



Can native grass species outcompete invasive goldenrods? Results of a replacement series experiment

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Summary

Invasion by alien species is a serious threat to the biodiversity and function of semi-natural grasslands and may impede restoration efforts in degraded meadows due to high competitiveness. Goldenrods (*Solidago* and *Euthamia* species) are considered among the most injurious invaders of grasslands in Central Europe. We tested the hypothesis that native grass species are able to outcompete the invasive goldenrods. A replacement series experiment was established to determine levels of interference between native grass taxa and goldenrods. In the experiment, four alien goldenrod species (*Solidago altissima*,

Solidago canadensis, *Solidago gigantea* and *Euthamia graminifolia*) and one native species (*Solidago virgaurea*) were studied. The native grasses were represented by *Lolium perenne* (forage and turf varieties) and *Festuca pratensis* (forage variety). Total biomass was higher in the mixture of species compared with that in monoculture. The higher total biomass was due to higher productivity of the goldenrod species, whereas that of the grasses was reduced. These results demonstrated the high competitiveness of alien goldenrods compared with native grass species.

Keywords: competition, biological invasions, replacement series experiment, grassland restoration.

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Introduction

Invasive species impact the functions and services provided by infested habitats and alter the composition and diversity of above- and below-ground organisms (Gioria & Osborne, 2014). Biological invasion by alien species is a serious environmental problem and has therefore been studied extensively (Holzmueller & Jose, 2009; Follak *et al.*, 2017). These studies have considered two basic questions: which traits enable species to invade new habitats (invasiveness) and which

characteristics of the habitats make them susceptible to invasion (invasibility). However, the factors that enable alien species to dominate the ecosystem in the new range are not fully understood (Thomson *et al.*, 2016).

Different hypotheses explain the mechanisms that allow alien species to invade new habitats (for review, see Holzmueller & Jose, 2009). The success of alien species is often associated with their competitiveness (Vilà & Weiner, 2004; Bottollier-Curtet *et al.*, 2013; Gioria & Osborne, 2014; Thomson *et al.*, 2016). The results of experiments where dominant native species

were compared with invasive species revealed the competitive superiority of invasive plants, at least in early life stages (Bottollier-Curtet *et al.*, 2013; Fenesi *et al.*, 2015a). Studies investigating the control of invasive species suggest that competition can occasionally reduce invasive plant growth more than other factors, such as herbivory (Vilà & Weiner, 2004). The process of competition also affects invasive species, as native vegetation can be resistant to invasion by competitive exclusion of the alien species (biotic resistant hypothesis) (Mangla *et al.*, 2011; Gioria & Osborne, 2014). Plants use different organs to compete above-ground for space and light and below-ground for nutrients, water and space (Casper & Jackson, 1997). Numerous studies have investigated above-ground competition (Gioria & Osborne, 2014), whereas below-ground competition studies are relatively rare (e.g. Kueffer *et al.*, 2007). Nevertheless, below-ground competition may be stronger and involve more neighbours than above-ground competition (Casper & Jackson, 1997).

Perennial grasslands offer many ecological and agronomical services, such as forage production, maintenance of biodiversity and carbon sequestration. More than 90% of semi-natural grasslands in Europe have been lost in the last 100 years due to intensified production, abandonment or afforestation (EEA, 2016). Many grassland species have declined or become extinct (Habel *et al.*, 2013). As a result, many semi-natural grasslands in the pan-European Nature 2000 network are now protected. Moreover, many grassland areas in Europe have been devastated by improper management, for example by drainage, over-fertilisation, excessive usage and/or introduction of inappropriate species, as well as by alien plant invasions (Török *et al.*, 2011). On the other hand, extensive areas of formerly arable lands have been abandoned in several regions of the world over the last few decades (Török *et al.*, 2011; Fenesi *et al.*, 2015b). This scenario provides an opportunity to re-wild these areas into open grasslands, which would benefit biodiversity and the human population (Navarro & Pereira, 2012). Degraded grasslands, as well as abandoned arable land, can be restored both by technical interventions and by using natural succession (Prach & Hobbs, 2008). However, spontaneous succession of former arable fields can be altered by invasion of alien species, making it impossible to develop species-rich grasslands (Fenesi *et al.*, 2015b). Competition, including the effect of invasive species, can also diminish the success of restoration of degraded meadows (Bartha *et al.*, 2014; Heckman *et al.*, 2017). Fast growing clonal species often monopolise resources and exclude other species. Thus, knowledge about intra- and interspecific competition of invasive and native plants is necessary for

appropriate grassland restoration. The optimal combination of desired plants, sowing density and proportion of species in a seed mixture must be determined to improve restoration success (Mangla *et al.*, 2011). However, restoration is only a first step in the long process of reconstructing a grassland (Bischoff, 2002), as further appropriate management is important.

Goldenrod taxa have a strong negative impact on grassland habitats (Hejda *et al.*, 2009; Bartha *et al.*, 2014). According to the European database of invasive plant species (Nobanis; Daise), goldenrods are exceptionally successful invaders throughout Europe. Goldenrods have negative impacts by decreasing biodiversity of vascular plant species in infested ecosystems (Hejda *et al.*, 2009) and hampering spontaneous succession of woody vegetation (Bornkamm, 2007). These effects are particularly pronounced when comparing invaded and uninvaded grasslands. Grasslands invaded by goldenrods support a smaller number of birds and breeding pairs (Skórka *et al.*, 2010), and the number and diversity of wild pollinators are lower (Fenesi *et al.*, 2015b). The inflorescences of goldenrods are attractive to insects; therefore, the number of visits to native flowers by pollinators decreases (Fenesi *et al.*, 2015b). Their effect on grasslands is related to its strong competitiveness (Weber, 2001; Fenesi *et al.*, 2015a). The invasive *Solidago* species (*Solidago altissima* L. (late goldenrod), *Solidago canadensis* L. (Canada goldenrod) and *Solidago gigantea* Aiton (tall goldenrod)) have similar competitive abilities and can outcompete native herbs (*Solidago virgaurea* L. (European goldenrod) and *Tanacetum vulgare* L. (common tansy)). Invasive species produce substantially (two to five times) more biomass than that of native species, suggesting that they better utilise the available resources (Szymura & Szymura, 2016). Their competitiveness is also related to prolific vegetative growth (Weber, 2001). As a result, goldenrods have a strong suppressive effect on regeneration of early established grasslands (Bartha *et al.*, 2014).

The aim of this study was to characterise the interactions between alien goldenrods and selected native grass species: *Festuca pratensis* Huds. (meadow fescue) and *Lolium perenne* L. (perennial ryegrass). Additionally, we compared growth of the grasses with a European native goldenrod species (*S. virgaurea*). *Festuca pratensis* and *L. perenne* are important components of permanent species-rich pastures and hay meadows because of their high productivity, very good nutritive value, high palatability and grazing tolerance (Sampoux *et al.*, 2011; Ergon *et al.*, 2016). Seed mixtures containing both species (*L. perenne* as short, grazing-tolerant species and *F. pratensis* as high grass) are suitable for alternately used (for hay and grazing)

grasslands (Sampoux *et al.*, 2011). The turf forms of *L. perenne* are commonly used on intensively trampled sites and slopes for ground stabilisation, as well as in ornamental and amenity areas (e.g. lawns and sports areas) (Turgeon, 2010). Alien goldenrod species (Asteraceae family) are perennial herbs with rhizomes. They often form large long-lasting single species stands in a new range. Among the invasive species, the range of *Euthamia graminifolia* (L.) Nutt is small and limited to a few locations (Weber, 2001), while three other introduced taxa (*S. gigantea*, *S. canadensis* and *S. altissima*) are expansive and widespread. The native goldenrod, however, is considered as a stable component of permanent grasslands and open forests without the tendency to expand (Kiełtyk & Mirek, 2014).

Based on the results of previous studies investigating interactions between grasses and alien *Solidago* species (Walck *et al.*, 1999; Rebele, 2000; Fenesi *et al.*, 2015a), we hypothesised that species growing in mixture will strongly compete with each other. However, the results of this interaction are not clear. Two detailed questions were posed in this study: (i) How does total biomass production differ between a monoculture and a mixture of species? And (ii) how does interspecific competition affect production and allocation of biomass in particular species?

Materials and methods

Species studied

In the experiment, four alien (*Solidago altissima*, *S. canadensis*, *S. gigantea* and *E. graminifolia*) and one native (*Solidago virgaurea*) goldenrod species were studied. The native grasses were represented by *L. perenne* and *Festuca pratensis*. Two types of *L. perenne* were used: forage (Temprano variety; *Lpp*) and turf (Talga variety; *Lpg*). *Festuca pratensis* was used as a forage type (Liherold variety; *Fpp*).

Experimental design

A replacement series experiment was performed. The seeds of goldenrods were collected from populations near Wrocław, Poland, Central Europe (51°6'54N, 17°7'42E). The seeds were stored frozen over the winter in an unheated room. The seeds of the grasses were obtained from the Plant Breeding and Acclimatisation Institute, which provides seeds for agriculture and greenery in Poland.

The experiment was conducted at the experimental station of the Wrocław University of Life and Environmental Sciences. The station is situated in Wrocław at an altitude of 115 m a.s.l. Mean annual temperature was 9.0°C (18.8°C in July and −0.4°C in January), and

mean annual precipitation was 583 mm, with a maximum during July–August. The growing season lasted 226 days. The most common wind directions were westerly and northerly.

Twelve plants per pot were cultivated in different combinations: 3x:9y (x and y denote two different taxa), 6x:6y, 9x:3y as well as monocultures of 12x and 12y. Each combination was planted in four replications. The experiment consisted of 212 pots in total (eight species planted in monocultures + three different combinations of mixtures of three grass taxa with five goldenrod species).

The seeds of grasses and juvenile goldenrod species were planted in plastic pots (22 cm in diameter and 25 cm deep) in April. Preliminary analysis of seed germination indicated that the grass species germinated very well, whereas the percentage germination of goldenrod species was approximately 50%. To accommodate the variation in germination between the taxa, goldenrod seeds were germinated in containers and transplanted as juveniles (three to five leaves). The seeds of grass species were sown at the same time as seeds of goldenrods. The seedlings were planted around the circumference of the pot, forming a single ring of equally spaced plants. The size of the pots and species proportions were selected based on previous studies (Walck *et al.*, 1999; Szymura & Szymura, 2016). The pots were placed outside at ground level, in full sunlight, and were filled with local soil (Anthropic Regosol; loamy sand texture, pH in KCl 4.6–6.0; mean concentrations of N, P₂O₅ and K₂O were 700, 410.0 and 157 mg kg^{−1} respectively). Weeds were removed manually. Manual irrigation (if necessary) was applied during the growing season. The pots were covered during winter to protect against freezing, and no fertiliser was applied. Individuals in mixtures of different species were planted as every other or every fourth plant, depending on the ratio of the combination. The within-species combination pots were arranged randomly and were placed approximately 0.75 m from each other to reduce the effect of shadowing by plants from neighbouring pots; the plants were grown for 4 years. The decayed ramets at the end of growing season were cut and removed during first years of experiment. In the last, fourth year, the plants were excavated for biomass analysis in October. The harvested plants were gently rinsed in water, divided into above- and below-ground parts, dried and weighed.

Data analysis

The following parameters were calculated: total relative yield ($RYT = RY_i + RY_j$) and relative yield of each species ($RY_i = Y_{ij}/Y_{ii}$), where Y_{ij} is yield of

species i when grown with species j and Y_{ii} is the mean yield of species i when grown in monoculture; RYT is RY_i of the monocultures. The proportion of RY_i for the above- to below-ground parts was calculated to assess biomass allocation. The RYT and RY values in a given species proportion were compared with the expected values and calculated based on the initial proportions, which were 1 (monoculture of 12 plants), 0.75 (9:3 mixture), 0.5 (6:6 mixture) and 0.25 (3:9 mixture). The replacement series diagrams show the RY value of a given species (RY_i) and the RYT value (RYT) as a function of the species proportion. The expected yield trends show the predicted values of RYT and RY, which were calculated based on the species proportion.

The relative increase or decrease in the biomass of a particular species growing in the mixture in relation to that expected based on the species proportion was expressed as the 'aggressivity index', which was calculated for a particular species as follows: $A_i = RY_i / (p - RY_j / q)$, where p and q are the proportions of species i and j , respectively, in the mixture ($p + q = 1$) (Walck *et al.*, 1999). This is a simple and general index that shows which species has gained or lost in a mixture.

The biomass per plant was also calculated, as the yield of a given species divided by the number of introduced individuals (seeds or seedlings) at the beginning of experiment. The differences between species in terms of biomass production and allocation were detected using the Kruskal–Wallis one-way analysis of variance by ranks. Multiple comparisons of medians with the Bonferroni correction were used as the post hoc test. Differences between the observed and expected RYT and RY values were identified using the Mann–Whitney U -test with Monte Carlo permutations to estimate the P level. The same method was used to detect differences in the RY_i proportions, allocated to the above- and below-ground parts between the monoculture and a given mixture, as well as to verify the differences in aggressivity index values between taxa. The computations were performed using the library 'coin' in R package and Statistica ver. 10 software.

Results

Growth of species in monocultures

All alien goldenrods produced two- to threefold more biomass than that of native *S. virgaurea* and the tested grass species (Table 1). *Solidago virgaurea* and *Lpp* had the highest biomass investment in above-ground parts. *Festuca pratensis* invested more biomass in above-ground parts than that of *Lpg*, which biomass

ratio did not differ significantly from that of *S. gigantea* and *S. canadensis*. *Euthamia graminifolia* and *S. altissima* invested the highest proportion of biomass in under-ground parts, compared with the remaining species (Table 1).

Influence of competition on biomass

The raw biomass production of species growing in different species mixtures is presented in Table S1. In the mixtures of grasses with invasive goldenrod species, the goldenrods account for the majority of the total biomass (Supporting Information Table S1). Biomass production divided by the number of initially introduced individuals is shown in Figure S1. Generally, the biomass production of invasive goldenrods decreased as the number of initially planted seedlings increased, while in case of grasses, the biomass increased. The exception was native species, *S. virgaurea*, and the grasses growing with it, where this trend was not observed, and biomass was more or less stable or has varied in rather erratic manner (Supporting Information Figure S1).

Effect of plant interactions on total productivity of the mixtures (RYT)

The RYT values generally increased when alien goldenrods were growing with grass taxa (Figs 1A–D, 2A–C and 3A,C,D), whereas the RYT did not differ from expected (Fig. 1E) or even decreased in cases of grass mixtures with native *S. virgaurea* (Figs 2E and 3E).

Table 1 Mean \pm standard deviation of total dry biomass (biomass), above- to below-ground dry biomass ratio (A/B) and results of statistical tests (H, p) for plants growing in monocultures

| Taxon | Biomass (d.w.g.) | A/B |
|--------------|---------------------------------|--------------------------------|
| <i>Fpp</i> | 24.7 ^c \pm 3.86 | 0.83 ^{a,b} \pm 0.22 |
| <i>Lpg</i> | 28.95 ^c \pm 6.83 | 0.59 ^{b,c} \pm 0.24 |
| <i>Lpp</i> | 26.7 ^c \pm 12.09 | 1.32 ^a \pm 1.10 |
| <i>Salt</i> | 57.8 ^b \pm 11.50 | 0.37 ^{d,e} \pm 0.11 |
| <i>Scan</i> | 78.0 ^{a,b} \pm 22.90 | 0.56 ^{c,d} \pm 0.36 |
| <i>Sgig</i> | 63.3 ^{a,b} \pm 6.30 | 0.51 ^c \pm 0.08 |
| <i>Egram</i> | 90.1 ^a \pm 41.20 | 0.30 ^e \pm 0.02 |
| <i>Svirg</i> | 29.6 ^c \pm 18.20 | 1.13 ^a \pm 0.60 |
| <i>H</i> | 40.23 | 40.25 |
| <i>p</i> | 0.000 | 0.000 |

Festuca pratensis – *Fpp*, turf type of *Lolium perenne* – *Lpg*, forage type of *Lolium perenne* – *Lpp*, *Solidago altissima* – *Salt*, *Solidago canadensis* – *Scan*, *Solidago gigantea* – *Sgig*, *S. virgaurea* – *Svirg*, *Euthamia graminifolia* – *Egram*.

Different uppercase letters denote a significant difference in mean values between species regarding a particular trait.

Effect of a mixture on relative species productivity (RY) and the aggressivity index

The RY value of alien goldenrods was generally higher in mixtures, whereas all grass taxa had lower than expected RY values (Figs 1A–D, 2A–D and 3A–D). The RY value of *S. virgaurea* in mixtures with grasses generally did not differ from expected, similar to the RY of the grass taxa (Figs 1E and 2E), except *Lpp*, where the RY of *S. virgaurea* was lower (Fig. 3E) than expected. Details of the test results are presented in Table S2.

The aggressivity index showed that all grass taxa had lower competitive ability than that of the goldenrod species, including native *S. virgaurea* (Table 2). Among the grasses, *Lpg* had the relatively highest aggressivity index value.

Biomass allocation

Solidago species, when growing in mixtures, generally invested more energy in producing above-ground parts than in monocultures (Figs 4A–C, 5A–C and 6A–C, Table S3) or did not differ significantly. The exception was *E. graminifolia*, which only sporadically invested more biomass in above-ground parts compared to the monocultures (Figs 4D and 5D), and *S. virgaurea* and grass taxa growing with it in mixtures usually lacked differences (Figs 3E, 4E and 5E). Details of the test results are presented in Table S3.

Discussion

The results showed that RYT increased when intraspecific competition was stronger than interspecific competition and decreased when interspecific competition was strongest. As a consequence of these interactions, the biomass of particular examined species could be relatively higher, lower or remained unchanged. The relative biomass changes in mixtures, expressed as A_i of particular species, indicated that species gain or lose biomass as a result of the interaction (Walck *et al.*, 1999; Jolliffe, 2000). When resources are limited, the intraspecific competition should be stronger than interspecific competition, because plants belonging to the same species have the same resource requirements (Goldberg & Barton, 1992; Ren & Zhang, 2009). The results demonstrated that the yield of a mixture can exceed the yield of monocultures. In practice, mixtures of grass species are used in grassland management because they produce higher yield than monocultures (Ergon *et al.*, 2016). This effect was particularly pronounced in our experiment, as the yield of the mixture increased a few folds compared with that of the

monocultures. In our experiment, the higher RYT of the mixtures likely resulted from reduced intraspecific competition of alien goldenrods for space. As grasses are relatively small, there was more free space for alien goldenrods to exploit compared with the monoculture. Another explanation is that different species utilise different resources, such as nutrients or water (Vilà & Weiner, 2004), which seems to be less probable, as the goldenrods produced most of the biomass (Supporting Information Table S1), and the biomass of grasses was strongly reduced. Therefore, the grasses could not efficiently exploit the resources. The increase in yield in mixtures is expected, but its magnitude was quite surprising. Similar effects were observed in a previous study when alien goldenrods were grown with the native perennial herbs *S. virgaurea* and *T. vulgare*, but the differences in biomass production were not as high (Szymura & Szymura, 2016) as found in this study. Perhaps further experiments are necessary to explain this effect better. Previous studies (see Vilà *et al.*, 2011 for meta-analysis) show that invasive alien plants could increase biomass production of the invaded community and this increase would be caused exclusively by alien, highly productive species (Vilà *et al.*, 2011). The negative impact of alien goldenrods on grassland communities is widely recognised (Hejda *et al.*, 2009; Skórka *et al.*, 2010; Fenési *et al.*, 2015b). It may be assumed that it is caused by the ability of the alien goldenrods to better exploit the available resources.

The grasses were outcompeted in mixtures with the alien goldenrods, as demonstrated by the higher biomass production by the alien goldenrods compared with grasses and native *S. virgaurea*. The alien goldenrods outcompeted the grasses in our experiment where disturbances causing loss of biomass, such as mowing and grazing, were excluded. The occurrence of semi-natural grasslands in Central Europe depends on human-caused disturbances, such as mowing, grazing or burning. A disturbance restricts the biomass production of late-successional plants, giving an advantage to grasses (Bartha *et al.*, 2014). Unfortunately, invasive goldenrods are quite resistant to moderate disturbances. It is known that burning reduces the shoot number of *S. canadensis*; however, it does not decrease its competitive superiority in relation to the native grass species *Elymus repens* (L.) Gould and *Brachypodium pinnatum* L. (Fenési *et al.*, 2015a). A single cut per year of a sward does not significantly reduce *Solidago* spp. shoot density, whereas sporadic cutting might even have the reverse effect by increasing the population density the following year (Weber & Jakobs, 2005). The most effective method for preventing alien plant invasion into grasslands is proper management, chosen according to environmental

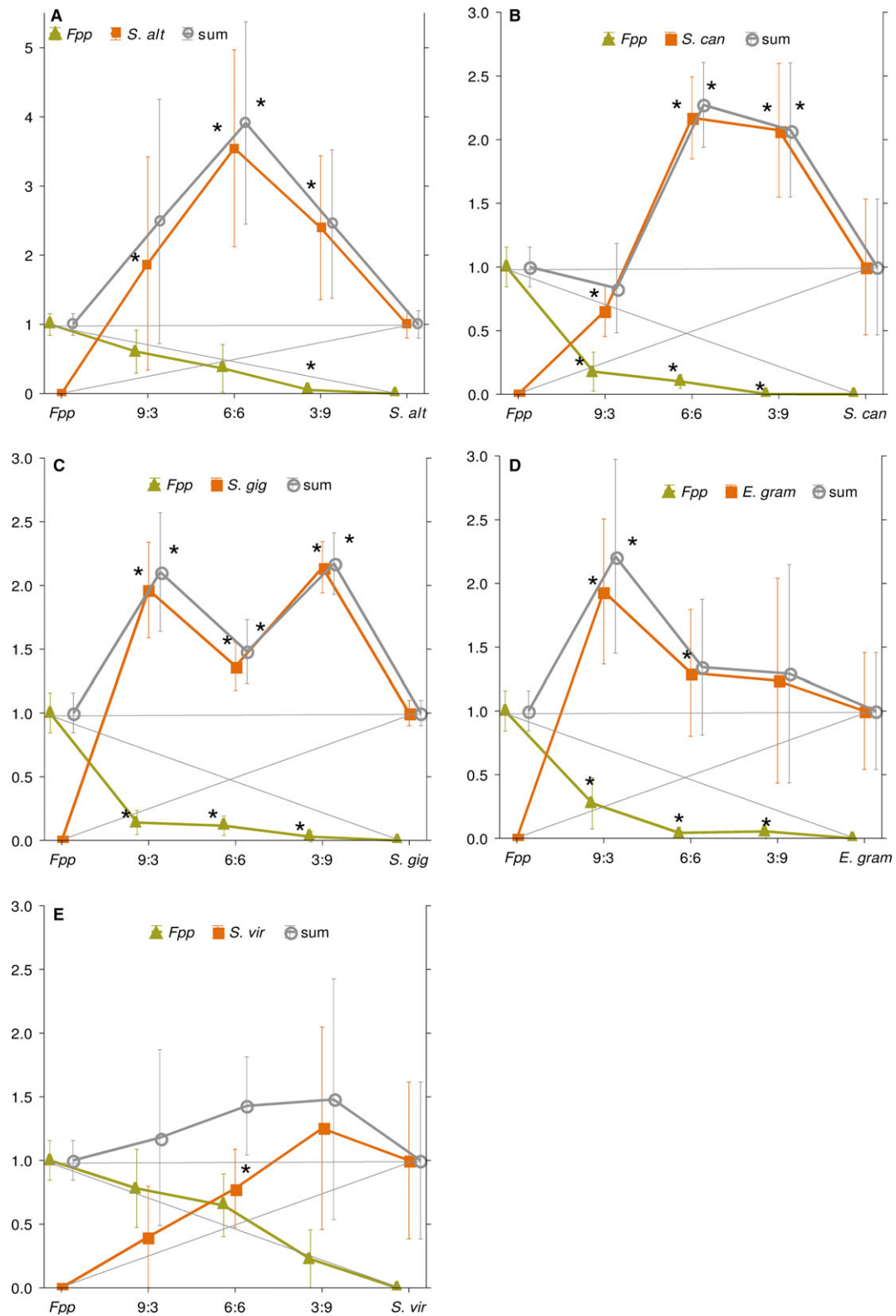


Fig. 1 Replacement series diagrams of mixtures of goldenrod species and *Festuca pratensis* (*Fpp*) showing the mean (points) and standard deviation (whiskers) for the relative yield of a given species (RY_i) and the total relative yield (RYT) as a function of the species proportion. The expected yield trends (dashed lines) show the expected RYT and RY values when species grew equally well in a mixture and monoculture. Asterisk (*) denotes a significant difference between the observed and expected values. Particular graphs (A–E) show results for a given pair of compared species. Abbreviations: *Fpp*–*Festuca pratensis*, *S.alt*–*Solidago altissima*, *S.can*–*S. canadensis*, *S.gig*–*S. gigantea*, *E.gram*–*Euthamia graminifolia*, *S.vir*–*S. virgaurea*. [Colour figure can be viewed at wileyonlinelibrary.com].

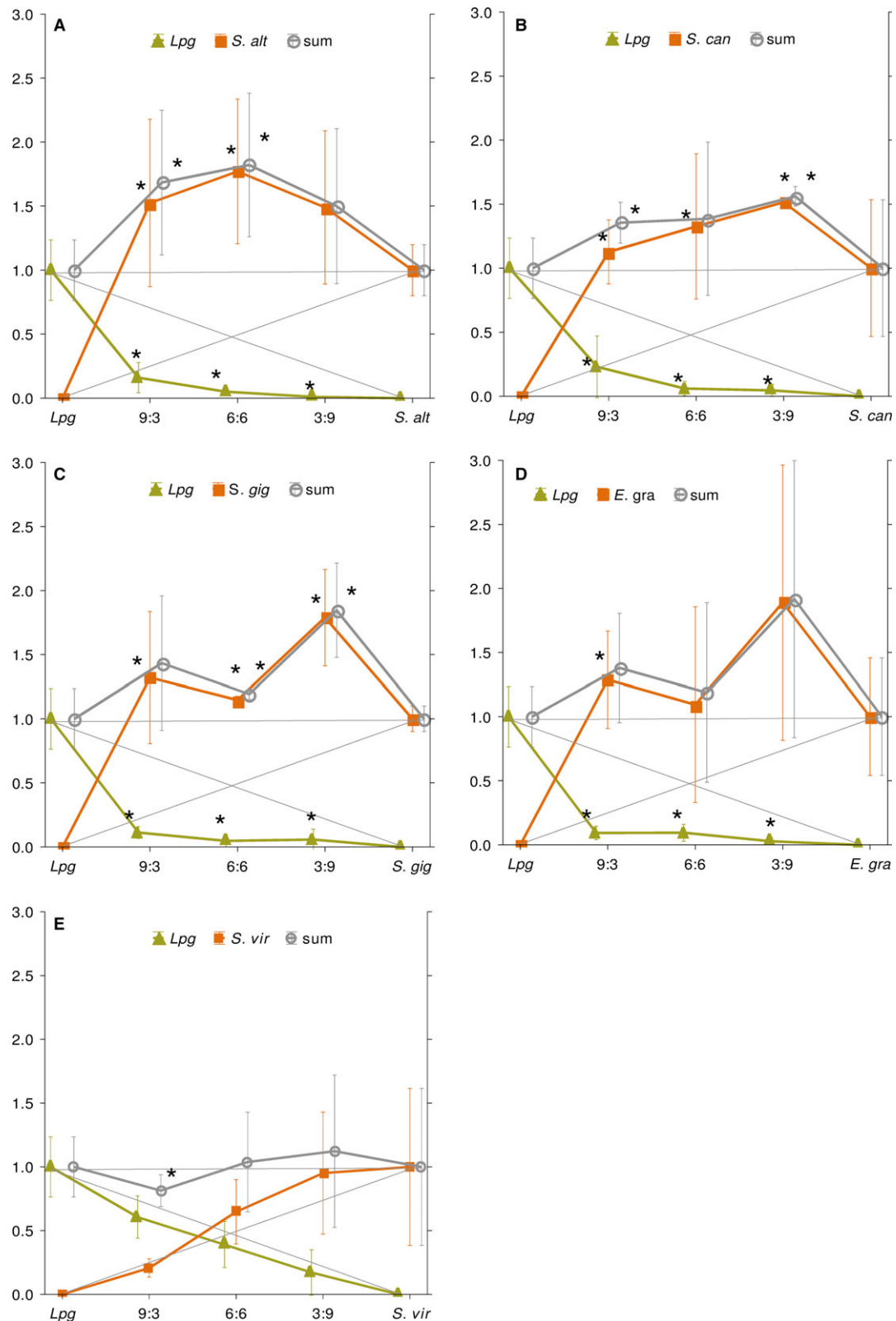


Fig. 2 Replacement series diagrams of mixtures of goldenrod species and the turf type of *Lolium perenne* (Lpg) showing the mean (points) and standard deviation (whiskers) for the relative yield of a given species (RY_i) and the total relative yield (RYT) as a function of the species proportion. The expected yield trends (dashed lines) show the expected RYT and RY values when species grew equally well in a mixture and monoculture. Asterisk (*) denotes a significant difference between the observed and expected values. Particular graphs (A–E) show results for a given pair of compared species. Abbreviations: Lpg–turf type of *Lolium perenne*, S.alt–*Solidago altissima*, S.can–*S. canadensis*, S.gig–*S. gigantea*, E.gra–*Euthamia graminifolia*, S.vir–*S. virgaurea*. [Colour figure can be viewed at wileyonlinelibrary.com]

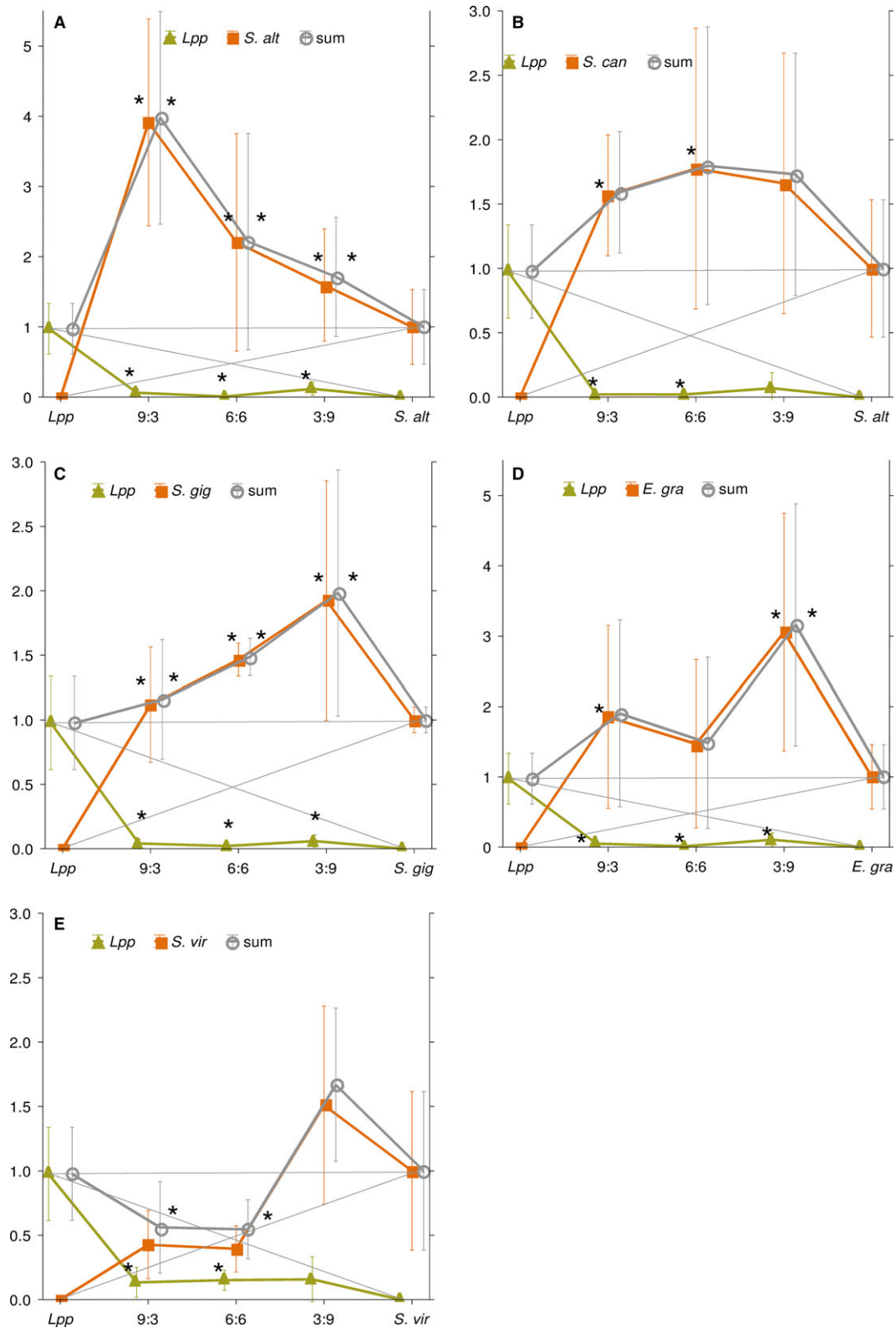


Fig. 3 Replacement series diagrams of mixtures of goldenrod species and forage type of *Lolium perenne* (*Lpp*) showing the mean (points) and standard deviation (whiskers) for the relative yield of a given species (RY_i) and the total relative yield (RYT) as a function of the species proportion. The expected yield trends (dashed lines) show the expected RYT and RY values when species grew equally well in a mixture and monoculture. Asterisk (*) denotes a significant difference between the observed and expected values. Particular graphs (A-E) show results for a given pair of compared species. Abbreviations: *Lpp*– forage type of *Lolium perenne*, *S.alt*–*Solidago altissima*, *S.can*–*S. canadensis*, *S.gig*–*S. gigantea*, *E.gra*–*Euthamia graminifolia*, *S.vir*–*S. virgaurea*. [Colour figure can be viewed at wileyonlinelibrary.com].

Table 2 Mean \pm standard deviation of the aggressivity index and results of statistical tests (z , P)

| Target taxon | Co-occurring species | | | | |
|--------------|--|--|--|--|--|
| | Salt | Scan | Sgig | Egram | Svirg |
| <i>Fpp</i> | -0.488 ± 0.292 $z = -3.940$, $P = 0.000$ | -0.263 ± 0.780 $z = -3.940$, $P = 0.000$ | -0.403 ± 0.222 $z = -3.532$, $P = 0.000$ | -0.314 ± 0.238 $z = -4.128$, $P = 0.000$ | -0.054 ± 0.069 $z = -2.824$, $P = 0.005$ |
| <i>Lpg</i> | -0.336 ± 0.178 $z = -3.940$, $P = 0.000$ | -0.238 ± 0.108 $z = -4.128$, $P = 0.000$ | -0.264 ± 0.147 $z = -4.128$, $P = 0.000$ | -0.289 ± 0.135 $z = -3.940$, $P = 0.000$ | -0.031 ± 0.042 $z = -3.047$, $P = 0.002$ |
| <i>Lpp</i> | -0.600 ± 0.573 $z = -4.128$, $P = 0.000$ | -0.325 ± 0.204 $z = -3.940$, $P = 0.000$ | -0.268 ± 0.115 $z = -4.128$, $P = 0.000$ | -0.386 ± 0.300 $z = -4.128$, $P = 0.000$ | -0.094 ± 0.092 $z = -3.493$, $P = 0.000$ |

Festuca pratensis – *Fpp*, turf type of *Lolium perenne* – *Lpp*, *Solidago altissima* – *Salt*, *Solidago canadensis* – *Scan*, *Solidago gigantea* – *Sgig*, *S. virgaurea* – *Svirg*, *Euthamia graminifolia* – *Egram*.

conditions, species composition and function of the grassland. Traditional management, such as regular mowing, grazing and balanced fertilisation, is likely to produce this result (Török *et al.*, 2011). Grazing or alternate utilisation, such as annual mowing with grazing, is the most effective method to increase or maintain biodiversity in lowland hay meadows, whereas mowing alone has a more positive effect in mountain grasslands (Tälle *et al.*, 2016).

Competitive interactions lead to differences in the allocation of above- to below-ground biomass (Gioria & Osborne, 2014). The results of studies that have examined above- and below-ground competition suggest that species with high competitiveness generally invest the higher biomass percentage in below-ground parts under competition than those growing alone (Aerts *et al.*, 1991). As a consequence, taller plants do not necessarily overgrow shorter plants. A short species (*E. graminifolia*) can overgrow taller taxa (*S. altissima*, *S. canadensis* and *S. gigantea*) due to high below-ground competitive ability (Szymura & Szymura, 2016). Our results show that the grasses are weak competitors; they were unable to compete with the alien goldenrods or force them to invest more biomass in below-ground parts. Even young, small goldenrod clones successfully outcompeted the grasses, and their growth was even more vigorous those in monocultures.

Restrictions of the experiment

The output of interspecific interactions in the field depends on many factors. Results can differ along resource gradients (Rebele, 2000; Čuda *et al.*, 2015) and vary with ontogeny of the plants; for example, small newly germinated plants are more prone to competitive exclusion than adults (Mangla *et al.*, 2011; Bottollier-Curtet *et al.*, 2013; Čuda *et al.*, 2015). Moreover, the conditions of plant growth in the pots in a garden are not the same as those observed in the field. Therefore, the results of replacement series experiments cannot be directly used to predict long-term interactions among plants under natural conditions (Jolliffe, 2000). Nevertheless, the garden experiments allowed us to control the environment and thoroughly study the interactions. Replacement series experiments do not allow us to distinguish between the effects of intra- and interspecific interactions or the exact definition of the interaction, for example competition vs. allelopathy (Jolliffe, 2000). Besides those limitations, quantifying the effect of plant interactions remains a valuable approach. The outputs of species interactions can change considerably with time (Rebele, 2000); thus, we ran our experiment for

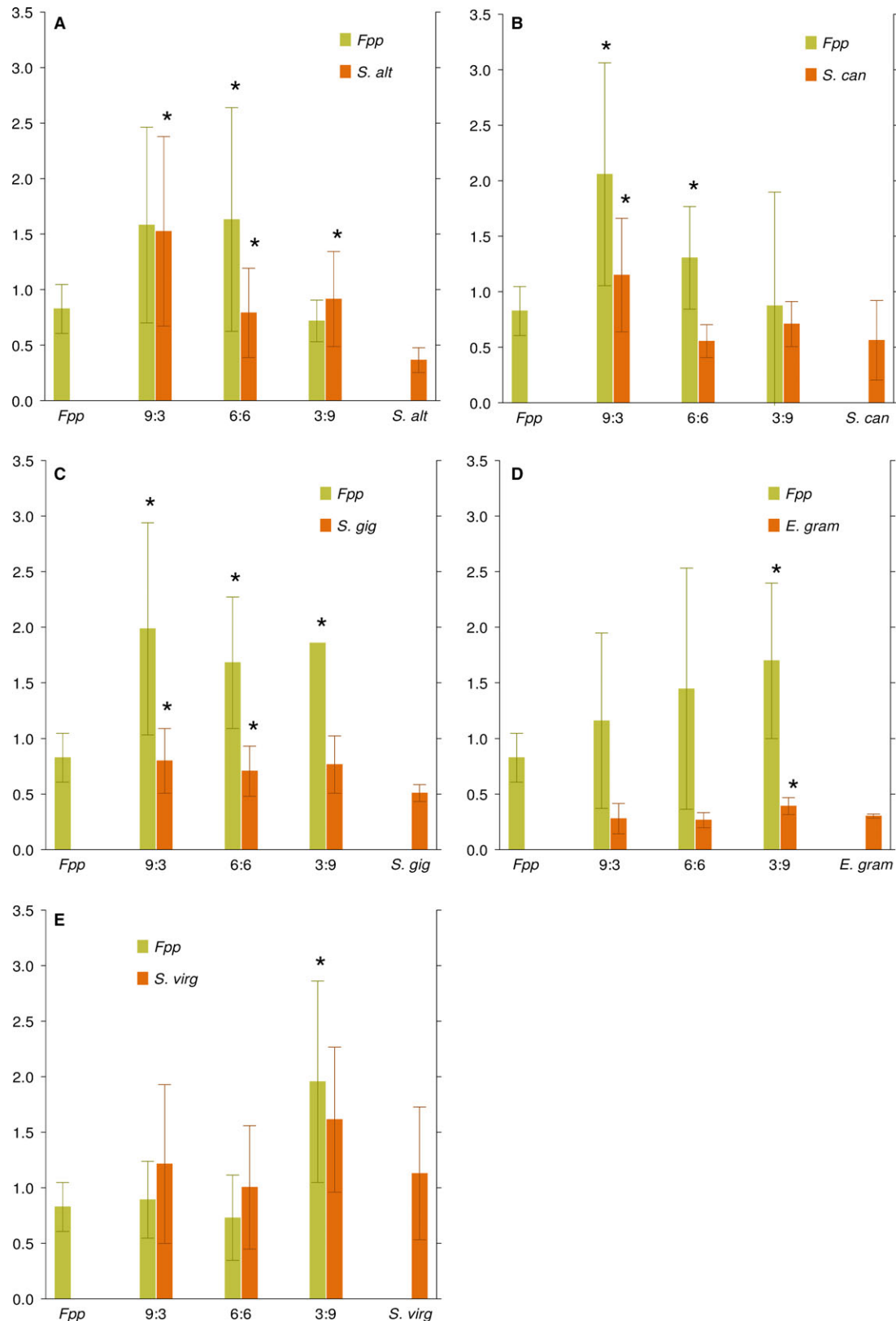


Fig. 4 Mean (bars) and standard deviation (whiskers) for the relative yield of a given species (RY_i) proportions, allocated to the above- and below-ground parts in mixtures of goldenrod species and *Festuca pratensis* (*Fpp*). Asterisk (*) denotes a significant difference in the above- to below-ground RY_i ratio between a monoculture and a given species mixture. Particular graphs (A–E) show results for a given pair of compared species. Abbreviations: *Fpp*–*Festuca pratensis*, *S.alt*–*Solidago altissima*, *S.can*–*S. canadensis*, *S.gig*–*S. gigantea*, *E.gram*–*Euthamia graminifolia*, *S.virg*–*S. virgaurea*. [Colour figure can be viewed at wileyonlinelibrary.com].

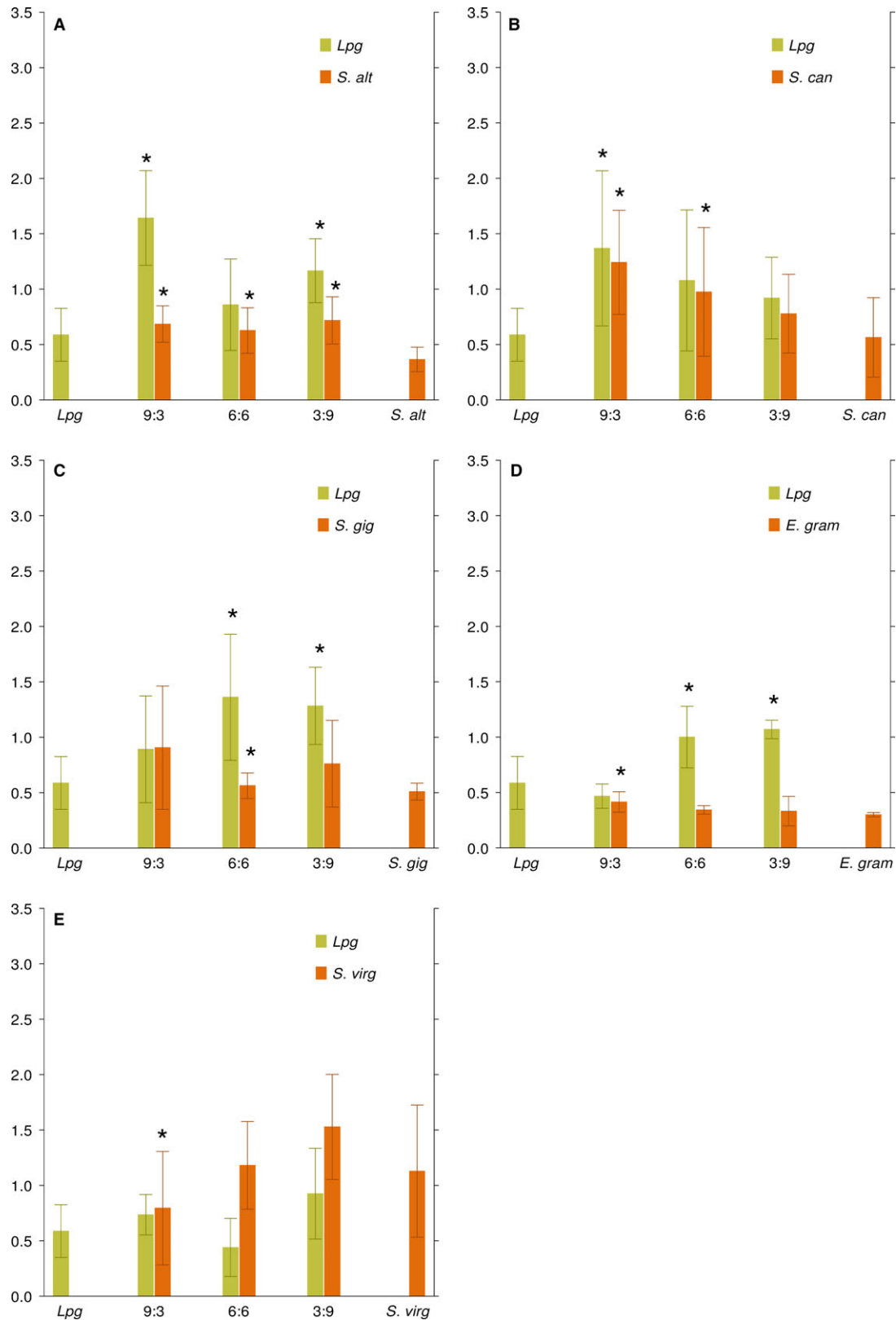


Fig. 5 Mean (bars) and standard deviation (whiskers) for the relative yield of a given species (RY_i) proportions, allocated to the above- and below-ground parts in mixtures of goldenrod species and the turf type of *Lolium perenne* (Lpg). Asterisk (*) denotes a significant difference in the above- to below-ground RY_i ratio between a monoculture and a given species mixture. Particular graphs (A-E) show results for a given pair of compared species. Abbreviations: Lpg—turf type of *Lolium perenne*, S.alt—*Solidago altissima*, S.can—*S. canadensis*, S.gig—*S. gigantea*, E.gram—*Euthamia graminifolia*, S.virg—*S. virgaurea*. [Colour figure can be viewed at wileyonlinelibrary.com].

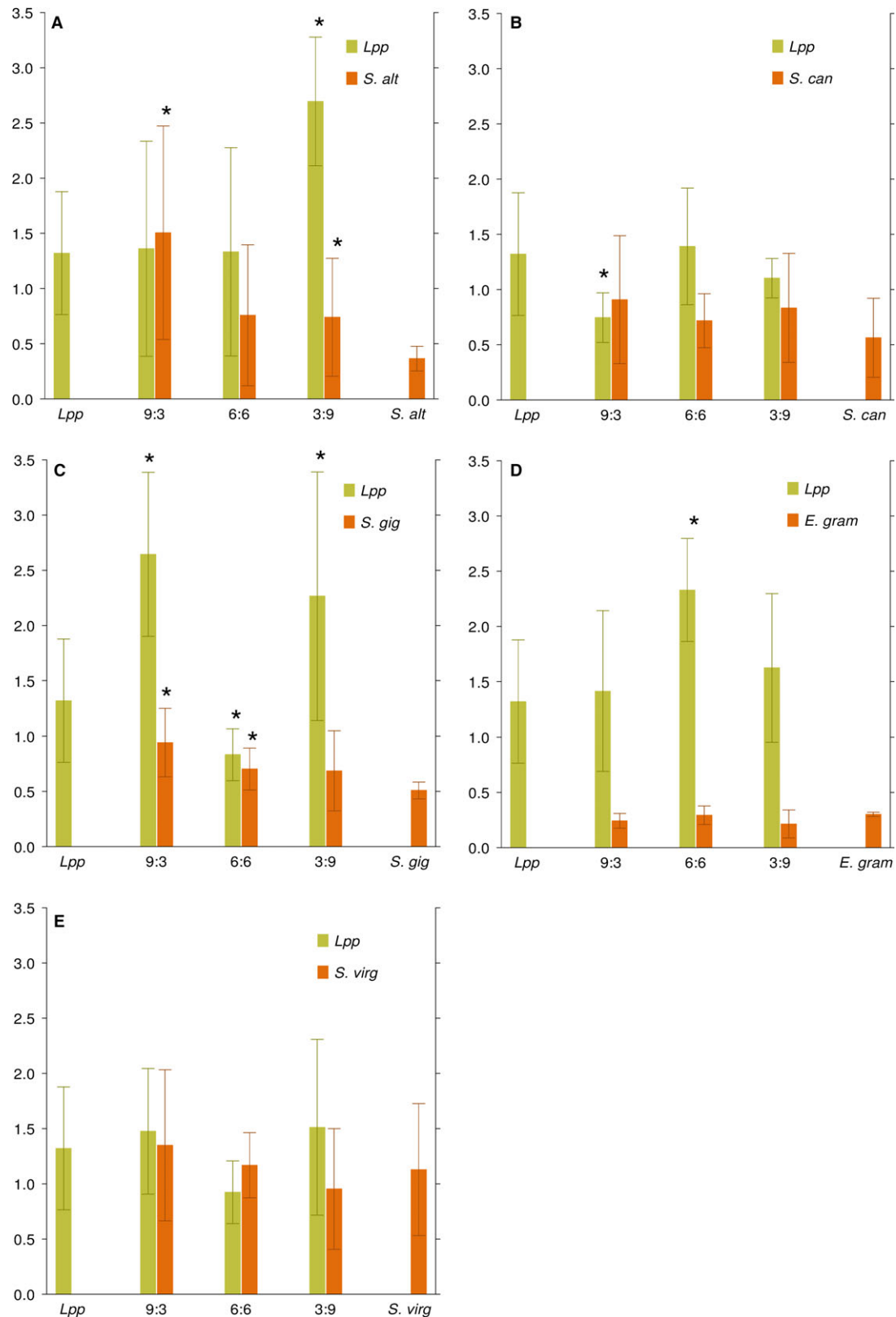


Fig. 6 Mean (bars) and standard deviation (whiskers) for the relative yield of a given species (RY_i) proportions, allocated to the above- and below-ground parts in mixtures of goldenrod species and the forage type of *Lolium perenne* (Lpp). An asterisk (*) denotes a significant difference in the above- to below-ground RY_i ratio between a monoculture and a given species mixture. Particular graphs (A-E) show results for a given pair of compared species. Abbreviations: Lpp– forage type of *Lolium perenne*, S.alt–*Solidago altissima*, S.can–*S. canadensis*, S.gig–*S. gigantea*, E.gram–*Euthamia graminifolia*, S.virg–*S. virgaurea*. [Colour figure can be viewed at wileyonlinelibrary.com].

4 years to examine the situation during a mid-succession stage. It can be assumed that the results of interaction change if some repeatable disturbances (e.g. mowing at least twice per year) are included. Moreover, in real field conditions, the plants can be shaded by adjacent individuals. In our experiment, we observed mostly the effect of plants from particular pots, as other pots were spaced 0.75 m apart to avoid interaction between the pots. In our experiment, we have also observed quite high levels of variability, resulting in large standard deviation of biomass production and RY (Table 1, Supporting Information Table S1 and Figs 1–3, Supporting Information Figure S1). In spite of high variability, the results are quite consistent and reflect general trends.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 Mean and standard deviation (SD) of total yield in different species proportions. The monocultures biomass is shown in Table 1. Abbreviations: *Salt*–*Solidago altissima*, *Scan*– *Solidago canadensis*, *Sgig*– *Solidago gigantea*, *Egram*–*Euthamia graminifolia*, *Svirg*–*S. virgaurea*, *Fpp*–*Festuca pratensis*, *Lpg*–turf type of *Lolium perenne*, *Lpp*–forage type of *Lolium perenne*.

Table S2 Results of statistical tests for comparisons between the observed and expected relative yield (RY) and total relative yield (RYT) values.

Table S3 Results of statistical tests for comparisons between observed and expected values of above to belowground relative yield (RY) ratio values for plants grown in a mixture and monoculture.

Figure S1 Mean (points) and standard deviation (whiskers) of dry biomass divided by the number of individuals introduced at the beginning of experiment.