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Investigating the impact of trees and hedgerows on landscape hydrology

Webb, Bid

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A thesis submitted to Bangor University by

Bid Webb

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School of Natural Sciences

Bangor University

Bangor, Gwynedd

LL57 2UW

UK

Declaration

I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards.

I declare that I am submitting this work with my supervisor's agreement.

Executive Summary

Anthropogenic climate change is inducing large-scale changes in rainfall intensity and frequency with a concomitant rise in flooding globally. Increasing ecological complexity through the integration of trees into the landscape creates multifunctional landscapes and can provide opportunities for 'natural flood management' through the regulation of streamflow. Whilst there is strong evidence to demonstrate an increase in streamflow from deforestation, evidence of a reduction in peak flow following afforestation is unclear due to a lack of empirical research. Moreover, the role of trees in hydrological regulation outside of forests, such as hedgerows, are little studied and often excluded from ecosystem service models. This thesis aims to understand tree species identity, richness and soil type on hydraulic function as well as the role of hedgerows in regulating soil water and the interaction with soil type, hedgerow age and time of year. Seven broadleaved tree species (*Alnus glutinosa* [L.] Gaertner, *Fraxinus excelsior* L., *Fagus sylvatica* L., *Betula pendula* Roth., *Castanea sativa* Mill., *Quercus robur* L. and *Acer pseudoplatanus* L.) grown in monoculture and a two species mixture on soil hydraulic properties were examined using a combination of root morphological characteristics collected from three soil layers (0-0.1, 0.1-0.2, 0.2-0.3 m) and soil physical properties from two soil layers (0-0.05, 0.1-0.15 m) at BangorDiverse, north Wales, whilst the interaction of *F. excelsior* with soil types of contrasting soil textures was examined at four sites across England and Wales. Fine root biomass (FRB) was positively correlation with field-saturated hydraulic conductivity (K_{fs}) and altered soil macroporosity and hydraulic function. Fine roots of *F. excelsior* were found to alter soil hydrology independently of soil type in the top 0.1 m of soil, where the majority of FRB is found, but below this, soil type mediated hydraulic function. In the mixed species plots, hydraulic conductivity was not affected by species richness *per se*, but by species identity. Tree species with contrasting functional traits, namely *B. pendula* and *C. sativa*, benefitted from a mutualistic relationship and belowground overyielding that resulted in a significant increase in K_{fs} compared to *C. sativa* in monoculture. Where mixtures consisted of species with similar functional traits e.g. *F. excelsior* and *B. pendula*, no belowground overyielding and a significant reduction in *F. excelsior* FRB and macroporosity was observed. Woody hedgerows in pasture-livestock farming systems were then used to investigate seasonality and soil type interactions on soil hydraulic properties. Soil matric potential was measured every 30 minutes for a year up- and downslope of a hedgerow on seasonally-wet (SW) and free draining (FD) soil types, and soil water retention curves determined. Soil macroporosity was 14-25% of total pore space under hedgerows, compared with 2-4% in pasture and 9-14% next to a stone wall, and soil moisture was significantly lower adjacent to hedgerows for 10-months of the year. At the SW site the hedgerow created a disconnect in lateral and vertical subsurface flow, whereas at the FD site no break in hydrological connectivity was observed. This thesis has shown that: (i) Soil macroporosity is increased by the presence of trees and the magnitude of change is tree species specific; (ii) widespread loss of *F. excelsior* from disease could have a large impact on local soil hydrology; (iii) species selection based on contrasting belowground functional traits to maximise niche differentiation should be considered where hydrological regulation is a key objective; and (iv) hedgerows can interrupt hydrological flow paths, and reduce flood risk, but the magnitude of change will depend on underlying soil types. These results suggest that the incorporation of trees into the landscape as hedgerows and forests has potential to improve flood risk management and that land managers and modellers should consider the traits of individual species when planning afforestation.

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Chapter 1 Introduction

1.1 Background

Trees and forests are fundamental to regulating the Earth's water, energy and carbon (C) cycles (Ellison et al., 2017). European woodland covers on average 35% of the land area (Forest Europe, 2020), whilst the extent of woodland cover in the UK is just 13% of the total land area (Forest Research, 2020). Hedgerows and tree shelterbelts were once common on farms throughout the UK but with the advent of the post-World War 2 drive for agricultural intensification, coupled with European Union incentives driven by the Common Agricultural Policy (CAP) reform, hedgerow extent has decreased (O'Connell et al., 2007). This transpired through activities such as the removal of small tree features and hedgerows for field enlargement, improving unviable land through establishment of land drains, channelization of watercourses and the removal of riparian buffer zones. Furthermore, land management and cultivation practices such as higher livestock stocking densities and deeper ploughing have resulted in compaction and exposed soils leading to increased overland flow and soil erosion from bare fields (Dadson et al., 2017; O'Connell et al., 2007).

Anthropogenically induced climate change is creating large-scale shifts in weather patterns, brought about by the release of CO_2 and other greenhouse gases. As a result, the occurrence and intensity of extreme weather and climate (e.g. rainfall and drought) is increasing (IPCC, 2014). Over the last 250 years, precipitation in the UK has increased significantly during the winter months and decreased significantly during the summer months with more pronounced winter precipitation in the uplands than in the lowlands (Dadson et al., 2017). Concurrent to a changing climate, ecosystem resilience to extreme events has reduced, as demonstrated by recent widespread flooding in the UK (Parry et al., 2020), and much attention has been given to the role agricultural land can play in improving ecosystem resilience (Mcintyre and Thorne, 2013).

Increasing ecological complexity in agricultural landscapes through the incorporation of trees creates a multifunctional landscape that can improve ecosystem service provision and benefits to humankind (Baudry et al., 2000). Ecosystem services (ES), defined broadly as the benefits to people from natural ecosystems, are used as a conceptual framework to understand human dependency on environmental services (Millenium Ecosystem

Assessment, 2005). Four categories define ES; provisioning (products from ecosystems), regulating (benefits from ecosystem process regulation), cultural (non-material benefits) and supporting services (supports all other ES). Regulating ES from trees and woodland include, mitigating climate change by retaining C in the biomass as well as in the soil (Lamb et al., 2016; Walter et al., 2003), habitat diversity and connectivity (Nelson et al., 2009) and soil quality enhancements through organic matter accumulation, diversity of root morphologies and greater soil macrofaunal activity (Walter et al., 2003). Additionally, woodland features can reduce erosion, keeping sediment and nutrients *in situ*, which in turn, improves downslope water quality (Viaud et al., 2005) and importantly, may also reduce downstream flooding (Dadson et al., 2017; Dixon et al., 2016; Wolton et al., 2014).

The Committee on Climate Change (2020) has set out its land strategy to meet the UK's 'Net Zero' target by 2050 to reduce climate change with a key policy to increase UK forestry cover to 17% by 2050 through afforestation, agroforestry, hedgerow creation and broadleaved tree management. It envisages the use of sustainable intensification approaches with the aim of releasing one fifth of current agricultural land for reducing emissions and sequestering C activities, whilst also recognising the non-carbon benefits such as hydrological regulation.

In the UK, approximately six million properties are at risk from flooding and the average economic cost of flooding in England and Wales is £1.2 billion annually (Ramsbottom et al., 2012). The use of hard engineering is no longer seen as a panacea to flooding as increases in storm frequency and intensity are increasingly breaching current flood defence structures. The cost of maintaining and building new structures, particularly in small catchments is increasingly unattainable and thus Natural Flood Risk Management (NFRM) alternatives are being explored (Parliamentary Office of Science and Technology, 2011) .

NFRM and the role of trees to mitigate against flooding have garnered particular interest throughout Europe (ALFA Project.eu) (Dusek and Vogel, 2016; Ghazavi et al., 2011) and the UK (Dixon et al., 2016; Marshall et al., 2013; Thomas and Nisbet, 2007; Wilkinson et al., 2014). The UK policy on NFRM states that "working with natural processes" must be considered when designing flood mitigation measures (Parliamentary Office of Science and Technology, 2011). Enthusiasts of 're-wilding' call for afforestation of the uplands (Monbiot, 2014) and grassroots organisations are implementing NFRM measures to try to reduce flood risk in their communities (e.g. see www.slowtheflow.net). However, a recent meta-analysis assessing the effect of trees to mitigate flood risk uncovered little evidence to support afforestation as a means to reduce channel discharge (Carrick et al., 2019). The authors cite the lack of empirical research as the primary barrier to confidence in the results and a high risk of publication bias. Small tree features, such as hedgerows are often excluded in landscape models used to understand catchment-scale water cycling and C storage contributions, principally due to a lack of empirical data (Cardinael et al., 2018; Dadson et al., 2017; Scholefield et al., 2016). Understanding the mechanisms by which trees, soil and water interact is a fundamental step in understanding the role forests, woodlands and trees outside of woodlands may have in both carbon cycling and reducing flood risk.

1.2 Research aims

I. To review the impact of trees and hedgerows on soil hydraulic function.
II. To understand the interactions between tree species identity, richness and soil type on soil hydraulic function.
III. To understand the role of hedgerows in regulating soil water and the interaction with soil type, hedgerow age and time of year.

1.3 Research hypotheses

1. Interspecific differences in tree fine root morphology affects soil hydraulic function (Chapter 3).
2. Soil type affects tree fine root biomass density and soil hydraulic conductivity (Chapter 3).
3. Fine root biomass of *F. excelsior* is not reduced when grown with a tree species of similar root morphology (Chapter 4).
4. Fine root biomass and morphological characteristics result in a greater hydraulic response when species grown in mixture possess contrasting functional traits. (Chapter 4).
5. Seasonality and soil type affect soil water storage capacity and air-filled pore space associated with woody hedgerows (Chapter 5).
6. Woody hedgerows increase hydraulic conductivity and interrupt hydrological connectivity across a hydraulic gradient (Chapter 5).

1.4 Thesis outline

The thesis is comprised of six chapters; an introduction (Chapter 1), a review of the literature (Chapter 2), three empirical chapters (Chapters 3-5), and a concluding chapter (Chapter 6) that draws together the different threads of the thesis. The title of each experimental chapter includes details of the authors, author contributions, and the current progress of each manuscript in relation to publication (e.g., published / submitted / draft).

Chapter 2: The impact of trees and hedgerows on soil hydraulic function

Reviews the impact of trees and hedgerows on soil hydraulic function, it considers soil and hydrological processes and the influence of trees on soil moisture and water yield. The role of tree age, species, seasonality, location and livestock are specifically considered, and key knowledge gaps are identified.

The following three empirical chapters take a mechanistic approach to investigate the impact of trees and hedgerows on soil hydraulic function and soil C storage.

Chapter 3: Variation in tree root morphology between tree species influences soil hydraulic conductivity and macroporosity

Investigates how root morphology and fine root functional traits of seven broadleaved tree species (*Acer pseudoplatanus* L.*, Alnus glutinosa* [L.] Gaertner*, Betula pendula* Roth.*, Castanea sativa* Mill*, Fagus sylvatica* L.*, Fraxinus excelsior* L. and *Quercus robur* L.), common to the UK and Europe, grown in monoculture interact with soil to influence hydraulic conductivity. Secondly, this chapter further explores how the interaction of *F. excelsior* and soil type influences soil hydraulic conductivity in four different soil types that span the UK.

Chapter 4: Contrasting root morphological traits in two-species admixture regulates fine root yield and hydraulic conductivity

Determines the relationship between species identity and fine root morphological traits of mixed species stands on soil hydraulic function. Two 2-species tree stands were investigated, the first consisting of species that follow similar successional pathways and produce a large amount of fine root biomass (*F. excelsior* & *Betula pendula*), the second with contrasting successional species and fine root biomass production (*B. pendula* & *Castanea sativa*). The role of species richness and species identity on hydraulic conductivity is considered.

Next, the research moves from an experimental to an applied setting, assessing the role of hedgerows in pasture-livestock farming systems on hydraulic connectivity.

Chapter 5: Abundance of air-filled soil pore space in hedgerows is increased by the presence of woody species and moderated by soil type

Determines the seasonality impacts of hedgerows on soil hydraulic properties in seasonally wet and free-draining soil environments. Specifically, the influence of hedgerows on soil structure and storage, the relationship of drainage and seasonal air-filled pore space and connectivity on a hydraulic gradient is examined.

Chapter 6: Discussion

Concludes by discussing the effects of tree species and tree diversity on hydraulic function and the role hedgerows play in regulating plot-scale hydrological ecosystem function. The wider implications for land management decision-making where hydrological regulation are key objectives are considered and recommendations are given for further research.

1.5 Multi-land project

The research presented here was conducted as a PhD studentship associated to the National Research Network for Low Carbon Energy and Environment (NRN-LCEE) Multi-land project. The NRN-LCEE was an initiative of the Welsh Government and the Higher Education Funding Council for Wales Sêr Cymru programme. One of eight pan-Wales research clusters, the Multi-land project was centred around enhancing agricultural productivity and ecosystem service resilience in multifunctional landscapes and drew together partners from Bangor and Aberystwyth universities, UK Centre for Ecology and Hydrology (Bangor), Woodland Trust, National Trust, Coed Cymru and Snowdonia National Park.

1.6 Field sites

The work contained within this thesis benefitted from access from several field sites. First, detailed empirical work on species' effect on soil properties (Chapters 3 & 4) was conducted at Bangor University's research field station Henfaes (53°14'15''N, 4°1'4''W) within the BangorDiverse biodiversity and ecosystem function experimental infrastructure (https://treedivnet.ugent.be/ExpBangor.html).

Second, Forest Research's Ash Provenance experimental research network (Cundall et al., 2003) was utilised for empirical work investigating the effect of soil type on fine root morphology (Chapter 3). The original network, established in 1992, consisted of six sites of *F. excelsior* in a randomised block design of contrasting provenance, of which three were used for the research; Hampshire (51° 12′ 02.02″ N, 001° 31′ 39.48″ W), Gloucestershire (51° 54′ 24.93″ N, 002° 18′ 39.68″ W) and Gwynedd (53° 14′ 19.38″ N, 004° 01′ 05.91″ W). A fourth site at Rothamsted Research in Devon (50° 46′ 12.14″ N, 003° 54′ 08.79″ W), established in 1987 was added to extend the diversity of soils used in the analysis.

Third, the Fferm Ifan group hosted the applied research component in the Conwy valley. Fferm Ifan are a group of 11 tenanted farmers situated on National Trust land near to Ysbyty Ifan in the upper River Conwy catchment, North Wales (centred on 53.04°N, 3.71°W). Covering 2 456 ha of agricultural land in the uplands (175-335 m asl), the group are collaboratively working to improve and manage natural resources sustainably at a landscape-scale through the Welsh Government's Sustainable Management Scheme. The farms are managed for mixed sheep and beef cattle production on permanent pasture on stagnogleys and brown earth soils. Hedgerows at two of the farms (Bryniau Defaid and Eidda Fawr) were instrumented for research carried out in 2017-2018 in Chapters 5. Additional C-related research was conducted here (Ford et al., 2021) and across ten farms from the group (Ford et al., 2019).

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Chapter 2 The impact of trees and hedgerows on soil hydraulic function

2.1 Soil & hydrological processes

Subsurface flow is influenced by soil texture, defining underlying soil porosity and its inverse, bulk density and is used to define soil hydraulic properties (Boorman et al., 1995; van Genuchten, 1980). However, there is evidence to suggest that land cover, porosity and soil organic carbon are better metrics to predict soil hydraulic function (Jarvis et al., 2013). Although related to soil texture, they can change through time and will be impacted by land use, management and climate change (Hirmas et al., 2018).

The hydraulic conductivity of soil is determined by the relationship between soil water potential and soil water content. Hydraulic conductivity, first described by Darcy in 1856 to calculate the rate of flow of water through saturated soil and later updated by the Richards equation (1931) to include unsaturated soil, assumes water flows from areas of high matric potential (higher water content) to low matric potential (lower water content). Soil water retention curves (SWRC) describe the relationship between water content of a given soil and the soil water matric potential. The SWRC and soil hydraulic conductivity are related, with small changes in the former leading to large changes in the latter (Schelle et al., 2013). Although the Darcy-Richards equation provides the theoretical basis for understanding hydraulic function, whether it adequately addresses the role of macropores and preferential flow is contested (Beven and Germann, 2013), but modifications account for bimodal flow in water retention models (Radcliffe and Simunek, 2010). Macropores are subject to gravitational drainage, whilst water in the remaining pores are held under tension (matric or capillary force). Field saturation, which accounts for occluded gas- filled pore space in large soil pores, occurs between field capacity (soil moisture at the conclusion of gravitational drainage) and saturation (all soil pore space filled with water) (Chandler et al., 2017). Small pore sizes have the greatest surface tension and fill first, while large pores are first to drain, creating hysteresis. Therefore, the soil’s resistance to flow is dependent upon pore-size distribution, water content and pore connectivity (Blume and van Meerveld, 2015) influenced by underlying soil conditions and slope (Bronstert et al., 2002; Ellis et al., 2006).

Preferential flow in the soil matrix dominates hydraulic conductivity and is associated with macropores, including artificial drainage (Marshall et al., 2009), macrofaunal pathways

(Bargues Tobella et al., 2014), biomat flow (Gerke et al., 2015) and root channels (Zhang et al., 2015). Where artificial soil drains are present, they can have a disproportionate influence on preferential flow, providing a direct connection for sub-surface flow to the river. Only when the soil has reached saturation is overland flow dominant (Bathurst et al., 2018; Marshall et al., 2009). However, the influence of drainage is mixed. Drainage of clay soils and permeable soils can both decrease and increase flooding at plot scales respectively. Where drainage has dried the soil, there is more storage capacity thereby reducing downstream flow, but once the soil saturated has no influence flow. Furthermore, open ditches are more reactive than sub-surface artificial drainage and so will have a greater influence on flow (Dadson et al., 2017).

Regardless of soil conditions, the depth of soil to bedrock will always limit infiltration. The soil depth can be artificially limited by the development of an impermeable layer within the profile (Gerke et al., 2015). This may be naturally occurring where there has been a deposit of impermeable material or anthropogenically-induced, such as through repeated ploughing to a certain depth creating a plough pan (Archer et al., 2015). Water accumulates on the impermeable layer producing a perched water table, infiltration is reduced and saturation overland flow common (Marshall et al., 2009).

Across the UK, soil is classified by soil type and the hydrological processes that occur in the soil and substrate. This classification system, known as Hydrology of Soil Types (HOST), categorises UK soils into 29 classes representing differences in hydrological properties (Boorman et al., 1995). The spatial heterogeneity of soil types means that hydrological response to an event or intervention can not be generalised (Fig. 2.1). However, soil type has been shown to be a dominant factor in run-off generation in wet, temperate climates (Geris et al., 2015).

2.2 Plant influence on soil moisture

Vegetation on the soil surface modifies soil hydraulic processes through physical and biological processes such as intercepting precipitation and protecting the soil from raindrop impact, adding organic matter and creating macrofaunal habitat, increasing surface roughness and impounding water for infiltration (Thompson et al., 2010; van Dijk and Keenan, 2007). Belowground, plant roots exert force on soil water influencing hydraulic movement and water balance by drawing water for transpiration and displacing water from deeper soil layers through hydraulic lift (Horton and Hart, 1998).

Tree roots create macropore pathways for water, organic matter and nutrients to move easily through the soil matrix (Bogner et al., 2010), changing pore size distribution and connectivity and consequently soil hydraulic properties (Bengough, 2012). Channels are created from

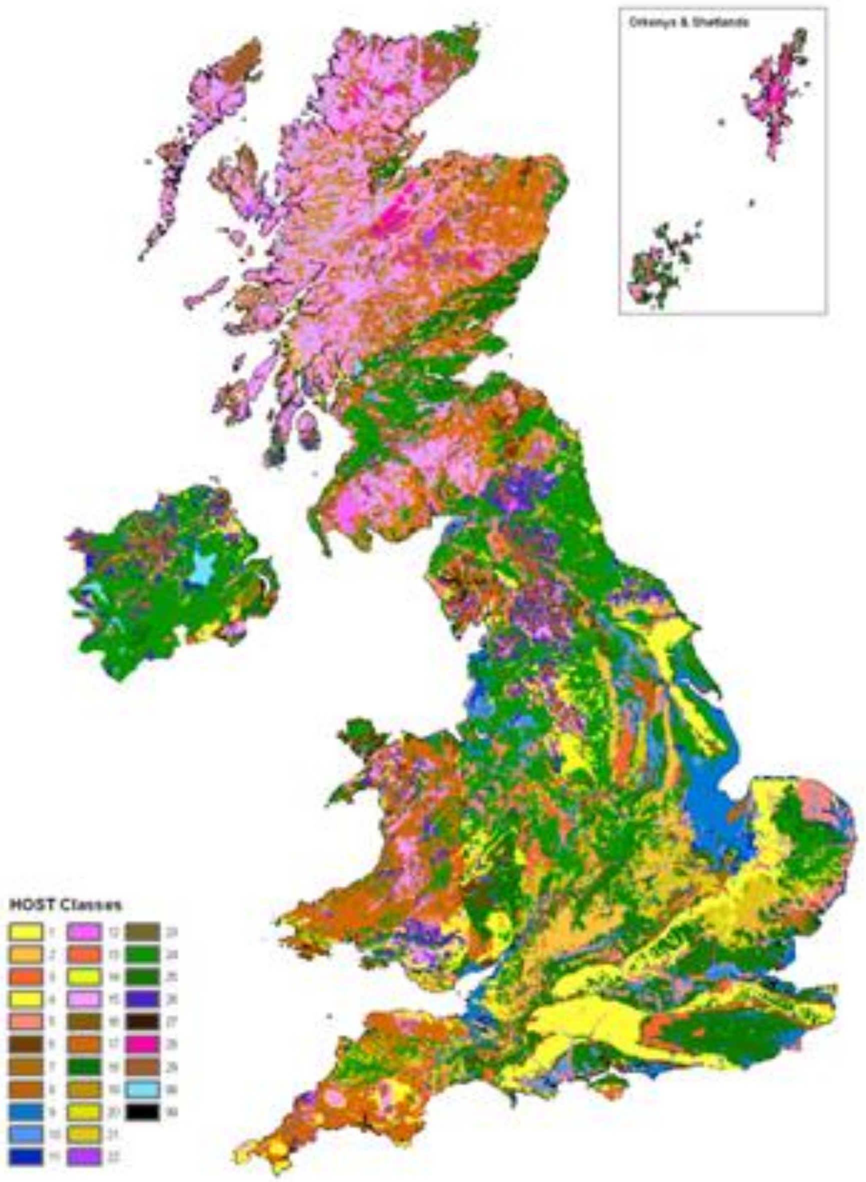

Figure 2.1. Distribution of Hydrology of Soil Types (HOST) classifications across the UK. Source: https://www.ceh.ac.uk/services/hydrology-soil-types-1km-grid

sloughed root cells and mucilages combining with soil particles behind the root apex and are strengthened by fungal mycelium (Ghestem et al., 2011) (Fig. 2.2). Even in stagnic, seasonally flooded soils, subsurface flow is strongly correlated with root density (Lange et al., 2009). Likewise in temperate stony forest soils, root systems dominate preferential flow pathways (Zhang et al., 2015). In arid regions too, tree roots aid preferential flow by enabling precipitation to infiltrate further down the profile, particularly during high intensity rainfall events, allowing for greater groundwater recharge (Mazzacavallo and Kulmatiski, 2015) and can outweigh the negative effects of trees on water availability, such as interception and evapotranspiration (Bargues Tobella et al., 2014; Ilstedt et al., 2016). Nevertheless, interception and evapotranspiration by trees is greater than other vegetation types (Farley et al., 2005) and can restrict soil water content. The recharge of groundwater under an oak woodland, for example, was estimated to be 55% less than under adjacent grass ley due to the extended length of time the soil is away from winter equilibrium soil moisture condition (Green et al., 2006).

The development of root channels is dependent on root diameter and length, orientation, sinuosity, climate, soil depth and topography (Ghestem et al., 2011). Where roots grow downwards, for example, efficient infiltration can take place, but lateral or upward growth can result in localised perched water table development. The depth to which tree roots grow depends on the species, soil depth and type and underlying geology, but is mediated by climate, land drainage, infiltration depth and frequency and groundwater accessibility (Fan et al., 2017). However, the majority of tree roots are typically found within the top 50-100 cm of the soil profile (Zhang et al., 2015), with greater than 50% found in the top 0.3 m of soil (Schenk and Jackson, 2002). Water is predominantly transported along root channels through the upper horizons and slows in the lower horizons where there is a significant decrease in root density (Bogner et al., 2010). Tree fine root production varies spatially and temporally but peaks during the spring and summer months with greater root dieback during the winter months (McCormack et al., 2014). Root decomposition can take days to years leaving empty root channels, which are then conduits for substantially faster preferential flow and new root growth (Bengough, 2012).

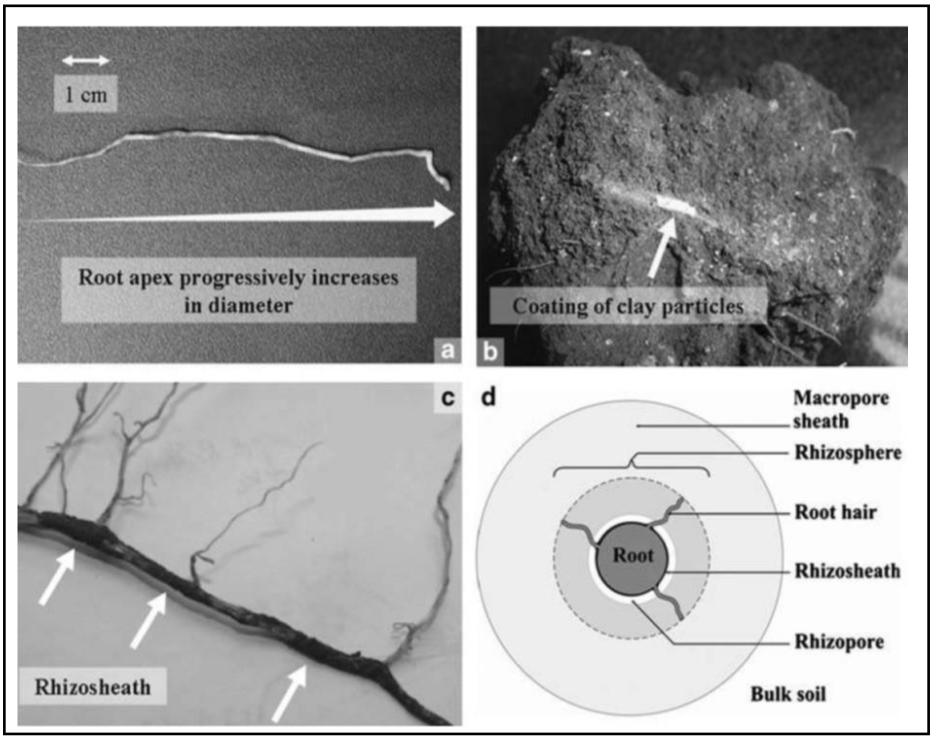

Figure 2.2. Development of macropore channels from root growth. The proportionally larger root tip (a) grows and sheds organic materials that then bind with soil particles (b) to create the root rhizosheath (c). Root hairs and rhizosheath develop the rhizosphere which is incorporated in the macropore sheath (d). Source: (Ghestem et al., 2011)

The interconnectivity of roots of different species that fill a greater proportion of the soil profile can increase preferential flow and infiltration (Ghestem et al., 2011). However, there is little understanding of the mechanisms that support this in wooded landscapes. Bens et al. (2007) investigated hydraulic function under a forest transformation chronosequence from monoculture *Pinus sylvestris* L. to mixed *P. sylvestris* and *F. sylvatica* to monoculture *F. sylvatica* forest. Hydraulic conductivity correlated with soil organic matter content, which increased within the process of forest transformation, but surface hydrophobicity was a confounding factor, leading to very low K and difficulty assessing the role of species identity belowground. Fine root growth in response to tree species diversity is disputed, with evidence of higher fine root productivity and turnover associated with tree species diversity (Jacob et al., 2014) as well as no increase in fine root biomass production (Meinen et al., 2009b). There is some evidence to support species identity not diversity as driving fine root yield (Jacob et al., 2014; Meinen et al., 2009a), with particular emphasis on specific species, such as *F. excelsior* (Jacob et al., 2013).

2.3 Water yield and tree cover

Globally, the effect of deforestation on increased flood risk is well acknowledged, but the effect of afforestation to reduce flood risk is contested (Ellison et al., 2017; Zhang et al., 2017). Long-term catchment-scale data from Plynlimon (UK) indicates that afforestation led to a reduction in flashiness and flow variation compared with the rough grazing control catchment, particularly over the summer months due to seasonal fluctuation in potential evapotranspiration (Archer, 2007). However, over the life of the plantation cycle, no impact on peak flow was shown (Robinson et al., 2013). The effect of plantation forests on water yield is influenced by plantation hydrology, tree physiology, plantation design, forestry operations and plantation management (van Dijk and Keenan, 2007). Artificially-drained plantation forests, for example, can increase peak streamflow compared with grassland by chanelling precipitation directly to rivers bypassing the opportunity for infiltration (Bathurst et al., 2018) but reduce annual streamflow as the forest matures (Birkinshaw et al., 2014).

Spatial and temporal variation in afforestation has a non-stationary effect on runoff and peak flow. Throughout the lifetime of a tree, leaf area index is greatest during the tree's formative period and is reduced during senescence reducing evapotranspiration losses over time as a result (Farley et al., 2005). Actual evaporation rates of plantation forests differ through time not just due to the ageing process but also as a reflection of forest growth, clear-felling and replanting, whereas grassland evapotranspiration rates remain relatively constant (Hudson et al., 1997). In areas where there is high rainfall, vegetation change has the largest impact on absolute run-off, but not on proportional runoff. In drier areas, streamflow is already low so the proportional impact on run-off of planting trees is much greater (Farley et al., 2005), rendering tree cover change in water-limited catchments more sensitive to annual run-off variation (Zhang et al., 2017).

However, evidence describing the relationship of trees and water cycling are biased towards fast growing plantation forests, often planned without water benefits in mind (Filoso et al., 2017) and do not consider the importance of groundwater flow and dry season flow (Ellison et al., 2017). Ilstedt et al. (2016) describe an 'optimal tree cover' theory (Fig 2.3) where intermediate tree cover strikes the balance between evapotranspiration losses and run-off, in contrast to trade-off theory , which assumes that a linear negative relationship exists between water yield and tree cover.

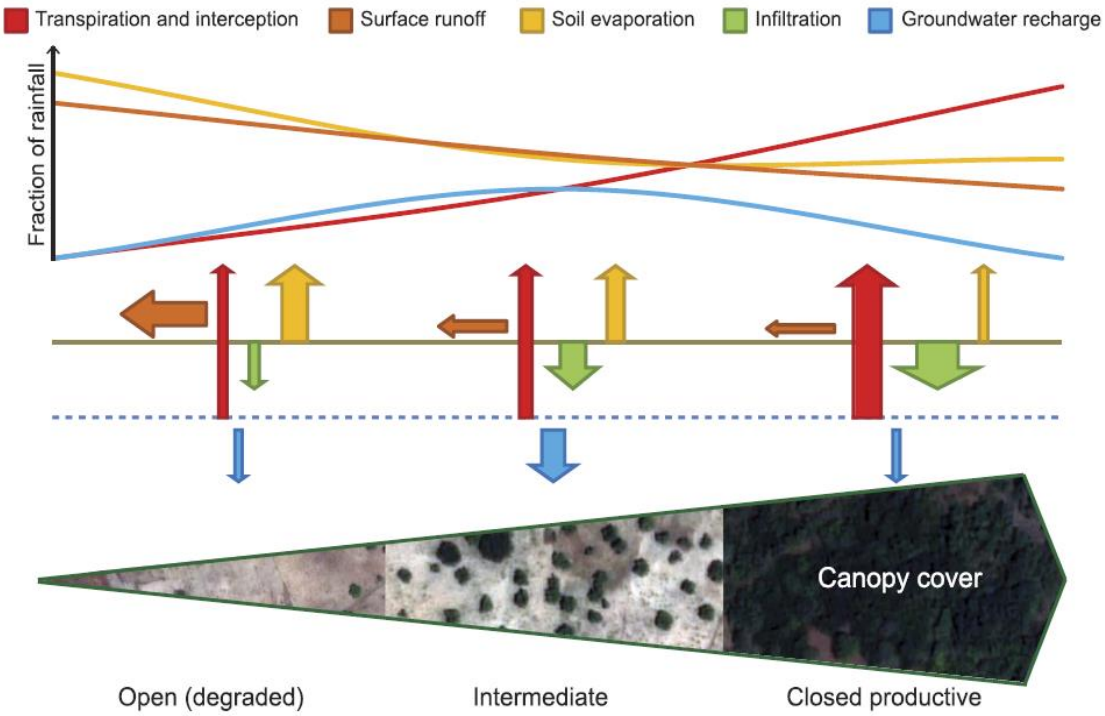

Figure 2.3. Conceptual description of an optimal tree cover theory. Open degraded landscapes have little infiltration and groundwater re-charge, losing most water to run-off and soil evaporation. Closed canopy forests also have little groundwater recharge because of transpiration and interception. Intermediate tree cover maximises groundwater recharge by balancing interception and transpiration losses against run-off and soil evaporation. Source: Ilstedt et al., 2016

2.4 Confounding variables

2.4.1 Tree age

Tree development passes through three stages; formative period, mature state and senescence. Growth rates are heterogenous between the stages and are subject to external influences such as availability of food, structural damage and environmental conditions and is further complicated by species choice (White, 1998). Nonetheless, the impact of trees on soil infiltration increase with age (Archer et al., 2013, 2015; Carroll et al., 2004; Greenwood and Buttle, 2014; Zema et al., 2021) although no effect of age has also been demonstrated (Bens et al., 2007). Forest maturity has been shown to be a better predictor of peak flows than forest coverage, principally due to an increase in interception, but also because of improved infiltration associated with older stands (Belmar et al., 2018). Soil under older woodland exhibits root structure diversity, larger pore spaces and soil aggregates and a greater organic matter content (Archer et al., 2015). Hydraulic conductivity of *Pinus nigra* Arn. spp. *Salzmannii* from 1- 120+ years increased with stand age due to a concurrent increase in associated soil organic matter (Zema et al., 2021). Typically, the formative period of tree growth is exponential as the tree becomes established, with a concurrent rise in water uptake. Soil infiltration, for example, was found to increase 60 times under two year old shelterbelt in Pontbren, Wales (Carroll et al., 2004).

However, the degree of influence of age is not uniform across sites. No difference in hydraulic conductivity (K) was found in a 30 year old *P. sylvestris* woodland compared with adjacent moss-dominant habitat on sandy soils in Slovakia (Homolák et al., 2009). *Pinus resinosa* Ait. plantation in Canada exhibited the same saturated hydraulic conductivity (K_{sat}) as 100 yr undisturbed grassland and recovery of K_{sat} to that of undisturbed mixed conifer hardwood took more than 40 years (Greenwood and Buttle, 2014). Six-year old *P. sylvestris* showed no significant difference in infiltration rates compared with adjacent pastureland in Scotland. Further comparison with 48 year old, 300 year old and ancient woodland suggested a correlation between increasing hydraulic conductivity and age (Archer et al., 2015) but not to the same degree exhibited in Pontbren (Carroll et al., 2004). The differences highlight the importance of land management and species choice. The two-year-old shelterbelt at Pontbren had excluded sheep, influencing infiltration rates, and consisted of broadleaf species, sampled during the growing season. Whereas, a soil pan had developed beneath the *P. sylvestris* site as a result of past tree harvesting, creating a perched water table that inhibited root development. Consequently, only roots of the ancient forest penetrated beyond the A horizon (Archer et al., 2015).

Changes in soil repellency from the presence of pine needles, for example, can exhibit a greater influence on soil hydraulic conductivity than age and species type (Archer et al., 2013). By creating a disparity in hydraulic conductivity between the biomat layer and the underlying horizons, it enables lateral movement of water for some distance before vertical percolation occurs (Gerke et al., 2015). Bens et al. (2007) attributed the similarity of K between stands of difference ages to the prevalence of hydrophobic soils, limiting K across the site. By contrast, Zema et al. (2021) found a negative correlation between stand age and soil repellency, further limiting the K of young stands.

2.4.2 Tree species identity

Tree species identity has been much overlooked as a driver of hydraulic processes and of the few published studies fewer than half demonstrate a between species effect (Chandler et al., 2018). Preferential flow in wooded ecosystems has been shown to be related to tree species; Luo et al. (2019) found that coniferous forests dominated by *Platycladus orientalis* (L.) exhibited greater preferential flow than deciduous forests dominated by *Quercus variabilis* Bl. Separately, a positive relationship ($r^2 = 0.91$) was found between macroporosity and tree roots of *Pinus coulteri* B. Don., but total porosity (and saturated conductivity) was greater under *Quercus dumosa* Nutt. and *Adenostoma fasciculatum* Hook., where conditions were more conducive to macrofaunal (e.g. earthworm) activity (Johnson-Maynard et al., 2002). Chandler (2018) tested the difference between *Acer pseudoplatanus* and *P. sylvestris* at contrasting tree density, finding that hydraulic conductivity under *P. sylvestris* was ~3 times greater than *A. pseudoplatanus*. However, the effect of land use (i.e. grazing) is postulated as a more important driver of hydraulic conductivity than within land cover change.

2.4.3 Livestock

Livestock can compact soil, reducing its bulk density and infiltration, which is exacerbated in areas where stock tend to gather, such as in gateways where sheep concentrate (Marshall et al., 2009). A recent meta-analysis of the effect of temperate silvopastoral interventions on water runoff, infiltration and hydraulic conductivity found that 55% of studies (n=22) demonstrated a significant positive effect (Jordon et al., 2020). However, the effect of livestock exclusion was found to be of similar or greater importance than the presence of trees, although the effects are cumulative. Marshall et al. (2013) found that over a five-year period, excluding sheep reduced run-off by 48% relative to grazed pasture, but 78% when combined with tree cover. The combination of both trees and livestock exclusion increased infiltration rates 67 times. Ungrazed woodland was found to have 1.8 times greater K_{sat} than grazed pasture across four catchments in Dartmoor (UK), but the relative effect of livestock exclusion and tree cover was not tested (Murphy et al., 2020). In arid southeastern Australia, soil compaction brought about by livestock trampling generated considerable overland flow but was absorbed by a livestock-excluded tree belt where infiltration rates were 46% than the adjacent pasture (Ellis et al., 2006). Likewise, arable farming is detrimental to soil hydraulic function but hedgerows provide a hydraulic break in the landscape to capture run-off. Holden et al. (2019) reported that woody hedgerows bounded by a grassy margin and adjacent to either arable fields or livestock-grazed pasture had significantly higher K_{sat} than any of the adjacent environments. Importantly, arable land was susceptible to run-off during small rainfall events, pasture during high intensity events (i.e. 4 times in sample year) but hedgerows only very rarely as K_{sat} was nearly three times the rainfall intensity of the most extreme event in 2001.

2.4.4 Seasonality

Interception and evapotranspiration are both greater in broadleaved trees than coniferous when in leaf (Nisbet, 2005), but the latter (except Larch species) retains leaf cover year round. Average interception and evapotranspiration losses in broadleaf trees is 400-640 mm per 1000 mm annual rainfall, compared with losses 550-800 mm per 1000 mm of annual rainfall from coniferous trees (Nisbet, 2005). In hedgerows, the effect of interception and evapotranspiration can extend far beyond the drip line (Ghazavi et al., 2008) and even in single parkland *Q. robur* trees affect K_{sat} beyond the canopy cover (Chandler and Chappell, 2008). During the winter months when precipitation is likely to be greatest, therefore, available soil water storage beneath broadleaved woodland compared with coniferous forest is reduced. However, the effect of seasonal soil drying can last into the winter months (Ghazavi et al., 2011, 2008), which can result in alternative stable states of soil moisture (Robinson et al., 2019).

Water losses from evapotranspiration and interception in hedgerow relative to adjacent pasture in Brittany created a depression of drier soil restricting flow to the finer pores and reducing hydrological connectivity between up- and downslope (Ghazavi et al., 2008) (Fig. 2.4). The subsequent soil re-wetting and groundwater recharge can be delayed by up to a month during a wet year and three months during a dry year (Ghazavi et al., 2011), and therefore has the potential to reduce run-off during periods of tree dormancy. Even where hedgerows surround riparian wetlands, increased drying is evident and a delay to rewetting by one month was observed (Caubel et al., 2003).

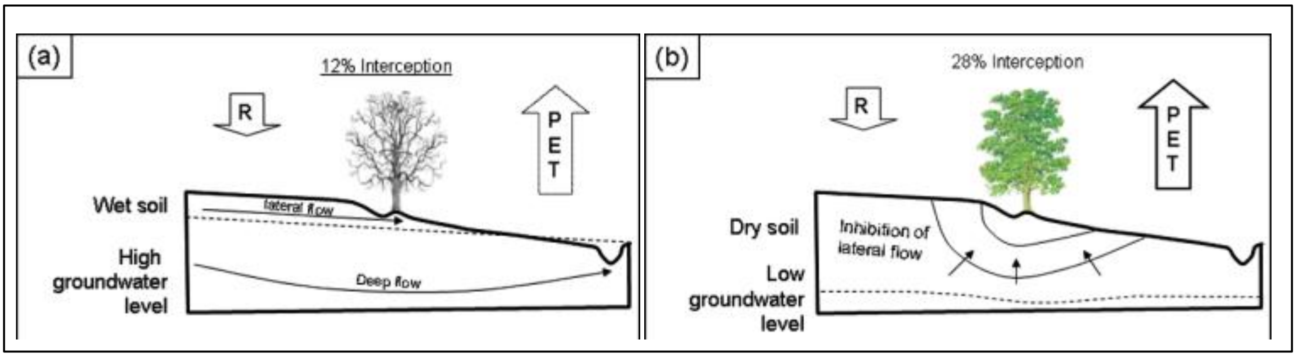

Figure 2.4. Schematic illustrating the effects of localised soil drying associated with hedgerows relative to adjacent pasture. During the leafless period (a), groundwater (dotted line) flows downslope uninhibited by the hedgerow. During the leaved period (b), interception and evapotranspiration create a depression of drier soil (solid lines), inhibiting lateral flow. Source: Ghazavi et al., 2008

2.4.5 Location

Planting configuration and location play a crucial role in soil water storage potential and runoff. Contour-planted hedgerows act as hydrological barriers, whereas perpendicular planting funnels water, accelerating overland flow (Merot et al., 1999). Contour hedgerows intercept eroding soil creating a deeper soil organic matter content on the upslope side of the hedgerow and increasing plant available water and infiltration compared with thinner soils at the top of the slope (Agus et al., 1997). Contour-planted bocages (hedgerows) in Brittany provide a hydrological buffering capacity of 15-40% through a reduction in connectivity, regardless of the hedge density. Even low-density bocage (39 m ha^{-1}) were found to disconnect flow pathways between upslope and the river (Merot et al., 1999). The barrier effect of hedgerows reducing runoff and erosion has been found to be consistent regardless of species (Bu et al., 2008).

Woodland planted on floodplains have limited storage capacity as the water table is high but still contributes to flood control through increasing surface roughness, which reduces peak flow, resulting in a longer duration event (Thomas and Nisbet, 2007). Nevertheless, the effect is small unless floodplain and river flow velocities are similar (Dadson et al., 2017). Desynchronisation of sub-catchment flows can increase or decrease flood risk. For example, restoring floodplain woodlands close to the catchment outflow can increase peak flow whereas forest restoration in the upper catchment has been shown to reduce peak flow (Dixon et al., 2016; Pattison et al., 2014; Thomas and Nisbet, 2007).

Climatic and slope influence the rate of evapotranspiration by limiting photosynthesis and transfer of energy through advection. Hedgerows, for example, can limit groundwater flow by 1.5 times compared with meadows during a sunny day on a steep slope, but have no comparable effect during a cloudy day on a flat area (Ryszkowski and Kedziora, 1993). Aspect can create climatic heterogeneity within a valley with north-facing slopes (in the Northern Hemisphere) remaining wetter for longer and therefore increasing the likelihood of overland flow (Merot et al., 1999). Similarly, the location of hedgerows in relation to groundwater has been shown to influence the shape and size of localised drying, with 60% of water use for transpiration sourced from groundwater (Thomas et al., 2012).

2.5 Key temperate research field sites

Temperate experimental research field sites assessing variation in catchment hydrology from afforestation or the impact of hedgerows on soil hydrology are limited. Much of the evidence presented above is drawn from a few key research sites in the UK and Europe, highlighting the need for an expansion in empirical research. Further information describing these sites are presented below.

2.5.1 Plynlimon

The Plynlimon catchment study is an important, long-term monitoring study originally established by the Institute of Hydrology (now Centre of Ecology and Hydrology) to analyse the impact of landuse change, namely plantation forestry, on the hydrological cycle. Since its inception, research at Plynlimon has gone beyond the original objectives and has been used to analyse hydrological and hydro-chemical impacts in over 500 published papers (Robinson et al., 2013) as well as used to develop UK policy and guidance (Marc and Robinson, 2007). The paired catchments, the Upper Wye (10.55 km^2) and the Upper Severn (8.7 km^2) are located at Plynlimon, mid-Wales. Originally, both were rough grazing grasslands with some heath and mire, but the Severn had 67% forest cover at the initiation of instrumentation in 1968, whilst the Wye has remained a rough grazing catchment (Archer, 2007).

2.5.2 Coalburn catchment

The Coalburn catchment experiment was established in 1966 to complement the Plynlimon catchment study by incorporating the commercial forestry establishment phase into the assessment of hydrological change. Instead of a paired catchment design, the purpose of this site was to compare land use change over a single site (Birkinshaw et al., 2014). Originally consisting of rough grazing on acid grassland, the 1.5 km^2 catchment benefitted from five years baseline monitoring before being plough drained and planted predominantly with *Picea sitchensis* (Sitka spruce) (Robinson et al., 1998).

2.5.3 Pontbren

By contrast, the Pontbren project, also located in mid-Wales, was a farmer-led project to investigate on-farm improvements to efficiency and productivity through planting hedges and trees for shelter and developing woodchip bedding (Keenleyside, 2012). Controlled trials began on-site in the early 2000s and developed to investigate the influence of hedgerows on infiltration and grazing (Carroll et al., 2004; Jackson et al., 2008; Marshall et al., 2009, 2013; Wheater et al., 2008). The Pontbren project was a heavily instrumented project and the first of its kind in the UK to specifically analyse the effects of hedgerows on soil hydrology.

2.5.4 Brittany

The French National Institute for Agricultural Research (INRA) have extensively researched the impacts of hedgerows on hydrological function. Based predominantly at two field sites in Brittany, it has contributed significantly to the body of research in temperate regions (Caubel et al., 2003; Ghazavi et al., 2011, 2008; Hao et al., 2014; Thomas et al., 2012; Walter et al., 2003). Research at Pontbren and INRA makes up the majority of relevant published research into the impact of hedgerows on soil hydrology (Wolton et al., 2014) but much is still unknown.

2.6 Limitations of experimental research

Evidence for the impact of trees on catchment hydrology is predominantly been limited to trees within forests, typically coniferous plantation forests (Ellison et al., 2017; Farley et al., 2005). Within the UK, this has been driven by concern over water use during rapid afforestation in the uplands during the 1960s and 1970s (Plynlimon/Coalburn catchment projects) (O'Connell et al., 2007). However, individual trees have greater evapotranspiration losses compared with forest stands due to the greater canopy cover and exposure (Nisbet, 2005). Little is known about the impact of linear tree features, such as hedgerows, on water use but there has been some evidence to suggest that the influence on water use is far beyond the drip line (Ghazavi et al., 2008). Hedgerows are likely to have a much greater edge effect than larger groups of trees due to increased localised turbulence with corresponding enhanced evaporation (Nisbet, 2005), and reduced competition enabling a more developed and extensive root network (Thomas et al., 2008).

In situ research specifically on the impact of hedgerows on catchment hydrology is limited to small plot or field-based trials, due to practical constraints of instrumentation. Extensive research at Pontbren has helped to understand the potential for hedgerows to reduce run-off and mitigate flooding, but the data gathered is site specific, short-term and may be dependent on soil conditions (Carroll et al., 2004; Marshall et al., 2009, 2013). Likewise, evidence from experimental studies investigating the hydrological effects from bocage (hedgerow) in Brittany are limited to one species (*Q. robur*) in one area (Benhamou et al., 2013; Caubel et al., 2003; Ghazavi et al., 2011, 2008; Thomas et al., 2012, 2008; Viaud et al., 2005b). Relying on these limited data to scale out to catchment scale is problematic. Sensitivity to land cover change is greatest in very large catchments (Zhang et al., 2017). Catchments also provide a much more heterogeneous landscape than small plots, with corresponding differences in response making it more difficult to account for non-linear effects such as groundwater recharge at this scale (Dadson et al., 2017; Ewen et al., 2013). Catchment response is further complicated by diverse farm management and water storage infrastructure (van Dijk and Keenan, 2007).

Many questions still remain (Marapara et al., 2020). Optimum species choice has been neglected in the literature and will almost certainly change soil hydrological response. Rooting architecture and depth vary across species and are influenced by climate, topography and environmental conditions of the growing medium (Fan et al., 2017; Ghestem et al., 2011). Below-ground interaction between tree species can affect yield through resource and niche partitioning and competition effects. However, the mechanism that drives yielding impacts and the consequences on hydraulic function are largely unknown. Tree age, too is a factor in the hydrological impact of trees (Archer et al., 2013, 2015; Carroll et al., 2004). Evidence suggests that ancient trees have the greatest effect on hydraulic conductivity and reduction in overland flow. However, rapid change is also evident in very young age classes, but the magnitude of change over time is disputed (Archer et al., 2013).

2.7 Limitations of modelled research

Modelling is beneficial in two distinct ways; it allows us to test various scenarios without having to change real world conditions and it allows us to predict outcomes at very large scales. The Budyko hydrological model, for example is designed to predict outcomes at very large catchment scale (>10,000 km^2). It uses physical catchment characteristics to predict catchment run-off and evapotranspiration rates related to different climatic scenarios and to produce the 'Budyko curve'. Vegetation characteristics are not included, but by incorporating vegetation characteristics such as leaf area, photosynthetic rate and rooting depth, it is argued that robust predictions at smaller scales (<1000 km^2) are possible (Dusek and Vogel, 2016). However, grouping by habitat can underestimate the importance of smaller features in the landscape. Using a modified version of the SWMS-2D model, Thomas et al. (2008) estimated transpiration rates of hedgerows in a spatially and temporally heterogeneous landscape for saturated and unsaturated flows. Data collected from from an oak hedgerow in Brittany (Caubel et al., 2003; Ghazavi et al., 2011) was used to validate modelled and collected values. Hedgerows extracted 115-140% of precipitation over summer and transpiration rates of hedgerows were nearly twice that of forest trees (Thomas et al. 2008), calling into question the exclusion of small landscape features in catchment-scale models (Dadson et al., 2017; Wolton et al., 2014).

Model resolution ranges from very large scale (Dusek and Vogel, 2016) to small, plot scale (Benhamou et al., 2013; Viaud et al., 2005a) validated with progressively coarse data as scale increases. Bronstert et al. (2002) argues that both the processes that lead to flooding as well as the the way in which these processes are represented within a model vary with scale and can not be compared. Localised flooding and regional flooding are likely to be resultant of very different hydrological processes (e.g. channel morphology and desynchronisation). SWAT model, for example, can not account for sub-surface artificial drainage (Schilling et al., 2014), despite the potentially large impact drainage can have (Dadson et al., 2017).

The accuracy and functionality of modelled data is limited by both scale, data accuracy (Schilling et al., 2014) and data availability. For example, Polyscape and its later iteration LUCI ecosystem service model (Jackson et al., 2013; Sharps et al., 2017) uses coarse resolution national soil data (NATMAP) and land cover monitoring (LCM) data to characterise and predict catchment response. Smaller variations in soil type and land cover, are excluded due to a paucity of data availability. Although user input is used to refine and calibrate data, further empirical data is required to strengthen accuracy of predictions. Vegetation influence on catchment hydrological response is either missing, such as in the Budyko hydrological model or limited to broad vegetation classes such as LCM data used in Polyscape and LUCI. Woodland impact on catchment response is well-represented (Archer et al., 2010; Dixon et al., 2016) but specific impacts of hedgerow features is not. Where attempts have been made to account for the influence of hedgerows, the interaction effect of species, age, location and seasonality are absent. It is clear that in order to build model robustness and performance, further *in situ* data are required to parametrise catchment response models.

2.8 Conclusion

Climate change is increasing the intensity and frequency of extreme weather events whilst concurrent land cover change is reducing landscape resilience. Increasingly severe and frequent incidences of flooding have led some to question the role of hard engineering in flood alleviation. The potential for trees, including small linear features such as hedgerows, are recognised as one way to mitigate against flooding through attenuation of surface and sub-surface flow. Evidence of a positive relationship between tree cover and reduced peak flow is lacking, however, principally due to a lack of empirical data. Underlying tree-soil-water relationships are poorly understood, particularly the influence of confounding variables such as tree species identity, age and diversity, the role of soil type and land use. Experimental evidence relating to trees outside of woodland, specifically hedgerows, and their relationship with soil hydraulic processes is lacking, with studies limited to a handful of sites. Predicting response to rainfall from forests and small tree features as well as the wider effect on catchment response is limited by difficulties of scale, limited data and the absence of small-scale tree features in models. In order to quantify and realise effective use of trees for hydraulic regulation, a greater understanding of the mechanisms driving changes in the tree-soil-water interface is needed.

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Chapter 3 Variation in tree root morphology between tree species influences soil hydraulic conductivity and macroporosity

Bid Webb[1]*, David A. Robinson[2], Miles R. Marshall[1], Hilary Ford[1], Tim Pagella[1], John R. Healey[1], Andrew R. Smith[1]

[1]School of Natural Sciences, Bangor University, Bangor, LL57 2DG, United Kingdom
[2]UK Centre for Ecology and Hydrology, Environment Centre Wales, Deiniol Rd, Bangor, LL57 2UW, United Kingdom

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Author contributions: BW, MM and AS conceived and planned the experiments, BW and HF carried out the data collection, BW the laboratory and statistical analyses, BW, DR and AS contributed to the interpretation of the results. BW took the lead in writing the manuscript. All authors provided critical feedback and helped shape the research, analysis and manuscript.

Abstract

Natural approaches to flood risk management are gaining interest as sustainable flood mitigation options. Targeted planting of trees has the potential to reduce local flood risk, however attention is generally focused on the hydrological impacts of catchment afforestation linked to generic tree features, whilst the species-specific impacts of trees on soil hydrology remain poorly understood. Here, we compare effects of different tree species on soil hydraulic properties with flood mitigation potential. Monocultures of *Alnus glutinosa*, *Betula pendula*, *Fagus sylvatica*, *Fraxinus excelsior*, *Acer pseudoplatanus*, *Castanea sativa* and *Quercus robur* were used to determine effects of tree-species identity on soil hydraulic properties in a sandy loam soil. The interaction of *F. excelsior* root properties and soil type on hydraulic conductivity was then examined in four different soils (sandy-silt loam, silty clay loam, limestone-rich silty clay loam and clay loam). Root biomass and morphological characteristics were determined at three depths (0-0.1 m, 0.1-0.2 m, 0.2-0.3 m), and complemented by *in situ* measurement of soil hydraulic conductivity (K). Root morphological traits were closely associated with species identity and strongly correlated with soil hydraulic conductivity near the soil surface (r^2=0.64 at 0-0.1 m depth; r^2=0.69 at 0.1-0.2 m depth) and pore size distribution. Root biomass of *F. excelsior* was six-fold greater than *C. sativa* (p<0.001), and the frequency of 0.01 mm radius soil pores under *F. excelsior* was twice that of *Q. robur*. Saturated hydraulic conductivity under *F. excelsior* was 7.91 ± 1.23 cm day^{-1}, double the mean rate of the other species. Soil class did not significantly influence on fine root biomass (p>0.05) or saturated hydraulic conductivity in 0.0-0.1 m depth soil, but conductivity tended to increase with depth. Species-specific traits of trees should be considered in landscape design to maximise the hydrological benefits of trees for local flood risk mitigation.

Keywords: Land use; Infiltration; Flood risk; Hymenoscyphus fraxineus; hydrology; Soil porosity; Soil classification.

3.1. Introduction

Anthropogenic activities are driving an acceleration of climate change and, as a result, the occurrence and intensity of extreme weather events is predicted to increase (IPCC, 2014). Precipitation in the UK over the past 250 years has increased during the winter and decreased during the summer (Dadson et al., 2017). Climate change has motivated greater attention to mitigating the impact of extreme events, such as flooding, with a policy focus on the role land use management can play (Mcintyre and Thorne, 2013). While the body of available evidence on natural flood management (NFM) suggests that flooding from high intensity rainfall events is unlikely to be prevented at the catchment scale, it indicates that NFM interventions may help reduce local flood risk during smaller rainfall events (Dadson et al., 2017) and are thus of importance at this scale.

Trees have the potential to mitigate local flooding by increased water infiltration into soil, evapotranspiration, interception and groundwater recharge, which all reduce overland flow (Dadson et al., 2017; Dixon et al., 2016; Lane, 2017; Wolton et al., 2014). There is little empirical evidence of the hydrological benefits of tree cover; much of the evidence that does exist is based on modelling (Carrick et al., 2019; Stratford et al., 2017), though its reliability is limited by a paucity of robust, underlying empirical data (Dadson et al., 2017). Ongoing debate over the heterogeneity and uncertainty of the data is attributed to the complexity of catchment processes at different scales and a lack of quantitative flow and effect-modifier data. The effect of tree characteristics such as species on water yield, for example, is largely unquantified (Creed and van Noordwijk, 2018; Stratford et al., 2017).

Plot-scale research has notably found that even when young (5-years old), trees can increase infiltration rate by 67 times compared with grazed pasture and reduce surface runoff by 78% (Marshall et al., 2013), but heterogeneity of effects on hydraulic conductivity at plot scale is also evident (Chandler and Chappell, 2008). The interplay between soil and vegetation shapes soil hydraulic functions but the relative importance of these functions are context specific. In arid zones, vegetation is highly influential in increasing hydraulic conductivity, whereas soil type dominates the process in humid tropical (Thompson et al., 2010) and temperate ecosystems (Geris et al., 2015). In contrast, soil type has generally been shown to have little effect on infiltration capacity, with interactions between soil fauna (e.g. earthworms), roots, plant species richness and soil structure of greater importance (Fischer et al., 2015; Jarvis et al., 2013).

The role of tree roots in shaping hydraulic response has often been overlooked (Chandler et al., 2018). Understanding of inter- and intra-species variation is largely based on the questionable assumption that root architecture and hydrological function can be predicted from above-ground morphological characteristics (Sinacore et al., 2017). Therefore, more thorough investigation of species-specific below-ground hydrological function is required. Macropores within soil can be associated with root channels that are developed through the process of root production and turnover, and enable preferential flow (Ghestem et al., 2011). Preferential flow in wooded ecosystems has been shown to be related to tree species; Luo et al. (2019) found that coniferous forests dominated by *Platycladus orientalis* (L.) exhibited greater preferential flow than deciduous forests dominated by *Quercus variabilis* (Bl.). Separately, a positive relationship ($r^2 = 0.91$) was found between macroporosity and tree roots of *Pinus coulteri* (B. Don.), but total porosity (and saturated conductivity) was greater under *Quercus dumosa* Nutt. and *Adenostoma fasciculatum* Hook., where conditions were more conducive to macrofaunal (e.g. earthworm) activity (Johnson-Maynard et al., 2002). Luo *et al.* (2019) found that whilst tree roots were strongly associated with macropore development and preferential flow, the interaction between macroporosity, total porosity and infiltration was less clear. Soil total porosity and infiltration rate can have a positive relationship (Sun et al., 2018), however Bodner et al. (2014) attributed an increase in infiltration to an increase in macroporosity in soil where total porosity remained unchanged. Inconsistent effects describing the relationships between total porosity, macroporosity, preferential flow and tree species imply that more work is required to understand these associations.

Preferential flow in the vadose zone mediates water infiltration and is associated with macropores, including artificial drainage (Bathurst et al., 2018; Marshall et al., 2009), macrofaunal pathways (Bargues Tobella et al., 2014), biomat flow (Gerke et al., 2015) and root channels (Zhang et al., 2015). Not all fine roots are conduits for preferential flow (Luo et al., 2019), suggesting that root size distribution may be more important than root biomass. For example, the metric root length density (cm cm^{-3}), has been shown to have a strong correlation with preferential flow (Zhang et al., 2015) but this relationship is spatially variable (Luo et al., 2019).

The difference in fine root production across a spectrum of the broadleaved tree species that are abundant in Europe, and the consequential effect on soil hydraulic conductivity, is largely unknown. Fine root production is known to be plastic in its response to antecedent hydrological conditions (Fan et al., 2017), which is influenced by the type of soil as well as by climate. Differences in hydrological response have been found between coniferous and deciduous forest ecosystems but the response was mitigated by spatially contrasting soil texture (Luo et al., 2019). The relative influence of tree species identity and soil type on infiltration capacity remains poorly understood. The aim of this study was to characterise the root morphology of seven species of broadleaved trees and investigate the relationship with soil hydraulic conductivity. Our objectives were to (i) investigate the variation in infiltration rate between seven tree species growing in the same soil type and (ii) compare the tree species' corresponding root morphological characteristics to (iii) determine whether soil hydraulic function depends on species' root characteristics, then (iv) to investigate the relative influence of tree roots and soil type on soil hydraulic function.

3.2. Methods

3.2.1 Site descriptions and experimental design

The BangorDiverse forest diversity and ecosystem function experiment, located at Abegwyngregyn, United Kingdom (53°14'15''N, 4°1'4''W) was used to determine the effect of tree species on hydraulic function. BangorDiverse was established as part of the global Tree Diversity Network of experimental sites (www.treedivnet.ugent.be) investigating tree diversity, ecological function and sustainability (Verheyen et al., 2016). The site comprises of two formally agricultural fields (2.36 ha total area) planted in randomised, replicated blocks (n=4) of 1-, 2- and 3-tree species mixtures (Ahmed et al., 2016) using a systematic hexagonal planting design (Aguiar et al., 2001) (Fig. 3.1). Planted as 0.6 m saplings in March 2004, species were selected based on their contrasting shade tolerance and successional characteristics and consisted of *Acer pseudoplatanus* L., *Alnus glutinosa* [L.] Gaertner, *Betula pendula* Roth., *Castanea sativa* Mill, *Fagus sylvatica* L., *Fraxinus excelsior* L. and *Quercus robur* L. (Ahmed et al., 2016).. Initial planting density was 10,000 stems ha^{-1} but trees were thinned to 2,500 stems ha^{-1} in 2012/2013 to facilitate continued tree development. The site also encompasses eight now defunct Free-Air Carbon dioxide Enrichment (FACE) experimental plots (Smith et al., 2013), but all trials took place outside of these plots. This study utilised the seven single-species plots replicated four times, each 81 m^2 in area.

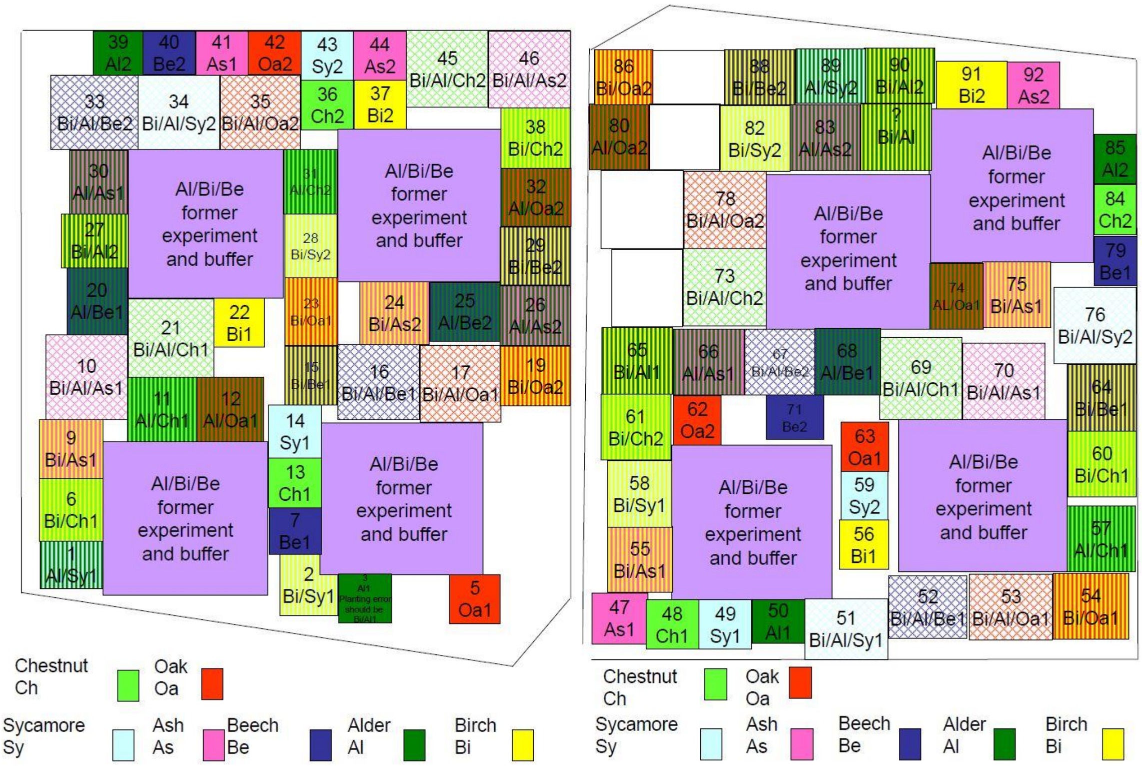

Figure 3.1 BangorDiverse experimental design; monoculture, two- and three-species mixtures, replicated (n=4) across two fields (treedivnet.ugent.be). Al/Bi/Be former experiment and buffer (purple squares) were part of the Free-Air Carbon dioxide Enrichment (FACE) experiments (Smith et al., 2013).

The soil at BangorDiverse is a Dystric Fluvic Cambisol, with a sandy loam/loam texture developed from glaciofluvial deposits (Smith et al., 2013) and pH ranging from 5.4 (surface) to 6.3 (1-m depth) (Ahmed et al., 2016). The site is hyperoceanic with a mean annual rainfall of ca. 950 mm and a mean annual temperature of 10.6 °C (Gunina et al., 2017).

Plots of *F. excelsior* planted in different sites across the UK with four contrasting soil types (IUSS Working Group WRB, 2015) were used to investigate how interaction of a single tree species with soil type influences hydraulic function. Originally established as part of a provenance trial in 1993 (Cundall et al., 2003) three sites, in Gloucestershire (England), Hampshire (England) and Gwynedd (Wales), were selected based on their soil types (Table 3.1) that best represent the range of textural characteristics (sand, silt or clay) commonly occurring across UK. Each experimental site consisted of three fully replicated randomised blocks of different provenances of *F. excelsior*. Saplings (same age from seed) were planted at 2500 stems ha^{-1} and had subsequently been thinned to 50% at the Gloucestershire site only. One plot from each block (n=3) comprised of *F. excelsior* trees of UK (Powys, Shropshire) or French (Normandy) provenance were selected for study. Due to the presence of the fungal pathogen *Hymenoscyphus fraxineus* at the Hampshire site only, plots were selected where only visibly healthy trees were found during the assessment detailed in Section 2.2.

To increase the diversity of soils used in this analysis (Table 3.1), an additional site with *F. excelsior* (provenance unknown) established in 1987 at Rothamsted Research, North Wyke, Devon (England) was selected. Here, three plots were randomly selected from two blocks, avoiding edge trees. All plots were planted with seedlings at 2500 stems ha^{-1} and had not been thinned. No obvious signs of *H. fraxineus* were present at North Wyke.

3.2.2 Hymenoscyphus fraxineus assessment

Each site was assessed for the presence of the fungal pathogen *Hymenoscyphus fraxineus* that causes ash dieback disease (ADB) using the methodology of Pliura et al. (2011) to score the damage to phenotypes. This was to ensure ADB could be accounted for when assessing the relationship between soil texture and hydraulic function. This method uses a scale of 1–7 as follows: 1, missing tree; 2, dead dry tree without significant development; 3, dry tree that produced shoots before dying; 4, heavily damaged living tree with dead main stem and resprouted stems with highly visible leaf and stem ADB lesions; 5, moderate damage with dry leading shoot and once or repeatedly re-sprouted leading shoot with highly visible leaf and stem ADB lesions; 6, limited damage with multiple brown dry or wilted leaves or peripheral shoot or/and brown lesions on stem or branches; 7, healthy tree with minimal signs of damage only on leaves (brown, dry or wilted leaves). Based on these scores, three plots per site were selected for soil and root sampling based on those plots containing the healthiest *F. excelsior* trees of UK or French provenances.

Table 3.1. Location of *Fraxinus excelsior* provenance experimental plots by World Reference Base soil classification (World Reference Base (WRB) for soil resources, 2006), UK county, Ecological Site Classification; accumulated temperature (AT) (day degrees above 5 °C), moisture deficit (MD) (mm), continentality (CONT) (Conrad index) and soil texture class (Soil Survey of England and Wales) (Avery, 1980).

WRB classification soil group	**Site (UK county)**	**Latitude Longitude**	**Climatic factors**			**Soil texture**
			AT	**MD**	**CONT**	
Dystric fluvic cambisol (CM)	Gwynedd	53° 14′ 19.38″ N 004° 01′ 05.91″ W	1773	157	6	Sandy silt loam
Haplic luvisol (LV)	Gloucestershire	51° 54′ 24.93″ N 002° 18′ 39.68″ W	1886	184	8	Silty clay loam
Rendzic leptosol (LP)	Hampshire	51° 12′ 02.02″ N 001° 31′ 39.48″ W	1909	193	10	Silty clay loam – limestone rich
Dystric gleysol (GL)	Devon	50° 46′ 12.14″ N 003° 54′ 08.79″ W	1728	132	8	Clay loam

3.2.3 Root morphology

Two soil cores of 0.08 m diameter were taken from three depths (0-0.1, 0.1-0.2, 0.2-0.3 m) equidistant between two trees, near the centre of each plot during dormancy (winter). Soil cores were placed into sealable polythene bags and transported to the laboratory on the day of field collection and stored at 4 °C for a maximum of 4 days before processing.

Each core was washed with water in a sieve stack (1 and 2 mm mesh size) to remove soil adhered to roots and separate roots into two size classes, fine (<2 mm ø), coarse (>2 mm ø). Tree species identity of the roots was based on morphological descriptions outlined by Mrak and Gricar (2016) and necromass was identified based on black or dark brown colour and a decaying fragmented appearance. Fine roots were scanned using an Epson 4990 scanner at a resolution of 300 dpi and images were analysed with WinRhizo (version 2005c Regent Instruments Inc, Quebec, Canada) to measure fine root length, surface area, surface volume, projected surface area and number of root tips, divided into 20 (0.1 mm) diameter classes (0-2 mm). Biomass of necromass, fine and coarse roots was determined after drying at 80 °C until constant mass. Data from the two soil cores collected per plot were averaged to avoid within-plot pseudo replication.

3.2.4 Soil hydraulic function

Minidisk Infiltrometers (Meter Group, Pullman, USA) were used to measure the rate of infiltration of water into soil and to calculate saturated hydraulic conductivity (K_{fs}) within each plot. Surface vegetation was carefully removed, and a thin layer of fine sand was applied to the soil surface to ensure optimal contact between the infiltrometer disc and the soil. The pressure head was set at 0.02 m to eliminate water flow through the heterogeneous macropores, to provide a more representative estimation of water flow through the soil matrix and to achieve steady-state infiltration rate. Saturated K_{fs} for the respective soil water potential was calculated using the method of Zhang (1997) and van Genuchten soil classification tables (Meter Group Inc, 2018). To measure K through the full range of soil pore sizes, a Saturo dual-head infiltrometer (Meter group, Pullman, USA) was used in each of the plots. However, the 0.05 m head of water required could not be maintained in approximately one third of the plots due to the stoniness of the soil and the method was abandoned.

At each plot, a 250 cm^3 UMS soil sampling core was taken at 0-0.05 m and 0.1-0.15 m depths. Cores were stored at 4 °C and then soaked for at least 24 hours in degassed, deionised water prior to analysis. Soil water retention was measured using a HYPROP 2 (Meter group, Pullman, USA) (Schindler et al., 2010), and dry bulk density and porosity was determined for the cores. The vapour equilibration technique (Scanlon et al., 2002) was used to measure the dry-end matric potential on sub-samples taken from each core. To account for the stoniness of the experimental plots, stones (>2 mm ø) were sieved out of the oven-dried soil and weighed. Soil water release curves were modelled using the HypropFit (Schindler et al., 2010) (UMS, Munchen, Germany) implementation of the Fredlund-Xing water retention model (Fredlund and Xing, 1994), underpinned by measured soil water retention, dry bulk density, porosity, dry end matric potential, volumetric moisture content and stoniness data.

Effective soil pore size distribution was estimated using the method outlined by Blonquist et al. (2006). Hydraulic capacity was estimated using data from the soil water release curve (modelled in HypropFIT) to derive the change in moisture over the change in hydraulic head ($d\theta_v/dh$)**.** Hydraulic capacity was plotted as a function of pore radius. The scaled effective pore size distribution associated with each tree species was then derived by taking the inverse relationship between pressure (h) from the water retention curve and log10 pore radius, resulting in a dimensionless, scaled, effective pore size distribution. The distribution is displayed as a function of effective pore radius ƒ(r) proportional to the abundance of each pore size within a given volume of soil.

To give context, *in situ* soil moisture was measured using ML3 ThetaProbe Soil Moisture Sensors (Delta_T Devices Ltd, Cambridge, UK) (n=9) in each plot at 10 cm depth. Particle size distribution was ascertained using an air-dried sub-sample from soil used for the HYPROP analysis, repeatedly quartered to mitigate selection bias (Lebron and Robinson, 2003). Particle size distribution was determined from a 0.5-0.8 g subsample of sieved (<2 mm) soil using a LS13 320 laser diffraction particle size analyser (Beckman Coulter Inc, Indianapolis, USA). Soil organic matter content was determined by Loss on Ignition (LOI) analysis of 10 g of sieved (<2 mm) soil (Ball, 1964). For quality assurance, two standard soil and two replicate samples were analysed alongside all LOI and particle size analyses.

3.2.5 Root characteristics

Root area index (RAI, m^2 m^{-2}) was derived from the root surface area divided by the surface area of the sampled core. Specific root area (SRA m^2 kg^{-1}) was calculated from the surface area of fine root divided by root dry mass (Lohmus et al., 1989). Specific root length (SRL m g^{-1}) was determined from the total length of fine roots divided by root dry mass (Ostonen et al., 2007). Root length density (RLD cm cm^{-3}), which indicates the proportion of soil occupied by fine roots, was estimated from the ratio of root length to the volume of the sampled core. For each of the aforementioned root metrics an arithmetic mean was calculated from data exported from WinRhizo output.

3.2.6 Statistical analyses

All statistical analyses were undertaken with SPSS v22.0 (IBM SPSS, Armonk, NY, USA) with p<0.05 used as the limit for statistical significance. Two statistical models were used to analyse the datasets: (i) For the data collected from BangorDiverse (n=4), a two-way ANOVA with species and depth as factor and root biomass, root morphological characteristics and field-saturated hydraulic conductivity (K_{fs}) as dependant variables; (ii) for data collected at the pan-UK *F. excelsior* provenance trial sites (n=4), a two-way ANOVA with soil type and depth as factors and root biomass, root morphological characteristics and K_{fs} as dependant variables. The Tukey HSD post-hoc test was used to determine within-factor significance for both statistical models. Relationships between dependent variables were explored using an ordinary linear regression. All data were tested for homogeneity of variance using Levene's test and normality using the Shapiro-Wilk's test. Root biomass, root morphological variables and K_{fs} data were log transformed to satisfy normality. To visualise the relationships between variables, the dimensionality of the dataset was reduced from forty-four parameters that included root morphological metrics (e.g., SRL, RAI, SRA, RLD) within three soil layers (0-0.1 m, 0.1-0.2 m and

0.2-0.3 m), K_{fs} at the soil surface and soil porosity within two soil layers (0-0.05 m and 0.10-0.15 m) by conducting a principal component analysis (PCA). Stepwise multiple regression (forward and backwards) was then used to determine the parameter that best predicts K_{fs}. All figures were produced using SigmaPlot v13.0 (Systat Software, San Jose, CA, USA).

3.3. Results

3.3.1 Hydraulic conductivity and root biomass

Mean field saturated hydraulic conductivity (K_{fs}) ranged from 3.47 ± 0.56 cm day^{-1} for *A. pseudoplatanus* to 7.91 ± 1.23 cm day^{-1} for *F. excelsior*, although there were no statistically significant differences (p=0.056) between any of the studied species (Fig. 3.2a). However, a strong relationship ($r^2 = 0.64$ (0-0.1 m depth) and $r^2 = 0.69$ (0.1-0.2 m depth)) was observed between species' fine root biomass and K_{fs}, but a high degree of variation around mean K_{fs} within some species (e.g. *Q. robur*) resulted in a significant correlation (p<0.05) at 0.1-0.2 m depth only.

A large difference in fine root biomass at a depth of 0-0.1 m was observed between *F. excelsior* and the other species, with a significant overall effect (p < 0.001; Fig 1b). The rank order of fine root biomass was *F. excelsior* (3.05 ± 0.4 kg m^{-2}) > *B. pendula* (1.12 ± 0.13 kg m^{-2}) > *A. pseudoplatanus* (0.87 ± 0.28 kg m^{-2}) > *Q. robur* (0.62 ± 0.29 kg m^{-2}) > *F. sylvatica* (0.55 ± 0.12 kg m^{-2}) > *C. sativa* (0.45 ± 0.09 kg m^{-2}). Fine root biomass of *F. excelsior* was between three-fold (*B. pendula*; p<0.001) and six-fold (*C. sativa*; p<0.001) greater than the other species. No differences were observed in coarse (>2 mm diameter) root biomass between species and soil depths (S.I. 3.1). In the 0.1 – 0.2 m soil layer, *C. sativa*, increased relative to other species, changing rank from sixth to fourth. However, *F. excelsior* fine root biomass (1.22 ± 0.31 kg m^{-2}) was only greater than *F. sylvatica* (0.35 ± 0.11 kg m^{-2}; p = 0.05) (S.I. 3.1). In the 0.2 – 0.3 m depth, *F. sylvatica* had the smallest fine root biomass (0.17 ± 0.04 kg m^{-2}) of all the species, more than fivefold less than *F. excelsior* (0.90 ± 0.32 kg m^{-2}; p < 0.01) and nearly four-fold less than *A. pseudoplatanus* (0.64 ± 0.19 kg m^{-}2; p < 0.05) (S.I. 3.1).

Soil total porosity (0-0.05 m depth; Fig 1c) was similar between all species (p>0.05). Despite the aforementioned relationship between K_{fs} and fine root biomass a similar relationship was not observed between fine root biomass and total porosity.

A positive linear relationship between the mean K_{fs} and fine root biomass of each species was observed, with 64%, 69% and 25% of the variation in K_{fs} explained by fine root biomass for the 0-0.1 m, 0.1-0.2 m and 0.2-0.3 m depths, respectively (Fig. 3.3a-c). *Alnus glutinosa* had a fine root biomass to necromass (B:N) ratio of 3.43 over the whole sampled soil profile, which was two- to three-times smaller than the other species, except *C. sativa* and Q. robur (S.I. 3.1). The rank order of the B:N ratios over the 0-0.3 m profile were *A. pseudoplatanus* (14.82 ± 6.65) > *F. excelsior* (12.01 ± 3.83) > *F. sylvatica* (10.68 ± 2.84) > *B. pendula* (9.30 ± 1.78) > *Q. robur* (4.57 ± 0.81) > *A. glutinosa* (3.43 ± 1.20) > *C. sativa* (1.97 ± 0.73). The B:N ratio of *A. pseudoplatanus* was significantly ($p < 0.05$) higher than *A. glutinosa* and *C. sativa* with in the 0 – 0.1 m soil layer and greater than *A. glutinosa*, *C. sativa*, *F. sylvatica* and *Q. robur* within the 0.1 – 0.2 m soil layer ($p < 0.05$).

3.3.2 Soil water retention and pore size distribution

The soil water retention curve (SWRC) describes the relationship between water content and soil water potential. Saturated soil water content was highest for *F. excelsior* (57%) and lowest for *F. sylvatica* (52%) in the 0-0.05 m soil layer (Fig. 3.4a). As soil water potential increased, the soil water content under *F. excelsior* dropped rapidly, becoming comparable to the other species. Further increases in soil water potential caused *F. excelsior* to drop to 6th rank in species' retention capacity. *Quercus robur* was ranked 5th at saturation but retained the highest percentage of soil water content at mid-range potentials. *Castanea sativa* had consistently low soil water content compared with the other species. It ranked 6th amongst species at saturation, dropping to 7th at higher potentials. Within the 0.10-0.15 m soil layer (Fig. 3.4b), *Q. robur* had the highest water content (57%) at saturation, whereas *F. excelsior* had the second lowest (50%), with *F. sylvatica* lowest (49%).

Figures 3c and 3d show the scaled effective pore size distribution. Soil developed under *F. excelsior* exhibited the highest abundance (0.24) of macropores, followed by *B. pendula* (0.20), whilst the pore size distributions of *Q. robur* and *C. sylvatica* are skewed towards smaller pore sizes. By contrast, the proportion of macropores deeper in the soil (0.1-0.15 m) are similar amongst the species, with the exception of *Q. robur* and *A. pseudoplatanus* (Fig 3d).

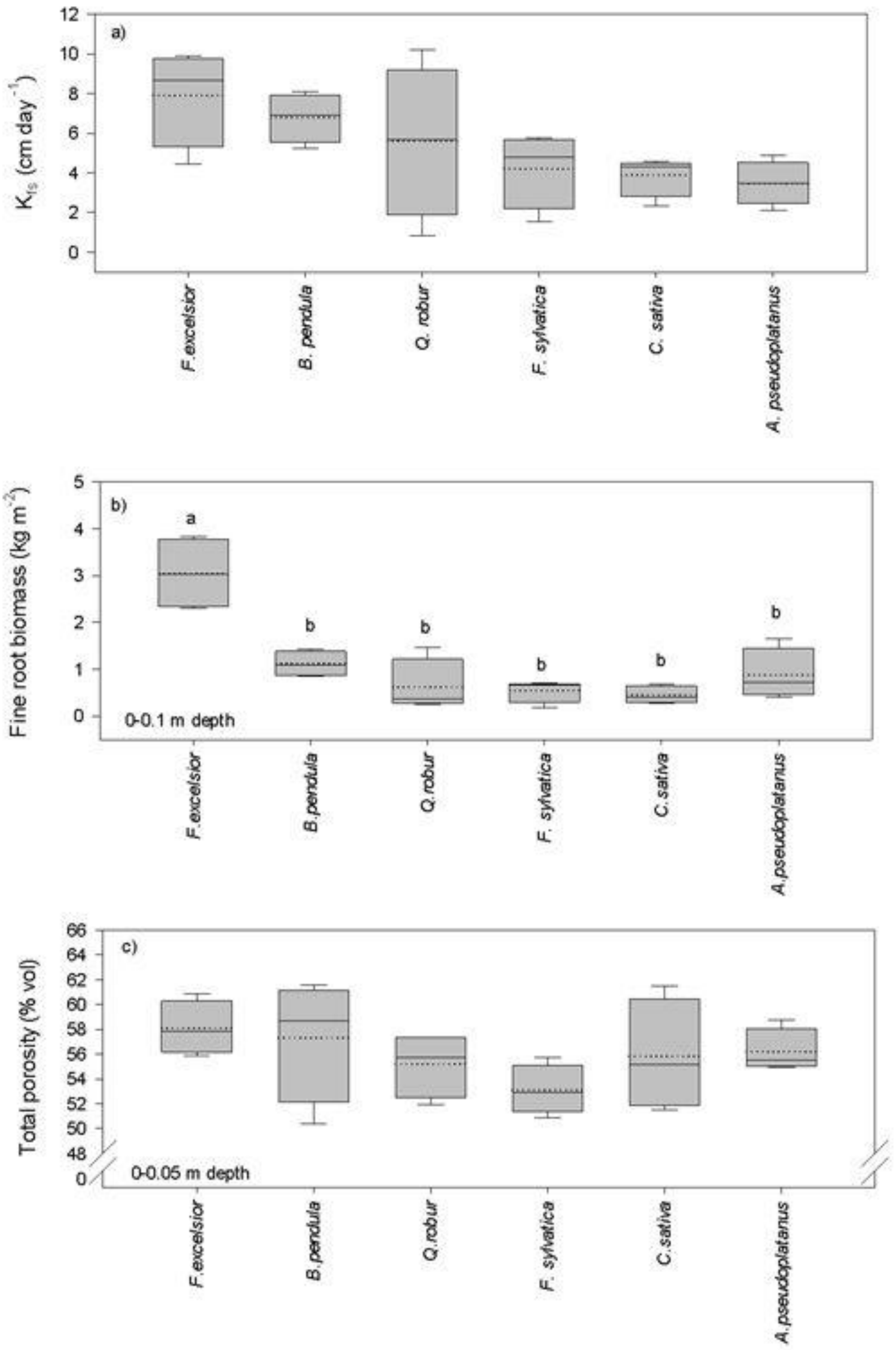

Figure 3.2. Variation in soil and fine root properties between plots of seven tree species (n=4): (a) Surface field saturated hydraulic conductivity (K_{fs}) (cm day^{-1}), (b) fine root biomass (kg m^{-2}) at 0-0.1 m depth, (c) total porosity (% vol) calculated from cores (excluding stone fraction) taken from 0-0.05 m depth. Data shown are mean (dashed horizontal line) and median (solid horizontal line) ± SE. Fine root biomass main effect p<0.001. No significance was found in K_{fs} or total porosity between species.

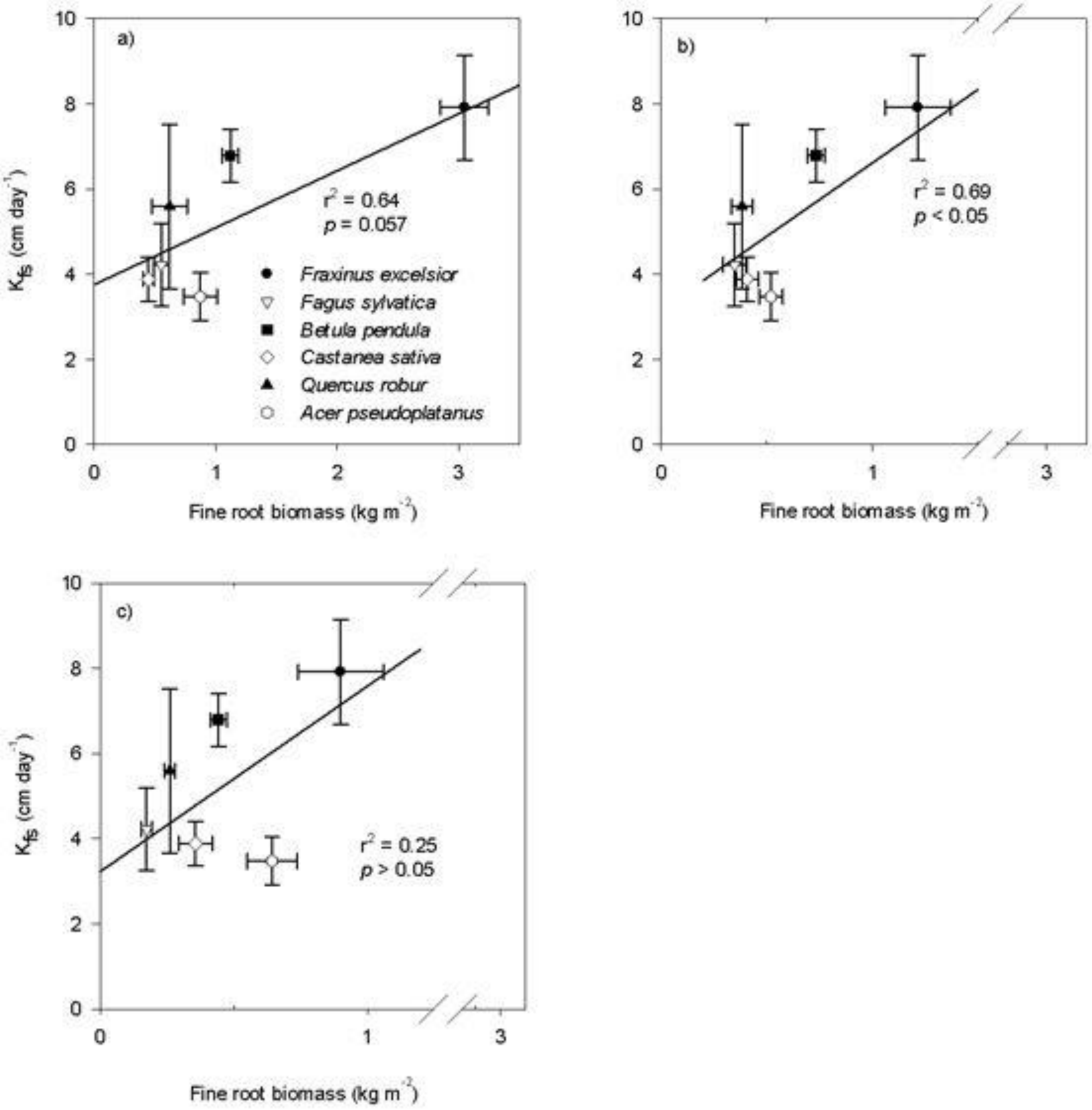

Figure 3.3. Relationship between mean surface field-saturated hydraulic conductivity (K_{fs}) (cm day^{-1}) and fine root biomass (kg m^{-2}) for plots (n=4) of six species *F. excelsior, B. sylvatica, B. pendula, C. sativa, Q. robur, A. pseudoplatanus* at (a) 0-0.1 m, (b) 0.1-0.2 m and (c) 0.2-0.3 m soil depths. Data shown are mean ± SE for each species.

3.3.3 Root morphological traits

An overall effect of species and depth was observed on all root traits ($p < 0.001$) except depth for SRA ($p > 0.05$), but there were no species × depth interactions (S.I. 3.2). In the 0-1.0 m soil layer, *F. excelsior* had greater RLD ($p<0.05$) and RAI ($p<0.01$) than all other species and greater RTD than *A. glutinosa* ($p < 0.001$), *C. sativa* ($p < 0.001$) and *Q. robur* ($p < 0.01$) (S.I. 3.3). The lowest RTD was associated with *C. sativa* (174.35 ± 17.17 000's m^{-2}), more than sevenfold less than *F. excelsior* (1275.01 ± 199.3 000's m^{-2}; $p < 0.001$). All species exhibited similar SRL at this depth, aside from a smaller SRL in *A. glutinosa* ($p < 0.01$). *Fraxinus excelsior* presented the greatest RLD, RAI, RTD and SRA in the 0.1-0.2 m soil layer ($p < 0.01$) but had similar SRL to all species other than *A. glutinosa* ($p < 0.01$). In the 0.2-0.3 m soil layer RLD and RAI of *Fraxinus excelsior* were greater relative to all other species except *A. glutinosa* ($p < 0.05$; S.I. 3.3).

Ordination analysis was used to examine the relationship between tree root morphological traits and soil physical properties developed under the different tree species. The dimensionality of the data was reduced to three principal components (PC) that explained 95% of the variation. Principal component 1 explained 63%, PC2 18% and PC3 14% of the variation (Fig. 3.5). Tree species were quite tightly grouped together with the exception of *F. excelsior*, which was strongly separated along the dominant PC1 and associated most strongly with fine root biomass, RAI, root tip density (RTD), RLD and root projected area. Necromass was weakly separated from other root traits along PC2 and associated with *A. glutinosa* and *F. excelsior* (Fig. 3.5a).Soil porosity at 0-0.05 m depth and K_{fs} were associated with each other along PC1 and weakly associated with *F. excelsior* and *A. glutinosa* along PC2 compared to the other five species, whereas conversely deeper in the soil (0.1-0.15 m) total porosity relates more strongly to the other five species than *F. excelsior* and *A. glutinosa*. Fine root biomass and other morphological traits (i.e. root projected area, RAI, RTD and RLD) are all closely associated with each other along PC1, and with *F. excelsior*. Stepwise multiple regression analysis (forward and backward) showed that root necromass was the sole best predictor of K_{fs} ($r^2 = 0.224$; $p<0.05$) with all other variables excluded during the analysis.

3.3.4 *Fraxinus excelsior* across soil classifications

Fine root biomass of *F. excelsior* did not differ significantly between the different soil types assessed across the UK ($p > 0.05$). However, fine root biomass was lowest in Rendzic Leptosol and the proportion of fine root necromass relative to fine root biomass in the 0.0-0.3 m layer was much greater (46%) in the Rendzic Leptosol than in the Haplic Luvisol (24%), Dystric Fluvic Cambisol (13%) and Dystric gleysol (33%) soils (S.I. 3.4). The relationship between fine root biomass and hydraulic conductivity previously observed across all species was reproduced when the relationship between *F. excelsior* fine root biomass and hydraulic conductivity was examined across the four soil types; the r^2 was 0.49 for the two soil layers 0-0.1 and 0.1-0.2 m and 0.43 for the 0.2-0.3 m soil layer.

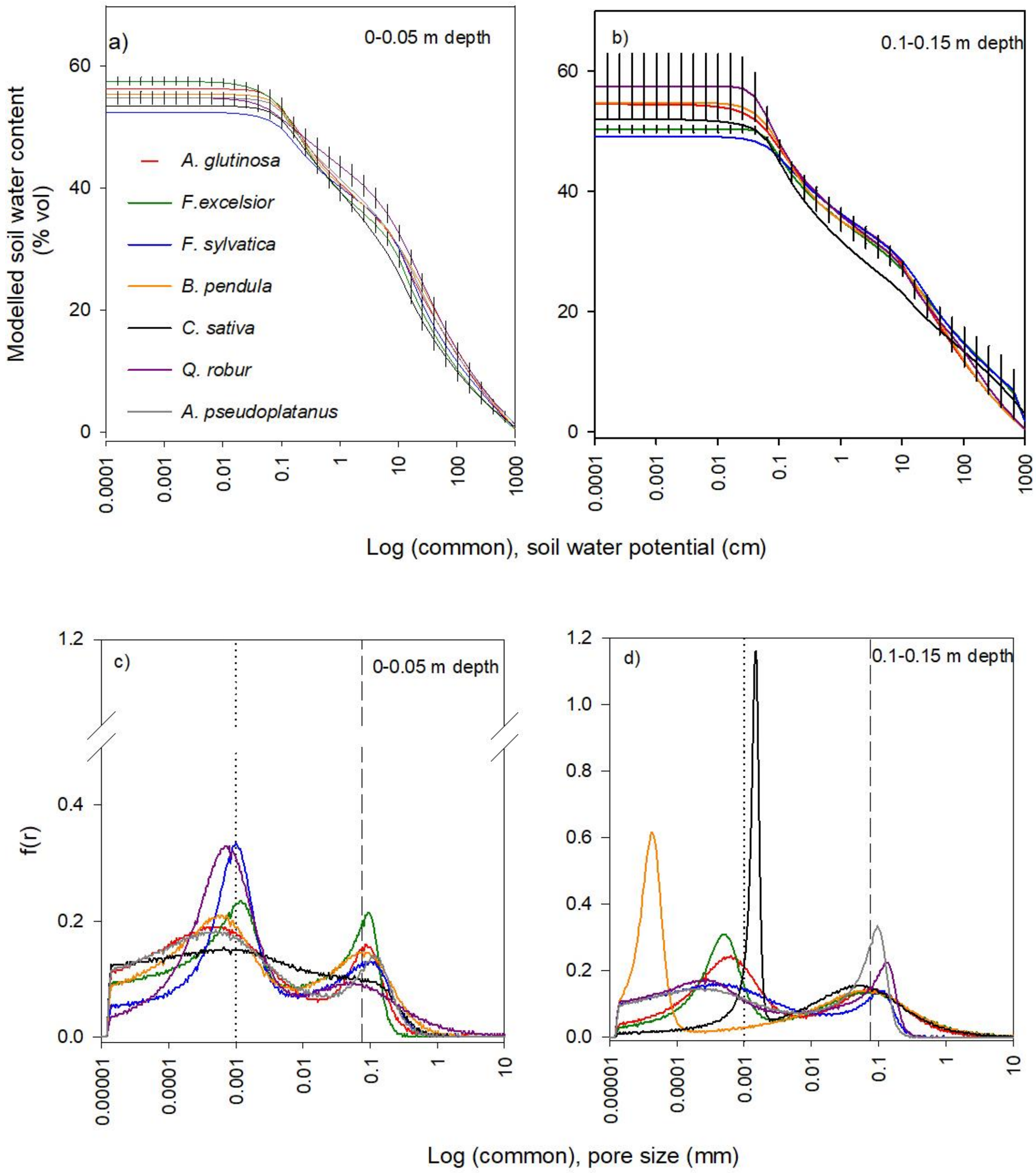

Figure 3.4. Mean soil water retention curves (SWRC) for plots (n=4) of seven species at (a) 0-0.05 m and (b) 0.01-0.15 m depths. The data are modelled using the bimodal Fredlund-Xing PDI model using measured soil water content (HYPROP) data. Modelled effective pore size radius distribution (Blonquist et al., 2006), displayed on a common log scale, of the seven species at (c) 0-0.05 m and (d) 0.1-0.15 m depths. The pore size distribution (f(r)) represents the proportional volume of the combined effective pore size radii. Values to the right of the dotted vertical line indicate pore radius sizes where capillary forces dominate water movement (Kosugi et al., 2002). Values to the right of the dashed vertical line indicate macropore radius sizes > 0.075 mm.

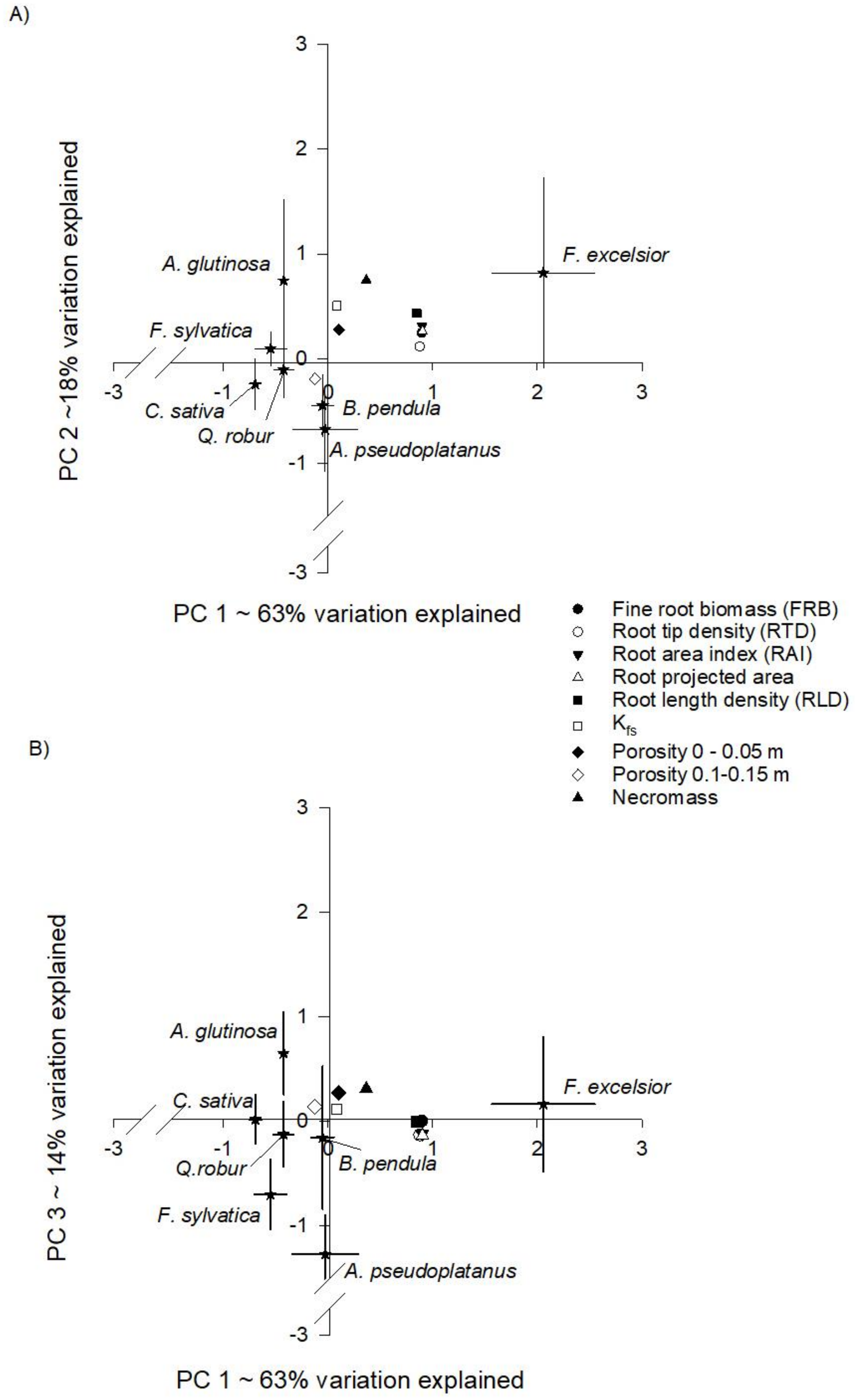

Figure 3.5. Principal component analyses examining the relationships between field saturated hydraulic conductivity (K_{fs}), species (*F. excelsior*, *B. pendula*, *F. sylvatica*, *C. sativa*, *Q. robur* and *A. pseudoplatanus*), fine root morphological variables (root biomass, root tip number, root area index, root projected area, root length density and necromass) and porosity (% volume) at two soil depths (0-0.05 m & 0.1-0.15 m). Error bars represent ± 1 SE.

Soil water retention curves were very similar under *F. excelsior* across all four soil types in the surface layer (Fig. 3.6a). At saturation, the soil water content at 0.0-0.05 m depth did not vary significantly and ranged between 61% and 57% for all the soil types. The shapes of the retention curves were also very similar throughout the range of water potential. Conversely, soil water retention curves from deeper in the soil profile (0.1-0.15 m) differed substantially (Fig. 3.6b). While the soil water retention curve of the gley soil from Devon retained the same form as the surface soils, all the other soils decreased their porosity and water retention with depth. The two silty clay loam soils at Gloucestershire and Hampshire showed the greatest change in porosity, reducing from ~58% to ~48% and ~42% respectively with depth. The silt loam Haplic luvisol soil had a unimodal pore size distribution, but the other soils all had a bimodal pore size distribution (Fig. 3.6c&d). For all four soils macro- and meso-size pores are clearly evident in the surface layer, but are reduced at depth, particularly the mesopores, with small pores becoming more prevalent at depth especially in the Dystric gleysol and Haplic luvisol soils.

Compared with reference soils in the ROSETTA database (Schaap et al., 2001), our soils retain greater volume of water at saturation, regardless of soil type (Fig. 3.7). The modelled soil water retention, based on physical soil characteristics of agricultural soils, is 15% - 50% less at saturation than our measured forested soils. Increasing soil water potential rapidly reduces the measured SWRC's and they become comparable with the predicted reference soils by pF 2.

3.4. Discussion

3.4.1 Soil type and hydrology

Our study explored whether within-species variation due to soil textural properties would temper the influence of forested landscapes on water retention capacity. Data was compared to agricultural soils with the same textural properties (loam, silty clay loam and clay loam) in the Rosetta database, to approximate hydraulic response. Soil structure, modified by the presence of trees, enabled a greater water retention capacity at saturation (Fig. 3.7). As water potential increased, which effectively excludes the influence of macropores, the forest SWRC's migrate much closer to the Rosetta predictions. We therefore argue that Landcover, specifically the presence of trees, mediates the influence of soil textural properties on hydraulic response, regardless of soil type.

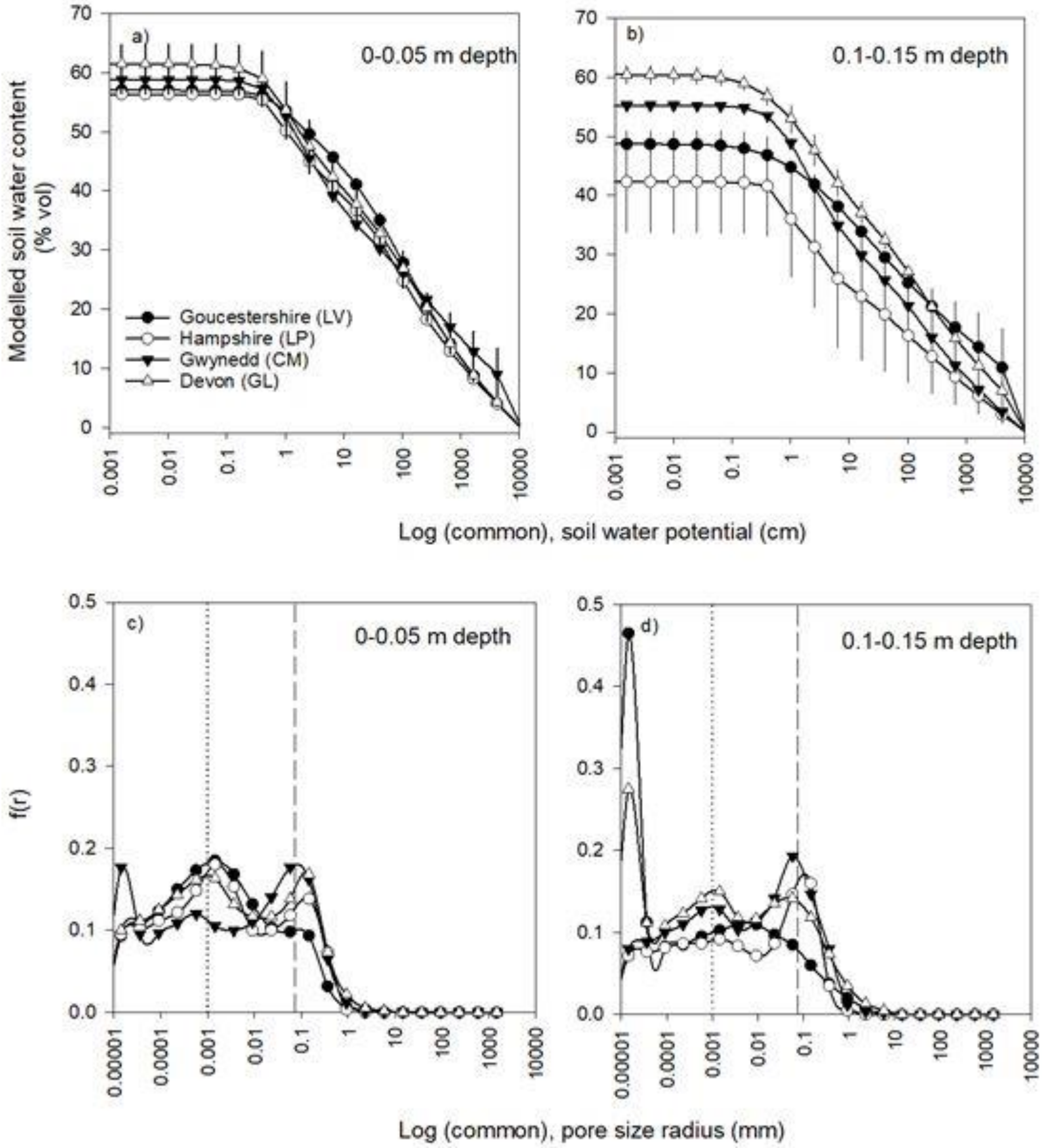

Figure 3.6. Mean soil water retention curves (SWRC) for four sites with contrasting soil classes: Haplic Luvisol (LV) silty clay loam; Rendzic Leptosol (LP) silty clay loam - limestone rich; Dystric Fluvic Cambisol (CM) sandy silt loam; and Dystric Gleysol (GL) clay loam, at (a) 0-0.05 m and (b) 0.01-0.15 m depths. The data are modelled using the bimodal Fredlund-Xing PDI model (Fredlund and Xing, 1994) using measured soil water content (HYPROP) data. Modelled pore size distribution (Blonquist et al., 2006) displayed on a common log scale from contrasting soil classifications at (c) 0-0.05 m and (d) 0.1-0.15 m depths. The pore size distribution (f(r)) represents the proportional volume of the combined effective pore size radii. Values to the right of the dotted vertical line indicate pore sizes where capillary forces dominate water movement (Kosugi et al., 2002). Values to the right of the dashed vertical line indicate macropore pore sizes > 0.075 mm.

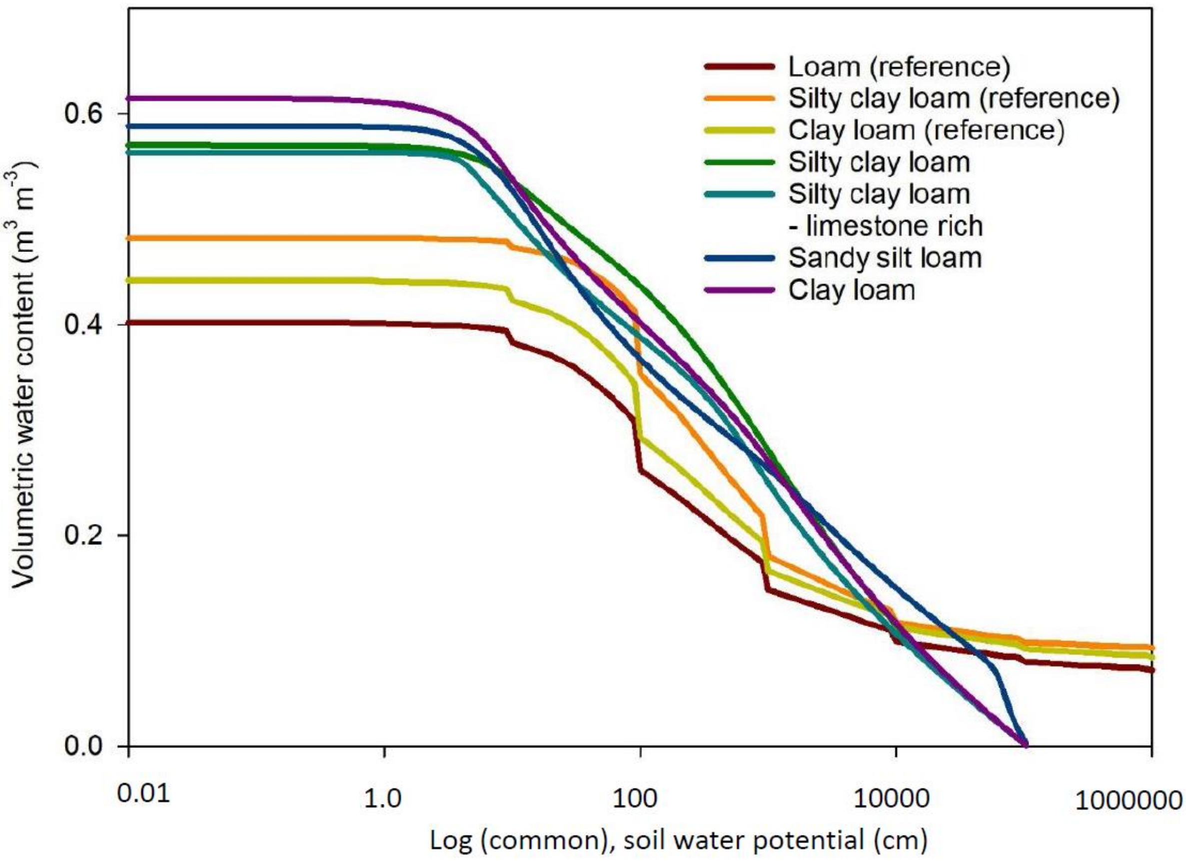

Figure 3.7. Soil water retention curves (SWRC) for the contrasting soil classes used in our study: Haplic Luvisol (LV) silty clay loam; Rendzic Leptosol (LP) silty clay loam - limestone rich; Dystric Fluvic Cambisol (CM) sandy silt loam; and Dystric Gleysol (GL) clay loam predicted solely from the soil texture using the Rosetta modelling framework for pedotransfer functions (Schaap et al., 2001).

Using *F. excelsior* as an example, our study showed that soil type (a considerable influence on ambient soil moisture) does not influence fine root growth near the soil surface. Furthermore, at 0-0.1 m depth, fine tree roots modified pore size distribution negating the effect of soil type on hydrological function. At this depth, where 50-58% of total fine root biomass of *F. excelsior* was found, little variation in soil water retention was observed between sites differing in soil type. Deeper in the soil, soil water retention is much more divergent between sites as the influence of fine roots decreases and soil type starts to dominate the hydraulic response. Hydraulic conductivity, therefore, is influenced by the interaction of root morphology and soil type, which varies with depth. Indeed, within-species variation in root morphology and rooting extent throughout the soil profile has been shown to be contingent on ambient hydrological soil conditions, oxygen availability and access to groundwater resources (Feng et al. 2017).

During very dry conditions, such as those recently preceding the study period (mean volumetric soil water content of 16%), soil type did have a nuanced effect on rooting morphology and macroporosity. The sandy silt loam and clay loam soil textures at the Gwynedd and Devon sites exhibited very similar pore size distribution. By contrast, the silty clay soil texture found in Gloucestershire was associated with a lower fine root biomass. In Gloucestershire there was a lack of organic matter, or limestone, in the soil that could disaggregate the clay compared with the other clay containing sites (i.e. Devon and Hampshire). The high clay content resulted in a substantially hardened soil that reduced plasticity and is likely to be the related to the observed lower abundance of macropores. Root dieback, however, caused by tree disease may have a greater (though time limited) impact on soil hydraulic function than soil type. Root dieback is positively associated with crown reduction due to infection from *Hymenoscyphus fraxineus* (Bakys et al., 2011). Where *H. fraxineus* was observed at a moderate - advanced stage (i.e. Hampshire), necromass accounted for half of the total fine root mass at 0-0.1 m depth, substantially more than the other clay-dominant sites (Gloucestershire, 29%, Devon, 33%). Once root necromass has fully decomposed, these root channels will be vulnerable to collapse, reducing hydraulic conductivity in the longer-term.

3.4.2 Tree root morphology and hydrology

Our study found that fine root biomass production is species-specific, broadly agreeing with Chandler et al. (2018). Notably, *F. excelsior*, a ubiquitous species across much of Europe, establishes fine roots far more extensively (up to six-fold greater biomass) than the other common European broadleaved species assessed. Across species, total soil porosity remained consistent but fine root biomass fluctuations changed soil macroporosity and soil water retention. Our data indicates that, although changes in species' root biomass roughly mirror that of K_{fs}, there was no relationship between root biomass and soil total porosity. *Fraxinus excelsior* had the highest water retention capacity at saturation (pF = 0) but the negligible variation between species indicates comparable total porosity. As soil water potential increased, the SWRC generated from soil collected under *F. excelsior* dropped rapidly, signifying the low bulk density and larger pore sizes (Radcliffe and Simunek, 2010) associated with this species.

Differences in pore size distribution, rather than total porosity, linked to species-specific differences in fine root morphology are likely to be driving the relationship between tree species and hydraulic conductivity. *Fraxinus excelsior* has the highest K_{fs}, root biomass and number of macropores, but the overall porosity was not statistically different from the soils under the other six tree species. Fine root biomass of *F. excelsior* might suggest adventitious root development and a greater RTN leading to the creation of macropores surrounding the root (Ghestem et al., 2011). However, it is apparent that fine root biomass, projected root area and RTN are not as strongly related to porosity as are other root traits (Fig. 3.5). Indeed, despite the high fine root biomass and hydraulic conductivity of *F. excelsior* we did not find a correspondingly high RTN suggesting that RLD rather than RTN is an important factor in the creation of macropore channels.

Despite nuanced relationships between live root morphological variables, macroporosity and K_{fs}, root necromass was the best predictor of K_{fs} suggesting that root turnover has an important role in soil hydraulic function. Fine root longevity in trees is complex, ranging from days to years (Bengough, 2012) and is dependent on root diameter, root density, N concentration, colonisation of mycorrhizal fungi and phenolic compound accumulation mediated by interaction with soil fauna (Eissenstat et al., 2000). During root development, exuded organic compounds contribute to the stability of the root channel, but following root death dehydration initially occurs, allowing gradual decomposition that creates progressively larger channels within the soil matrix available for preferential flow, and subsequently sub-surface sediment transfer causes channels to collapse or fill over time (Bengough, 2012; Ghestem et al., 2011). Variation in root turnover rates should have a large influence on the size and longevity of root-derived macropores (Wang et al., 2020).

Tree root morphological traits in our study better explained K_{fs} near the soil surface (0-0.2 m) than deeper in the soil (0.2-0.3 m depth). Root length density was greatest near the soil surface facilitating connectivity of root-induced macropores and greater opportunity for infiltration. A similar strong relationship between macroporosity near the soil surface and preferential flow in three tree species (*Sophora japonica* Linn., *Platycladus orientalis* Franco, and *Quercus dentata* Thunb.), which diminished with depth has also been reported (Zhang et al. 2015). A comparison with pedotransfer functions, largely used for agricultural soils, indicated that, by excluding sub-surface flow through macropores, hydraulic functions quickly converge with those predicted by the pedotransfer functions for the given soil texture in the 0-0.2 m soil layer, however, deeper in the profile (0.2-0.3 m) where the density of fine roots is lower, soil texture had a greater influence over soil hydraulic conductivity. Our results combined with the apparent lack of accountability for macropore generated by trees in pedotransfer functions suggests that improvement could be made to the parameterisation of hydrological models and NFM management based on the belowground characteristics of vegetation.

3.4.3 Implications for land managers

Fraxinus excelsior had the greatest potential to improve water infiltration and storage regardless of soil type. A ubiquitous species in much of Europe, *F. excelsior* is likely to have a disproportionately large influence on the landscape hydraulic function than the other species assessed here due to its root morphology and changes to macroporosity, which potentially makes an important contribution to natural flood risk management. Therefore, loss of *F. excelsior* in the landscape due to the fungal pathogen *H. fraxineus* could have serious implications for local natural flood resistance throughout Europe. We argue that consideration of hydraulic function should be a major consideration for the selection of alternative tree species to replace *F. excelsior*, and that a species' root morphological traits and influence on soil hydrology should be used as a criterion to select tree species in the future to maximise the potential benefits of NFM interventions. However, whilst our results show that tree species-specific root morphological traits have a role in altering soil hydraulic function at the plot scale, the complex interactions that influence catchment hydrology (e.g. field boundaries, land use, drainage) suggest that caution should be exercised before extrapolating our finding to the landscape scale.

3.5. Conclusion

Species-specific variation in fine root morphological characteristics of seven common European broadleaved tree species were found to alter soil macroporosity and hydraulic function. Fine root length density and necromass was correlated with an increased abundance of macropores within the soil, facilitating greater hydraulic conductivity, despite little change in total porosity. Notably, *F. excelsior* had up to a six-fold greater fine root biomass than the other species studied, however, RLD rather than fine root biomass was found to be the strongest driver of the observed changes in macroporosity.

Soil water retention curves and porosity data indicated that tree roots influence soil structural characteristics in the 0-0.1 m layer of the soil, where more than 50% of the fine root biomass was found, maximising macroporosity regardless of soil texture. Species with the greatest RLD exhibit correspondingly greater macropore abundance and higher hydraulic conductivity when soils are at or close to saturation.

The species-specific influence of trees to hydrological function and the associated impact of tree diseases, such as *F. excelsior* to ADB, suggests that changes to the tree species present in the landscape could have implications for hydrological regulation and the resilience of ecosystems to extreme weather events. Further work is necessary to determine if hydrological models can be improved by the incorporation of belowground tree trait data to improve selection of species for NFM interventions.

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3.7 Supplementary information

S.I. 3.1. The relationship between mean fine and coarse root biomass and necromass of seven tree species (*Alnus glutinosa, Fraxinus excelsior, Fagus sylvatica, Betula pendula, Castanea sativa, Quercus robur* and *Acer pseudoplatanus*) at 3 depths grown in monoculture (n = 4) are presented. Mean fine root biomass at each depth is given as a proportion of the whole profile (0-0.3 m) fine root biomass (%), B:N describes the biomass:necromass ratio, mean necromass at each depth is given as a proportion of total fine root mass (necromass + biomass) in the whole profile (0-0.3 m)(%).S.E. = ±1 standard error. Small letters denote post hoc comparison ($p < 0.05$) between species within each soil depth.

	Fine root biomass (kg m^{-2})		Proportion of total fine root biomass (%)	Necromass (kg m^{-2})		B:N ratio		Proportion of necromass to total fine root (%)	Coarse root biomass (kg m^{-2})	
0–0.1 m		S.E			S.E		S.E.			S.E
Alnus glutinosa	0.84^{b}	± 0.15	60.31	0.25	± 0.05	4.21^{b}	± 1.53	22.93	2.90	± 2.26
Fraxinus excelsior	3.05^{a}	± 0.40	59.01	0.36	± 0.14	12.17^{ab}	± 3.69	10.57	4.30	± 1.51
Fagus sylvatica	0.55^{b}	± 0.12	51.36	0.03	± 0.01	16.85^{ab}	± 3.69	5.91	0.17	± 0.11
Betula pendula	1.12^{b}	± 0.13	48.71	0.14	± 0.05	10.08^{ab}	± 2.13	10.79	2.89	± 1.44
Castanea sativa	0.45^{b}	± 0.09	36.91	0.07	± 0.04	5.56^{b}	± 2.81	14.12	0.23	± 0.15
Quercus robur	0.62^{b}	± 0.29	49.10	0.12	± 0.07	7.30^{ab}	± 2.51	16.67	0.47	± 0.21
Acer pseudplatanus	0.87^{b}	± 0.28	42.88	0.08	± 0.06	37.19^{a}	± 16.73	8.85	1.64	± 1.02
0.1–0.2 m		S.E			S.E		S.E.			S.E
Alnus glutinosa	0.26	± 0.07	19.04	0.15	± 0.05	3.27^{b}	± 1.92	36.17	1.47	± 0.90
Fraxinus excelsior	1.22	± 0.31	23.56	0.11	± 0.03	15.16^{ab}	± 4.73	8.29	6.14	± 3.05
Fagus sylvatica	0.35	± 0.11	32.45	0.05	± 0.02	6.60^{b}	± 3.76	12.99	2.10	± 1.86
Betula pendula	0.74	± 0.08	31.99	0.06	± 0.02	14.05^{ab}	± 2.42	7.73	5.74	± 2.47
Castanea sativa	0.41	± 0.10	33.62	0.17	± 0.06	1.05^{b}	± 0.40	29.09	1.23	± 0.24
Quercus robur	0.38	± 0.10	30.29	0.08	± 0.03	5.23^{b}	± 1.23	17.48	4.44	± 2.49
Acer pseudoplatanus	0.52	± 0.11	25.51	0.03	± 0.02	103.9^{a}	± 54.77	5.28	3.46	± 0.39
0.2–0.3 m		S.E			S.E		S.E.			S.E
Alnus glutinosa	0.29^{ab}	± 0.05	20.66	0.11	± 0.03	3.82	± 1.95	28.27	1.11	± 0.17

Fraxinus excelsior	0.90^{a}	± 0.32	17.43	0.11	± 0.06	10.67	± 2.73	11.23	4.53	± 2.67
Fagus sylvatica	0.17^{b}	± 0.04	16.18	0.02	± 0.00	8.96	± 2.80	11.33	0.50	± 0.22
Betula pendula	0.44^{ab}	± 0.06	19.30	0.08	± 0.01	6.95	± 1.86	14.47	2.90	± 2.26
Castanea sativa	0.36^{ab}	± 0.13	29.47	0.05	± 0.02	2.57	± 1.05	12.58	2.71	± 1.23
Quercus robur	0.26^{ab}	± 0.04	20.61	0.09	± 0.03	3.78	± 1.05	26.21	3.32	± 2.96
Acer pseudoplatanus	0.64^{a}	± 0.19	31.61	0.12	± 0.05	12.61	± 6.33	15.20	3.53	± 2.19
0–0.3 m		S.E			S.E		S.E.			S.E
Alnus glutinosa	1.39^{b}	± 0.26	N/A	0.51	± 0.11	3.43	± 1.20	26.94	5.47	± 0.17
Fraxinus excelsior	5.16^{a}	± 0.71	N/A	0.58	± 0.17	12.01	± 3.83	10.16	14.97	± 2.67
Fagus sylvatica	1.07^{b}	± 0.26	N/A	0.11	± 0.03	10.68	± 2.84	9.21	2.77	± 0.22
Betula pendula	2.30^{ab}	± 0.12	N/A	0.27	± 0.05	9.30	± 1.78	10.58	11.52	± 2.26
Castanea sativa	1.21^{b}	± 0.24	N/A	0.29	± 0.10	1.97	± 0.73	19.42	4.16	± 1.23
Quercus robur	1.26^{b}	± 0.34	N/A	0.30	± 0.09	4.57	± 0.81	19.07	8.24	± 2.96
Acer pseudoplatanus	2.04^{ab}	± 0.56	N/A	0.23	± 0.07	14.82	± 6.65	10.11	8.62	± 2.19

S.I. 3.2. Between-subject effects of species and depth on fine root traits (specific root length (m g^{-1}; SRL), root area index (m^2 m^{-2}; RAI), specific root surface area (m^2 kg^{-1}; SRA), root length density (cm cm^{-3}; RLD), root tip density (thousands m^{-2}; RTD). ****p*<0.001, ns = not significant.

		df	F-stat	*p*
Species	Specific root length (m g^{-1})	6	21.825	***
	Root Area Index (m^2 m^{-2})	6	22.757	***
	Specific root surface area (m^2 kg^{-1})	6	19.549	***
	Root length density (cm cm^{-3})	6	29.519	***
	Root tip density (thousands m^{-2})	6	25.816	***
Depth	Specific root length (m g^{-1})	2	76.572	***
	Root Area Index (m^2 m^{-2})	2	22.994	***
	Specific root surface area (m^2 kg^{-1})	2	0.591	ns
	Root length density (cm cm^{-3})	2	39.089	***
	Root tip density (thousands m^{-2})	2	57.046	***
Species*Depth	Specific root length (m g^{-1})	12	0.395	ns
	Root Area Index (m^2 m^{-2})	12	0.826	ns
	Specific root surface area (m^2 kg^{-1})	12	0.392	ns
	Root length density (cm cm^{-3})	12	0.852	ns
	Root tip density (thousands m^{-2})	12	1.108	ns

S.I. 3.3. Fine root metrics (specific root length (m g^{-1}), root area index (m^{2} m^{-2}), specific root surface area (m^{2} kg^{-1}), root length density (cm cm^{-3}), root tip density (thousands m^{-2}) of seven tree species (*Alnus glutinosa, Fraxinus excelsior, Fagus sylvatica, Betula pendula, Castanea sativa, Quercus robur* and *Acer pseudoplatanus*) at three soil depths (0-0.1, 0.1-0.2, 0.2-0.3 m). S.E. = ±1 standard error. Small letters denote Tukey post hoc comparisons ($p < 0.05$) of root traits within each soil depth.

Root trait	**Depth**	***Fraxinus excelsior***	***Betula pendula***	***Acer pseudoplatanus***	***Alnus glutinosa***	***Quercus robur***	***Castanea sativa***	***Fagus sylvatica***
Specific root length (m g^{-1})	0-10	22.23^{a} ± 3.62	14.88^{ab} ± 1.58	22.43^{a} ± 3.57	8.27^{b} ± 1.94	20.20^{a} ± 3.04	13.43^{ab} ± 1.22	26.38^{a} ± 3.22
	10-20	10.09^{ab} ± 0.45	6.36^{abc} ± 0.29	9.42^{ab} ± 0.38	4.13^{c} ± 0.41	9.88^{ab} ± 2.50	5.79^{bc} ± 0.83	13.45^{a} ± 3.85
	20-30	8.98^{ab} ± 0.73	5.35^{bc} ± 0.57	6.52^{bc} ± 1.12	3.37^{c} ± 0.45	9.31^{abc} ± 1.06	5.53^{bc} ± 0.95	11.78^{a} ± 1.66
Root area index (m^{2} m^{-2})	0-10	6.02^{a} ± 0.86	1.27^{b} ± 0.19	1.25^{b} ± 0.32	0.88^{b} ± 0.27	0.78^{b} ± 0.26	0.51^{b} ± 0.09	0.96^{b} ± 0.26
	10-20	2.59^{a} ± 0.64	0.76^{ab} ± 0.11	0.70^{b} ± 0.17	0.28^{b} ± 0.07	0.45^{b} ± 0.09	0.47^{b} ± 0.10	0.50^{b} ± 0.16
	20-30	1.78^{a} ± 0.57	0.42^{b} ± 0.06	0.74^{ab} ± 0.20	0.29^{b} ± 0.05	0.37^{b} ± 0.05	0.39^{b} ± 0.12	0.26^{b} ± 0.05
Specific root surface area (m^{2} kg$^{-1)}$	0-10	19.40^{a} ± 0.41	11.14^{bc} ± 0.78	14.90^{abc} ± 1.47	10.29^{c} ± 1.87	14.32^{abc} ± 1.36	11.58^{bc} ± 0.60	16.97^{a} ± 1.73
	10-20	21.13^{a} ± 0.89	10.17^{b} ± 0.36	13.17^{b} ± 0.66	10.80^{b} ± 0.68	13.74^{b} ± 2.74	11.59^{b} ± 1.28	15.60^{ab} ± 1.96
	20-30	20.15^{a} ± 1.30	9.50^{c} ± 0.60	11.92^{bc} ± 1.27	9.95^{c} ± 0.70	14.15^{a} ± 0.85	11.68^{bc} ± 0.94	15.92^{a} ± 1.69
Root length density (cm cm^{-3})	0-10	6.56^{a} ± 0.65	1.70^{b} ± 0.33	1.82^{b} ± 0.43	0.70^{b} ± 0.24	1.03^{b} ± 0.27	0.57^{b} ± 0.07	1.51^{b} ± 0.42
	10-20	2.42^{a} ± 0.60	0.94^{ab} ± 0.15	0.96^{ab} ± 0.20	0.21^{c} ± 0.05	0.61^{b} ± 0.10	0.43^{bc} ± 0.07	0.72^{b} ± 0.19
	20-30	1.55^{a} ± 0.47	0.46^{bc} ± 0.05	0.77^{ab} ± 0.19	0.19^{c} ± 0.04	0.48^{bc} ± 0.09	0.33^{bc} ± 0.07	0.37^{bc} ± 0.06
Root tip density (RTD) (thousands m$^{-2)}$	0-10	1275.01^{a} ± 199.30	625.53^{ab} ± 150.04	528.29^{ab} ± 116.41	242.89^{bc} ± 45.28	348.08^{bc} ± 88.43	174.35^{c} ± 17.17	515.07^{abc} ± 127.84
	10-20	512.43^{a} ± 132.38	307.72^{ab} ± 23.23	246.19^{abc} ± 36.84	63.31^{d} ± 11.36	205.66^{abc} ± 39.54	104.35^{cd} ± 14.62	260.47^{abc} ± 64.56
	20-30	314.58^{a} ± 84.47	137.32^{ab} ± 12.12	205.31^{a} ± 38.81	59.83^{c} ± 9.99	157.04^{ab} ± 25.09	85.35^{b} ± 16.00	130.93^{abc} ± 17.09

S.I. 3.4. The relationship between mean fine and coarse root biomass and necromass of *F. excelsior* grown in four contrasting soil textures (Hampshire, silty-clay loam – limestone rich; Gloucestershire, silty-clay loam; Gwynedd, sandy silt loam; Devon, clay loam) at 3 depths grown in monoculture (n = 3). Mean fine root biomass at each depth is given as a proportion of the whole profile (0-0.3 m) fine root biomass (%), B:N describes the biomass:necromass ratio, mean necromass at each depth is given as a proportion of total fine root mass (necromass + biomass) in the whole profile (0-0.3 m) (%). S.E. = ±1 standard error.

	Fine root biomass (kg m^{-2})		Proportion of total fine root biomass (%)	Necromass (kg m^{-2})		B:N ratio	Proportion of necromass to total fine root (%)	Coarse root biomass (kg m^{-2})	
0-10 cm									
Hampshire	2.24	± 0.61	55.01	2.29	± 0.04	0.98	50.55	4.77	± 0.27
Gloucestershire	1.99	± 0.12	50.63	0.80	± 0.23	2.49	28.67	2.84	± 0.46
Gwynedd	2.88	± 0.71	51.91	0.37	± 0.07	7.78	11.38	5.90	± 0.80
Devon	3.53	± 0.15	57.61	1.72	± 0.27	2.05	32.76	8.86	± 3.58
10-20 cm									
Hampshire	0.99	± 0.37	24.33	0.69	± 0.11	1.43	41.07	1.59	± 0.58
Gloucestershire	1.23	± 0.14	31.38	0.26	± 0.03	4.73	17.45	3.91	± 1.38
Gwynedd	1.21	± 0.36	21.85	0.25	± 0.05	4.84	17.12	1.23	± 0.42
Devon	1.78	± 0.17	29.06	0.84	± 0.19	2.12	32.06	9.34	± 7.69
20-30 cm									
Hampshire	0.84	± 0.20	20.66	0.55	± 0.10	1.53	39.57	1.41	± 0.53
Gloucestershire	0.71	± 0.05	17.99	0.18	± 0.03	3.94	20.22	1.29	± 0.69
Gwynedd	1.46	± 0.70	26.24	0.21	± 0.07	6.95	12.57	0.66	± 0.46
Devon	0.82	± 0.18	13.33	0.45	± 0.06	1.82	35.43	0.77	± 0.28
0-30 cm									
Hampshire	4.07	± 1.13	-	3.52	± 0.17	1.16	46.38	7.77	± 0.99
Gloucestershire	3.93	± 0.22	-	1.24	± 0.24	3.17	23.98	8.04	± 0.37
Gwynedd	5.56	± 1.73	-	0.84	± 0.17	6.62	13.13	7.79	± 0.62
Devon	6.13	± 0.44	-	3.01	± 0.50	2.04	32.93	19.0	± 4.86

Chapter 4 Contrasting root morphological traits in two-species admixture regulates fine root yield and hydraulic conductivity

Bid Webb[1], David A. Robinson[2], Andrew R. Smith[1]

[1] School of Natural Sciences, Bangor University, UK
[2] UK Centre for Ecology and Hydrology, Bangor, UK

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Abstract

Trees moderate soil hydraulic function via belowground processes. The relationship between species identity and hydraulic conductivity has been identified in monoculture, but the influence of species richness on hydraulic function is little understood. This study aimed to characterise tree root morphology of two-species plots of *Fraxinus excelsior* – *Betula pendula* and *Betula pendula* – *Castanea sativa* and the relationship with soil hydraulic properties. Hydraulic conductivity was determined at the soil surface by minidisk, soil water retention curves (SWRC) from soil cores (0-0.5 m & 0.1-0.15 m depths) and root morphology from soil cores collected at 0-0.1, 0.1-0.2, & 0.2-0.3 m depths from Bangor Diverse monoculture and two species plots (n=4). The results showed that hydraulic conductivity is not affected by species richness but is dependent on species identity and competition between species. Tree species that possessed contrasting functional traits, namely *B. pendula* and *C. sativa* had a net biodiversity benefit from a mutualistic relationship that resulted in a significant increase in field-saturated hydraulic conductivity (K_{fs}) from *C. sativa* in monoculture. *Fraxinus excelsio*r and *B. pendula*, species with similar functional traits, had no effect on K_{fs}. The most prolific producer of fine root biomass (FRB) in monoculture, *F. excelsior*, experienced the greatest reduction in FRB when grown in admixture with *B. pendula* and was associated with a low abundance of macropores. Selection of species based on contrasting belowground functional traits to maximise niche differentiation should, therefore, be considered where hydrological regulation is a key objective of afforesting with mixed species.

4.1 Introduction

Managing over- and under-supply of water is of global importance as climate change alters the magnitude and periodicity of precipitation events increasing the risk of flooding and drought worldwide (UNDRR, 2019). Trees have the potential to moderate water cycling by reducing overland flow through interception, evapotranspiration and infiltration (Ellison et al., 2017). Soil textural properties (sand, silt, clay), bulk density and organic matter have been widely used to estimate soil hydraulic properties (van Genuchten, 1980) but more recent research points to the importance of land cover, porosity and organic carbon as better predictors of soil hydraulic conductivity (Jarvis et al., 2013). These factors are more dynamic, influenced by climate change, land use and management. To support land use and management decision-making and maximise the hydrological benefits from greater tree cover (and minimise the disbenefits), it is important to understand how species identity and competition affect belowground hydraulic function.

Species-specific differences in fine root morphology have potential to alter K_{fs} through root induced changes to soil structure. Species identity has been found to have an inconclusive effect on hydraulic conductivity in mixed species stands with some finding an effect for example between *Pinus sylvestris* and *Acer pseudoplatanus* (Chandler et al., 2018), and *Quercus dumosa*, *Adenostoma fasciculatum* and *Pinus coulteri* (Johnson-Maynard et al., 2002) while others found no effect (Eldridge and Freudenberger, 2005; Jost et al., 2012). In Chapter 3 of this thesis a comparison of seven common broadleaved tree species (*Acer pseudoplatanus* L., *Alnus glutinosa* [L.] Gaertner, *Betula pendula* Roth., *Castanea sativa* Mill, *Fagus sylvatica* L., *Fraxinus excelsior* L., *Quercus robur* L.) grown in monoculture, revealed that FRB was correlated to field-saturated hydraulic conductivity (K_{fs}) ($r^2 = 0.64$ & $r^2 = 0.69$, 0-0.1 m & 0.1-0.2 m depths respectively). Despite thisrelationship, fine root necromass was found to be the best predictor of K_{fs}, suggesting that fine root turnover has an effect on K_{fs}. It appears likely that channels generated by the growth of fine roots increases soil macroporosity, which when combined with organic matter inputs can improve both the soil water retention capacity and hydraulic conductivity. This has important implications for species choice for hydraulic regulation. Tree diseases, such as *Hymenoscyphus fraxineus* (Ash Dieback) that target specific tree species, could therefore have a disproportionate influence on overland flow and consequently flood risk.

The role mixed tree species stands play in hydraulic conductivity is poorly understood. In grassland ecosystems, Fischer et al., (2015) reported that plant species richness modifies soil porosity as well as indirectly through soil organic carbon and root biomass, explaining infiltration capacity. However, the relationship between hydraulic conductivity and mixed forested ecosystems are largely unknown. Bens et al. (2007) investigated hydraulic function under a forest transformation chronosequence from monoculture *Pinus sylvestris* L. to mixed *P. sylvestris* and *F. sylvatica* to monoculture *F. sylvatica* forest. Hydraulic conductivity correlated with soil organic matter content, which increased within the process of forest transformation, but surface hydrophobicity was a confounding factor, leading to very low K and difficulty assessing the role of species identity belowground.

The extent to which root growth and morphology of species grown in monoculture is altered when species are grown in mixed groupings is contested (e.g. Brassard et al., 2011; Ma et al., 2019; Meinen et al., 2009b). Overyielding of root biomass when species are grown in mixture is one possible mechanism that could improve K_{fs} of soils (Lei et al., 2012; Ma et al., 2019). The concept of overyielding emerges from an increase in productivity from mixed forest stands that is greater than what could be expected from the same species grown in monoculture. Total production (above- and below-ground) might be expected to both increase in response to species richness, however, biomass overyielding has been found to occur disproportionately belowground (Fruleux et al., 2018; Ma et al., 2019; Meinen et al., 2009a). Indeed, Jacob et al. (2014) showed that species richness was associated with higher fine root productivity and turnover, with fine roots occupying more of the vertical soil profile (Brassard et al., 2011; Lei et al., 2012). *Fagus sylvatica*, for example, benefits from being grown in admixture with *B. pendula* despite the greater FRB of *B. pendula*, due to niche partitioning of fine roots (Curt and Prevosto, 2003). In young trees (5-6 years old), niche differentiation can account for 95% more FRB compared with monoculture (Lei et al., 2012). However, where trees occupy the same niches in vertical rooting patterns, no FRB overyielding between monoculture, three and five-species mixtures was found (Meinen et al., 2009b). It is therefore argued that species identity, rather than richness per se, is key to the overyielding of FRB (Jacob et al., 2014, 2013; Meinen et al., 2009a). Fine root productivity, for example, was not affected by different levels of species richness (i.e., 1, 2 or 3 species mixes ; Jacob et al., 2014) nor in the 1, 3 or 5 levels of species richness used in the study of Meinen et al., (2009b), but overyielding has been associated with specific tree species, such as *F. excelsior* (Jacob et al., 2013).

One approach to determine the relative function of each species when planted in mixture, with reference to monoculture is through additive partitioning of biodiversity effects (Loreau and Hector, 2001). Niche differentiation, where species occupy different 'niches' in the soil and species facilitation, where the functional traits of one species is advantageous to the other, are collectively referred to as complementarity (Loreau and Hector, 2001). Positive complementarity can arise from resource partitioning, where species growing in resource-rich parts of the soil benefit more than roots in resource-poor soil, from mutualistic relationships and/or from a reduction in pests and diseases (Hector, 2006). Selection assumes that species with advantageous functional traits in monoculture, such as large volumes of FRB, will exhibit the same benefit in mixture, bolstering overall community performance. The additive partitioning method assesses species' performance in relation to each other i.e., a complementarity effect, or as an individual contribution i.e., a selection effect.

The aim of this study was to investigate the relationship between soil hydraulic properties and the tree root morphology of species grown in two species mixture. Specifically, we investigated how root morphology was altered when *F. excelsior*, *B. pendula* and *C. sativa* were grown in two-species mixture (*F. excelsior – B. pendula* & *B. pendula – C. sativa*) and compared the results to the same species grown in monoculture. The net biodiversity effect (i.e. over- or under-yielding) were explored using additive partitioning of biodiversity effects where the relative effect of complementarity (competition) and selection (species) were identified and linked to the vertical stratification of roots within the available soil volume and the soil hydraulic function. It was hypothesised that species identity would determine FRB, competition response and vertical fine root distribution, which in turn alters hydraulic response. Specifically, we tested the hypotheses that: (i) the FRB of *F. excelsior* is not reduced when planted with a tree species of similar root morphology; and (ii) FRB and morphological characteristics result in a greater hydraulic response when species grown in mixture possess contrasting functional traits.

4.2 Method

4.2.1 Site description and experimental design

The BangorDiverse forest diversity and ecosystem function experiment, located at Abergwyngregyn, United Kingdom (53°14'15''N, 4°1'4''W) was used to determine the effect of tree species on hydraulic function (see Chapter 3; Fig. 3.1). Two species mixes of *B. pendula* and *A. glutinosa* were planted as 0.6 m saplings in March 2004 with one of five other tree species: *A. pseudoplatanus, C. sativa, F. sylvatica, F. excelsior* and *Q. robur* (Ahmed et al., 2016). Two mixed plot combinations were used for this study (*B. pendula – F. excelsior* and *B. pendula – C. sativa*) based on complementary and contrasting FRB density (Chapter 3) respectively. Species combinations were limited by the original experimental design but *B. pendula*, the second most prolific FRB producer (Chapter 3), was considered complementary to *F. excelsior* and contrasting to *C. sativa*.Initial planting density was 10,000 stems ha^{-1} but trees were thinned to 2,500 stems ha^{-1} in 2012/2013 to facilitate continued tree development. Randomised replicate plots (121 m^2) of each species (n=4) were blocked across two adjacent fields.

The soil at BangorDiverse is a Dystric Fluvic Cambisol, with a sandy loam/loam texture developed from glaciofluvial deposits (Smith et al., 2013) and pH ranging from 5.4 (surface) to 6.3 (1 m depth) (Ahmed et al., 2016). The site is hyperoceanic with a mean annual rainfall of ca. 950 mm and a mean annual temperature of 10.6 °C (Gunina et al., 2017).

4.2.2 Root morphology

Two soil cores of 0.08 m diameter were taken from three depths (0-0.1, 0.1-0.2, 0.2-0.3 m) equidistant between two trees, near the centre of each plot during dormancy (winter). Soil cores were placed into sealable polythene bags and transported to the laboratory on the day of field collection and stored at 4 °C for a maximum of 4 days before processing.

Each core was washed with water in a sieve stack (1 and 2 mm mesh size) to remove soil adhered to roots and separate roots into two size classes, fine (<2 mm ø), coarse (>2 mm ø). Tree species identity of the roots was based on morphological descriptions outlined by Mrak and Gricar (2016) and necromass was identified based on black or dark brown colour and a decaying fragmented appearance. Live fine roots were scanned using an Epson 4990 scanner at a resolution of 300 dpi and images were analysed with WinRhizo (version 2005c Regent

Instruments Inc, Quebec, Canada) to measure fine root length, surface area, surface volume, projected surface area and number of root tips, divided into 20 (0.1 mm) diameter classes (0-2 mm). Biomass of necromass, fine and coarse roots was determined after drying at 80 °C until constant mass. Data from the two soil cores collected per plot were averaged to avoid within-plot pseudoreplication.

Fine root data was converted to matrices to enable comparisons across the groups. Fine root biomass indicates the density of fine roots (kg m^{-2}) extrapolated from the weight found in the sampled core. Root length density (RLD cm cm^{-3}), which indicates the proportion of soil occupied by fine roots, was estimated from the ratio of root length to the volume of the sampled core. Root tip density (RTD) was calculated as thousands per m^{-2}. Root area index (RAI, m^2 m^{-2}) was derived from the root surface area divided by the surface area of the sampled core. Specific root area (SRA m^2 kg^{-1}) was calculated from the surface area of fine root divided by root dry mass (Lohmus et al., 1989). Specific root length (SRL m g^{-1}) was determined from the total length of fine roots divided by root dry mass (Ostonen et al., 2007). For each of the aforementioned metrics an arithmetic mean was calculated from data exported from WinRhizo output.

4.2.3 Soil hydraulic function

Minidisk Infiltrometers (Meter Group, Pullman, USA) were used to measure the rate of infiltration of water into soil and to calculate saturated hydraulic conductivity (K_{fs}) within each plot. Surface vegetation was carefully removed, and a thin layer of fine sand was applied to the soil surface to ensure optimal contact between the infiltrometer disc and the soil. The pressure head was set at -0.02 m to eliminate water flow through the heterogeneous macropores, to provide a more representative estimation of water flow through the soil matrix and to achieve steady-state infiltration rate. Saturated K_{fs} for the respective pressure head was calculated using the method of Zhang (1997) and van Genuchten soil classification tables (Meter Group Inc, 2018). Predicted median K_{fs} was calculated from the average median of each component species in monoculture.

At each plot, a 0.00025 m^3 UMS soil sampling core was taken at 0 - 0.05 m and 0.1 - 0.15 m depths. Cores were stored at 4 °C and then soaked for at least 24 hours in degassed, deionised water prior to analysis. Soil water retention was measured using a HYPROP 2 (Meter group, Pullman, USA) (Schindler et al., 2010), and dry bulk density and porosity of the cores was determined following analysis. Sub-samples of the cores were taken and the vapour equilibration technique (Scanlon et al., 2002) was used to measure the dry-end matric potential. To account for the stoniness of the experimental plots, stones (>2 mm ø) were sieved out of the oven-dried soil and weighed. Soil water retention curves (SWRC) were modelled using the HypropFit (Schindler et al., 2010) (UMS, Munchen, Germany) implementation of the Fredlund-Xing water retention model (Fredlund and Xing, 1994), underpinned by measured SWRC, dry bulk density, porosity, dry end matric potential, volumetric moisture content and stoniness data.

Effective soil pore size distribution was estimated using the method outlined by Blonquist et al. (2006). Hydraulic capacity was estimated using data from the SWRC (modelled in HypropFIT) to derive the change in moisture over the change in hydraulic head ($d\theta_v/dh$). Hydraulic capacity was plotted as a function of pore radius. The scaled effective pore size distribution associated with each tree species was then derived by taking the inverse relationship between pressure (h) from the water retention curve and log10 pore radius, resulting in a dimensionless, scaled, effective pore size distribution. The distribution is displayed as a function of effective pore radius ƒ(r) proportional to the abundance of each pore size within a given volume of soil.

4.2.4 Biodiversity effects

The net biodiversity effect is estimated from the sum of complementarity and selection effects on observed yield as described in Loreau and Hector (2001). Complementarity is calculated from the deviation of expected relative yield in mixture from yield in monoculture. Selection effect is calculated from the co-variance of the expected yield in mixture relative to monoculture. The null hypothesis returns a value of 0 illustrating no effect, whilst positive values indicate a net benefit (overyielding), negative values a net cost (underyielding).

4.2.5 Statistical analyses

All statistical analyses were undertaken with SPSS v22.0 (IBM SPSS, Armonk, NY, USA) with $p < 0.05$ used as the limit for statistical significance. A one-way ANOVA with Tukey post hoc test were used to describe the effect of tree species and mixture by grouping according to species and co-species (i.e. 'group') on surface K_{fs}, soil porosity at 2 soil depths (0-0.05 & 0.10-0.15 m) FRB and necromass at three soil depths (0-0.1, 0.1-0.2, 0.2-0.3 m). All data satisfied normal distribution (Shapiro-Wilk) and Levene's test used to verify homoscedasticity. To predict the

K_{fs} rate if each species retained the same K_{fs} exhibited in monoculture, the median of the 2 component species in monoculture were averaged to find the ‘expected median’.

Multivariate GLM were used to isolate the overall effects of species and depth as well as the interaction effects on vertical distribution of FRB using species and tree configuration (i.e. monoculture or admixture) as factors. Simple main effects of group were then examined using one-way analysis of variance (ANOVA) with Tukey post hoc test at each soil depth. Logged diameter class distribution of RLD and RTD were also defined using multivariate GLM to examine overall species and configuration effects. Root length density was described over 20 diameter classes (0-2 mm), whereas RTD over 10 diameter classes (0-1 mm) because few root tips were found with diameters > 1mm. One-way ANOVA with Tukey post hoc tests described the group effect at each diameter class as well as total RLD (0-2 mm) and RTD (0-1 mm).

4.3 Results

4.3.1 Two-species mixture and hydraulic conductivity

Overall there was a tree species and mixture effect on K_{fs} ($F_{(1,4)} = 3.403$, $p = 0.036$; Fig 4.1A). Field saturated hydraulic conductivity associated with *C. sativa* was more than two-fold greater ($p < 0.05$) when grown in admixture with *B. pendula* than when grown in monoculture. In contrast, when *F. excelsior* was grown in admixture with *B. pendula* no difference in K_{fs} was observed in comparison to the same species grown in monoculture. Assuming an expected median K_{fs} of each mixed species group lying between that of each species in monoculture, the expected median of *F. excelsior* – *B. pendula* (7.79 cm day^{-1}) is higher than the actual median (6.99 cm day^{-1}) but within the range, whilst the inverse is true for *B. pendula* – *C. sativa* (expected 5.62 cm day^{-1}; actual 7.72 cm day^{-1}). Species identity had no effect on soil porosity near the soil surface (0-0.05 m) or deeper in the soil (0.1-0.15 m).

The effect of tree species identity on FRB identified in monoculture (Chapter 3) is not replicated with species mixture (Main effects $F_{(1,4)} = 13.1$, $p<0.001$; Fig. 4.1B). No difference was found between FRB of *F. excelsior* and *B. pendula* grown in monoculture and when grown together. By contrast, stands of *B. pendula* – *C. sativa* have an additive benefit from co-location with a mean increase of total FRB of 47% and 268% compared with monoculture *B. pendula* and *C. sativa* respectively, demonstrating a significant increase from monoculture *C.*

sativa (p=0.05). Necromass, however, was unaffected by species identity or richness (Fig. 4.1C).

Vertical distribution of fine roots did not differ when species were grown in monoculture or in admixture with other species (Fig. 4.2). However, there was a monoculture/two-species effect on *F. excelsior* FRB density at 0 - 0.1 m ($F_{(6,21)}$ = 12.3, p <0.001) and at 0.1 - 0.2 m ($F_{(6,21)}$ = 4.750, p < 0.01) depths. Fine root biomass of the *F. excelsior* component of *F. excelsior – B. pendula* mixture decreased by 57% in the 0 – 0.1 m soil layer (p < 0.001) and 63% at 0.1 – 0.2 m soil layer (p < 0.05) compared with *F. excelsior* in monoculture (Figs. 4.2A & 4.2B). In contrast, FRB of *B. pendula* component in *F. excelsior – B. pendula* mixture was not significantly different than in monoculture at any depth (Figs. 4.2A & 4.2C). *Betula pendula* had similar distribution when grown in monoculture as in admixture with *C. sativa* (Figs. 4.2D, 4.2E, 4.2F). Proportionally, mean *C. sativa* FRB was evenly spread in monoculture (40%, 33%, 27% at 0-0.1, 0.1-0.2, 0.2-0.3 m depths) but in admixture was skewed towards the soil surface (52%, 19%, 29% at 0-0.1, 0.1-0.2, 0.2-0.3 m) (SI 4.1). However, variance of the vertical distribution of *C. sativa* in admixture was too large to denote a significant difference.

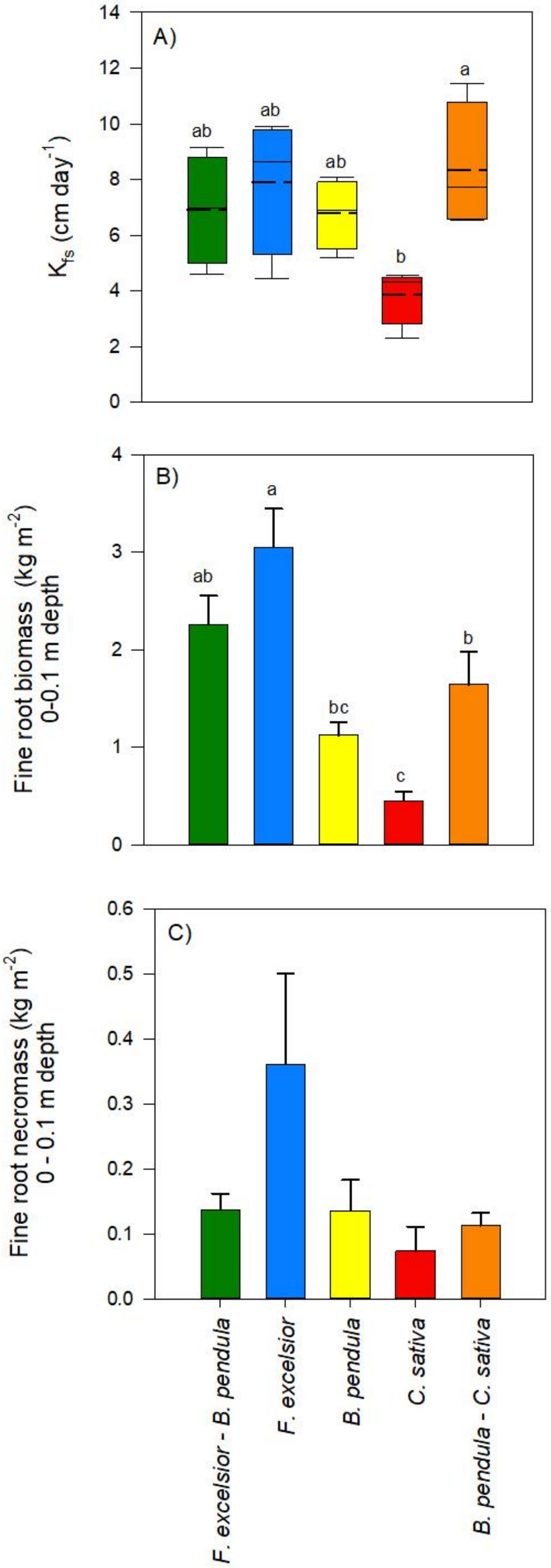

Figure 4.1. Field-saturated hydraulic conductivity (K_{fs}) (cm day-1) of two-species polyculture (*F. excelsior – B. pendula* & *B. pendula – C. sativa*) and in monoculture (*F. excelsior*, *B. pendula*, *C. sativa*) (A). Solid line is median, dashed line is mean. Main effect $F_{(4,15)} = 3.403$, $p < 0.05$. Species' mean fine root biomass (FRB) (B) and necromass (C) at 0-0.1 m soil depth. Main effects $F_{(4,15)} = 13.1$, $p < 0.001$. Post hoc multiple comparisons $p < 0.05$.

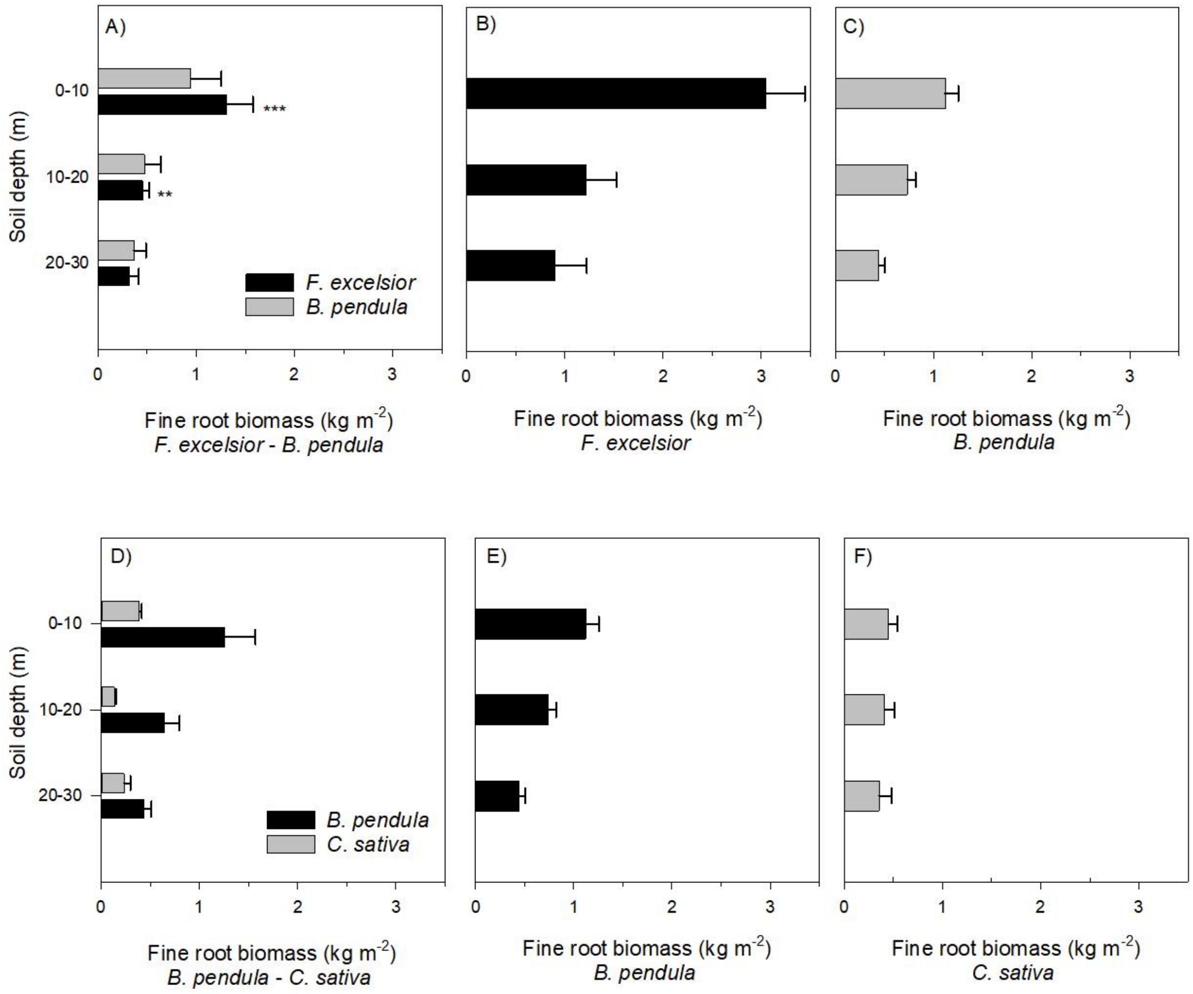

Figure 4.2. Vertical distribution of fine root biomass (FRB) of *F. excelsior* – *B. pendula* mix component parts (A) and species in monoculture (*F. excelsior* (B); *B. pendula* (C)). Panel D describes FRB of *B. pendula* and *C. sativa* when grown together and in monoculture (*B.* pendula (E), C. sativa (F)). *** $p < 0.001$, ** $p < 0.01$ species grown in admixture compared with monoculture.

4.3.2 Overyielding and net biodiversity effects.

Two-species mixed groups has a net biodiversity benefit to *B. pendula* and *C. sativa* but not to *F. excelsior* (Fig. 4.3). When co-located with *F. excelsior*, *B. pendula* FRB and RLD at 0 – 0.1 m depth (Fig. 4.3A) both overyield by 137% but when co-located with *C. sativa*, *B. pendula* FRB overyields by 250%, a nearly two-fold difference from co-occurrence with *F. excelsior*. The more modest biodiversity benefit to RLD (167%) and RAI (179%) (SI 4.2) suggests that the morphology of the additional fine roots produced are different from those in monoculture.

Castanea sativa also benefits from polyculture, despite facing competition from a more prolific producer of fine roots (*B. pendula*). The biodiversity benefit to *C. sativa* FRB (145%) is not matched by RLD (100%) and RAI (55%) signifying root morphological change in response to polyculture. *Fraxinus excelsior* exhibits net negative biodiversity effects for FRB (-28%), RLD (-19%) and RAI (-22%) but SRL, SRA overyield considerably with a net biodiversity effect of 221% and 211% respectively (SI 4.2). Root branching is positively associated with admixture at 0 – 0.1 m depth, denoted by a net biodiversity gain in RTD for all species, but *B. pendula* and *C. sativa* experience a much more substantial gain (168-179%) than *F. excelsior* (21%). Small negative selection effects are offset by large complementarity benefits driving overall net yield gain in *B. pendula* and *C. sativa* at 0 – 0.1 m depth (Fig. 4.3B). Both species benefit from complementarity in all matrices, with *B. pendula* exhibiting the greatest yielding effects. Mixed planting is to the detriment of *F. excelsior* compared with monoculture here, with selection effect under-yielding in all matrices apart from a small benefit to RLD of 4%. Similarly, competition from *B. pendula* has a negative effect on FRB (-15%) and RLD (-22%) but delivers a positive yielding effect on RTD (62%).

Deeper in the soil, the net biodiversity benefits are reduced (Fig. 4.3C). *Fraxinus excelsior* and *C. sativa* underyield at 0.1 - 0.2 m depth when grown with *B. pendula* in FRB (-1% & -66%), RLD (-24% & -50%) and RTD (-41% & -19%). Functional root traits of *B. pendula* mixed with *F. excelsior* demonstrate a mixed response to co-location, overyielding FRB (59%) but not RLD (-25%) or RTD (-14%). However, co-location with *C. sativa* is advantageous, overyielding 151%, 45% and 49% in FRB, RLD and RTD respectively. Selection has a small negative effect deeper in the soil for all species and positive complementarity benefits to *B. pendula* only, grown with *F. excelsior* (FRB 81%, RLD 12%) and with *C. sativa* (FRB 164%, RLD 59%, RTD 57%) (Fig. 4.3D). Biodiversity yield benefits *B. pendula* and *C. sativa* grown in admixture (16% - 206%) in the deepest soil layer (0.2-0.3 m) but not *F. excelsior* (FRB -39%, RLD -41%, RTD -52%) (Fig. 4.3E). Selection disadvantages all species (apart from small gain for *C. sativa* RTD 8%) but complementarity drives overall benefit, particularly *B. pendula* FRB grown with *F. excelsior* (123%) and *C. sativa* (206%) (Fig. 4.3F). Negative selection effects for almost all root traits across all species indicate that species-specific performance is reduced when mixed. However, the interaction between species in polyculture (complementarity) is beneficial to *B. pendula* and *C. sativa* but not *F. excelsior*.

4.3.3. Diameter class distribution

Fine root morphological change in response to competition is also species- and co-species-specific (Fig. 4.4). Overall, monoculture-grown species had significantly more RLD ($p < 0.001$ – $p < 0.05$) than in two species mix in 16 out of the 20 diameter classes (i.e. not 0-0.0., 0.01-0.02, 0.12-0.13, 0.13-0.14 mm classes) (SI 4.3). However, an interaction effect of species and configuration was evident at three diameter classes only (0.7-0.8, 0.8-0.9, 0.9-1.0 mm; SI 4.3) with *F. excelsior* the only species' RLD that was significantly reduced by growing in admixture ($p < 0.05$) at these diameter classes, as well as in total (i.e 0-2 mm diameter) ($p < 0.05$). Within each species pair, *F. excelsior* RLD produced more RLD than *B. pendula* in the smaller diameter classes (0.02-0.03, $p < 0.01$; 0.03-0.04, $p < 0.05$), but was very similar from ~0.8 mm diameter and larger (Fig. 4.4A). Average *B. pendula* RLD was greater than *C. sativa* in three diameter classes (0.05-0.06, $p < 0.05$; 0.07-0.08, $p < 0.05$; 0.08-0.09, $p <0.05$), but the distribution shape of each component species was similar up to 1.2 mm (Fig. 4.4B).

Root tip density reduced in admixture in the 0.7-0.8 mm diameter class ($F_{(1,18)} = 5.246$, $p < 0.05$) only. Interactions between tree species and configuration were evident in four diameter classes (0.2-0.3, 0.3-0.4, 0.4-0.5, 0.6-0.7) (SI 4.4), but no individual species' RTD in admixture was different to that in monoculture at each diameter class or in total. Root tip density associated with *F. excelsior* was almost an order of magnitude more than *B. pendula* in 2 diameter classes (0.2-0.3, & 0.3-0.4 mm, $p < 0.05$) (Fig. 4.4C), but *B. pendula* had significantly more RTD than *C. sativa* in three diameter classes (0.2-0.3, $p < 0.05$; 0.5-0.6, $p < 0.05$; 0.6-0.7, $p < 0.01$) (Fig. 4.4D).

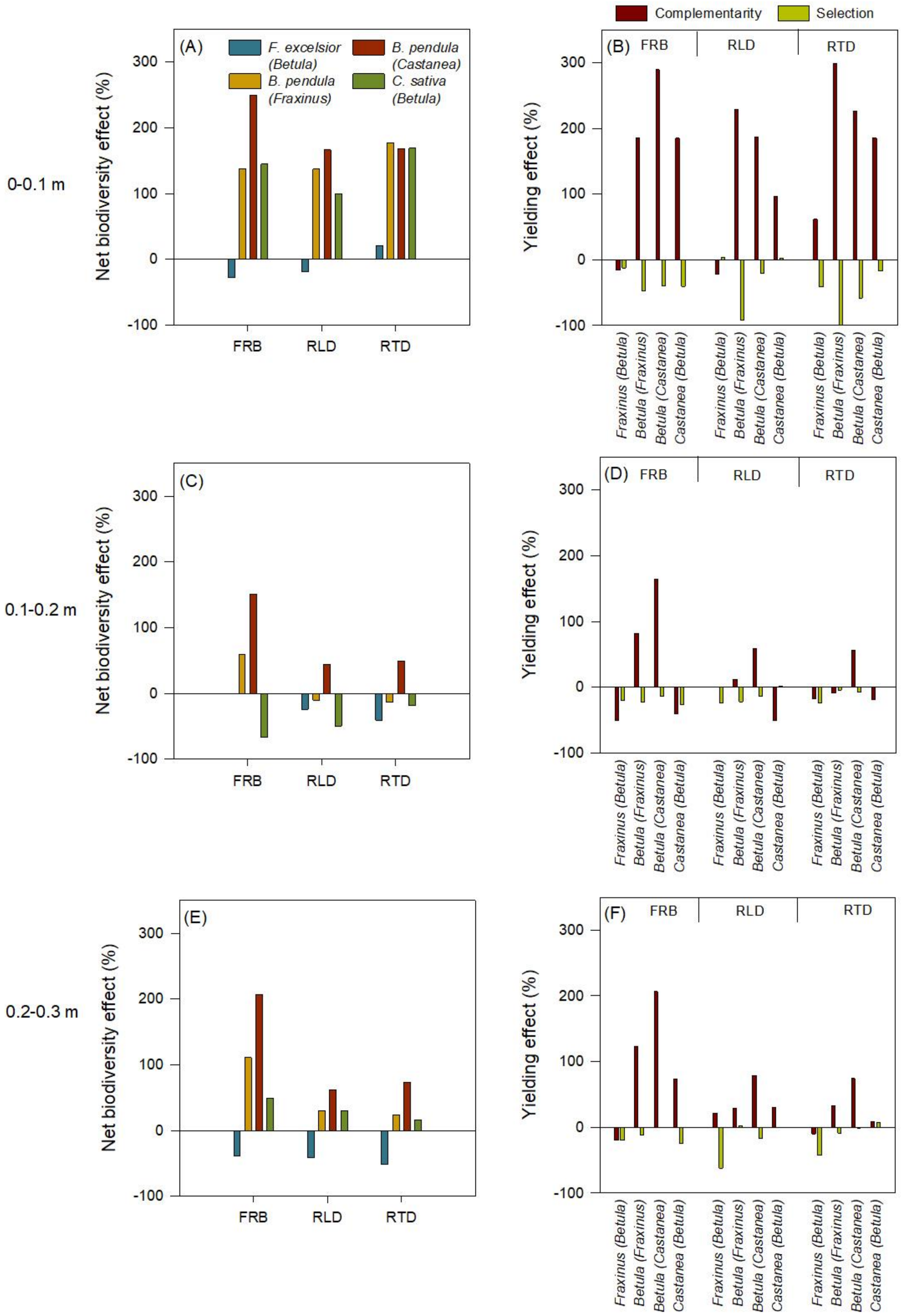

Figure 4.3. The net biodiversity effect on fine root morphological traits (FRB – fine root biomass, RLD – root length density, RTD – root tip density) performance of each species in two-species stands compared with monoculture at 0-0.1 m (A), 0.1-0.2 m (C), 0.2-0.3 m (E) depths and the relative contributions of complementarity and species selection at 0-0.1 m (B), 0.1-0.2 m (D), 0.2-0.3 m (F) depths. Genus names of co-located species are given in brackets. Positive values indicate over-yielding, negative values indicate under-yielding.

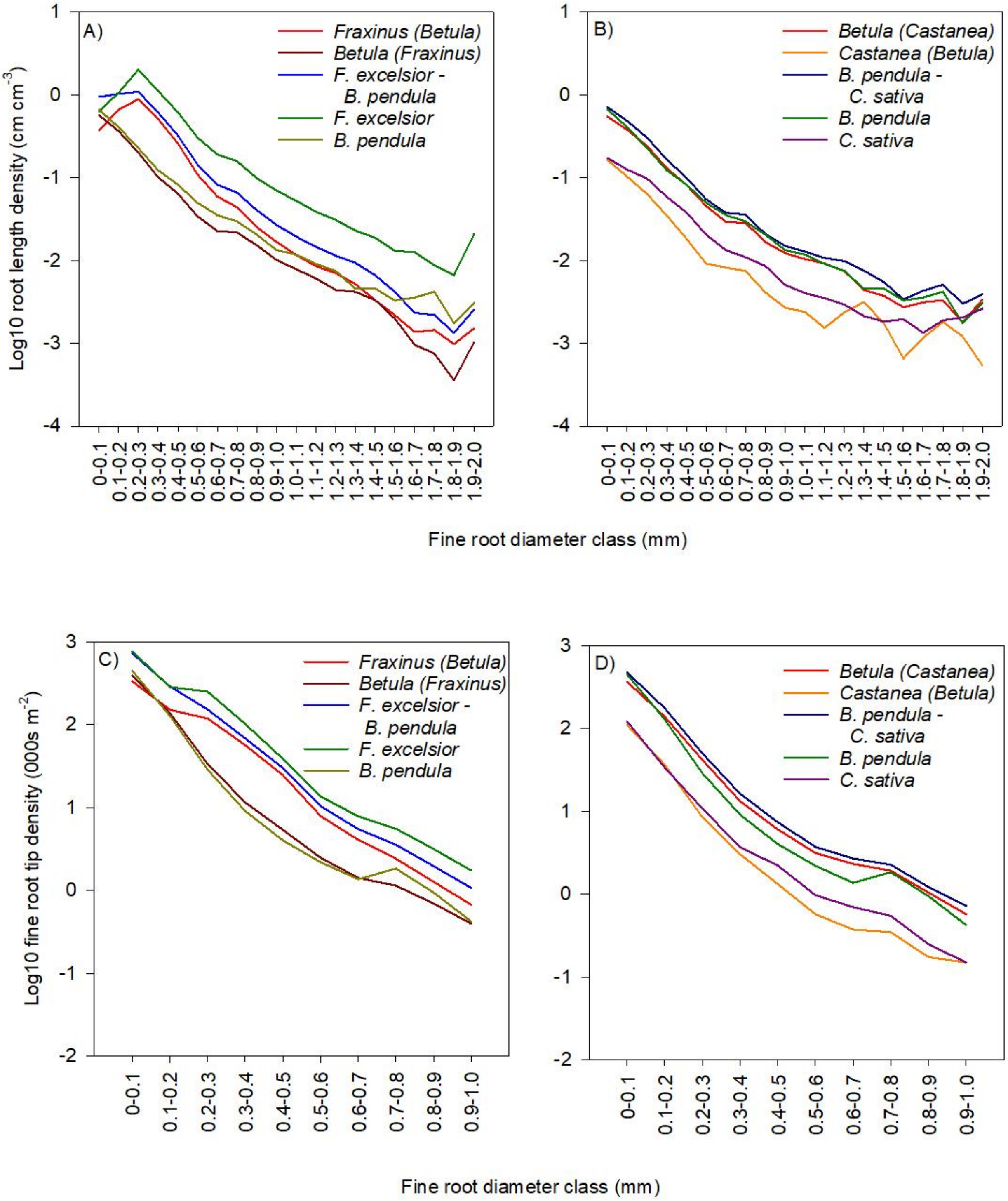

Figure 4.4. Mean root length density (RLD) of *F. excelsior – B. pendula* (A) and *B. pendula – C. sativa* (B) mixed stands over 20 root diameter classes (0 – 2 mm). Mean root tip density (RTD) *F. excelsior – B. pendula* (C) and *B. pendula – C. sativa* (D) over 10 root diameter classes (0 – 1 mm). Each species in the mix is denoted by its genus name with the genus of the co-located species in brackets. Figures also show the total volume of the component species combined (i.e. *F. excelsior - B. pendula* & *B. pendula – C. sativa*) and is compared against monoculture density of each species.

4.3.4 Soil structure and water retention

Soil water retention curves indicated that soil water content was similar throughout the measured soil potential range (1 – 10000 cm), but was ~5% higher and outside the margin of error when *F. excelsior* was grown in mixture with *B. pendula* than all other species and mixtures at potentials ranging between 1 and 100 cm (Fig. 4.5A). Species grown in mixture had very similar soil water content through the soil potential range at 0.1 - 0.15 m soil depth but tended to have higher soil water content (~4%) than in monoculture between 10 and 1000 cm potentials (Fig. 4.5B).

Both monoculture and mixed tree species follow a bimodal pore size distribution. The abundance of macropores (pore size radius > 0.075 mm) at 0 - 0.05 m depth (Fig. 4.5C) follows the same rank order as FRB (*F. excelsior*, *F. excelsior – B. pendula*, *B. pendula – F. excelsior*, *B. pendula*, *C. sativa*) with the notable exception of mixed *F. excelsior* - *B. pendula*, which has the least macropore abundance and is consequently more unimodal. Deeper in the soil (0.1 – 0.15 m depth) (Fig 4.5D), both single and mixed species exhibit much more variation in micro- and mesopores sizes. All species in monoculture exhibit very similar macropore abundance at this depth and are all more abundant than mixed species.

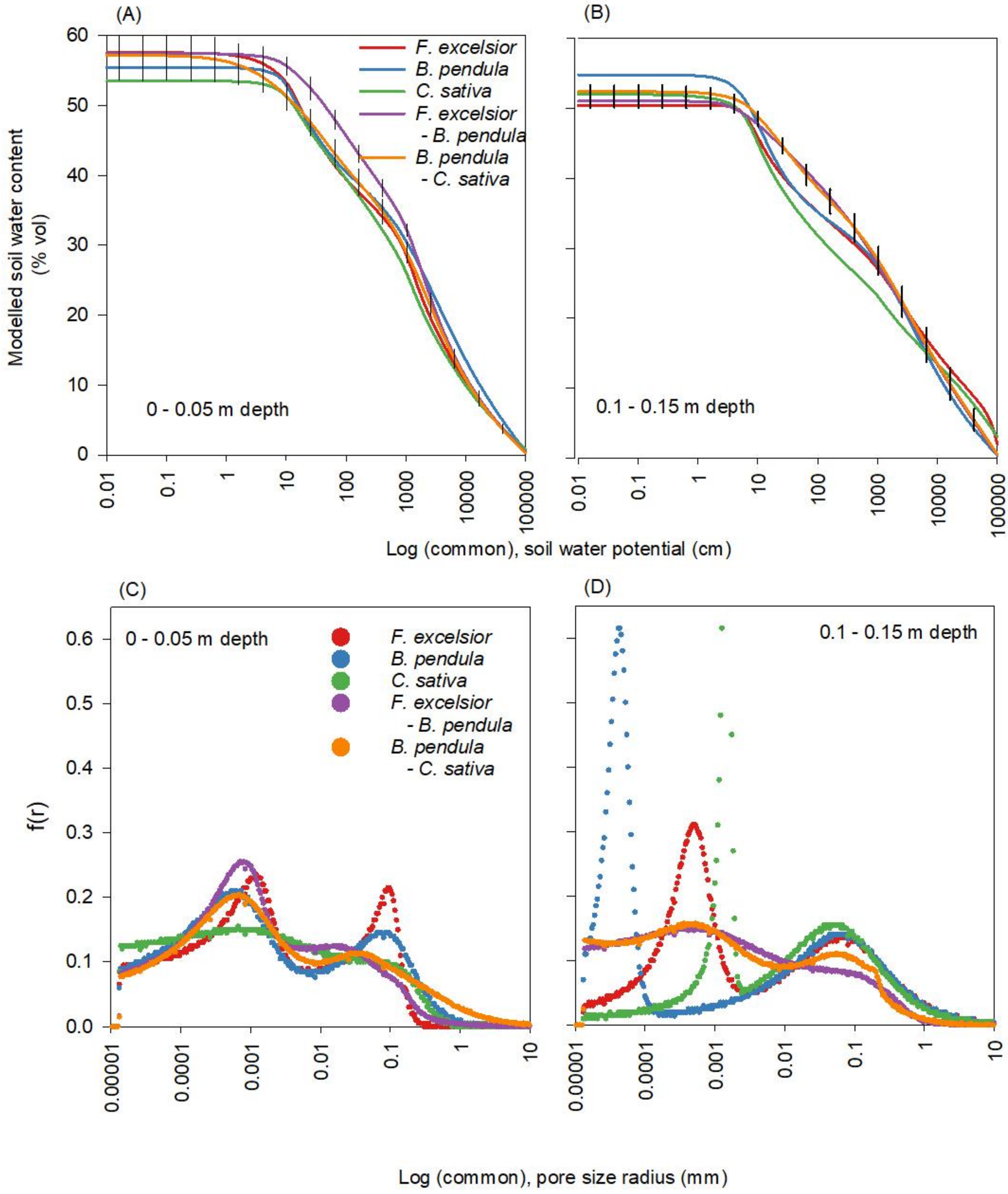

Figure 4.5. Mean soil water retention curves (SWRC) for three tree species in monoculture (*F. excelsior*, *B. pendula*, *C. sativa*) and polyculture (*F. excelsior – B. pendula* & *B. pendula – F. excelsior*) at (A) 0-0.05 m and (B) 0.01-0.15 m depths. The data are modelled using the bimodal Fredlund-Xing PDI model using measured soil water content (HYPROP) data. Modelled effective pore size radius distribution (Blonquist et al., 2006), displayed on a common log scale, for monoculture and polyculture tree species at (C) 0-0.05 m and (D) 0.1-0.15 m depths. The pore size distribution (f(r)) represents the proportional volume of the combined effective pore size radii. Standard error is displayed for mixed species SWRC with vertical black lines.

4.4 Discussion

4.4.1 Tree mixture effects on hydraulic conductivity

In our study, species identity and the functional root traits of tree individual species was found to be more important to soil hydraulic function than species richness *per se*. In monoculture, FRB near the soil surface (0-0.1 m depth) was correlated with K_{fs} (Chapter 3). Hydraulic conductivity measured under the same species grown in monoculture and in admixture with one other species was within the same margin of error, however, the small but significant effect on K_{fs} associated with *C. sativa* indicates a species identity interaction effect. Co-location of *B. pendula* and *C. sativa* has an overyielding effect on fine root traits, resulting in an additive K_{fs} that is greater than component species grown in monoculture due to positive net biodiversity effects on all root traits of both species. Hydraulic conductivity was highest in *F. excelsior* in monoculture, but there was no significant difference in K_{fs} between the *F. excelsior – B. pendula* mixture, or the component species grown in monoculture. This can be explained by the negative net biodiversity effect on *F. excelsior* FRB and RLD offsetting the positive net biodiversity effect on *B. pendula*.

4.4.2 Overyielding effects

Fine root biomass of *F. excelsior* underyields when grown in admixture with *B. pendula* whereas the FRB of *B. pendula* and *C. sativa* overyields when grown in mixture with each other. Modest selection effect yield loss of all root traits at every depth are largely offset by substantially greater complementarity benefits to *B. pendula* in both tree mixes and *C. sativa*, but *F. excelsior* gains nothing (apart from root tips) from competition with *B. pendula*. Our results contrast with Jacob et al. (2014) who identified *F. excelsior* as a key species in a mixed *Fagus sylvatica* L., *Carpinus betulus* L. *Tilia cordata* Mill., *Acer pseudoplatanus* L, *F. excelsior* woodland with 30% higher fine root productivity in treatments associated with *F. excelsior* than with other species. They hypothesise that species with high root productivity in monoculture dominate total root productivity in mixed stands (i.e., a selection effect), rather than species richness. Our results strongly disagree that selection determines root productivity as we have shown that growing *F. excelsior*, a prolific producer of FRB in monoculture, in admixture with *B. pendula* resulted in competition for resources and a lower overall FRB. In contrast, the mutualistic relationship of *B. pendula* (high FRB in monoculture) and *C. sativa* (low FRB in monoculture) resulted in a positive complementarity effect and overyielding of FRB that concurrently increased K_{fs}. This demonstrates that species identity is not the key determinant of fine root productivity in mixture, but rather to maximise the benefit of mixing species it is necessary to understand the functional traits of the species and select only species possessing contrasting functional traits to maximise complementarity and overyielding potential.

4.4.3 Vertical stratification and morphology of roots

Selection effects reduce the overall *F. excelsior* biomass in mixture, explaining the significant FRB reduction from monoculture in the top two soil depths. In response to co-location with *B. pendula*, *F. excelsior* fine root vertical distribution was inelastic. Fine root biomass density maintained the same vertical distribution proportionately but produced fewer roots down to 0.2 m depth. Our results contradict Rust and Savill (2000) who found that *F. excelsior* responds favourably to competition (*F. sylvatica*), by spreading fine roots more evenly through the soil profile, conferring an advantage by improving access to water. *Betula pendula* too maintained the same vertical distribution as in monoculture, but benefitted from the relationship, overyielding FRB, RLD and RTD particularly where the majority of fine root is located (0-0.1 m depth, ~47% of the total FRB), giving *B. pendula* the advantage. *Fraxinus excelsior* and *B. pendula* are both early to intermediate successional species (Beck et al., 2016a, 2016b). As such, they are both shallow rooting, rapidly exploiting the resources available near the soil surface to become quickly established. Both species are in competition for the same resources, concentrating fine root growth in the same soil space. *Castanea sativa* is, in contrast to *B. pendula*, a slower growing and later successional species (Conedera et al., 2016), with contrasting fine root morphological traits.

Competition from species diversity has been shown to increase fine root production in boreal mixed forests, which was partially attributed to a diversion of resources from aboveground to belowground (Ma et al., 2019). However, our results indicate that belowground response to competition is more nuanced, with root morphological response contingent upon the functional traits of each constituent species.

Species in the *B. pendula* – *C. sativa* admixture displayed a mutualistic relationship, evidenced by the extent of net biodiversity benefit to all root functional traits of both species in the same soil space (0-0.1 m). *Betula pendula* maintained similar vertical FRB distribution in admixture as in monoculture. Vertical distribution of *C. sativa* FRB was relatively homogenous in monoculture, but tended to skew towards the 0-0.1 m soil depth in admixture (SI 4.1) to the detriment of FRB at 0.1-0.2 m soil depth, concentrating the majority, on average, of both species' FRB (~52 %) near the soil surface. However, large variance in *C. sativa* FRB vertical distribution prevented observation of any overall significant difference at each soil depth between monoculture and admixture indicating that 0.1 m soil depth categories may be too coarse to distinguish nuanced vertical root response. Niche differentiation, therefore, may be occurring within each depth category providing advantageous resource partitioning and accounting for the additive effect on yield from being grown together. Contrary to our results, Valverde-Barrantes et al. (2015) found that species identity was unrelated to niche differentiation, observing all species foraging equally in resource rich areas, despite variance in FRB. Instead, they explain disparity in fine root biomass production in mixed stands as the result of phylogenetic diversity amongst constituent species, with trees that share genetically-related evolution overyielding FRB, which cannot explain the mutualistic relationship displayed by unrelated species (i.e., *B. pendula* and *C. sativa*) in this study. Changes to functional root traits influences the soil structure associated with each species. A reduction in RLD, particularly in *F. excelsior*, may explain the lower abundance of macropores in *F. excelsior – B. pendula* stands. Macropores develop around growing roots as the proportionally larger root tip physically creates a soil channel and sloughed root exudates strengthen the channel walls (Bengough, 2012). Macropores associated with root channels, therefore, may increase in size as root diameter increases. Root length density of *F. excelsior* is strongly skewed towards the smaller diameter classes, whilst the opposite is true of *B. pendula*. Whilst this may have had little effect on total macropore abundance associated with *F. excelsior* in monoculture where total FRB was significantly more than other species, the significant reduction in FRB and RLD in admixture limits macropore abundance relative to other species. The largest biodiversity benefit to SRL and SRA was observed in *F. excelsior* at all three depths indicating that more biomass was allocated to finer diameter roots. The *F. excelsior* fraction accounts for more than half the total biomass of *F. excelsior – B. pendula* mix and therefore may have a disproportionate effect on macropore abundance and water retention. The RLD of *C. sativa*, although less than *B. pendula*, follows roughly the same distribution across the diameter classes. The combined larger diameter roots may be responsible for greater abundance of macropores relative to *F. excelsior – B. pendula* mix, particularly macropores with > 0.1mm pore size radius. Fewer roots at depth (0.1 – 0.15 m) reduces overall macropore abundance and increases the influence of soil type relative to tree roots on hydraulic conductivity (Chapter 3). The magnitude of the mixed-species variation in soil water retention and macropore abundance is small but is consistent with the functional root trait data.

4.5 Conclusion

Hydraulic conductivity of soil can be maximised during afforestation through the selection of trees with contrasting functional traits. Species identity and competition, not richness regulates the fine root morphological response of trees grown in mixture. The contrasting functional traits of *B. pendula* and *C. sativa* result in a FRB overyielding effect in both species that significantly increased the K_{fs} associated with *C. sativa* grown in monoculture. Calculation of biodiversity effects suggest that *C. sativa* and *B. pendula* benefit from niche differentiation and/or a mutualistic relationship that result in overyielding of FRB, RLD and RTD, particularly near the soil surface (0-0.1 m depth). *Fraxinus excelsior*, a prolific producer of FRB in monoculture, yielded up to six-fold the FRB than monoculture *C. sativa* (Chapter 3), yet K_{fs} does not increase when *F. excelsior* is grown in admixture with *B. pendula*. The results show an interesting but small effect of species interaction rather than diversity *per se* on K_{fs}. This has implications for species choice in the management of tree planting schemes where hydrological regulation is a key objective. Further investigation with greater replication across a variety of species combinations would give greater confidence in extrapolation of the observed results.

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4.7 Supplementary information

S.I. 4.1. Proportion of fine root biomass (%) of *F. excelsior*, *B. pendula* and *C. sativa* grown in monoculture and each component species in admixture from three soil depths (0-0.1, 0.1-0.2, 0.2-0.3 m).

		Fine root biomass (%)		
		0-0.1 m	0.1-0.2 m	0.2-0.3 m
Monoculture	*F. excelsior*	60.89	22.57	16.54
	B. pendula	48.31	32.59	19.10
	C. sativa	39.88	33.10	27.02
Admixture	*F. excelsior*	61.97	23.22	14.81
	B. pendula	46.79	31.43	21.77
	Total *F. excelsior – B. pendula*	57.69	24.63	17.69
Admixture	*B. pendula*	52.67	27.03	20.30
	C. sativa	52.30	18.79	28.91
	Total *B. pendula – C. sativa*	52.82	24.86	22.33

S.I. 4.2. Net biodiversity effect (%) derived from additive partitioning of biodiversity effects (Loreau and Hector, 2001) of 6 fine root traits of *F. excelsior*, *B. pendula* and *C. sativa* planted in admixture at three soil depths (0-0.1, 0.1-0.2, 0.2-0.3 m). Genus of co-species is denoted in brackets. FRB = fine root biomass, SRL = specific root length, SRA = specific root area, RAI = root area index, RTD = root tip density, RLD = root length density

		Fine root morphological trait net biodiversity effect (%)					
		FRB	SRL	SRA	RAI	RTD	RLD
0 - 0.1 m	*Fraxinus* (*Betula*)	-27.75	220.81	210.59	-22.25	20.78	-18.50
	Betula (*Fraxinus*)	137.59	185.01	155.63	104.88	176.96	137.35
	Betula (*Castanea*)	249.72	134.33	135.17	178.65	167.75	166.61
	Castanea (*Betula*)	144.98	130.44	90.73	54.52	168.68	99.88
0.1 - 0.2 m	*Fraxinus* (*Betula*)	-0.62	271.90	200.55	-50.70	-40.80	-24.45
	Betula (*Fraxinus*)	59.02	100.22	126.62	1.30	-13.58	-10.18
	Betula (*Castanea*)	150.74	79.95	108.86	70.62	49.04	44.59
	Castanea (*Betula*)	-66.17	221.22	145.21	-83.29	-18.88	-49.64
0.2 - 0.3 m	*Fraxinus* (*Betula*)	-38.69	220.82	177.27	-52.70	-52.11	-41.11
	Betula (*Fraxinus*)	110.64	83.73	126.30	63.67	23.98	30.42
	Betula (*Castanea*)	206.24	66.02	117.37	107.39	72.94	62.00
	Castanea (*Betula*)	48.98	75.21	88.95	8.10	15.85	30.39

S.I. 4.3. Main effects of tree configuration and tree species on root length density of *F. excelsior*, *B. pendula* and *C. sativa* grown in monoculture and in 2 two-species mixtures (*F. excelsior – B. pendula* & *B. pendula – C. sativa*) over 20 diameter classes. Statistical significance is denoted by **p*<0.05, ***p*<0.01, ****p*<0.001.

	Tree configuration			Tree species		
Diameter class (mm)	df	F	*p*-value	df	F	*p*-value
0-0.1	1	2.952	0.102	2	0.482	0.625
0.1-0.2	1	2.267	0.149	2	0.608	0.555
0.2-0.3	1	5.804	0.026*	2	2.133	0.146
0.3-0.4	1	6.897	0.017*	2	2.227	0.135
0.4-0.5	1	8.191	0.010**	2	2.136	0.146
0.5-0.6	1	17.936	0.000***	2	3.513	0.050
0.6-0.7	1	13.932	0.001***	2	3.015	0.073
0.7-0.8	1	12.966	0.002**	2	5.338	0.014*
0.8-0.9	1	14.262	0.001***	2	4.205	0.031*
0.9-1.0	1	8.775	0.008**	2	4.050	0.034*
1.0-1.1	1	5.005	0.037*	2	2.998	0.074
1.1-1.2	1	4.988	0.038*	2	2.509	0.108
1.2-1.3	1	2.856	0.107	2	2.050	0.156
1.3-1.4	1	1.956	0.178	2	2.269	0.131
1.4-1.5	1	5.191	0.034*	2	1.773	0.197
1.5-1.6	1	8.939	0.008**	2	1.181	0.329
1.6-1.7	1	12.424	0.002**	2	2.181	0.140
1.7-1.8	1	8.308	0.010**	2	0.615	0.551
1.8-1.9	1	12.686	0.002**	2	0.623	0.547
1.9-2.0	1	22.626	0.000***	2	3.482	0.051

S.I. 4.4. Main effects of tree configuration and tree species and the interaction between configuration and species on root tip density of *F. excelsior*, *B. pendula* and *C. sativa* grown in monoculture and in 2 two-species mixtures (*F. excelsior – B. pendula* & *B. pendula – C. sativa*) over 10 diameter classes. Statistical significance is denoted by **p*<0.05, ***p*<0.01, ****p*<0.001.

	Tree configuration			Tree species			Configuration x species		
Diameter class (mm)	df	F	*p*-value	df	F	*p*-value	df	F	*p*-value
0-0.1	1	2.068	0.167	2	13.725	0.000***	2	3.116	0.068
0.1-0.2	1	0.352	0.560	2	28.534	0.000***	2	2.592	0.101
0.2-0.3	1	2.29	0.147	2	71.443	0.000***	2	4.734	0.021*
0.3-0.4	1	1.947	0.179	2	61.403	0.000***	2	3.852	0.039*
0.4-0.5	1	1.823	0.193	2	47.323	0.000***	2	4.308	0.029*
0.5-0.6	1	2.182	0.156	2	26.462	0.000***	2	2.053	0.156
0.6-0.7	1	3.314	0.084	2	38.222	0.000***	2	5.202	0.016*
0.7-0.8	1	5.164	0.035*	2	16.006	0.000***	2	0.775	0.475
0.8-0.9	1	2.046	0.169	2	18.692	0.000***	2	2.294	0.128
0.9-1.0	1	0.771	0.391	2	7.841	0.003**	2	2.753	0.089

Chapter 5 Abundance of air-filled soil pore space in hedgerows is increased by the presence of woody species and moderated by soil type

Bid Webb[1], David A. Robinson[2], Andrew R. Smith[1]

[1] School of Natural Sciences, Bangor University, UK
[2] UK Centre for Ecology and Hydrology, Bangor, UK

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Author contributions: BW and AS conceived and planned the experiments. BW collected field and laboratory data. Statistical analysis and interpretation of the results was conducted by BW under the supervision of DR and AS. BW led the writing of the manuscript and all authors provided critical feedback.

Abstract

Globally, agricultural intensification has reduced hedgerow cover and agroecological complexity, in turn reducing hydrological regulation. Hedgerows have been shown to improve infiltration, reduce erosion and provide sub-surface hydrological barriers in limited settings. However, broader evidence of hedgerow effects on soil hydraulic function is sparse and the influence of confounding variables such as soil type and time of year have not been widely considered. Here we investigate the influence of hedgerows in permanent pasture on soil structure, water storage capacity and hydraulic conductivity on two soil types with contrasting drainage (free draining (FD) and seasonally wet (SW)). The effect of time of year on air-filled pore space available for infiltration is considered as well as hydrological connectivity intersected by hedgerows. Soil matric potential and saturated hydraulic conductivity (K_{fs}) was measured at a depth of 0.08-0.13 m for one year 1 m and 10 m up- and downslope from a hedgerow on FD and SW soil types. To compare effects with an abiotic boundary, soil cores were taken at 0 - 0.05 m and 0.08 - 0.13 m depths from three transects perpendicular to a stone wall on the FD soil type and next to each tensiometer to derive soil water retention curves (SWRC). Soil porosity was unchanged by treatments, but the pore size distribution associated with hedgerows had greatly increased macropore abundance, making up 14-25% of total pore space compared with pasture (2-4%) and stone wall (9-14%). Soil was significantly drier ($p<0.05$) for ten months of the year than the adjacent pasture suggesting that the increased soil macroporosity under hedgerows was promoting faster drainage of soil water. At the FD site, vertical sub-surface flow dominated and no break in connectivity was

observed, whilst at the SW site the hedgerow interrupted consistent lateral sub-surface flow where improved drainage capacity facilitated vertical infiltration resulting in consistently drier pasture downslope. Our data suggests that hedgerows can create soil structural heterogeneity in the landscape to provide fill and spill zones that interrupt hydrological lateral flow paths, but the magnitude of change will depend on underlying soil type.

5.1 Introduction

Agricultural intensification globally has decreased agroecological diversity, in turn reducing soil and water quality, biodiversity and hydrological regulation (Tilman et al., 2001). Improving ecosystem function through increasing agroecological diversity can derive multiple ecosystem benefits from agricultural land (Palomo-Campesino et al., 2018). Anthropogenic climate change is increasing global air temperatures, with concomitant increases in the intensity and frequency of rainfall events as well as the likelihood of drought (IPCC, 2014). Effective hydrological regulation through for example, tree cover, is therefore imperative to maintain landscape resilience to extreme events. Hedgerows, once ubiquitous in agricultural landscapes, have been widely removed during the expansion and intensification of agriculture, halving in density in Belgium, France and United Kingdom, for example, during the 20th century (Deckers et al., 2005; Robinson and Sutherland, 2002; Walter et al., 2003). Defined as linear woody features, they can include both heavily managed (cut or bent to the desired shape) lines of trees and shrubs as well as lightly managed lines of mature trees or a combination of both (Baudry et al., 2000). Commonly, hedgerows are used as stock-proof boundaries and as such, stone walls are sometimes referred to as hedgerows in the literature (Kovář et al., 2011). Hedgerows may include in-field lines of agriculturally productive trees (alleys), which can be used for fodder, shelter and fuel whether in-field or boundary-grown (Quinkenstein et al., 2009; Vandermeulen et al., 2017).

Assessment of landscape-scale hydraulic regulation has predominantly been limited to different types of land use, particularly the potential role of woodland in promoting water infiltration, storage, and decreasing overland flow (Bathurst et al., 2018; Birkinshaw et al., 2014; Murphy et al., 2020; Robinson et al., 2013) with little attention paid to the hydraulic function of hedgerows or stone wall field boundaries. Hedgerows are thought to improve soil organic matter content, infiltration and above- and below-ground biodiversity (Holden et al., 2019; Tscharntke et al., 2005) whereas stone walls simply act as a physical barrier to surface run-off (Kovář et al., 2011), which can be important for reducing erosion. Individual trees and small tree features are likely to have greater edge effects than woodland, due to micro-climatic features (e.g. localised turbulence, temperature variation) enhancing evapotranspiration (Nisbet, 2005; Vanneste et al., 2020) and reduced competition enabling a more developed and extensive root network (Thomas et al., 2008). Infiltration rates have been shown to increase by 60 times compared to grazed pasture in hedgerows planted and established over two years in a livestock-excluded area (Carroll et al., 2004) and by 67 times after five years with a reduction in overland flow by up to 78% (Marshall et al., 2013). In mixed arable and pasture farming systems, soil associated with hedgerows exhibited significantly higher saturated hydraulic conductivity, taking on average an hour longer to saturate during rainfall events, regardless of the time of year (Holden et al., 2019). Roots of woody species have been shown to reduce both surface and sub-surface flow by altering soil structure and increasing macroporosity resulting in higher hydraulic conductivity (Ghestem et al., 2011; Chapter 3). In deciduous species, however, seasonality can affect soil hydrology through changes in leaf area (i.e. senescence and abscission) that reduces leaf interception of rainfall and stemflow, or physiologically through reductions in evapotranspiration (Nisbet, 2005). Contour-planted hedgerows can therefore act as a sub-surface barrier (Caubel et al., 2003; Ghazavi et al., 2008; Merot et al., 1999) where temporal hydrological function can be altered by species composition. Ghazavi et al. (2008) showed that soil in bocage, field boundary lines of mature trees in French hedgerow-pasture systems (Aviron et al., 2016), soil matric potential increases significantly away from the hedgerow (e.g. -800 cm within 1 m; 50 cm at 12 m away) illustrating the drying effect of hedgerow relative to pasture, with a delay to field saturation by up to three months. Where hedgerows are present, hydraulic conductivity can be interrupted by a soil moisture deficit that interrupts hydrological lateral flow (Caubel et al., 2003) and delayed rewetting can extend this period of disconnectivity into the winter season when the leaves of deciduous species have abscised (Ghazavi et al., 2008, 2011).

Existing research shows success of hedgerows in regulating hillslope hydrology in limited settings but empirical evidence to understand the effect of soil type, drainage, spatial and temporal variation at the sub-catchment scale is lacking (Rogger et al., 2017). Empirical studies assessing hydrological regulation of heavily managed hedgerows (e.g. flailed, laid, coppiced), typical of the UK is limited to few sites (e.g. Holden et al., 2019; Marshall et al., 2009, 2013). The role of stone walls, also common in parts of the UK, in influencing hydrology is poorly understood. Modelling approaches to assess the impact of small tree features on hydrological function are limited by a paucity of empirical data (Dadson et al., 2017) and lack fine-scale consideration of hedgerow cover as well as the interaction with soil drainage and seasonality on hydraulic function (Emmett et al., 2017; Ewen et al., 2013; Jackson et al., 2013).

Ultimately, resilience to extreme rainfall events is dependent on the soils capacity to infiltrate rainfall and reduce overland flow. Although limited by soil depth, the proportion of soil pore space available (i.e. air-filled) for infiltration of rainfall and sub-surface hydraulic connectivity is integral to landscape resilience. The objective of this study was to determine the impacts of seasonality upon the soil hydraulic properties of woody hedgerows in seasonally wet and free-draining soil types over the period of one year in north-west Wales, UK. Specifically, the study hypotheses were: (i) seasonality and soil type affect soil water storage capacity and air-filled pore space associated with woody hedgerows; and (ii) woody hedgerows increase hydraulic conductivity and interrupt hydrological connectivity across a hydraulic gradient.

5.2 Methods

5.2.1 Site description and experimental design

The study was conducted at two farms in the Conwy valley near the village of Ysbyty Ifan, North Wales, UK located at Bryniau Defaid (53.033457°, −3.747871°) and Eidda Fawr (53.037096°, −3.712010°) farms. The area is characteristic of Welsh upland farms with hedgerows or stone walls typically used as field boundaries to semi-improved permanent pasture (e.g. *Lolium perenne*, *Trifolium* spp.). Mixed sheep and beef cattle livestock farming predominate with the sward in some fields mechanically cut and removed in summer to provide winter silage (Table 5.1). The study area is situated in a maritime climate with high annual rainfall (~2500 mm), mid-range UK mean monthly temperatures (12 °C max, 6 °C min) (Ford et al., 2021) and predominantly S-SW winds.

Study sites were identified based on the presence of contour-planted hedgerows/stone wall with contrasting soil drainage types and are classified for this study as seasonally-wet (SW) or free-draining (FD) (Table 5.2). The Stagnogley (Stagnosol) soil afforded a seasonally wet site with a silty-clay texture and lower bulk density (0.64 g cm^{-3} ± 0.04) than the FD site (0.89 g cm^{-3} ± 0.04). Although similar in mineral soil texture (silty-clay loam), the free-draining Brown

Earth (Cambisol) had proportionally much lower mean organic matter content (~14%; SW site ~24%) in the pasture. Three boundaries were studied across the two locations; a hedgerow on seasonally-wet soil, a hedgerow on free-draining soil and a stone wall, as an abiotic boundary, on free-draining soil.

Table 5.1. Site and boundary characteristics at study sites across two study locations. SW = seasonally wet; FD = free-draining

Boundary category	**SW Hedgerow**	**FD Hedgerow**	**FD Stone wall**
Location	Eidda Fawr	Bryniau Defaid	Bryniau Defaid
Field boundary	Hedgerow	Hedgerow	Stone wall
Slope	~5-7°	~10°	~10°
Aspect	SE	SE	SE
Soil type[1]	Stagnogley	Brown Earth	Brown Earth
Drainage	Seasonally-wet, impeded	Free-draining	Free-draining
Altitude (MASL)	~270	~220	~220
Land use	Mixed grazing; sheep, beef cattle (May-June)	Mixed grazing; sheep, beef cattle (March-November)	Mixed grazing; sheep, beef cattle (March-November)
Silage cut	Yes (but not during study period)	No	No
Dominant hedgerow species	*Corylus avellana, Prunus spinosa*	*C. avellana, P. spinosa, Crataegus monogyna*	NA
Age	40 years	10 years	100 years
Size	W = 2 m, H = 2m	W = 1 m, H = 2m	W = 0.6 m, H = 1.2 m
Stock-exclusion fencing	Yes, both sides	Yes, both sides	No

[1] www.landis.org.uk/soilscapes/ (UK Soilscapes Soil Map)

Each hedgerow had livestock exclusion fencing on either side 2 m apart and were dominated by *Corylus avellana*, *Crateagus monogyna* (FD only) and *Prunus spinosa*. The hedgerow understorey largely consisted of *Urtica dioca* and *Galium aparine* (SW) and *U. dioca*, *Cirsium vulgare* and *Ranunculus repens* (FD), However, the older hedgerow at the SW site occupied more space between the livestock exclusion fencing than at the FD site, reducing the space available for ground cover to develop (Plate 5.1). Hedgerows were kept at approximately 2 m height and were managed by flailing (when sufficiently mature) every two years. No active management took place during the study period. The stone wall was approximately 0.6 m (W) x 1.2 m (H) with no stock exclusion fencing (Plate 5.2). Three transects were established that crossed perpendicular to each boundary, with four sample points at <1 m and 10 m both upslope and downslope from the boundary centre point (Fig. 5.1) over the period of one year (n=3). Measurements are grouped according to boundary and soil type (e.g. SW pasture) and where appropriate, further divided by location upslope or downslope of the boundary denoted by the abbreviation US (upslope) or DS (downslope). Data downslope of the stone wall (<1 m and 10 m) was compromised by stoniness, limiting soil core collection to fewer than three replicates for each treatment and soil depth (n=1, 0-0.05 m, n=2, 0.08-0.13 m). Meteorological data (rainfall (mm), temperature (°C) and wind speed (ms^{-1}) & direction) were collected using two Vantage Pro2 weather stations (Davis, Hayward, California) situated close to the study sites at each study location. Due to vandalism of the meteorological equipment at the FD site, the weather station was replaced with a tipping bucket rain gauge (Casella, Kempston, UK) for the final three months of the project (April – June). Missing rainfall data (18/10 – 28/11 and 15/03 - 27/04) was determined from rainfall data from SW site.

Table 5.2. Soil characteristics of the study sites (adapted from (Ford et al., 2021))

Soil type	**Seasonally wet (SW)**	**Free-Draining (FD)**
Soil classification (UK)	Stagnogley	Brown Earth
Soil classification (Worldwide)	Stagnosol	Cambisol
Soil texture	Silty-clay	Silty-clay loam
Sand / silt / clay (%)	0-20 / 40–60 / 40-60	0-20 / 40-73 / 27-40
Soil organic matter (%)[1]	24.41 ± 1.29	13.84 ± 0.61
pH	5.7 ± 0.1	5.5 ± 0.1
Bulk density (g cm^{-3})	0.64 ± 0.04	0.89 ± 0.04

[1] Field measurements taken during study

Plate 5.1 Free-draining hedgerow (FD hedgerow) (A) with insert showing space between the hedgerow and fence and (B) close up of the seasonally wet hedgerow (SW hedgerow) showing the hedgerow filling the available space behind the livestock exclusion fence, with insert of the same hedgerow and adjacent pasture.

Plate 5.2 Unfenced free-draining stone wall (FD stone wall) adjacent to double fenced free-draining hedgerow (FD hedgerow). The weather station recorded rainfall, air temperature, wind direction and speed above the influence of either boundary type.

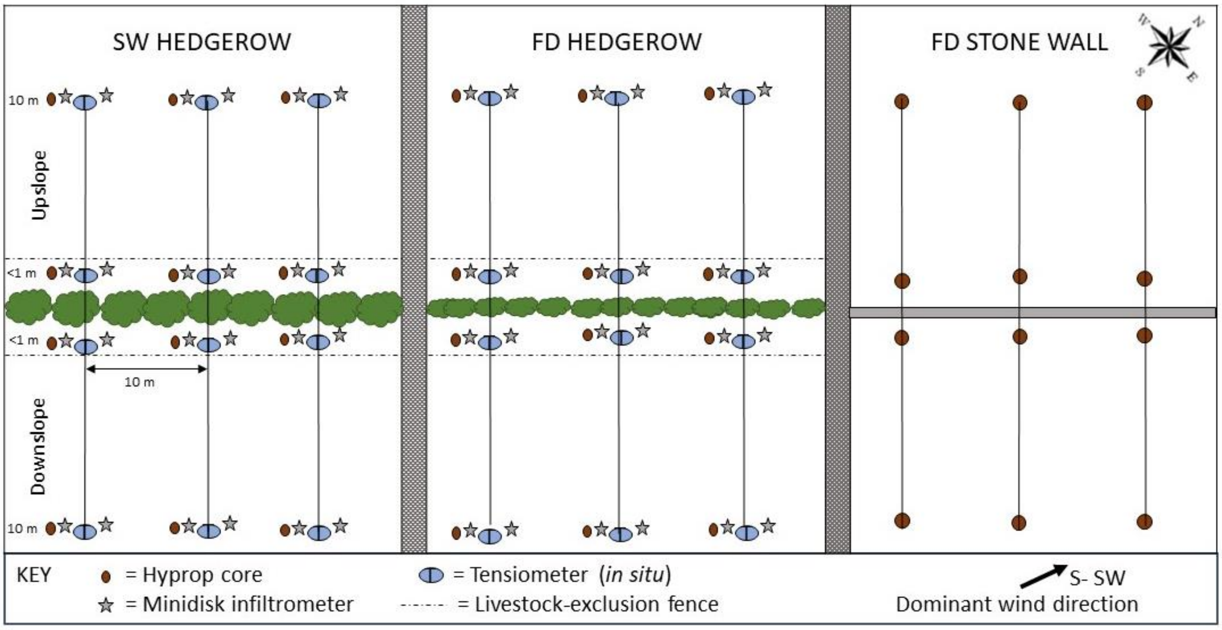

Figure 5.1. Experimental design at seasonally-wet hedgerow (SW hedgerow), free-draining hedgerow (FD hedgerow) and free-draining stone wall (FD stone wall) sites. Three replicate transects were established perpendicular with the field boundary, 10 m apart. Soil sampling took place along each transect within 1 m and at 10 m from the hedgerow centre point or stone wall edge, both upslope and downslope. In situ UMS Tensiometers installed at 0.08 – 0.13 m depth at four points along the hedgerow transects measured soil matric potential

every 30 minutes for one year. Two tension minidisk infiltrometers (-2 cm) measured infiltration and field-saturated hydraulic conductivity on either side of each tensiometer. Soil Hyprop cores were taken at two depths (0 – 0.05 m & 0.08 – 0.13 m depths) along all transects to determine soil water retention curves (SWRC) using the Hyprop 2 system. Dominant wind direction is southerly and south-westerly.

5.2.2 Soil water storage and movement

Soil cores were taken at 0 - 0.05 m and 0.08 – 0.13 m depths, two distances from the treatment; 1 m (within fencing, where applicable) and 10 m (in the pasture) from the hedgerows/stone wall. Soil cores were stored at 4 °C and soaked in deionised and degassed water for at least 24 hours prior to analysis. Soil water retention curves (SWRC) were measured using Hyprop 2 (Schindler et al., 2010) (Meter group, Pullman, USA). Oven-dried (105 °C) Hyprop cores were sub-sampled according to Lebron and Robinson (2003) to mitigate selection bias and used to obtain moisture retention values for the low end of the retention curve using the vapour equilibration technique (Scanlon et al., 2002). Soil organic matter (SOM) was estimated using Loss on Ignition (LOI) (Ball, 1964) analysis, utilising a muffle furnace and bulk density (BD) was estimated from change in moisture content of oven-dried (105 °C) soil. A change in technique to thermogravimetric analysis (TGA) was used part-way through to estimate both BD and LOI of the remaining soil samples. Repeated measurements of BD and LOI from different soils using both techniques ensured compatibility and replicability of both techniques. Two known standard soils and two replicates were included in each analysis for quality assurance. Oven-dried (105°C) soil samples were sieved to 2 mm and weighed to account for stone content when calculating BD, porosity, organic matter content and deriving SWRC.

The HypropFit (Schindler et al., 2010) (UMS, Munchen, Germany) implementation of the unconstrained van Genuchten bimodal PDI water retention model, weighted in favour of retention fit, was used to derive SWRC. The model was supported by dry BD, porosity, dry end matric potential and stoniness data. Data from each replicate were averaged to find mean plot values. Soil water storage capacity was estimated from the difference between water retention at field capacity (pF 2.6) and wilting point (pF 4.2). Effective soil pore size distribution was estimated using the method outlined by Blonquist et al. (2006). Hydraulic capacity was estimated using data from the SWRC (modelled in HypropFIT) to derive the change in moisture over the change in hydraulic head $(d\theta_v/dh)$. Hydraulic capacity was plotted as a function of pore radius. The scaled effective pore size distribution associated with each tree species was then derived by taking the inverse relationship between pressure (h) from the SWRC and log10 pore radius, resulting in a dimensionless, scaled, effective pore size distribution. The distribution is displayed as a function of effective pore radius ƒ(r) proportional to the abundance of each pore size within a given volume of soil.

To monitor soil matric potential, four 0.5 m UMS tensiometers (T4e) (METER group, Munchen, Germany) were installed *in situ* along each transect (Fig. 5.1). The tensiometers were inserted to a depth of 0.13 m allowing the 0.05 m porous cup to measure tension from 0.08 – 0.13 m depth. All tensiometers were connected to data loggers, which recorded matric potential every 30 minutes, and data were downloaded monthly. Tensiometers were protected from livestock damage by a plastic cage enclosure and grass within the cage was cut monthly to mimic grazing. To calculate available pore space, matric potential (kPa) was converted to pressure head (h) (1 cm h = 0.0980665 kPa), and pF calculated as log10 h. Actual water content (% vol) was deduced from the SWRC based on pF. Air-filled pore space (% vol) was calculated as the difference between saturated water content (i.e. water content where pF=-3) and actual water content (% vol). In order to account for differences in porosity across the treatments, the volume of actual air-filled pore space (cm^3) was estimated based on mean total porosity at 0.08-0.13 m depth.

Tension minidisk infiltrometers (METER Group, Pullman, USA) were used to measure infiltration and calculate field saturated hydraulic conductivity (K_{fs}). Field saturation, which accounts for occluded gas-filled pore space in large soil pores, occurs between field capacity (soil moisture at the conclusion of gravitational drainage) and saturation (all soil pore space filled with water) (Chandler et al., 2017). Tension was set at -2 cm limiting hydraulic conductivity to pore sizes less than 0.75 mm, excluding flow through the largest macropores. Two measurements were taken at each sampling point along the transects (either side of the tensiometers) at SW hedgerow and FD hedgerow sites (n=3 per site). To account for hydraulic conductivity through all soil pores, a SATURO Dual-head infiltrometer (Labcell, Alton, UK) was used to estimate K_{fs}. Although successful in FD pasture, measurement in FD hedgerow was discontinued as a stable 5 cm pressure head could not be achieved.

5.2.3 Statistical analyses

Data was organised in three ways; by 'site' (FD/SW), 'treatment' (hedgerow, pasture, stone wall) and 'group' (SW pasture, SW hedgerow, FD pasture, FD hedgerow, FD wall). One-way ANOVA with Tukey post hoc tests ($p < 0.05$) were used to individually investigate the effect of site, treatment and group on SOM, Porosity, SWSC at 2 depths (0-0.05 and 0.08-0.13 m) and surface K_{fs}. All data were assessed for normality using the Shapiro-Wilk test and homoscedasticity using Levene's test. Where homoscedasticity was violated (i.e. SWSC 0 – 0.05 m depth by site and treatment; SOM 0-0.05 by site), the Welch statistic and Games-Howell post hoc test was used. A multifactorial repeated measures ANOVA was used to explore the interaction between month, treatment, slope position and site (factors) on available pore space (dependent variable). The dependent variable was log-transformed to meet the assumption of normality. The data violated Mauchley's test of sphericity and so the more conservative Greenhouse-Geisser univariate test was used to determine within-subject effects to minimise Type I errors. All statistical analyses were performed using IBM SPSS Statistics 25 (IBM SPSS, Armonk, NY, USA).

5.3 Results

5.2.1 Soil structure and hydraulic conductivity

Soil porosity and organic matter content were within the range of values typical in Welsh soils across a range of land uses (Fig. 5.2). The SW site is distinguished from FD site by its greater SOM content at 0 - 0.05 m ($F_{(1, 11.69)} = 17.69$, $p = 0.001$) and 0.08 - 0.13 m ($F_{(1, 30)} = 28.629$, $p < 0.001$) depths (Fig. 5.3). The exponential relationship between BD and SOM is evident near the soil surface (0-0.05 m) both across all three treatments ($r^2 = 0.83$), as well as at site level (r^2=0.56, 0.71, 0.51 (FD hedgerow, SW hedgerow, FD stone wall). Yet, this relationship disappears at 0.08 - 0.13 m depth. Soil porosity did not differ between treatments (Fig. 5.4A), but did between groups ($F_{(4,31)} = 18.35$, $p < 0.001$). Total soil porosity (0-0.05 m), a function of BD, was significantly greater at SW hedgerow than FD pasture ($p < 0.001$), FD hedgerow ($p = 0.001$) and FD wall ($p < 0.01$) groups (Fig 4B), reflecting the higher overall SOM. Deeper in the soil (0.08-0.13 m), total soil porosity was greater at SW hedgerow than FD pasture ($p < 0.01$) and FD hedgerow ($p < 0.05$) only. Despite disparity in total porosity, there was no site effect on K_{fs}. Both treatments at SW were associated with similar K_{fs} but at FD, where porosity between treatments was comparable, K_{fs} was significantly higher in hedgerow than pasture ($p < 0.05$).

5.2.2 Soil Water Storage Capacity

Bimodal pore size distribution was evident at both hedgerow sites, with an abundance of macropores (>0.075 mm) associated with hedgerows (0-0.05 m), whilst micro- (< 0.03 mm) and mesopores (<0.075 mm) dominated the pasture (Fig. 5.5). The mean proportion of total pore space defined as macropores associated with the hedgerow at the FD site was 22% (US), 14% (DS), whereas pasture along the same transects had ~3% macropore abundance. Similarly, hedgerow macropore abundance at the SW site was 22% and 25% up- and downslope respectively, compared with 2-4% in the pasture. Mean macropore abundance made up 9% and 14% up and downslope adjacent to the FD stone wall and 5% and 10% up and downslope in the pasture. Macropore abundance in pasture varied with soil depth exhibiting a more bimodal distribution deeper in the soil (0.08 – 0.13 m), whereas distributions of hedgerow soil at two depths varied little (Fig 5A-D). Near to the soil surface, where the difference in macropore abundance between pasture and hedgerows is stark, no clear delineation in pore size abundance along the stone wall transects was observed, demonstrating relative homogeneity regardless of treatment (Fig 5E-F).

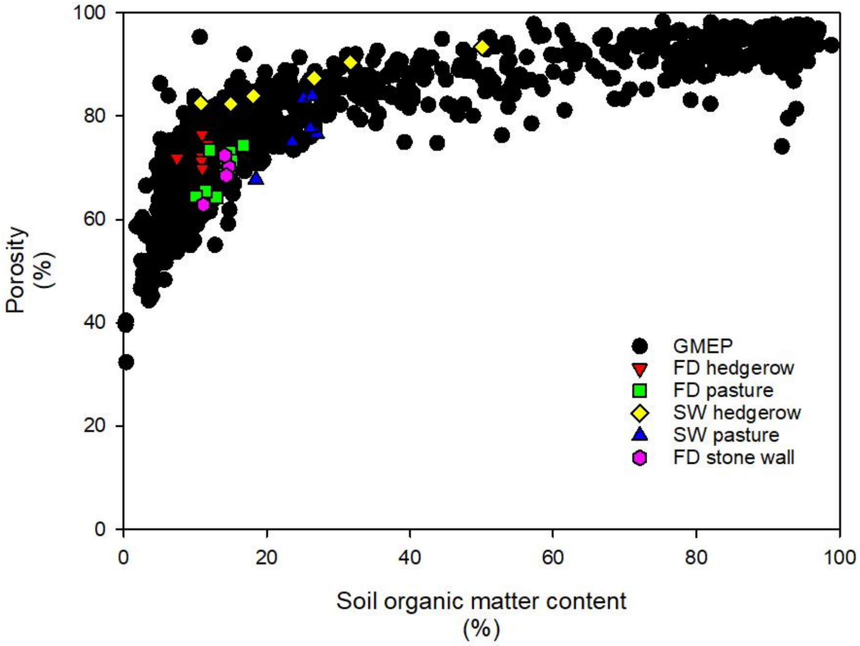

Figure 5.2. Soil porosity and organic matter content (0-0.05 m depth) from SW hedgerow, SW pasture, FD hedgerow, FD pasture and FD stone wall superimposed over Welsh soil data obtained during the Glastir Monitoring and Evaluation Programme (GMEP) 2013-2016 (0 – 0. 15 m depth)(Emmett et al., 2017).

Modelled SWRC in the top 0.05 m of FD hedgerow and FD pasture had similar retention at saturation but when pressure is applied, water retention drops sharply at FD hedgerow US and FD hedgerow DS by up to 20% and remains differentiated over three orders of magnitude (Fig. 5.6A). The SW hedgerow retained the greatest volume of water at saturation in the top 0.05 m, reflecting the significantly greater ($p < 0.01$) organic matter content here compared with FD hedgerow, FD pasture and FD stone wall (Fig. 5.2). When pressure is applied, soil water retention drops immediately by the hedgerow but remains unchanged in pasture over 2 orders of magnitude (Fig. 5.6C). Deeper in the soil (0.08 – 0.13 m), soil water retention becomes more homogenous with differentiation between hedgerow and pasture less apparent (Fig. 5.6B & 5.6D).

Variability of SWSC between the treatments is greatest in the top 0.05 m of soil with mean SWSC volume of 34%, 27% and 25% in the pasture, hedgerow and stone wall respectively (Table 5.3). No treatment effect was found at the SW site but more SWSC was observed in pasture than both hedgerow ($p = 0.001$) and stone wall ($p < 0.05$) at the FD site. In all cases, SWSC is reduced deeper in the profile (0.08-0.13 m) and values are similar.

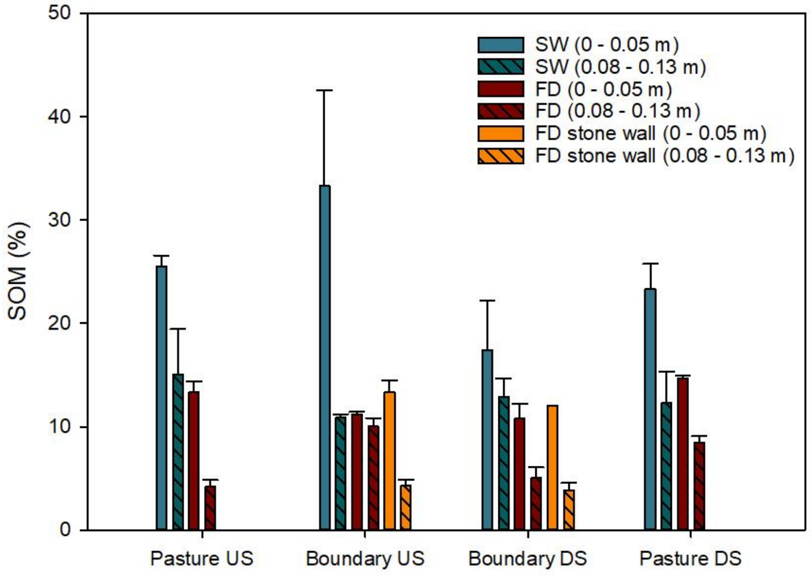

Figure 5.3. Mean soil organic matter (SOM) content % at seasonally-wet (SW), free-draining (FD) and free-draining stone wall sites at four points along each transect; 10 m upslope of the boundary in the pasture (Pasture US), <1 m upslope of the boundary (Boundary US), <1 m downslope of the boundary (Boundary DS), 10 m downslope of the boundary in the pasture (Pasture DS). Each measurement was taken at two soil depths; 0 – 0.05 m & 0.08 – 0.13 m. At each soil depth, SW site had significantly more SOM than FD (0-0.05 m, $p = 0.001$; 0.8-0.13 m, $p < 0.001$). No overall treatment effect on SOM content was identified.

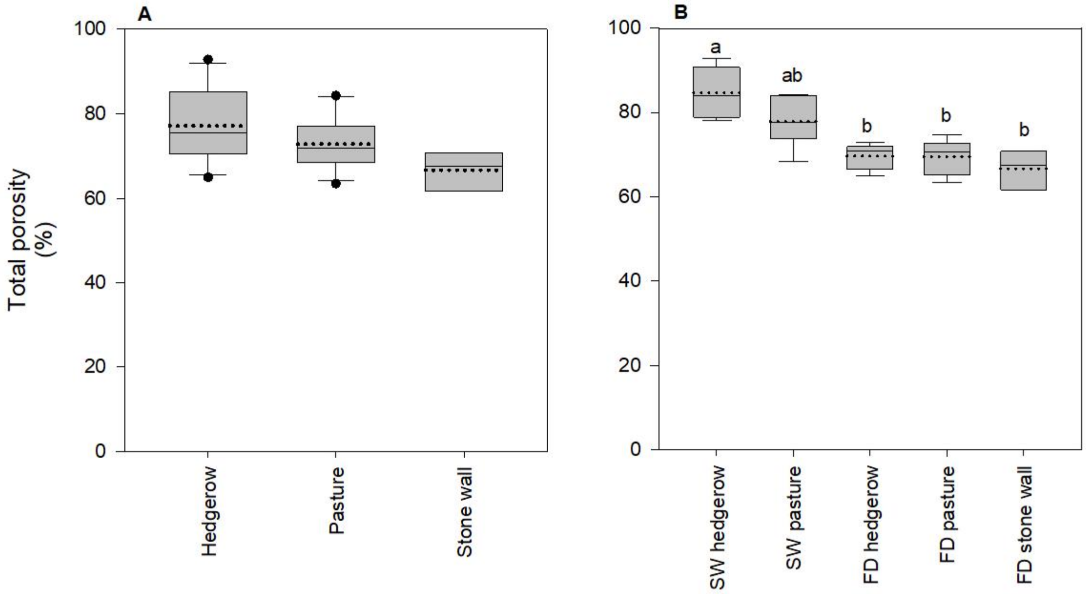

Figure 5.4. Total porosity (%) of soil at 0-0.05 m depth within 1 m of the boundary (i.e. next to hedgerow/stone wall) and 10 m from the boundary (i.e. in the pasture). Panel A shows porosity grouped by boundary type and panel B shows total porosity grouped by treatment

(upslope + downslope) at each site. Solid horizontal lines show the median and dashed horizonal lines show the mean. Statistical significance is denoted by letters ($p < 0.01$). SW = seasonally wet, FD = free-draining.

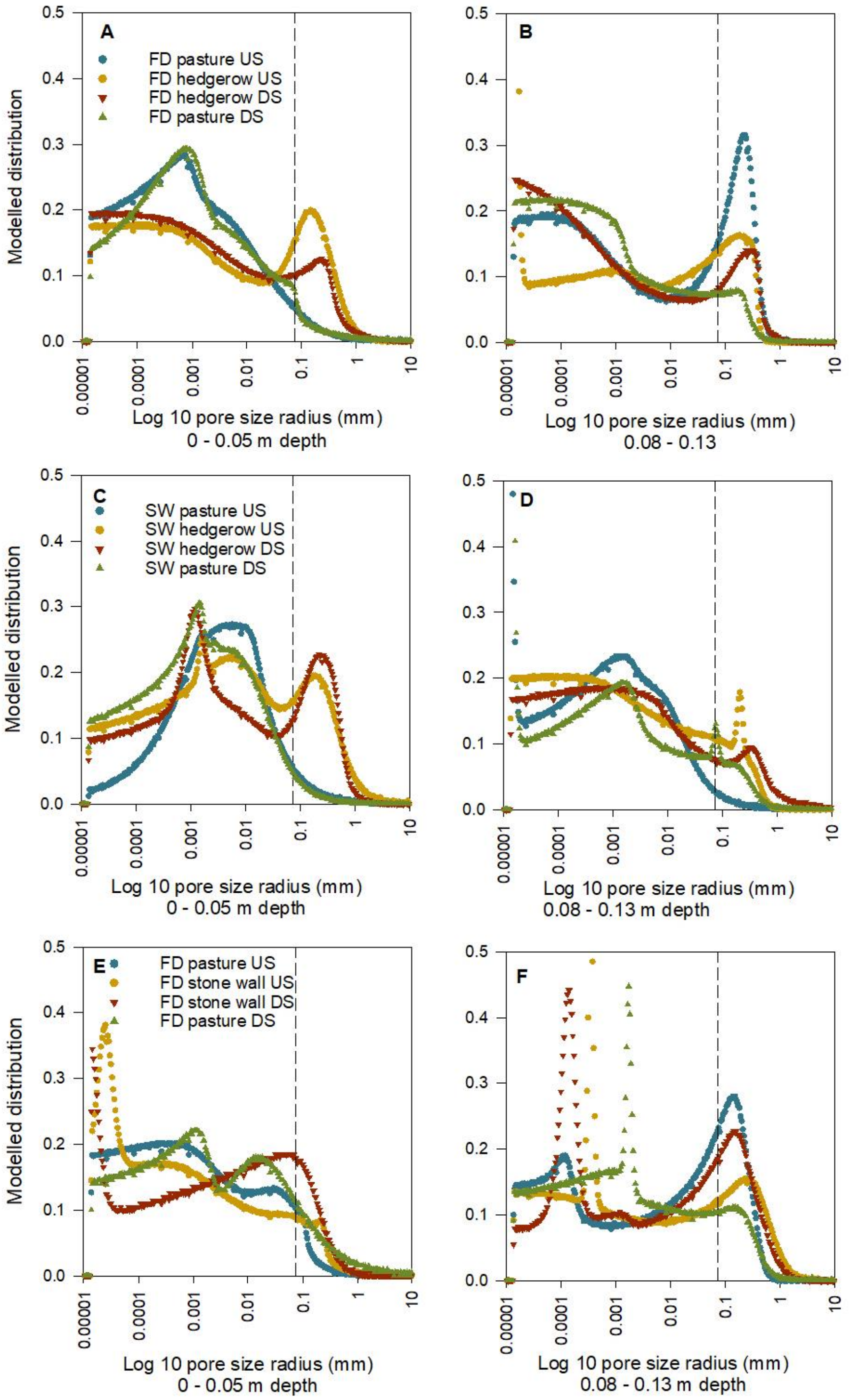

Figure 5.5. Modelled pore size distribution (log10) (mm radius) at two soil depths (0-0.05 m & 0.08-0.13 m) 10 m upslope from boundary in the pasture (pasture US), within 1 m upslope of boundary (hedgerow/stone wall US), within 1 m downslope of the boundary

(hedgerow/stone wall DS) and 10 m downslope from the boundary in the pasture (pasture DS). FD = free-draining site (5A & 5B; 5E & 5F), SW = seasonally-wet site (5C & 5D). Values to the right of the dashed vertical line indicate macropore radius sizes (> 0.075 mm).

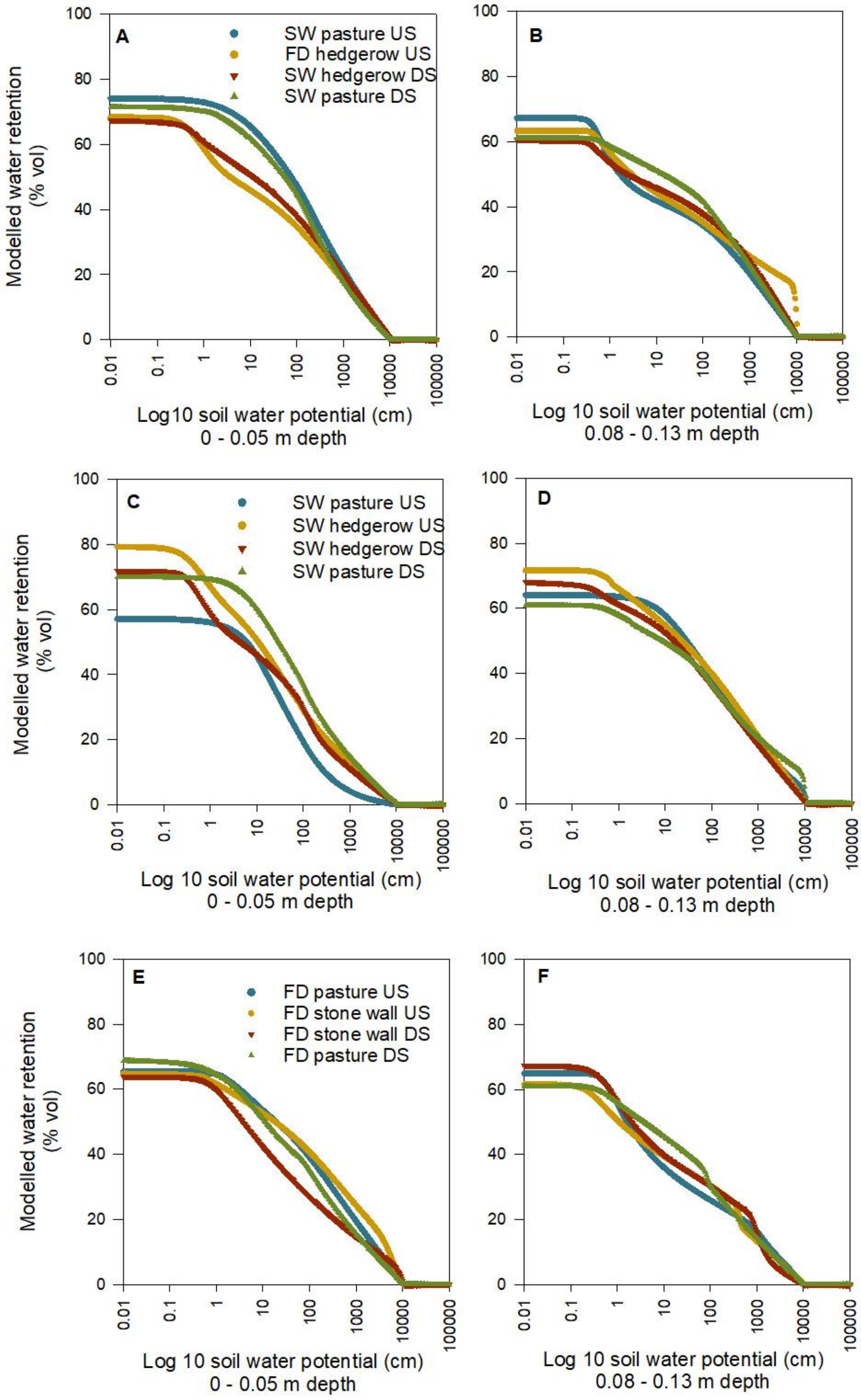

Figure 5.6. Modelled soil water retention curves (SWRC) at two soil depths (0-0.05 m & 0.08-0.13 m) 10 m upslope from boundary in the pasture (pasture US), within 1 m upslope of

boundary (hedgerow/stone wall US), within 1 m downslope of the boundary (hedgerow/stone wall DS) and 10 m downslope from the boundary in the pasture (pasture DS). FD = free-draining site (6A & 6B; 6E & 6F), SW = seasonally-wet site (6C & 6D).

Table 5.3. Soil water storage capacity (SWSC) indicating the difference in water retention (% volume) at field capacity (pF=2.6) and wilting point (pF=4.2), derived from modelled soil water retention curves (SWRC). SW = seasonally wet, FD = free-draining. Main effects across both sites ($F_{(2, 10.34)} = 6.07$, $p = 0.018$) was driven by a pairwise site effect at FD, denoted by letters, between pasture and hedgerow ($p = 0.001$) and pasture and stone wall ($p < 0.05$) at 0-0.05 m soil depth.

Site	Treatment	Mean SWSC (%)	
		0 – 0.05 m	0.08 – 0.13 m
SW	Pasture	31.18	29.03
	Hedgerow	28.31	29.51
FD	Pasture	35.30^a	23.37
	Hedgerow	26.52^b	19.28
	Stone wall	23.94^b	24.01
Both	Pasture	33.58^a	26.26
	Hedgerow	27.41^b	24.40
	Stone wall	24.99	24.15

5.2.3 Hydraulic connectivity and soil response of hedgerow landscapes

The volume of available pore space, i.e. pore space not filled with water at any given time, was differentiated by treatment, slope position, site and time of year (Figs. 5.7 & 5.8). Over the time period, FD hedgerow (Fig. 5.7B) and SW hedgerow (Fig. 5.8B) were drier (i.e. more available pore space) than the pasture equivalent (Figs. 5.7A & 5.8A) and the disparity was accentuated at drier times of year. FD pasture US (Fig. 5.7A) was an exception, with similar available pore space to FD hedgerow US. However, FD pasture US was more responsive to rainfall (i.e. quicker to fill, slower to drain) than the hedgerow equivalent. Multivariate analysis revealed a significant main effect of time (seasonality) (Wilks Lambda (WL) =0.003, $F_{(11,6)}=162.693$, $p<0.001$), and interaction effects of time and site (WL = 0.008, $F_{(11,6)} = 65.857$, $p<0.001$), time and treatment (WL = 0.059, $F_{(11,6)} = 8.739$, $p<0.01$) time and slope position (WL = 0.085, $F_{(11,6)} = 5.850$, $p<0.05$) and time, site and slope position (WL=0.082, $F_{(11,6)} = 6.110$, $p<0.05$) on available pore space (Table 5.4). Bonferroni-adjusted pairwise differences of available pore space were significant between SW and FD sites ($p < 0.001$) and treatment (p

< 0.01) but not slope position. For ten months of the year, hedgerow treatments were significantly drier ($p < 0.05$) than the adjacent pasture treatment. However, when grouped by site, a treatment effect was evident in all time periods at SW site ($p < 0.05$) but none at FD site.

Rainfall throughout the study period was fairly uniform, with little associated seasonality (Figs. 5.7C & 5.8C). Temperature, although exhibiting some annual fluctuation, varied only by 10 °C mean temperature between the hottest time of year (June/July/Aug, 13.9 °C) and the coldest time of year (December/January/February, 3.9°C). Soil response to rainfall differed seasonally, within and between sites (Table 5.4). During the active growing season (April – September) (Fig. 5.9A & 5.9C), the volume of air-filled pore space is greater in the hedgerow treatments than during the dormant period (October – March) (Fig. 5.9B & 5.9D). By contrast, the pasture treatments return to a similar volume of air-filled pore space following rainfall events throughout the year. At the FD site, there is a parallel response to rainfall under all treatments, with a slight delay from the hedgerow during the growing season. FD pasture US is dry throughout, with comparable air-filled pore space to the hedgerow (US). However, during the dormant period, FD hedgerow US remains consistently dry and less responsive to rainfall than the pasture counterpart, which fluctuates heavily. Downslope, the hedgerow is much wetter and lies on the windward side of the dominant south south-westerly wind. At the SW site, the pattern is reversed, with the downslope side of the hedgerow substantially drier than the upslope side, despite the same orientation of both hedgerows. Soil in all plots follow a similar pattern in response to rainfall, albeit with treatment-specific actual volumes of air-filled pore space. During the dormant period, available pore space is reduced adjacent to the hedgerow but is rarely saturated, whilst the pasture treatments often reach saturation during rainfall regardless of time of year.

Hydraulic connectivity across the hedgerow boundaries is site dependent (Fig. 5.10). Where the underlying soil is FD, the positive difference in air-filled pore space between upslope and downslope (mean difference ~20 cm^3) indicates that upslope of the hedgerow boundary is consistently drier than downslope. By contrast, the predominantly negative difference where it is SW (mean difference ~-5 cm^3) signifies a break in hydraulic connectivity.

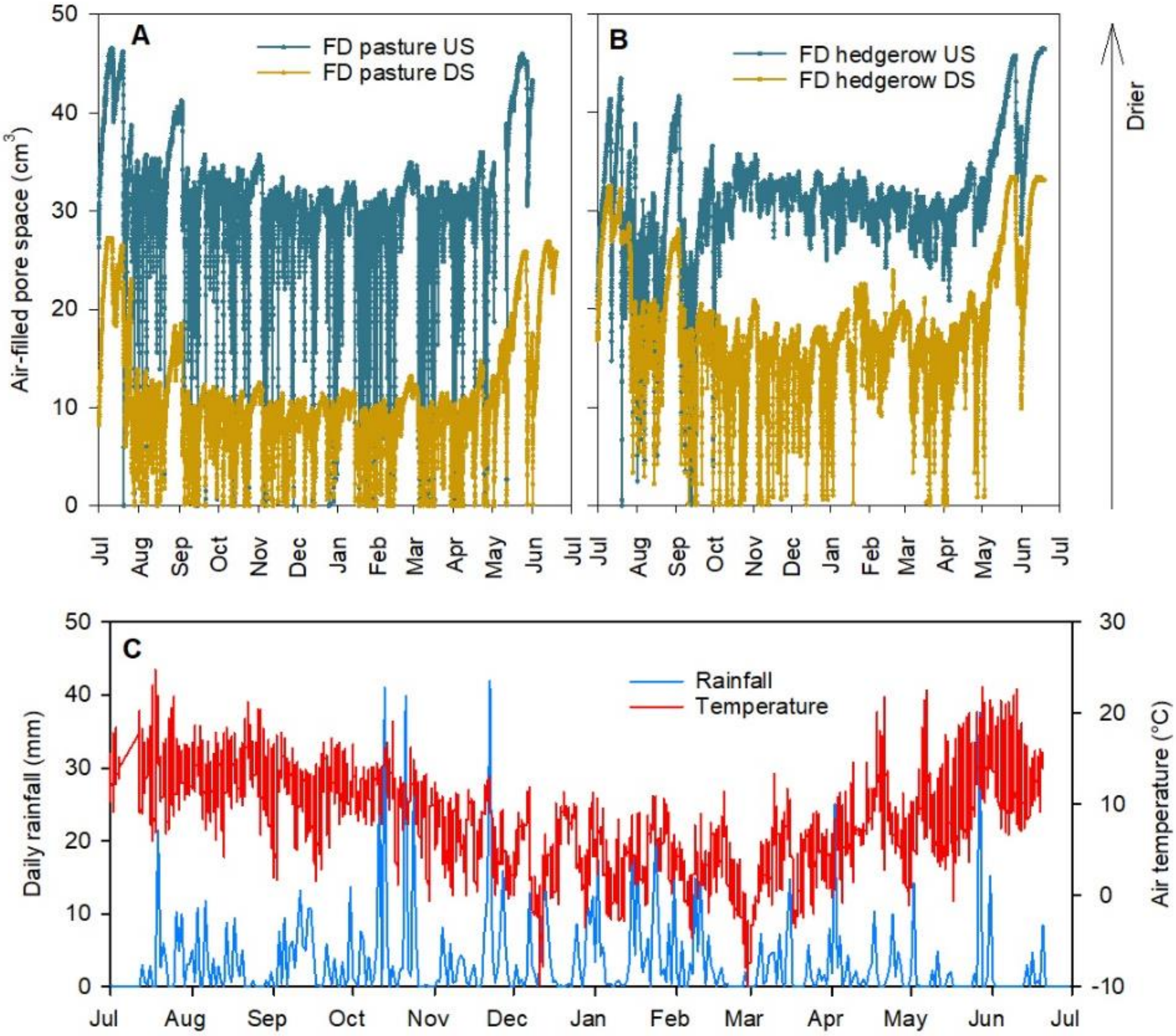

Figure 5.7. Volume of available (air-filled) pore space (saturated soil moisture- actual soil moisture) at free-draining (FD) site over the study year period in (A) pasture, 10 m upslope and downslope of the hedgerow and (B) within 1m of the hedgerow up- and downslope. Higher values indicate drier soil. Soil response is contextualised by daily rainfall (mm) and temperature (°C) at 30-minute intervals over the study period (C).

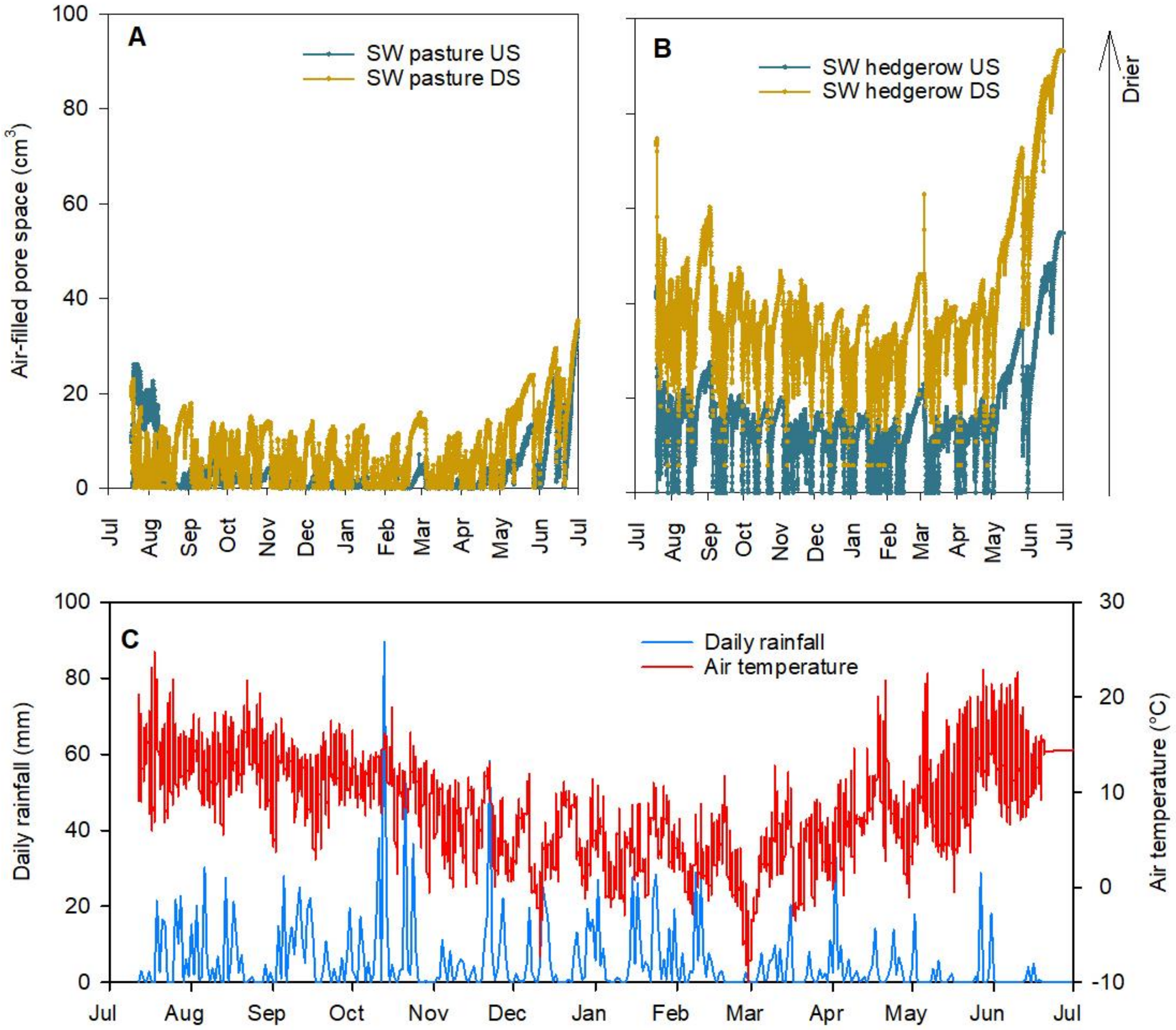

Figure 5.8. Volume of available (air-filled) pore space (saturated soil moisture - actual soil moisture) at seasonally-wet (SW) site over the study year period in (A) pasture, 10 m upslope and downslope of the hedgerow and (B) within 1m of the hedgerow up- and downslope. Higher values indicate drier soil. Soil response is contextualised by daily rainfall (mm) and temperature (°C) at 30-minute intervals over the study period (C).

Table 5.4. Main effects (Wilks' Lambda, df = 11, error = 6) and within-subject effects (Greenhouse-Geisser (G-G), df = 2.118, error = 33.889) of multiple factors on air-filled pore space from repeated measures ANOVA. Significance is denoted by ***p < 0.001, **p < 0.01, *p < 0.05, ns = not significant.

	Wilks' Lambda value	**Main effects F-statistic**	**Main effects Significance**	**G-G F-statistic**	**G-G Significance**
Time	0.003	162.693	***	28.519	***
Time*Site	0.008	65.857	***	9.373	***
Time*Treatment	0.059	8.739	**	0.952	ns
Time*Slope	0.085	5.850	*	1.035	ns
Time*Site*Treatment	0.282	1.391	ns	0.581	ns
Time*Site*Slope	0.082	6.110	*	5.138	*
Time*Treatment*Slope	0.162	2.813	ns	0.286	ns
Time*Site*Treatment*Slope	0.214	2.004	ns	0.566	ns

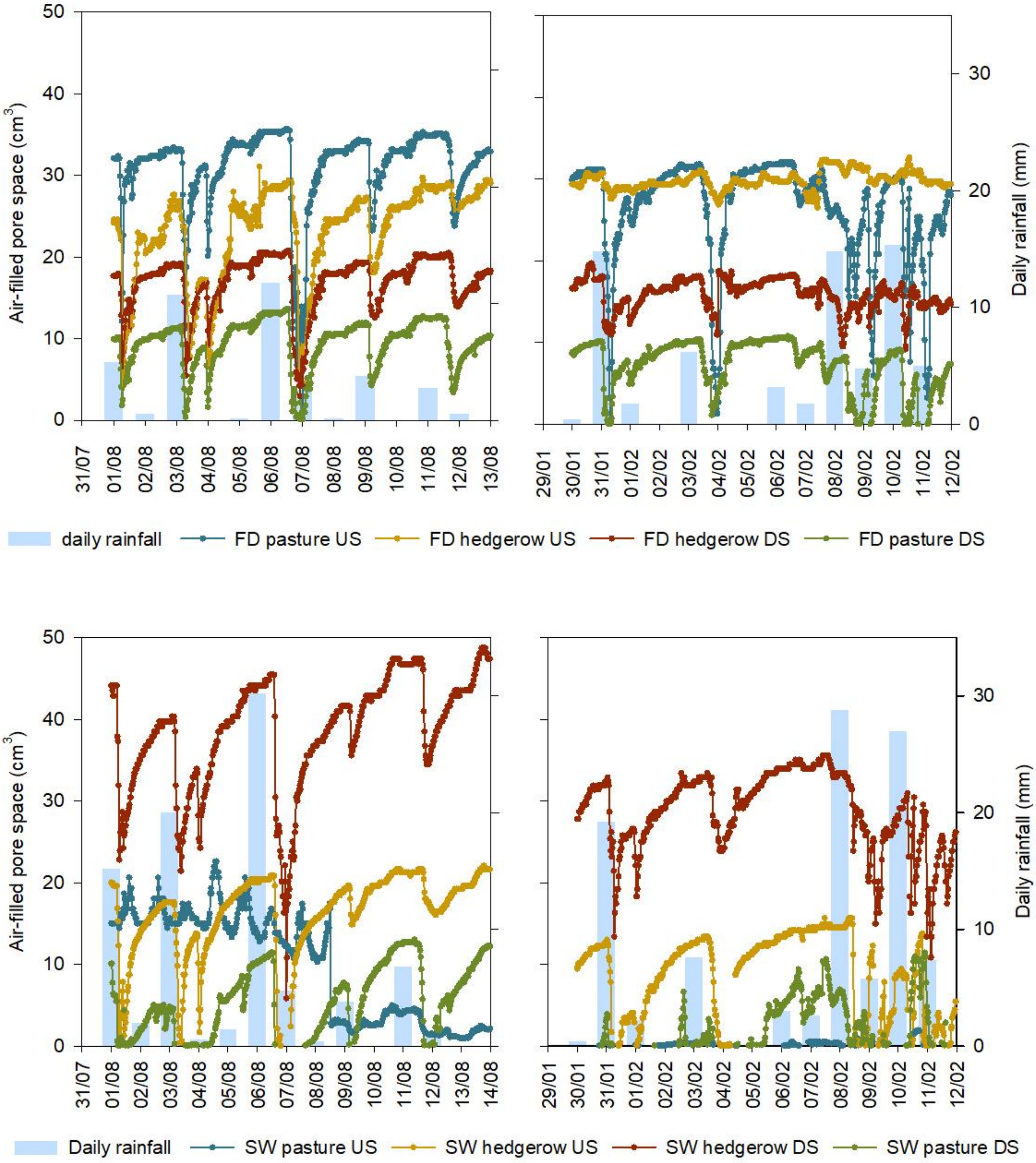

Figure 5.9. Volume of air-filled pore space (cm^3) in the pasture 10 m upslope of the hedgerow (pasture US), <1 m upslope of the hedge (hedgerow US), <1 m downslope of the hedgerow (hedgerow DS) and in the pasture 10 m downslope of the hedgerow (pasture DS) at (A) free-draining (FD) site during summer growing period and (B) the winter dormant period; seasonally wet (SW) site during the summer growing period (C) and winter dormant period (D). Soil response is contextualised by daily rainfall (mm) at each site.

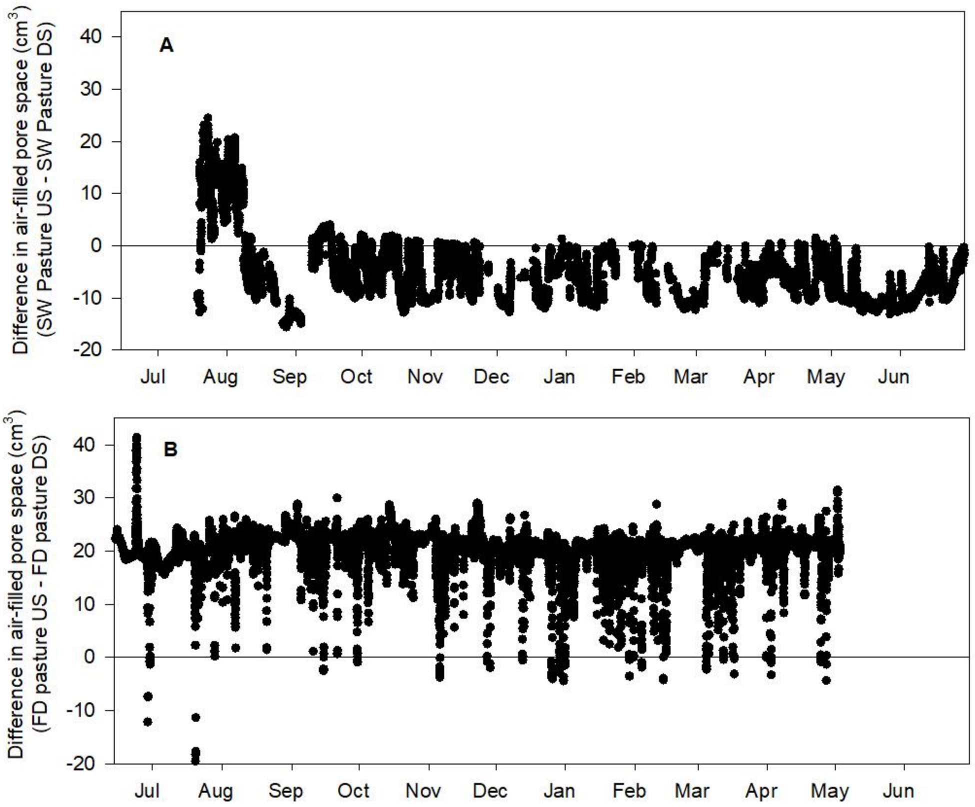

Figure 5.10. The difference in air-filled pore space (cm^3) between pasture 10 m upslope and 10 m downslope of the hedgerow throughout the study period at (A) seasonally wet (SW) and (B) free-draining (FD) sites. Positive values indicate drier soil upslope of the hedgerow and negative values indicate drier downslope of the hedgerow.

5.4 Discussion

5.4.1 Soil structure and hydraulic conductivity

Our data showed that woody roots of hedgerow species modified soil structure by creating an increased abundance of macropores, to the detriment of micro- and mesopores. These changes in soil pore size distribution were apparent in the SWRC that followed a more unimodal curvature in pasture and when adjacent to stone walls but was bimodal in soil associated with hedgerows. In Chapter 3 we showed that tree roots mediated an increased abundance of macropores, which drove changes in the hydraulic gradient rather than total soil porosity. Contour-laid stone walls, like hedgerows, create a physical barrier in the landscape obstructing overland flow that provides time for infiltration and has been shown to reduce run-off by 60% in extreme (1 in 100-year) rainfall events (Kovář et al., 2011). However, without the presence of woody roots, pore size distribution and soil water retention remain unchanged and therefore the hydraulic gradient was similar to adjacent pasture, validating results from Chapter 3.

Macropore abundance in the hedgerow at both sampled soil depths was similar, whereas the soil of either pasture, or pasture next to the stone wall were dominated by small (micro- and mesopores) radius pore sizes. The fine grass roots of the grazed pasture had limited influence on pore size distribution in either the root zone (0-0.05 m depth) or beyond (0.08-0.13 m depth). Coarse roots of leguminous species, such as *Trifolium* spp. often used as a N-fixing species in pasture sward, has been shown to increase interaggregate pore space increasing macropore abundance in cover crops (Bodner et al., 2014). In our study, greater macropore abundance was not observed in the root zone of pasture suggesting that the root morphology of the unimproved pasture sward did not contain sufficient abundance of large diameter roots.

Compaction from grazing pressure at the study sites was negligible as no difference in BD were observed between treatments. However, BD at the study sites was too insensitive to detect soil structural and soil hydraulic changes, instead, SWRC demonstrated the effect of tree roots relative to pasture on soil macroporosity and soil water retention. At the FD site, median K_{fs} was more than twice as great in the hedgerow than the pasture ($p < 0.05$). Field-saturated hydraulic conductivity was measured under a pressure head of -2 cm, effectively excluding the flow through the largest pore sizes. Attempts to directly measure K_{fs} (i.e. flow through all available soil pores) using a dualhead infiltrometer were thwarted by high permeability under the hedgerow preventing equilibration, demonstrating the importance of the largest pore sizes to hydraulic conductivity. In the pasture, equilibrium was easily met reflecting the differential macropore size and abundance between hedgerow and pasture. In the SW site, the pattern was reversed; K_{fs} (-2 cm tension) was similar in the pasture relative to hedgerow despite much greater macropore abundance associated with the hedgerow. Evidence of a historical stone wall was noted beneath the SW hedgerow, which may have impeded accurate estimation of surface K_{fs} here relative to the pasture.

Isolating the effect of hedgerows relative to pasture on soil hydraulic function requires disentangling the confounding effects of soil compaction from grazing. Soil moisture was positively associated with grazing occurrence at both FD and SW sites (Ford et al.2021). This study did not distinguish between grazed and ungrazed treatments and so interpretation of the results should be treated with caution. However, no association was found between BD and grazing occurrence in this study, suggesting that observed differences in soil structure and associated hydraulic function associated with hedgerows are driven largely by the presence of tree roots rather than an absence of grazing.

Soil structure and infiltration are affected by both plant roots and soil macrofauna, particularly earthworms. Pasture is associated with greater earthworm density in farmed environments than in hedgerows where the drier and cooler soil negatively affects earthworm density relative to pasture (Holden et al., 2019). However, in acidic soils such as soil at the study sites, earthworm survival and reproduction is limited (Spurgeon et al., 2013). Preliminary unpublished data collected at the SW and FD field sites revealed no difference in earthworm abundance at < 2 m and 10 m from the FD boundary (0.10 m depth) suggesting that bioturbation is less important than other processes to hydraulic function at this site.

Soil type, alongside land cover type (i.e. hedgerow/pasture/stone wall), played a pivotal role in determining soil hydraulic conductivity. Slow loss of soil water from pasture and adjacent to the stone wall relative to hedgerows means these sites stay wetter for longer, reducing aeration. In soils with a high SOM content and soil water holding capacity this results in an oxygen-limited environment (e.g. SW site), biological productivity as well as pasture productivity is likely to be reduced away from the hedgerow, hindering yield. Hedgerows in

SW environments, therefore, may contribute to improvements in below-ground biological activity and consequently on-farm productivity. The disparity in SOM between the sampled soil depths at SW may be creating a seasonal perched water table inducing infiltration-excess overland flow. Seasonally wet pasture contained approximately 10% more SOM at 0 – 0.05 m depth compared with 0.08 – 0.13 m depth. We observed a reduction of soil water retention with depth, which correlates with the SOM content of the soil (Fig. 5.5). This is in agreement with the theory that available water holding capacity of soil increases 1.5 – 1.7 times with every 1% increase in SOM (% weight) (Libohova et al., 2018). The effect of an increase of 1% SOM is greatest at saturation (2.95 mm H_2O 100 mm soil^{-1}) followed by field capacity (1.61 mm H_2O 100 mm soil^{-1}) (Minasny and McBratney, 2018), which is typically within the range of soil moisture at the SW site due to rainfall patterns in the uplands of Wales. During winter, saturated soil (pooling water) was observed at the soil surface of the SW site, but soil was visibly drier at the 0.08 – 0.13 m depth in the pasture. This phenomenon was not observed in the hedgerow, where we believe that roots improved surface macropore abundance, ameliorating a perched water table. Further research is required to determine the lateral extent of hedgerow roots in pasture and the extent of the influence of roots on pore size distribution.

5.4.2 Soil water storage

Our data showed that soil associated with hedgerows had a greater abundance of empty (air-filled) pore space to fill with water during rainfall events than adjacent pasture. Typically, macropores filled with water drain faster than water in micro- and mesopores held by the soil's matric potential. Therefore, the greater the macropore abundance, the lower the SWSC, and conversely the greater the volume of air-filled pore space. Whilst greater soil macropore abundance is correlated with faster drainage, during high intensity or persistent rainfall events, there is the potential for the soil to reach saturation, however during our study period this rarely occurred under either of the hedgerows.

Pasture exhibited a similar volume of air-filled pore space during dry periods throughout the year whereas under hedgerows the soil was driest during the growing season when the hedgerow was in leaf, suggesting that a combination of reduced throughfall, increased interception, and the effect of evapotranspiration likely resulted in drier soils. Following rainfall, gravitational drainage of macropores returns the soil to field capacity and soil moisture content is held under tension. Rainfall was relatively consistent for 10 months of the year and mean temperature fluctuated little. Consequently, air-filled pore space in the pasture was similar over this time period. The consistency of rainfall allows untangling of the effects of climate and hedgerow on air-filled pore space.

Soils under hedgerows consistently stayed drier than the adjacent pasture soils but no seasonal lag time was observed. In contrast, lag times of 1-3 months were observed in Brittany, coinciding with above- and below-average rainfall periods (Caubel et al., 2003; Ghazavi et al., 2011, 2008). During the study year, precipitation from summer, autumn and winter months lacked the strong seasonality of the French studies. This highlights the importance of climate to the influence of hedgerows on soil hydrology. During the last two months of the study year (May - June), an increase in temperature and a decrease in rainfall brought about drought conditions (Ford et al., 2021). During this time, potential evapotranspiration increased accelerating soil drying and accentuating the difference in the volume of air-filled pore space in hedgerow soil compared with pasture. However, this trend may not have continued beyond the study period as the degree of localised soil drying is limited by groundwater/soil moisture plant availability during extended dry periods, decreasing to half actual evapotranspiration observed during wet growing seasons (Thomas et al., 2012). Climate change is predicted to result in an increase of extreme weather events for Wales (i.e. summer droughts, higher temperatures and high intensity rainfall in winter) (IPCC, 2014). Upland areas in Wales may experience greater drying during summer and a delay to soil re-wetting becoming more consistent with observations made in Northern France. Land management changes, such as increased presence of hedgerows in the landscape to promote ecosystem service provision in conjunction with summer droughts could result in low soil moisture and physiochemical changes to soil structure (Robinson et al., 2016) that carry over into the following year (Viaud et al., 2005).

Soil water storage and available air-filled pore space associated with hedgerows were site specific. Soil saturation limits root growth in hedgerow-pasture systems (Grimaldi et al., 2009) explaining the greater macropore abundance and drainage on the downslope side at SW but on the upslope side at FD. At the FD site, the soil was much drier upslope on the more sheltered, leeward side of the hedge. In conditions such as these, roots of hedgerows can preferentially grow upslope for stability, to access nutrients from higher concentrations of

SOM or to avoid saturated soil (Caubel-Forget et al., 2001). On this site, macropore abundance was greater upslope rather than downslope relative to the hedge, reducing SWSC. The pattern was reversed at SW; the downslope side of the hedgerow was substantially drier than the upslope, despite facing the windward direction. Soil upslope of the hedgerow and in the pasture was near saturation for the majority of the year. Lateral sub-surface flow provided a constant water supply to the upslope side of the hedge, where it intercepts soil altered by the presence of the hedgerow with a greater abundance of macropores that expediated water infiltration. Vertical drainage is then facilitated by the abundance of macropores associated with the hedgerow. During intermittent rainfall and dry periods, only the upslope side is affected, whereas during more persistent rainfall, soil water begins to fill pores on the downslope side, reducing the volume of air-filled pore space. In the FD site, the pasture upslope of the hedgerow is much drier, dominated by vertical rather than lateral sub-surface flow, and therefore does not have the same effect. Low soil moisture content of the soil below hedgerows has the potential to interrupt lateral sub-surface flow, interrupting hydraulic connectivity downslope in groundwater dominated catchments (Ghazavi et al., 2011). Evidence of this effect is seen at the SW site, where the pasture downslope is consistently drier than upslope. By contrast, the hydraulic gradient is not disconnected by the hedgerow where there is effective drainage (FD). It is possible that water initially drains vertically until reaching more impermeable and/or wetter soil and then flows laterally but is beyond the measurement depth of the study. Both sites are in rainfall-fed, not groundwater dominated catchments, but the high SOM content in SW creates a shallow water table throughout most of the year, facilitating lateral sub-surface flow.

5.5 Conclusion

Hedgerows have traditionally been used as a physical barrier in the landscape and are well-known to have a positive effect on biodiversity (Baudry et al., 2000). Here we show that hedgerows can also provide complexity and storage capacity in the subsurface, which introduces fill and spill zones across the landscape, changing the lateral speed of water flow. This may be important for surface water flows and it may impede soil erosion development. The growth of woody hedgerow roots modifies soil structure, namely macroporosity, facilitating faster drainage leaving a greater volume of air-filled soil pores available to infiltration. During the leafed period, evapotranspiration and interception further dry the soil relative to the pasture, enhancing the volume of available pore space. The field-scale hydrological effect of hedgerows is mediated by the underlying drainage conditions, dependent on soil type. Where the soil is already free-draining, localised drying occurs, but hydrological connectivity with downslope remains. However, in a seasonally wet environment, hedgerows can interrupt lateral flow, facilitating vertical drainage and enabling greater capacity to absorb rainfall downslope. We show that hedgerows in pasture affect soil hydraulic function and the effect is soil type specific. Hydrological models used to predict landscape-scale change should consider both smaller wooded features, such as hedgerows as well as soil type.

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Chapter 6 Discussion

6.1 Introduction

In this chapter, the experimental work presented in Chapters 3-5 is summarised and discussed in relation to the common themes and initial aims of the thesis. These were to review the existing evidence of the impact of trees and hedgerows on soil hydraulic function. Secondly to understand the interactions between tree species identity, diversity and soil type on soil hydraulic function. The third aim was to understand the role of hedgerows in regulating soil water and the interaction with soil type, hedgerow age and time of year. Detailed discussion of the empirical work of this thesis are described in each chapter. Here, I present a synthesis of the results in relation to the research hypotheses and consider the wider implications of the findings.

6.2 Synthesis of findings

6.2.1 Tree stands and hydraulic function

The belowground role of tree species in influencing soil hydraulic function has been little studied with a paucity of studies examining how species-specific roots relate to hydraulic conductivity (Chapter 2). This study established a relationship between K_{fs} and FRB density in monoculture, with RLD and necromass also playing a key role in determining hydraulic function. Fine root biomass density is species-specific, with *F. excelsior* highlighted as the dominant species producing significantly more FRB than six other common European tree species. Fine roots altered the soil structure by increasing macroporosity, not total porosity, facilitating greater sub-surface flow, leading to acceptance of the hypothesis that tree species identity affects tree fine root morphology and soil hydraulic function. Surprisingly, soil texture had no effect on hydraulic conductivity in *F. excelsior* stands nor on FRB density near the soil surface (0-0.1 m). Deeper in the soil where the proportion of fine tree roots was much reduced (> 0.1 m), soil texture not FRB moderated soil hydrological response. Soil type, therefore, does affect tree FRB and soil hydraulic conductivity, as stated in the second hypothesis, but only affects soil hydraulic function deeper than 0.1 m where typically less than half the FRB is growing.

When combined, species' functional traits do not mirror that in monoculture. Species richness *per se* did not affect hydraulic conductivity but rather the interaction of each species within the mix. There was an under-yielding effect on *F. excelsior* fine root functional traits associated with co-location with *B. pendula*, contrary to overyielding demonstrated in the literature when co-located with other species. We reject the hypothesis that FRB of *F. excelsior* is not reduced when grown with a tree species of similar root morphology. The combination of tree species from similar successional stages resulted in the dominant species under-yielding as both inhabited similar soil spaces. Conversely, combining species from contrasting successional stages had an additive effect, overyielding fine root functional traits of both species due to resource partitioning from niche differentiation and mutualism, thereby increasing K_{fs}. Consequently, the species associated with the lowest K_{fs} in monoculture (*C. sativa*) gained the most from polyculture, with a significant increase in K_{fs}. Therefore, the hypothesis that FRB and morphological characteristics result in a greater hydraulic response when species grown in mixture possess contrasting functional traits is accepted.

Although this work has contributed more pieces to the puzzle, there are still many questions left unanswered. What, for example, is the effect of tree identity and successional status on fine root functional traits as the trees age? It is possible that *F. excelsior* and *B. pendula* are the dominant tree species with the greatest effect on K because experimental work took place on relatively young trees (~13-14 years). Heterogenous fine root growth and functional trait development during the growing phase may be related to species identity and/or successional stage. The rank order of tree species facilitating the greatest K of much older trees, therefore, may be different. The interaction between co-located species resulted in a small in magnitude but significant difference in K worthy of further investigation. Repeating the experiment with a greater number of replicates and a more diverse range of polyculture (i.e. contrasting species and species richness) would give greater confidence in the effect of species on K_{fs}. Further research is needed to investigate the hypothesis that combining contrasting successional tree species results in an additive effect on fine root production and K whilst combining similar successional tree species is detrimental.

Soil texture can impede the growth of tree fine roots, but this study demonstrated that for species with prolific FRB production (i.e. *F. excelsior*), there is no effect (within the first 0.1 m of soil), nor on associated K_{fs}. However, how less productive species would interact with contrasting soil types is unknown. Testing the relationship between species identity, soil texture and K across a bigger cross-section of soil types could establish a tipping point where moderation of soil structure and K is insignificant compared with soil texture. This would enable land managers to offset other objectives against hydrological moderation objectives when choosing species to plant in different contexts.

6.2.2 Hedgerows and hydraulic function

Hedgerows are often ignored in modelling when quantifying farmland ecosystem service delivery. This study demonstrated that hedgerows could affect hydraulic function, but soil type and drought modified the response. Hedgerows modify soil structure by increasing macroporosity. Faster drainage facilitated by greater macroporosity left a greater volume of air-filled pore space available for infiltration close to hedgerows, an effect that was accentuated during the growing season due to plant water use. However, the effect of localised drying on hydrological connectivity was mediated by soil type and thus the hypothesis that seasonality and soil type affect soil water storage capacity and air-filled pore space associated with woody hedgerows is accepted. In seasonally wet soil, the hedgerow acted as a hydrological barrier interrupting connectivity between up- and downslope, creating greater capacity downslope to absorb rainfall. But in FD soil, hydrological connectivity remained conferring no additional absorption capacity downslope. The results lead to rejection of the final hypothesis that woody hedgerows increase hydraulic conductivity and interrupt hydrological connectivity across a hydraulic gradient. This contrasts with data from Brittany which found that drying beneath the hedgerow during the growing season created a hydrological barrier to downslope lateral water flow from well-drained soil. However, there were two important differences between the studies. Firstly, hedgerows in the Brittany studies were ‘unmanaged’ and consisted of a line of single species mature trees (*Q. robur*) whereas ours were a heavily managed mix dominated by *P. spinosa*, *C. monogyna* and *C. avellana*. Secondly, for 9-10 months of the study year, there was little seasonal variation in rainfall at the study site, compared with broadly typical temperate seasonal rainfall experienced in Brittany. The differences highlight the importance of considering soil type and climate when assessing the effectiveness of hedgerows along a hydraulic gradient.

Climate change scenarios predict increasing periods of intensive rainfall as well as droughts, which could change hydrological connectivity associated with hedgerows. A warming climate could shift rainfall patterns experienced in North Wales to become more similar to Brittany.

The effect of hedgerow density and management on fine root growth could also moderate hydrological processes. Our study was on heavily managed hedgerows, regularly flailed (cut), typical of hedgerow management in Wales. However, changes in agricultural policy may see people use hedgerows for a multitude of benefits. Management, therefore, may become more varied such as coppicing for fuel, occasional cutting to increase biodiversity or grazed by ruminants for tree fodder, the effect of which on hydraulic function are largely unknown.

Soil type, climatic events and management could all influence the results described in this study. Further research exploring these variables could be used to parameterise models seeking to understand the hydrological ecosystem service provision from woody hedgerows in livestock-based pasture systems. The existing hydrological dataset could be further developed by building a model (e.g. using Hydrus) to predict the hillslope flow regime of hedgerow-pasture land cover on different soil types and rainfall intensities. Predictions could then be used to determine the size of rainfall event that would induce overland flow and therefore determine the capacity of hedgerows and pasture to absorb rainfall.

6.2.3 Implications for policy makers and land managers

The effects of ADB on *F. excelsior* is likely to have a greater impact on soil hydraulic function in monoculture stands than in mixed woodlands (Chapters 3&4). Land managers concerned with hydrological regulation who seek to replace *F. excelsior* in woodlands with an alternative could consider either a monocultural replacement using a species with prolific fine root growth (e.g., *B. pendula*) or a mixed stand of species with contrasting functional traits (e.g., *B. pendula* and *C. sativa*) depending on the wider objectives for the site. Fine root dieback, in the short-term, will increase macroporosity and K as decomposing roots increase available space in root channels (Bevan and Germann, 2013; Zhang et al., 2015; Chapter 3). In the medium to long-term, root channels will collapse reducing macroporosity and K (Bengough, 2012). The time taken for dead-root channels to break down depends on root resistance to decay, soil texture, sub-surface erosion and climate (Ghestem et al., 2011). Depending on duration of dead-root channel decay, land managers may therefore decide that natural regeneration from surrounding woodland may be sufficient to ameliorate the long-term effect on K locally.

Managing *F. excelsior* replacement, whether through natural regeneration or planting, will require a careful balance of competing objectives. Land managers will also need to carefully consider site-specific species diversity, soil and climatic conditions to maximise benefits from post-*F. excelsior* woodlands. In the UK, natural tree regeneration in ADB-affected unmanaged broadleaved woodlands (where *F. excelsior* >10%) is likely to be dominated by *A. pseudoplatanus* and *F. sylvatica* following establishment of shrub species such as *C. avellana*, *Cornus sanguinea* L., *P. spinosa* and *C. monogyna* (Broome et al 2019). However, the adaptability of *F. excelsior* to colonise a wide diversity of sites means that woodland tree species composition and replacement species from natural regeneration may vary on sites at the extremes of *F. excelsior*'s soil and climatic range. Mitchell et al. (2014) provide a list of 22 replacement species for *F. excelsior*, ranked in terms of similarity in nutrient cycling, litter decomposition, succession, species richness and biodiversity. Based on similar characteristics, Hill et al. (2019) developed a model to identify regions of the UK which are the most vulnerable to *F. excelsior*-like functional trait loss by weighting traits based on the importance to ecosystem services. Both studies omitted consideration of functional root traits. Vulnerability to flood protection estimated by Hill et al. (2019) is determined from litter decomposition, mycorrhizal type and Ellenberg's nutrient indicator values. Functional root trait data and its impact on hydraulic function identified in Chapters 3 & 4 could significantly refine the model to highlight areas where changes in hydrological regulation are likely and examine the trade off with other ecosystem services from selection of replacement species.

The Committee on Climate Change (2018) recommends that hedgerow networks in the UK expand by 30-40% by 2050. Research presented in Chapter 3 & 4 indicates that species choice and richness can impact hydrological functioning inside woodlands; the next step is to establish whether the same relationships apply in hedgerows. Hedgerows, like woodland edge trees, have greater access to resources (light, nutrients, water) but also greater susceptibility to wind and heat stress than trees inside woodlands (Reinmann & Hutyra, 2017; Vanneste et al., 2020). In temperate woodlands, edge effects have been shown to promote growth of aboveground biomass, but with no corresponding change in belowground biomass (Reinmann & Hutyra, 2017). Regular cutting of hedgerows can decreases shoot to root ratio influencing fine root turnover (Axe et al., 2017) with implications for K, while preferential growth for stability, to access nutrients from higher concentrations of SOM or to avoid saturated or compacted soil (Caubel-Forget et al., 2001; Jackson et al., 2000) can create heterogeneity in hydrological impact. More research is required to understand the full effects of management and adjacent land use on functional root traits and hydraulic function, but what is evident is that trees both inside and outside of woodlands alter soil pore size distribution with consequences for K.

In hedgerow settings, the greater total available pore space relative to pasture significantly increases K (Chapter 5). Estimating available pore space through time considers the effect of preceding weather conditions, interception and evapotranspiration on soil moisture content and the ability of the landscape to absorb water during precipitation events. Considering two contrasting months of the study year, August and February, illustrates the hedgerow impact on hydraulic function during growth and dormant periods on different soil types explained in Chapter 5 (Table 6.1). During the growing season (August) in the seasonally wet environment, soil pore space capacity associated with the hedgerow upslope was exceeded for 15 hours only and not at all downslope. In the adjacent pasture 10 m from the hedgerow, capacity was exceeded for 199 hours and 115.5 hours upslope and downslope respectively. During the dormant period (February), total exceedance increased to 28 hours and 0.5 hours immediately upslope and downslope of the hedgerow but 340 hours and 184.5 hours in the pasture. The hedgerow is clearly having an important impact on the soil's capacity to absorb rainfall close to the hedgerow as well as downslope, regardless of leaf cover.

By contrast, on free-draining soil, the capacity to absorb rainfall was not exceeded at all under the hedgerow during August or February and only in the pasture for 0.5 hours upslope and 10 hours downslope during February. Here, the relative impact of hedgerows is slight due to the underlying soil conditions. The importance of hedgerows on free draining soil may be more important during high intensity rainfall events where the additional soil available pore space afforded by hedgerows may provide resilience in the face of extreme precipitation events. Concentrating the proposed expanded hedgerow network on contour-planted hedgerows cutting across large expanses of pasture on sloping ground, could increase the ability of the landscape to absorb precipitation, reducing overland flow with implications for flood risk. Greater emphasis on expanding the hedgerow network in sites with free draining soil may mitigate the effect of predicted higher intensity precipitation events, brought about by climate change, on overland flow. Further work with existing data will develop a model to predict hedgerow resilience to different magnitude and periodicity rainfall events on contrasting soil types to support hedgerow expansion decision-making.

Table 6.1 Total number of hours where no available pore space (i.e., no soil capacity to absorb precipitation) was recorded adjacent to the hedgerow upslope (US) and downslope (DS) and in the pasture, 10 m US and DS from the hedgerow. Data from 1-31 August 2017 and 1-28 February 2018 representing periods where the hedgerow is actively growing (August) and dormant (February). Maximum daily rainfall recorded during each month at each site is given for context.

		Hedgerow US	Hedgerow DS	Pasture US	Pasture DS	Max daily rainfall
August (growing period)	Seasonally wet (SW)	15	0	199	115.5	30.2
	Free draining (FD)	0	0	0	0	11.8
February (dormant period)	Seasonally wet (SW)	28	0.5	340	184.5	28.8
	Free draining (FD)	0	0	0.5	10	15.4

6.3 Conclusion

Increasing tree cover is often suggested as a way to both sequester carbon and facilitate greater subsurface flow during precipitation, reducing peak flow and flood risk. However, the effect of trees to achieve those objectives is contested due to a complex interaction of variables, some of which were explored in this study. Extirpation of *F. excelsior* from large swathes of UK and Europe from fungal pathogen *H. fraxineus*, for example, could result in a disproportionate effect on hydraulic conductivity from monoculture stands. However, where *F. excelsior* was part of a mixed stand with *B. pendula*, the hydrological impact would be reduced. Overyielding of *F. excelsior* with *F. sylvatica* described in the literature supports the results of this study suggesting that successional status of co-located species is likely to influence hydraulic conductivity. This has implications for land managers deciding on replacement tree species following natural dieback or controlled felling of *F. excelsior* due to Ash dieback. Contour-planted hedgerows provide complexity in the landscape, creating a mosaic of spill and fill opportunities, interrupting overland and sub-surface lateral flow with the potential to reduce sediment loss. Introducing or restoring hedgerows in pasture farmland could help regulate water flow pathways with implications for flood risk. However, soil type and future climatic changes must be taken into consideration when designing tree features into the landscape in order to meet hydrological regulation objectives.

6.4 Questions for future research

- What is the effect of tree identity and successional status on fine root functional traits and hydraulic function as trees age?
- Does tree successional status determine soil hydraulic conductivity associated with trees in polyculture? Does this change with increasing species richness?
- What is the relationship between tree species identity, soil texture and hydraulic conductivity across a wide range of soil types?
- Does hedgerow management and density affect woody species' root morphology, and soil hydraulic function? Is there an interaction effect with soil type?
- How does extreme weather events (e.g. drought) affect hydrological connectivity associated with contour-planted hedgerows on a wide range of soil types?

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