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FAILURE OF AN *AMYNTHAS AGRESTIS* (GOTO&HATAI 1899) (OLIGOCHAETA: MEGASCOLECIDAE) POPULATION TO EXPAND ITS RANGE WITHIN A SUGAR MAPLE (*ACER SACCHARUM*) STAND.

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ABSTRACT

Earthworms in the genus *Amynthas* Kinberg have been associated with horticulture but were recently reported from forested ecosystems where they are limited to distinct patches. Little is known about whether these earthworms spread beyond their original invasion patch. We observed an invasion from a patch of a successful population into a neighbouring patch in 2013. *Amynthas agrestis* was the sole species in the original patch. There were 6 Lumbricidae species present in the newly invaded patch. The invasion may have been triggered by runoff events that could have washed *A. agrestis* down a gentle slope in early summer 2013. Even though the newly invaded patch had up to half the abundance of the original patch, the invasion failed. Already in the year of the invasion juveniles did not develop into adults and by October 2013 the total abundance in the newly invaded patch had all but collapsed. In the following year *A. agrestis* was absent from the newly invaded patch but abundance at the original patch reached 200 individuals m^{-2} in July 2014. The cause of the collapse of the new population is not known. Speculatively, earthworm diversity, presence of parasites of adults and predation of smaller individuals may have caused the invasion failure.

Key words: Vermont, Oligochaeta, Megascolecidae, *Amynthas agrestis*

ÖZET

Amynthas Kinberg cinsi solucanlar bahçecilik ile ilişkilendirilmiş fakat son zamanlarda belli arazi parçalarıyla sınırlandırılan orman ekosistemlerinden geldikleri rapor edilmiştir. Bu solucanların istila ettikleri original toprak alanın ötesine yayılıp yayılmadıkları az bilinmektedir. Biz 2013 yılında etkin bir nüfusun olduğu alandan komşu alana olan bir istila gözlemledik. Başlangıçtaki ve henüz istila edilmiş araziler aynı orman alanında ve özdeş toprak ve bitki örtüsüne sahipti. *A. agrestis* asıl alandaki tekstür idi. Henüz şimdi istila edilmiş alan 6 adet Lumbricidae türü vardı. Bu, 2013 yazı başındaki hafif bir eğimle aşağıya doğru yıkanmış olabilen *Amynthas agrestis* istilası güçlü yağışlardan kaynaklanmış olabilir. Yeni işgal edilmiş alan, başlangıçtakinin miktarından yarısı kadar olmak zorunda olsa da, istila başarısız oldu. İstila olduğu yılda bile gençler yetişkin haline gelmedi ve 2013 yılı Ekim ayına kadar yakın zamanda istila edilmiş alandaki toplam yoğunluk tamamlanmış fakat çökmüştü. Ertesi yılda *A. agrestis* yeni istila edilmiş alanda yoktu, fakat 2014 yılı Temmuz ayında başlangıçtaki alanda m2'ye 200 sayıya ulaştı. Yeni popülasyonun çökmesinin sebebi bilinmemektedir. Kuramsal olarak solucan çeşitliliği, küçük bireylerin predasyonu ve yetişkinlerdeki parasitlerinin varlığı, istilanın başarısızlığına sebep olmuş olabilir.

Anahtar Kelimeler: Vermont, Wyoming, Oligochaeta, Megascolecidae, *Amynthas agrestis*

ZUSAMMENFASSUNG

Regenwurmarten in der Gattung *Amynthas* Kingberg sind häufig mit Gartenbau verbunden aber inzwischen auch in Wäldern anzufinden. Obwohl sie dem Waldökosystem schaden können, sind sie scheinbar auf Mikrohabitate beschränkt. Ob und in wie weit die Verbreitung über ein ursprüngliches Invasionshabitat hinaus erfolgt ist nicht bekannt. Wir haben in 2013 eine Invasion von einem dieser bewaldeten Mikrohabitate in einen benachbarten Waldbereich mit identischem Boden und Vegetationbedingungen verfolgt. Die Invasion erfolgte wahrscheinlich auf Grund starker Regenfälle im Juni und Juli 2013, die *Amynthas agrestis* Individuen das leichte Gefälle herab geschwemmt haben könnten. Im ursprünglichen Mikrohabitat waren lediglich *A. agrestis* präsent. Im anliegenden Habitat waren noch 6 Arten der Familie Lumbricidae vorhanden. Anfänglich war die *A. agrestis* Population im neuen Invasionsbereich ein viertel (Ende Juli) bis halb (Anfang August) so groß wie die ursprüngliche Population. Die Invasion war nicht erfolgreich und vor allem kleinere Individuen entwickelten sich schon im Invasionsjahr nicht zu adulten Individuen. Die Gesamtabundanz im neuen Invasionsbereich brach schon im Oktober zusammen. Im folgenden Jahr war *A. agrestis* gänzlich vom neuen Invasionsbereich verschwunden. Der Grund des Populationszusammenbruchs ist unbekannt. Vermutlich könnte der Zusammenbruch mit der Regenwurmartenvielfalt im neuen Invasionsbereich, Parasiten adulter Regenwürmer und Prädationsdruck auf kleinere Individuen zusammenhängen.

Stichwörter: Vermont, Oligochaeta, Megascolecidae, *Amynthas agrestis*

RÉSUMÉ

Les vers de terre appartenant au genre *Amynthas* Kinberg ont été associés à l'horticulture mais ont été récemment signalés dans les écosystèmes forestiers où ils sont limitées à des parcelles distinctes. Peu est connu à savoir si ces vers de terre se sont propagés au-delà de leurs points invasion d'origine. Nous avons observé une invasion réussie d'une population dans une parcelle avoisinante en 2013. *Amynthas agrestis* était la seule espèce dans la parcelle originale. Il y avait six espèces de Lumbricidae présentes dans la nouvelle parcelle envahie. L'invasion peut avoir été déclenché par des événements de ruissellement qui pourraient avoir lavés *A. agrestis* le long d'une pente douce au début de l'été 2013. Même si la nouvelle parcelle envahie avait jusqu'à la moitié de l'abondance de la parcelle d'origine, l'invasion a échoué. Déjà, dans l'année de l'invasion, les juveniles ne se sont pas transformés en adultes et en octobre 2013, la population dans la nouvelle parcelle envahie s'est essentiellement effondrée. L'année suivante, *A. agrestis* était absente de la parcelle initialement envahie mais l'abondance dans la parcelle d'origine a atteint 200 individus m^{-2} en Juillet 2014. La cause de l'effondrement de la nouvelle population n'est pas connue. On peut supposer que la diversité des vers de terre, la présence de parasites affectant les adultes et la prédation des petits individus peuvent avoir causé l'échec de l'invasion.

Mots-clé: Vermont, Oligochaeta, Megascolecidae, *Amynthas agrestis*

RESUMEN

Las lombrices de tierra del género Amynthas Kinberg se han asociado con la horticultura, pero se informó recientemente de su presencia en ecosistemas forestales limitadas a diferentes parches. Poco se sabe acerca de si estas lombrices de tierra se extienden más allá del parche invadido originalmente. Se observó en 2013, una invasión en un parche de una población que tuvo éxito en un parche vecino. *Amynthas agrestis* fue la única especie en el parche original y se encontraron seis especies Lumbricidae en el parche recién invadido. La invasión puede haber sido provocada por las lluvias que al escurrir el agua podría haber arrastrado a *A. agrestis* o deslizarla por una suave pendiente a principios del verano de 2013. A pesar de que el parche recién invadido tenía hasta la mitad de la abundancia de individuos del parche original, la invasión fracasó. En el año los juveniles invasores no desarrollaron hasta adultos y en octubre de 2013, la población en el parche recién invadido había colapsado. En el siguiente año *A. agrestis* estaba ausente en el parche recién invadido, pero la abundancia en el parche original llegó a 200 individuos m^{-2} en julio de 2014. La causa del colapso de la nueva población no se conoce. Especulativamente, la diversidad de lombrices de tierra, la presencia de parásitos en los adultos y la depredación de los individuos más pequeños pudo haber causado el fracaso de la invasión.

Palabras clave: Vermont, Oligochaeta, Megascolecidae, *Amynthas agrestis*

INTRODUCTION

Until recently, earthworms in the genus *Amynthas* Kinberg were reported in New England mainly from horticultural installations (Reynolds, 2010). However, they now occur in gardens and in the wild (Reynolds, 2012; Görres and Melnichuk, 2012) where they have the potential to damage native woodlands as reported for other earthworms (Hale *et al.*, 2006). Others have also reported *A.* spp. from woodlands in the Southern Appalachians (Callaham *et al.*, 2003; Snyder *et al.*, 2009) and from New York State (Burtelow *et al.*, 1998; Bernard *et al.*, 2009). In most of these cases *A.* spp. occurred in confined patches. We have been following the annual growth of a population of *A. agrestis* (Goto and Hatai, 1899) that had been limited to a woodland patch in the Champlain Valley of Vermont for at least 6 years prior to the investigation. In 2013, the patch expanded unexpectedly. We took this opportunity to compare the development of the populations in the original and the newly colonized patches.

We wondered about the expansion of *A. agrestis* patches and whether the population in the newly invaded patch would persist given the relative stability of the spatial extent of the original patch. While there is research on the effect of expansion of Lumbricidae species in northern North American woodlands (Hale *et al.*, 2005), there is little known about the spatial dynamics of *A.* spp. when they migrate beyond invasion foci. There is some evidence that they migrate in response to temperature and moisture gradients. For example the spatial extent of *A. agrestis* in a patch in the Great Smoky Mountain National Park was dynamic, expanding during wet years and being confined to wetter areas during dry conditions (Snyder *et al.* 2011).

METHODS

We tracked a population of *A. agrestis* in a mixed deciduous forest stand dominated by sugar maple (*Acer saccharum,* Marshall). The site was at the Horticultural Research Center of the University of Vermont (44° 25' 53" N, 73° 11' 58" W) in South Burlington. But it had been limited to a patch approximately 60 m by 30 m where it was the only earthworm species. In 2013, we found that the patch had expanded to approximately twice its original width between mid-June and the end of July. Several shallow channels connected the original patch with the newly invaded area. The newly invaded patch was on the same soil and had the same vegetation. Although the soil in the stand was mapped as a Duane-Deerfield series it was more like an excessively drained Windsor series (mixed, mesic Typic Udipsamments) on a 2-3% slope.

A similar expansion was observed during the same period for a patch of *A. agrestis* in Huntington, Vermont (44° 20' 38" N, 72° 59' 38" W). No information was available about how long this population had been present there. This population was in an oak-maple (*Quercus-Acer*) woodland on terraces of soils that were mapped as a Groton fine sandy loam (Typic Eutrochrepts) on a 30-60% slope but *A. agrestis* probably originated in some cultivated beds further upslope. The newly invaded patch was on a Munson-Raynham silt loam (Aeric Haplaquepts) on a 6 to 12% slope that was grading into a wetland with emergent vegetation. The forest there was dominated by white pine (*Pinus strobus*) with an admixture of 40% deciduous trees. Here the two areas were connected by a path leading down the steep slope.

We concentrated our quantitative sampling on the site in South Burlington. The original patch, OP, and the newly invaded patch, NIP, were sampled on July 31st, August 12th, August 2nd, September 6th, and October 16th, 2013. We also sampled throughout the season in 2014 (data not shown). We hand-sorted earthworms from litter and soil taken from five 50 cm × 50 cm quadrats. Each quadrat was sampled only once with quadrats being separated by at least 5 m apart from any previously excavated quadrats. We found *A. agrestis,* an epi-endogeic species, to a depth of 5 cm. For this study we examined the top 20 cm of soil to make sure that we did not miss any individuals that might have migrated to lower depths when temperature and moisture conditions at the surface were unfavourable. When soils showed disturbance at 20 cm depth we excavated soils to 30 cm. We classified individuals of *A. agrestis* into juveniles and adults by the presence or absence of a clitellum. The earthworms were returned to the quadrats post data collection. We also noted the presence of other species.

Weather records were taken from the NOAA weather station at Burlington International Airport, South Burlington, Vermont. This station is 5 km from the South Burlington site and 18 km from the Huntington site. Soil temperatures in 2014 were recorded by a thermochron iButtons (MaximIntegrated, San Jose, California).

Two-way ANOVA was carried out separately for adult, juvenile and total abundance for the South Burlington plots (JMP, SAS-Institute, Cary, North Carolina, USA). Effect factors were sampling date and patch, *i.e.*, OP and NIP. When ANOVA showed differences t-tests were conducted. We used a significance level of 5% to infer differences.

RESULTS

In the OP patch, *A. agrestis* was the sole species present. In the NIP, six species other than *A. agrestis* were found in 2013: *Apporectodea tuberculata, Apporectodea rosea, Dendrobaena octaedra, Lumbricus rubellus, Lumbricus terrestris*, and *Octolasion cyaneum*. These species were still present in the NIP in 2014. However, *A. agrestis* was absent from NIP in 2014. In Huntington *A. agrestis* was the only species at the upslope, originally invaded site. The downslope site was inhabited by *Apporectodea tuberculata, Apporectodea rosea, Apporectodea turgida, Dendrobaena octaedra, Lumbricus rubellus, Lumbricus terrestris*, and *Octolasion cyaneum* prior to invasion by *A. agrestis.* To our knowledge, these are the first reports of *O. cyaneum* in Vermont as it was absent from the survey by Reynolds (2010).

A. agrestis was absent from the NIP site on June 17, 2013 when we carried out routine maintenance of equipment and earthworm surveys in this stand. The first *A. agrestis* at NIP was observed on July 16th, 2013, when we recorded its presence, but not its abundance, as part of an earthworm survey study.

Two-way ANOVA determined that there were differences among abundances in time and location in South Burlington ($F = 22.4, 39.4, 9.89$ with corresponding p values $< 0.0001, 0.0001, 0.0001$ for total, juvenile and adult abundances, respectively) in 2013. The comparison with 2014 abundance data was trivial as there were no *A. agrestis* found at NIP in 2014. However, at OP this species was present in 2014 with total abundance reaching 200 m^{-1} in June 2014. The first adults in 2014 were observed in early August about a month later than in previous years. Adult abundances were still very low at 7 individuals m^{-1} in late August 2014 significantly lower than in previous years when adult abundances were as high as 80-120 m^{-2} in late August/early September (data not shown).

Figure 1 gives the time course of the total, juvenile and adult abundance of *A. agrestis* at NIP and OP in 2013. Total abundance in the OP area was significantly greater than in the NIP for all but one sampling date. After reaching a peak on August 12, 2013, total abundance declined at NIP. Most of that decline was due to a significant reduction of juveniles while adult abundances remained the same statistically over most of the sampling period. Between September and October, total abundance at NIP was greatly reduced. In contrast, at OP, total abundance remained the same through the end of August but declined slightly in September and more rapidly in October, probably due to frost (Görres *et al.*, 2014). Adult abundance steadily increased from July through August in both areas. At the same time juveniles declined. While total abundance at OP decreased by 30% of the August level in September, it remained the same from September into October when the NIP population crashed.

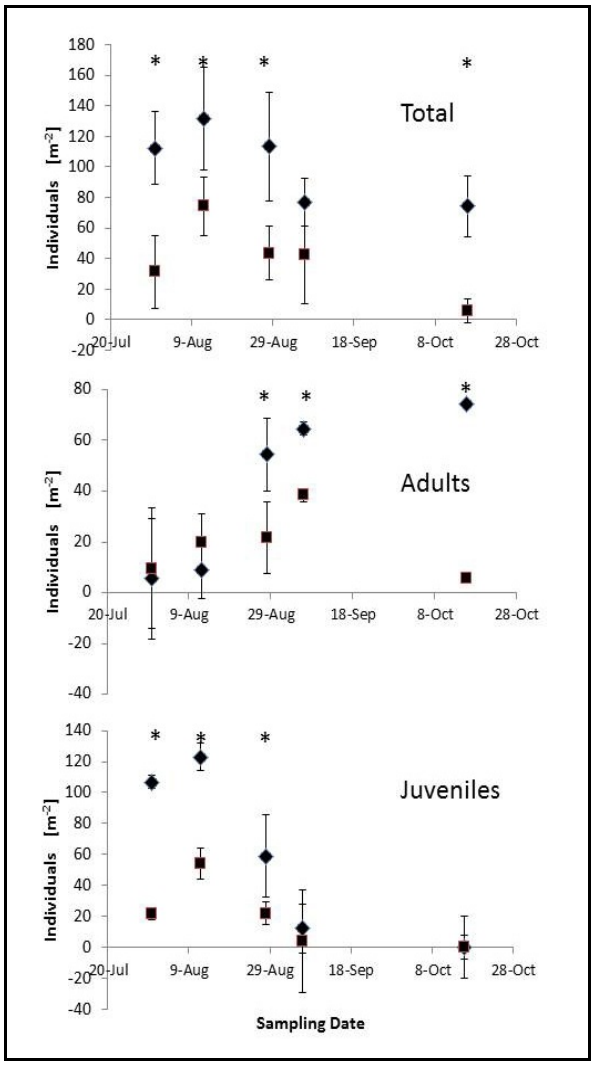

Figure 1. Total, adult and juvenile abundance of *A. agrestis* at an original (diamonds) and newly invaded patch (squares) at the Horticultural Research Center of the University of Vermont. Error bars give ± two standard errors. Error bars that do not overlap indicate that population means are different at the 5% level. Asterisks show significant difference for comparison between NIP and OP on the same sampling date.

DISCUSSION

We expected that the NIP population would persist as soil and vegetation conditions at OP and NIP were the same. We also expected that the competitive nature of *A. agrestis* would result in a reduction in Lumbricidae species at NIP. This did not happen. The earthworm species assemblies in Huntington and South Burlington were the same in 2014 as prior to invasion in 2013. No *A. agrestis* was detected in the NIP in 2014.

Our findings are consistent with the observations of others that at the stand scale, distributions of *Amynthas spp*. are patchy in northeastern US forests (Burtelow *et al.*, 1998). Reasons for this patchiness are not as well-understood as for variability at the regional scale, where several factors may contribute to spatial variation. For example, the notable absence of earthworms including *Amynthas* spp. from the Adirondack Mountains in New York State has been linked to the reduction in soil base saturation that was caused by acid deposition (Bernard *et al.*, 2009). The length of the growing season may also constrain this annual earthworm as it requires about 90 days to reach reproductive maturity (Görres and Melnichuk, 2012). At the patch scale, spatio-temporal variations of *A. agrestis* populations are thought to be driven by soil moisture and temperature gradients (Snyder *et al.*, 2011). Support for this also comes from laboratory studies that identified temperature and moisture ranges required for the survival of *A. agrestis* (Richardson *et al.*, 2009).

At the study site in South Burlington, *A. agrestis* migrated within a forest stand with apparent uniform microclimate, soil and vegetation. Yet, the migration did not result in a successful expansion of the original patch boundaries as *A. agrestis* was not present in the NIP a year after the migration. The migration event occurred sometime between mid-June and the end of July 2013 during or after the end of a very wet period in the Champlain Valley. From mid-May to mid-July, 2013, the NOAA weather station at Burlington Airport recorded 543 mm of rainfall. The greatest 24-hour storm during that period had a volume of 55 mm, just short of the 2-year, 24-hour storm for this part of Vermont. Yet the high antecedent soil moisture caused by the frequent rain events had likely generated several overland flow events, rare on this very sandy soil. At the end of July, this was evident from scouring marks, consistent with water flow, on the forest floor material especially within the shallow channels that connected the OP with the NIP. We speculate that the flow of water may have assisted in this migration. A similar expansion of a patch of *A. agrestis* was observed in Huntington, Vermont, 16 km from the South Burlington site. We did not quantify *A agrestis* abundances in Huntington. However, the area downslope from an existing *A. agrestis* population was free of *A. agrestis* in June 2013 when we surveyed the earthworm community. By the end of July 2013 this patch had a sizeable *A. agrestis* population. At Huntington the two patches were connected by a steep path that acted as a flow concentration with clear signs of overland flow after the wet period of May to July. On returning to the sites in 2014 the original *A. agrestis* populations had persisted but the down-slope population had vanished. Unlike the South Burlington sites, the Huntington sites differed considerably in both soils and vegetation. The landscape position near a wetland and the pine canopy may both have prevented a successful colonization of the patch. However, these factors alone may not explain the failure of *A. agrestis* to colonize this patch as a successful invasion of this earthworm had previously been reported on a floodplain soil with a canopy dominated by white pine (Görres and Melnichuk, 2012).

These migration patterns match those observed in Great Smoky Mountains National Park by Snyder *et al.* (2011) where a patch of *A. agrestis* expanded during wet conditions and contracted during dry conditions. What sets this study apart from Snyder *et al.* (2011) is that the migration at the South Burlington site occurred within a forest stand with uniform soils and no difference in drainage class.

A potential reason for the loss of the population at NIP was the exceptionally low soil temperatures which reached to -24° C during the winter of 2013/2014. However, these temperatures would also have affected the original populations. The population data suggests that factors other than the cold temperatures had caused the failure of *A. agrestis* to persist at NIP. The population at NIP began to decline in August 2013 seemingly affecting the juvenile population greatly. Very few juveniles appeared to become adults at NIP and the population had dropped to seven *A. agrestis* m^{-2} by mid-October down from 78 m^{-2} two months earlier. In contrast, at the OP, the decline began later in the year and most of the juveniles appeared to have grown into adults. By the end of October there were still 74 *A. agrestis* m^{-2} almost all of which were adults. Adverse conditions were probably already acting on the NIP population during the growing season of 2013.

At NIP adult abundance remained relatively constant over the sampling period while the number of juveniles steadily declined. Either the juveniles did not mature into adults or they did mature but the adults did not survive. Juveniles may be more susceptible to

predation by salamanders (Maerz *et al.*, 2005; Maerz *et al.*, 2009; Migge-Kleian *et al.*, 2006). Small adults that develop later in the season may also become prey for salamanders and subject to ectothermic cooling (Görres *et al.*, 2014). But, *A. agrestis* adults may also be affected by gregarine parasites (*Monocystis spp*.) which feed on sperm in the earthworm's seminal vesicles. Gregarine parasites have been found in other *A.* spp. (Bhowmik *et al.*, 2012; Bandyopadhyay *et al.*, 2006). In the Champlain Valley *L. terrestris* are ubiquitously infected with *Monocystis lumbrici*. But, gregarine parasites were also found in the seminal vesicles of several *A. agrestis* adults at the OP in 2014 but were absent from immature ones (Schall, pers. comm.). It should be noted that there is no evidence that these parasites affect mortality or fecundity. Infected *L. terrestris* for example exist at high densities at some sites in Vermont even when all adults are infected (Schall, pers. comm.) suggesting that the populations are not limited by the parasite.

CONCLUSION

This study shows that there are limits to the expansion of *A. agrestis* and that the migration of this organism from established sites does not always result in viable populations in newly colonized patches. Populations at the South Burlington sites developed very differently in a newly invaded patch and the original habitat patch during one growing season resulting in the demise of *A. agrestis* in the NIP while the population in the OP persisted. The mechanisms of this extinction remain elusive.

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Web Site for *Nomenclatura Oligochaetologica – Editio Secunda*
A catalogue of names, descriptions, and type specimens of the Oligochaeta:
http://wwx.inhs.illinois.edu/people/mjwetzel/nomenoligo