1 and Kanon F1), suggesting poorer nutritional quality and/or production of plant metabolites that impeded larval development (Awmack & Leather, 2002; Bawin et al., 2015; Krechemer & Foerster, 2017; Pereyra & Sanchez, 2006). A high C/N ratio in the leaves can lead to a low survival rate and a longer development cycle of the leafminer (Han et al., 2014). Leite et al. (2000) also found that higher concentrations tridecan-2-one (produced by type VI glandular trichomes of *Lycopersicon hirsutum*) slowed the development of *T. absoluta* larvae. *Lycopersicon hirsutum* has antixenotic and antibiotic effects against *T. absoluta*. It is more toxic for male larvae than females because of their lower weight and the relatively higher rate of penetration of the allelochemical through the male cuticle, since the latter have a smaller body volume. Zingiberene contained in type VI and IV glandular trichomes (Gonçalves et al., 2006) is also toxic to *T. absoluta* larvae (Azevedo et al., 2003; Lima et al., 2015).

The duration of the biological cycle of *T. absoluta* varied over the different tested varieties (between 22 and 26 days). These values are close to those reported by Razuri & Vargas (1975) (27 days), Fernández &Montagne (1989) (24 days) and Cherif et al. (2019) (24 days) for experimental temperatures close to ours (24 and 28° C). Lebdi-Grissa et al. (2011), working on a Tunisian *T. absoluta* strain, under temperature conditions close to ours (25±2°C) reported much longer developmental cycles (i.e. 37 days), including pupal development of up to 14 days, much more than the one we observed in our study (8 days). In herbivorous insects, a shorter development period is a key indicator of a good food quality (Awmack & Leather, 2002; Pereyra & Sanchez, 2006).

Based on our results, we conclude that two varieties available on the Burkinabe market, namely Kanon F1 and Cobra 26 F1, have better abilities to slow *T. absoluta* development. A slowed development cycle increases the probability for the pest to be found by one of its natural enemy (e.g. *Nesidicoris tenuis*) which is known to prefer young larvae (Siqueira et al., 2000; Urbaneja et al., 2008).

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