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The distribution and abundance of the stem-galling fly, *Cecidochares connexa* (Macquart) (Diptera: Tephritidae), a biological control agent of *Chromolaena odorata* (L.) (Asteraceae), in Ghana

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Chromolaena odorata (L.) R.M. King and H. Robinson (Asteraceae: Eupatorieae) is one of the worst invasive weeds in West Africa, and a serious biotic threat to food security. The stem-galling fly, *Cecidochares connexa* (Macquart) (Diptera: Tephritidae), a biological control agent for *C. odorata*, was released in the Ivory Coast in 2003 and first detected in Ghana in 2014. The spatiotemporal distribution and abundance of *C. connexa* in Ghana was determined by country-wide surveys from 2015 to 2016. Galls were found in varying densities across Ghana but gall densities were consistently low east of Lake Volta. A limited survey conducted in the extreme west of Togo in 2016, found the gall fly also in low numbers. There was a significant correlation between *C. connexa* gall densities and the distance from the release sites in the Ivory Coast. The distribution and abundance of the gall fly in Ghana could be explained by its spread from the original release sites over time and/or the much drier conditions east of Lake Volta. *Cecidochares connexa* has dispersed a distance of about 1000 km over a 10-year period and, while there is some evidence that the gall fly is still dispersing towards the east, its range and population size could be limited by the dry climatic conditions in the east of Ghana and in Togo. Actively redistributing the agent over this dry corridor to the more humid and higher rainfall areas of Nigeria, may result in the spread of this agent through the rest of West and Central Africa, thereby aiding the control of *C. odorata* in the region.

Key words: weed biological control, gall fly, agent dispersal, spatiotemporal distribution, climatic suitability, West Africa.

INTRODUCTION

Chromolaena odorata (L.) King and Robinson (Asteraceae: Eupatorieae), often referred to as 'Akyeampong' in Ghana, is a neotropical shrub that has invaded numerous countries in Africa, Asia and the western Pacific, threatening biodiversity and food security (Zachariades *et al.* 2009). The weed was first detected in Ghana in 1969, at the Legon Botanical Garden (LBG) (Hall *et al.* 1972), and two decades later, it had invaded about 75 % of the total land area of the country, occupying many different habitats (Timbilla & Braimah 1996).

Biological control of *C. odorata* in West Africa began in the 1970s, when two biocontrol agents, *Pareuchaetes pseudoinsulata* Rego Barros (Lepidoptera: Erebidae) and *Apion brunneonigrum* Béguin-Billecocq (Coleoptera: Brentidae) were introduced unsuccessfully into Nigeria and Ghana (Cock & Holloway 1982). In the early 1990s, *P. pseudoinsulata* was re-introduced in Ghana, as part of a new biological control programme against *C. odorata* (Timbilla & Braimah 2000) and subsequently established (Braimah & Timbilla 2002). However, nine years after an earlier study reported its



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success in Ghana (Timbilla & Braimah 2000), a re-evaluation of the agent showed that the insect's densities had declined over time (Uyi *et al.* 2009). Braimah *et al.* (2013) reported that the decline in densities of *P. pseudoinsulata* in Ghana was due to the decline in densities of *C. odorata* from about 85 % cover in the early 1990s to about 34 % cover by 2013, as *P. pseudoinsulata* tends to thrive in high abundance of *C. odorata* (Braimah & Timbilla 2002). Nevertheless, 30 % cover of *C. odorata* is not low enough to curb its impact on biodiversity and agriculture (Braimah & Timbilla 2002), and the impact of *P. pseudoinsulata* on *C. odorata* is insufficient to control the plant much further (Uyi *et al.* 2009).

With *C. odorata* still widespread and difficult to manage, its threat to human welfare and food security remain significant (Uyi & Igbiosa 2013). Therefore, other biological control agents, such as the gall fly *Cecidochares connexa* Macquart (Diptera: Tephritidae), are required to help manage the weed in the region (Zachariades *et al.* 2009). The gall fly lays eggs in both the terminal and axillary buds of *C. odorata* and the developing larvae induce galls on the plant stems (McFadyen *et al.* 2003). The induced galls act as 'nutrient sinks' and reduce metabolic functions, such as shoot growth, and flower head and seed production (Cruz *et al.* 2006). High densities of galls can lead to the death of branches, stems and plants, consequently reducing densities of the weed over time (Harris & Short-house 1996; McFadyen *et al.* 2003; Day *et al.* 2013a).

Cecidochares connexa is host specific to *C. odorata*, having been tested against over 135 plants in eight countries (*e.g.* McFadyen *et al.* 2003; Day *et al.* 2016). It has been deliberately released into 12 countries and has established in 11 (Winston *et al.* 2014). In Papua New Guinea (PNG), Indonesia, and Guam, post-release studies have shown that the gall fly establishes easily, spreads rapidly and can reduce densities of *C. odorata* to below thresholds that threaten food security and biodiversity (Soekisman 1999; Muniappan *et al.* 2007; Day *et al.* 2013a; Reddy *et al.* 2013), thereby improving the livelihoods of the indigenous people (Day *et al.* 2013a).

The gall fly is now considered to be the most successful biocontrol agent of *C. odorata* worldwide, and has the ability to establish populations in landscapes where *C. odorata* is distributed, either as thickets or scattered patches (Cruz *et al.* 2006; Day *et al.* 2013a). However, the success of *C. connexa* as a biological control agent appears to be influenced by climate (Day *et al.* 2013b). For

example, unlike PNG and Guam where *C. connexa* has provided significant control of *C. odorata*, it has been less successful in Timor Leste. In Timor Leste, climatic conditions are generally drier than PNG and are less conducive for the gall fly (Day *et al.* 2013b). This suggests that prolonged dry conditions, such as low rainfall and humidity or drought, play crucial roles in determining the ability of the gall fly to increase to sufficient numbers to control *C. odorata* and spread to new areas.

In 2003, the gall fly was introduced into Ivory Coast, around Soubre and Okrouyo, close to the Liberian border (Winston *et al.* 2014; R. Desmier de Chenon, pers. comm. to C. Zachariades 2009). Although establishment was confirmed, little post-release evaluation was conducted. In 2014, *C. connexa* was reported in Ghana, having spread from Ivory Coast (Paterson & Akpabey 2014). Here, we examine the abundance and distribution of *C. connexa* in Ghana, investigate the rate of spread from the original release sites, and identify factors that could limit the spread of the agent. This is the first post-release evaluation of *C. connexa* in West Africa and we offer recommendations of how to improve its use as a biological control agent of *C. odorata* in the region.

MATERIAL AND METHODS

Distribution of Cecidochares connexa

Two field surveys were conducted across southern Ghana between June 2015 and March 2016, covering most of the known distribution of *C. odorata* in Ghana (Djietror 2012). The first survey sampled 85 sites between June and September 2015 and the final survey was conducted between January and March 2016. This survey sampled 27 sites, which included 10 sites previously visited in the first survey. All six regions in southern Ghana, except the Western region, were sampled in both 2015 and 2016. Detailed surveys were not conducted in the Western region, as surveys by Paterson & Akpabey (2014) had already determined that the gall fly was well established there. The intention of these surveys was to determine the current distribution of *C. connexa* in the country and investigate any possible changes to its distribution over time. *Chromolaena odorata* plants along roadsides, open vegetation and farmlands were visually examined for the presence or absence of galls by a team of three persons for approximately four hours per location. A limited survey was also conducted

opportunistically in the extreme west of Togo in July 2016.

Density of Cecidochares connexa

Five sites were randomly selected from locations in each of the Ashanti, Central, Eastern, Greater Accra and Volta regions of southern Ghana where *C. connexa* galls were present. Average distances of the selected sites in the aforementioned regions from the release sites in Ivory Coast were 625, 820, 650, 800, 910 km, respectively. In all sampling events, five quadrats (1 m²) were thrown randomly on a patch of *C. odorata* at each site and the number of galls within each quadrat was recorded. Only young galls (prior to adult eclosion) within the quadrat were recorded in this study, because this is the only way to be certain that the fly is present at the site at the time of each survey. Data were recorded monthly from June 2015–March 2016 to determine the change in gall density at each site over time. The monthly average number of galls/m² were obtained for each of the 25 locations and then grouped according to the five regions.

Cecidochares connexa gall densities recorded across the five regions in October 2015 and March 2016 were tested for normality with Shapiro & Wilk's test and Quantile-Quantile (Q-Q) plots. Following satisfaction of the assumptions for normality and homogeneity of variances, a one-way analysis of variance (ANOVA) was used to test for differences in mean gall densities between the five regions. Where differences were significant, comparisons between means were conducted with Bonferroni *post hoc* tests.

The distances from the release sites in Ivory Coast to the study sites in Ghana were calculated by the Geography and Resource Development Department (GRDD), University of Ghana (UG), Legon. The Pearson's product-moment correlation analysis was then used to test the relationship between the calculated distances and gall densities in Ghana. All statistical analyses were performed in Genstat 9.2 Lawes Agricultural Trust (Rothamsted Experimental Station).

RESULTS

Distribution of Cecidochares connexa

The two surveys in Ghana covered a total of 102 locations, in six regions: Ashanti, Central, Eastern, Greater Accra, Western and Volta. Six sites with *C. odorata* were sampled in western Togo. *Cecido-*

chares connexa galls were found in all six sampled regions of Ghana and two of the six sites in the extreme west of Togo (Fig. 1). In both the first and second surveys, galls were found in the west and east of Lake Volta, albeit in low densities in the east. The farthest location in Ghana from the release sites in Ivory Coast, where *C. connexa* galls were found, was Hohoe (7°09'06.66"N 0°28'25.78"E), over 800 km from the release sites. The gall fly was detected at two (Noepe 6°15'37.71"N 1°02'13.45"E and Badja 6°22'34.30"N 0°59'08.35"E) of the six locations sampled in Togo, which were approximately 50 km east of the Ghana border. These are the first records of *C. connexa* in Togo and were over 950 km from the release sites in Ivory Coast.

Cecidochares connexa was found at almost all sites in all regions in the first survey in 2015, which corresponded with the rainy season. The gall fly was also found at almost all sites in the Ashanti, Central and Eastern regions during the second survey in 2016, suggesting that it is well established in those regions (Fig. 2). However, there was a substantial decrease in the proportion of sites in Greater Accra and Volta that supported *C. connexa* populations in early 2016, as compared to late 2015 (Fig. 2).

Density of Cecidochares connexa

Cecidochares connexa gall densities showed similar population trends at all monitored sites in each of the Ashanti, Central, Eastern, Greater Accra, and Volta regions (Fig. 3). The change in densities of *C. connexa* galls across the five regions showed similar oscillations during the wet (June–October) and dry (November–March) seasons. Gall densities peaked in October–November in most regions except the Central region, where peaks occurred around November–December at most sites and the Volta region, where densities were much lower, and peaks occurred from October–December (Fig. 3). The highest average density of galls (16/m²) per region was recorded in the Ashanti region (Fig. 4). Galls were never absent at any time in these regions, despite the decline in gall densities across all study regions during the dry periods (Fig. 4).

There was a significant difference in the mean density of *C. connexa* galls between regions in both October 2015 ($F_{4,20} = 45.32, P < 0.001$) when populations were highest and February 2016 ($F_{4,20} = 10.26, P < 0.001$) when they were lowest (Fig. 5).

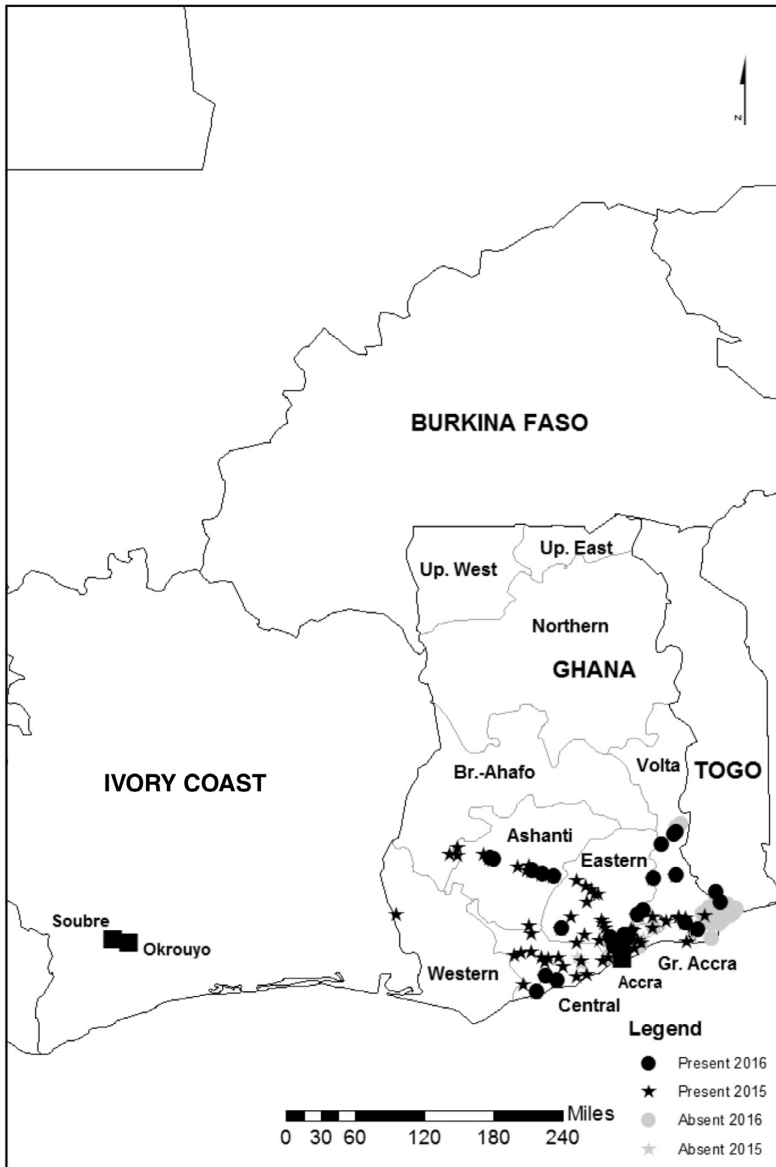


Fig. 1. Map showing the presence and absence of *Cecidochares connexa* in Ghana and Togo during field surveys conducted in 2015 and 2016.

Overall, regardless of seasons, populations tended to be higher in the Ashanti and Eastern regions (Fig. 5).

There was a significant negative correlation between the average *C. connexa* gall density and the distance from release sites in Ivory Coast ($r = -0.60$, $F_{1,24} = 26.19$, $P < 0.001$), with gall fly densities decreasing as distance from the release sites increased (Fig. 6). However, when sites from the

Volta region were excluded from the analysis, there was no significant correlation ($r = -0.09$, $F_{1,19} = 0.14$, $P = 0.92$).

DISCUSSION

Cecidochares connexa is well established in Ghana, occurring in all six regions of southern Ghana where *C. odorata* has invaded, albeit in varying

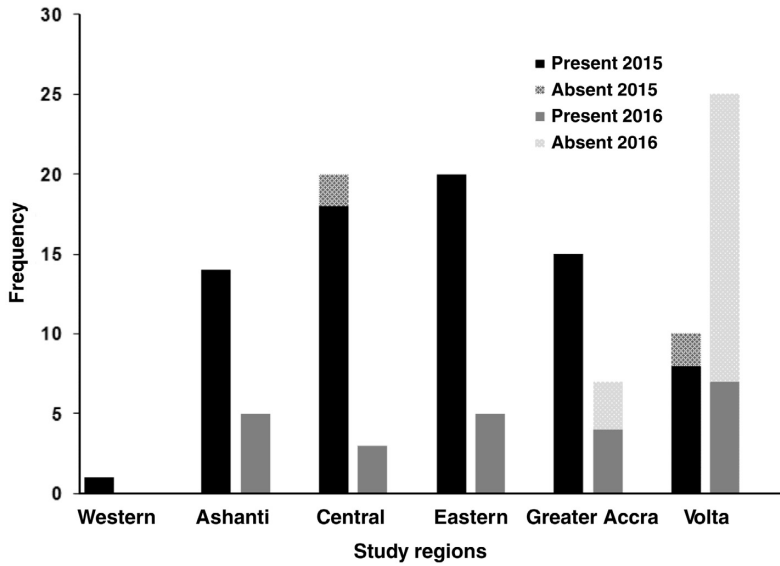


Fig. 2. Spatiotemporal regional distribution and change in the occurrence of *Cecidochares connexa* within regions across southern Ghana.

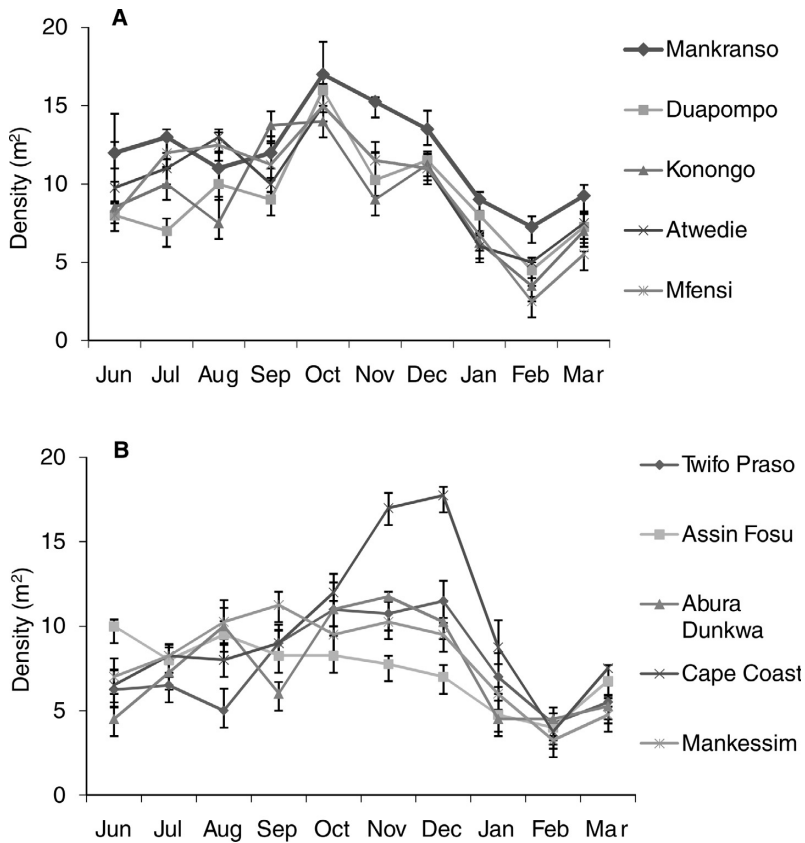


Fig. 3. Mean (\pm S.E.) of *Cecidochares connexa* galls at different sites in the (A) Ashanti, (B) Eastern, (C) Greater Accra, (D) Central and (E) Volta regions during June 2015 to March 2016. (Continued on p. 476.)

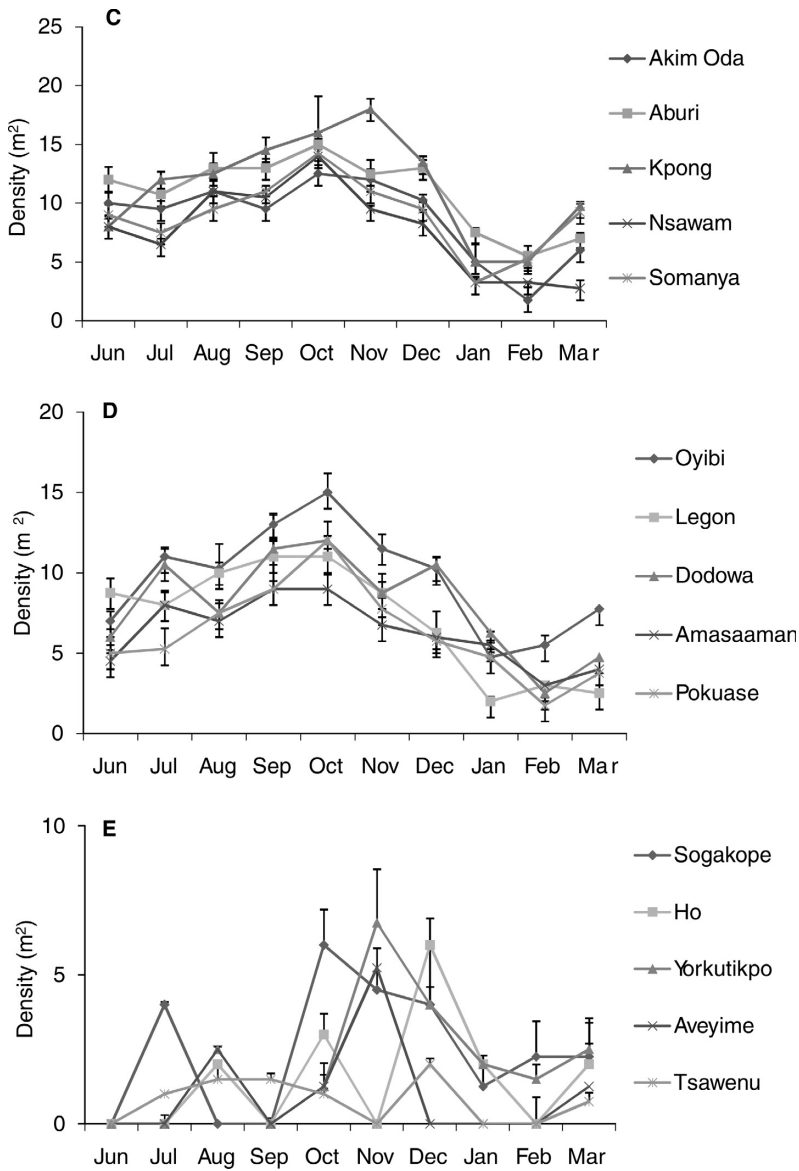


Fig. 3 (continued)

densities across the country. The gall fly was also confirmed in Togo for the first time. Although there is no record of how long *C. connexa* has been in Ghana or in Togo, prior to being first reported by Paterson & Akpabey (2014) or here, respectively, *C. connexa* has spread about 1000 km in the 11 years since its intentional release in Ivory Coast in 2003. Such dispersal over time by *C. connexa* was also observed in PNG (Day *et al.* 2013a) and Timor Leste (Day *et al.* 2013b). The pattern of spread and

dispersal ability demonstrated by *C. connexa* is neither unexpected nor exclusive to the gall fly, and is comparable with other biocontrol agents with strong dispersal abilities (Day *et al.* 2003; Urban *et al.* 2011; Winston *et al.* 2014).

Gall densities were generally higher in the west of Ghana (wetter region) and decreased farther east, where conditions are drier. This trend could be attributed to the greater distances in the east from the release sites in Ivory Coast, suggesting

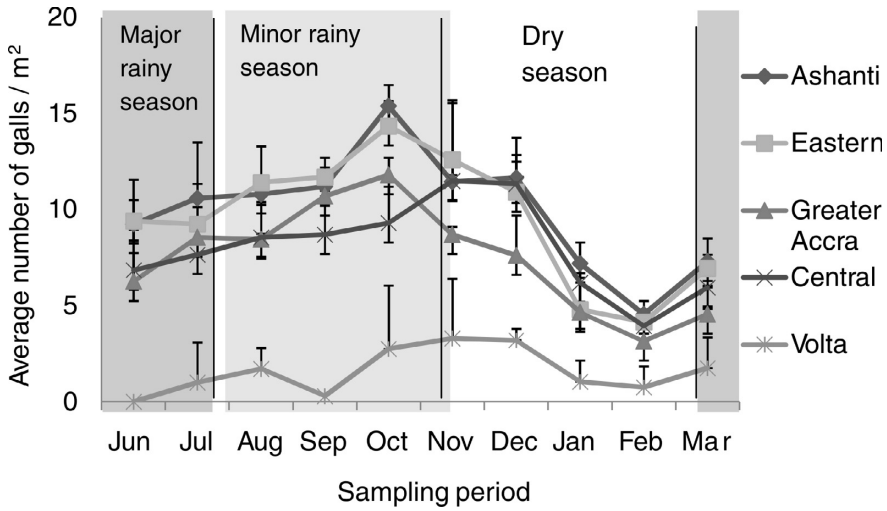


Fig. 4. Regional population trends of *Cecidochares connexa* galls recorded during June 2015 to March 2016 as indicated by mean (\pm S.E.) number of gall per quadrat per region.

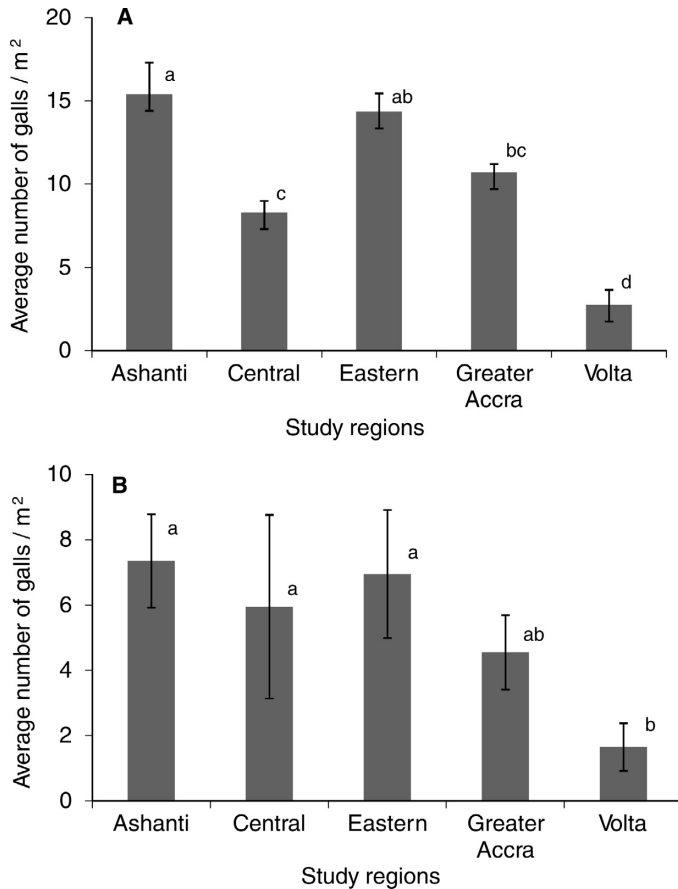


Fig. 5. Mean (\pm S.E.) regional abundance of *Cecidochares connexa* galls in Ghana during (A) October 2015, and (B) March 2016. Means with the same lower case letters are not significantly different (Bonferroni's test: $P < 0.05$).

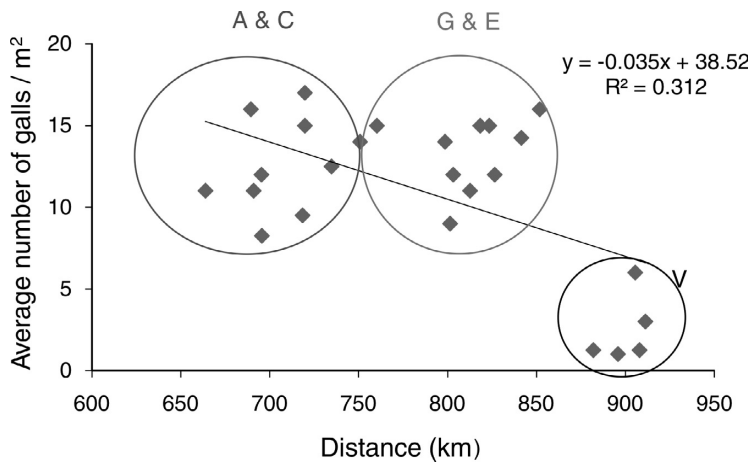


Fig. 6. Relationship between the density of *Cecidochares connexa* galls in Ghana and distance from the release sites in Ivory Coast. **A & C** = Ashanti and Central regions, **G & E** = Greater Accra and Eastern regions and **V** = Volta region. Only gall densities recorded in October 2015 (when recorded in their highest numbers) were used for the analysis.

that the gall fly is still dispersing to new areas, or is being constrained by adverse climatic factors, or both. Certainly, the distribution of the gall fly in Ghana reported here is greater than that reported by Paterson & Akpabey (2014). Since the latter authors surveyed primarily in the western regions of Ghana, it is possible that the gall fly was already present in the eastern regions but was not detected. However, the change in the frequency of the fly in this current study is most likely due to the reduction of locations sampled in 2016.

The negative correlation between gall densities in Ghana and the distance from the release sites in Ivory Coast could be explained probably by two hypotheses. First, the fly is a relatively recent incursion into Ghana, and spreading eastwards. Therefore, populations in the east are likely to be smaller than populations in the west, which are closer to the release sites in Ivory Coast. Second, the drier climatic conditions in the extreme east of the country, where gall densities were consistently low throughout this study, could be influential as they were in Timor Leste (Day *et al.* 2013b)

Temperature and humidity have a significant impact on the establishment, dispersal, geographical range, population densities and overall success of biological control agents (May & Coetzee 2013; Cowie *et al.* 2016). In particular, low humidity is challenging for many insect species, as it disrupts or hinders development, impedes oviposition and/or reduces life expectancy (Cowie *et al.* 2016). Humidity, inferred from the amount of rainfall, appeared to have influenced densities

of *C. connexa* populations in our surveys in both time and space. *Cecidochares connexa* gall densities consistently declined in all five study regions throughout the dry season, popularly regarded as 'Harmattan' in West Africa. There was a subsequent and expected increase in gall densities at the onset of the major rainy season, clearly indicating the susceptibility of the fly to prolonged dry conditions. The major rainy season in West Africa is characterised by periodic heavy rainfalls often accompanied with strong winds, while the minor rainy season is characterised by sporadic rainfalls, accompanied sometimes with oscillating mild winds. The dry season is characterised mainly by the dry dusty northeast trade winds, the same blowing across the Sahara Desert. The susceptibility of *C. connexa* to climate conditions such as temperature and humidity has been previously documented (see Day *et al.* 2013b, 2016).

Further surveys are warranted to determine the distribution of *C. connexa* elsewhere in Ghana, such as the northern region, where *C. odorata* is present, albeit in fragmented patches (Djietror 2012). Further surveys are also needed in Togo, with attention focused towards its border with the Republic of Benin to determine how far east *C. connexa* has become distributed. Surveys for *C. connexa* are also warranted in Nigeria, and Central Africa where the impact of *C. odorata* on food security and livelihoods has been historically correlated with that in West Africa (*e.g.* Hoevers & M'Boob 1996).

In areas where *C. connexa* is absent, we recom-

mend its re-distribution across areas with less favourable climatic conditions in the east of Ghana, in Togo, and further into the wetter parts of West Africa, such as southwestern Nigeria, through a sub-regional concerted alliance that is geared towards the integrated control of *C. odorata* in West Africa. This could significantly speed up the distribution of the gall fly in the region, consequently alleviating the socio-ecological impact of the weed on the indigenous people. The impact of *C. odorata* on people's livelihoods in West Africa, and other parts of Africa, has, for a long time, been neglected (see Zachariades *et al.* 2009; Uyi & Igbinosa, 2013). We do not anticipate any risks following the re-distribution of *C. connexa* across West Africa, because the host specificity of the fly has previously been tested against 136 non-target

plant species in eight countries (see Day *et al.* 2016), with no reports of non-target impacts (Winston *et al.* 2014).

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