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A novel grass hybrid to reduce flood generation in temperate regions

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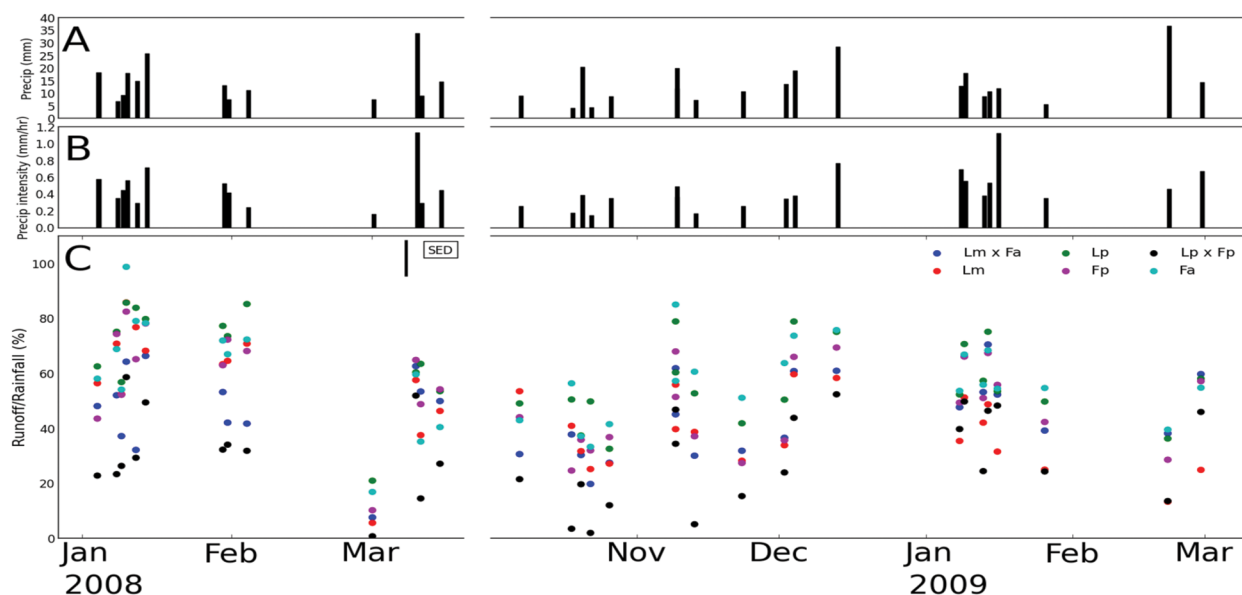
We report on the evaluation of a novel grass hybrid that provides efficient forage production and could help mitigate flooding. Perennial ryegrass (*Lolium perenne*) is the grass species of choice for most farmers, but lacks resilience against extremes of climate. We hybridised *L. perenne* onto a closely related and more stress-resistant grass species, meadow fescue *Festuca pratensis*. We demonstrate that the *L. perenne* × *F. pratensis* cultivar can reduce runoff during the events by 51% compared to a leading UK nationally recommended *L. perenne* cultivar and by 43% compared to *F. pratensis* over a two year field experiment. We present evidence that the reduced runoff from this *Festulolium* cultivar was due to intense initial root growth followed by rapid senescence, especially at depth. Hybrid grasses of this type show potential for reducing the likelihood of flooding, whilst providing food production under conditions of changing climate.

Global precipitation patterns are changing with drought in some areas and rainfall, including rainfall intensity, increasing in others[1], especially in the northern hemisphere[2]. Increased rainfall intensity causes greater runoff and streamflow[3] and potential for increased likelihood of flooding[4]. Winter stream flow in particular is increasing in central, northern and western Europe[5]. Understanding the role of agricultural land management in flood prevention is a key challenge[6,7]. Grasslands cover 69% of global agricultural land[8] and therefore offer great potential to intercept rainfall or modify runoff generation and potentially mitigate flood risk[9].

Hybrid formation and consequent persistence and fecundity are important contributors to plant speciation and evolution. They are often necessary for the successful colonisation of environments previously beyond the range of adaptation of their parent genotypes. The grasses that comprise the *Festuca* genus are excellent examples where hybridisation has provided enhanced adaptations to climatic and edaphic (soil environment) extremes[10]. Several *Festuca* (fescue) species hybridise readily with the major agricultural forage grasses of the *Lolium* (ryegrass) genus, providing plant breeders with opportunities to combine their complementary traits[11]. In particular, there is potential to integrate the rapid establishment, growth rate and forage quality of *Lolium* with the large well developed root systems and efficient water and nutrient capture of *Festuca* species[11]. As intergeneric hybrids, cultivars classified as *Festulolium* are being developed[11] that may have the required developmental and phenotype plasticity necessary to combat climatic extremes such as flooding or drought. The choice of the appropriate *Lolium* x *Festuca* species combination will depend on where the crop will be grown and the climatic and edaphic stresses anticipated.

Results

Reduced plot scale runoff generation from a *Festulolium* hybrid. As part of a long-term breeding programme to understand the genetic basis of trait variation in grasses, we have developed *Festulolium loliaceum* cv Prior (hereafter Prior). Here, we show that Prior had a significant impact on rainfall runoff compared to either parental species. Over a two-year period, Prior reduced event runoff by 51% compared to the UK National Listed perennial ryegrass cultivar *L. perenne* cv AberStar, and by 43% compared to a meadow fescue cultivar *Festuca pratensis* Huds. cv. Bf993, a progenitor of cultivar S215, the fescue parent of Prior (over two years, replicated randomized-block design) (Figure 1). Of the six grass cultivars tested, comprising two *Festulolium* hybrids (the other being a *Lolium multiflorum* x *Festuca arundinacea var glaucescens* cultivar, hereafter 99/1) and their respective parental species, Prior had consistently the least runoff in 29 out of 33 individual rainfall runoff events whereas

Figure 1 | Time series of total precipitation, precipitation intensity and reduced plot scale runoff in *Festulolium* hybrid over a two year period. Box A total precipitation (n = 2) time series for runoff events. Box B precipitation intensity (mm/hr) time series for runoff events. Boxes C and D mean plot scale runoff/rainfall (%) ((runoff (surface and 0–30 cm) for the event duration divided by the rainfall for the event duration)*100) (n = 3) from six grasses (*Lp-Lolium perenne* cv AberStar, *Fp-Festuca pratensis* cv Bf993, *LpxFp- L. perenne x F. pratensis* cv Prior, Lm-*Lolium multiflorum,*cv AberEpic, Fa-*Festuca arundinacea* cv Dovey, and LmxFa-*L. multiflorum* x *F. arundinacea var glaucescens* cv 99/1). Statistical analysis of the runoff coefficients with variable time steps used a power function-the simplest correlation structure, where the power index is the absolute time in days between the assessments. Restricted maximum likelihood (REML) was used to determine if such a model was required. The models were compared using the difference between the residual deviances (−2*log likelihood). The difference in deviances is 84 on 1 degree of freedom (this is a chi-square statistic and is highly statistically significant). Standard error of differences of means (SED) is presented. Runoff measurements were made using high resolution (one min) data collection from laboratory and field calibrated tipping buckets from March 2007. Analysis of the time series datasets identified 33 individual rainfall events.

L. perenne cv AberStar had the highest incidence of runoff in 17 rainfall runoff events. The *Festulolium* hybrid 99/1 initially had the second lowest runoff (after Prior), but following the 2008 growing season 99/1 was less effective at reducing runoff compared to its ryegrass parent (Figure 1). This is the first report that supports a clear multifunctional role for *Festulolium* as a sustainable agricultural crop bred to endure abiotic stresses[12] that also provides a regulatory ecosystem service[13] of major economic importance in temperate regions by significantly reducing runoff and the likelihood of flooding.

Rainfall accumulations (% of 1961-90 average) and return period estimates for the South West of England for 2008 and 2009 were 110% and 2–5 years, indicating average rainfall amounts. The flow in the River Taw (which the Rowden plots drain into) was 109% in 2008 and 97% in 2009 and were classed as normal flows[14]. In 2008 and 2009, rainfall during the winter months (October to March) provided 56% of the annual precipitation compared to 63% for the 1961–2000 long term average. For the duration of the rainfall-runoff events, rainfall for the winter months from January 2008 to March 2009 was 825 mm compared to 973 mm for the 1961–2000 long term average.

We did not measure transpiration directly in the North Wyke rainfall-runoff plot experiment. This study presents rainfall-runoff events from the months of October to March, which for 2008 had lower levels of average FAO Penman-Monteith calculated daily potential evapotranspiration (ET) of 0.6 mm d^{-1} (0.3 s.d.), compared to the daily average for the months April to September of 1.4 mm d^{-1} (0.5 s.d.).

Root growth and turn-over. We tested whether these favourable effects on runoff were caused by differences in root growth and turn-over[15]. We conducted root development studies on the two *Festulolium* hybrids and their respective parental species over a two year growing period. We found in all cases that, subsequent to an initial six month establishment phase during which major root development occurred, there followed a phase of significant root senescence (P < 0.001) (Figure 2). Only in the *F. pratensis* cultivar
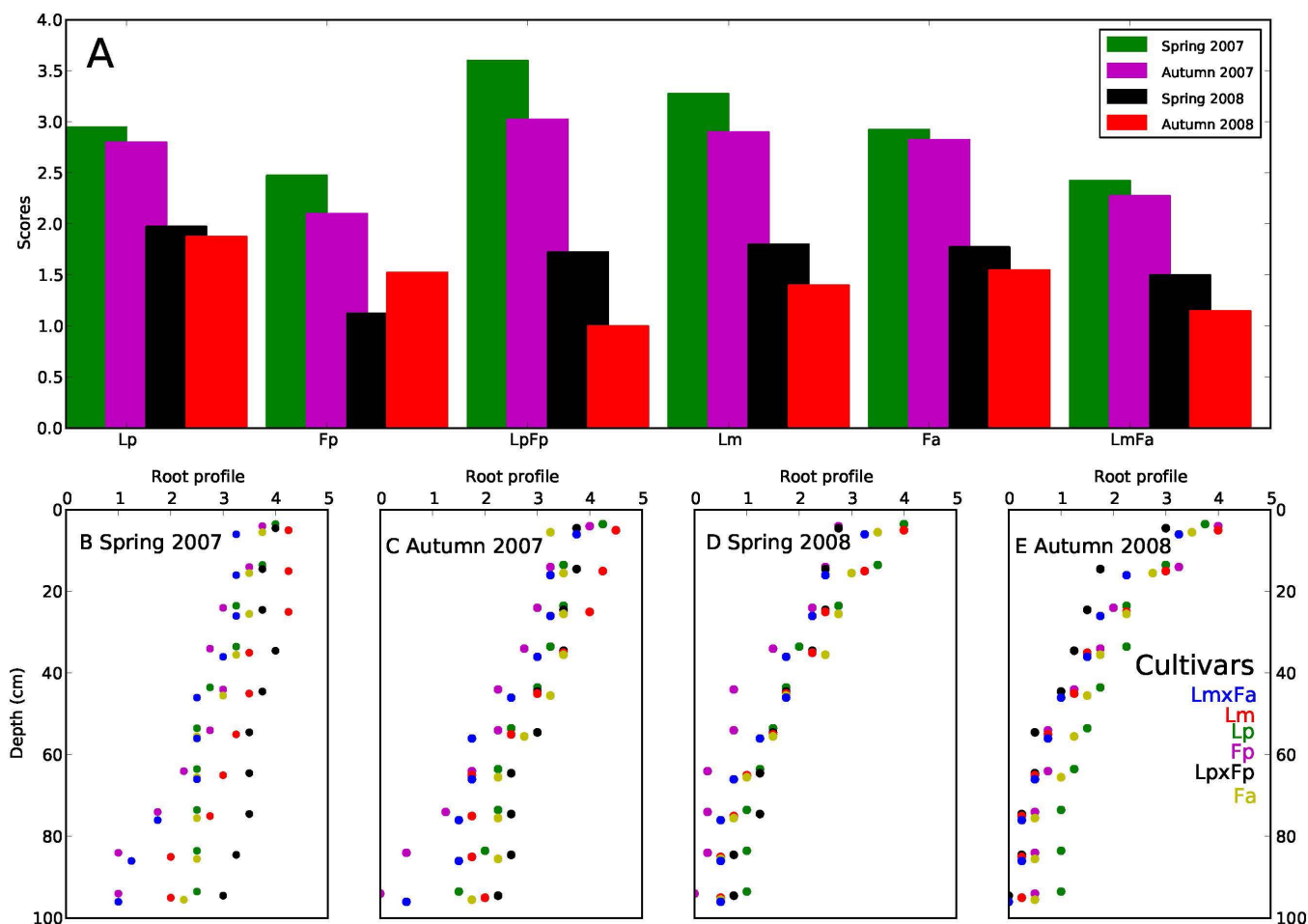
Figure 2 | Changes over two consecutive years to root system size in *Lolium* and *Festuca* species and their hybrids. Box A shows significant degeneration ($P < 0.001$) in overall root system size following an initial 6 months establishment of forage grass cultivars *Lolium perenne* cv AberStar (*Lp*), *Festuca pratensis* cv Bf993 (*Fp*), *L. perenne x F. pratensis* cv Prior (*LpxFp*), *Lolium multiflorum* cv AberEpic (*Lm*), *Festuca arundinacea* cv Dovey (*Fa*), and *L. multiflorum* x *F. arundinacea var glaucescens* cv 99/1 (*LmxFa*) throughout one meter soil columns (n = 4) observed on April 16th and September 17th over two growing seasons. Boxes B-E "dissect" these root systems (shown in A) into consecutive 10-cm fractions distributed along the one meter soil columns to show significant ($P < 0.001$) root growth and senescence (scale 0 = no visible root system; 4 = very extensive root systems) (n = 4) at the same timepoints[25].

Bf993 was there evidence for root system recovery during the second summer. A significant difference between cultivars was found in both overall root size and distribution through a one meter soil column ($P < 0.001$). In April, six months after establishment, Prior had produced both the largest and most extensively distributed root system throughout the one meter soil cores. However, after two years' growth, Prior retained the lowest number of roots throughout the soil core amongst all six cultivars, with new root growth confined to near the soil surface (Figure 2). In the field hydrological study, equivalent root growth and senescence was also observed in Prior using soil core samples and root measurements[16]. The *Festulolium* cultivar 99/1 had, in contrast to Prior, a comparatively small root system, which was smaller in size to either its parental species and was less able to limit rainfall runoff. One of the 99/1 parental species *L. multiflorum* had a similar pattern of root turn-over to Prior (Figure 2), but its overall root size and the consequent effect on soil hydrology was inferior in 2008 (Figure 1).

Herbage growth characteristics. The *Festulolium* cultivar Prior was found to have similar above ground growth characteristics in terms of biomass yield as its parental species *L. perenne* cv AberStar (Table 1). Whereas the *Festulolium* cultivar 99/1 was found to have significantly ($P = 0.05$) lower biomass yields at all time points

compared to its parental species *L. multiflorum* cv AberEpic. *L. multiflorum* cv AberEpic was only second to *Festuca arundinacea* cv Dovey in terms of above ground biomass produced over the duration of the experiment (Table 1). This data shows that the *Festulolium* hybrid Prior was not the tallest grass or had the greatest biomass. There is in general, a positive relationship between grass height (and leaf area index; which we did not measure) and rate of ET[17]. In a related microcosm experiment (unpublished data) we measured predawn leaf water potential and found no significant differences between the grass cultivars.

Soil matric potential. Automated tensiometers were used to monitor how the soil water status was changing within the experimental plots between the six grass cultivars over time. Changes in matric potential at 20 and 60 cm during 2008 from the two sets of runoff end members (pairs of cultivars with the lowest and highest average rainfall runoff percentages over 2008 events) are presented in Figure 3. This data indicates that the rapid growth and turnover of roots in the *Festulolium* hybrids resulted in greater soil water storage capacity in the plots with observed lower rainfall runoff.

Electrical resistivity tomography. We used Electrical resistivity tomography (ERT) to monitor spatial patterns of soil moisture[18,19]

Table 1 | Plot grass growth characteristics (2007–2009). Dry matter biomass (for first cut and total for five cuts) and sward height (first cut only) is presented for six grasses (*Lp-Lolium perenne* cv AberStar, *Fp-Festuca pratensis* cv Bf993, *LpxFp- L. perenne x F. pratensis* cv Prior, Lm-*Lolium multiflorum,*cv AberEpic, Fa-*Festuca arundinacea* cv Dovey, and LmxFa-*L. multiflorum* x *F. arundinacea var glaucescens* cv 99/1)

	2007			2008			2009		
	First cut[a]		All five cuts[b]	First cut		All five cuts	First cut		All five cuts
	Height (cm)	Biomass (kg DM/ha)	Biomass (kg DM/ha)	Height (cm)	Biomass (kg DM/ha)	Biomass (kg DM/ha)	Height (cm)	Biomass (kg DM/ha)	Biomass (kg DM/ha)
Lp-*Lolium perenne* cv AberStar	26.5	1912	8117	18.2	2810	8946	22.2	1480	11827
Fp-*Festuca pratensis* cv Bf993	30.7	2202	8392	21.5	3296	10214	20.1	1288	10156
LpxFp- *L. perenne x F. pratensis* cv Prior	30.5	2040	8518	23.8	3054	9170	24.0	1759	11468
Lm-*Lolium multiflorum* cv AberEpic	46.9	2901	10272	35.1	3427	10980	37.0	2698	13284
Fa-*Festuca arundinacea* cv Dovey	42.3	3316	11301	31.3	3593	12126	36.5	2241	12851
LmxFa-*L. multiflorum x F. arundinacea var glaucescens* cv 99/1	31.6	2072	7906	25.6	2884	9114	25.3	1449	11008
F pr	<0.001	<0.001	<0.001	<0.001	0.036	<0.001	<0.001	<0.001	0.001
LSD (5%)	3.55	460	993	3.63	509	709	2.77	477	1177

[a]Cut taken during week no 16. [b]Cuts taken during week nos: 16, 23, 29, 33 and 38.

to non-invasively obtain 2D maps of the variation in soil electrical resistivity. This allowed us to infer changes in soil moisture[18,19] due to the activity of the different grasses (Figure 3). We found significantly ($P < 0.01$) higher resistivity in Prior compared to *L. perenne* cv

AberStar and *F. pratensis* cv Bf993 at two separate time points that spanned the rainfall runoff results (Figure 4). ERT data showed that the soil in the root-zone of Prior had a much higher electrical resistivity than the other grasses on both occasions (Figure 4). This
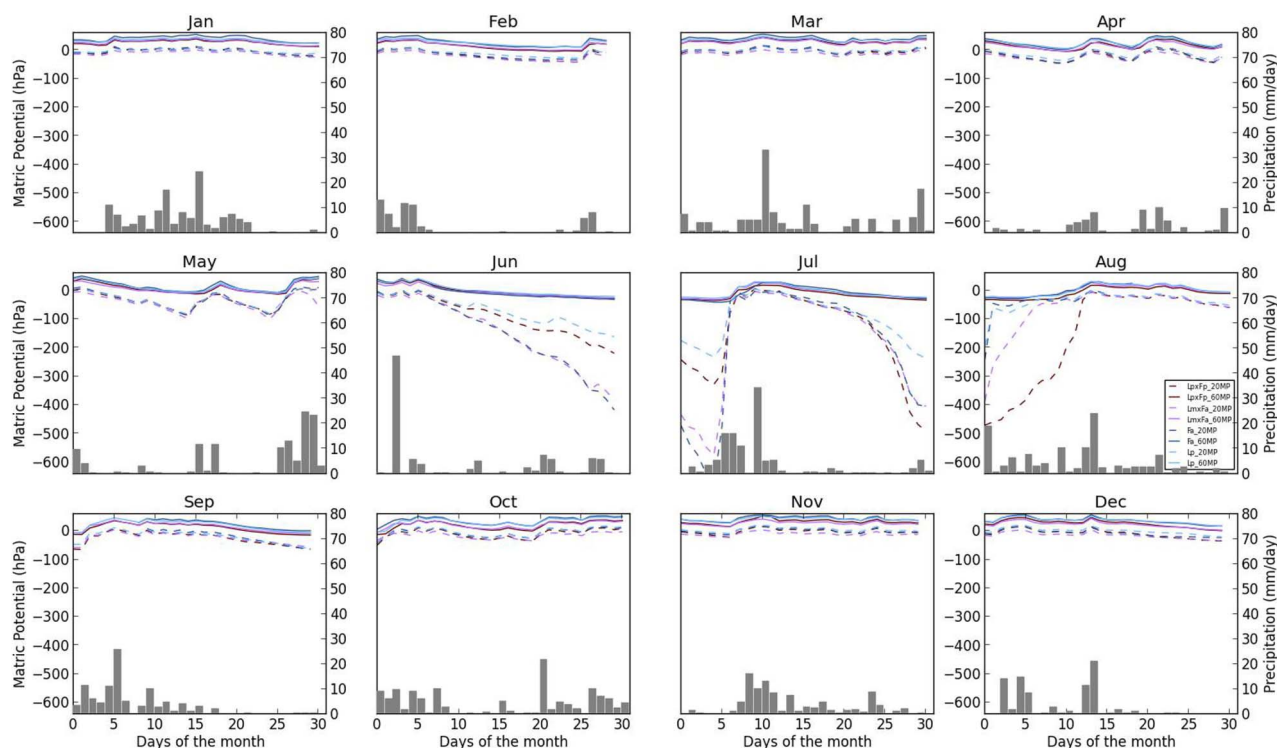
Figure 3 | Changes in soil matric potential during 2008 indicating greater soil water storage capacity in the Festulolium plots. The lower soil matric potentials at 20 and 60 cm in the *LpxFp- L. perenne x F. pratensis* cv Prior and LmxFa-*L. multiflorum* x *F. arundinacea var glaucescens* cv 99/1 Festulolium hybrids (which had the lowest average rainfall runoff percentages for the 2008 events) compared to *Lolium perenne* cv AberStar and *Festuca arundinacea* cv Dovey (which had the highest average rainfall runoff percentages for the 2008 events).

is due to the rapid growth and senescence of Prior's roots, resulting in greater storage in the soil profile and lower water content of the surface soil layers.

Tension-infiltration. We carried out field based tension infiltration measurements on four occasions (May 2007, October 2007, May 2008 and July 2008), where the flux of water into the soil was measured at a range of negative pressures (-2, -1.5, -1.0, -0.5 and 0 kPa)[20]. This technique measures the hydraulic properties of the surface soil. We found that the greatest infiltration rate was in *Lolium perenne* cv AberStar, followed by *Festuca arundinacea* cv Dovey, *L. multiflorum* x *F. arundinacea var glaucescens* cv 99/1, *L. perenne x F. pratensis* cv Prior and *Lolium multiflorum,* cv AberEpic.

Discussion

Poor infiltration of water into soil is sometimes explained in terms of biologically induced water repellence[21], but we found no difference ($P = 0.117$) in the wettability (as measured with the capillary rise method[22]) for soils in the different grass plots[20]. We conclude that the differences in infiltration (Figure 1) and soil water content of the profile (Figures 3 and 4) are due to differences in the spatial organization of soil, commonly referred to as soil structure. There are two likely mechanisms responsible for changes to soil structure. First, the soil used in the experiments is known to shrink on drying and, in a parallel laboratory experiment, we observed cultivar differences in drying rates likely to cause soil shrinkage and therefore induced soil structure. Second, we suggest that the senescing roots that penetrated the deeper soil layers are likely to leave bio-pores that can transmit water to depth, resulting in a greater soil water storage capacity. The tensiometer data (Figure 3) indicates that for long periods of time the water table was near the surface, resulting in the high rainfall runoff percentages. This data also indicates that there is a decrease in the water table in the plots between events.

The rapid root development and senescence (Figure 2) in the Prior cultivar is likely to be an important control on runoff generation and therefore the likelihood of flooding. The longevity of these effects on runoff generation is unknown. Though, vertical cylindrical pores (like those created by grass roots) have been shown to be more stable compared to interaggregate pores[23]. Further research is required to assess when and to what degree improvements in plot to landscape scale soil water storage capacity can contribute to reducing runoff generation and mitigating the risk of flooding.

The resilience of the *Festulolium* cultivar Prior against climatic and edaphic stresses found commonly throughout temperate regions of the world, makes possible its widespread use as both a support to sustainable agricultural practice and a safeguard against flooding.
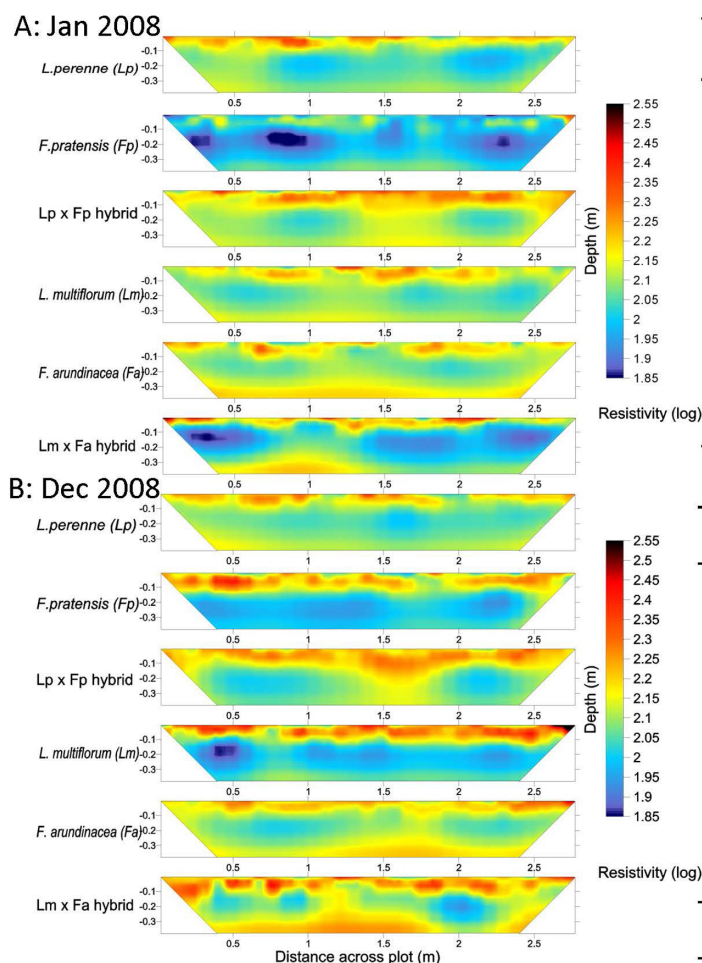
Cultivar	0–20 cm	0–40 cm
L. perenne	135.2	133
F. pratensis	100.8	101.7
Prior hybrid	152.2	148.2
L. Multiforum	135.1	134.2
F. Arundinacea	134.1	137.6
99/1 hybrid	135.6	139.1
sed	1.4	0.9
Cultivar	0–20 cm	0–40 cm
L. perenne	135.4	134.5
F. pratensis	139.8	131.8
Prior hybrid	152.7	146.2
L. Multiforum	150.3	140.2
F. Arundinacea	141.2	142.2
99/1 hybrid	152.1	152.8
sed	1.8	1.1

Figure 4 | Differences in plot scale 2D electrical resistivities indicating *Festulolium* induced soil surface drying. Higher surface resistivities in Prior treatment compared to other grass cultivars indicates lower water content in January 2008 (A) and December 2008 (B). Data are 2D electrical resistivities, log10(resistivity in Ohm-m). from electrical resistivity tomography, determined using a 32-electrode 2.9 meter length Wenner array with 0.09 meter minimal electrode spacing. The computed electrical resistivity measures the ability of the soil to restrict flow of electrical current laterally and vertically. The six treatments were *Lp-Lolium perenne* cv AberStar, *Fp-Festuca pratensis* cv Bf993, *LpxFp- L. perenne x F. pratensis* cv Prior, Lm-*Lolium multiflorum,*cv AberEpic, Fa-*Festuca arundinacea* cv Dovey and LmxFa-*L. multiflorum* x *F. arundinacea var glaucescens* cv 99/1. Average values over 0–20 and 0–40 cm depths across 2D transects. Statistics carried out using a two-way ANOVA with Genstat 13th edition.

This is a timely finding during a period of increasing rainfall intensity[1,2] and flooding[4].

Methods

Experimental design and plant material. Three replicate 10 × 3 m plots of *Lolium perenne* cv AberStar (Lp) (diploid), *Festuca pratensis* cv Bf993 (Fp) (diploid), *L. perenne* × *F. pratensis* cv Prior (LpxFp) (tetraploid), *Lolium multiflorum* cv AberEpic (Lm) (diploid), *Festuca arundinacea* cv Dovey (Fa) (hexaploid), and *L. multiflorum* x *F. arundinacea var glaucescens* cv 99/1 (LmxFa) (tetraploid) were established on a planar hillslope (5°) on a clay rich soil (Typic Haplaquept (USDA classification) or Dystric Gleysol (FAO classification)), and subsequently maintained over three entire growing seasons (2006-2009) at Rothamsted's North Wyke Research, Devon, UK. The Rowden research platform of which these plots were part of is situated on the Hallsworth soil series. This soil series represents the most common hydrologic soil type in England and Wales, covering approximately 13.9% of the land area according to the Hydrology of Soil Types classification system[24]. The study site was carefully chosen to have a homogeneous soil texture so as to remove the potential for soil texture to influence the soil water balance.

The rainfall runoff plots were drilled in an identical manner using a professional small plot drill (Hege seed drill) operated by an experienced member of staff. The plots were drilled along their length (10 meter) with a buffer (2 meter) on the upper and lower boundaries to ensure no mixing of different grass seeds. At the start of each plot and buffer area the correct mass of seeds was added to the drill and seeds planted. The spacing of the rows was 11.5 cm. The sowing rate accords with commercial field trials throughout Europe: 2.2 g m² for diploids (*Lolium perenne* cv AberStar, *Lolium multiflorum*,cv AberEpic and *Festuca pratensis* cv Bf993) and 3.3 g m² for the tetraploids and hexaploids (*L. perenne x F. pratensis* cv Prior, *L. multiflorum* x *F. arundinacea var glaucescens* cv 99/1 and *Festuca arundinacea* cv Dovey). The seeds of diploid grasses are smaller, so require a smaller mass of seed to produce an equivalent ground cover. Visual checks were made after six months of growth to ensure plots had been drilled with the correct grass material. A homogeneous sward was maintained by manual weeding from June 2006 until the end of 2009.

The plots were fertilized at the start of the growing season and following five herbage cuts for which dry matter yield was determined gravimetrically (middle of April, then at the start of June, July and August and then in the middle of September). In total approximately 250 kg/ha of mineral N fertilizer was added with 90 kg/ha P and 120 kg/ha of K per annum in line with guidelines at the time and soil testing for P and K. Soil cores were taken from the field plots in the Autumn of 2007 and 2008 and root mass determined gravimetrically after washing[16].

During an identical period (summer 2006), five equal sized clones comprising five representative genotypes of the six cultivars were established and maintained in heated (min temp 8°C) glasshouse conditions in freely draining polythene-lined one meter deep pipes filled with John Innes No3 Potting Compost (n=4)[25]. Above ground growth was determined at the same time points in 2007 and 2008 as the field experiment. Plants were cut back to five cm and dry matter determined gravimetrically. Root growth measurements were made by non-destructive scoring of visible roots in 10 cm sections viewed through the one meter polythene sleeve extracted from the glasshouse pipes at IBERS in April and September 2007 and 2008 concurrent with foliage harvest[25]. The maximum depth at which roots were visible was recorded and root density for each 10 cm section was scored on a scale of 0 (no roots visible) to 4 (extremely dense rooting). The proportion of roots that were white or very pale colour were classed as "new roots"[26]. Other roots were classed as "old roots". Root system size was the sum of scores for all these sections and root profile was the regression coefficient for a line fitted through the root from the lowest section to the surface.

Plot herbage production. Plot herbage dry matter yield and sward height was determined at five time points each year in 2007-2009 (during weeks 16, 23, 29, 33 and 38). Sward height was measured by taking 10 measurements at one meter intervals along the length of each plot. Herbage yield was determined by measuring the mass of an eight meter strip of each plot using a Haldrop small plot harvester. Subsamples were taken from each plot and the moisture content was determined gravimetrically through drying (at 100°C) to a constant mass. The grass cultivars in the IBERS microcosm were harvested during the same weeks.

Plot rainfall runoff. Rainfall was measured using two Delta T RG1 rainfall gauges (standard meteorological equipment) within the plots. The plots were hydrologically isolated from lateral flows through gravel drainage ditches top and bottom and plastic sheeting inserted to 40 cm depth (10 cm above soil surface) along the plot sides. Visual inspections were made at regularly intervals to ensure that water was not flowing onto or off the plots through the side surface barriers. Runoff was collected along two hydrological pathways: the upper capturing water moving across the vegetated soil surface and to a depth of five cm (through careful insertion of plastic sheeting 10 cm into the plot that fed plastic guttering); and a lower pathway to a depth of 30 cm in the clay Bg horizon. The Bg soil horizon is a clay and has a low saturated hydraulic conductivity ($<10^{-10}$ ms^{-1})[27]. The assumption is that vertical losses and gains of water through the subsurface will be low, especially when the soil is saturated and over short durations (the events reported in this paper). A number of hydrological studies on the Rowden experimental platform have found these to be the main hydrological pathways during saturated conditions, with some loss to the groundwater[28]. This later pathway fed to a plastic lined trench that was backfilled with 40 mm gravel drainage and a slotted drainage pipe. Water in these two hydrological

pathways was measured using calibrated (laboratory and field) tipping buckets[29] both recording at one minute intervals. In this paper the combined runoff from these two hydrological pathways is presented as ((runoff for the event duration divided by the rainfall for the event duration)*100).

Soil matric potential. In 2007, UMS T4 (without external refilling) pressure transducer tensiometers were inserted to 20 and 60 cm in one block of the grass cultivar treatments. Readings of matric potential were automatically recorded at one minute intervals and regularly downloaded from Delta T GP1 data loggers. The T4 tensiometers were chosen since they can provide reliable outdoor measurements of soil water tension from +100 kPa to −85 kPa. The tensiometers were installed according to manufactures guidance[30]. At the end of September 2007 and 2008 the tensiometers were removed to check for the presence of air bubbles and to recalibrate, before the start of the winter drainage season.

Electrical resistivity tomography (ERT). We collected 2D electrical resistivities using D.C. resistivity metering applied with a 32 electrode Wenner array on a fixed support (0.09 m spacing and 2.9 m length). D.C. resistivity metering measures the ability of the soil to restrict the flow of electrical current laterally and vertically. A GEOPULSE resistance meter and multiplexor switching unit enabled computer controlled automatic survey collection over two cycles of repeated measurements. Good contact between the electrodes (three cm) and soil was tested for using the GEOPULSE resistance meter. Spatial variation in resistivity was determined using four-electrode measurements. Two electrodes were used to establish an electrical circuit with measurement of the potential difference between two additional electrodes enables determination of apparent resistivity[31]. The aim of resistivity measurements was to derive the distribution of electrical properties of the subsurface from a set of measurements taken from the soil surface. Given the surface apparent resistivities (data) then an "inverse problem" was solved to produce a distribution of electrical properties (model) to explain the data. The inverse problem was solved as a regularized optimization problem involving the minimising of an objective function and a penalty term of deviation from desired model attributes[31]. The average (n=2) resistivities underwent an inversion using a quadrilateral finite element mesh with the Profiler inversion software[31,32]. Soil electrical resistivities are dependent on temperature; the output resistivities were adjusted[33] using soil temperature data collected at the time of resistivity surveys using in-situ thermistor temperature probes at 10, 20, and 40 cm depths (ST2, Delta T).

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Author contributions

C.J.A.M., M.W.H. and P.M.H.conceived the project. C.J.A.M. and A.J. set up the North Wyke plots and collected the data. C.J.A.M., M.W.H. and L.T. carried out the data processing. W.R.W., A.B. and C.W.W. helped carry out the soil physical and geophysical observations and analysis. M.W.H. led the plant aspects of the project. M.W.H., L.T., S.H., S.O. and L.S. provided plant cultivars and carried out the IBERS pipe experiment. M.W.H., P.M.H. and W.R.W. helped C.J.A.M. write the paper.

Additional information

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