A mesocosm-based assessment of whether root hairs affect soil erosion by simulated rainfall

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Abstract
Although plant canopies are widely recognized to protect the soil and help mitigate soil erosion, recent research has shown that the majority of soil scour prevention can be attributed to the roots. Because roots are more difficult and time-consuming to measure than shoots, research in this area has largely been limited to understanding the influence of large roots and/or whole root systems, and there is little understanding on how smaller root traits, such as root hairs, contribute to the root system's ability to mitigate soil erosion. Therefore, this study subjected a root hairless mutant (brb) of barley (Hordeum vulgare L. cv. Pallas) and its wild-type (WT) genotype to simulated rainfall. The results showed that increasing root presence significantly reduced soil erosion, but the impact of root hairs was less clear. Soil detachment significantly decreased as root length density increased, with no apparent genotypic difference in this relationship. The brb root systems produced significantly thinner (0.8-fold) roots and a higher percentage (1.1-fold) of fine roots, with both traits previously associated with increased ability to mitigate soil erosion. However, brb mesocosms produced a similar quantity of eroded soil to WT mesocosms, suggesting that root hairs in WT plants could have compensated for their root systems' reduced ability to mitigate soil erosion.

Highlights
- It is not known whether root hairs affect a root system's ability to mitigate soil erosion.
- Soil yield following simulated rainfall was compared for a root hairless mutant (brb) and its WT.
- Root traits of brb favoured erosion mitigation, but brb and WT mesocosms eroded to the same degree.

KEYWORDS
barley, brb, root hairs, roots, simulated rainfall, soil erosion
1 | INTRODUCTION

Erosion of agricultural soil is of global concern (Borrelli et al., 2017; Quinton, Govers, Oost, & Bardgett, 2010) due to severe financial implications and threats to food security (Posthumus, Deeks, Rickson, & Quinton, 2015; Verheijen, Jones, Rickson, & Smith, 2009). Soil can be eroded by both wind and water, with water being the prominent cause in the UK (Verheijen et al., 2009). The mechanisms that cause soil to erode via water are governed by the detachment force of water versus the cohesive and adhesive bonds between the soil particles (Laflen, Elliot, Simanton, Holzhey, & Kohl, 1991). Plants have long been known to influence these interactions between soil and water, resulting in a reduction in soil erosion (Acostasolis, 1947; Singer, Blackard, & Huntington, 1980).

Although most research has focused on the impact of aboveground plant matter (such as leaves and stems), the relative contribution of roots to preventing soil erosion can outweigh the contribution of aboveground matter (Zhou & Shangguan, 2007). Up to 95% of a plant’s ability to reduce soil erosion, caused by overland flow, can be attributed to its root system (Burylo, Rey, Mathys, & Dutoit, 2012; De Baets, Poesen, Gyssels, & Knappen, 2006; Zhou & Shangguan, 2007). Similar results have also been found with simulated rainfall (Ghidey & Alberts, 1997; Zhou & Shangguan, 2007, 2008). Determining the quantitative variation in the contribution of the root system to amelioration of soil erosion requires an understanding of the mechanisms by which roots mediate erosivity.

Previous studies have found that a variety of root parameters are significantly correlated with reducing sediment yield, including root surface area (Li, Zhu, & Tian, 1991; Prosser, Dietrich, & Stevenson, 1995; Zhou & Shangguan, 2007, 2008), root length density (Bui & Box, 1993; De Baets et al., 2006; Ghidey & Alberts, 1997; Mamo & Bubenzer, 2001), root density (Gyssels & Poesen, 2003; Tengbeh, 1993) and diameter (Burylo et al., 2012; Li et al., 1991), percentage of fine roots (Burylo et al., 2012), and a combination of the above (Burylo et al., 2012; Shit & Maiti, 2012). Therefore, all root systems do not have an equal impact on erosion mitigation.

At just a cell thick, root hairs are only just visible to the naked eye, but have been associated with characteristics attributed to reducing soil loss. For example, their abundance throughout the root system means that over 90% of root surface area can be attributed to root hairs (Gilroy & Jones, 2000). Root hairs can grow as long as 1.5 mm (Brown, George, Neugebauer, & White, 2017) and their total length can be 20 times that of the rest of the root system (Wulfsohn & Nyengaard, 1999). Due to their small diameter, root hairs can physically penetrate and enmesh soil aggregates (Keyes et al., 2013; Rasse, Rumpel, & Dignac, 2005). Further to this, White and Kirkegaard (2010) show that roots actively increase root hair density to increase soil contact. As well as physical enmeshment, root hairs are considered the main water uptake pathway into the root system (Wasson et al., 2012). So, theoretically the presence of root hairs should have an impact on erosion mitigation.

Root hairs have been shown to play a role in anchoring plant roots to the soil (Czarnes, Hiller, Dexter, Hallett, & Bartoli, 1999; Ennos, 1989), but investigations into the inverse of this relationship are lacking. The only recorded mechanism by which root hairs influence soil reinforcement is by binding soil to the root through the formation of the rhizosheath, where root hairs are believed to be a key component alongside mucilage production (Brown et al., 2017; McCully, 2005; Pang, Ryan, Siddique, & Simpson, 2017; Watt, McCully, & Canny, 1994). The strength of rhizosheaths has previously been estimated in sonic baths (Brown et al., 2017), but their resistance to rainfall erosion is yet to be explored. So, although root hairs have been shown to reinforce soil at the root:soil interface and provide anchorage for roots, their impact on the whole root system’s ability to mitigate soil erosion is currently unknown.

In this paper, a root hairless mutant (brb) from barley (Hordeum vulgare L. cv. Pallas) was grown in adapted mesocosms, subjected to simulated rainfall, and compared to its respective wild-type (WT) genotype (with root hairs), with the aim to investigate whether the presence of root hairs ameliorates soil erosion. We hypothesized that the presence of root hairs would provide greater soil reinforcement and result in less soil detachment in comparison to a root system lacking root hairs.

2 | MATERIALS AND METHODS

2.1 | Mesocosms

The mesocosms were constructed out of 2lL plastic containers (Euro Container ref. 9230001, Schoeller Allibert Ltd, Winsford, UK), with internal dimensions of 55.5 cm length × 3.6 cm width × 11.5 cm height (Figure 1). Drainage holes were drilled in the base in a 5cm grid to aid drainage during growth. The top 2.5 cm of the front edge was removed (Figure 1a) so that the surface of the soil would be above the edge of the plastic, with 1.5 cm leeway, to remove any obstacles to drainage. The detached section was temporarily reattached during the growth stage to maintain the front edge of the soil profile.
Guttering was constructed out of a 40mm pipe with a 90° bend solvent welded to one end and affixed to the box with small nuts and bolts; silicone sealant was used to prevent leakage. The whole box was then affixed to a piece of 18mm thick marine plywood, cut with corresponding drainage holes and oversized to allow handles to be attached to either side of the box. The plywood and handles were necessary to minimize any disturbance to the soil structure whilst moving the mesocosms.

The mesocosms had a 20mm layer of gravel lining the bottom to aid drainage and were then filled with a sandy loam textured topsoil (Bailey’s of Norfolk Ltd, Norwich, UK; 12% clay, 28% silt, 60% sand and 3% gravel, D50 6 mm, no particles greater than 8 mm). The soil was added in 3 cm increments and packed to a bulk density of 1.4 g cm\(^{-3}\); the surface of each layer was scoured to achieve a uniform profile.

The experiment consisted of three treatments, a barley root hairless mutant, its WT and an unplanted control. Due to time and growth space constraints, these three treatments were grown in four blocks (one of each treatment per block). Each block was prepared, watered, and exposed to simulated rainfall at the same time. The mesocosms were kept in a walk-in controlled environment room set at 24°C during the day and 19°C at night, with a 12 hr photoperiod. To limit any effect of climatic variation in the walk-in controlled environment room, all three treatments per block were grown adjacent to each other in a random order. Although regular spatial rotation of the mesocosms would have been preferable, they were too heavy and fragile to move repeatedly.

The barley root hairless mutant (brb [bald root barley]) is a spontaneous mutation with its genetic background in Pallas, a spring barley cultivar. Seeds were germinated directly in the soil. Five trenches were dug laterally across each mesocosm, approximately 1 cm deep and spaced at 11.5cm intervals. Assuming an 80% germination rate, 12 seeds were planted per row to achieve a density of 245 seeds m\(^{-2}\). The trenches were then filled in and the surface smoothed over and wetted. For continuity, this process was also carried out on the unplanted mesocosms (minus the seeds). Each mesocosm was watered until a film of water appeared on the surface, using a watering can with a spray rose attached, every 2–3 days for 35 days until harvest. This was sufficient water for the barley to grow; any more resulted in excessive movement of surface soil.

2.2 | Rainfall simulator

This experiment used a gravity-fed rainfall simulator (Armstrong, Quinton, & Maher, 2012), approximately 3 m above the mesocosm surface (Figure 2). The simulator consisted of 958 hypodermic needles (25G × 25 mm, BD
Microlance™ 3, Fisher Scientific, Loughborough, UK) in 27 staggered rows of 35 and 36 needles in a grid of 47.25 × 72.00 cm, producing a rainfall rate of approximately 23 mm h⁻¹ (CU = 86.6). A 2mm mesh was suspended approximately 20 cm below the needles to disperse the water droplets and make them less uniform in size and distribution on the mesocosm surface. The simulator was run with tap water and there is a weir and outlet pipe in the chamber above the needles to ensure a consistent water pressure through the needles.

The day before harvest, the mesocosms were left standing in approximately 5 cm of water overnight for pre-wetting from the base to achieve a consistent soil water content. Soil moisture measurements, made using a soil moisture probe (HH2 Moisture Meter with a ML3 probe, Delta-T Devices Ltd, Cambridge, UK), before each experiment proved that this method was effective (WT = 33.8 ± 1.0%, brb = 33.1 ± 0.9%, and unplanted = 32.5 ± 1.2%; p = 0.208); however, there was a significant block effect (p < .01) on soil moisture content (ANOVA table can be found in the Supplementary Material). The rainfall simulator was turned on 1–2 h before the experiment, to give time for the needle reservoir chamber to fill. The shoots and leaves were removed with care so as not to disturb the surface soil immediately prior to each test. Any large gaps (approx. > 3 mm) that formed as a result of soil shrinkage or movement of the temporary barrier were filled with plumber’s putty (Plumbers Mait, Evo-Stik, UK); this also served to reinforce the front edge of the soil, preventing it from slumping.

Each mesocosm was then placed on a 6% slope under the rainfall simulator for 1 hr. Sediment and runoff were continually collected in a beaker: at 5min intervals the contents of the gutter were washed into the beaker using a measured amount of water from a 60ml syringe and the beaker replaced with an empty one. The beaker contents were weighed and then washed into a metal tray to be dried in an oven at 105°C.

### 2.3 Statistical analysis

The amount of erosion for each interval was equal to the weight of the dry soil collected in the container every 5 min and is displayed as soil detachment rate (SDR). The amount by which the presence of roots reduced the quantity of eroded soil in comparison to their respective unplanted mesocosms (relative soil detachment reduction rate [RSDR]) is calculated as a percentage decrease from the unplanted mesocosms:

$$\text{RSDR} = \left( \frac{E_c - E_r}{E_c} \right) \times 100,$$

where $E_c$ is the sum of the erosion from the control unplanted mesocosm and $E_r$ is the sum of the erosion from the rooted mesocosm; RSDR was calculated for each of the four replicates.

The amount of runoff was calculated from the weight of the beaker’s initial content, minus the weight of soil and beaker. Sampling the roots from the whole mesocosm was impractical, so roots were harvested from the top 1.5 cm using a modified guillotine, as this was easily accessible due to the removable front section of the mesocosm. The roots were washed out of the soil, stored in a 50% ethanol and DI water solution and kept at approximately 4°C until they were measured. The roots were then scanned at 600 DPI using an Epson expression 11000 XL pro scanner and analysed using WinRHIZO (2013a Pro, Regent, Canada).

Root length density (RLD) was calculated as follows:

$$\text{RLD} = \frac{\text{RL}}{V_s},$$

where RL is the total length of live roots (cm) and $V_s$ is the volume of soil sampled (cm³). Root surface area density was similarly calculated:

$$\text{RSAD} = \frac{(\pi D) \times \text{RL}}{V_s} = \frac{\text{RSA}}{V_s},$$

where $D$ is the diameter (cm) of the root and RSA is the root surface area (cm²), under the assumption that the root is cylindrical. Percentage of fine roots is calculated using the diameter threshold described by Burak (2019). Pearson’s correlation and ANOVA were used to assess the root data and two-way ANOVA was used to assess the amounts of erosion and runoff produced as well as the soil water content of the mesocosms. Linear relationships

### Table 1 Summary statistics for the measured root parameters

| Parameter          | Averages | WT       | p value |
|--------------------|----------|----------|---------|
| Diameter (mm)      | 0.188 ± 0.012 | 0.223 ± 0.005 | .035    |
| Fine roots (%)     | 89.39 ± 2.01  | 79.37 ± 1.52  | .007    |
| RLD (cm cm⁻³)      | 3.37 ± 1.25   | 1.48 ± 0.57    | .220    |
| RSAD (cm² cm⁻³)    | 0.13 ± 0.04   | 0.07 ± 0.03    | .287    |
| Volume (cm³)       | 1.68 ± 0.49   | 1.13 ± 0.40    | .415    |

Notes: Data are means ± SE of four replicates. P values are from ANOVA; full ANOVA tables can be found in Tables S4 to S8. Abbreviations: RLD, root length density; RSAD, root surface area density.
between RLD and RSDR for both brb and WT mesocosms were assessed by ANCOVA. Full ANOVA tables can be found in the Supplementary Material (Table 1).

3 | RESULTS

3.1 | Erosion

The impact of roots on soil detachment rate (SDR) was initially delayed (Figure 3). Because it took 25 min of rainfall for the mean of the unplanted mesocosms to exceed that of both the rooted treatments, 25 min was taken as the threshold for root impact. The mean total amount of erosion produced in the first 25 min, before roots became influential, was 29.3 ± 4.6 g for unplanted, 29.9 ± 13.1 g for brb and 24.1 ± 5.7 g for WT mesocosms. Assuming erosion occurred uniformly across the mesocosms, this would equate to an average eroded depth of 0.10 ± 0.01 mm across all treatments. Due to the lack of discernible root influence during the first 25 min, these data are discarded from further analysis of erosion rates.

In the subsequent 35 min, there was a significant treatment effect ($p < .05$) and a significant block effect

| TABLE 2 | A list of Pearson’s correlation coefficients for all measured root parameters |
|------------------|------------------|------------------|------------------|------------------|
| Diameter (mm)    | Fine roots (%)   | RLD (cm cm$^{-3}$) | RSAD (cm$^2$ cm$^{-3}$) |
| Fine roots (%)   | −0.96***         |                  |                  |
| RLD (cm cm$^{-3}$) | −0.91**         | 0.82*            |                  |
| RSAD (cm$^2$ cm$^{-3}$) | −0.87**        | 0.79*            | 0.99***          |
| Volume (cm$^3$)  | −0.80*           | 0.73*            | 0.95***          | 0.98***         |

Abbreviations: RLD, root length density; RSAD, root surface area density.

*p < .05,
**p < .01,
***p < .001.
The rooted mesocosms produced the least mean total erosion (32.6 ± 14.4 g and 34.5 ± 11.8 g for WT and brb, respectively) in comparison to the unplanted mesocosms (57.1 ± 10.4 g). These results equate to reductions in SDR associated with plant roots of 44.0 ± 16.8% for the WT and 40.7 ± 10.8% for the brb. However, although both rooted treatments consistently produced less erosion than their respective unplanted mesocosms, only the reduction from the WT mesocosms was significant (p < .05 and p = .067 for WT and brb, respectively).

### 3.2 | Runoff

Unlike erosion rates, runoff rates were much less susceptible to temporal fluctuations. After a brief peak 10 min into the experiment, the runoff rates remained relatively steady for the rest of the hour (Figure 4). However, total runoff and erosion (for the whole hour of rainfall) were significantly positively correlated (R = 0.82, p < .05). As with erosion rates, there was a delay in the observable difference between rooted and unplanted mesocosms. The mean of the unplanted mesocosms consistently exceeded that for both the rooted treatments after the first 20 min of rainfall, in comparison to the first 25 min with erosion rates. The runoff from both unplanted and brb mesocosms seemed to increase over time but runoff from WT mesocosms appears to decrease over time. In the last 40 min of the experiment, runoff from WT (2.29 ± 0.48 L) and brb (2.30 ± 0.39 L) mesocosms was less than that for unplanted mesocosms (2.66 ± 0.27 L) by 14.6 ± 5.5% for brb and 11.8 ± 7.5% for WT mesocosms. However, unlike with erosion, there was no significant treatment effect across the blocks (p = .24), although there was a significant block effect (p < .01).

### 3.3 | Root parameters

There were genotypic differences in some of the root traits (Table 1). Wild-type root systems had a significantly greater average diameter than the brb root systems (18.6%, p < .05). This difference in average diameter is most likely driven by the significant difference in percentage of fine roots (p < .01); in WT fine roots made up 11.3% less of the root system than in brb. Other root traits differed but not significantly. For example, for each block, the WT produces less root length density (RLD) than its respective brb, resulting in a mean RLD more than twice that of the WT (2.2-fold greater), in the top 1.5 cm of the mesocosms, although overall these differences were not statistically significant. Table 2 illustrates that all measured root parameters were autocorrelated. However, although all the measured root parameters were positively correlated with relative soil detachment rate (RSDR) for brb (Table 3), except percentages of fine roots, which were negatively correlated, only RLD was significantly correlated with RSDR for both the WT and brb.

Compared to the unplanted mesocosms, less soil was detached as RLD increased in both genotypes (Figure 5).
Each unit increase in RLD equates to an extra 14% reduction in eroded soil in comparison to the unplanted mesocosms. WT roots appeared to be more effective than brb roots at reducing erosion (in comparison to unplanted soil) as RLD increased, although the interaction between RLD and genotype was not significant ($p = .06$).

4 | DISCUSSION

The initial delay of 25 min before a root effect on erosion (Figure 3) is likely to be due to the presence of easily eroded surface soil (Armstrong & Quinton, 2009). In the subsequent period of rainfall, both brb and WT roots reduced erosion similarly, but only WT roots significantly reduced soil detachment compared to the unplanted treatment. Because the thicker roots and lower percentage of fine roots in WT plants should have resulted in increased soil erosion (Burylo et al., 2012), the lack of genotypic differences suggests an important role of root hairs in erosion mitigation.

Roots are known to reduce runoff by increasing the amount of water able to penetrate the soil, either by lowering the soil water content through evapotranspiration or physically increasing infiltration by increasing either soil porosity (Stokes, Atger, Bengough, Fourcaud, & Sidle, 2009) or hydraulic conductivity (Carminati, 2013). To eliminate potential effects of evapotranspiration and porosity, the soil was intentionally saturated before initiating the simulated rainfall. As there were no genotypic differences in runoff rates, it can be assumed that WT and brb root systems had similar impact on soil porosity and hydraulic conductivity.

Consistent with previous studies (Bui & Box, 1993; De Baets et al., 2006; Ghidey & Alberts, 1997; Mamo & Bubenzer, 2001), the presence of roots consistently decreased soil loss from both rooted treatments compared to the unplanted mesocosms (Figure 3). However, the effect of root hairs on erosion cannot be assessed in isolation from the differences in other root traits (such as root length density, diameter and percentage of fine roots; Table 2).

Increased root length density (RLD) is one of the most recognized traits by which a root system can mitigate erosion (Bui & Box, 1993; De Baets et al., 2006; Ghidey & Alberts, 1997; Mamo & Bubenzer, 2001). Although RLD and relative soil detachment rate (RSDR) were correlated, genotypic differences in RLD were not significant (Figure 5). Like RLD, root diameter is positively correlated with erosion rates and percentage of fine roots negatively correlated with erosion rates (Burylo et al., 2012); therefore, differences in average root diameter and percentage of fine roots in a root system also impact a root system's ability to reduce erosion. Thus, brb root systems with significantly smaller diameter roots (0.8-fold) and with significantly greater percentage of fine roots (1.1-fold) than WT root systems, should have been more effective at reducing erosion. This was not the case and it is hypothesized that the presence of root hairs may have compensated for the thicker roots and less abundant fine roots of the WT root systems; this explains why there was no difference between the soils eroded from the WT mesocosms and those from the brb mesocosms. However, more replication and/or a greater range of root length densities is needed to adequately test this hypothesis.

5 | CONCLUSION

In the absence of aboveground plant matter, this study showed that root systems with and without root hairs can reduce soil erosion, and increasing root length density clearly enhanced this effect. The impact of root hairs, however, was less clear. Barley brb root systems had significantly thinner root diameters and higher percentage of fine roots, traits associated with erosion reduction, suggesting that brb root systems (without root hairs) should reduce erosion more than WT (with root hairs) root systems. However, mesocosms permeated with brb roots and WT roots were eroded to a similar degree, suggesting that the presence of root hairs on WT roots may have increased soil resistance to erosion, although further work is required to test this hypothesis.

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AUTHOR CONTRIBUTIONS

Emma Burak: Conceptualization; methodology; formal analysis; investigation; writing - original draft. Ian Dodd: Conceptualization; supervision; writing-review and editing. John Quinton: Conceptualization; supervision; writing-review and editing.
DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available from the corresponding author upon reasonable request.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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