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The Effect of Latitude, Litter and
Vegetation type on the Performance of
the Invasive Species *Impatiens*
glandulifera

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Natural Resources Management

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ABSTRACT

- **Background and Aims** *Impatiens glandulifera* is a blacklisted invasive alien plant species that exhibits high phenotypic variation along latitudinal gradients in its invaded range in Europe, with a preference for riparian, roadside and other moist or disturbed habitats. However, limited information exists on how different latitudinal populations perform in contrasting vegetation types. Furthermore, the impact of *I. glandulifera* litter on the performance of co-occurring species within different vegetation types has not been assessed.
- **Methods** In a greenhouse experiment, we compared performances of different latitudinal populations of *I. glandulifera* in two vegetation types (roadside vs. riverside) and with or without litter using a life-history trait-based approach.
- **Key Results** Performance of *I. glandulifera* was much lower in graminoid-dominated roadside vegetation turfs than in the herbaceous-dominated riverside vegetation turfs. Although the northern plants exhibited faster onset of flowering, they had lower growth rates, height at maturity and biomass than individuals from central and southern latitudes. Especially the northern plants had lower performance in the highly competitive roadside vegetation compared to the rest of the populations. Interestingly, *I. glandulifera* litter facilitated the performance of the invader but did not limit the biomass accumulation of the co-occurring species.
- **Conclusions** Our findings indicate that the performances of contrasting latitudinal populations of *I. glandulifera* depend on the invaded vegetation type. The southern and central latitudinal populations of *I. glandulifera* exhibited higher performances than the northern population. Although litter of *I. glandulifera* did not limit the performance of native species in invaded vegetation in our study, we show that litter can facilitate the invader's performance.

Key words Competitive limitation, Himalayan Balsam, *Impatiens glandulifera*, invasiveness, invasibility, latitudinal gradient, life-history traits, litter, vegetation type.

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INTRODUCTION

Invasive alien species are a hot topic in conservation and management of biodiversity today because of their potential to negatively affect native diversity, distort ecosystem functions such as soil nutrient cycles and mutualisms essential for pollination, and due to the economic costs related to their control (Daehler, 2003, Gurevitch and Padilla, 2004, Charles and Dukes, 2007, Hejda et al., 2009, Vilà et al., 2011). Any species that has considerably spread after having been introduced, and naturalized outside its natural range can be regarded as invasive (Richardson et al., 2000, Colautti and MacIsaac, 2004).

Plants form the majority of known invasive alien species in Europe (Genovesi and Shine, 2004). It is becoming progressively clearer that countermeasures against their spread such as herbicides and bio-control agents are not that proficient because they focus on already established invasive plant populations rather than the causes and pathways of these invasions (Sheley and Krueger-Mangold, 2003). For instance, the persistence of *Spartina anglica* invasion in Northern Irish estuaries may be attributed to deficient efforts in controlling the mechanistic factors leading to this invasion such as disturbance regimes, colonisation pathways and resident species performance (Hammond and Cooper, 2002, Genovesi, 2005). Thus, it is imperative that we understand the biotic and abiotic mechanisms influencing the performance of invasive plants, so as to formulate efficient measures to counteract their spread (Wittenberg and Cock, 2001). An intriguing feature of most invasive alien plants is their difference in phenotypic expression and growth morphology along key environmental gradients that has been documented in several species such as *Verbascum thapsus* in North America (Reinartz, 1984), *Impatiens glandulifera* (Kollmann and Bañuelos, 2004) and the perennials *Solidago altissima* and *S. gigantea* across Europe (Weber and Schmid, 1998). However, the driving factors prompting such differentiation

and their significance in most of the problematic alien plant invasion processes are not clearly understood.

Plant invaders are associated with characteristics such as high phenotypic plasticity, high fecundity, short generation times, high growth rates and habitat generality (Elton, 1958, Rejmánek and Richardson, 1996, Dethier and Hacker, 2005, Drenovsky et al., 2012). Traits of these invasive plants may bear similarity across native and invaded geographical ranges or they may have evolved thereby increasing the competitive ability (Daehler, 2003, Maron et al., 2004, Facon et al., 2006, Acharya, 2014). Although rapid evolution and phenotypic plasticity have often been noted as important mechanisms in most plant invasions, a majority of successful invasion processes are also dependent on habitat characteristics within the introduced range (Elton, 1958, Tilman, 1997, Kostrakiewicz-Gierałt and Zajac, 2014). Thus, the invasiveness of alien plant species needs to be associated with limited competition in the invaded range and environmental modification through novel weapons to spread in new habitats (Callaway and Ridenour, 2004, Sharma et al., 2005, Mitchell et al., 2006, Theoharides and Dukes, 2007, Del Fabbro and Prati, 2015).

Limited competition in invaded ranges is often associated with the nature and assemblage of plant functional types (Tilman, 1997, Turnbull et al., 2005, Mitchell et al., 2006, Richardson and Pyšek, 2006, Funk et al., 2008). For instance, the dense mats of graminoid species dominant in roadside vegetation may exert greater competitive limitation on a new alien species than herbaceous growth forms dominant in riverside vegetation (Sheley et al., 1999, Brooker, 2006, Bond, 2008). The greater competition exerted on the recruitment and establishment of new alien species in graminoid dominated vegetation types could indeed lead to poor performance of most annual plant invaders (Symstad, 2000, Rice and Dyer, 2001, Luis et al., 2008). On the other

hand, the broadleaved herbaceous species dominant in vegetation types such as those found in riverside habitats, often dominate through shading out the rest of the species but leave open ground spaces that can easily be exploited by arriving propagules of an invasive plant (Davis et al., 2000, Grime, 2006). In such communities with herbaceous assemblages of broadleaved species, and native individuals exhibiting considerable variation in timing of sprouting, growth rates and plant heights, there could be limited competition resulting from open niches (ground spaces) that could easily be exploited by the arriving propagules of invaders. In such a functional type, an invasive plant with good recruitment capabilities and rapid growth rates will in most scenarios have a head start in a race for limited resources such as light.

Plant invaders can also modify their environments through “novel weapons” so as to outcompete other dominant native species. Environmental modification often occurs through production of allelochemicals that inhibit the performance of co-occurring species while facilitating that of the invader (Vivanco et al., 2004, Lind and Parker, 2010). Such inhibitory allelochemicals can be released through decomposition of plant litter or as exudates from plant roots (Smith, 2013, Ruckli et al., 2014, Loydi et al., 2015). Given the high growth rates and high biomass accumulation of invasive plants in most invaded ranges, litter could indirectly act as a “novel weapon” that greatly influences their performance in new habitats (Callaway and Ridenour, 2004, Evans et al., 2011). For instance, *Pueraria montana* and *Alliaria petiolata* in the USA rely on accelerated growth rates and litter-mediated allelopathy to dominate new areas (Barto et al., 2010, Rashid et al., 2010).

Understanding the driving mechanisms most influential to invasiveness may be achieved through studying trends in growth phenology and morphology across key environmental gradients in invaded ranges (Kollmann and Bañuelos, 2004, Arévalo et al., 2005, Dietz and

Edwards, 2006, Hoffmann and Sgrò, 2011). Plant morphological and phenological traits vary with changes in the abiotic and/or biotic limitations along a given environmental gradient (Jonas and Geber, 1999, Sexton et al., 2009). In some cases, benign abiotic limitations at lower latitude localities facilitate higher performance of both invasive and resident plant species as opposed to the harsher adverse environmental conditions at higher latitudes. Abiotic limitations like low temperatures and delayed growing seasons may play a major role in regulating performance of invasive plants at higher latitudes compared to biotic limitations like intraspecific and interspecific competition that are usually a major limiting factor at lower latitudes (Beerling, 1993, Huston, 1999, Colautti et al., 2009). Under a similar set of conditions, populations of temperate invasive plants originating from lower latitudes have been documented to have higher biomass accumulation and faster growth rates than their conspecifics from higher latitudes implying that they may be better competitors (Weber and Schmid, 1998, Kollmann and Bañuelos, 2004, Sexton et al., 2009). This is because they are accustomed to greater biotic limitations at lower latitude localities as opposed to the higher latitude localities where abiotic limitations may be more prominent.

Here we study *Impatiens glandulifera*, a blacklisted and problematic invasive alien annual plant species in Europe that expresses phenotypic differences among populations along latitudinal gradients (Kollmann and Bañuelos, 2004, Helmisaari, 2010, Acharya, 2014). This invader mainly occurs in riparian habitats, roadsides and other areas with some level of disturbance. It has been documented to outcompete and reduce the performance of co-occurring species like *Urtica dioica*, *Agrostis stolonifera* and *Tanacetum parthenium* especially in riparian vegetation types (Beerling and Perrins, 1993, Perrins et al., 1993, Hulme and Bremner, 2006). In a replicated removal experiment, Hulme and Bremner (2006) reported that extensive growth of *I.*

glandulifera has the potential to reduce species richness by ca. 25%. Differences in phenotypic expression and morphology among latitudinal populations could lead to varying performances and effects among different vegetation types in invaded ranges (Müller-Schärer et al., 2004, Strayer et al., 2006). A great deal of research has been centered on which habitats are most prone to invasion by *I. glandulifera* and which traits make the plant invasive (Beerling and Perrins, 1993, Hejda and Pyšek, 2006, Hulme and Bremner, 2006, Skálová et al., 2012, Tanner et al., 2013). However, limited information exists on how the plants from contrasting populations along latitudinal gradients perform in different vegetation types. Furthermore, a lot of attention has been diverted to the control of *Impatiens glandulifera* such as mowing before seed maturation to prevent its spread (De Waal et al., 1994). However, to our knowledge, no studies have assessed the impact of the litter from this species.

We assessed the performance of *I. glandulifera* in different vegetation types by using a life-history trait-based approach. We sowed seeds from three third-generation controlled greenhouse populations of *I. glandulifera* originating from different localities along a latitudinal gradient into vegetation turfs from roadside and riverside vegetation. We also installed a control treatment without native vegetation. We determined growth, reproduction and survival of the *I. glandulifera* individuals to test the following hypotheses: (i). There is a greater competitive limitation on the performance of *I. glandulifera* in graminoid-dominated roadside compared to herbaceous-dominated riverside vegetation types. (ii). Invasive plants from lower latitude localities are better competitors than those from higher latitudes due to adaptations to higher biotic limitations in benign habitats at lower latitudes. (iii). Litter of *I. glandulifera* facilitates its performance by limiting growth of co-occurring species.

MATERIALS AND METHODS

Study species and vegetation types

I. glandulifera, commonly known as the Himalayan balsam, is a blacklisted invasive plant in most temperate regions of Europe, North America and New Zealand (Pyšek and Prach, 1995, Helmisaari, 2010, Tanner et al., 2014). It was first introduced in Europe as an ornamental plant in the first half of the 19th century and has now been recorded as invasive in most of the European countries. It is an invasive annual known to thrive in riparian or disturbed areas, forest patches and moist roadsides (Hejda and Pyšek, 2006, Kostrakiewicz-Gierałt and Zajac, 2014). It can grow up to 2-3 m in height and produces a large number of > 130 zygomorphic flowers which are both self and insect pollinated (Beerling and Perrins, 1993, Acharya, 2014). Flowers of *I. glandulifera* are often in racemes of 2-13 and protandrous with the stamens maturing before the pistil (Clements et al., 2008). Flowers vary in colour from white to pink and purple, but plants in this experiment mainly exhibited pink inflorescences. Though the plant flowers are morphologically well designed for pollination by bumble bees, the genetic origins of floral colour variation are not completely clear (Titze, 2000). *I. glandulifera* relies on production of greater quantities of nectar with higher sugar content compared to that of other co-occurring species to attract more pollinators (Chittka and Schürkens, 2001). The plant exhibits ballistochorous seed dispersal with individual capsules releasing on average 4 to 16 seeds (Beerling, 1993, Willis and Hulme, 2004). We sampled populations of *I. glandulifera* along a latitudinal gradient from Amiens (northern France; 49.9 °N 2.2 °E), Lund (southern Sweden; 56 °N 12.8 °E) and Trondheim (central Norway; 63.5 °N 11 °E) to test the variation in performance of these plants in two different vegetation types (Figure 1). The three latitudinal populations

were sampled to respectively represent the invasive populations of *I. glandulifera* from southern, central and northern localities along a latitudinal gradient in Europe.

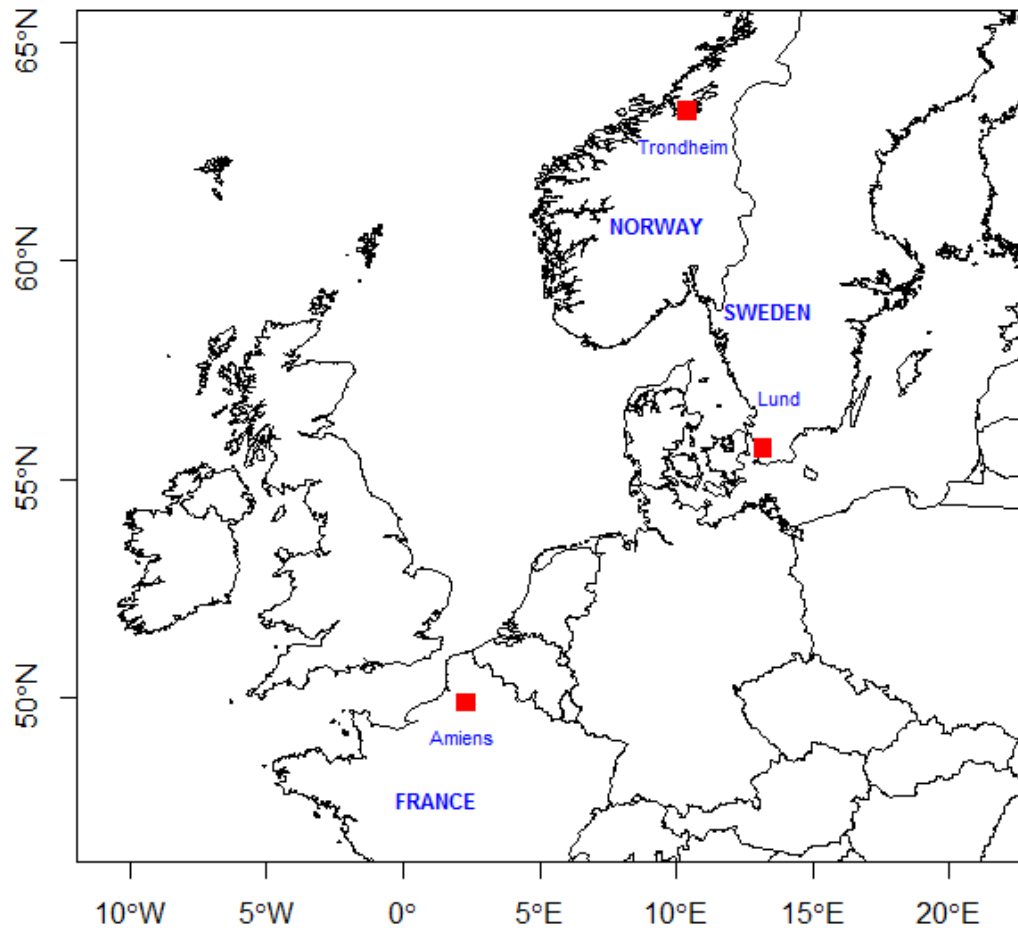


Figure 1: The used latitudinal gradient in Europe and sampled *I. glandulifera* populations.

We sampled thirty vegetation turfs of 20 cm diameter and 20 cm depth from each of the homogeneous roadside and riverside habitats where *I. glandulifera* typically grows (Helmisaari, 2010). In total, 60 vegetation turfs were sampled during early autumn 2013 in the Stjørdal-Trondheim area, Norway (63.5 °N 11.2 °E). A typical sampled roadside vegetation turf was dominated by dense graminoid species such as *Phleum pratensis* (32%), *Agrostis stolonifera*

(27%), *Dactylis glomerata* (9%), *Poa pratensis* (6%), and some few herbs, mainly *Taraxacum officinale* (6%) and *Urtica dioica* (4%). A sampled riverside turf was dominated by mainly herbaceous species such as *Filipendula ulmaria* (54%), *Ranunculus repens* (15%), *Urtica dioica* (13%), *Taraxacum officinale* (5%), *Epilobium hirsutum* (3%), *Geum rivale* (3%) and *Anemone nemorosa* (2%). We considered composition of each species as the mean percentage biomass in pots where a given species occurred. The graminoid-roadside species were all nearly of the same height and sprouted at nearly the same time thus leaving very limited open ground as opposed to the sparse herbaceous-dominated riverside turfs with different heights and sprouting times.

Experimental design

Each of the sampled vegetation turfs was inserted in pots of 20 cm diameter and 30 cm height, with potting soil in the lower 10 cm of the pot. We clipped resident vegetation until 1.5 cm above the ground level of all the vegetation turfs in preparation for the sowing of *I. glandulifera* seeds. For each of the three latitudinal origins, 20 seeds were sown in each of the 10 turfs of riparian, 10 turfs of roadside vegetation and 10 pots of control treatment without vegetation (for a total of 90 pots). The sown seeds were obtained by controlled random mating of individuals within populations of identical latitudinal origin from two previous generations of *I. glandulifera* grown in the greenhouse (Acharya, 2014). Half of all the pots were covered with litter from *I. glandulifera* (Appendix 1). The amount of added litter was estimated by taking into account the densities of *I. glandulifera* stands in colonized sites in Trondheim. We estimated the amount of expected litter per unit area by taking an average biomass of harvested plants from a 2 m × 2 m plot within a dense stand of *I. glandulifera* during the autumn of 2013. The harvested litter was dried at room temperature for four weeks and then saved in plastic bags for storage at 4

°C. It was then cut into pieces of < 8 cm, sorted and added to the pots with sown seeds of *I. glandulifera* during early November 2013 at an application rate of 0.52 kg m⁻². The pots were cold stratified for eight weeks to break dormancy of the seeds through exposure to cold-outdoor Trondheim temperatures (average daily min and max temperature; -0.2 °C to 5.3 °C) during November and December 2013 (yr.no, 2015).

During the second week of January 2014, we transferred all the pots into a single greenhouse room (Appendix 1 & 2). After germination, the seedlings were thinned to keep one individual of *I. glandulifera* per pot. All the pots were given similar treatment in terms of water, nutrients, light and temperature. The temperature was maintained at an average of 10 °C for both day and night during the first month in the greenhouse, and later raised to 18 °C during the day (0600 h – 1800 h) while keeping the night temperatures at 10 °C (1800 h – 0600 h). Watering was carried out as needed every four days throughout the whole six months duration of the experiment. Nutrients were added once a week starting after a month of growth. The nutrition applied was set at a low concentration of a 0.64 g l⁻¹ solution of the added water and contained two equally pre-composed mixtures; *Superex* (N 11%, P 4%, K 25% and micronutrients) and *Calsinit* (N 15.5%, Ca 19%, CaO 26.5% and micronutrients). The plants were grown under 16/8 hour (light/dark) light regime for the subsequent four months in the greenhouse until the beginning of April 2014. We rotated pots systematically every four days until flowering to avoid any unintentional variation in environmental conditions within the greenhouse. After flowering, we hand-pollinated and isolated the fertilized stigmas using light paper tea bags. Stamens were transferred from the pollen parent to the stigma of the seed parent using tweezers. Crosses were done between plants of the same population so that the resultant seeds maintained their parental origin on both sides (Silvertown and Charlesworth, 2009).

Measurements

We recorded the germination percentage, growth rates, specific leaf area (SLA), onsets of flowering, flower number, biomass and height at maturity, seed mass, seeds per capsule and reproductive output of *I. glandulifera* in all pots. All these life-history traits are known to affect performance of invasive plants during key invasion stages of dispersion, colonisation and naturalization (Elton, 1958, Grime, 2006, Hulme and Bremner, 2006, Pyšek and Richardson, 2007). A life-history trait-based approach was used to discern the significance of the different life history characteristics in successful invasion of different vegetation types by *I. glandulifera*. We recorded germination potential as the percentage emerged seedlings divided by the amount of sown seeds. The plant height was measured every four days and growth rate calculated as $Growth\ rate = \sum [h_i / 4n]$; where h_i is the plant height measured during an interval of measurement i , and n the number of time intervals after the four months. At this time, flowering had started and the rate of height increment had considerably slowed down. For SLA, we harvested the largest leaf from each plant at the end of May 2014, scanned it and computed the leaf area with *ImageJ* software (Abràmoff et al., 2004). Leaves were oven dried at 60 °C for 48 hours and weighed, and SLA computed as a ratio of the area to the dry weight of the leaf. We recorded onset of flowering as the time difference between germination and the emergence of the first flower (Weiher et al., 1999, Cornelissen et al., 2003). After pollination and ripening of capsules, we harvested the seeds, and the number and mass of seeds per capsule were counted and measured respectively. The seed mass was calculated as the mass of all seeds per capsule divided by number of seeds in that capsule. During the first week of June 2014, we counted the total number of flowering buds and capsule scars and measured the height at maturity. We then recorded reproductive output as the product of flowering buds and the average number of seeds

per capsule to represent the potential seed production of an individual plant under ideal pollination conditions. The plants were then harvested, oven dried at 60 °C for 72 hours and the dry weight (total aboveground biomass) measured. Additionally, we measured the dry aboveground biomass of co-occurring species to capture the effect of litter on the co-occurring species.

Data analyses

To test if the performance of *I. glandulifera* was limited by competition, we analysed the responses of several life-history traits of *I. glandulifera* growing in the different vegetation types and in the control without vegetation using analysis of variance (ANOVA). We fitted “*TukeyHSD*” and “*lm*” models in R-3.1.2 using the *stats* package (RCoreTeam, 2014). We also tested for significant differences in life-history traits among the different latitudinal populations and with or without litter treatments using similar ANOVA models. Non-normal response variables were transformed to meet the conditions of normality and homogeneity of variances of the statistical tests (see Table 1). “*Latitude*”, “*Litter*” and “*Vegetation*”, plus all possible interaction terms were used as predictor variables in our null linear models. Our modelling approach involved a step-by-step elimination process of a single predictor with the least effect (highest *p*-value) from a null model hence leaving only significant variables ($p \leq 0.05$). A Principal Component Analysis (PCA) was used to visualize the correlations among life-history traits. Estimates of growth rate, height at maturity, biomass and seed per capsule were all positively correlated, but negatively correlated with SLA (Appendix 3). Onset of flowering exhibited negative correlations with other reproductive traits such as flower number,

reproductive output, seed mass and germination percentage. Reproductive output was correlated with flower number but less so with seeds per capsule.

RESULTS

Vegetation type effect on life history traits of *I. glandulifera*

With the exception of SLA (ANOVA; $F_{2,84} = 2.8$, $p = 0.07$), individuals of *I. glandulifera* differed significantly in all their life-history traits when growing in different vegetation types (Table 1). All populations of *I. glandulifera* performed best in the control pots without vegetation and poorest in the roadside vegetation.

Table 1: Effects of latitude (Amiens-France, Lund-Sweden & Trondheim-Norway), litter (litter vs. no-litter) and vegetation type (control, roadside & riverside) on life-history traits of *I. glandulifera* (only significant predictors shown).

Trait (response)	DF	Model R ²	Significant Predictor	P-Value	F-Value	Estimates ± s.e. (+/- as direction)
Germination [%]	86	0.537	Litter	< 0.001	66.58	Intercept (83.22 ± 3.73) No litter (-30.44 ± 3.73)
			Vegetation	< 0.001	16.65	Riverside (+0.33 ± 4.57) Roadside (-22.67 ± 4.57)
Seeds per capsule	79	0.268	Vegetation	0.041	3.32	Intercept (7.55 ± 0.42) Riverside (+0.72 ± 0.60) Roadside (-0.92 ± 0.62)
Log (Seed mass [mg])	77	0.455	Latitude	0.006	5.48	Intercept (2.70 ± 0.05) Lund (+0.09 ± 0.06) Trondheim (-0.11 ± 0.06)
			Vegetation	< 0.001	20.99	Riverside (-0.28 ± 0.06) Roadside (-0.38 ± 0.06)
Log (Onset of flowering [Days from germination])	79	0.490	Latitude	< 0.001	12.09	Intercept (3.93 ± 0.07) Lund (-0.11 ± 0.06) Trondheim (-0.32 ± 0.06)
			Vegetation	< 0.001	20.76	Riverside (+0.21 ± 0.09) Roadside (+0.27 ± 0.09)
			Vegetation: Litter	0.010	4.86	Riverside: no-litter (-0.07 ± 0.12) Roadside: no-litter (+0.31 ± 0.13)
√(Flower number)	87	0.721	Vegetation	< 0.001	112.48	Intercept (22.00 ± 0.71) Riverside (-2.96 ± 1.00) Roadside (-14.21 ± 1.00)

$\sqrt{(\text{Reproductive output})}$	73	0.627	Vegetation	< 0.001	80.76	Intercept (57.85 ± 3.31) Riverside (-3.90 ± 4.69) Roadside (-28.15 ± 5.4)
			Latitude: Vegetation	0.005	4.07	Lund: Riverside ($+5.14 \pm 6.72$) Trondheim: Riverside (-10.04 ± 6.63) Lund: Roadside ($+2.55 \pm 7.24$) Trondheim: Roadside (-22.89 ± 7.35)
S.L.A [cm ² g ⁻¹]	84	0.083	No significant differences	> 0.05	NA	NA
Growth rate [cm day ⁻¹]	78	0.765	Latitude	< 0.001	10.25	Intercept (2.95 ± 0.16) Lund (-0.49 ± 0.22) Trondheim (-0.83 ± 0.22)
			Litter	0.036	4.58	No litter (-0.35 ± 0.16)
			Vegetation	< 0.001	104.84	Riverside (-0.49 ± 0.19) Roadside (-1.81 ± 0.19)
			Latitude: Litter	0.014	4.51	Lund: no-litter ($+0.54 \pm 0.22$) Trondheim: no-litter (-0.06 ± 0.22)
			Latitude: Vegetation	0.044	2.58	Lund: Riverside ($+0.02 \pm 0.27$) Trondheim: Riverside ($+0.64 \pm 0.27$) Lund: Roadside ($+0.41 \pm 0.27$) Trondheim: Roadside ($+0.55 \pm 0.27$)
Height at maturity [cm]	81	0.590	Latitude	< 0.001	12.40	Intercept (208.70 ± 10.91) Lund (-26.80 ± 15.43) Trondheim (-67.60 ± 15.43)
			Vegetation	< 0.001	39.10	Riverside (-35.20 ± 15.43) Roadside (-101.10 ± 15.43)
			Latitude: Vegetation	0.015	3.31	Lund: Riverside ($+11.80 \pm 21.82$) Trondheim: Riverside ($+51.00 \pm 21.82$) Trondheim: Roadside ($+29.00 \pm 21.82$)
$\sqrt{(\text{Biomass [g]})}$	82	0.780	Latitude	< 0.001	8.89	Intercept (7.11 ± 0.35) Lund ($+0.03 \pm 0.30$) Trondheim (-1.08 ± 0.30)
			Vegetation	< 0.001	130.91	Riverside ($+0.32 \pm 0.42$) Roadside (-3.83 ± 0.42)
			Litter: Vegetation	0.013	4.56	Riverside: No litter (-1.76 ± 0.60) Roadside: no-litter (-1.21 ± 0.60)
$\sqrt{(\text{Biomass of Co-occurring species [g]})}$	48	0.789	Vegetation	< 0.001	171.69	Riverside (2.63 ± 0.45) Roadside ($+2.32 \pm 0.64$)

Seed mass, growth rate, flower number and reproductive output were significantly higher in control pots as opposed to the roadside and riverside vegetation types (Figure 2). Onset of flowering was also significantly earlier in the control treatment, implying faster flower development for pots with potting soil compared to those with vegetation turfs. Plants in the

riverside vegetation turfs exhibited significantly more seeds per capsule, higher biomass, and germination potential compared to plants in the roadside turfs. Plants in the roadside vegetation exhibited the poorest performance in almost all considered reproductive and morphological traits (Figure 3 & 4). For instance, height at maturity was much lower in roadside (mean \pm s.e. 107.6 ± 15.43 cm; $n=30$) compared to the rest of the treatments (Figure 4B).

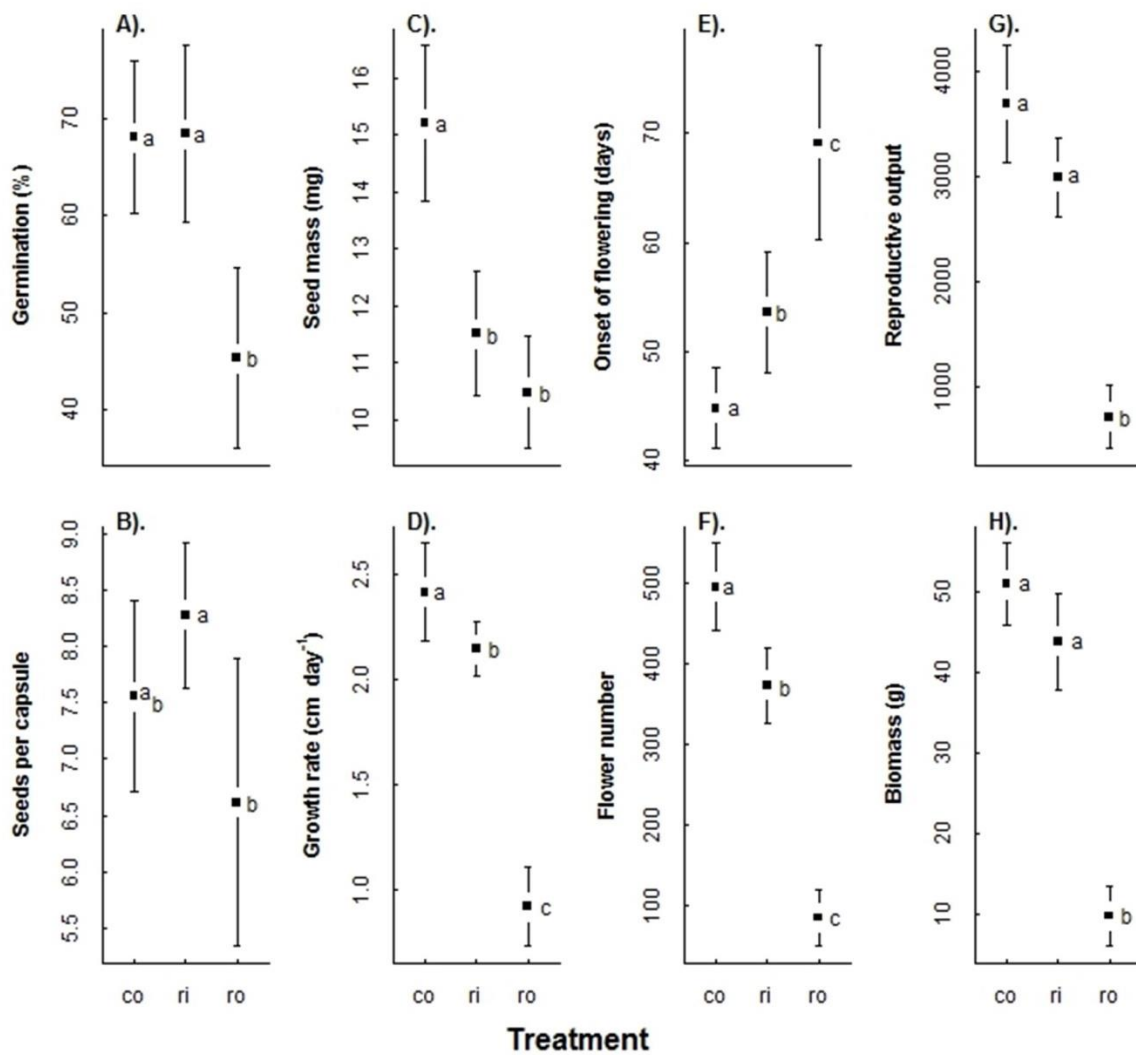


Figure 2: Variation in life history traits (means and 95% CIs) of *I. glandulifera* among the different treatments; co: control, ri: riverside vegetation and ro: roadside vegetation. Different letters represent significant differences between treatments. See Table 1 for significance values.

Population of origin (latitude) effect on life history traits of *I. glandulifera*

Seed mass, growth rate, onset of flowering, biomass and height at maturity were highly variable between the different latitudinal populations (Table 1). However, we recorded no significant variation between the germination percentages ($F_{2,84} = 2.67$, $p = 0.08$), seeds per capsule ($F_{2,76} = 0.49$, $p = 0.62$), flower numbers ($F_{2,84} = 0.76$, $p = 0.47$), reproductive outputs ($F_{2,73} = 1.5$, $p = 0.23$) and SLA ($F_{2,84} = 1.17$, $p = 0.32$) of the different populations of origin. The northern population exhibited faster flowering times compared to the rest of the populations (Figure 3D). Plants from this population also exhibited significantly lower plant biomass compared to the rest. On the other hand, both the southern and central populations exhibited significantly faster growth rates resulting in higher recorded heights at maturity as opposed to that of the northern plants. For seed mass, significant differences existed only between the northern and central populations and surprisingly not between the southern and northern populations (Table 1, Figure 3C).

Within the control treatment, the northern plants had significantly faster flowering times compared to the southern and central plants (Table 1, Figure 3D). Biomass was also lower in the northern plants compared to those from the central population within the control pots. Within the riverside vegetation, significant variation existed between the onsets of flowering of the northern and southern populations ($F_{2,24} = 6.01$, $p \leq 0.01$). Biomass of the northern plants was also significantly lower than that of central plants in the roadside pots (Figure 6c; $F_{2,24} = 5.03$, $p \leq 0.05$). The northern plants exhibited lower performances especially in the highly competitive roadside vegetation type compared to the central and southern populations (Figure 3 & 4).

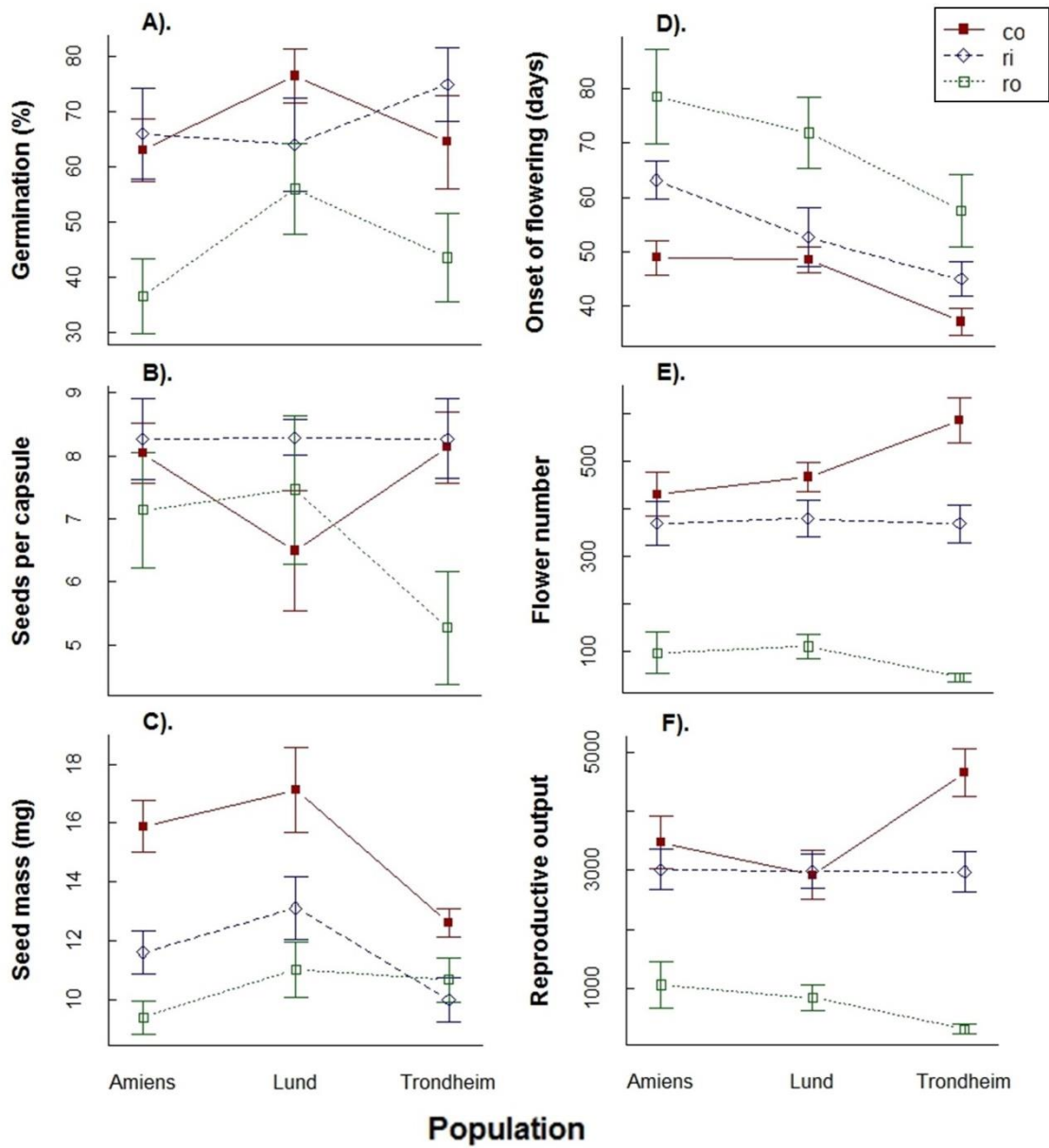


Figure 3: Variation in reproductive traits (means \pm s.e.) of the three latitudinal populations of *I. glandulifera*; Amiens-France (southern), Lund-Sweden (central) and Trondheim-Norway (northern) within different treatments (co: control, ri: riverside and ro: roadside). See Table 1 for significance values.

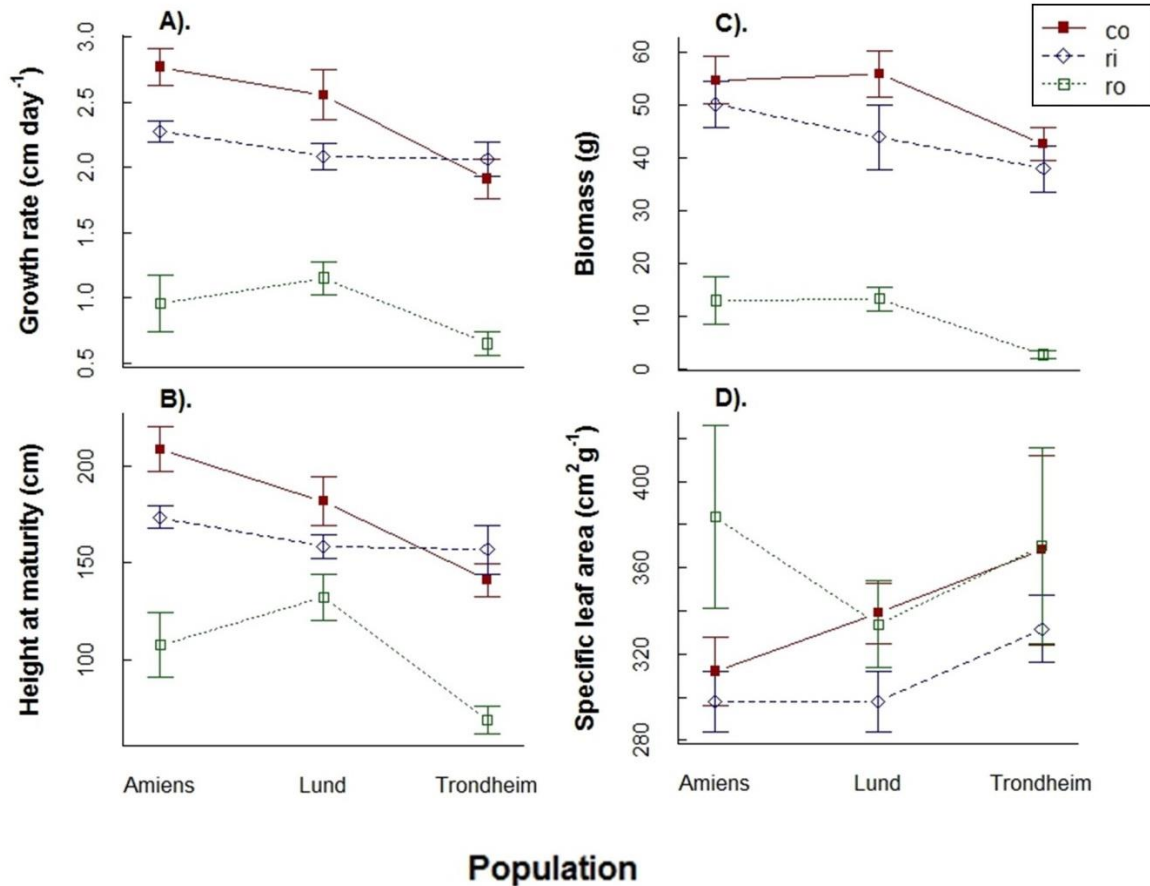


Figure 4: Variation in morphological traits (means \pm s.e.) of the three latitudinal populations of *I. glandulifera*; Amiens-France (southern), Lund-Sweden (central) and Trondheim-Norway (northern) within different treatments (co: control, ri: riverside and ro: roadside vegetation). See Table 1 for significance values.

Litter effect on life history traits of *I. glandulifera*

Litter had a significant effect on the growth rate and germination percentage of *I. glandulifera* (Figure 5). Plants in pots with litter had slightly faster growth rates (difference in means \pm s.e. 2.94 ± 0.16 cm day⁻¹, n=45) and higher germination (difference in means \pm s.e. 30.44 ± 3.73 %, n=45) than those without litter. However, litter had no significant effect on the total biomass of co-occurring species ($F_{2,48} = 0.004$, $p = 0.95$).

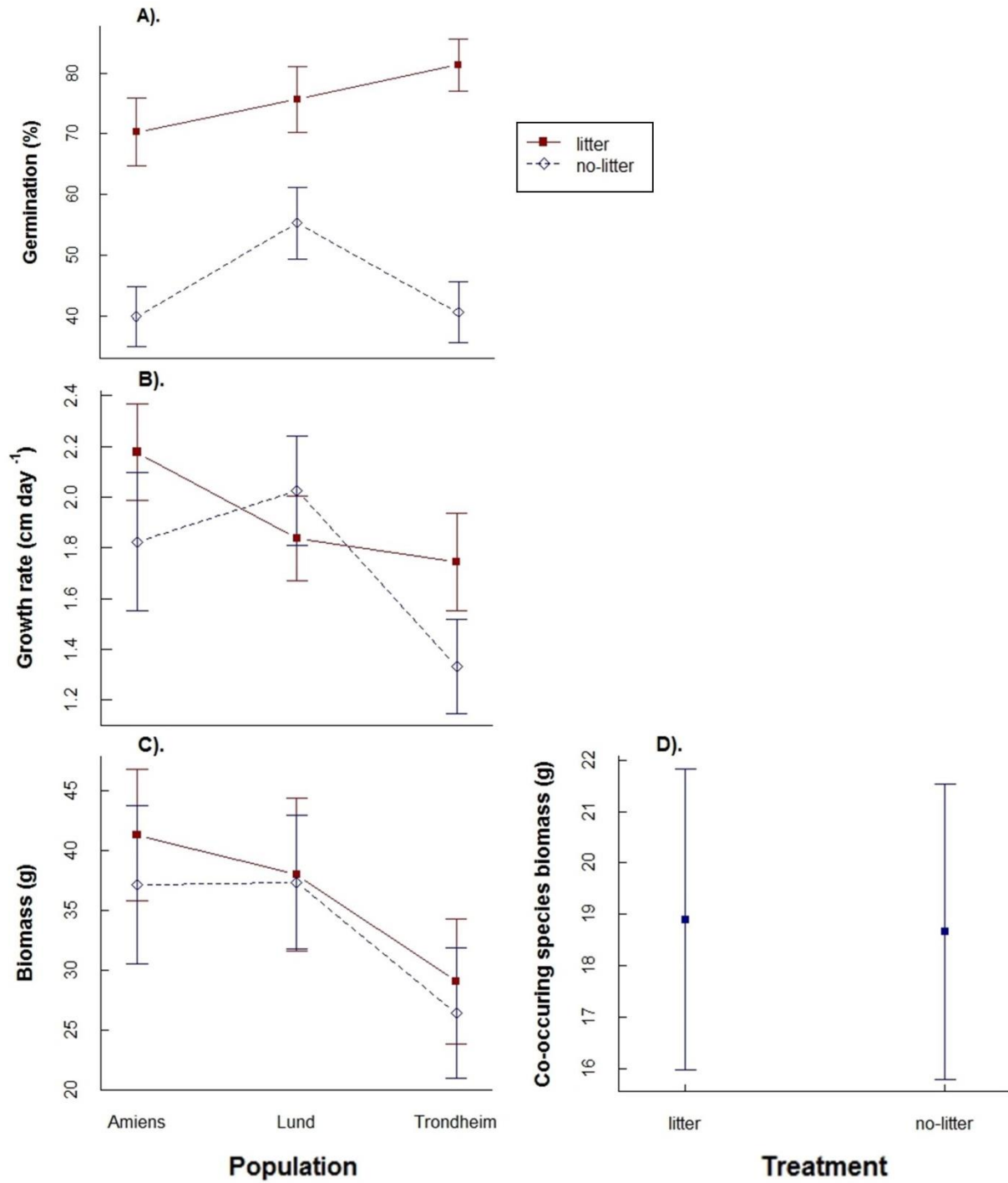


Figure 5: Effect of litter presence on life history traits (means \pm s.e.) of the three latitudinal populations of *I. glandulifera* (A, B & C), and biomass (means \pm s.e.) of co-occurring species (D).

DISCUSSION

Our results clearly show that graminoid dominated roadside vegetation exerts greater competitive limitations on the performance of *I. glandulifera* compared to the herbaceous dominated riverside vegetation. Patterns of variation for both morphological and reproductive traits of the three populations were divergent in the different vegetation types. Although the northern plants had faster onsets of flowering compared to the central and southern populations, their performance was particularly lower in the roadside vegetation. Litter had no effect on the biomass of the co-occurring species but strongly facilitated the recruitment of *I. glandulifera*.

Germination percentages, growth rates, flower numbers and heights at maturity were all significantly lower in the roadside compared to the riverside turfs. These are traits associated with competitive limitations on arriving propagules (seeds) of an alien plant within a new vegetation community (Elton, 1958, Daehler, 2003, Pyšek and Richardson, 2007, Drenovsky et al., 2012). The highly competitive graminoid species dominant within the roadside turfs form dense mats of vegetation with a complex adventitious rooting system that greatly limit the recruitment capabilities, establishment and growth of *I. glandulifera*. In a race for valuable resources such as light and other nutrients, a poor start will in most scenarios lead to decreased performance of an alien species throughout its life history within a new plant community (Dyer et al., 2000, Rice and Dyer, 2001, Luis et al., 2008). Indeed germination percentage which was also much lower in roadside compared to riverside turfs, exhibited high correlation with growth rate and biomass in our experiment. Within the herbaceous dominated communities, variable sprouting among species could give the invasive plant propagules enough time to establish in that vegetation type. The herbaceous species dominant within the riparian vegetation most likely did not impose enough competitive limitations on the recruitment capabilities and establishment

of a rapidly growing and tall annual such as *I. glandulifera*. Furthermore, the composite dominant tall-herbaceous species in riverside vegetation such as *Filipendula ulmaria*, which are in particular functionally similar to *I. glandulifera*, are considerably outcompeted due to the early germination, rapid growth rates and height of this invader (Pyšek and Prach, 1995, Maron et al., 2004, Mitchell et al., 2006). The combination of these factors may explain the considerably poorer performance of *I. glandulifera* populations in the roadside vegetation as opposed to that in the riverside vegetation. On the other hand, graminoid species as a functional group could in particular have higher ecological resistance to invasion by *I. glandulifera* compared to herbaceous species (Symstad, 2000). Further research is needed to test whether graminoid dominated vegetation types have higher resistance to invasion by *I. glandulifera* compared to that of herbaceous dominated vegetation types.

However, our synthesis for the greater competitive limitation in our roadside experimental turfs poses an important question as to why there are documented established populations of *I. glandulifera* within graminoid dominated communities such as roadsides. This could be explained by the high propagule pressures and disturbance levels where most of these presences have been sighted (Lake and Leishman, 2004, Helmisaari, 2010, Schmitz and Dericks, 2010). Roadside habitats are typical in receiving a high number of propagules of ornamental invasive plants such as *I. glandulifera* seeds since they border gardens (Hulme, 2007, Kowarik and von der Lippe, 2007). It is easy to disperse seeds into roadside vegetation via practices of transportation and disposal of garden remnants which increases the invaders propagule pressure in such a habitat. The high propagule pressure coupled with some disturbances related to unintentional human modification and maintenance operations along roadsides could explain the considerable increase in the invasiveness of *I. glandulifera* in such habitats (Turnbull et al., 2000,

Hansen and Clevenger, 2005, Eschtruth and Battles, 2009, Helmisaari, 2010). In light of this, possibilities for high invasion success of *I. glandulifera* within novel undisturbed habitats dominated by graminoid species are probably limited.

Comparisons between the different latitudinal populations revealed strong differences in growth rate, height at maturity and biomass of *I. glandulifera* especially between the northern population vs. the rest (see also Kollman & Bañuelos 2004; Acharya 2014). The northern plants exhibited faster flowering compared to the rest of the populations implying a direct adaptive response towards the shorter and delayed growing seasons at higher latitudes. At higher latitudes, abiotic limitations inducing environmental stress may be more prominent than biotic factors. An invasive alien plant will need to develop tolerances or adaptations to the shorter growing season and colder year-round temperatures at such localities (Beerling, 1993, Maron et al., 2004, Theoharides and Dukes, 2007, Sexton et al., 2009, Hoffmann and Sgrò, 2011). Plants from the northern population had low growth rate, height at maturity and above ground biomass in all our treatments. The plants from the northern population were particularly poorer competitors within the highly competitive roadside vegetation compared to their southern and central conspecifics. The higher growth rates and rapid biomass accumulation make the southern and central populations the more aggressive phenotypes since these traits are associated with high competition for resources such as light and nutrient uptake (Weber and Schmid, 1998, Jonas and Geber, 1999, Kollmann and Bañuelos, 2004, Mitchell et al., 2006, Pyšek and Richardson, 2007). With the exception of onsets of flowering, there was no latitudinal trend in the variation of reproductive traits. For instance, there was limited latitudinal variation in seed mass which is an important trait associated with the chance of dispersal and recruitment ability of an invasive plant

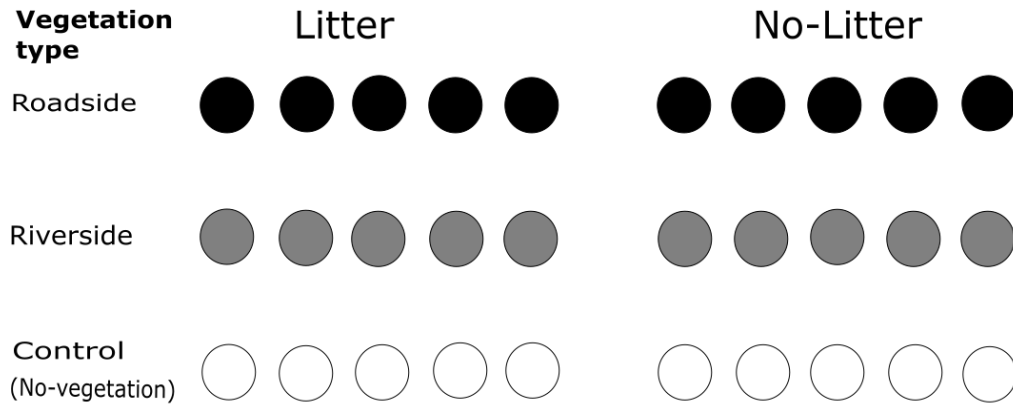
in the face of a variety of biotic and abiotic limitations at a given locality (Weiher et al., 1999, Pyšek and Richardson, 2007).

Alien plants may also increase their invasive performance through habitat modification by reliance on “novel weapons” that inhibit the performance of co-occurring vegetation while facilitating that of the invader itself (Callaway and Ridenour, 2004, Lind and Parker, 2010, Smith, 2013, Loydi et al., 2015). These “novel weapons” are mainly allelochemicals such as Naphthoquinones (secondary metabolites in *I. glandulifera*) leached from plant litter decomposition or as exudes from roots (Ruckli et al., 2014). Given the massive amounts of litter produced by *I. glandulifera* plants, litter could act as a novel weapon that increases the performance of the plant. In our study, presence of litter enhanced growth rate and germination of the invader but did not inhibit biomass accumulation of co-occurring species. These results are contradictory to findings in previous studies such as Smith (2013) and Ruckli et al. (2014) that employed bioassays to test allelopathy in *I. glandulifera*. Our contradictory results may be explained by the contrasting approach we used in our study whereby *I. glandulifera* litter was directly added to natural vegetation turfs, rather than the often relied on bioassay technique of using aqueous extracts from invasive plant shoots and roots as additives to growth mediums. There were probably insufficient concentrations and/or fast decomposition rates of the allelopathic chemicals leached from the litter within our vegetation turfs, hence rendering them ineffective in limiting the performance of co-occurring species (Reigosa et al., 1999, Del Fabbro and Prati, 2015). Further research is needed to test the allelopathic effects of *I. glandulifera* in more realistic settings that mimic environmental conditions in the natural environment.

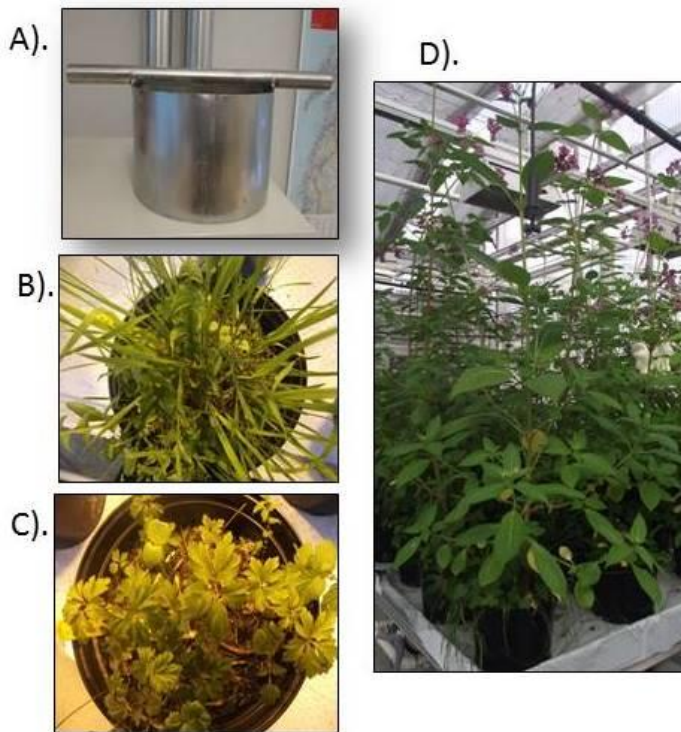
To conclude, our results indicate that the dense graminoid dominated vegetation type with a complex adventitious rooting system and no or very few open spaces can greatly limit the

recruitment and establishment of *I. glandulifera* populations. Especially the northern plants had lower performance in the highly competitive roadside vegetation type. The southern and central populations of *I. glandulifera* had higher performance compared to the northern population. *I. glandulifera* litter did not limit the biomass accumulation of co-occurring species but did facilitate the performance of the invader. For better management, we recommend removal of *I. glandulifera* litter after any kind of control procedure.

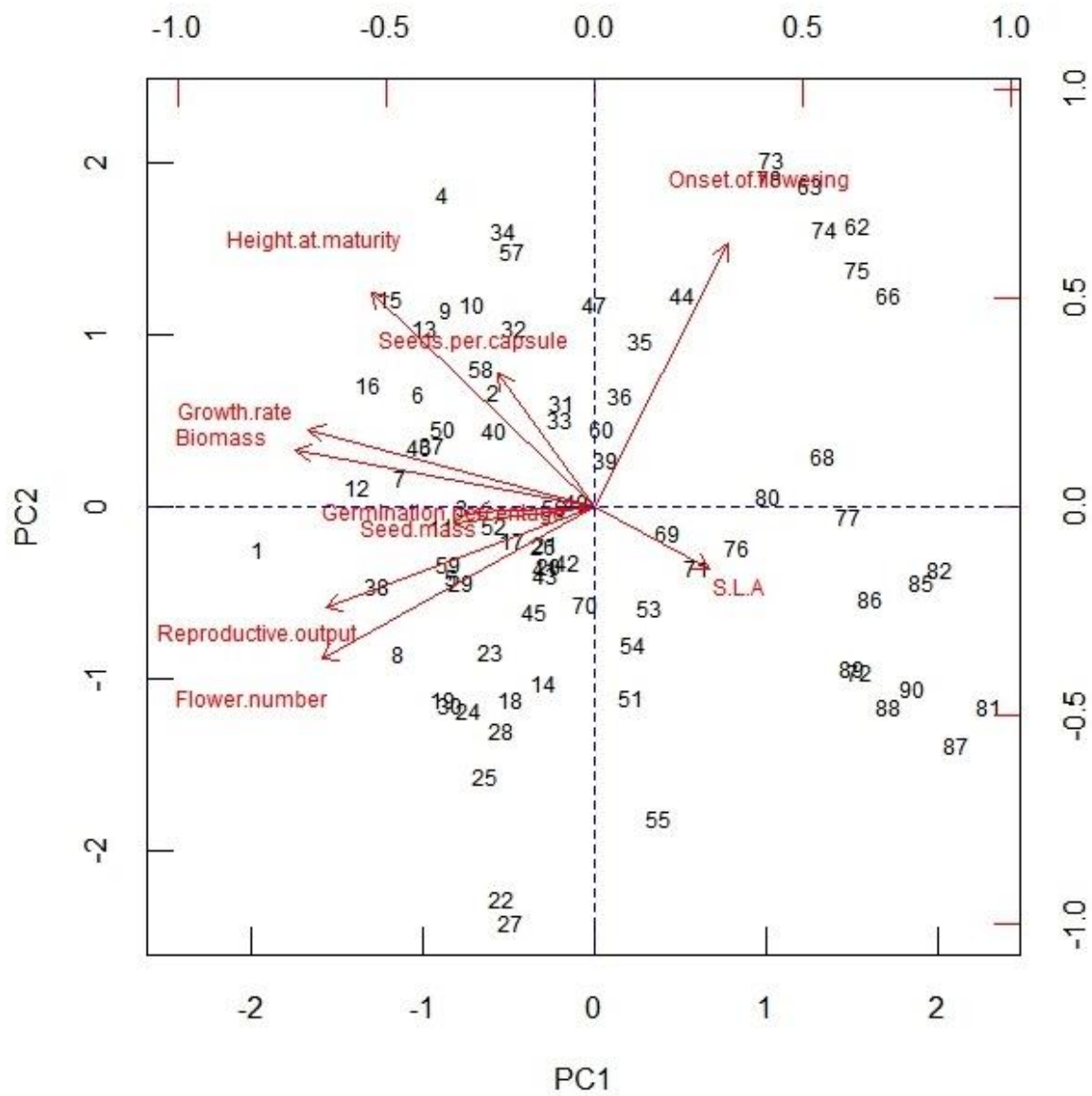
APPENDICES



Appendix 1: Experimental setup for a single latitudinal population of *I. glandulifera*. This setup was replicated three times, one for each of the three populations along the latitudinal gradient. ● - Represents a roadside vegetation turf dominated by graminoid species, ● - a riverside vegetation turf dominated by herbaceous species and ○ - a control pot without vegetation.



Appendix 2: Pictures showing; A - equipment used to extract the vegetation turfs, B - a roadside vegetation turf in pot, C - a riverside vegetation turf in pot and D - some of the tall mature *I. glandulifera* plants in the greenhouse.



Appendix 3: Biplot showing the correlation between the different traits of *I. glandulifera* used as predictor variables. Axis one explains 39.7 % and axis two 16.1 % of the variation.

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