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ORIGINAL PAPER

Increased adaptive phenotypic plasticity in the introduced range in alien weeds under drought and flooding

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Abstract Phenotypic plasticity is an essential mechanism by which plants respond to changes in their environment, but our understanding of the evolution of plasticity is still limited. Comparing plasticity of introduced alien species across native and introduced provenances can indicate potential evolution of adaptive plasticity. We examined reaction norms across an experimental soil moisture gradient for native and introduced provenances of two *Rumex* spp. to ask whether plasticity was (a) adaptive or maladaptive, (b) greater in the more widespread *R. obtusifolius*, and (c) greater in the introduced range. We cloned genotypes from the United Kingdom (native range) and New Zealand (introduced range) and grew them under drought, mesic or flooded conditions. We measured biomass and functional traits to assess differences in, and fitness implications of, trait means and plasticity, where plasticity was quantified as the slope of the reaction norm. Plasticity to drought was often positively correlated with biomass and likely adaptive, while plasticity to flooding was sometimes negatively correlated with biomass and thus potentially maladaptive. Plasticity to drought was greater in *R. obtusifolius* than in the less widespread *R. conglomeratus*, as expected, although no difference was found under flooding. Compared to plants from the native range, introduced provenance *R. obtusifolius* had greater plasticity in chlorophyll content and water use efficiency under drought, both of which were positively correlated with biomass, suggesting that greater adaptive plasticity may have evolved in New Zealand. This capacity for adaptation could increase their range and exacerbate their impact in the future.

Keywords Climate change · Clonal · Exotic · Fitness homeostasis · Functional traits · Specific leaf area

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Introduction

Alien plants provide a compelling opportunity to evaluate the role and evolution of phenotypic plasticity in response to climate extremes and changing abiotic environments (Moran and Alexander 2014). Plants can respond to these selective pressures through adaptive phenotypic plasticity, where trait expression is sensitive to environmental conditions in a way that improves fitness (Bradshaw 1965; van Kleunen and Fischer 2005; Richards et al. 2006; Ghalambor et al. 2007; Nicotra et al. 2010; Chevin et al. 2010; Pauls et al. 2013). It has long been suggested that invasive alien plant species should have high levels of phenotypic plasticity, either inherently or following evolution in the introduced range (Ghalambor et al. 2007; Matesanz et al. 2010), allowing them to establish in novel or stressful habitats (Baker 1974; Sultan 2000; Richards et al. 2006; Wennersten and Forsman 2012; Forsman 2015). If naturalized alien species are highly responsive to changing conditions in the introduced range, then understanding their plastic and evolutionary responses to environmental conditions may be important for forecasting their spread and impact (Diez et al. 2012; Moran and Alexander 2014; Felton and Smith 2017). Studies in the introduced range have demonstrated high plasticity in alien plants (Davidson et al. 2011; Liao et al. 2016). But fewer studies have compared plasticity between genotypes from native and introduced provenances to test for potential evolution of plasticity in plants following their introduction and whether such plasticity is actually beneficial (Matesanz et al. 2010). Some studies have indicated that the evolution of increased plasticity can occur quite rapidly following invasion (Sultan et al. 2013). Nonetheless, it is still unclear in many cases whether phenotypic plasticity is adaptive, the extent to which it varies between populations, and whether it has evolved to increase in the introduced range (van Kleunen and Fischer 2005; Hulme 2008; Colautti and Lau 2015; Colautti et al. 2017; Matesanz and Ramírez-Valiente 2019).

Phenotypic plasticity is itself a heritable trait, which can vary within a species and can evolve in response to natural selection, particularly in highly variable environments (Lee and Gelembiuk 2008; Chevin et al. 2010; Chevin and Hoffmann 2017). Conditions in the introduced range may therefore select for increased plasticity, particularly if species are more likely to establish in variable environments, or if environmental conditions in the introduced range differ from those in the native range (Ghalambor et al. 2007; Franks et al. 2014; Valladares et al. 2014; Chevin and Hoffmann 2017). Intraspecific comparisons between the native and introduced ranges of naturalized species can therefore provide a model for evolutionary responses to novel environments (Hulme and Barrett 2013; Moran and Alexander 2014). Not all plasticity improves fitness, however. Some plasticity promotes fitness by shaping plant traits to better match environmental optima, but some shifts in plant traits are a passive result of stress or a mismatch between environmental cues and plant responses (van Kleunen and Fischer 2005). Such plasticity may have no effect on fitness or can be maladaptive, decreasing fitness relative to genotypes with low plasticity. Studies comparing plasticity in native and introduced ranges must therefore consider not only the magnitude, but the direction of trait change and the resulting fitness consequences of plasticity (van Kleunen and Fischer 2005; Hulme 2008; Matesanz et al. 2010), however this is still not consistently done. Constraints and costs of plasticity may also limit the extent and evolution of plastic responses (van Kleunen and Fischer 2005; Murren et al. 2015) and in some cases mean trait values may be more important than trait plasticity, or the two may interact to determine fitness outcomes (Godoy et al. 2012; Conti et al. 2018). For example, trait means and plasticity may be correlated and respond jointly to selection, and differences in plasticity may be confounded by differences in means unless both are taken into account (van Kleunen and Fischer 2005; Ghalambor et al. 2007). Many evolutionary studies focus on shifts in trait means, but understanding the evolution of plasticity in response to the environment requires considering the interaction between changes in trait means and trait plasticity in response to environmental variability (Matesanz et al. 2010; Godoy et al. 2012; Colautti et al. 2017). Patterns of variation in plasticity between populations or ranges can influence species persistence and range shifts, but these patterns are rarely tested and the costs and trade-offs between them are not well understood (Matesanz et al. 2010; Valladares et al. 2014; Colautti and Lau 2015; Matesanz and Ramírez-Valiente 2019; De Kort et al. 2020). Therefore, to better understand the functional role and evolution of phenotypic plasticity, detailed studies that evaluate the fitness consequences of plasticity across multiple traits using both native and introduced provenances are needed (Matesanz and Ramírez-Valiente 2019).

Using two *Rumex* species (Polygonaceae) that differ in their impact and spread, we tested for evidence of increased adaptive plasticity in the introduced range. If overcoming introduction barriers and establishment in novel environments selects for greater phenotypic plasticity, we might expect a higher degree of plasticity in the introduced than in the native range in those functional traits that promote fitness homeostasis, which could further exacerbate the spread of alien weeds. Because it has a broader range of environmental tolerances, we expect *R.*

obtusifolius, a globally significant weed, to show greater adaptive plastic responses, particularly to drought, than the less abundant *R. conglomeratus*, which is often restricted to wetlands and riparian habitats (Holm et al. 1977; Lousley and Kent 1981; Zaller 2004; Grime et al. 2007). Soil moisture is a key environmental gradient to consider for these *Rumex* species as they grow across environments that show a wide range of precipitation and soil moisture and exhibit differences in their soil moisture tolerances (Lousley and Kent 1981; Webb et al. 1988). This means that plasticity to soil moisture is likely to be important for their success across the landscape, particularly in their introduced range in New Zealand, which has strong precipitation gradients (NIWA Taihoro Nukurangi 2019). To understand the implications of increased plasticity, it is essential to consider not only whether traits change, but the effects of any plasticity on fitness or a fitness proxy, since only adaptive plasticity promotes plant success and should be under selection (van Kleunen and Fischer 2005). By using the slope of the reaction norm as a measure of phenotypic plasticity and testing for associations between this plasticity and biomass, we can robustly assess whether adaptive plasticity has evolved in the introduced range. We therefore used genotypes derived from multiple native and introduced populations and measured the relationships between four key functional traits (i.e. chlorophyll, root shoot ratio, specific leaf area, water use efficiency) and biomass across an experimental soil moisture gradient to ask:

1. Which traits show adaptive plasticity, defined as an association between the slope of a reaction norm and increased biomass, under drought and flooding in *Rumex* species?
2. Does the more widespread alien *Rumex obtusifolius* have greater phenotypic plasticity than the more locally naturalized species, *R. conglomeratus*?
3. Have genotypes from the introduced range evolved greater adaptive plasticity than genotypes from the native range?

Materials and methods

Species

Both *Rumex obtusifolius* L. and *R. conglomeratus* Murray are fast-growing herbaceous biennials or perennials native to Eurasia and have been introduced around the world (Cavers and Harper 1964; Grime et al. 2007, USDA, Agricultural Research Service, National Plant Germplasm System 2019). Classed as one of the world's worst weeds (Holm et al. 1977) both in its native and introduced ranges, *R. obtusifolius* occurs across a broad environmental range while *R. conglomeratus* has a more limited habitat distribution, often restricted to waterways, and is rarely considered a problematic species (Cavers and Harper 1964; Holm et al. 1977; Lousley and Kent 1981; Grime et al. 2007). Both species were likely accidental introductions to New Zealand from the United Kingdom arriving in the mid-1800s and are now found across low-elevation environments in New Zealand (Webb et al. 1988). Although many studies of plasticity use half-sib families or coarser levels of genetic resolution, *Rumex* spp. are easily propagated from root cuttings, which allowed us to assess plasticity of individual genotypes across a range of environmental conditions (Richards et al. 2006). Because these *Rumex* spp. typically overwinter as a rosette and flower in their second growing season after attaining sufficient rosette size, we used total biomass as a proxy for fitness, as biomass is strongly related to seed production in these ruderal species (Pino et al. 2002; Grime et al. 2007).

Seed sources

We collected seeds of *R. obtusifolius* and *R. conglomeratus* from the native range in the United Kingdom (n = 11–12 populations per species) and the introduced range in the South Island of New Zealand (n = 11 populations per species; Fig. S1 in Supporting Information) across a range of climates, habitats, and latitudes. New Zealand has strong precipitation gradients over relatively short distances (NIWA Taihoro Nukurangi 2019), creating an environment in which we might expect selection for plasticity (Ghalambor et al. 2007). We collected native provenance individuals from the UK because it is the predominant source from which these *Rumex* spp. were introduced to New Zealand (Darwin 1845 p. 454). As *Rumex* spp. were historically common seed contaminants, introduction likely occurred over many years and from multiple sources (Holm et al. 1977). We therefore included sites that spanned a substantial portion of the range of climates within both the UK and NZ where these *Rumex* spp. are found. This captured a wide range of variation within both the native and the introduced range so that any differences are likely to represent true differences between provenances, whether adaptive or a result of processes like genetic drift, rather than simply reflecting sampling biases or within-country clines. Populations were separated from each other by 35 ± 3.5 km (mean ± SE) and had on average 106 ± 20 fruiting individuals within a 25 m radius (mean ± SE). We used seeds collected from two individuals at least one metre apart where possible. Seeds were collected in the autumn in both countries, in September and October, 2016 in the UK and from late February to early May, 2017 in NZ and stored dry at room temperature until needed. Seeds from the UK were imported into NZ under Ministry for Primary Industries permit 201661142.

Selected functional traits and environmental gradient

Soil moisture is a known driver of *Rumex* distributions (Cavers and Harper 1964; Lousley and Kent 1981; Grime et al. 2007) and may exert selective pressure towards the evolution of plasticity in key traits related to water use (Felton and Smith 2017; Ummenhofer and Meehl 2017), particularly given recent and expected increases in drought and flooding as a result of climate change (Knapp et al. 2008; Seneviratne et al. 2012; Coumou and Rahmstorf 2012; Dai 2013). However, determining which traits show adaptive plasticity in response to water availability gradients has been challenging (Nicotra and Davidson 2010). Under drought, excessive water loss through stomata compels plants to reduce stomatal openings to prevent xylem cavitation, but this limits the uptake of CO_2 needed for photosynthesis (Chaves et al. 2003; McDowell et al. 2008). To counter this, plants may invest in roots (root shoot ratio) to improve water uptake, or produce smaller, thicker leaves (specific leaf area, SLA) to reduce water loss (Chaves et al. 2003; Nicotra and Davidson 2010). Drought tolerant plants also maintain or increase chlorophyll content under drought conditions (Ashraf and Harris 2013) which may compensate for decreased leaf size and promote rapid recovery when conditions improve (Avramova et al. 2015). These changes along with changes in enzyme expression in photosynthetic pathways may increase water use efficiency (WUE) (Nicotra and Davidson 2010), as has been seen in *R. obtusifolius* under drought (Gilgen et al. 2010). Under flooded conditions, where gas exchange to improve aeration is more important than water conservation, many of these traits are expected to respond in the opposite direction, with greater allocation towards aboveground biomass, larger and thinner leaves as well as high transpiration and low water use efficiency (Mommer et al. 2006). Based on these a priori expectations, we therefore examined plasticity in root shoot ratio, SLA, chlorophyll content and WUE in response to flooding and drought using plant biomass as a fitness proxy to test for adaptive plasticity in genotypes of these *Rumex* spp. from the native and introduced ranges.

Greenhouse experiment

Seeds from two maternal lines per population were planted in the greenhouse in potting soil in August, 2017. We chose to plant only two lines per population to maximize the number of populations tested and emphasize quantifying variation across the geographic range rather than within populations. This approach maximizes the diversity captured across the native and introduced ranges and more robustly tests for differences between provenances, rather than differences within populations, consistent with our research questions. However, one maternal line of *R. conglomeratus* could not be used, resulting in only a single maternal line within that UK population. After two months, the largest seedling from each maternal line, chosen to maximize survival and ability to clone, was transplanted into a 2 L pot and grown in potting soil (1:4 pumice:bark, Osmocote 16–3.9–10 N–P–K 3 g/L, horticultural lime 1 g/L, Hydraflo 1 g/L) for three months (*R. conglomeratus*) or seven months (*R. obtusifolius*) before cloning. Cloning occurred immediately before the experiment began, when greenhouse space was available. *Rumex obtusifolius* root fragments (12.8 ± 0.3 g) were larger than *R. conglomeratus* fragments (9.7 ± 0.2 g) at the start of the experiment, but within species there was no difference in growing time between our treatments or between native and introduced range individuals, and initial fragment weight was accounted for in our models. We cloned individuals by cutting the root collar longitudinally into pieces, retaining one leaf per piece wherever possible and removing all other leaves. Each fragment was weighed, dipped in rooting hormone (3 g/kg beta indolylbutyric acid, Seradix 2, Rhône-Poulenc) and planted in a 50:50 sand:sieved topsoil mix in 10 L planter bags (PB 18, Egmont) for the experiment. The experiment included a total of 172 plants from 43 genotypes or clone lines (2 ranges × 11 populations × 2 genotypes) of *R. conglomeratus* and 184 plants from 46 genotypes (2 ranges × 11–12 populations × 2 genotypes) of *R. obtusifolius*. Each genotype was cut into four clones, one clone for each of four water treatments. The cuttings established over two weeks under well-watered conditions, and clones from each individual were haphazardly assigned to the four water treatments. Pots were randomly assigned to one of three blocks across the greenhouse such that all clones of a genotype, but not necessarily both genotypes from a population, were together in the same block to minimize variation within clones from sources other than the treatment. Each block included approximately equal representation of genotypes from native and introduced provenances.

The water treatment comprised a series of exponentially increasing water availability, where pots were watered to create a broad moisture gradient ranging from hard dry soil, which caused wilting, to completely saturated soil with standing water in trays at the base of each pot. This resulted in measured mean soil moisture values of 5% (drought), 8% (dry), 18% (mesic) and 34% (flooded). We define drought by soil moisture, as this is a robust measure of water availability (Slette et al. 2019). However, because the drought and dry treatments had similar soil moisture and trait and fitness distributions overlapped for these two treatments, we have combined these into a single drought treatment for the analyses. To retain water in the two highest treatments, much of which would otherwise be lost at the time of application, individual trays were placed under each of those pots. For plants in the highest water treatment, this generally resulted in permanent standing water around the bottom ~ 3 cm of the pot and helped mimic a waterlogged soil environment, such as might be found along stream or pond margins or as a result of flooding. This allowed us to separately assess genotype responses to drought (lowest two soil moisture treatments) and flooding (highest soil moisture treatment), with plants grown in mesic conditions (soil moisture ~ 18%) as the control in each comparison. Pots were watered every 3–4 days in summer and autumn and once per week in winter to account for changes in evapotranspiration and to maintain the soil moisture gradient. Artificial lighting was provided in winter to increase the effective day length. Water treatments were maintained for 10 weeks, at which point the plants were harvested. Plants in natural populations typically grow most vigorously in spring and early summer, and plant size at this time is important to determine flowering success (Grime et al. 2007). After 10 weeks in the greenhouse, plants in the mesic treatments had filled the space available in the pots and had a mean of 12 (*R. obtusifolius*) to 34 (*R. conglomeratus*) leaves. Soil moisture was measured regularly throughout the experiment using an HH2 Moisture Meter with an ML2x ThetaProbe (Delta-T Devices). For each set of measurements, we haphazardly selected 15 individuals in each treatment and measured soil moisture in the upper layer of soil near the plant stem (Table S1; Fig. S2).

At harvest, we collected data on plant biomass and key traits related to plant water use and photosynthesis. Leaf-level data were collected on the youngest fully expanded leaf, which developed during the course of the experiment and thus reflected plant strategies under the soil moisture treatment regime. For each plant, we measured gas exchange between approximately 10:30 am and 1:30 pm using a LI-6400 (LI-COR) with red/blue LED light source and integrated CO_2 mixer, with the temperature set for the expected mean temperature for that period each day (mean leaf temperature 21.8 °C, range 19.09–26.43 °C). We also measured chlorophyll as an average of three readings from the leaf using a SPAD-502 Chlorophyll Meter (Konica Minolta Sensing, Inc.). The leaf was imaged using a flatbed scanner to measure leaf area and then dried and weighed. Leaf area was calculated from the images using ImageJ (Rasband 2012) and the package 'LeafArea' (Katabuchi 2017) in R (R Core Team 2018). We recorded the clean, fresh weight and dry weight of the aboveground and belowground biomass for each plant. For one lost sample, shoot dry weight was imputed from the wet weight, with which it is very highly correlated (r = 0.97), using a model based on the interaction between fresh weight and treatment. We used these data to calculate the root to shoot ratio (root dry weight/shoot dry weight), specific leaf area (SLA, leaf area/leaf dry weight in $cm^2 g^{-1}$), and water use efficiency (WUE, photosynthetic rate/transpiration rate in $\mu mol CO_2 mmol H_2O^{-1}$). Additionally, we measured soil moisture at three points haphazardly spaced around each pot at harvest.

We excluded two *R. obtusifolius* plants (one in drought and one in the flooding treatment, from different genotypes) which had died above-ground or retained only a single old leaf, as this severely distorted the trait data. We also excluded two *R. conglomeratus* plants from the flooding treatment where the difference in pot-level soil moisture between the flooding and mesic treatments within the genotype was less than 2%, as in this case the flooding treatment did not represent an increase in soil moisture over the mesic treatment.

Data analysis

For each genotype, we calculated mean trait values and the slope of the reaction norm for two soil moisture comparisons, each moving across the changes in soil moisture from mesic to increasing water stress (either drought or flooded). Measuring plasticity using a reaction norm (Reed et al. 2011), instead of the coefficient of variation or other metrics (Valladares et al. 2006), allows us to assess not only the magnitude, but also the direction of trait change, which is particularly important where the direction changes between genotypes (van Kleunen and Fischer 2005) and provides a more interpretable connection between trait change and biomass. Furthermore, measuring plasticity as the slope of the reaction norm allows us to calculate change across the measured soil moisture values, rather than relying on less precise treatment categories. Mean trait values and biomass were calculated by taking the mean of the trait or biomass across treatments within a genotype (e.g. mean of drought and mesic trait values for a clone line). We calculated trait means across treatments so that means and the slope of the reaction norm could be considered simultaneously in our analyses, as plasticity can only be calculated across treatments. Furthermore, plants are expected to experience a range of soil moisture conditions over time and therefore mean trait values are relevant for understanding overall performance of a genotype across treatments.

To examine whether trait plasticity (slope of the reaction norm) in response to drought or flooding was associated with increased performance, and therefore putatively adaptive (Q1), we used linear mixed effects models. We modelled mean biomass across the soil moisture treatments as a function of the slopes of the reaction norms and trait means. Because plant functional traits are often correlated or demonstrate tradeoffs, plasticity is likely to vary across multiple traits simultaneously either directly as a result of selection or due to genetic or physiological constraints (Ghalambor et al. 2007).

Therefore, to account for correlations between traits, assess the role of multiple traits within a single model, and improve the interpretability of the results, we first conducted principal components analyses (PCA). To derive a measure of multi-trait plasticity, we ran a PCA on the slopes of the reaction norm for each trait for each individual genotype (multi-trait plasticity PCA). This approach has been recommended when examining plasticity at the individual plant or population level (Lande and Arnold 1983; Forsman 2015). We assessed whether multi-trait plasticity was adaptive by testing for a significant effect of PC axes on biomass. We determined which traits contributed most to any adaptive multi-trait plasticity using the loadings for PC axes significantly related to biomass. The traits with reaction norm slopes that were most strongly correlated with the PC axes contributed most to any adaptive multi-trait plasticity, if the relationships were positive, or indicated maladaptive plasticity, if the relationships were negative. This approach therefore allowed us to distinguish between adaptive and maladaptive plasticity and examine suites of traits that together affect fitness. We also conducted a similar PCA using the means of each trait across treatments for each genotype (multi-trait mean PCA). A significant effect of a multi-trait mean PC axis on biomass indicated a benefit of traits correlated with that axis. Whether high or low trait values were beneficial was determined from the sign of the loading of the trait on the PC axis.

We therefore modelled mean biomass across treatments as a function multi-trait plasticity (multi-trait plasticity PCA axes 1 and 2) and multi-trait means (multi-trait plasticity PCA axes 1 and 2). We used the first two PC axes for each PCA as the first two axes together represented 69–80% of the original variation (Table S2). In *R. obtusifolius*, there were also strong correlations between some trait means and their plasticity under drought (chlorophyll and WUE, $r > 0.4$, $p \leq 0.0015$), and therefore for this model we used a single PCA (multi-trait combined PCA) that included both means and plasticity to improve interpretation. In this case, we included the first three PC axes to represent 67% of the variation. Native or introduced provenance was also included as a fixed effect and the models accounted for the mean fresh weight of the initial root fragment across treatments as a fixed effect and block and population as random effects. For all models, we assessed significance of fixed effects using parametric bootstrapped 95% confidence intervals and random effects were assessed using likelihood ratio tests (Bolker et al. 2009). We also examined model diagnostics, influential points and R^2 values (Nieuwenhuis et al. 2012; Lefcheck 2016) and only considered effects which were robust to the removal of outliers or influential points.

To compare phenotypic plasticity between species (Q2), we used linear mixed effects models to test for a significant difference in the magnitude of plasticity to drought and flooding for each of the four traits. As in the previous analyses, plasticity was measured as the slope of the reaction norm. In order to test for differences in adaptive plasticity, we accounted for the direction in which plasticity was associated with increased biomass, if at all, based on the modelling results from Q1. Where the slope of the reaction norm differed in sign between species, we multiplied one set of plasticity values by -1 so that in both cases increasingly positive values indicated greater adaptive plasticity. We included species as a fixed effect and species-specific block and population as random effects. This allowed us to directly test whether adaptive plasticity, the response variable, was greater in the more widespread species, *R. obtusifolius*, which we assessed using likelihood ratio tests.

To evaluate the differences in traits and their change in response to soil moisture between native and introduced provenances, we modelled biomass and trait values as a function of soil moisture, provenance and the interaction between the two for each species separately using linear mixed effects models (Q3). These models accounted for greenhouse block and source population as random effects and separate models were run for each species and trait and for drought and flooding treatments. The model of biomass also included fragment weight as a fixed effect to account for any initial differences in size. Significance of the terms in the model was assessed using likelihood ratio tests.

All mixed models were run in R (R Core Team 2018) using the package 'lme4′ (Bates et al. 2015). Plots were created using the package 'ggplot2′ (Wickham 2009).

Results

(Q1) Which traits show adaptive plasticity under drought and flooding?

Plant biomass and all functional traits showed significant differences across soil moisture treatments (Fig. 1; Fig. S3). Plants in drought conditions only reached half of the biomass of plants in mesic conditions (*R. conglomeratus* 49 ± 6%, *R. obtusifolius* 46 ± 6% of mesic, $p < 0.0001$) while flooding had a minor impact on biomass (*R. conglomeratus* 91 ± 9%, *R. obtusifolius* 90 ± 11% of mesic, $p \leq 0.04$). The greatest plasticity, measured as the slope of the reaction norm, occurred in chlorophyll content and WUE under drought for *R. obtusifolius*, while the reaction norms show less response to flooding in both species (Fig. 2). Under flooding, the slope of the reaction norm varied in both magnitude and direction between genotypes within a species and provenance, while under drought the direction of the reaction norms was more consistent, indicating that it was essential to consider not only the magnitude but also the direction of plasticity in further analyses. Plasticity in chlorophyll content and WUE tended to covary, while plasticity in SLA and root shoot ratio tended to trade off with each other and were less correlated with chlorophyll and WUE (Table S2).

Multi-trait plasticity, measured with a PCA of trait reaction norms, was an important predictor of biomass in genotypes of *R. obtusifolius* under both drought and flooding, as were multi-trait mean values (Fig. S4). Across mesic and drought treatments, higher biomass was explained by multi-trait plasticity that increased chlorophyll content and WUE with drought, and by greater mean root shoot ratio and lower mean SLA. These traits were associated with the significant multi-trait combined PC first axis, where the PCA included

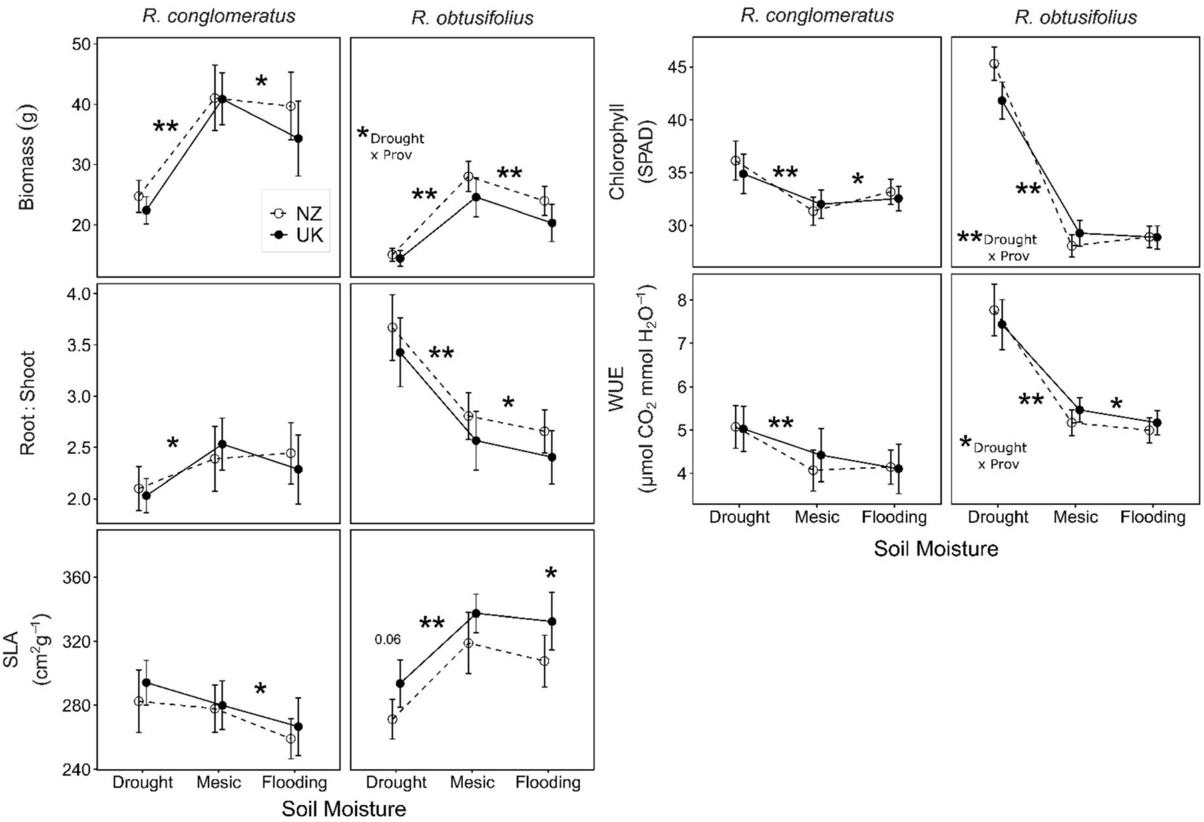

Fig. 1 Trait means and 95% confidence intervals for four key traits and total dry biomass under drought, mesic or flooded conditions for genotypes of *Rumex conglomeratus* and the more invasive *R. obtusifolius* from the native (UK, dark circles) and introduced (NZ, open circles) range. Stars indicate significance (***< 0.0001, **< 0.001, *< 0.05) where stars over the line between treatments indicate a significant main effect of soil moisture, and stars over the points indicate a significant main effect of provenance. A significant interaction between provenance and soil moisture across drought is indicated with text

both reaction norm slopes and trait means (Fig. 3; Table S2), while random effects had no explanatory power (marginal and conditional $R^2 = 0.66$). Reaction norm slopes varied across genotypes from no response to drought to marked trait change, and this variation was well represented by a linear relationship with the relevant multi-trait combined PC axis (Fig. S5). Across flooding, greater mean root shoot ratio (multi-trait mean PC first axis) predicted higher biomass (Fig. 3; Table S2). Plasticity that increased SLA and decreased root shoot ratio (multi-trait plasticity PC second axis) under flooding also increased biomass, although the effect was not as strong (Fig. S5). Interestingly, genotypes varied in both the magnitude and direction of their reaction norm slopes. Some genotypes displayed maladaptive plasticity, as indicated by plasticity in a direction that decreased biomass (Fig. S5). Both fixed effects and the random effect of block ($p = 0.047$) were important in the model and the explanatory power was high (marginal $R^2 = 0.78$, conditional $R^2 = 0.89$).

Similarly, for *R. conglomeratus*, multi-trait plasticity was a significant predictor of biomass under drought, and trait means were significant predictors under both drought and flooding (Fig. S4). Biomass across mesic and drought treatments increased with a greater mean root shoot ratio and WUE (multi-trait mean PC second axis) and a shift towards investment in shoots with drought (multi-trait plasticity PC second axis; Fig. 4; Table S2), in contrast to *R. obtusifolius* where plasticity increased investment in roots (Fig. 2). Root shoot ratio generally shifted towards increasing investment in shoots, but not always, with some genotypes showing maladaptive plasticity that increased investment in roots instead (Fig. S6; Fig. 4). Under flooding, high mean root shoot

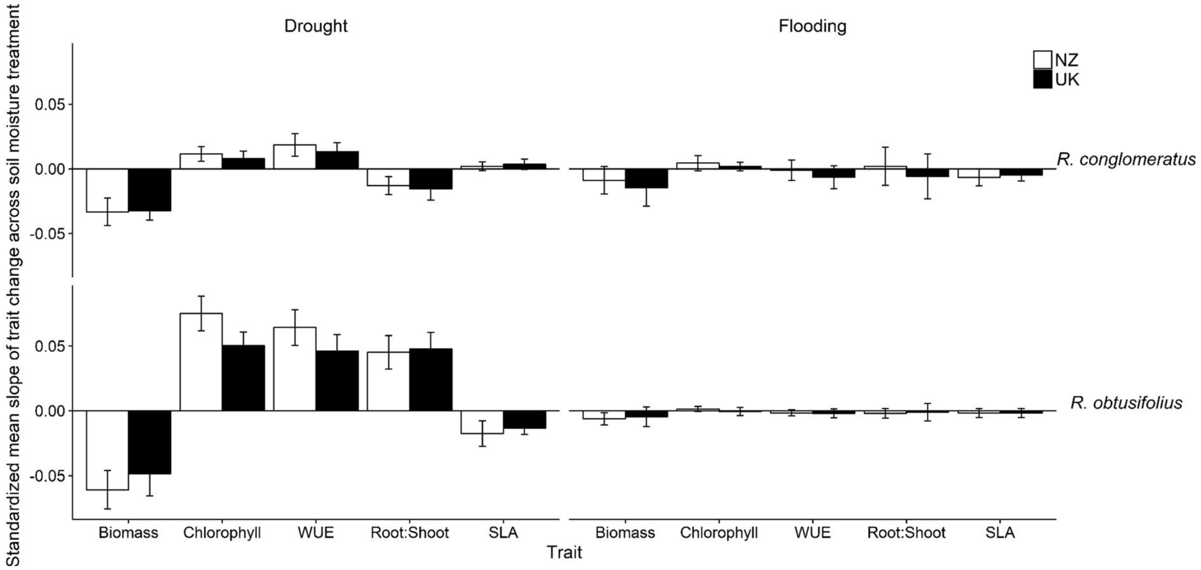

Fig. 2 Standardised mean slope of the reaction norm (plasticity) of traits for *Rumex conglomeratus* and the more invasive *R. obtusifolius*. Plasticity is calculated as the slope of the reaction norm across decreasing (drought) or increasing (flooding) soil moisture and standardized by dividing both the mean and the 95% confidence intervals (bars) by the mean trait value under mesic conditions, resulting in a standardized plasticity that indicates change as a proportion of the mesic value. Thus, a standardized plasticity of 0.01 indicates that per 1% change in soil moisture, the trait changed by 1% of its mean under mesic conditions

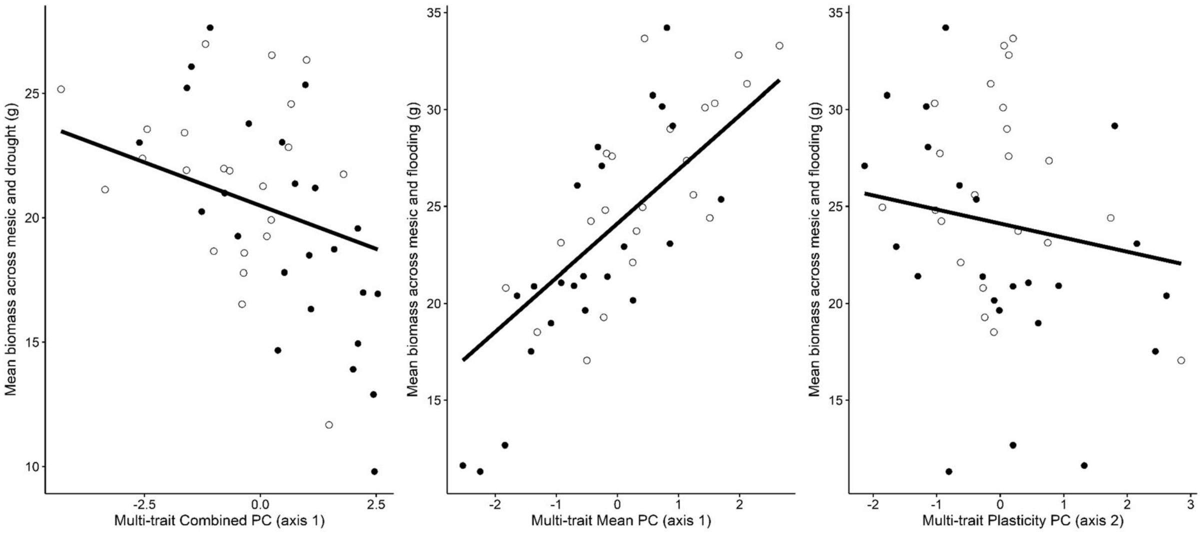

Fig. 3 The effects of multi-trait plasticity, multi-trait means, or multi-trait combined plasticity and means, represented by PC axes, on mean final biomass of *Rumex obtusifolius* across drought (left) and flooding (centre, right) gradients. Points represent individual genotypes with introduced (NZ) genotypes in unfilled circles and native (UK) provenance individuals in filled circles. The lines show a partial regression from mixed effects models across all points. Only significant effects are shown

ratio and WUE were associated with greater biomass (multi-trait mean PC first axis; Fig. 4; Table S2). The explanatory power of the models was moderate across both flooding (marginal $R^2 = 0.58$, conditional $R^2 = 0.65$) and drought (marginal $R^2 = 0.46$, conditional $R^2 = 0.58$) and was due largely to fixed effects.

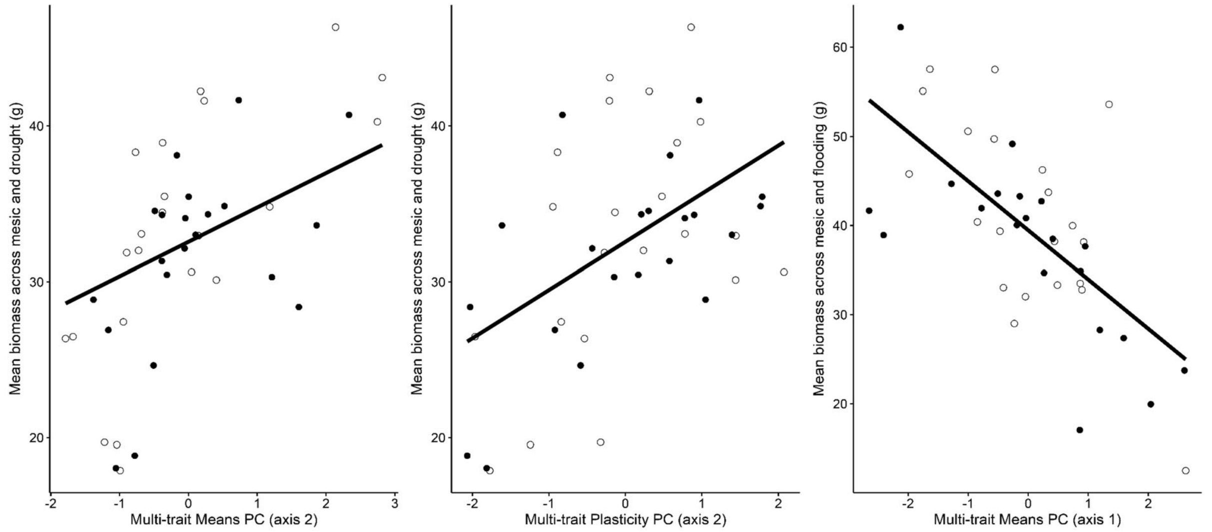

Fig. 4 The effects of multi-trait plasticity and multi-trait mean PC axes on mean biomass of *Rumex conglomeratus* across drought (left, centre) or flooding (right) gradients. Trait plasticity is measured as the slope of trait change moving from mesic to stressful conditions. Points represent individual genotypes with introduced (NZ) genotypes in unfilled circles and native (UK) provenance individuals in filled circles. The lines show a partial regression from mixed effects models across all points. Only significant effects are shown

(Q2) Does the more widespread alien *Rumex obtusifolius* have greater plasticity?

Across all traits under drought, *R. obtusifolius* exhibited between four- and six-fold larger reaction norm slopes than its congener (likelihood ratio tests: all $p \leq 0.03$), even where this plasticity was not associated with increased biomass in *R. obtusifolius* (Fig. 2). There were no significant differences in reaction norms between species under flooding (likelihood ratio tests: $p > 0.07$). Loss of biomass in response to drought and flooding was similar between species (likelihood ratio tests: $p > 0.2$).

(Q3) Have genotypes from the introduced range evolved greater adaptive plasticity?

In *R. obtusifolius*, there was a significant interaction between provenance and soil moisture for chlorophyll content and WUE across the mesic and drought treatments (Fig. 1) indicating significantly greater plasticity to drought in chlorophyll ($p < 0.0001$) and WUE ($p = 0.016$) in introduced range genotypes (Fig. 2). Genotypes of *R. obtusifolius* from the introduced range also had lower SLA under mesic and flooding treatments than genotypes from the native range ($p = 0.02$) as well as under mesic and drought treatments, though this was marginally non-significant ($p = 0.06$). The interaction between provenance and soil moisture in all other traits was not significantly different between provenances. All traits showed a significant response to low soil moisture ($p < 0.0001$), and root shoot ratio and WUE showed a significant response to flooding ($p \leq 0.04$). Source population was not a significant random effect in any model, indicating that variation is not strongly partitioned by population. Biomass decreased significantly in response to flooding and drought ($p < 0.0001$) and the decline in biomass was greater for native provenance plants under drought (provenance x soil moisture $p = 0.0013$).

In *R. conglomeratus*, there were significant changes in chlorophyll content under both flooding and drought, SLA under flooding, and WUE and root shoot ratio under drought ($p < 0.026$). Because the slopes of the reaction norms differed from zero, this indicates significant plasticity in these cases. Provenances did not differ for any trait (Fig. 1), nor were there significant provenance by treatment interactions and therefore no significant differences in plasticity between provenances (Fig. 2). There was significant variation between populations (root shoot ratio under drought, $p = 0.025$) and genotypes within populations (SLA, WUE both drought and flooding, $p < 0.0001$).

Biomass also decreased in response to both flooding and drought ($p < 0.015$; Fig. 1), but this was not different between provenances.

Discussion

Phenotypic plasticity, particularly in chlorophyll content, WUE and root shoot ratios, was an important predictor of biomass, our fitness proxy, for both *Rumex* species across a broad soil moisture gradient. Plasticity to drought was greatest in the widespread *R. obtusifolius*, consistent with its broader distribution and greater abundance in dry areas, while plasticity to flooding did not differ between species. Differences between native and introduced provenances indicated potentially adaptive evolution of mean SLA and drought-induced chlorophyll and WUE plasticity in the introduced range for *R. obtusifolius*. Continued survival and growth despite severe drought and waterlogging and greater plasticity in the introduced range in *R. obtusifolius* indicates that *R. obtusifolius* is likely to persist and may increase in abundance under future climate extremes.

Though it has long been assumed that plasticity benefits colonizing species (Baker 1974; Richards et al. 2006), our results demonstrate that it is essential to consider not only the magnitude, but also the direction of plasticity and its relationship with fitness, as not all plasticity is adaptive (van Kleunen and Fischer 2005; Hulme 2008; Funk 2008; Davidson et al. 2011). Measuring both trait plasticity, as the slope of the reaction norm, and a fitness proxy, biomass, allowed us to assess changes in the magnitude and direction of plasticity and their putative significance for fitness (van Kleunen and Fischer 2005; Hulme 2008) as well as the effect of mean trait values (Godoy et al. 2011, 2012). This has rarely been undertaken for invasive alien species. In the more invasive *R. obtusifolius*, we saw adaptive multi-trait plasticity to both drought (i.e. increased chlorophyll, WUE) and flooding (i.e. decreased root shoot ratio, increased SLA), as well as a benefit of mean trait values in drought (lower SLA, greater root shoot ratio), all consistent with expectations (Chaves et al. 2003; Heschel et al. 2004; Mommer et al. 2006; Nicotra and Davidson 2010; Ashraf and Harris 2013; Avramova et al. 2015). Using the slopes of the reaction norms aggregated across traits with a PCA, we found multi-trait plasticity had a greater effect on biomass under drought than under flooding, and also showed greater consistency in direction across genotypes, perhaps reflecting past selective pressure for adaptive plasticity (Lee and Gelembiuk 2008). By contrast, plasticity in *R. conglomeratus* was less consistent with our expectations. Under drought, biomass of *R. conglomeratus* increased with increasing investment in shoots, perhaps because watering from the surface meant that deeper roots were not advantageous. Surprisingly, even though *R. obtusifolius* showed greater reaction norm slopes and multi-trait plasticity more often reduced biomass loss in response to drought and flooding, proportional biomass loss between species was quite similar. This suggests that plasticity is more important for maintaining growth under adverse conditions for *R. obtusifolius* than it is for *R. conglomeratus*. This is consistent with the hypothesis that plasticity is more important in the widespread species, even though the more restricted *R. conglomeratus* performed better than expected under drought conditions. Additionally, we found evidence of correlations and trade-offs between variables. Relationships between traits, or between a trait mean and its reaction norm, as found in *R. obtusifolius* under drought, can affect the evolution of plasticity, as can conflicting selection pressures in different environments (van Kleunen and Fischer 2005; Valladares et al. 2007; Hulme 2008; Godoy et al. 2012; Murren et al. 2015; Conti et al. 2018). In our study, however, the relationships between variables shifted between drought and flooding, suggesting that these associations may arise from integrated responses rather than physical or genetic constraints.

Differences between genotypes from the native and introduced provenances suggest that adaptive evolution may have occurred and may help explain the broad distribution and high abundance of *R. obtusifolius* in the introduced range in New Zealand. Plasticity in chlorophyll content and WUE under drought were important components of adaptive multi-trait plasticity and were greater in *R. obtusifolius* genotypes from the introduced range. Similarly, genotypes of *R. obtusifolius* from the introduced range had lower SLA, which was beneficial across both drought and flooding. Perhaps as a result, genotypes of *R. obtusifolius* from the introduced range lost less biomass under drought than those from the native range. By contrast, although plasticity did improve performance for *R. conglomeratus*, the level and direction of plasticity did not vary between provenances. Because we have limited replication within populations, we are cannot robustly assess the extent to which populations within a range vary from each other. The presence of notable variation between individual genotypes, even from the same population, suggests that differences in plasticity are likely to be heritable, as they are in other species in the Polygonaceae (Sultan et al. 2013), but our study did not directly test this. Further research into within-population variation and the strength of the heritability of plasticity could provide greater insight into contemporary evolution, particularly given that our study did show substantial variation between genotypes within provenance. For the purposes of this study, however, we focused on sampling broadly across the ranges, to provide greater confidence that differences between provenances are not due solely to sampling effects within the range (Colautti and Lau 2015). Overall, the ability of genotypes to survive and grow across the full range of soil moisture emphasizes that both these *Rumex* spp. are highly adaptable. High survival across both drought and flooding combined with intraspecific variability in traits and in the strength and direction of plasticity, including differences between provenances, suggests a capacity for evolutionary change in response to extreme weather events (Matesanz et al. 2010; Valladares et al. 2014), which may further exacerbate the impact of these species, particularly *R. obtusifolius*, in the introduced range and under future climate regimes.

By measuring phenotypic plasticity and its relationship to performance in genotypes from populations of two species across both the native and introduced ranges, we have demonstrated putative adaptation in the more invasive species within the introduced range. High plasticity may explain why both species have successfully naturalized around the world, and greater plasticity to drought may explain the greater abundance of *R. obtusifolius* and its status as a globally significant weed. Furthermore, *R. obtusifolius* demonstrated not only high plasticity, but also evolution in the introduced range, which may partly explain the greater success of *R. obtusifolius* in New Zealand. Given that climate change could lead to increases in the frequency or severity of local droughts and floods (Seneviratne et al. 2012; Coumou and Rahmstorf 2012; Ummenhofer and Meehl 2017), the capacity for evolutionary change, indicated by high survival and intraspecific variation, may be especially important for the persistence and impact of these species.

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Author contributions JLB and PEH planned and designed the research. JLB conducted the experiment, processed and analysed the data. JLB and PEH wrote the manuscript.

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Data availability The data associated with this paper are archived at Figshare. https://doi.org/10.6084/m9.figshare.14430470 (Bufford and Hulme 2021).

Code availability Code will be provided upon reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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