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RESEARCH PAPER

Regrowth patterns and rosette attributes contribute to the differential compensatory responses of *Arabidopsis thaliana* genotypes to apical damage

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ABSTRACT

A plant's compensatory performance refers to its ability to maintain or increase its reproductive output following damage. The ability of a plant to compensate depends on numerous factors including the type, severity, frequency and timing of damage, the environmental conditions and the plant's genotype. Upon apical damage, a cascade of hormonal and genetic responses often produces dramatic changes in a plant's growth, development, architecture and physiology. All else being equal, this response is largely dependent on a plant's genotype, with different regrowth patterns displayed by different genotypes of a given species. In this study, we compare the architectural and growth patterns of two *Arabidopsis thaliana* genotypes following apical damage. Specifically, we characterise regrowth patterns of the genotypes Columbia-4 and Landsberg *erecta*, which typically differ in their compensation to apical meristem removal. We report that Landsberg *erecta* suffered reductions in the number of stems produced, maximum elongation rate, a delay in reaching this rate, lower average rosette quality throughout the growing period, and ultimately, less aboveground dry biomass and seed production when damaged compared to undamaged control plants. Columbia-4 had no reductions in any of these measures and maintained larger rosette area when clipped relative to when unclipped. Based on the apparent influence of the rosette on these genotypes' compensatory performances, we performed a rosette removal experiment, which confirmed that the rosette contributes to compensatory performance. This study provides a novel characterisation of regrowth patterns following apical damage, with insights into those measures having the largest effect on plant performance.

INTRODUCTION

Plants are often damaged in nature, whether by abiotic (*e.g.* wind, lightning) or biotic (*e.g.* parasites, herbivores) means. Due to their sessile nature, plants are presumably under strong selective pressure to either prevent damage or to at least maintain reproductive output upon sustaining damage (*i.e.* to compensate for damage). Leaf damage, for example, often stimulates a localised or systemic chemical response in the plant to prevent further tissue loss (Agrawal 1998). In contrast, damage by apical meristem-feeding insects (*e.g.* tipworms and other mining insects) and mammalian herbivores disrupt the production of auxin, a plant hormone that inhibits lateral meristem development (Sachs & Thimann 1967). Damage to or removal of the apical meristem thus often leads to a release of apical dominance, which causes a change in plant architecture that may subsequently impact plant growth, survivorship and/or reproductive success (Sachs & Thimann 1967; Maschinski & Whitham 1989). For example, a study of the branching responses of *Medicago truncatula* revealed that damaged plants generally averaged more stems per plant relative to undamaged plants under most combinations of timing and intensity of damage (Gruntman & Novoplansky 2011). Such changes in plant architecture may then lead to compensation for damage in terms of reproductive output, or even increased plant fitness following damage (*i.e.* overcompensation; Strauss & Agrawal 1999; Agrawal 2000; Stowe *et al.* 2000). For example, studies of the monocarpic biennial *Ipomopsis aggregata* showed that when naturally browsed by ungulate herbivores, plants displayed a 4.1-fold increase in the number of stems produced on average relative to undamaged controls, ultimately resulting in a 2.4-fold increase in total seed yield (Paige & Whitham 1987). Damage compensation has also been observed in numerous plant species, including *Ipomopsis arizonica* (Maschinski & Whitham 1989), *Arabidopsis thaliana* (Mauricio *et al.* 1997; Weinig *et al.* 2003), *Gentianella campestris* (Lennartsson *et al.* 1997), *Sanicula arctopoides* (Lowenberg 1994) and *Ipomoea purpurea* (Hougen-Eitzman & Rausher 1994), among many others. Substantial variation in compensatory performance, ranging from under-compensation to over-compensation, can occur within a species when comparing different genotypes, families and populations (*e.g.* Paige 1992, 1999). Apart from changes in plant architecture following damage, mechanisms contributing to compensation are proposed to include the reallocation of

stored carbon reserves (Van der Meijden *et al.* 1988), increased photosynthetic output of undamaged tissues (McNaughton 1979) and the mitigation of phenological delays following damage (English-Loeb & Karban 1992; Tucker & Avila-Sakar 2010; Hoque & Avila-Sakar 2015; see Tiffin 2000 for review). Constraints on these processes, evidence of their promotion *via* natural selection and the generalisability of their ecological and evolutionary implications remain unclear, however (Stowe *et al.* 2000; Fornoni 2011).

Despite intraspecific variation for fitness compensation, the relatively consistent compensatory performance of individual genotypes suggests the trait has a strong underlying genetic basis. For example, studies of *A. thaliana* have demonstrated that the Columbia-4 genotype often over-compensates following apical damage, whereas the Landsberg *erecta* genotype generally under-compensates (Scholes & Paige 2011, 2014; Scholes *et al.* 2013; Siddappaji *et al.* 2013). The genetic basis of these differences in compensatory performance is evident upon the crossing of these two genotypes; offspring of a Columbia-4× Landsberg *erecta* cross display a wide range of compensatory abilities intermediate to and even beyond those of the parents (Scholes *et al.* 2013; Siddappaji *et al.* 2013; Scholes & Paige 2014), as expected upon the recombination of the genes underlying this polygenic trait. Targeted studies of the genetic basis of compensatory abilities using these two genotypes have implicated two pathways of particular importance – the oxidative pentose phosphate pathway (OPPP) and endoreduplication. The OPPP is a generalised metabolic pathway that supplies 5-carbon sugars as raw material for biosynthesis in the Calvin cycle (Kruger & von Schaewen 2003). Among other compounds, OPPP intermediates are used to produce DNA nucleotides that likely support endoreduplication – the replication of the genome without mitosis such that cellular ploidy increases (Lee *et al.* 2009). Because of the exponential increase in gene copy number with each replication, and its commonality across cell types and taxa (Leitch & Leitch 2012), endoreduplication is assumed to play generalised roles in cell expansion, gene expression and metabolism (Nagl 1976; Lee *et al.* 2009). The degree to which both the OPPP and endoreduplication are up-regulated following apical damage is positively associated with the compensatory abilities of these *A. thaliana* genotypes (Scholes & Paige 2011; Scholes *et al.* 2013; Siddappaji *et al.* 2013). Furthermore, recent manipulative studies using Columbia-4 and Landsberg *erecta* confirm that both the OPPP and endoreduplication contribute directly to the compensatory response (Siddappaji *et al.* 2013; Scholes & Paige 2014), and likely a wide range of environmental stressors generally (Scholes & Paige 2015).

Although differences in fitness compensation and the genetic basis of these differences have been documented among many genotypes of *A. thaliana*, characterisation of the outward expression of these genetic differences, *i.e.* the whole-plant phenotype, has so far not been made with regard to compensatory performance. In this study, we seek to characterise the regrowth patterns of *A. thaliana* Columbia-4 and Landsberg *erecta* following apical meristem damage to determine if, and how greatly, damaged plants differ from undamaged controls in aspects of their architecture, growth potential and biomass generation through time and biomass and fitness at senescence in an effort to understand the basis of their differing compensatory abilities. Among the myriad phenotypic measures assessed, our results suggest that rosette size and quality significantly impact regrowth of these damaged *A. thaliana* genotypes, and we therefore additionally performed a rosette removal experiment to directly evaluate the rosette's impact on inflorescence growth and fitness compensation. Collectively, this study provides a characterisation of plant regrowth following apical damage for these two commonly studied genotypes and yields general insights into the basis for the differential compensatory performances of *A. thaliana*.

MATERIAL AND METHODS

Study species, growth and experimental clipping

Arabidopsis thaliana is a monocarpic, long-day annual native to Europe but with a naturalised range spanning the Eurasian continent and northern Africa (Nottingham Arabidopsis Stock Center, http://www.arabidopsis.info). Populations may be found worldwide, however, likely established *via* the introduction or release of laboratory populations. Naturally, *A. thaliana* plants develop in early spring as rosettes and produce a flowering inflorescence (*i.e.* they bolt) in late spring. The inflorescences elongate, produce flowers and primarily self-fertilise to produce siliques (*i.e.* seed pods) that each contain numerous small seeds (Abbott & Gomes 1988).

Thirty plants each of *A. thaliana* genotypes Columbia-4 (Col-4; TAIR stock number: CS933; The Arabidopsis Information Resource, http://www.arabidopsis.org) and Landsberg *erecta* (L*er*-0; TAIR stock number: CS20) were grown in a greenhouse at approximately 21 °C on a 12-h light/dark cycle. When elongating inflorescences reached 6 cm in height, approximately 6 weeks after planting, the inflorescences of half (15) of the plants of each genotype were clipped with scissors, leaving approximately 1 cm of stem height. Studies indicate that this clipping regimen is comparable and has the same effect on plant architecture as the natural damage imposed on *A. thaliana* by rabbits in its native Europe (D. R. Scholes, J. Dalrymple, J. M. Mesa, J. A. Banta and K. N. Paige unpublished).

Phenotypic measures

Fitness

Upon the completion of senescence (*ca.* 12 weeks after planting), the number of siliques was counted for each plant. The number of seeds per silique was measured for ten siliques per plant, and for each plant, the total number of siliques was multiplied by the average number of seeds per silique for each genotype × treatment group to estimate each plant's seed yield.

Growth potential

To assess the degree to which the rosette is capable of promoting growth (or regrowth) as the primary photosynthetic tissue, rosette area and 'greenness' were measured over time. For these and all other phenotypic characters measured over time, Day 0 is defined as the day before primary inflorescence elongation began for unclipped plants, and the day before the lateral inflorescences began to elongate for clipped plants. From Day 0, photographs of the rosette of each plant were taken approximately every fourth day with a Nikon P5100 (12.1 megapixels; Nikon, Tokyo, Japan) camera under no flash, fixed zoom

settings, with the rosette positioned against a white background, consistent overhead greenhouse lighting, and at a distance of 1 m from the camera lens such that measurements across photographs were standardised and directly comparable (see Fig. 1A for an example photograph). Using GIMP (v.2.8.0; http://www.gimp.org) photo-editing software, a selection of pixels was made for each image such that only the rosette was included in the analysis (Fig. 1B). The histogram application was then used to determine the number of pixels within the rosette (as a measurement of total rosette area; Fig. 1C), which was divided by 10,000 for scaling purposes. A value for the level of 'green' in the rosette was determined by the mean value reported in the histogram application green channel, ranging from 0 (black) to 255 (bright green; Fig. 1C). This measurement served as a proxy for rosette chlorophyll content, and thus rosette leaf photosynthetic potential (hereafter referred to as rosette 'quality', with higher values assumed to indicate higher quality). Chlorophyll content is known to be positively correlated with photosynthetic activity and negatively correlated with leaf age (Šesták 1963). Our measure was verified as a general assessment of quality upon analysis as all rosettes decreased in our 'quality' measure as expected leading up to senescence (see Results).

An estimate of stomatal density, assumed to correspond to gas exchange and transpiration potential, was measured for each plant by applying a thin layer of clear nail polish to the adaxial (upward-facing) surface of the most basal cauline (inflorescence) leaf, peeling the nail polish from the surface when dry, affixing it to a microscope slide with clear tape, and counting the number of stomata in three non-contiguous, representative fields of vision (~237 mm^2) per leaf *via* a Zeiss Axiovert 200M microscope (Carl Zeiss, Oberkochen, Germany) viewed with a 20 × /0.8NA objective (CFI Plan Apochromat VC Series; Nikon Instruments, Melville, NY, USA) controlled by Zeiss Axiovision (version 4.5, Carl Zeiss AG, Oberkochen, Germany) software (see Fig. 1D for an example image). Previous studies using Col-4 and L*er*-0 have shown that stomatal density is positively related to stomatal conductance and negatively related to transpirational efficiency (*i.e.* the ratio of transpiration to photosynthesis rates; Masle *et al.* 2005).

Biomass

The length of all stems (primary, secondary and tertiary, if applicable) was measured daily from the induction to the termination of inflorescence elongation. At the completion of senescence, the belowground and inflorescence dry biomasses

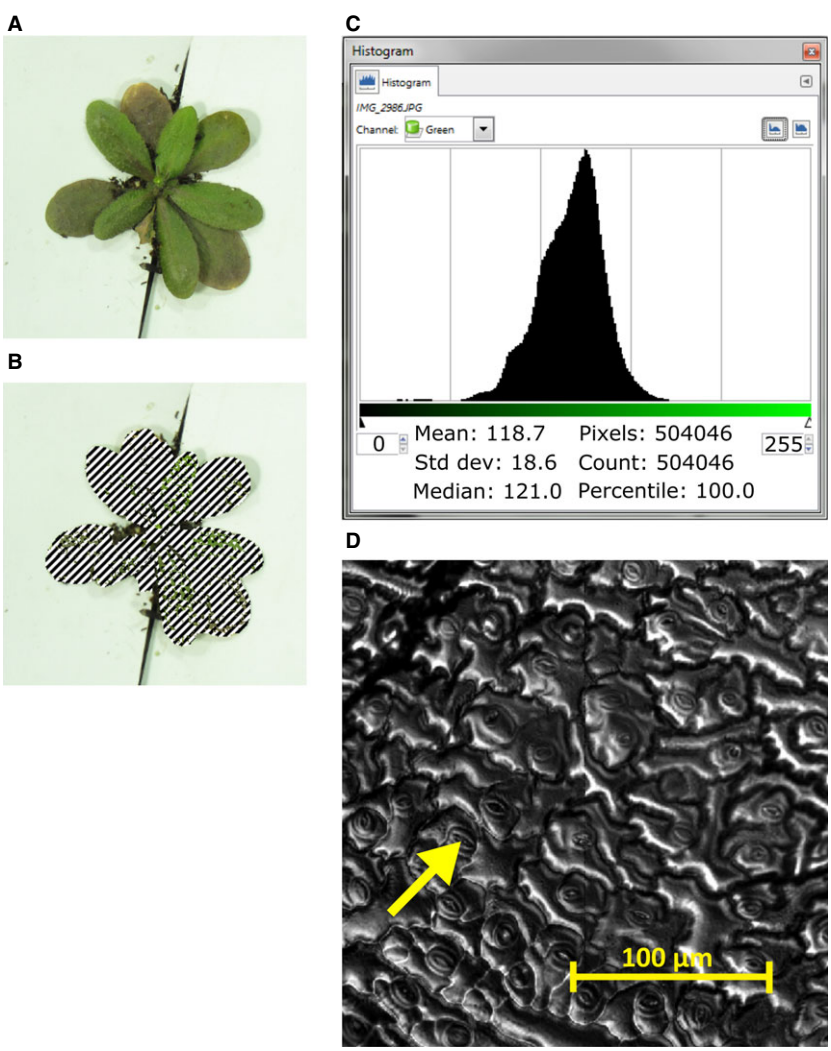

Fig. 1. Estimation of rosette area, quality and stomatal density. A: A typical photograph used for analysis. B: Only the rosette tissue is selected (selected area indicated by black-and-white stripes) for analysis. The selection is continuous although leaf portions appear to be unselected. C: The histogram application in GIMP (version 2.8.0) provides the number of pixels within the selection (*i.e.* rosette area) and the mean green channel value of the selection (*i.e.* 'greenness' of the rosette, a proxy for chlorophyll content). Values (*e.g.* mean, SD, *etc.*) are reproduced here in larger font for legibility. D: Nail polish epidermal peel showing cauline leaf adaxial stomatal density at 20 × magnification. The yellow arrow identifies one stomate. Photographs in A., B. and D. have been cropped for space. See Methods for detailed procedures.

of each plant were measured and their ratio (belowground:inflorescence, *i.e.* root:shoot dry biomass ratio) was calculated.

Rosette removal

Upon analysis of the first group of plants, we performed a rosette removal experiment to directly assess the degree to which the rosette affects compensatory performance. An additional 70 plants of each genotype were grown under greenhouse conditions. We note that while these plants were grown in the same facility as our first set of plants, some greenhouse conditions that are influenced by the external environment (*e.g.* temperature, humidity) could have differed between plants assessed for regrowth characterisation and those used to test the effects of rosette removal. At the time the elongating inflorescences reached 6 cm in height, inflorescences of 35 plants of each genotype were clipped. Of the 35 plants of each clipping treatment, the rosette leaves of 17 unclipped and 18 clipped plants were concurrently removed, creating four treatment groups per genotype (unclipped, unclipped with rosette removed, clipped, clipped with rosette removed). Total seed yield and inflorescence dry biomass were measured at senescence as described above.

Statistical analysis

Fitness

Statistical analyses for all measures were conducted in SAS (version 9.4; Cary, NC, USA). Silique and seed yields were analysed among all genotype × treatment groups *via* ANOVA (PROC GLM), with comparisons between unclipped and clipped plants for each genotype made *via* linear contrasts.

Growth potential

Estimates of rosette area and quality were each analysed across time using PROC REG linear regression with repeated measures over a time series. Values at each time point were transformed as a percentage of their maximum (*i.e.* the maximum value during inflorescence elongation period = 100%) to standardise for differences among plants in area and quality values. Data were fit to the linear function:

$$\text{Dependent variable} = \beta_0 + \beta_1 \bullet \text{day} + \varepsilon$$

where β_0 is the *y*-intercept, β_1 is the slope, *day* is the day identity (number of days after the induction of stem elongation that the stem measurement was taken), and ε is the experimental error. Differences among genotype × treatment groups were determined with general linear models *via* PROC GLM, comparing the slopes and *y*-intercepts pair-wise among genotype × treatment groups. For each plant, the average area and quality value were calculated across all days measured and compared among treatments for each genotype *via* ANOVA and linear contrasts to determine if, on average through the stem elongation period, rosette area and quality differed between control and damaged plants of each genotype. The numbers of stomata for each field of vision were averaged for each plant, and stomatal density was compared between treatments of each genotype by ANOVA and linear contrasts.

Stem elongation and biomass

The sums of all stem lengths (primary, secondary and tertiary, if applicable) over time among genotype × treatment groups were analysed *via* logistic regression with repeated measures over a time series. Length measurements at each time point were converted to percentage of maximum length achieved to control for variation in total stem length among plants. Data were fit to the logistic function:

$$\text{Percent of total stem length} = \beta_1/(1 + \beta_2 \bullet e^{-\beta_3 \bullet day}) + \varepsilon$$

where β_1, β_2 and β_3 are parameters by which the logistic function is fit, *e* is Euler's number, *day* is the day identity and ε is experimental error. To test for significant differences among growth curves, parameters were tested for significance by comparing pair-wise differences of each β_1, β_2 and β_3 against zero among genotype × treatment groups (Col-4 unclipped, Col-4 clipped, L*er*-0 unclipped, L*er*-0 clipped). Comparisons were not made among β_1, β_2 and β_3 within or among genotype × treatment groups. To better visualise the rate of change and timing of stem elongation for each genotype × treatment group, the first derivative of the logistic function, representing the change in the percentage of maximum stem length per day, was calculated and plotted. Inflorescence dry biomass, belowground dry biomass and root:shoot biomass ratios were compared between treatments of each genotype by ANOVA and linear contrasts.

RESULTS

Fitness

Clipped Col-4 displayed no difference in silique yield relative to Col-4 unclipped plants (*i.e.* Col-4 equally compensated for silique production; $t(56) = 0.9$, $P = 0.371$), while L*er*-0 displayed a near significant reduction in its silique yield upon clipping ($t(56) = 1.89$, $P = 0.0634$). Clipped Col-4 plants did not differ from unclipped plants in their total seed yield ($t(56) = 1.06$, $P = 0.2916$), but L*er*-0 clipped plants experienced a significant reduction in their seed yield relative to unclipped controls ($t(56) = 2.29$, $P < 0.05$; Fig. 2).

Growth potential

All genotype × treatment groups displayed significant reductions in rosette area through time ($\beta_1 < 0$, all $P < 0.0001$). The rate of rosette area reduction through time did not differ between Col-4 unclipped and clipped plants (*i.e.* unclipped β_1 = clipped β_1; Table 1A) nor between treatments of L*er*-0 (all $P > 0.05$; Table 1A). Clipped Col-4 plants had larger average rosette area over the inflorescence elongation period (*i.e.* from the induction to the termination of inflorescence elongation) than unclipped plants ($t(55) = 2.26$, $P < 0.05$), with no significant difference between treatments of L*er*-0 for this measure ($t(55) = 1.65$, $P = 0.1055$).

All genotype × treatment groups displayed significant reductions in rosette quality through time ($\beta_1 < 0$, all $P < 0.05$), although the rate of rosette quality reduction did not differ between unclipped and clipped plants of either genotype

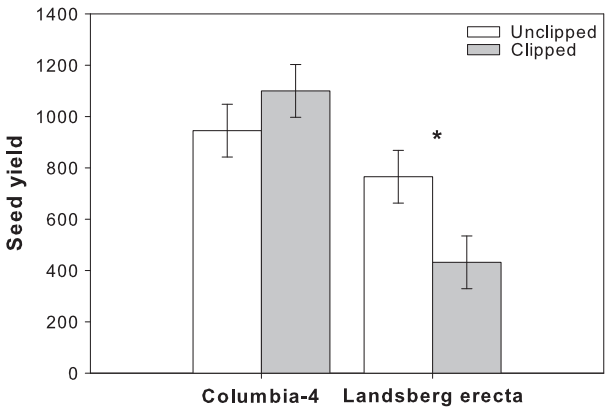

Fig. 2. Effects of damage on fitness. Seed yield for Col-4 and L*er*-0 unclipped and clipped plants. Shown are means ± SE (n = 15 plants per genotype × treatment group). Asterisks (*) indicate that unclipped and clipped plants of a genotype differ significantly ($\alpha = 0.05$).

(*i.e.* unclipped β_1 = clipped β_1, all $P > 0.05$; Table 1B). Unclipped and clipped Col-4 plants also displayed comparable quality when averaged over the inflorescence elongation period ($t(55) = 0.64$, $P = 0.5218$). L*er*-0 clipped plants, however, were of significantly lower quality relative to unclipped plants when averaged over this period ($t(55) = 2.73$, $P < 0.01$). Finally, clipped plants of both genotypes had significantly fewer stomata per unit area relative to unclipped controls (Col-4: $t(142) = 9.45$, $P < 0.0001$; L*er*-0: $t(142) = 5.51$, $P < 0.0001$).

Stem elongation and biomass

All genotype × treatment groups displayed logistic stem elongation (Fig. 3A and B). Stem elongation curves did not differ between unclipped and clipped Col-4 plants (unclipped *versus* clipped for β_1, β_2 and β_3: all $P > 0.05$; Table 1C, Fig. 3A), with no significant differences in the maximum stem elongation rate (unclipped: 7.62% day^{-1}, clipped: 6.67% day^{-1}) nor the time at which the maximum rate was achieved (unclipped: day 9.4, clipped: day 11; Fig. 3C) between unclipped stems and those stimulated by damage. There was also no difference in the total number of stems produced by unclipped and clipped Col-4 plants ($t(52) = 1.48$, $P = 0.1452$), nor in their total stem length (combined length of all stems; $t(52) = 1.51$, $P = 0.1372$).

There was a significant difference in the stem elongation curves between treatments in L*er-0* (unclipped *versus* clipped β_3: $P < 0.05$; Table 1C, Fig. 3B), where stems of clipped plants had a 15.6% reduction in the maximum rate of elongation (unclipped: 8.34% day^{-1}, clipped: 7.04% day^{-1}) and a 31.2% delay in the time at which the maximum elongation rate was achieved (unclipped: day 7.7, clipped: day 10.1; Fig. 3D). Clipped L*er*-0 plants produced significantly fewer stems than unclipped plants ($t(52) = 2.58$, $P < 0.05$), although with no significant difference in total stem length ($t(52) = 0.93$, $P = 0.358$).

Col-4 unclipped and clipped plants did not significantly differ in inflorescence dry biomass at senescence ($t(53) = 1.13$, $P = 0.2615$), although L*er*-0 clipped plants had a marginally significant reduction in inflorescence dry biomass relative to unclipped plants ($t(53) = 1.97$, $P = 0.0546$; Fig. 4A). Unclipped and clipped plants did not differ in their production of belowground (root) biomass for either genotype (Col-4: $t(55) = 1.27$, $P = 0.2083$; L*er*-0: 0.66, $P = 0.5105$; Fig. 4B), although both had significant increases in their belowground:inflorescence (*i.e.* root:shoot) biomass ratios (Col-4: $t(53) = 2.39$, $P < 0.05$; L*er*-0: $t(53) = 2.05$, $P < 0.05$; Fig. 4C) due to trends toward decreasing and increasing inflorescence and belowground biomass, respectively, upon clipping for both genotypes.

Rosette removal

In our follow-up experiment, both Col-4 and L*er*-0 equally compensated for seed yield when clipped relative to when unclipped ($t(114) = 1.42$, $P = 0.158$, and $t(114) = 0.21$, $P = 0.831$, respectively; Fig. 5A). Upon removal of the rosette at the time the elongating inflorescence reached 6 cm, unclipped plants experienced a significant reduction in seed yield for both genotypes (Col-4: $t(114) = 5.5$, $P < 0.0001$; L*er*-0: $t(114)$: 5.84, $P < 0.0001$; Fig. 5A). An even larger reduction in seed yield was observed for Col-4 upon clipping and rosette removal (rosette removed *versus* rosette removed + clipped: $t(114) = 3.87$, $P < 0.001$), although the further reduction was not significant for L*er*-0 ($t(114) = 1.65$, $P = 0.1008$; Fig. 5A).

Inflorescence dry biomass measures of Col-4 significantly differed among treatments in the following order (from largest to smallest): unclipped, clipped, rosette removed, rosette removed + clipped (unclipped *versus* clipped: $t(114)$: 2.3, $P < 0.05$; clipped *versus* rosette removed: $t(114) = 4.39$, $P < 0.0001$; rosette removed *versus* rosette removed + clipped: $t(114) = 3.99$, $P < 0.0001$; Fig. 5B). Biomass measures followed the same treatment order in L*er*-0, but without significant differences between unclipped and clipped plants for both categories of rosette removal (unclipped *versus* clipped: $t(114) = 1.06$, $P = 0.2896$; clipped *versus* rosette removed: $t(114) = 4.57$, $P < 0.0001$; rosette removed *versus* rosette removed + clipped: $t(114) = 1.64$, $P = 0.1046$; Fig. 5B). When unclipped, Col-4 rosettes were significantly larger than those of L*er*-0 ($F(1,121) = 9.07$, $P < 0.01$).

DISCUSSION

Our results provide a characterisation of the regrowth patterns for two commonly studied *A. thaliana* genotypes that typically differ in their abilities to compensate for apical damage (*i.e.* Col-4 generally compensates to a greater degree following damage than L*er*-0, as reported by Scholes & Paige 2011, 2014; Scholes *et al.* 2013; Siddappaji *et al.* 2013; current study). Among the many measures by which clipped plants differed from unclipped plants, a few key differences in the regrowth patterns between genotypes were identified that may help elucidate the basis of these genotypes' differential compensatory performances. Specifically, relative to unclipped controls, clipped L*er*-0 plants had a significant reduction in the number of stems produced, maximum stem elongation rate, a delay in reaching this rate, lower average rosette quality throughout the stem elongation period, and ultimately, less inflorescence dry biomass and seed production. Col-4 did not display reductions in any of these measures, maintained larger average rosette area throughout the growing period, and ultimately suffered no biomass or seed yield losses when damaged. Differences between the genotypes in their compensatory abilities thus seem to be

Table 1. Phenotypic measures through time. Estimates, SE) and 95% confidence limits (95% CL) for regression parameters of each genotype × treatment group (Group). Rosette quality reflects the green value obtained from photographs (see Methods for a complete description of value measurement and regression models). Letters represent statistical significance groups determined by linear contrasts among genotype × treatment groups for each parameter.

parameter	group	estimate	SE	95% CL	significance
A. rosette area					
β_0	Col-4 U	109.9	3.40	103.2 to 116.7	A
	Col-4 C	93.08	2.25	88.62 to 97.53	B
	L*er*-0 U	114.0	3.29	107.4 to 120.5	A
	L*er*-0 C	86.26	3.12	80.05 to 92.47	B
β_1	Col-4 U	−1.860	0.114	−2.08 to −1.63	AB
	Col-4 C	−1.741	0.104	−1.95 to −1.53	A
	L*er*-0 U	−2.404	0.116	−2.63 to −2.18	C
	L*er*-0 C	−2.218	0.201	−2.62 to −1.82	BC
B. rosette quality					
β_0	Col-4 U	90.44	2.73	85.05 to 95.83	A
	Col-4 C	79.67	2.73	74.27 to 85.06	B
	L*er*-0 U	91.50	3.66	84.25 to 98.75	A
	L*er*-0 C	80.13	3.09	74.00 to 86.28	B
β_1	Col-4 U	−0.638	0.0913	−0.818 to −0.458	A
	Col-4 C	−0.622	0.1263	−0.872 to −0.373	A
	L*er*-0 U	−0.609	0.1291	−0.864 to −0.354	A
	L*er*-0 C	−0.505	0.1983	−0.900 to −0.111	A
C. stem length					
β_1	Col-4 U	96.61	1.06	94.54 to 98.69	A
	Col-4 C	95.42	1.29	92.90 to 97.95	A
	L*er*-0 U	97.75	0.93	95.92 to 99.58	A
	L*er*-0 C	97.78	1.27	95.30 to 100.30	A
β_2	Col-4 U	19.38	2.48	14.51 to 24.25	AB
	Col-4 C	21.48	2.77	16.04 to 26.91	A
	L*er*-0 U	14.52	1.74	11.10 to 17.93	B
	L*er*-0 C	18.11	2.34	13.51 to 22.70	AB
β_3	Col-4 U	0.32	0.014	0.287 to 0.344	AB
	Col-4 C	0.28	0.013	0.254 to 0.305	B
	L*er*-0 U	0.34	0.016	0.311 to 0.372	A
	L*er*-0 C	0.29	0.014	0.260 to 0.315	B

reflected in their differential abilities to maintain stem production, biomass production and growth rates following clipping, perhaps in part due to aspects of the rosette.

A primary proposed mechanism contributing to damage tolerance is compensatory growth following the release of apical dominance (Aarssen 1995; Cline 1997; Tiffin 2000). Specifically, increased lateral branching has been observed in a number of species, including *Ipomopsis aggregata*, *Urtica dioica*, *Zea mays*, *Gossypium hirsutum*, *Gentianella campestris*, and *Scrophularia nodosa*, among many others (Paige & Whitham 1987; Mutkainen *et al.* 1994; Rosenthal & Welter 1995; Sadras 1996; Lennartsson *et al.* 1997, 1998; Strauss & Agrawal 1999; Hambäck *et al.* 2011). In this study, *A. thaliana* Col-4 not only increased its lateral stem number when damaged relative to when undamaged, but Col-4's resultant inflorescence biomass also increased while L*er*-0 had reductions in both measures. The propensity for compensatory regrowth, as measured by stem number and inflorescence biomass, therefore seems to be an important difference between these genotypes in accordance with their compensation for fitness. Further, Col-4's increase in these attributes was presumably due to its ability to reduce phenological delay, which is another factor proposed to contribute to damage tolerance in *A. thaliana*, since damage at early ontogenetic stages is more detrimental to tolerance than damage occurring later in phenology (Tucker & Avila-Sakar 2010; Hoque & Avila-Sakar 2015). In our study, Col-4 displayed no difference in its average or maximum stem elongation rate, nor the time at which the maximum rate was achieved, when clipped relative to when unclipped; L*er*-0, in contrast, suffered reduced average and maximum stem elongation rates, as well as a delay in reaching the maximum rate. In this study, Col-4's mitigation of such phenological delay combined with its propensity for compensatory regrowth likely contributed to its increase in stem number, inflorescence biomass and ultimately maintained seed production while L*er*-0 under-compensated.

Despite their differences in inflorescence regrowth patterns, both genotypes displayed trends toward increased belowground biomass following clipping, resulting in significant increases in their root:shoot biomass ratios. Theory suggests that the ability of a plant to tolerate damage to aboveground tissues may be influenced by the degree to which the plant has stored belowground carbon reserves and its ability to reallocate those resources to replace the removed tissues (Strauss & Agrawal 1999; Stowe *et al.* 2000; Tiffin 2000). There is even some empirical evidence supporting the importance of this process of carbon reallocation (*e.g.* Richards & Caldwell 1985; Mabry & Wayne 1997). Across the literature, however, the increase in belowground biomass following damage has been observed widely among taxa and often contributes to increased root:

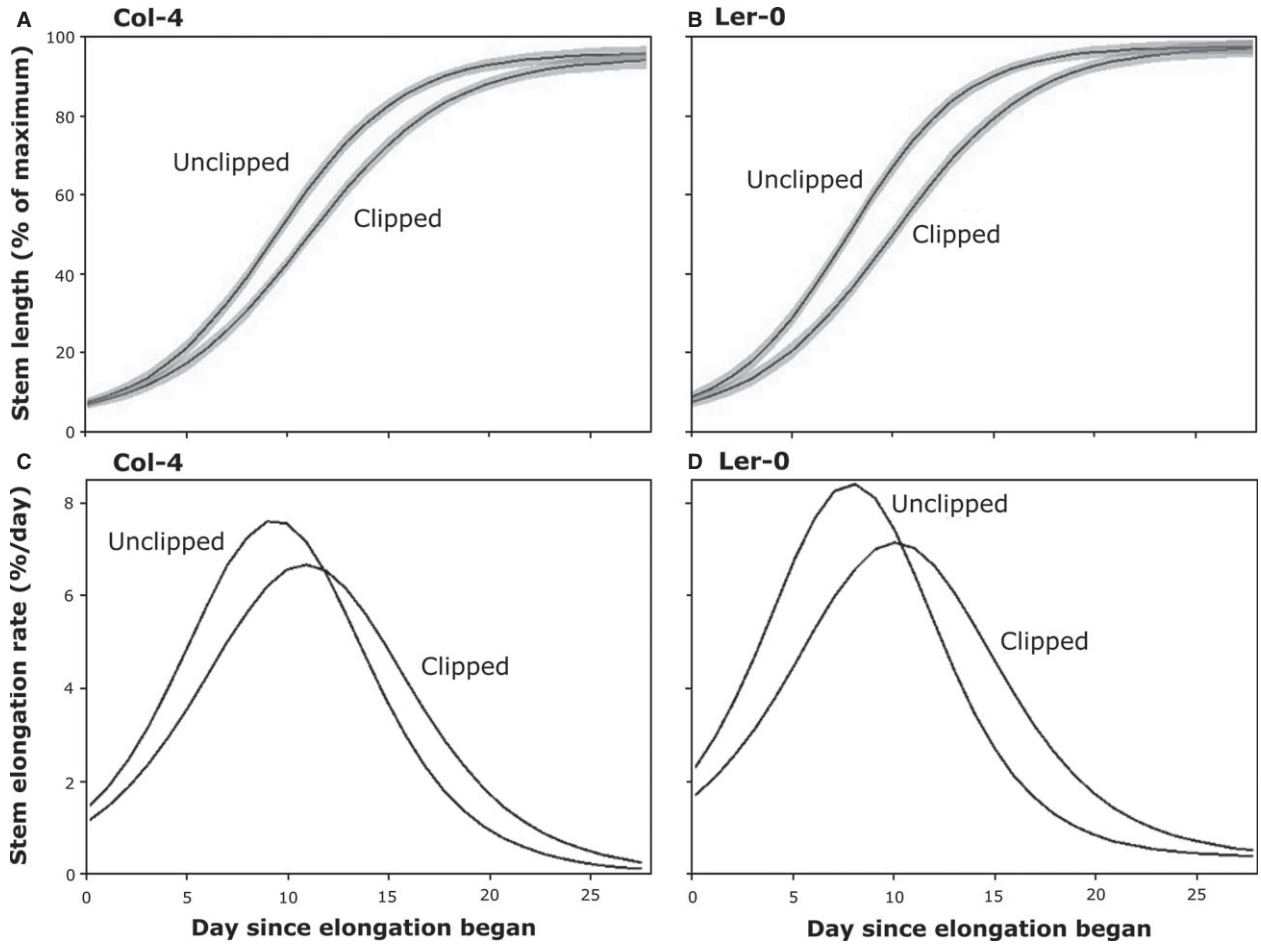

Fig. 3. Stem elongation curves. Percentage of maximum total stem length through time and total stem elongation rates for Col-4 (A, C) and L*er*-0 (B, D) unclipped and clipped plants. Shaded regions around logistic growth curves (A., B.) are 95% confidence bands for the mean of the respective genotype × treatment group. Only Days 0–28 are plotted since logistic growth curves asymptote to 100% from Day 28 to senescence.

shoot biomass ratios as plants search for water and soil nutrients for regrowth (Danckwerts 1993; Welter & Steggall 1993; Briske *et al.* 1996). In *A. thaliana*, plants with a higher propensity for root growth and/or naturally larger root:shoot biomass ratios are generally more tolerant of damage (Hoque & Avila-Sakar 2015; Kornelsen & Avila-Sakar 2015). Evidently, if the trend toward increased belowground biomass observed here is truly due to the allocation of photosynthate to the roots for growth or storage, as has been observed in other species (Caldwell *et al.* 1981; Danckwerts 1993; Briske *et al.* 1996; Mabry & Wayne 1997), Col-4's ability to compensate for inflorescence biomass and ultimately seed yield is not likely due to the reallocation of stored belowground resources to inflorescence production. Reallocation of stored belowground resources may therefore not be as important to the compensation for aboveground biomass as has been previously theorised, where compensatory growth and the mitigation of phenological delay are presumably supported *via* other means.

Further, since Col-4 maintained a larger rosette of similar quality over the growth period when clipped relative to when unclipped, it is also unlikely that the rosette was used as a source of stored nutrients for reallocation, which would likely have reduced rosette size and quality through catabolism. In theory, compensatory growth and damage tolerance may alternatively be afforded through increased photosynthetic capacity of the remaining undamaged tissues (Tiffin 2000), with some evidence for this phenomenon (see Welter 1989 for review). The rosette, as the only remaining aboveground tissue, may therefore have supported regrowth *via* its post-damage photosynthetic output. In our study, not only did Col-4 have a larger rosette than L*er*-0 when undamaged, but clipped Col-4 plants actually retained a larger rosette area of similar quality throughout the inflorescence elongation period relative to unclipped Col-4. While L*er*-0 clipped plants maintained a comparable rosette area throughout the growing period relative to unclipped L*er*-0, they were of significantly lesser quality relative to undamaged controls. The ability to maintain or increase the relative rosette area and quality following damage could have contributed to the differential compensatory performances of these genotypes, particularly if clipping of the initial inflorescence caused an increased demand for photosynthate for inflorescence regrowth from the remaining undamaged rosette leaves. Under this pressure, it appears that the relatively low quality rosette of clipped L*er*-0 plants (*via* our proxy measure based on colour) was unable to fulfil the demand necessary for compensatory regrowth and fitness production. Col-4's maintenance of rosette quality and area upon clipping, in contrast, corresponded with maintained stem number, stem elongation

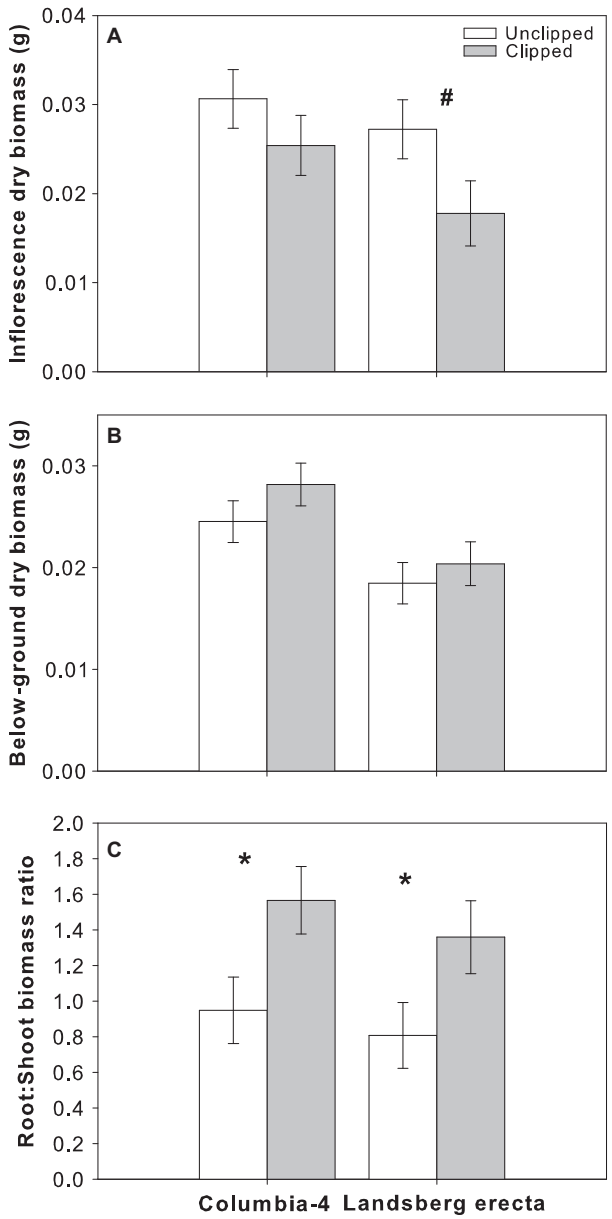

Fig. 4. Effects of damage on biomass. A: Inflorescence and B: belowground dry biomass, and C: the belowground:inflorescence dry biomass ratio (*i.e.* root:shoot biomass ratio) at the completion of senescence for Col-4 and L*er*-0 unclipped and clipped plants. Shown are means ± SE. Asterisks (*) indicate that unclipped and clipped plants of a genotype differ significantly ($\alpha = 0.05$; # $P = 0.0546$).

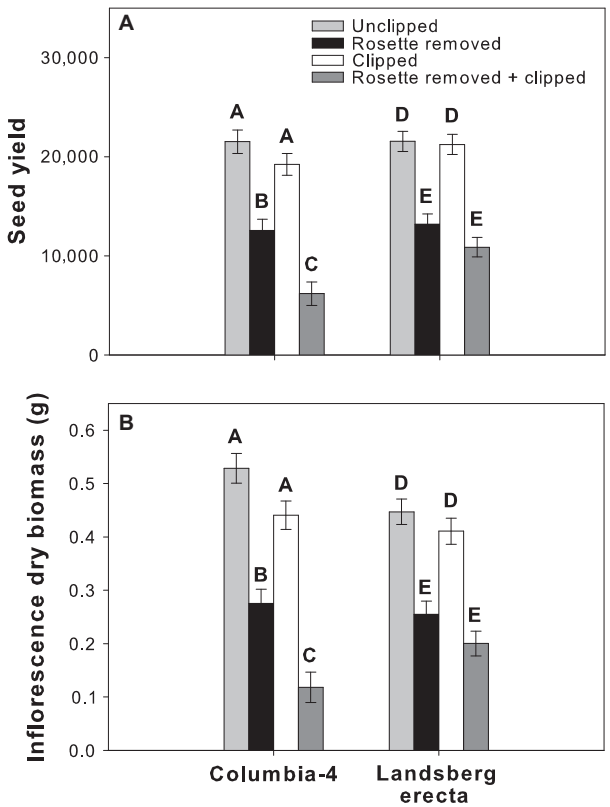

Fig. 5. Effects of rosette removal on growth and fitness. A: Seed yield and B: inflorescence dry biomass of unclipped (light grey bars), rosette removed (black bars), clipped (white bars), and rosette removed + clipped (dark grey bars) for Col-4 and L*er*-0 plants. Shown are means ± SE. Letters indicate significant differences ($\alpha = 0.05$) among treatments of each genotype for the given measure; no direct comparisons were made between genotypes for any treatment group.

rate, inflorescence dry biomass and ultimately silique and seed yield. Rather than stored resource reallocation, differences in photosynthetic carbon assimilation in the rosettes of these genotypes may have therefore contributed more strongly to their different regrowth and compensatory abilities.

Following these results, our rosette removal experiment sought to directly test the importance of the rosette in normal growth and compensatory regrowth. First, rosette removal decreased inflorescence biomass and seed yield of unclipped plants of both genotypes, suggesting that aspects of the rosette contribute significantly to normal growth and fitness (although experimental removal of these rosette aspects is inherently confounded with damage to the rosette leaves). When clipped in this follow-up experiment, both genotypes equally compensated for fitness measures. Employing rosette removal concurrently with clipping caused Col-4 to significantly undercompensate, where clipped plants with rosettes removed displayed the lowest seed yield and inflorescence biomass of all treatment groups. L*er*-0 maintained its equal compensation in this experiment even when rosettes were removed. Given that Col-4 has a larger rosette than L*er*-0, clipped Col-4 plants maintain a larger rosette throughout regrowth relative to unclipped Col-4 plants, and that Col-4 typically compensates better for damage than L*er*-0, the larger negative impact of rosette removal on compensation for Col-4 relative to L*er*-0 may be due to Col-4's greater reliance on photosynthesis of the rosette during regrowth, such that removal represents a proportionately larger loss for Col-4 than for L*er*-0. While our results clearly show that the rosette is important for normal growth and fitness of both genotypes (comparing unclipped plants to unclipped plants with rosettes removed), and for the compensatory regrowth of Col-4 (comparing compensation with rosettes intact to compensation with rosettes removed), our ability to make direct comparisons of compensatory performance between genotypes is limited due to both genotypes equally compensating for damage. Although Col-4 typically compensates for damage to a greater degree following damage

than L*er*-0 (Scholes & Paige 2011, 2014; Scholes *et al.* 2013; Siddappaji *et al.* 2013; and the current study), experiment-to-experiment variation in a genotype's compensatory performance can occur with environmental variation (Siddappaji *et al.* 2013). The specific influence of the interaction between genotype, the environment and rosette attributes on regrowth patterns and ultimately compensation therefore remains unclear.

With the initial investment into vegetative growth, the importance of the rosette for the growth and reproductive efforts of rosette plants is expected and has been demonstrated in other species (*e.g.* Gross 1981). Studies on the perennial *Arabidopsis lyrata*, a species closely related to *A. thaliana*, have demonstrated that rosette leaf damage has a large negative effect on fruit production in the following year (Puentes & Ågren 2012). In fact, leaf damage caused a larger reduction in future reproductive success than did concurrent damage to leaves and inflorescences (Puentes & Ågren 2012), demonstrating the importance of vegetative rosette growth on plant fitness. Our results here corroborate those observed for *A. lyrata*, where rosette removal had a substantial negative impact on seed production of both genotypes. We did however observe an even larger reduction in seed yield when inflorescence clipping was performed concurrently with rosette removal for Col-4, which might attest to the substantial importance of the rosette in Col-4's ability to typically compensate for apical damage alone. Assessments of the effects of rosette leaf damage on *A. thaliana* have additionally observed that its intensity is positively related to the reduction in fitness (Akiyama & Ågren 2012; Puentes & Ågren 2012). Our damage treatment may be considered the most intense among those applied in previous studies, as our 100% rosette defoliation produced a 42% reduction in seed yield for Col-4 compared to undamaged control plants. This reduction in fitness is actually less than that observed for a less intense defoliation intensity (a 60% reduction in seed yield on average following 50% leaf removal; Akiyama & Ågren 2012) for a natural population of *A. thaliana*, demonstrating both the substantial genetic variation that exists for damage tolerance in this species and the relative resilience of Col-4 to damage.

Collectively, and in light of other recent studies, the ability of Col-4 to maintain its growth rate, biomass production and seed yield upon damage may be due in part to its regulation of the oxidative pentose phosphate pathway (OPPP). Specifically, Col-4 plants significantly up-regulate the expression of *GLUCOSE-6-PHOSPHATE DEHYDROGENASE1* (*G6PD1*), an important OPPP regulator, during regrowth after clipping relative to before clipping, while L*er*-0 experiences no such up-regulation (Siddappaji *et al.* 2013). The OPPP is a generalised metabolic pathway that produces metabolites for primary biosynthesis, intermediate molecules for secondary metabolism and ribo- and deoxyribonucleotides for RNA and DNA production, among other molecules (Kruger & von Schaewen 2003; Scharte *et al.* 2009). Beyond utilising these metabolites for general growth, metabolism and potentially defensive chemistry, the nucleotides produced by the OPPP may be used in a process of genome re-replication, termed endoreduplication. Endoreduplication involves the replication of the genome without mitosis, which exponentially increases a cell's ploidy with each replication (Sugimoto-Shirasu & Roberts 2003; Lee *et al.* 2009; Breuer *et al.* 2014). This process is considered important in the growth and differentiation of cells due to the increases in cell size, metabolism and gene expression accompanying the increase in gene copy number (Sugimoto-Shirasu & Roberts 2003; Lee *et al.* 2009; Breuer *et al.* 2014). The up-regulation of *G6PD1*, and presumably the OPPP generally, in Col-4 coincides with the increase in endoreduplication relative to unclipped control plants, but neither of these increases is observed in L*er*-0 (Scholes & Paige 2011, 2014; Scholes *et al.* 2013; Siddappaji *et al.* 2013). In fact, the experimental induction of the OPPP and endoreduplication both independently improve plant regrowth and fitness compensation following damage (Siddappaji *et al.* 2013; Scholes & Paige 2014), and may even be involved in plant tolerance to a wide range of environmental stressors (Scholes & Paige 2015). Because of the demonstrated role of the OPPP and endoreduplication in compensation, and the known differences in their induction in Col-4 *versus* L*er*-0, the genotypes' differential regrowth patterns and compensatory abilities are potentially a product of genetic differences in these two pathways.

Overall, these results reveal differences in the regrowth patterns of two commonly studied *A. thaliana* genotypes following apical damage and suggest that aspects of the rosette may be particularly important in contributing to their different compensatory abilities. While recent research has focused on the genetics of compensation, this study provides insights into the collective phenotypic expression of the genetic differences between these genotypes of *A. thaliana*. With an improved understanding of how the patterns of growth, development, architecture and physiology of these genotypes compare and contrast, our results may serve as a starting point for molecular methods to be employed in a more targeted fashion to elucidate the genetic underpinning of not only compensation for seed yield but also biomass, stem length, regrowth rates, *etc.* that may be of interest or of potential application. On a basic level, this study yields a characterisation of the regrowth response and reveals patterns linked to compensatory performance from the whole-plant perspective.

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