

Distribution and growth dynamics of invasive goldenrod (*Solidago canadensis*) in its introduced range in Estonia, and some Australian comparisons

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ABSTRACT

Understanding the distribution and population dynamics of invasive plant species is fundamental to our capacity to appropriately predict and manage plant invasions. The invasion biology of non-native *Solidago canadensis* in Estonia was investigated for the first time by assessing its distribution patterns and growth dynamics. First, fifty-two peri-urban populations were surveyed, and population location, size, adjacent communities, number of shoots as well as shoot height were recorded. Then, thirty genets were excavated from previously surveyed populations in order to analyze their age and growth traits in the vicinity of Tartu. The majority of *S. canadensis* populations were small, i.e. occupying less than 50 m², had 1 to 50 plants per population and were located predominantly on disturbed roadsides. The surveyed populations were young, with the average age of genets estimated to be five years at the time of sampling in 2006. We suggest that *S. canadensis* is well adapted to a wide range of habitats but predominantly occurs in human-disturbed habitats adjacent to settlements and roads. We found that *Solidago canadensis* genet age did not affect significantly its growth traits suggesting that growth traits are similar between younger and older genets.

KEYWORDS: Asteraceae, disturbance, invasive species, perennial, rhizome, vegetative growth

INTRODUCTION

Plant invasions pose a significant threat to the conservation of ecosystems worldwide and have major impacts on economics (Simberloff et al., 2013, Pimentel, 2011). With increasing globalization, plant species are currently being introduced to novel ecosystems at an unprecedented rate (Eschtruth and Battles, 2009). The impacts of human-mediated plant invasions have been well documented (Pyšek et al., 2012, Gaertner et al., 2009). For example, invasive species have been reported to directly alter ecosystem functioning and composition and indirectly affect nutrient dynamics, disturbance regimes and hydrologic cycles (Pimentel et al., 2005, Yelenik and D'Antonio, 2013, Mack and D'Antonio, 2003).

A number of studies indicate that there is a positive correlation between human introduction and plant invasive success (Donaldson et al., 2014, Gravuer et al., 2008). Although often careful in their introduction and cultivation (Dawson et al., 2008), botanical gardens have been recognized to play a central role in the spread of invasive plants (Hulme, 2015, Marco et al., 2010). For instance, Hulme (2011) found that 19 out of 34 of the world's worst invasive species were introduced and cultivated by botanical gardens. In Australia, Flax-

leaf Broom (*Genista linifolia*), a shrub to 3 m high and listed as a weed of national significance (WoNS) was first cultivated at the Adelaide Botanic Gardens (South Australia) in 1858 (Parsons and Cuthbertson, 1992) and is now naturalized in Western Australia as well. Similarly, Lantana (*Lantana camara*), also listed as WoNS and naturalized in Western Australia, earliest record for Australia is from 1941 in the old Botanic Gardens in Adelaide (DECC, 2011). Other WoNs are known garden escapees, e.g. Boneseed (*Chrysanthemoides monilifera* subsp. *monilifera*), Water Hyacinth (*Eichhornia crassipes*) and Madeira Vine (*Anredera cordifolia*), all present in Western Australia as well.

The focus of this study is *Solidago canadensis* s.l.l. (Canada goldenrod) which was introduced to Europe from North America as a garden ornamental in the 17th century (Weber 1998; Weber 2001) and is now widely distributed across Europe, Asia, Australia and New Zealand (Weber, 2001, Nolf et al., 2014). In Australia, earliest herbarium specimen recorded of *Solidago canadensis* dates back to 1935 (GBIF, 2013). *Solidago canadensis* is now naturalized or invasive in Queensland, New South Wales, Victoria, Tasmania and Western Australia (ALA, 2017). Although not all Atlas of Living Australia (ALA) *S. canadensis* records are accurate as some may have been misidentified and are actually *S. chillens* or *S. altissima* (A. Uesugi pers. observation).

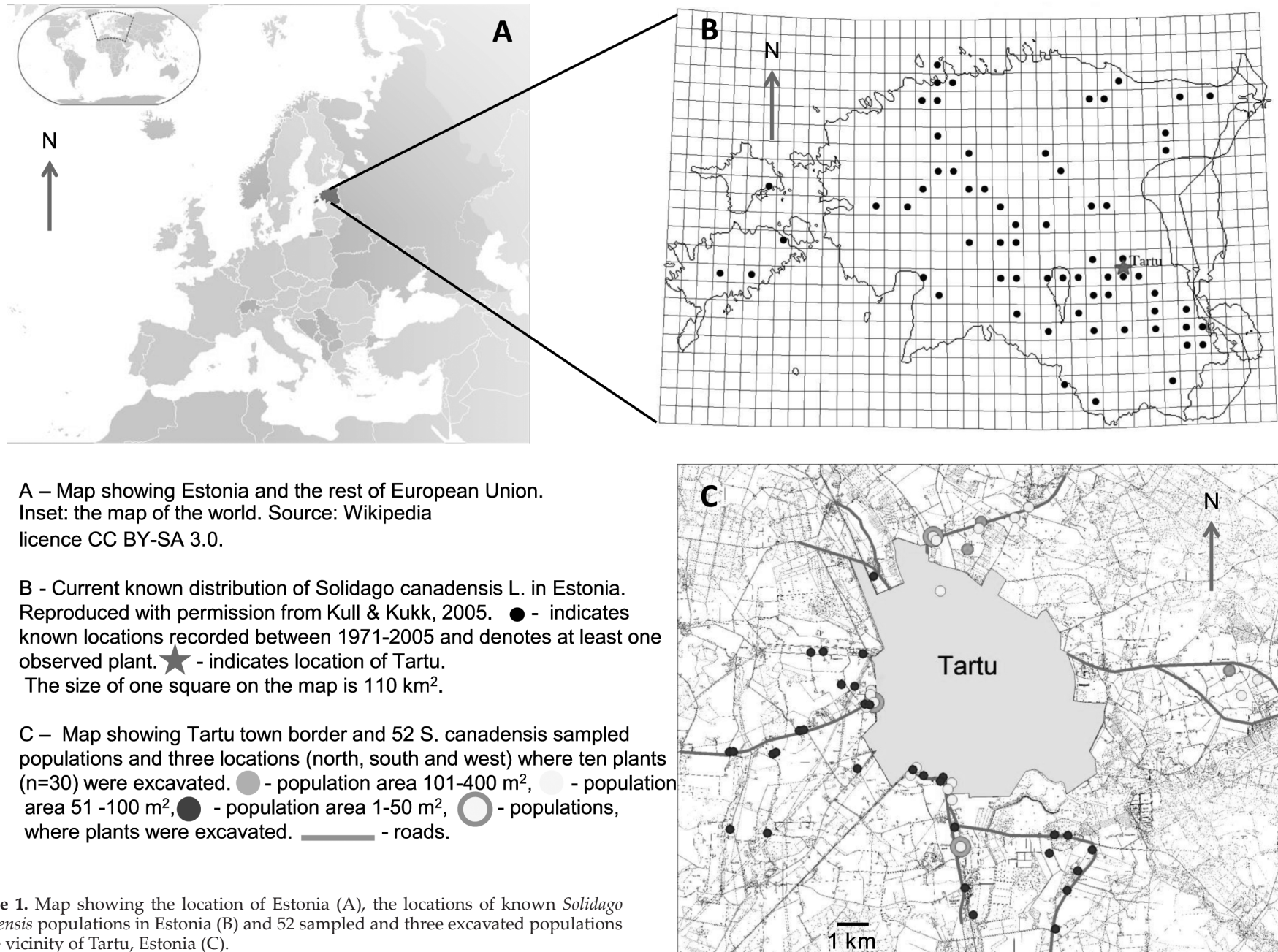


Figure 1. Map showing the location of Estonia (A), the locations of known *Solidago canadensis* populations in Estonia (B) and 52 sampled and three excavated populations in the vicinity of Tartu, Estonia (C).

The first record of *S. canadensis* in Estonia was from 1807 when it was cultivated in the Tartu University botanical garden (Kangur et al., 2005). As many other invasive or naturalized plants in Estonia, the present wild populations of *S. canadensis* in Estonia are most likely garden escapees (Kangur et al., 2005) (Fig. 1b). *Solidago canadensis* is considered an invasive or naturalised species in Estonia (Ööpik et al., 2013).

Solidago canadensis invades a wide range of habitats, e.g., semidry grasslands, riparian forests, lowlands, mountainous vegetation, abandoned fields, roadsides and pastures (Nolf et al., 2014, Dong et al., 2005). In its introduced ranges, *S. canadensis* has been reported to promote monocultures due its fast growth rates, prolific reproduction as well as strong allelopathic effects on native species (Dong et al., 2005). Allelopathy is the phytotoxicity of a compound or a group of compounds released from plant parts by leaching and root exudation to susceptible plants (Inderjit et al., 2006). The negative effects of allelopathic plants on co-occurring plants include reduction of seed germination and seedling growth (Hierro & Callaway, 2003). Overall, the invasion biology and environmental impacts of *S. canadensis* have been recently widely documented in its introduced ranges in Austria (Nolf et al., 2014), China (Guo et al., 2016, Tong et al., 2012), Germany (Schittko & Wurst, 2013), Latvia (Priede, 2008) and Poland (Szymura & Szymura, 2016). There are no published records of *S. canadensis* ecological impacts in Australia of which we are aware.

Although *S. canadensis* is widely recognized as one of the most widespread invasive species in Europe, there is little knowledge on its distribution and biology in Estonia. Until now, no comprehensive reports of its population biology in Estonia have been published. The objectives of this paper were thus to (i) investigate *S. canadensis* distribution in the vicinity of Tartu, Estonia, (ii) assess its vegetative and generative growth and (iii) estimate the age of *S. canadensis* genets in the vicinity of Tartu. The results are aimed to fill the gaps in the knowledge on the distribution and biology of the invasive *S. canadensis* in Estonia.

METHODS

Study species

Solidago canadensis L. (Asteraceae) is a rhizomatous, perennial, erect, herb with yellow flowers that can grow up to 2 meters tall (Werner et al., 1980). *Solidago canadensis* can reproduce sexually with obligatory outcrossing (Mulligan & Findlay, 1970) and asexually through rhizome propagation (Dong et al., 2006, Sun & He, 2010). Short-distance dispersal occurs mostly by rhizomes and *S. canadensis* can rapidly become a dominant plant in abandoned or disturbed old fields (Dong et al., 2006). Long-distance dispersal occurs by seeds, which can be disseminated by wind (Priede, 2008). The seeds are small and are produced in large numbers (an individual shoot can produce up to 10,000 seeds) with a long pappus which facilitates wind dispersion (Priede, 2008). Seed germination rate has been reported to be up to 80% in favorable conditions (Werner, 1979).

Habitat survey

Solidago canadensis populations were surveyed and mapped using a GPS device between the end of August and beginning of October (peak flowering season) in 2004, in the vicinity of Tartu, Estonia (58.3833° N, 26.7167° E) following a modified survey protocol from Holm (2004). All populations were visited once and surveyed by the same person. We excluded sections of the protocol that specifically targeted plant eradication. The surveyed populations were confined to the vicinity of south Tartu and proximity to the laboratories due to logistic reasons. A total of fifty-two discrete sites with *S. canadensis* plants (henceforth populations) was recorded (Fig. 1c). For each population the following details were visually estimated and recorded: 1) population location (e.g., roadside, garden, roadside and garden, none of the above/other); 2) adjacent communities (urban, forest, urban and forest, none of the above/other); 3) number of shoots counted (1–50; 51–100; 101–150; 151–200; > 200) in population; 4) population area (m²) visually estimated (< 50; 51–100; 101–400); 5) average height of plants (m) measured with a tape (< 1; 1–1.5; 1.5–2).

Clonal growth

In August of 2006, three random medium sized populations (i.e. 51–100 m²) from north, west and south of Tartu from the 52 previously surveyed populations were selected. From each population, ten genets were physically excavated and transported to the laboratory where their rhizomes were cleaned of soil residue. A genet is defined as a group of genetically identical individuals produced asexually in plants from a single ancestor. Only these genets were chosen for excavation for which we were able to excavate all rhizomes to avoid losing rhizome connections (e.g. rotted rhizomes) in older individuals which would lead to underestimation of the genet age. For each genet, we measured its radius and calculated its circumference (mm) using formula $2 \times \text{Radius} \times \pi$. We estimated its age by counting the annual rhizome increments. *Solidago canadensis* has a sympodial rhizome growth and in Estonia its shoots are annual. Thus, each sequential sympodial unit (see Bell & Tomlinson, 1980) of its rhizome (each rhizome branch) denotes one year of growth. Then we counted the number of all living shoots in each genet and the total number of inflorescences per individual shoot. Mean number of inflorescences/genet was used for the analyses. We counted the number of ramets (i.e. an independent member of a genet). We also measured the length (mm) of each shoot and length of its adjacent rhizome branch as well as the length of older rhizome branches (thus obtaining the annual clonal mobility of a genet, see Tamm et al. 2001; Sammul et al. 2004).

ANALYSIS

Distribution data were analyzed using chi-square goodness of fit test. We tested whether the location and population area affected the number of plants in a population and whether location affected population area. Clonal growth data were analyzed using one-way ANOVA and linear mixed model with genet age as a fixed factor and population was a random factor. Data were visually inspected for homogeneity and normality

assumptions of ANOVA. Residuals were inspected visually to check model assumptions. Data was Ln transformed when it did not meet these assumptions. Using linear mixed effects models we assessed in separate models whether genet age affected genet size (i.e. circumference), annual increment, number of shoots, height of shoots and number of inflorescences. Distribution data were analysed in SPSS v. 21 (SPSS IBM, USA). Clonal growth data were analysed and all figures were plotted in R programming language (version 3.2.2) (R Core Team, 2015).

RESULTS

Distribution

31 out of 52 *Solidago canadensis* populations in the vicinity of Tartu covered an area of less than 50 m² and only three populations had an area of greater than 100m² (Fig. 2a). 33 out of 52 populations had up to 50 individual shoots recorded per population (Fig. 2b). Majority of the plants surveyed were 1–1.5 m tall (Fig. 2c). The number of shoots in a population was similar across different population locations ($\chi^2 = 10.96$, d.f. = 12, $P =$

0.53), and population area was not affected by location ($\chi^2 = 10.93$, d.f. = 6, $P = 0.09$). The number of plants was positively related to population area ($\chi^2 = 60.03$, d.f. = 8, $P < 0.001$). 35 out of 52 populations were found growing along roadsides (Fig. 2d) and adjacent communities to *S. canadensis* populations included both urban areas and forest sites (Fig. 2e).

Clonal growth

The mean age of thirty excavated genets was 5.4 (± 0.3) years with mean circumference of 623.7 mm (± 37.1) (Fig. 3a). The number of ramets was similar for younger and older genets (Fig. 3b). Mean annual increment of a rhizome for all plants was 36.7 mm (± 2.0) (Fig. 3c). Mean number of shoots per genet was 11.2 (± 0.9) (Fig. 3d) with mean height of 1027 mm (± 31) (Fig. 3e) and mean number of inflorescences per shoot was 27.7 (± 1.5) (Fig. 3f). Overall, we found no effect of genet age on size (i.e. circumference), number of shoots and ramets, height of shoots, number of inflorescences and annual increment of a rhizome (Table 1). There were no significant differences between the three populations in the growth traits with an exception of annual increment of a rhizome, which was marginally different between populations ($F_{2,27} = 2.63$, $P = 0.09$).

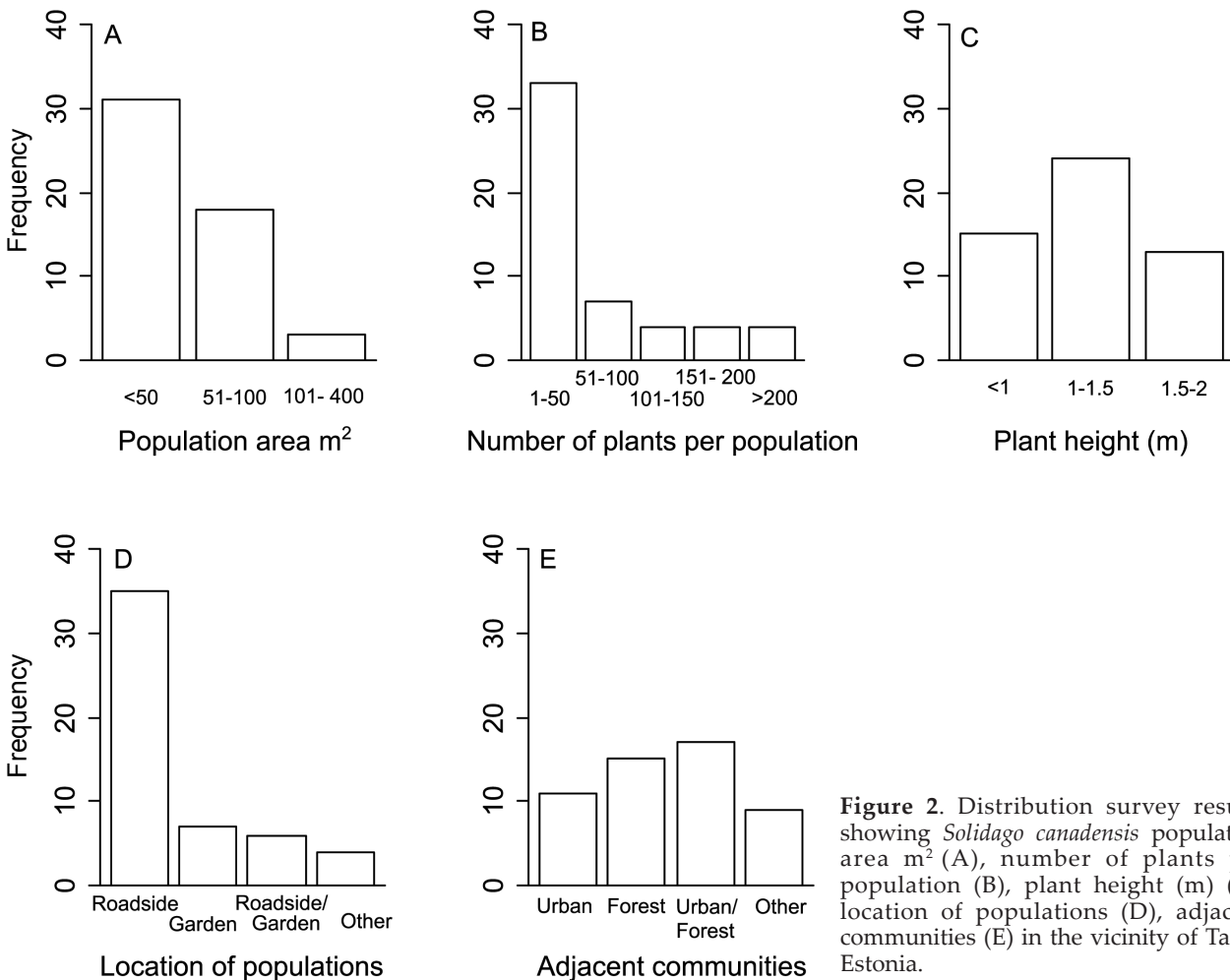


Figure 2. Distribution survey results showing *Solidago canadensis* population area m² (A), number of plants per population (B), plant height (m) (C), location of populations (D), adjacent communities (E) in the vicinity of Tartu, Estonia.

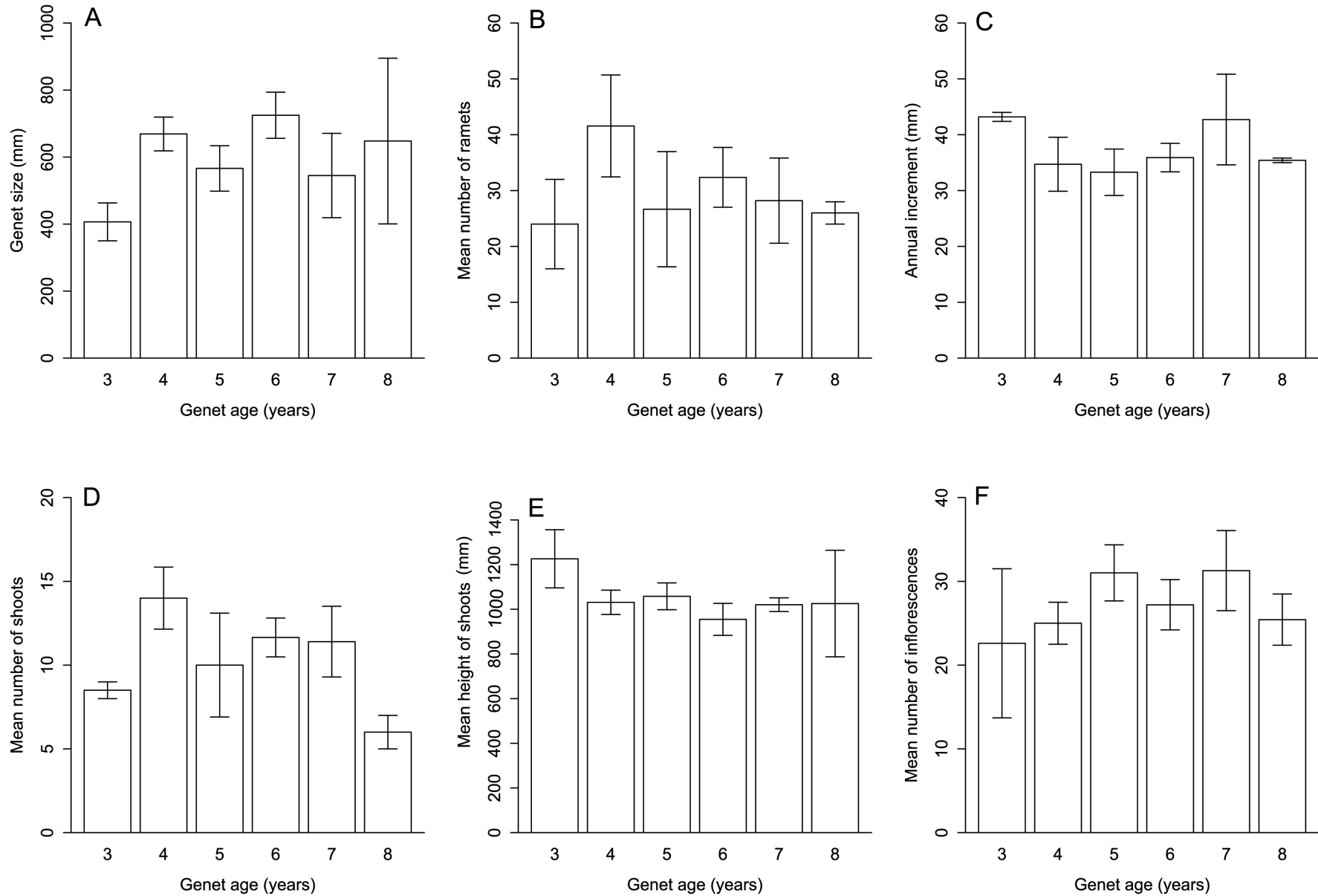


Figure 3. Histogram showing mean (\pm S.E.) genet size (mm) (A), number of ramets (B), annual rhizome increment (mm) (C), number of shoots (D), mean height of shoots (E) and the number of inflorescences (F) for 3 (n=2), 4 (n=7), 5 (n=6), 6 (n=8), 7 (n=5) and 8 (n=2) year old genets for thirty *Solidago canadensis* plants excavated in the vicinity of Tartu, Estonia.

Table 1

Summary of the linear mixed effects models showing the effect of genet age on *Solidago canadensis* clonal growth traits based on thirty excavated genets from the vicinity of Tartu, Estonia.

Parameter	Estimate	S.E.	t-value	P-value
Factor: Age				
Response variable				
Circumference (mm)	12.93	27.69	0.47	0.35
Annual increment (mm)	0.59	1.504	0.39	0.36
Number of shoots	-0.06	0.06	-1.13	0.21
Number of ramets	-0.06	0.08	-0.83	0.27
Height of shoots	-19.72	22.48	-0.87	0.26
Number of inflorescences	1.36	1.12	1.22	0.18

DISCUSSION

We found that *S. canadensis* occurred predominantly on roadsides and adjacent to urban areas (gardens) from where it plausibly could have escaped (Ööpik et al., 2008). This is in accordance with previous evidence on *S. canadensis* distribution patterns in non-native ranges in Europe (Kabuce & Priede, 2010, Priede, 2008) and in China (Guo et al., 2016). It is well established that invasive plants often colonize sites with high levels of disturbance, particularly roadsides that also serve as vectors of spread (Mortensen et al., 2009, Rentch et al., 2005). Disturbance increases resource availability such as light and soil nutrients (Lake & Leishman, 2004). Roadsides are often rich in nutrients such as phosphorus due to run off waters (Leishman, 1990) and some authors have found a positive correlation between increased levels of phosphorus and average vegetative mobility and rhizome branching of clonal plants (Sammul et al., 2003). This explains why clonal, invasive species like *S. canadensis* may thrive on disturbed sites such as nutrient rich roadsides. Studies in Australia have found similar results for invasive species that thrive in high nutrient soils, e.g. English Broom (*Cytisus scoparius*) in the Mt Lofty Ranges (Adelaide) (Fogarty & Facelli, 1999). A study conducted across twenty-four sites in northern Sydney across urban bushland and national parks found that the increase of many soil nutrients, rather than phosphorus alone, contributed to the invasion of exotics into the urban bushland (King & Buckney, 2002). In Western Australia, Hobbs & Atkins (1988) showed that invasives had increased growth in sites that experienced both, disturbance and fertilization, suggesting that introduced species respond to a combination of nutrient addition and soil disturbance in the Western Australian wheatbelt.

The number of *S. canadensis* plants was significantly affected by the population area. The majority of *S. canadensis* populations occupied on area of less than fifty square meters with up to fifty plants per population, which suggests that at the time of field census, i.e. in 2004, these populations were relatively young. This is further supported by our findings that the average age of genets from investigated populations was five years as estimated in 2006, which implies that these surveyed populations are likely to have started to expand around 2001 in the vicinity of Tartu, at least in the three

populations we studied. The rhizome increment values (i.e. 36.7 mm) were comparable to previous findings from early successional *S. canadensis* plants in Canada (i.e. rhizome increment values between 21–40 mm, Bradbury & Hofstra 1976).

Solidago canadensis is considered an exceptionally successful invader worldwide largely due to its prolific vegetative and generative growth that makes it a superior competitor over native species (Weber, 2001, Fenesi et al., 2015). This is particularly the case in open, low growing vegetation such as is found in many parts of Estonia. A study in China emphasized the importance of establishment opportunities as there was limited invasion of the species in the surrounds of the focal point of infection from Lushan Botanical Garden isolated on a mountain within dense forest, while there was extensive invasion from Wuhan Botanical Garden in a more open alluvial landscape (Guo et al. 2016). In Australia, *S. canadensis* has been recorded as far north as Roebourne, Western Australia's Pilbara region and in southern parts of Tasmania, suggesting that this species can occupy a broad ecological niche with diverse climates (ALA, 2017). *Solidago canadensis* is comparable to some introduced species in Australia that reproduce both by seed and vegetatively from rhizomes, e.g. Asparagus Fern (*Asparagus aethiopicus*), although *S. canadensis* is not as prolific. Although sporadically present across almost all states and territories in Australia, *S. canadensis* has nevertheless not become as abundant as in Central Europe possibly due to naturally low soil nutrient levels in Australian, and especially Western Australian soils as it spreads predominantly along roadsides and waste places that are rich in nutrient runoff.

In conclusion, our results support findings from earlier studies that showed *S. canadensis* occurs predominantly along disturbed roadsides. A more comprehensive across-Estonia survey and mapping of this species' distribution may be needed in the future to accurately assess its potential current and future impacts on natural ecosystems in Estonia. Our study paves the way for future research about the population biology of *S. canadensis* in Estonia and contributes to improved understanding of this species' biology in its introduced ranges.

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