Plant Ecology (2024) 225:705–712
https://doi.org/10.1007/s11258-024-01429-2

Defoliation tolerance in *Plantago* seedlings varies with neighbour environment

Mick E. Hanley[1] · **James Buckley**[1] · **Laoise Hunter-Martin**[1] · **Jessica J. S. Thomas**[1]

Received: 19 December 2023 / Accepted: 22 April 2024 / Published online: 11 May 2024

Abstract

Environmental selection during early ontogeny influences plant species representation in mature vegetation. Chief amongst these selective forces is the interplay of herbivore selection and seedling defence/tolerance. Although some species can recover from almost complete cotyledon loss, it remains unclear whether tolerance is impacted by other critical early life-history hazards like competition. This study examines early seedling tolerance of two sympatric *Plantago* species (*P. lanceolata* and *P. major*) for individuals grown in isolation, monoculture (i.e., with conspecifics) and mixed assemblages (with congenerics). The effects of 95 and 50% cotyledon removal at 14-d-old on plant growth and root:shoot allocation was established in 28-d and 100-d old plants. Although damage and neighbour environment consistently limited subsequent growth of *P. major*, there was no interaction between these factors. Nonetheless, individuals subjected to 95% defoliation in mixed assemblages were substantially smaller than those without neighbours. A similar response to cotyledon removal was evident for *P. lanceolata* at 28-d, although plants with conspecific neighbours tended to be larger. The defoliation effect disappeared at 100-d, and plants grown with neighbours were now smaller. Mortality and root:shoot allocation did not vary across treatments. While we underscore the negative impact that early ontogenetic damage and the influence of neighbour environment has on subsequent plant growth, we failed to elucidate obvious interactions between these factors. Nonetheless, we highlight how the remarkable tolerance of *Plantago* seedlings to almost complete defoliation in the face of intra-/inter-specific competition, may yet be impacted by anthropogenic disruption of environmental filters operating at the regeneration stage.

Keywords Defoliation · Overcompensation · Root:Shoot allocation · Seedling herbivory · Tolerance

Introduction

The interaction between plants and their environment during early establishment is critical to understanding the ecological patterns and processes that underpin plant community assembly, species coexistence and persistence (Harper 1977; Fenner & Thompson 2005; Parmesan & Hanley 2015). Seedlings are by far the most vulnerable phase of a plant's life history (Grime 2001; Fenner & Thompson 2005) and many different factors, including competition, nutrient limitation, disease, and drought limit seedling recruitment and even eliminate entire cohorts (Moles & Westoby 2004; Fenner & Thompson 2005; Chang-Yang et al 2021). Nonetheless, chief amongst the hazards to seedling survival is herbivory (Moles & Westoby 2004), and it is perhaps no surprise therefore that different plant species exhibit a range of early life history traits that imbue their seedlings with the capability to deter herbivores or recover from herbivore attack when it happens (Barton & Hanley 2013).

A wide variety of chemical defences are expressed in seedlings (see Elger et al 2009; Hanley et al 2018) and in tandem with the selective preferences of different herbivores, conspire to shape the composition and structure of

Communicated by Hank Stevens.

✉ Mick E. Hanley
mehanley@plymouth.ac.uk

James Buckley
james.buckley@plymouth.ac.uk

Laoise Hunter-Martin
laoise95@gmail.com

Jessica J. S. Thomas
jessica-thomas1@outlook.com

[1] School of Biological & Marine Sciences, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK

established plant communities (Hanley et al 1996; Burt-Smith et al. 2003; Hensgen et al 2011; Liang et al. 2019). The mechanism by which this happens reflects likely trade-offs between allocation of resources to (seedling) defence, and growth (competitive ability). In an experiment with two clover species for example, Hanley & Sykes (2009) showed how by varying the numbers of snails, the intensity of herbivory, coupled with species-specific variation in seedling growth and anti-herbivore defence, dictated which species came to dominate the mature community. In the absence of herbivory, *Trifolium pratense* dominated the established community presumably by virtue of its greater competitive ability at the seedling stage. In the most heavily grazed treatments by contrast, snails removed the majority of *T. pratense* seedlings, leaving *T. repens* to dominate. In natural plant communities, spatio-temporal variation in the number and activity of seedling herbivores likely interacts with seedling growth-defence trade-offs to dictate recruitment success for different plant species and in so doing, contribute to the maintenance of biodiversity and species coexistence (Hanley & Sykes 2014; Liang et al. 2019).

Also important in our understanding of early ontogenetic plant responses to herbivory is the ability of seedlings to recover from almost complete early cotyledon/leaf removal. Despite an assumption that seedlings are heavily constrained by resource limitation in their ability to tolerate tissue damage (Haukioja and Koricheva 2000) experiments demonstrate considerable species-specific variation in tolerance at the seedling stage (see Hanley & May 2006; Hanley & Fegan 2007; Barton 2013). The mechanistic explanation for plant tolerance has traditionally focussed on resource allocation trade-offs and especially the supposed negative relationship between anti-herbivore tolerance and resistance (Strauss and Agrawal 1999; Salgado-Luarte et al. 2023; but see Koricheva et al. 2004; Leimu & Koricheva 2006). More recently however, the process of endoreduplication (Scholes & Paige 2014) has been proposed as an explanation for growth recovery from plant damage (although this has yet to be evidenced for seedlings). While this mechanism has been shown to facilitate upregulation in both plant chemical defence (resistance) and plant growth potential (tolerance) in *Arabidopsis* (Scholes & Paige 2014; Mesa et al. 2017), experiments by Mesa & Paige (2023) suggest that upregulation of anti-herbivore resistance still imposes a cost in tolerance. Moreover, despite examples of relatively higher tolerance abilities in younger ontogenetic stages (Weltzin et al. 1998; Barton 2008), generally speaking, early tissue loss has long-term impacts on plant size and reproductive output, even if the plant can recover from almost complete cotyledon loss (Hanley & May 2006; Hanley & Fegan 2007; Hanley 2012; Barton 2013).

Importantly however, studies on seedling (and often established plants) tolerance have imposed tissue loss on plants grown in isolation from additional stressors, including competition with other seedlings (but see Parmesan 2000). This is an extremely unlikely scenario. In field conditions germination and recruitment is cued by synchronous seed release and/or seasonally variable environmental change (Fenner & Thompson 2005), and consequently, there is an expectation that intra- and interspecific competition with high densities of neighbours is almost inevitable for any individual (Harper 1977; Fenner & Thompson 2005). The impacts of density-dependent mortality are widely reported for seedling cohorts from many different plant species (Harper 1977; White 1985; Watkinson 1997). Indeed, the competition-density principle is one of the most long-standing in plant ecology and the 'self-thinning' rule (Reineke 1933) used widely to understand plant population dynamics and predict agricultural and forestry yields (Harper 1977; Vospernik & Sterba 2015). In addition to conspecifics (even siblings), most seedlings emerging in natural plant communities find themselves competing with similar-aged recruits drawn from many different species. While generally assumed to be less intense than intraspecific competition (Adler et al. 2018), the effects of interspecific competition in natural plant communities are highly unlikely to be symmetrical between species, even, or perhaps especially, at the seedling stage (see Kelly & Bowler 2005; Kelly & Hanley 2005). This presents a complex set of potential interactions for any individual seedling to surmount, even in the absence of losing tissue to herbivory.

When taken together, it seems highly probable therefore that seedling response to early defoliation will be moderated by how that species copes with simultaneous exposure to intra- or inter-specific competition. As far as we are aware however, only one previous study has explored that interaction at the seedling stage. Parmesan (2000) reported how *Collinsia torreyi* plants were surprisingly less affected by early ontogenetic tissue loss in highly (intra-specific) competitive environments than conspecifics with little or no competition. In this study, we examine whether species-specific differences in defoliation tolerance observed when seedlings are grown in isolation from potential competitors are retained, lost, or magnified when they are simultaneously grown in association with conspecific or sympatric congeneric neighbours.

Materials and methods

Plant species collection and cultivation

In July 2022, seeds of two epigeal, dicotyledonous, herbaceous species (*Plantago lanceolata* L. and *Plantago* *major* L.) were collected from a minimum 30 parent plants each, from a coastal grassland habitat at Wembury, Devon, England (50°18′58″N, 04°06′17″W). A sympatric, congeneric pair offers a shared evolutionary history and so a fundamental physiological similarity, increasing the likelihood and intensity of competition across their shared Eurasian native ranges (Sagar and Harper 1964; Kelly and Hanley 2005). A study of seedling recruitment in grasslands by van der Toorn and Pons (1988) suggests that *P. lanceolata* is the competitive dominant of the two species during early ontogeny.

In early October 2022, seeds were set to germinate on dampened filter paper in Petri dishes and placed in a growth room set at 15°C and a 12-h day/night illumination cycle. Immediately after germination (emergence of the radicle), seedlings were transferred into the centre of 70 × 70 × 80 mm plastic pots filled with John Innes No. 2 compost, such that there was a total of 324 pots. Fifty-four pots for each species were then set aside and received no further seedlings (‘Single’). The remaining pots were planted with either six seedlings drawn from the same species (‘Conspecific’), or six from the congener (‘Congeneric’). These seedlings were planted around the central seedling in a hexagonal array such that the distance between all seedlings remained constant (20 mm) (see Hanley & Sykes 2009). The pots were retained in the controlled growth room at 15°C and the 12-h day/night illumination cycle. Any seedlings that died during the first 7-d following transplant into experimental pots was replaced by a seedling of similar age.

Defoliation treatments

When seedlings were 14-d-old, the central individual in each pot received one of three defoliation treatments, i.e., no defoliation (‘0%’), half of each cotyledon removed (‘50%’), or most of each cotyledon removed to the nodes (‘95%’). This yielded 18 replicates in each defoliation/seedling array treatment group for each species. Although achieved using scissors, artificial defoliation facilitates consistent replication (effectively impossible using invertebrate herbivores on such small seedlings) and thus more precise assessment of plant tolerance to tissue loss (Tiffin & Inouye 2000).

After defoliation, the pots were randomly arranged on an unheated glasshouse bench and grown in natural daylight until the plants were 28-d-old (November), at which time nine pots from each treatment group were selected at random. From these, the central individual was carefully removed from the pot, cleaned of any adhering compost, separated into roots and shoots before oven-drying at 50°C for 24 h. The total dry weight biomass (and root:shoot ratio) attained during the 14-d period after cotyledon damage was taken as a measure of plant growth (and biomass allocation) following defoliation of 14-day old individuals. Mean daily temperatures during this time varied between 12.9 °C ± 0.3 (min) and 21.8 °C ± 0.5 (max). The remaining plants were cultivated in glasshouse conditions [7.9 °C ± 0.2 (min) and 18.3 °C ± 0.2 (max)], until they were 100 days old (i.e., 86 days post-cotyledon damage; January 2023), at which time the central plant from all pots ($n = 9$ per treatment/species group) was harvested, processed, and weighed as described above.

Statistical analysis

Separate ANOVA models were used to explore the effects of ‘Competition’ (‘Single’, ‘Conspecific’, ‘Congeneric’) and ‘Defoliation’ (0%, 50%, 95%), and the ‘Competition’ × ‘Defoliation’ interaction on the response variables, total dry biomass, and root:shoot ratio at 28 days and 100 days old. Model fit was assessed by examining plots of residuals against fitted values and quantile–quantile plots to identify deviations from that expected under normality. Where necessary, square root or $\log_{10}$ transformations of the response variable were used to improve model fit. Specifically, $\log_{10}$ transformations were used for most analyses, with square root transformation only used for those modelling total and shoot dry mass for *P. lanceolata* and *P. major* at 28 d, and total, shoot and root dry mass for *P. lanceolata* at 100 days old. All statistical analyses were conducted in R statistical software version 4.1.1 (R core team 2021).

Results

Total plant mass

In *P. major,* cotyledon loss (‘Defoliation’) had consistent negative effects on the subsequent total dry weight biomass at both 28-day ($F_{2,72} = 16.14$; $P < 0.001$) and 100-day old ($F_{2,71} = 10.27$; $P < 0.001$) (Fig. 1). Similarly, ‘Competition’ also reduced plant size at 28-d ($F_{2,72} = 8.99$; $P < 0.001$) and 100-d ($F_{2,71} = 16.24$; $P < 0.001$), but we found no ‘Defoliation’ × ‘Competition’ interaction for either age group (28-d – $F_{4,72} = 1.48$; $P = 0.218$; 100-d – $F_{4,71} = 0.19$; $P = 0.942$). Nonetheless, it was noteworthy that 14 days after damage was inflicted, individuals subjected to 95% defoliation in both the mixed assemblages were about half the size of those subject to the same amount of cotyledon loss but grown in isolation. This fell to less than one third the relative size at the final harvest.

The responses of *P. lanceolata* at 28-day harvest were broadly similar to those shown by *P. major* for ‘Defoliation’ ($F_{2,71} = 5.30$; $P = 0.007$). Interestingly however, the ‘Competition’ effect ($F_{2,71} = 3.57$; $P = 0.033$) signalled a relative increase in plant size in

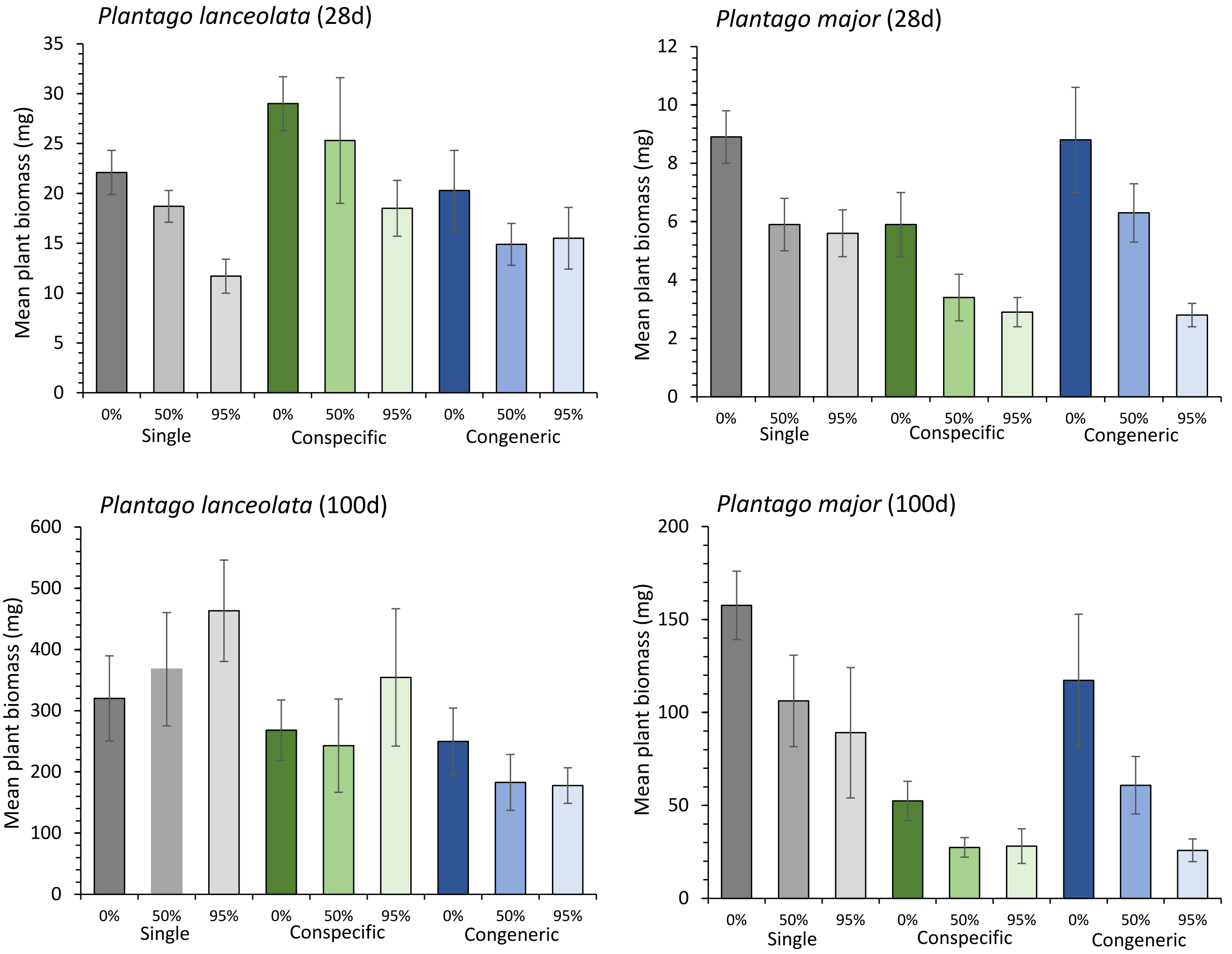

Fig. 1 The effect of seedling defoliation imposed 14 d after germination, on the subsequent growth (mean dry biomass ± SE) of *Plantago lanceolata* and *P. major.* Summary data are shown for plants grown in pots without neighbouring seedlings ('Single'), six conspecific seedlings ('Conspecific'), or six congeneric seedlings ('Congeneric') and compare responses of individuals 14-d (i.e., 28-d-old) or 86-d (i.e., 100-d-old) after 50% or 95% cotyledon loss with untreated controls (0%)

mixed assemblages. This was especially pronounced in the conspecific treatment where the mean total biomass of plants experiencing 95% defoliation was over 150% larger than plants subject to the same defoliation but grown without neighbours (Fig. 1). There was however no 'Defoliation' × 'Competition' interaction ($F_{4,71} = 0.52$; $P = 0.725$). These effects had however, disappeared or were reversed by 100-d-old; the 'Defoliation' ($F_{2,70} = 0.68$; $P = 0.509$) and 'Defoliation' × 'Competition' ($F_{4,70} = 0.51$; $P = 0.730$) effects were no longer significant, while the 'Competition' ($F_{2,70} = 4.36$; $P = 0.018$) effect highlighted a reduction in plant size in mixed assemblages. This shift was most apparent for 95% defoliated plants where individuals exposed to cotyledon damage were 76% (conspecific) and 38% (congeneric) the mass of plants subject to similar cotyledon loss but grown in isolation.

Root:Shoot ratios

Relative biomass allocation to roots and shoots was largely unaffected by defoliation or competition treatments (Fig. 2). For *P. major* harvested at 28 day old, there was a 'Defoliation' effect ($F_{2,72} = 4.45$; $P = 0.015$), but neither 'Competition' ($F_{2,72} = 1.22$; $P = 0.302$), nor the 'Defoliation' × 'Competition' interaction ($F_{4,72} = 2.26$; $P = 0.071$) influenced relative Root:Shoot biomass allocation. The 'Defoliation' effect may have been associated with a marked increase in Root:Shoot ratios (i.e., higher relative allocation to shoots) for 95% cotyledon defoliated plants in 'Single' and 'Congeneric' treatments, compared to the 50% and undamaged plants in the same assemblages (although this pattern did not hold in the 'Conspecific' assemblage). No variation in Root:Shoot ratios was evident for the 100-day harvest ('Defoliation' $F_{2,71} = 0.77$;

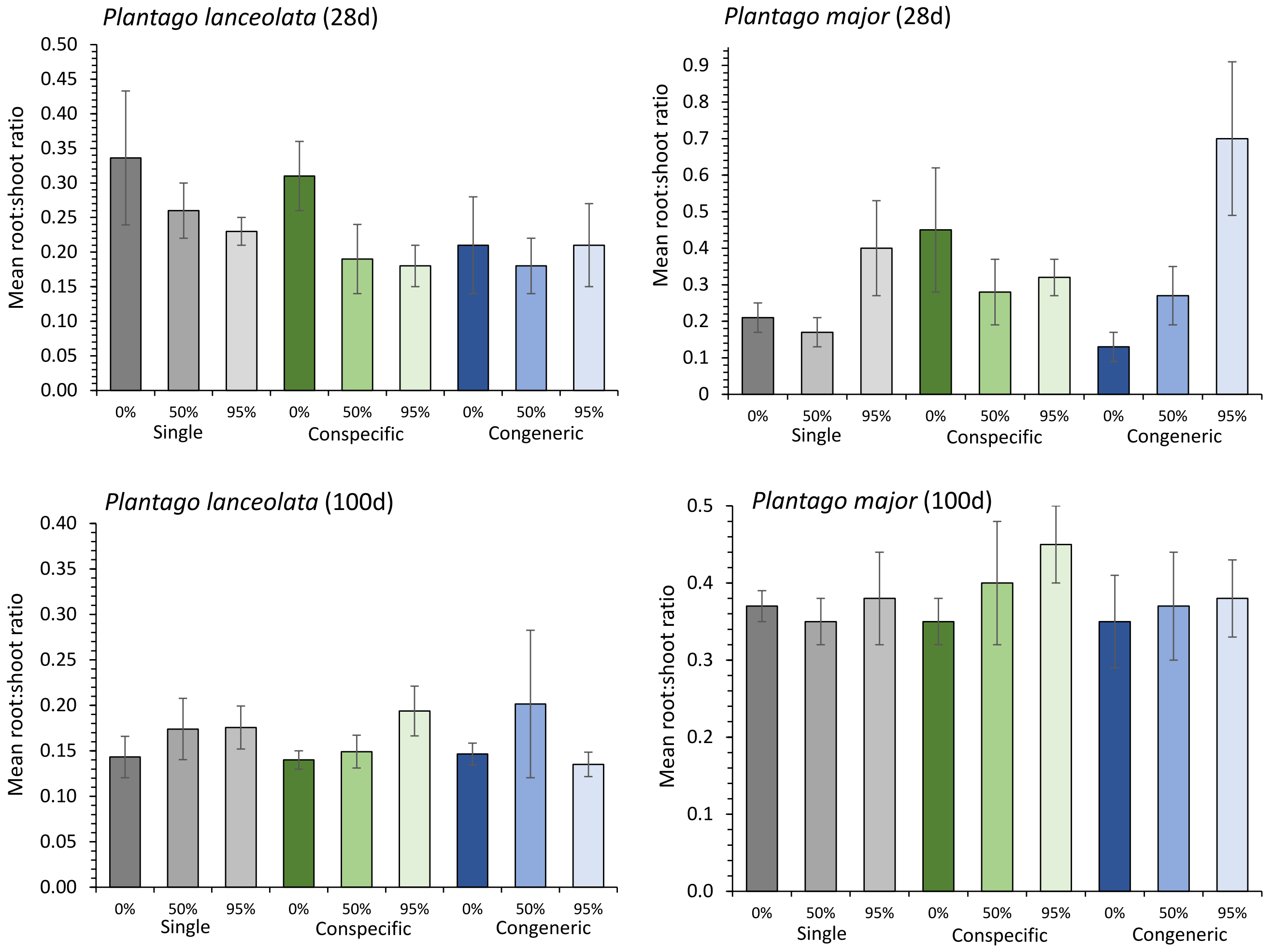

Fig. 2 The effect of seedling defoliation imposed 14-d after germination on subsequent biomass allocation to roots and shoots (mean root:shoot ratio ± SE) of *Plantago lanceolata* and *P. major*. Summary data are shown for plants grown in pots without neighbouring seedlings ('Single'), six conspecific seedlings ('Conspecific'), or six congeneric seedlings ('Congeneric') and compare responses of individuals 14 days (i.e., 28-d-old) or 86 days (i.e., 100-d-old) after 50% or 95% cotyledon loss with untreated controls (0%)

$P = 0.466$; 'Competition' $F_{2,71} = 1.17$; $P = 0.317$; 'Defoliation' × 'Competition' $F_{4,71} = 0.21$; $P = 0.930$).

Similarly, Root:Shoot ratios of *P. lanceolata* showed no variation 28 days ('Defoliation' $F_{2,71} = 0.93$; $P = 0.401$; 'Competition' $F_{2,71} = 1.89$; $P = 0.159$; 'Defoliation' × 'Competition' $F_{4,71} = 0.39$; $P = 0.814$), or 100 days after cotyledon removal ('Defoliation' $F_{2,70} = 0.69$; $P = 0.503$; 'Competition' $F_{2,70} = 0.20$; $P = 0.818$; 'Defoliation' × 'Competition' $F_{4,70} = 0.66$; $P = 0.619$) (Fig. 2).

Discussion

For the most part, our results support the predicted and widely observed negative effect that early ontogenetic tissue removal has on subsequent plant establishment and growth (Strauss and Agrawal 1999; Haukioja and Koricheva 2000; Barton & Koricheva 2010). *Plantago major* (28- and 100 days old) and 28-day harvest *P. lanceolata* plants subjected to 50 and 95% defoliation at 14 days old, were consistently smaller (although the effect was not always statistically significant) than undamaged controls in the same neighbour environment. Nonetheless, the response of *P. lanceolata* at final harvest also underscores how some plants show a remarkable ability to tolerate early ontogeny tissue loss (see Thomson et al. 2003; Hanley & May 2006; Barton 2008, 2013), even when also exposed to competition from neighbouring plants (Parmesan 2000). Weltzin et al., (1998) argued that early ontogenetic tolerance may reflect more effective physiological performance before cotyledons senesce with seedling development (see Ampofo et al. 1976), but since we removed around 95% of the cotyledon tissue, this explanation seems implausible for *P. lanceolata* in our study.

More likely perhaps, *P. lanceolata* seedlings were able to mobilize reserves stored elsewhere, but the lack of any significant shift in relative Root:Shoot biomass allocation at both harvest points indicates that any reallocation to shoot growth was not at the medium/long-term expense of root biomass. Nonetheless, our data closely corroborate Barton (2013) who ascribed higher relative damage tolerance in *P. lanceolata* to enhanced photosynthetic rates and root/shoot allocation plasticity compared to *P. major*. More generally, seedlings that invested more biomass to roots than shoots prior to damage had higher tolerance, an observation that Barton (2013) used to explain why *P. lanceolata* was able to better recover from early ontogenetic tissue loss than *P. major,* and (although we did not quantify this) which may also hold for our experiment.

Our primary goal was however, to determine how an interaction with neighbouring seedlings might affect these well described patterns of post-damage establishment. There was remarkably little mortality (only four plants died in total with no more than one individual from any one treatment group) and despite 'Defoliation' and 'Competition' exerting an influence on plant growth when examined in isolation, there was no instance of any significant 'Defoliation' × 'Competition' interaction for either species. The significant 'Competition' effect for *P. major* at 100-d-old is intuitive given plants were fully established in the relatively small pots and competitive interactions between neighbours would seem inevitable. It is noteworthy however, that for both species, a 'Competition' effect was evident for 28-day old plants, showing that the influence of neighbours was manifest as quickly as 14-d after cotyledon damage to seedlings.

Even though there was no significant 'Defoliation' × 'Competition' interaction, for *P. major*, the 'Competition' effect signalled a marked decline in the size of the most severely defoliated (95%) individuals. More unexpected however, was the apparent early positive effect on plant size that association with neighbours seemed to have for *P. lanceolata*. Classical theory predicts, and experiments often demonstrate, that plant size decreases with increased neighbour density (Harper 1977; Grace 1990; Tracey & Aarssen 2011), yet 14 days after damage was imposed, *P. lanceolata* seedlings, including the most severely damaged, grew larger when in association with conspecific and congeneric neighbours than when without any competitors. This result mirrors closely the Californian field study by Parmesan (2000), showing how early ontogenetic tissue loss in *Collinsia torreyi* had more marked long-term effects on fecundity (seed set) in adults in relatively competitor-free sites than those surrounded by high densities of conspecifics. Interestingly, Parmesan (2000) also observed remarkably low mortality following anything less than total seedling defoliation.

Plant (over)compensation from herbivory is context dependent and can be mediated by soil nutrient and water availability, plant size, and the degree and frequency of damage (Wise & Abrahamson 2007; Ramula et al 2019). Parmesan's (2000) explanation for apparent overcompensation in a field study conducted on very low nutrient soils, was that at high seedling densities, water-limitation prevented carbon fixation being as restrictive for defoliated seedlings as it was in low-competition sites. This explanation highlights the importance of interacting environmental factors during early ontogeny but is unlikely to explain a similar pattern of response to defoliation and neighbour environment in our greenhouse study. It is possible that defoliated *P. lanceolata* seedlings were able to detect the presence of neighbours and mobilize nutrients (internally and/or from the relatively nutrient-rich compost) and use these to achieve rapid, early overcompensation. This reallocation may have had long-term consequences for plant growth; at 100 days, the 95% defoliation plants were smaller than their equivalents in the single plant treatment, but individual survival had been achieved. As Bonser & Aarssen (2009) point out, plants vary not only in maximum attainable size, but also in their minimum reproductive threshold sizes (MPTS). Thus, many individuals reproduce effectively even when their maximum growth is compromised due to factors like competition and herbivory. Although we did not have the opportunity to assess reproductive fitness, the surviving plants likely achieved the MPTS for the species (e.g., they were similar size as flowering individuals in Hanley & Fegan 2007). Indeed, Hanley & May (2006) report that while flowering was delayed, the total number of inflorescences produced by *P. lanceolata* individuals 100-d later was unaffected by complete cotyledon removal in 7-d-old seedlings.

Intuitively (see Hanley & Sykes 2009), we expected cotyledon loss to lead to different recruitment outcomes for the two *Plantago* species depending on their neighbour environment. As consistently the larger of the two species (this includes seed mass and dry biomass of 14-day old seedlings – Hanley unpublished data), *P. lanceolata* is the presumed competitive dominant (see also van der Toorn and Pons 1988), but except for the 95% defoliation treatment at 100 day harvest, there was limited indication that the composition of the neighbour environment affected plant biomass. In this treatment group moreover, average plant size in the congeneric neighbour assemblage was about half that of plants in the conspecific group; presumed competitive dominance over *P. major* would suggest the opposite pattern more likely. Similarly, while *P. major* exhibited little variation in plant size in different neighbour environments at 28- or 100 d harvest in the undamaged and 95% defoliation treatments, at both harvest points, the 50% defoliated plants were unexpectedly larger when grown in association with *P. lanceolata*. The reason for these departures from expectation remain unclear. The presumed dominance of *P. lanceolata* over *P. major* may be unfounded, and/or compromised by how the seedling recovers from defoliation in different environments. Our increasing appreciation of the role of endoreduplication in plant tolerance (Scholes and Paige 2014; Mesa & Paige 2023), may provide the enhanced mechanistic understanding needed to tease apart the complex biosynthetic interactions that dictate how and why plants recover form herbivory.

Our results underscore how the neighbour environment could be one of many external factors that influence patterns of early ontogenetic plant tolerance. Ultimately this is important since spatio-temporal variation in seedling germination, and the number and activity of seedling herbivores will likely conspire with seedling growth-defence trade-offs, including tolerance, to dictate recruitment success for different plant species (Grubb 1977; Barton & Hanley 2013; Liang et al. 2019). A large body of research has shown how selective seedling herbivory by molluscs in particular, interacts with variation in seedling defence and competitive ability to dictate patterns of plant generation in temperate grassland ecosystems (Hanley et al 1995, 1996; Burt-Smith et al 2003; Hanley 2004; Barlow et al 2013). Naturally occurring environmental fluctuations that affect any of these parameters can, consequently, tip the balance towards or away from recruitment success in different species, and so contribute to the maintenance of species diversity in plant communities (Grubb 1977; Hanley and Sykes 2014). Similarly, anthropogenic disruption of natural environmental fluctuation, e.g., through climate-induced shifts in herbivore populations and activity, and/or the expression of seedling ecophysiological traits (Parmesan & Hanley 2015), is likely to disrupt long-established patterns of recruitment, with possible lasting negative consequences for species persistence and community pattern and process.

Author contributions MEH, L H-M and JJST contributed to the study concept and design. Material preparation, data collection and analysis were performed by all authors. The first draft of the manuscript was written by MEH and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding The authors have not disclosed any funding.

Declarations

Competing interests The authors declare no competing interests.

References

Adler PB, Smull D, Beard KH et al (2018) Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. Ecol Letts 21:1319–1329

Ampofo ST, Moore KG, Lovell PH (1976) The influence of leaves on cotyledon photosynthesis and export during seedling development in Acer. New Phytol 76:247–255

Barlow SE, Close AJ, Port GR (2013) The acceptability of meadow plants to the slug *Deroceras reticulatum* and implications for grassland restoration. Ann Bot 112:721–730

Barton KE (2008) Phenotypic plasticity in seedling defense strategies: compensatory growth and chemical induction. Oikos 117:917–925

Barton KE (2013) Ontogenetic patterns in the mechanisms of tolerance to herbivory in *Plantago*. Ann Bot 112:711–720

Barton KE, Hanley ME (2013) Seedling-herbivore interactions: Insights into plant defence and regeneration patterns. Ann Bot 112:643–650

Barton KE, Koricheva J (2010) The ontogeny of plant defense and herbivory: characterizing general patterns using meta-analysis. Am Nat 175:481–493

Bonser SP, Aarssen LW (2009) Interpreting reproductive allometry: individual strategies of allocation explain size-dependent reproduction in plants. Persp Plant Ecol Evol Syst 11:31–40

Burt-Smith GS, Grime JP, Tilman D (2003) Seedling resistance to herbivory as a predictor of relative abundance in a synthesised prairie community. Oikos 101:345–353

Chang-Yang C-H, Needham J, Lu C-L et al (2021) Closing the life cycle of forest trees: the difficult dynamics of seedling-to-sapling transitions in a subtropical rainforest. J Ecol 109:2705–2716

Elger A, Lemoine DG, Fenner M, Hanley ME (2009) Plant ontogeny and chemical defence: older seedlings are better defended. Oikos 118:767–773

Fenner M, Thompson K (2005) The ecology of seeds. Cambridge University Press, Cambridge, UK

Grace JB (1990) On the relationship between plant traits and competitive ability. Persp Plant Comp 2:51–65

Grime JP (2001) Plant strategies, vegetation processes and ecosystem properties. Wiley, Chichester, UK

Grubb PJ (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol Rev 52:107–145

Hanley ME (2004) Seedling herbivory and the influence of plant species richness in seedling neighbourhoods. Plant Ecol 170:35–41

Hanley ME (2012) Seedling defoliation, plant growth and flowering potential in native- and invasive-range *Plantago lanceolata* populations. Weed Res 52:252–259

Hanley ME, Fegan EL (2007) Timing of cotyledon damage affects growth and flowering in mature plants. Plant, Cell Environ 30:812–819

Hanley ME, May OC (2006) Cotyledon damage at the seedling stage affects growth and flowering potential in mature plants. New Phytol 169:243–250

Hanley ME, Sykes RJ (2009) Impacts of seedling herbivory on plant competition and implications for species coexistence. Ann Bot 103:1347–1353

Hanley ME, Sykes RJ (2014) Seedling herbivory and the temporal niche. In: Kelly CK, Bowler MA, Fox GA (eds) Environmental fluctuation, temporal dynamics and ecological process. Cambridge University Press, pp 102–122

Hanley ME, Fenner M, Edwards PJ (1995) An experimental field study of the effects of mollusc grazing on seedling recruitment and survival in grassland. J Ecol 83:621–627

Hanley ME, Fenner M, Edwards PJ (1996) Mollusc grazing and seedling survivorship of four common grassland plant species: the role of gap size, species and season. Acta Oecol 17:331–341

Hanley ME, Shannon RWR, Lemoine DG et al (2018) Riding on the wind: volatile compounds dictate selection of grassland seedlings by snails. Ann Bot 122:1075–1083

Harper JL (1977) Population biology of plants. Academic Press, London

Haukioja E, Koricheva J (2000) Tolerance to herbivory in woody vs. herbaceous plants. Evolutionary Ecol 14:551–562

Hensgen F, Albrecht C, Donath TW, Otte A, Eckstein RL (2011) Distribution of gastropods in floodplain compartments and feeding preferences for river corridor plant species: is there an effect of gastropod herbivory on the distribution of river corridor plants? Flora 206:534–543

Kelly CK, Bowler MG (2005) A new application of storage dynamics: differential sensitivity, diffuse competition and temporal niches. Ecol 86:1012–1022

Kelly CK, Hanley ME (2005) Juvenile growth and palatability in congeneric British herbs. Am J Bot 92:1586–1589

Koricheva J, Nykanen H, Gianoli E (2004) Meta-analysis of tradeoffs among plant anitherbivore defenses: are plants jacks of all trades, masters of all? Am Nat 163:E64–E75

Leimu R, Koricheva J (2006) A meta-analysis of tradeoffs between plant tolerance and resistance to herbivores: combining the evidence from ecological and agricultural studies. Oikos 112:1–9

Liang AJ, Stein C, Pearson E et al (2019) Snail herbivory affects seedling establishment in a temperate forest in the ozarks. J Ecol 107:1828–1838

Mesa JM, Paige KN (2023) Molecular constraints on tolerance-resistance trade-offs: is there a cost? Plant-Environ Interact 4:317–323

Mesa JM, Scholes DR, Juvik JA, Paige KN (2017) Molecular constraints on resistance–tolerance trade-offs. Ecol 98:2528–2537

Moles A, Westoby M (2004) What do seedlings die from and what are the implications for evolution of seed size. Oikos 106:193–199

Parmesan C (2000) Unexpected density-dependent effects of herbivory in a wild population of the annual *Collinsia torreyi*. J Ecol 88:392–400

Parmesan C, Hanley ME (2015) Plants and climate change: complexities and surprises. Ann Bot 115:849–864

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria (https://www.R-project.org/)

Ramula S, Paige KN, Lennartsson T, Tuomi J (2019) Overcompensation: a 30-year perspective. Ecol 100:e02667

Reineke LH (1933) Perfecting a stand-density index for even-aged forests. J Agric Res 46:627–638

Sagar GR, Harper JL (1964) *Plantago major* L., *P. media* L. and *P. lanceolata* L. J Ecol 52:189–221

Salgado-Luarte C, Gonzalez-Teuber M, Madriaza K, Gianoli E (2023) Trade-off between plant resistance and tolerance to herbivory: mechanical defenses outweigh chemical defenses. Ecol 104:e3860

Scholes DR, Paige KN (2014) Plasticity in ploidy underlies plant fitness compensation to herbivore damage. Mol Ecol 23:4862–4870

Strauss SY, Agrawal AA (1999) The ecology and evolution of plant tolerance to herbivory. Trends Ecol Evol 14:179–185

Thomson VP, Cunningham SA, Ball MC, Nicotra AB (2003) Compensation for herbivory by *Cucumis sativus* through increased photosynthetic capacity and efficiency. Oecol 134:167–175

Tiffin P, Inouye BD (2000) Measuring tolerance to herbivory: accuracy and precision of estimates made using natural versus imposed damage. Evol 54:1024–1029

Tracey AJ, Aarssen LW (2011) Competition and body size in plants: the between-species trade-off for maximum potential versus minimum reproductive threshold size. J Plant Ecol 4:115–122

van der Toorn J, Pons TL (1988) Establishment of *Plantago lanceolata* L. and *Plantago major* L. among grass. Oecol 76:341–347

Vospernik S, Sterba H (2015) Do competition-density rule and self-thinning rule agree? Ann for Sci 72:379–390

Watkinson AR (1997) Plant population dynamics. In: Crawley MJ (ed) Plant ecology, 2nd edn. Blackwells, Oxford, UK, pp 359–400

Weltzin JF, Archer SR, Heitschmidt RK (1998) Defoliation and woody plant (*Prosopis glandulosa*) seedling regeneration: potential vs realized herbivory tolerance. Plant Ecol 138:127–135

White J (1985) The thinning rule and its application to mixtures of plant populations. In: White J (ed) Studies on plant demography. Academic Press, London, pp 291–309

Wise MJ, Abrahamson WG (2007) Effects of resource availability on tolerance of herbivory: a review and assessment of three opposing models. Am Nat 169:443–442