Valesca Harezlak

Filters and plant trait strategies

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FILTERS AND PLANT TRAIT STRATEGIES: WHAT STEERS VEGETATION DYNAMICS IN FLOODPLAINS OF REGULATED LOWLAND RIVERS?

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"We're lost again," said Big Panda
"When I'm lost," said Tiny Dragon, "I find it helps to go
back to the beginning and try to remember why I started."
Big Panda and Tiny Dragon by James Norbury

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Summary

Regulated rivers differ from natural flowing rivers in, amongst others, how they interact with their floodplains. The floodplains within the active meandering plane of natural flowing rivers are strongly influenced by hydrodynamic and morphological processes, like discharge dynamics, and erosion and sedimentation. Those processes shape floodplain vegetation composition, resulting in rich biodiversity. Regulated rivers interact less with their floodplains as through engineering works the course of rivers has been fixed, and discharge dynamics are affected by dams and embankments. Consequently, the lack of hydro-morphodynamic rejuvenation causes floodplains of regulated rivers to become, without human intervention, overgrown with forests, which not only leads to impoverished biodiversity but also jeopardizes water safety.

To manage both water safety and biodiversity within the floodplains of regulated rivers, insight is required into how vegetation, as the base for biodiversity, is shaped in these types of systems. The so-called filter-trait concept could be useful, as this concept links filters (i.e. processes) to trait strategy composition (i.e. vegetation species composition). The rationale of this concept is that those trait strategies are selected that 'pass through' (i.e. thrive under) specific combinations of filters. In natural flowing rivers, for example, trait strategies are selected that can cope with highly dynamic filters, while in the less dynamic floodplains of regulated rivers biological interactions, like competition, are a dominant filter for trait strategy selection. Note that different species can have the same trait strategy: a trait strategy therefore represents clusters of species. However, albeit the premise the filter-trait concept holds, the applicability of the concept for floodplains of regulated rivers is not without debate.

To research whether the filter-trait concept can generate insights that contribute to balancing water safety and biodiversity goals in floodplains of regulated rivers, the following main question was posed, in which the filter-trait concept was used as the leading principle:

What are the main steering processes shaping vegetation patterns in floodplains of regulated lowland rivers and how can this knowledge be used in floodplain management?

With the following sub-questions:

1. *What does the filter-trait concept add to the understanding of vegetation composition in floodplains of regulated lowland rivers?*
2. *What are the main filters that govern vegetation dynamics in floodplains of regulated lowland rivers and are those filters scale-independent?*
3. *How can the knowledge of the filter-trait concept, as underpinning for the dynamics of plant trait strategies in floodplains of regulated rivers, be translated into a modelling approach?*

Based on field and satellite data, and the application of linear programming as a modelling approach, the filter-trait concept was tested and explored as a potentially useful concept for floodplain management. In the field study, data on environmental filters and plant traits of grasses and herbaceous vegetation was collected in three floodplains along the regulated Dutch Rhine branches. Next, statistical clustering techniques were used on this data to identify links between filters and trait strategies. For the satellite data, LandSat data from missions 5 and 8 were used (spatial resolution 30*30m, covering a period of 35 years). The data was translated to landcover classes, which were subsequently analysed in terms of succession and retrogression rates and linked to filters. The modelling approach was, by using linear programming, aimed at simulating trait strategy competition along resource gradients to explore 1) how trait strategies compete over resources and 2) if linear programming is a suitable approach to simulate trait strategy competition. As a test case, the competition between two herbaceous trait strategies along a light and nutrient gradient was simulated. Modelling results were verified against prevailing hypothesis found in literature.

The field study revealed that, at least for grass and herbaceous vegetation, disturbances (excavation and summer flooding) and resource gradients were the main filters shaping vegetation composition. The field study also indicated that when species, instead of trait strategies, were used, less insight into the main filters was given. The satellite data identified management and interventions as the main filters shaping land cover composition. The use of the two different approaches, therefore, revealed the nesting of filters: the filters identified during the field study operate within the boundaries of the large-scale filters identified through satellite data. Additionally, as the satellite data comprised a 35-year-long time series, spatiotemporal changes in dominant filters for land cover composition were identified using succession and retrogression rates of those land covers.

The use of linear optimization as a modelling technique for the competition of two herbaceous trait strategies along a light and nutrient gradient demonstrated not only how the filter-trait concept can be translated into vegetation competition, but also showed the importance of including intra-specific variation. Besides that, the model also demonstrated that linear optimization gives clear insight into the main filters while solving competition for the different trait strategies simultaneously. Both features are not common in many competition models. So, even though the model is not yet able to simulate the complete findings of the field and satellite data, the model concept could eventually strengthen the understanding of how filters and trait strategies result in the vegetation patterns found in floodplains of regulated, lowland rivers.

To conclude, in the floodplains of the large regulated Dutch lowland rivers, interventions and management are the main filters shaping vegetation at the floodplain scale. However, nested within those main filters, are filters such as natural disturbances by floods and resource gradients that further detail floodplain vegetation composition. The identified filters can be included in models to test hypotheses and explore scenarios and as such support floodplain management. So, the research showed that the filter-trait concept can be applied to floodplains of large, regulated lowland rivers as it can identify the dominant filters for trait strategy composition, concomitantly revealing essential information to balance water safety and biodiversity aims within floodplains of those types of rivers.

Samenvatting

Gereguleerde rivieren verschillen van natuurlijk stromende rivieren in, onder meer, de interactie met hun uiterwaarden. De uiterwaarden die in het actieve meandervlak van natuurlijk stromende rivieren liggen, worden sterk beïnvloed door hydrodynamische en morfologische processen, zoals afvoerdynamiek en erosie en sedimentatie. Deze processen zijn bepalend voor de samenstelling van de vegetatie in de uiterwaarden, en zorgen daarmee voor een rijke biodiversiteit. Gereguleerde rivieren, daarentegen, interacteren minder met hun uiterwaarden, omdat door middel van engineeringswerken de loop van rivieren is vastgelegd en de afvoerdynamiek beïnvloed wordt door dammen en dijken. Door de verminderde interactie, en zonder menselijke tussenkomt, raken uiterwaarden van gereguleerde rivieren overwoekerd met bossen. Dit leidt niet alleen tot een verarmde biodiversiteit, maar brengt ook de waterveiligheid in gevaar.

Om zowel de waterveiligheid als de biodiversiteit in uiterwaarden van gereguleerde rivieren te beheersen, is inzicht nodig in hoe vegetatie, als de basis voor biodiversiteit, in deze systemen wordt gestuurd. Het zogeheten filter-trait concept kan hiervoor waardevol zijn, aangezien dit concept filters (d.w.z. processen) koppelt aan de samenstelling van de trait strategieën (d.w.z. vegetatiesamentelling). De basisgedachte van dit concept is dat die traitstrategieën worden geselecteerd die gedijen onder specifieke combinaties van filters. In natuurlijk stromende rivieren worden dan bijvoorbeeld trait strategieën geselecteerd die bestand zijn tegen zeer dynamische filters, terwijl in uiterwaarden van gereguleerde rivieren biologische interacties, zoals concurrentie, een dominant filter voor de samenstelling van traitstrategieën kan zijn. Ondanks de belofte van het filter-trait concept is de toepasbaarheid van het concept voor uiterwaarden van gereguleerde rivieren niet zonder discussie.

Om te onderzoeken of het filter-trait concept inzichten kan geven die bijdragen aan het balanceren van waterveiligheids- en biodiversiteitsdoelen in uiterwaarden van gereguleerde rivieren, is de volgende hoofdvraag gesteld, waarbij het filter-trait concept als leidend principe is gebruikt:

> *Wat zijn de belangrijkste stuurprocessen voor vegetatiepatronen in uiterwaarden van gereguleerde laaglandrivieren en hoe kan deze kennis worden gebruikt voor het beheer van deze uiterwaarden?*

Met de volgende deelvragen:

1. *Wat draagt het trait-filter concept bij aan het begrip van de vegetatiesamenstelling in uiterwaarden van gereguleerde laaglandrivieren?*
2. *Wat zijn de belangrijkste filters voor vegetatiedynamiek in uiterwaarden van gereguleerde laaglandrivieren en zijn deze filters schaalonafhankelijk?*
3. *Hoe kan kennis van het filter-trait concept over de dynamiek van plant trait strategieën in uiterwaarden van gereguleerde rivieren vertaald worden naar een modelbenadering?*

Op basis van de veld- en satellietdata en de toepassing van lineaire programmering als modelleringstechniek, is het filter-trait concept getest en verkend als mogelijk bruikbaar concept voor management van uiterwaarden. De deelvragen zijn beantwoord door een combinatie van veldonderzoek, satellietdata en modelontwikkeling. In het veldonderzoek is data verzameld van plantentraits van grassen en kruidachtige vegetatie en milieufilters in drie uiterwaarden langs de Nederlandse Rijntakken. Vervolgens zijn door statistische clusteringstechnieken relaties gelegd tussen filters en traitstrategieën. Voor de satellietdata is LandSat-data van de missies 5 en 8 gebruikt (ruimtelijke resolutie 30*30m, over een periode van 35 jaar). De data is vertaald naar vegetatieklassen. Deze klassen zijn geanalyseerd in termen van successie- en retrogressiedynamiek en gekoppeld aan filters. De modellering was, door het gebruik van lineaire programmering, gericht op het simuleren van competitie tussen trait strategieën langs resource-gradienten om te onderzoeken 1) hoe trait strategieën concurreren om resources en 2) of lineair programmeren een geschikte methode is voor het simuleren van competitie tussen trait strategieën. Als testcase werd de competitie tussen twee kruidachtige traitstrategieën langs een licht- en nutriëntengradiënt gesimuleerd. De resultaten zijn getoetst aan geldende hypothesen.

De resultaten van de veldstudie lieten zien dat, in ieder geval voor grassen en kruidachtige vegetatie, verstoringen (afgravingen en zomeroverstromingen) en resource gradiënten (water en nutriënten) de sturende filters zijn voor de samenstelling van de trait strategieën. Ook toonde de veldstudie aan dat wanneer soorten, in plaats van traitstrategieën, gebruikt worden, minder inzicht werd verkregen in de sturende filters. Een combinatie van de veld- en satellietdata identificeerde een ruimtelijke hiërarchie in de filters: de tijdens de veldstudie gevonden filters opereren binnen de grenzen van de grootschalige filters van beheer en menselijke interventies. De combinatie van de twee onderzoeksmethode was daarmee waardevol om een diepgaander inzicht te krijgen in de filters en hun ruimtelijke schaal. Daarnaast benadrukte de tijdreeks van de satellietdata dat filters in ruimte en tijd kunnen veranderen.

Lineaire programmering toonde aan dat deze techniek niet alleen bruikbaar is om de competitie van twee kruidachtige traitstrategieën langs een licht- en nutriëntengradiënt te simuleren, maar ook het belang van intraspecifieke variatie. Het model liet ook zien dat lineaire optimalisatie helder inzicht geeft in de belangrijkste filters, en daarnaast wordt de concurrentie tussen de traitstrategieën simultaan opgelost. Deze beide eigenschappen zijn niet gebruikelijk in veel bestaande competitiemodellen. En hoewel het ontwikkelde model nog niet in staat is om alle bevindingen vanuit de veldstudie en satellietdata te simuleren, kan het gebruikte modelconcept bijdragen aan het begrip van hoe filters en trait strategieën leiden tot de vegetatiepatronen die worden aangetroffen in uiterwaarden van gereguleerde laaglandrivieren.

Concluderend, in de uiterwaarden van de grote gereguleerde Nederlandse laaglandrivieren zijn beheer en menselijke ingrepen de belangrijkste filters die de uiterwaardvegetatie vormgeven. Binnen deze grootschalige filters detailleren andere filters, zoals natuurlijke verstoringen door overstromingen en gradiënten in resources, de samenstelling van de vegetatie in de uiterwaarden. De geïdentificeerde relaties tussen traitstrategieën en filters kunnen worden opgenomen in modellen om hypothesen te testen en scenario's te verkennen en zo het beheer van uiterwaarden te ondersteunen. Het uitgevoerde onderzoek heeft daarmee aangetoond dat het filter-trait concept toepasbaar is voor de uiterwaarden van grote, gereguleerde laaglandrivieren: het concept was in staat om de dominante filters voor de samenstelling van de trait strategieën te identificeren, waardoor essentiële informatie beschikbaar komt voor het balanceren van waterveiligheids- en biodiversiteitsdoelen in uiterwaarden van dit type rivieren.

Chapter 1

Introduction

1.1 Introduction

River landscapes, or riverscapes, are valued for their high biodiversity and other services they offer. The high biodiversity of riverscapes results from processes on several spatiotemporal scales (Naiman and Decamps, 1997). The spatial scales comprise a nested system of processes: climate, geology, and topography control the intermediate-scale geomorphic processes, which in turn shape distinct habitats on the small(er) scale. However, those smaller scale processes feed-back to the larger scale processes (Naiman et al., 2002; Figure 1.1).

Along the longitudinal dimension, climate, geology, and topography change, and as such the geomorphic processes and the resulting habitats (Ward et al., 2002). In the lateral dimension, the river shapes floodplain habitats through disturbances due to flooding and sediment dynamics. Those disturbances vary in space and time through year-to-year variation, but also through river meandering and small-scale variations in topography (Tockner et al., 2008). Once established, floodplain vegetation may interact with riverine processes by, for example, influencing a river's plan form (Tockner and Stanford, 2002; Gurnell, 2014).

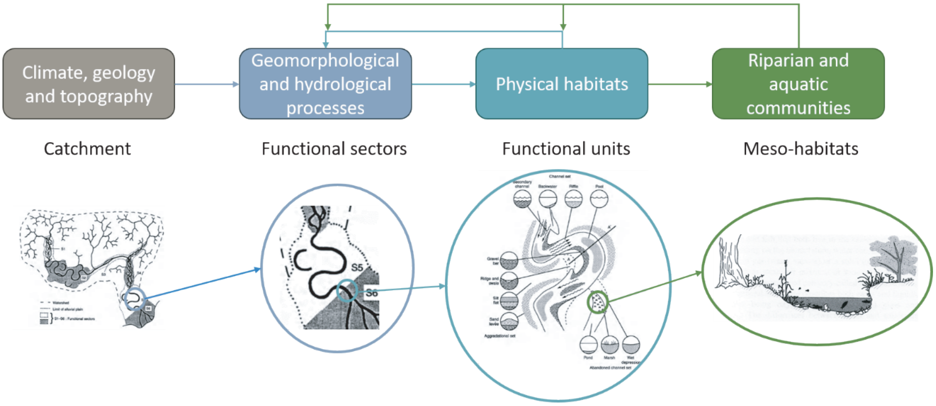

Figure 1.1: *Overview of the different processes, their scales, and their feedbacks. The terminology 'functional sectors, functional units and meso-habitat' stems from Petts and Amoros (1996) and is used to indicate that within catchments different combinations of processes lead to different sectors, units and therefore habitats. Adapted from Naiman et al., 2002 and Petts and Amoros, 1996.*

However, the ecological functioning of rivers and therefore their biodiversity is under threat, as rivers throughout the world are altered for human benefit. In the Northern hemisphere alone, almost 80% of the 139 largest rivers have been impacted by engineering works by the early 1990s (Dynesius and Nilsson, 1994), and this percentage has been increasing ever since (Richter and Thomas, 2007).

The drawbacks of these engineering works are all too evident. In the Netherlands, a country well-known for its water engineering, the dynamic processes of a natural riverscape has dwindled and the once biodiverse floodplains have either become frozen in time by floodplain management or evolved towards climax vegetation (Geerling et al., 2008).

To understand how river regulation affects the natural functioning of rivers and how this impacts biodiversity, this introduction describes firstly the context of the research: how river regulation and management affect the natural functioning of rivers and subsequently biodiversity. Then, the concept behind floodplain vegetation dynamics (the so-called 'filters') is introduced, which are the (a)biotic processes that select for certain combinations of characteristics of plant species (i.e. plant trait strategies). The introduction then continues with a description of the main filters in natural flowing rivers and how these are changed through anthropogenic interferences, like engineering works and management. This chapter concludes with the research questions and how these questions will be answered.

1.2 River regulation and floodplain management

Like in the rest of the world, the large lowland rivers of the Netherlands are also heavily engineered. To protect against flooding, dykes were built and to promote navigability and to safeguard arable floodplains, rivers were straightened and groynes were constructed (Havinga and Smits, 2000). However, this river course fixation contributed also to river bed incisions caused by increased flow velocities, decreased upstream water retention capacity, and reduced sediment availability due to upstream dams and bank and river bed protection (Bravard et al., 1999). Besides blocking sediment transport, the upstream dams, built to ensure water for drinking, irrigation, and electricity generation, also distort downstream discharge dynamics. This distortion, together with the hampered material transport, affects the ecological functioning of the river considerably (Buijse et al., 2002; Tockner and Stanford, 2002).

River engineering works not only impacted the main channel itself, but they also impacted the river's floodplains. Increasing levels of river regulation decreased the exchange of energy and materials (i.e. morphological interaction) between rivers and floodplains thereby changing the dominant selecting processes for floodplain vegetation (Ward, 1989). As a result of the dwindled morphological interaction between the river and its floodplain, floodplain vegetation evolved to its climax stadium (i.e. forest) instead of diverse and dynamic vegetation compositions. And exactly these diverse and dynamic compositions are key for the high biodiversity of floodplains of natural flowing rivers (e.g Tockner & Stanford 2002; Naiman et al. 2008; Tockner et al. 2008; Loheide & Booth 2011; Beechie et al. 2010).

Besides lower biodiversity, forested floodplains of regulated rivers may endanger flood protection due to increased flow resistance and subsequent higher water levels. Therefore, the area covered by shrubs and forests in floodplains of regulated rivers is often curtailed by interventions and management: excavation and redesign (e.g. creation of side gullies, lakes), clear-cutting of forests, active mowing and grazing by cattle (Baptist et al. 2004; Geerling et al. 2008). This rigorous floodplain management is at odds with environmental laws within the Netherlands, as many floodplains have been assigned as nature areas (NW4, 1999). Several regional and national programs, like 'Plan Ooievaar' (De Bruin et al., 1987), 'Room for the River' and 'Streamline' (Oosterloo and Otermann, 2016), were launched to comply with nature legislation while ensuring flood protection.

'Plan Ooievaar' was aimed at restoring nature and natural processes in former agricultural floodplains. The reduced morphological interaction and autonomy of biotic processes indeed allowed for vegetation succession, increasing the roughness of the floodplains. The risk of this was demonstrated during the major floods in 1993 and 1995 as the rivers' water levels rose dangerously high. To prevent the recurrence of those dangerous situations, the national programme "Room for the River" (Ministries of VROM and V&W, 1997) was launched in 2006. This programme aimed at preventing high water levels by increasing the area available for water conveyance during high discharges, and not by heightening dykes. The program also adopted the concept of cyclic rejuvenation, which focuses on restoring the floodplains' biodiversity potential, while still ensuring water safety (Duel et al., 2001). Cyclic rejuvenation mimics the effect of fierce fluvial erosion processes on vegetation by large-scale artificial removal of shrubs and forests in floodplains leading to a patchwork of succession stages while also (temporarily) reducing the roughness of the Dutch floodplains. The artificial removal of shrubs and forests was executed through project Streamline (2015/2016, Oosterloo and Otermann, 2016) and the management of floodplain vegetation for both water safety and biodiversity continues to be a focal point of the Dutch water authority (RWS, 2023).

To further the understanding of how the dwindled connection between regulated lowland rivers and their floodplains impact vegetation dynamics, this research investigates what processes (filters) in floodplains of lowland rivers alter vegetation dynamics, to support more effective floodplain management. As part of the RiverCare programme (Hulscher et al., 2016; RiverCare, 2013), the aim of this study supports the overall aim of the RiverCare programme, which was to develop knowledge and methods to gear towards self-sustaining multifunctional rivers. As such, the programme spanned a broad spectrum, divided over several subprojects that were as diverse as, amongst others, the functioning of longitudinal dams, sediment dynamics, valuation of ecosystem services and governance of floodplains (https://kbase.ncr-web.org/rivercare/).

1.3 Vegetation: traits and filters

A framework to understand how floodplain vegetation is steered by fluvial processes and human activity is the ‘filter-trait’ concept. Ever since Darwin’s ‘Origin of Species’ (Darwin, 1872), it is evident that environmental and biological conditions are steering floral and faunal composition and dynamics. In principle, abiotic and biotic processes, or ‘filters’, select species with specific traits or a set of traits (i.e. trait strategy) capable of coping with the prevailing conditions (Keddy 1992). So, along a gradient of one filter, for example soil moisture, different compositions of trait strategies are selected: high soil moisture select for trait strategies capable to manage anoxic root conditions and low soil moisture select for trait strategies specialized in water saving (Figure 1.2).

The first structured conceptual models on the filter-trait concept appeared in the early 1970ies and have been developed further since then. In 1974, Grime presented his C-S-R scheme (i.e. <u>C</u>ompetition, <u>S</u>tress tolerant and <u>R</u>uderal strategies) in which it was demonstrated that specific plant characteristics, like life span and growth rate, could be coupled to environmental conditions, thereby providing a mechanistic approach to how environmental conditions select for certain plant trait strategies (Grime, 1974) . In the decades that followed the publication of Grime, the C-S-R scheme evolved into the global spectrum of plant form and function (Diaz et al., 2016). This global spectrum comprises six major plant traits that explain the presence and absence of plant species across the earth’s terrestrial biomes: adult plant height, stem specific density, leaf area, leaf mass per area, nitrogen content per unit leaf mass, and diaspore mass.

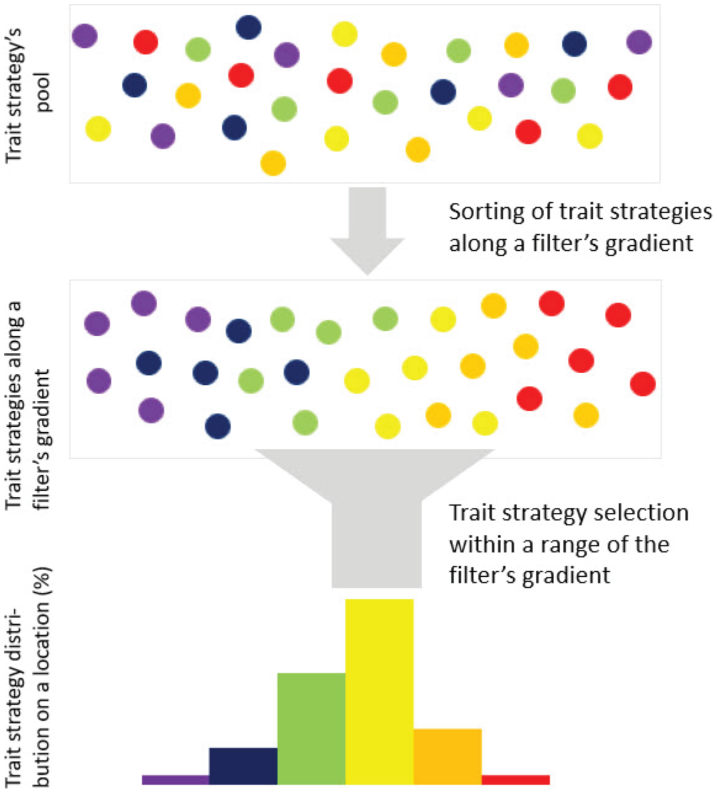

Figure 1.2: *Schematic representation of the filter-trait concept. At the top the trait strategy's pool is depicted as a random composition of trait strategies. Along a gradient of a filter, the trait strategies are ordered (mid part), and when looking at a specific location, the filter's prevailing value selects for a certain distribution of trait strategies (lower part). Adapted from Laughlin et al. (2012).*

In fluvial systems, the filter-trait concept has also been successfully applied. For example, in floodplains of natural flowing rivers the lifespan and lifeform of plant species have been related to the recurrence time of floods (Southwood 1988; Merritt et al., 2010). However, the sparse studies on the filter-trait interaction in floodplains of regulated rivers and their vegetation did not find univocal evidence of such links (Ordoñez et al., 2010; Douma et al., 2012; Baastrup-Spohr et al., 2015; Baattrup-Pedersen et al., 2015). Additional research might disclose the potential of the concept for managing flood protection and nature in those floodplains.

If the most dominant filters for vegetation dynamics in floodplains of regulated rivers can be identified and linked to specific trait strategies, this allows for predicting the development of floodplain vegetation by models: where and how quickly does vegetation develop, and what measures would lead to optimization of water safety and nature in terms of costs, efficiency, and biodiversity? The existing river-floodplain models that explore the effects of for example management on floodplain vegetation development mostly rely on the effects of physical drivers for vegetation development and empirical relations between river dynamics and plant demography (i.e Benjankar et al., 2011; Harper et al., 2011; Stella and Battles, 2010). Also in the Netherlands (conceptual) models are used, like those of Peters et al. (2002), Baptist et al. (2004) and Straatsma et al. (2019). However, those models lack an explicit mechanistic link between filters and plant trait strategies and omit plant (trait strategy) competition as a process, which is, in floodplains of regulated rivers, an important filter (Bornette et al., 2008).

In a multi-stressor system, which floodplains of regulated rivers are, the general modelling approaches result in a (too) simplified and limited representation of the effects of river regulation and measures on floodplain vegetation dynamics. One of the causes of the simplification is a limited understanding of the dynamic interaction between filters and trait strategies. Additionally, as models often focus on specific species rather than trait strategies, the mechanistic link between filters and species may remain both implicit and geographically specific. And lastly, modelling plant (trait strategy) competition is challenging and has often several shortcomings, like solving competition on a first come first serve principle in terms of code (e.g. Kiniry et al., 1992) or a biomass or plant volume ratio (e.g Soussana et al., 2012; DeMalach et al., 2016). Providing a link between filters and trait strategies and adding competition as a filter, allow those models to become more realistic as, for example, the effects of interacting measures can be simulated as well as the resilience of plant trait strategies to the effects of climate change, measures, or management.

1.4 Filters in natural flowing rivers

In natural flowing rivers, the filters shaping the trait strategy composition originate directly or indirectly from a river's flow regime. The flow regime comprises five components regarding a river's discharge: magnitude, frequency, duration, timing and the rate of change of discharges (Poff and Ward, 1989). Each of these five components is an important filter and are the base for other important filters, like the morphological filter, of a river's ecosystem. Directly connected to a river's flow regime are for example seasonal peaks and inter-annual peaks in discharge. Seasonal peaks may act as cues for floral and faunal characteristics and dynamics, like plant species life span and growth form, or fish migration and spawning. Inter-annual peaks may rejuvenate floodplains and remove alien species that are not suited to survive flooded conditions, from the system. Indirectly, annual high flows shape the channel morphology providing various substrates that accommodate different vegetation, macrofauna and fish species, while base flows may ensure water and lead to increased prey density (Poff et al., 1997). As the flow-regime and morphology filters are tightly coupled, these filters are in the remainder of this chapter referred to as the hydro-morphological filter.

An important aspect of the flow regime and concurrent filters is its four dimensions: longitudinal, lateral, vertical and temporal (Figure 1.3, Petts and Amoros, 1996). The longitudinal dimension was first formalized in the River Continuum Concept (Vannote et al., 1980), which was later broadened by the lateral dimension in the Flood Pulse Concept (Junk et al., 1989; Junk and Wantzen, 2004). The third dimension, the vertical one, is the interaction of the river with groundwater flows and the river's sediments (Hynes, 1983). The temporal dimension is often implicitly woven into the other three dimensions, by assuming changes in the river's discharge, i.e. its flow regime. Those four dimensions differ spatially, fuelling the high biodiversity values and productivity of fluvial ecosystems (Ward, 1989; Junk et al. 1989).

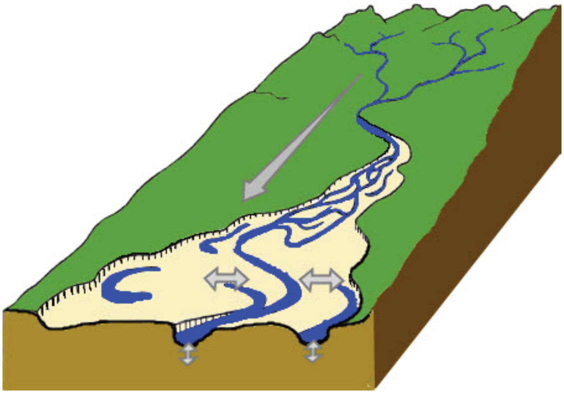

Figure 1.3: *Overview of three spatial dimensions in a fluvial system. Indicated with grey arrows are the longitudinal, lateral and vertical dimensions (adapted from Petts and Amoros, 1996).*

Because of the dominance of the hydro-morphological filter in floodplains of natural flowing rivers, those floodplains accommodate a multitude of patches of different plant trait strategy compositions (Naiman and Decamps, 1997). This filter selects for trait strategies that can quickly colonize bare sediments and reproduce before erosion washes away the substrate (e.g. Bravard et al. 1986; Petts & Amoros 1996; Naiman et al. 2010). The dominance of the hydro-morphological filter is governed by a floodplain's topography and the distance to the river: on higher grounds and farther away from the river, this filter becomes weaker and other fluvial filters, like inundation and soil moisture, become more pronounced in filtering plant trait strategies. Gurnell et al. (2016) conceptualized this by coupling distance to the river to prevailing filters and concurrent plant trait strategies (Figure 1.4).

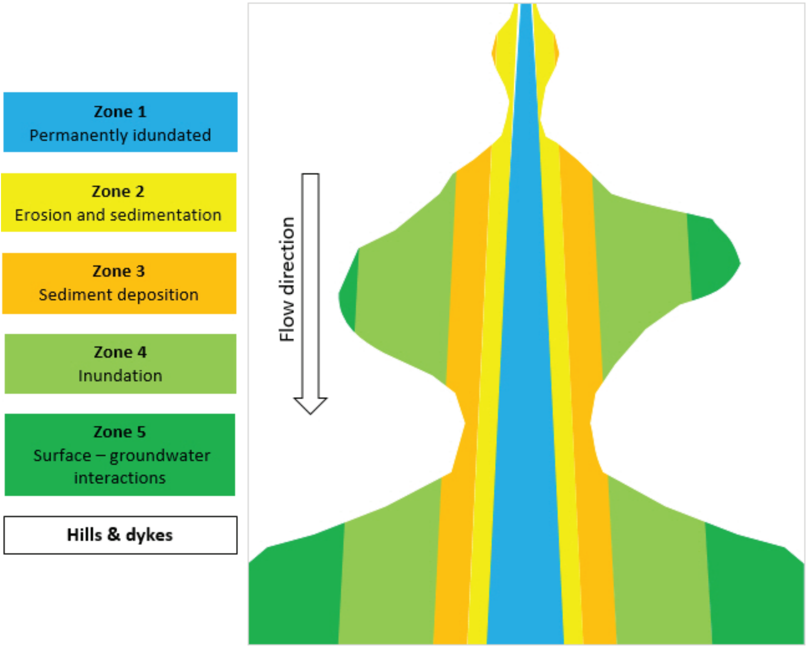

Figure 1.4: *Schematic representation of five zones where different filters for vegetation composition prevail (adapted from Gurnell et al., 2016). Note that the presence of side gullies is lacking.*

1.5 Filters in regulated rivers

The dwindled importance of the hydro-morphological filter for plant trait strategy composition in floodplains of regulated rivers is apparent: without human intervention, those floodplains become much more uniform and forest dominated compared to floodplains of natural flowing rivers (Petts & Amoros 1996; Hughes et al. 2001; Tockner & Stanford 2002) as the dominant filters for floodplain vegetation change (Ward, 1989). But what exactly changes when rivers become regulated? What processes become dominant and hence what filters emerge from changed fluvial processes that shape trait strategy composition? Generally, by changing a river's natural dynamics that have been shaping its floral and faunal community for centuries (Naiman and Decamps, 1997, Poff et al., 1997), anthropogenic interference leads to the dominance of more indirect filters, like inundation, drought and competition filters at the expense of the hydro-morphological filter (Bornette et al., 2008). It depends on the anthropogenic interference of how a river and its floodplains are impacted.

River channelization and dams distort a river's longitudinal and temporal dimensions by affecting the components of the flow regime (Poff et al., 1997). However, the effect of those river-engineering works on those dimensions differs. River channelization shortens the river length, leading to increased magnitude and rate of change of discharges, and a decreased duration of peak flows. Dams alter water flow by storing and releasing water and by that modifying high and low flows and the general dynamics of peak flows (Bunn and Arthington, 2002). Changes in frequencies, duration and timing of peak flows alter the inundation dynamics of floodplains, and often lead to drier floodplains as frequencies and duration of peak flows decrease (Tockner and Stanford, 2002). The text below explains in more detail the different effects and is summarised in Figure 1.5.

Changes in inundation dynamics through changes in frequencies, duration and timing of peak flows filter specific trait strategy composition of floodplain vegetation. For example, the timing of the growth, flowering or senescence season may change (Greet et al., 2011, 2013), as well as the need for aerenchyma formation, a survival mechanism to withstand longer periods of anoxic conditions (Van Eck et al., 2004). Moreover, more competitive (terrestrial) trait strategies are selected for when river channelization and dams lead to drier floodplains: the need to cope with adverse effects of periodically wet conditions, either by inundation through surface or groundwater, lessens (Londo, 1975).

Besides affecting a river's flow regime, river channelization increases the flow energy. This reduces sedimentation within the main channel due to higher flow velocity and causes river bed incision (Howard et al., 1994). The consecutive effect of river bed incision is, besides undermining constructions and cables, increased drought periods in floodplains because of lowered groundwater tables and a decreased flooding frequency (Bornette and Heiler, 1994; Bravard et al., 1997; Hupp and Rinaldi, 2007). So, also via river incision and groundwater lowering, river channelization may filter more competitive plant trait strategies compared to plant strategies of unchanneled rivers (Merritt et al., 2010).

Dams too have effects on trait strategy composition. Besides changing the discharge regime, dams trap sediments and plant tissues like seeds and vegetative parts. This trapping not only reduces the nourishment of sediment downstream of the dam but also hampers the passive dispersion of species pools (Naiman and Decamps, 1997). The effect of hampered passive dispersion may have a relative effect on the species pool downstream of the dam (Poff et al., 1997), and hence plant trait strategy composition. Diminished sediment loads enhance river incision, leading (also) to drier floodplains and hence impacting trait strategies. Diminished sediment loads caused by dams also reduce sedimentation and change sediment size composition within floodplains. The combination of landscape layout and sediment size composition is a spatially heterogeneous filter for plant trait strategy composition (Nilsson and Svedmark, 2002; Wassen et al., 2003) as the combination governs sediment texture and hence water retention capacity and nutrient availability (Middelkoop and Van der Perk, 1998; Huang et al., 2013).

Dykes and groynes distort mostly the lateral dimension by fixating both the course of the river and the area prone to flooding (Junk et al., 1989). This lateral distortion reduces the extent of exchange of both material and energy. Dykes confine the flood-prone areas, leading to greater inundation depths when flooded and may therefore recharge groundwater. Greater inundation depths may filter plant trait strategies that can cope with longer periods without oxygen (aerenchyma) and diminished light (elongation) (van Eck et al., 2004).

Groynes reduce sediment loads by fixating the course of the river: no new areas, either lateral or vertical, can be eroded easily because of armoured river banks and beds. And, again, a shortage of sediment leads to less sedimentation and hence river channel incision (Bravard et al., 1999), in which the bed lowering of 2 cm/year of the Dutch part of the River Rhine is confirmed by the data analysis of Berends et al. (2021). This lowering of the bed translates to the drying of floodplains and corresponding plant trait strategies. Reduced suspended sediments (including associated compounds like nutrients) decrease sedimentation in floodplains, reducing the nutrient availability for plant uptake. This may lead to the selection of plant trait strategies tailored to nutrient-poor conditions. Also, less sediment input may lead to a different, more homogeneous sediment size composition compared to a situation without groynes (Vauclin et al., 2019).

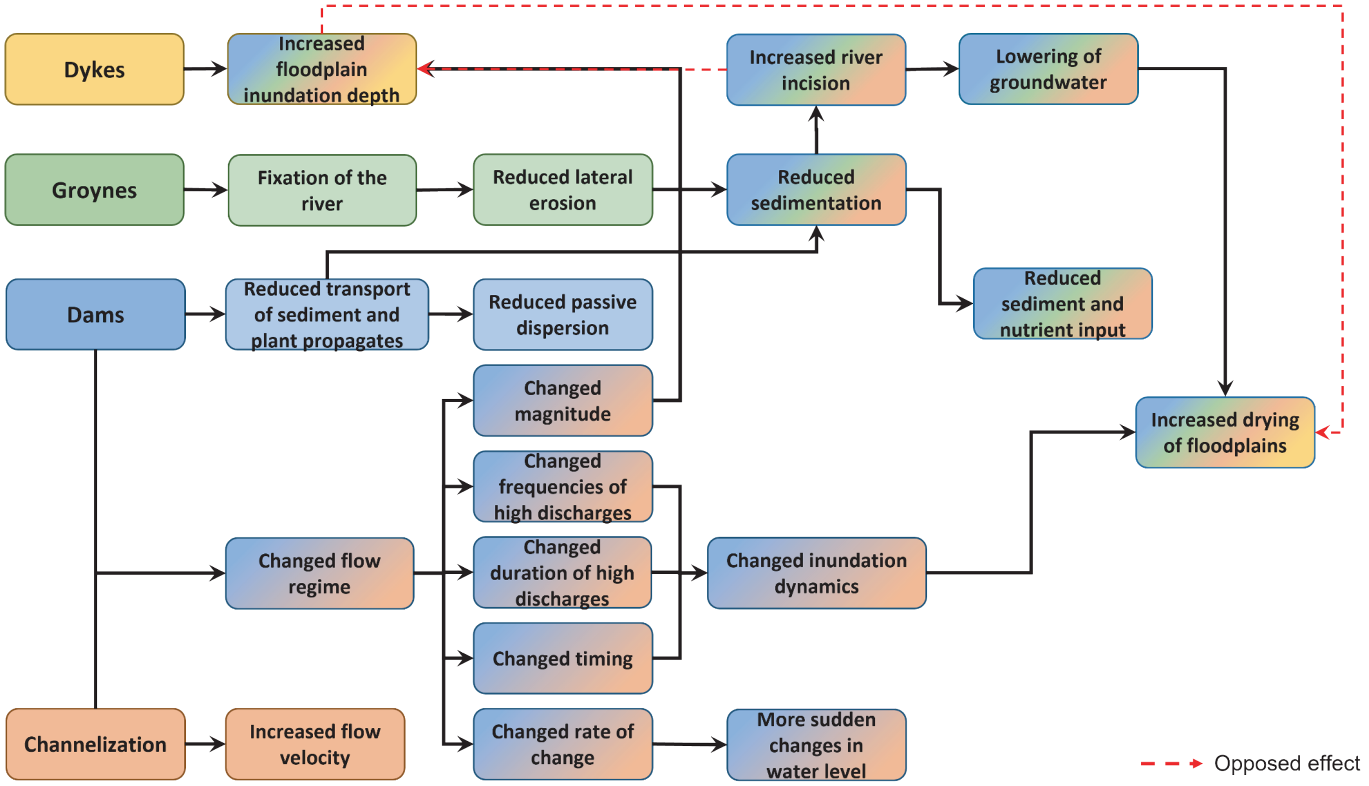

Figure 1.5: *Flow chart of general impacts of engineering works on the filters for vegetation composition in floodplains compared to natural flowing rivers. The links between the boxes are explained in the text of section 1.4. The different coloured boxes represent different types of engineering works: yellow: dykes, green: groynes, blue: dams, and orange: channelization. The multi-coloured boxes represent the effect of multiple engineering works and the red arrow indicates the opposed effect of what is written in the boxes.*

Besides the effects of engineering works on fluvial ecological functioning and its effects on trait strategy composition in floodplains, another source of potential filters is floodplain management. In the Netherlands, management of vegetation in floodplains of regulated rivers often comprises excavation and redesign, clear-cutting of forests, and active mowing and grazing by cattle of grass and herbaceous vegetation (Baptist et al. 2004; Geerling et al. 2008). These measures emanated from the idea that vegetation succession is allowed where it does not interfere with water safety, allowing for a variety of vegetation age structures while not putting water safety at risk. This is a daunting task as insight is required into where nature may develop, where reset is mandatory and how vegetation develops, to be able to steer towards a heterogenous floodplain vegetation composition while water safety standards are still met.

1.6 Research aim & outline of the thesis

The filter-trait concept holds a great premise to improve the understanding of vegetation development in floodplains of regulated rivers and hence to use that knowledge in management tools to improve the management of those floodplains. However, the usefulness of the concept for floodplains of regulated rivers could not yet be demonstrated, and as such, it remains unclear whether the concept can be used to pinpoint filters and link them to trait strategy compositions. As such it also remains unclear whether this concept can be used to make predictions on how trait strategy compositions change when measures are taken, management changes or due to climate change. Therefore, the main research question of this thesis is:

> *What are the main steering processes shaping vegetation patterns in floodplains of regulated lowland rivers and how can this knowledge be used in floodplain management?*

With the following sub-questions:

1. What does the filter-trait concept add to the understanding of vegetation composition in floodplains of regulated lowland rivers?
2. What are the main filters that govern the vegetation dynamics in floodplains of regulated lowland rivers and are those filters scale-independent?

3. How can the knowledge of the filter-trait concept, as underpinning for the dynamics of plant trait strategies in floodplains of regulated rivers, be translated into a modelling approach?

The main and sub-questions are answered in Chapters 2 through 5, in which a combination of field studies, satellite images, and models are used (Figure 1.6). This combination of three different research approaches, or triangulation approach, combines the advantages of the three approaches and overcomes limitations of each of them:

- field studies are precise but labour-intensive, expensive and limited in temporal resolution,
- satellite images are easy to come by and have a high temporal resolution, but have a coarse spatial resolution and have no to limited information on actual processes,
- models can be precise with high spatiotemporal resolution but are only as good as the knowledge or data that is available through, amongst others, field studies and earth observation data. Additionally, models can pinpoint what knowledge is missing in understanding floodplain vegetation dynamics.

In Chapter 2 the field research is described, in Chapter 3 the research based on satellite image and Chapter 4 presents the developed model. Below the details of the chapters are presented. Chapter 5 encompasses the synthesis of the foregoing chapters, the conclusions and recommendations.

Chapter 2: Linking plant strategies to environmental processes in floodplains of lowland rivers

In this chapter, the first sub-question is addressed by collecting and analysing field data. In each of three floodplains along the regulated Dutch Rhine branches ten 1 m^2 field plots were marked. In these plots, vegetation was mapped, several traits of the dominant plants were measured, soil samples were taken and the height of the plot relative to the mean summer river water level was measured. The soil samples were taken to extract information on filters like soil moisture, grain size, nutrient and carbon content. Those filters were complemented with information on grazing, summer inundation and being excavated or not. Using clustering techniques, links between filters and trait strategies were identified. The findings of the fieldwork also contribute to answering sub-question 2 by identifying filter-trait relations on field scale.

Chapter 3: Revealing 35 years of landcover dynamics in floodplains of trained lowland rivers using satellite data

This third chapter also contributes to sub-question 2, as it describes how satellite data was used to link filters to landcover classes. LandSat data (LandSat missions 5 and 8, 30*30 m spatial resolution) was classified into six landcover classes: water, bare substrate, grass, herbaceous vegetation, shrubs and forest. Succession and retrogression rates of those land cover classes were analysed for the available period of 35 years on three different scales: the whole regulated Dutch Rhine river, its three Dutch branches, and five floodplains within those branches. On floodplain scale, the succession and retrogression rates of the different land cover classes were linked to interventions (e.g. floodplain lowering) and management (e.g. grazing pressure) filters.

Chapter 4: Linear Programming as a tool for understanding plant species interactions

Chapter 4 addresses the third sub-question, as in this chapter a mechanistic model is developed that explicitly includes the filter-trait strategy concept, including the competition filter to allow for a better understanding of what is driving trait strategy composition. The model is based on literature and field data from Chapter 2, and uses a combination of linear programming and differential equations, in which the linear programming is used to model competition to overcome often encountered difficulties in plant competition models regarding resource acquisition and use. The model includes a light and nutrient gradient and two trait strategies: a competitive trait strategy and a nutrient-conservative trait strategy. The developed model demonstrated how linear optimization allows for in-depth analyses of the dominant filter(s) for trait strategy composition and has the potential to include resilience of trait strategies against disturbances (natural or anthropogenic). The presented modelling approach can therefore aid in understanding how spatiotemporal dynamics steer plant trait composition, hence supporting effective floodplain management.

Chapter 5: Synthesis

This chapter reflects on the three sub-questions answered in chapters 2 through 4 and how the three different research approaches (field data, remote sensing data and model use) complement each other. Based on this reflection the main research question is answered.

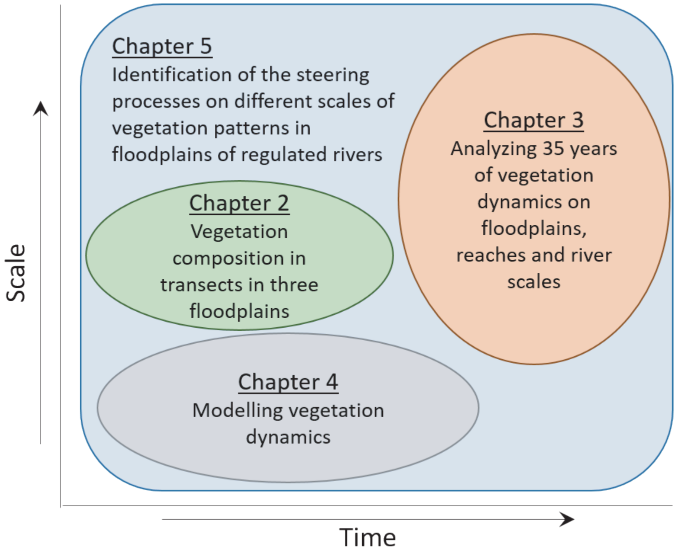

Figure 1.6: *Relation between the spatiotemporal scales of the different chapters, with the time scale on the x-axis and the spatial scale on the y-axis.*

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Chapter 2

Linking plant strategies to environmental processes in floodplains of lowland rivers

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Abstract

The successful use of relations between environmental processes (filters) and either plant trait or plant strategy (i.e. concurrent species traits) composition has boosted ecological research. Various studies identified environmental filters shaping plant species composition. However, this approach is scarce in research on vegetation succession in floodplains of heavily modified rivers. Especially in these ecosystems, mechanistic knowledge is needed to understand ecological effects of human interventions and to develop strategies for floodplain rehabilitation. The aim of this study is therefore to explore whether the application of the filter—strategy concept reveals a better understanding of environmental drivers for vegetation succession than analyses of just species composition. And if so, could this information support floodplain management? Ten plots (1 m^2) with herbaceous vegetation were marked in each of three floodplains along two distributaries of the Rhine River in the Netherlands. For each plot, environmental filters for establishment of plant species were measured (e.g. soil moisture, soil nutrient content and grain size). Data on species composition of vegetation and plant strategies, like life and growth form, were collected.

The data were analyzed using the combination of fuzzy clustering and multiple regression trees. Both species composition and filter-plant strategy composition reflected a soil moisture and nutrient gradient, but the filter-plant strategy analyses also revealed the importance of disturbances (excavation and summer inundation) for shaping vegetation composition. The plant strategy composition supplemented species surveys and benefitted understanding species assembling by anthropogenic disturbances and the tipping points of filters for plant strategy composition. Moreover, application of the filter-plant strategy concept can provide insight in functional diversity, biomass and hydraulic roughness of vegetation and may support decision making on the optimization of floodplain functions.

2.1 Introduction

Plant communities are structured through environmental filtering (Keddy 1992). Environmental filters select those species that have the most fit traits or set of traits (i.e. strategies) to establish viable populations. The interaction between plant strategies and abiotic and biotic processes (i.e. the filter-strategy concept) is not species specific and allows for mechanical understanding and prediction of how vegetation dynamics are steered by environmental filters. The filter-trait concept has been successfully applied in various field studies and for different filters and traits and strategies (Douma et al., 2012; Baastrup-Spohr et al., 2015; Laughlin et al., 2015). The concept was also used for the development of both conceptual (Wright et al. 2004; Merritt et al., 2010; Gurnell et al., 2016; Diaz et al. 2016) and mathematical plant trait models (Shipley et al. 2006; Laughlin et al. 2012).

The filter – trait concept has also been applied to riverine ecosystems. In natural flowing rivers, fluvial disturbances steers vegetation composition in areas that are permanently, frequently, and regularly inundated. In occasionally or rarely inundated areas, inundation and soil moisture are the dominant steering filters for vegetation composition (Bornette et al. 2008; Gurnell et al., 2016). Nowadays, the hydromorphology of most rivers in temperate areas is modified, leading to unnatural disturbance regimes in river channels and adjacent floodplains. Straightening of channels increases flow velocity and discharge, while the construction of embankments blocks the exchange of sediment, nutrients and biota between rivers and their floodplains and increases inundation depths. Inundation is also more sudden and last longer (Sýkora et al. 2009), but local depressions in floodplains may still experience gradual inundation dynamics because of coupled groundwater - river level dynamics (Ledoux et al. 1989).

In heavily modified river systems the areas that were frequently and regularly inundated are greatly diminished in size, yet, those heavily modified rivers still influence vegetation composition in their floodplains by the timing, frequency, predictability, duration and magnitude of flooding, but in an indirect way (Mahoney and Rood, 1998). During flooding, oxygen concentrations and light availability are lowered. The impact on vegetation depends on the timing of the inundation. The effect is more pronounced during the growing season, than during winter, when vegetation survives through either seeds or belowground organs (Van Eck et al. 2004). Another indirect effect of flooding is the supply of sediments and nutrients to floodplains, which results in spatial heterogeneous floodplain sediments (Middelkoop and Van der Perk, 1998). The sediment composition subsequently controls physical and chemical soil characteristics such as soil moisture (Huang et al. 2013), which is on its turn steered by ground water dynamics (Woessner 2000).

The flow regime of a river and a floodplain's topography both control the spatial sediment composition and hence soil moisture and nutrients concentrations in the floodplains of heavily modified rivers. As such, those two drivers steer floodplain vegetation composition of heavily modified rivers (Vervuren et al., 2003; Van Eck et al., 2006; Thonon et al., 2007). When those floodplains are also managed to, for example, provide flood protection, grazing pressure or mowing regimes are also important filters, and may even overrule natural biotic processes (Baptist et al. 2004; Geerling et al., 2008).

Several studies indicate the convergence of plant strategies under specific environmental filters. On sandy, dry sediments, plant strategies are filtered that can cope with poor water and nutrient conditions, like the so-called scleromorphs (Ellenberg and Leuschner, 2010), the conservative species of the leaf economic spectrum (LES, Wright et al. 2004; Diaz et al. 2016) and the grass growth form (Grime et al. 1997). In contrast, resource rich sediments select for more competitive plant strategies, like phreatophytes (Londo 1975), hygromorphs and mesomorphs (Ellenberg and Leuschner, 2010), the acquisitive strategies of the leaf economic spectrum (Diaz et al. 2016), and forbs (Grime et al. 1997). When an area is grazed or mowed, sturdier leaves are favored (an increase in leaf mass per leaf area) and the rosette growth form is more abundant then in non-grazed or — mown areas (Golodets et al. 2009; Violle et al. 2011). Additionally, specific floodplain conditions such as the amount of grazers, large open areas and the timing of the retreat of winter flooding may filter specific seed morphology (e.g. nuts, feathers and hooks) and timing of germination (Römermann et al. 2005). Figure 2.1 schematizes the environmental filtering of floodplain plant with various strategies to cope with of altered disturbance regimes in heavily modified rivers.

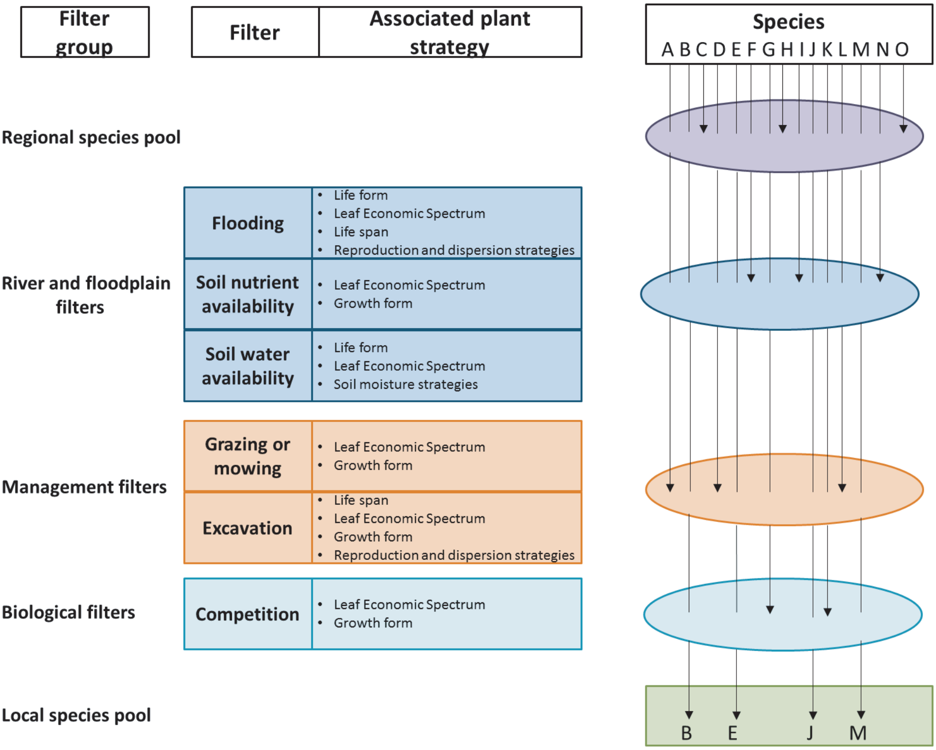

Figure 2.1: Conceptual framework of relations between various types of environmental filters and plant strategies. Left: the different levels of filter groups, middle: the different filters connected to strategies, and right: a schematic overview of how species are filtered.

In the Netherlands, the floodplains of the major rivers, which has been actively modified since hundreds of years (ten Brinke, 2005), fulfil several functions, of which flood protection and nature conservation are the key ones, but they are but conflicting (Geerling et al. 2008). And even though measures are taken to optimize those two functions, mechanistic knowledge on vegetation dynamics is lacking. As the premise of the filter-strategy concept is to mechanistically link environmental filters to plant traits or strategies and vice versa, the goal of this study is to analyze whether 1) the filter—strategy concept could identify and discern between dominant filters better than species composition alone, and 2) if this information could be helpful in assisting floodplain management. The fieldwork set-up is based on elevation gradients and focused on grass and herbaceous vegetation, as those vegetation types react faster to changes in filters than shrubs and trees (Stromberg and Merritt 2016).

2.2 Material and methods

The research was a combination of fieldwork, labwork, and data-analyses. This order is kept in the description of this section, and to facilitate ease of reading, this order is depicted in Figure 2.2.

2.2.1 Study sites

In 2016, fieldwork was carried out in three floodplains along two distributaries of the Rhine River in the Netherlands (Figure 2.3). Two floodplains are adjacent to each other and located along the Waal River: the Erlecomse Waard (56 ha) and the Millingerwaard (365 ha). The third floodplain, the Duursche Waarden (120 ha), is located along the IJssel River. The Duursche Waarden has been converted from agriculture to nature in 1989. Since the early nineties the Millingerwaard has been gradually converted from agriculture to nature. The Erlecomse Waard followed about 10 years later. The Duursche Waarden is grazed year-round by 0.2 Highland Cattle/ha and 0.15 Shetland ponies/ha. The Millingerwaard is also grazed year-round by 0.6 grazers per ha (Galloways and Konik horses). The Erlecomse Waard is grazed by 0.9 Galloway cows per ha during April and November only. During May and June of 2016, a summer flood partially inundated all floodplains.

2.2.2 Data collection

In each floodplain, ten plots (1 m^2) with herbaceous vegetation were marked. To maximize coverage of the elevation, and hence water and nutrient gradients, the plots were laid out in transects. Such an experimental set-up allows for detection of drivers and response variables in multivariate systems (Kreyling et al., 2018). Ideally, in all three floodplains, the plots should have covered the main levee to reflect a broad elevation gradient. This was accomplished in the Duursche Waarden only, as in the Erlecomse Waard a full gradient was prevented due to restricted access because of endangered bird species and in the Millingerwaard dense shrubs blocked further access. The exact plot locations were set by dividing the transects into elevation segments. In each segment the location was picked randomly. Additionally, in the Duursche Waarden long-time exclosures were present. Two plots were placed within the exclosures and two plots adjacent to the exclosures for researching possible effects of grazing. Possible effects of excavation were looked into by placing three plots in a newly excavated area in the Millingerwaard. To compare with no excavation, three plots were selected at the same height in the Erlecomse Waard. Figure 2.3 gives an overview of the elevation of the plots and their aerial view.

Throughout fieldwork in June 2016, soil samples were collected during one event. For each plot, three cores at 0–10 cm depth were taken. Those cores were mixed, and subsequently analyzed for soil water and organic matter content, grain size distribution, carbon, nitrogen and calcium concentrations. Table 2.1 lists the used analyses techniques and the proxies used to represent filters. In the remainder of the paper, proxies are referred to as filters. Supplementary material S2.A lists the collected data on filters.

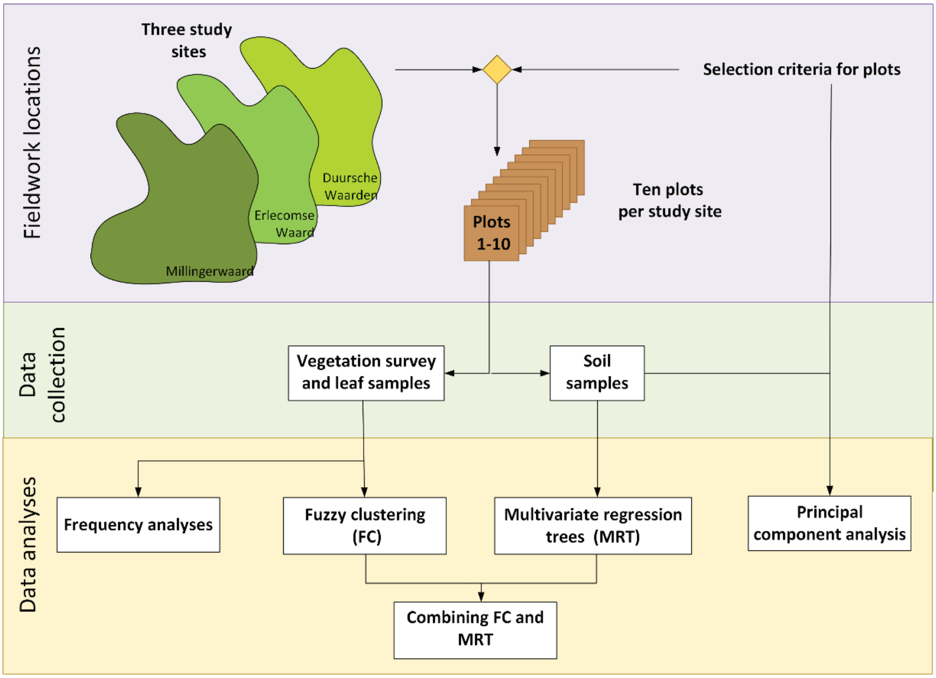

Figure 2.2: Overview of the workflow of the research. The upper compartment contains the fieldwork set-up, the middle compartment what data has been collected and the lower compartment the different data analysis techniques used.

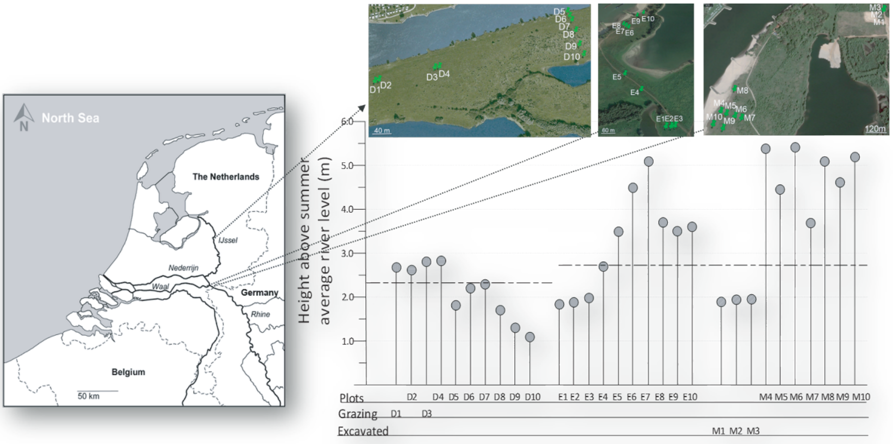

Figure 2.3: Elevation of the field plots relative to summer average river level. The plots are ordered by floodplain and according to plot number. The interrupted, horizontal line indicates the inundated plots (below) and the non-inundated plots during the summer flood of 2016. Above the plot elevation the field locations of the plots in the three floodplains (Google Earth), and at the left-hand side the location of the floodplains within the Netherlands.

In mid-July 2016, one vegetation survey was performed for all 30 plots using the Braun-Blanquette method. The vegetation compositions were used to obtain a) species coverage and b) plant strategy coverages (e.g. life span, growth form, groundwater dependence). Information on plant strategies was extracted from the TurboVeg database (Hennekens and Schaminée, 2001), except for the leaf economic spectrum (LES), as this spectrum uses measured leaf nitrogen, mass and area. Per dominant species (plot coverage >8%, chosen for pragmatic reasons) 12 leaves of several healthy-looking individuals were collected. For some of the dominant grasses no leaves could be collected as leaves were collected two weeks after the vegetation survey and by then some grass species ceased flowering, obstructing species identification with high certainty.

The used data analyses (see below), allows for only one dataset for the filters, one for the species and one per plant strategy. As for the leaf economic spectrum, often several species per plot were measured, and to avoid averaging of the measured values, the data for the leaf economic spectrum were split in two datasets, LES_H and LES_L. LES_H contained the species with the highest leaf nitrogen and associated leaf mass per area and leaf area per plot. LES_L contained the species with the lowest leaf nitrogen and associated leaf mass per area and leaf area per plot. Table 2.1 lists the links between strategies and filters, together with the methods used for data collection. Note that a strategy comprises several classes, for example, the strategy life span is comprised of the four classes annuals, biannuals, herbaceous perennials and woody perennials (i.e. tree saplings). Supplementary material S2.B lists the strategy classes together with a short explanation and Supplementary materials S2.C and S2.D the collected vegetation compositions and concurrent plant strategies.

Table 2.1: *Overview of the filters and strategies (between brackets, where applicable, the used abbreviation, classes and units), data collection method, what the proxy represents or what the strategy indicates and key references.*

Filters	Method	Proxy	References
Soil moisture availability (SoilM, mass %)	Oven dried, 24h at 105°C	Water availability	Silvertown et al. 1999; Silvertown et al. 2015.
Soil total carbon (CSoil, mgC/g soil)	Fisons NA 1500 NCS mass spectrometer	Organic matter content of soil and thereby nutrient availability	Van der Werf et al. 1993
Soil total nitrogen (NSoil, mgN/g soil)	Fisons NA 1500 NCS mass spectrometer	Nutrient availability	Van der Werf et al. 1993
Soil calcium content (Ca, mgCa/g soil)	Thermo Scientific XRF	pH value	Bohn et al., 1985
Soil organic matter content (L550, %)	Loss on ignition at 550^{0}C	Nutrient availability	Pansu and Gautheyrou 2006
Grain size (Lutum, Silt, and 6 sand fractions,-)	Sieving	Water availability, nutrient availability.	Kettler et al. 2001; Wösten et al. 2001; Huang et al. 2013
Soil type (Stype, classes 1-3, -)	Combination of grain size and soil type classification	Water availability	Wösten et al. 2001
Being flooded in summer of 2016 (Flooded, classes 1-4, -)	Comparison of river level summer 2016 and plot elevation	Light and/or oxygen deprivation	Blom and Voesenek 1996; Mommer et al. 2006; Van Eck et al. 2006
Excavation (Exc, yes/no)	Excavated plots	Secondary succession	Geerling et al. 2008

Table 2.1 (continued)

Strategies		**Indication**	
Leaf Economic Spectrum (LES, ordination coordinates)	SIOX plug-in FIJI software (leaf area); Leaf mass (dry weight): balance; LMA: Leaf mass/Leaf area; LeafN: Fisons NA 1500 NCS mass spectrometer	Water and nutrient economics, grazing pressure, acquisitive vs conservative strategy	Givnish 1987; Westoby et al. 2000; Westoby et al. 2002; Wright et al. 2004; Diaz et al. 2016
Life form (8 classes)	Turboveg software[2]	Harshness of living conditions	Raunkiaer 1934
Life span (4 classes)	Turboveg software[2]	Magnitude of river dynamics	Merritt et al. 2010
Growth form (4 classes)	Turboveg software[2]	Acquisitive vs conservative strategy, grazing pressure	Siebenkäs et al. 2015
Anatomy (5 classes)	Turboveg software[2]	Gas and water exchange capabilities	Mueller-Dombois and Ellenberg 1974
Groundwater dependence (5 classes)	Turboveg software[2]	Wetting of seeds for germination, water availability, nutrient availability	Londo 1975
Onset of flowering (5 classes)	Turboveg software[2]	Competition, disturbance (grazing, flooding)	Weiher et al. 1999
Pollination method (2 classes)	Turboveg software[2]	Open vs closed vegeation	Culley et al. 2002
Seed morphology (7 classes)	Turboveg software[2]	Dispersal method	Römermann et al. 2005
Germination period (11 classes)	Turboveg software[2]	Timing to right conditions	Blom and Voesenek 1996

[1]: Those indicators are combined into LES_H and LES_L, see main text for explanation.

[2]: Hennekens and Schaminée 2001.

2.2.3 Data analyses

To characterize the floodplains, a principle component analyses (PCA, mean = 0, SD = 1) on the filters was performed, followed by a frequency analyses of the strategies. To be able to link filters to species and plant strategy composition, two clustering techniques were used. The first clustering technique was fuzzy clustering (FC) and is an unconstrained clustering technique and hence clusters the plots together that resemble each other in terms of species or strategy composition. Besides, the FC analyses shows how much a plot belongs to different clusters, giving information on how well a cluster suits a plot (Kaufman and Rousseeuw 1990). FC was applied to the species dataset and per plant strategy dataset. To actually link filters to a plot's species and plant strategy composition multivariate regression trees (MRTs, De'ath 2002) were used. Unlike generalized linear models and generalized additive models, MRTs can handle nonlinear relationships and higher order interactions. The key of using FC and MRTs together is that combined results of both techniques indicate the strength of the link identified by the MRT (Borcard et al., 2011).

Comparing the results of the FC and the MRT analyses can give three different results: 1) both techniques separate the same clusters, suggesting a strong link between the identified filter and the species or plant strategy composition, 2) several FC clusters are combined into one MRT cluster, suggesting missing filters as the FC analysis identified differences but the MRT analyses could not attribute those differences to a filter, and 3) one FC cluster is spread over several MRT clusters. There are three causes for this latter phenomenon: a) different filters select for similar plant strategy composition, b) plant strategy composition does not prove critical given the used filters (i.e. the strategy is redundant), and c) fuzziness of the FC clustering: the plots in a cluster bear only weak resemblance.

All data analyses were executed with R software (R Core Team 2017, version 3.4.0). The FC analyses were performed by using R's package 'cluster', function 'fanny'. Dissimilarity matrices were used as input. Those matrices were created by firstly transform the species and the plant strategy composition data with the Hellinger method, followed by calculating Jaccard distances. The default membership coefficient of 2.0 was used for the strategies, and a membership coefficient of 1.3 was required for the species dataset. The number of FC clusters was based on the strength of the clusters. The MRTs were constructed using the R package 'mvpart', which allows for cross validation of the MRTs (Borcard et al. 2011). Raw filter data served as constraint on the species and on each of the plant strategy composition data sets. The same dissimilarity matrices as for the FC were used. The number of leaves of a MRT was chosen based on inspection of the results, but was always within one standard deviation from number of leaves selected by 'mvpart' itself.

2.3 Results

2.3.1 Floodplain scale

The plot locations based on elevation did indeed comprise clear gradients in water and nutrients. The PCA on filters explained 82.8% of the variance on the first to axes and showed high correlation between several filters (Figure 2.4). The first PCA axis contrasted plots that were not inundated, contained coarse sized substrates, and had low resource availability with plots that were inundated, contained small sized substrates and had high resource availability. The second axis aligned very fine and extra fine sand, high calcium soil content and excavation. The values of the filters ranged considerably, but still there were some overall dominant plant strategy classes Most of the species were perennials (96%), surviving the winter period through below ground organs (81%) and the majority of the species depended neither on groundwater (85%) nor were tailored to wet or dry conditions (58%) (for more results see Supplementary material S2.E).

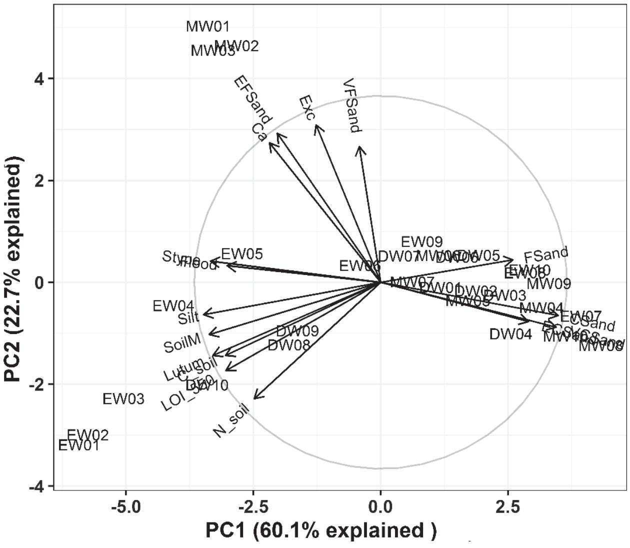

Figure 2.4: Principal component analysis of the environmental filters for plant species in floodplains. Abbreviations of the filters are listed in Table 2.1. The thirty plots are indicated by abbreviation of floodplain and serial number.

2.3.2 Cluster analyses

The **"**vials**"** in Figure 2.5 result from the MRT analyses and combines these results with the FC analyses. Each of the colored circles represents one plot and circles having the same color belong to the same FC cluster. For every FC analysis (species and plant strategy composition) the plots grouped together may vary as well as the resemblance of the plots within a cluster. The color of the groups indicates the order of the clustering process: red is the first group, green the second, and this continues via blue, turquoise, pink, yellow, and grey. Supplementary material S2.F lists the results of the FC analyses per plot.

2.3.2.1 Species

The combination of the FC and MRT analyses (Figure 2.5) linked three distinct plot clusters (red, pink and grey) to three levels of higher soil moisture concentrations. A geographical component in the species composition was also identified, as the turquoise, yellow and partly the blue FC clusters were assigned to specific floodplains. The green FC cluster, which was comprised of plots that were intermediate between other FC clusters (high fuzziness), could not be linked to a specific filter by the MRT.

2.3.2.2 Resource gradient

The 'Anatomy' and both 'leaf economic spectrum' (LES_H and LES_L) datasets were linked to a water and/or nutrient gradient. The red FC cluster of the 'Anatomy' strategy was linked to high soil moisture and nutrient concentrations. This red cluster was comprised of relatively high shares of 'Anatomy' classes adapted to moist and shaded conditions (for more detail on plant strategy classes see Supplementary material S2.B). Compared to the red FC cluster, the green FC cluster contained plots with lower shares of 'Anatomy' classes adapted to moist and shaded conditions and was linked to lower soil moisture and nutrient concentrations. The turquoise and blue FC clusters had relatively high shares of 'Anatomy' classes capable of withstanding drier conditions, and the MRT linked both FC clusters to lower soil moisture and nutrient concentrations, but no split was made between those two FC clusters.

LES_H was linked to soil nutrient concentrations. The red and green FC clusters were linked to higher soil nutrient concentrations and both clusters had relatively high leaf nitrogen, low leaf mass per area and larger leaves. The blue and turquoise clusters were linked to more nutrient poor location and had relatively low leaf nitrogen, higher leaf mass per area and smaller leaves. The other LES dataset, LES_L, was linked to a soil moisture gradient. The plots belonging to the red FC cluster were linked to wetter conditions and had relatively high leaf nitrogen, low leaf mass per area and larger leaves. The green and blue FC clusters were linked to drier conditions and had relatively lower leaf nitrogen, higher leaf mass per area and smaller leaves. Considering both LES_H and LES_L data sets, it was found that the cluster with the highest leaf nitrogen and lowest mass per leaf area were found on the most nutrient rich locations, while the cluster with the lowest leaf nitrogen and highest leaf mass per area was found on the driest locations.

Pollination strategy (wind or insect driven) was linked to organic soil content, and hence to a resource gradient, and geographical location. The MRT attributed solely plots belonging to the green FC cluster, consisting of plots with a high share of wind pollination, to high organic soil content. However, this was only a part of the green FC cluster. The other part of the green FC cluster was attributed to lower organic soil content. The link of FC clusters to geographic location was partially separating FC clusters. The blue and turquoise FC clusters, both having relatively high shares of pollination by insects, were assigned to the Erlecomse Waard and the Millingerwaard. The red FC cluster, with almost equal shares in wind and insect pollination, became scattered over the two identified geographical locations.

2.3.2.3 Resource gradient and disturbance

The strategies 'Onset of flowering', 'Groundwater dependence' and 'Germination period' were linked both to a resource gradient and to disturbance by summer inundation and/or excavation. The red FC cluster of the 'Onset of flowering' strategy consisted of plots that started flowering predominantly in June and was linked to relatively high soil moisture and nutrient concentrations. The plots within the pink FC cluster tended to start flowering in either April until June or August and those plots all contained higher shares of tree saplings and three out of four were excavated. The MRT linked the mix of the timing of flowering to excavation. The onset of flowering of the green (June), blue (May) and turquoise (July) FC clusters was not linked to a filter.

The strategy 'Groundwater dependence' was linked to flooding duration and excavation. The blue FC cluster comprised plots with a mix of 'Groundwater dependence' classes and was linked to excavation. The red FC cluster was split between 'not or shortly inundated' and 'inundated for a longer duration'. The red FC plots belonging to the latter had higher shares of species bounded to groundwater dynamics. Plots of the red FC cluster with lower shares of species bounded to groundwater dynamics were not or only shortly inundated and were grouped with the green FC cluster. This green FC cluster was composed of the plots having the highest shares of species indifferent to groundwater dynamics and were linked to lower soil moisture concentrations.

Even though the FC analysis of the 'Germination period' strategy resulted in fuzzy FC clusters, the MRT analysis linked the plots that germinated in late spring and summer (red FC cluster) to longer inundation. The plots of both the green and blue FC clusters were scattered based on the extra fine sand fraction. The MRT was therefore unable to link the green cluster, consisting of a mix of germination periods, and the blue cluster, consisting of classes germinating in early autumn and winter, to a specific filter.

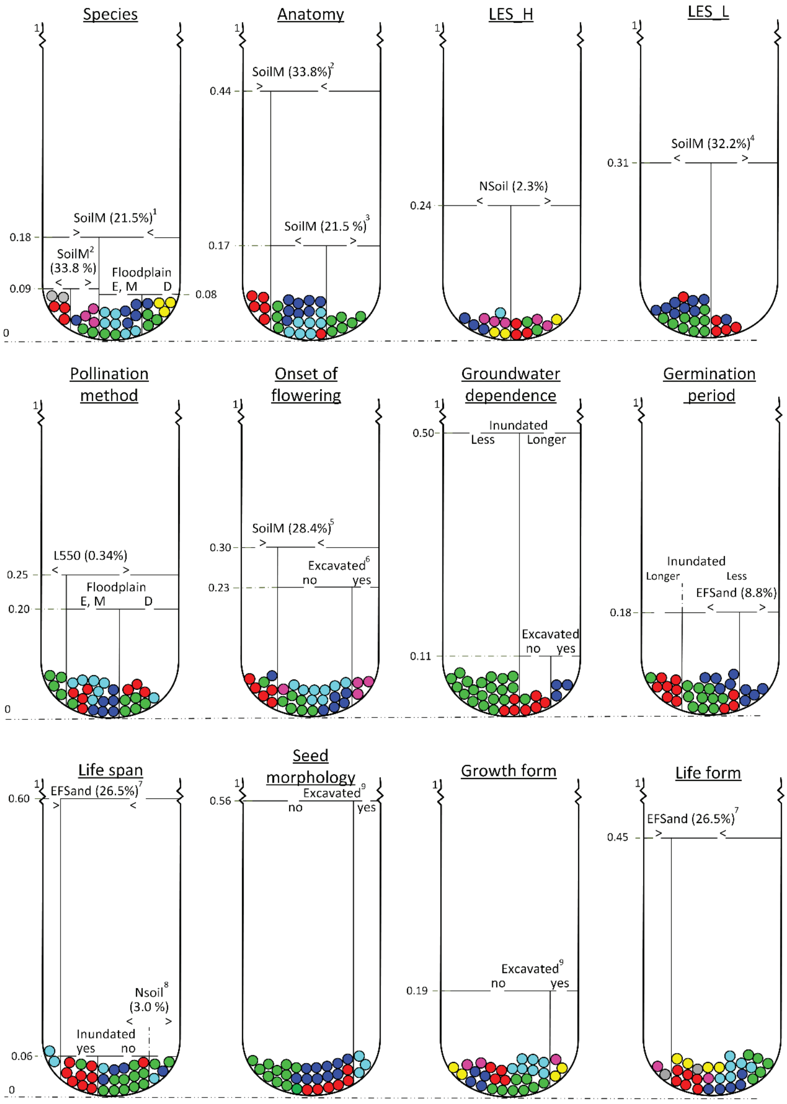

Figure 2.5: Results of the fuzzy clustering (FC, colored circles) and multivariate regression tree (MRT, presented as splitting filters and their values) analyses. Each field plot is depicted as a colored circle (FC). The colors are not plot specific: they may change for each FC analyses as they represent the output of the FC analyses. The MRT results are represented by the vials. The left side of each vial shows how much variation the mentioned filter explained. The '>' or '<' indicates the higher and lower values of a filter. The dotted, vertical lines in the vial of 'Life span' and 'Germination period' discriminate between the first split (i.e. the 'upper' filter) and the second split (i.e. the 'lower' filter). The superscripts indicate the identical results for another filters: 1: Lutum (3.0%), 2: NSoil (4.0%), 3: Lutum (3.0%), Silt (29.6%), VCSand (10.2%), CSand (16.9%), 4: Csoil (48.0%), 5: Csoil (45.7%), Nsoil (3.0%), 6: Ca (4.7%), CSand (5.1%), VCSand (1.9%), Inundated (1-3 vs 4), 7: VCSand (0.5%), 8: VFSand (14.3%), CSoil (45.7%), 9: Ca (4.7%), EFSand (22.3%).

2.3.2.4 *Disturbance*

Only the ‘Life span’ strategy was solely influenced by disturbances. The red FC cluster consisted of the herbaceous perennial life strategy only and was inundated during the 2016 summer flood. The one red plot not being inundated, was a very dry plot. The excavated plots, represented by the turquoise FC cluster, were not kept together by the MRT. Although all excavated plots and one other plot contained high shares in woody perennial life class (saplings), the lower shares in herbaceous perennial life strategy were considered the critical factor for the MRT. The MRT linked very low shares of herbaceous perennial life span to high percentages of extra fine sand and low shares of herbaceous perennial life span to higher percentages of very fine sand. The green and most of the blue FC clusters contained high shares of the herbaceous perennial life span class and were scattered based on soil nutrient concentrations.

2.3.2.5 *Missing filters and discord between FC and MRT*

The three strategies ‘Seed morphology’, ‘Life form’ and ‘Growth form’, either indicated missing filters or resulted in a discord between the FC and the MRT analyses. For example, even though the turquoise FC cluster of the ‘Seed morphology’ strategy, comprising a mix of different seed morphologies, was linked to excavation, the MRT was unable to link the other three FC clusters to a filter, despite the different seed morphology class composition: the red FC cluster had a high share in dispersal by ants, and the green and blue FC cluster had low shares of species with specific adaptations. The six FC clusters of the ‘Growth form’ strategy consisted of different shares in grass, rosette and non-rosette forb. The MRT did not detect this and grouped most of the clusters together but separated the excavated plots. These excavated plots were not clustered together by the FC analysis. The MRT result for the ‘Life form’ strategy also disagreed with the FC result. The gradient reflected in the shares in hemicryptophytes (surviving winter through perennial storage organs just below the soil surface) by the FC clusters (red, green, blue, turquoise and yellow) and the two distinct clusters with higher shares in woody chameophytes (overwintering through buds on shoots, grey cluster) and phanerophytes (overwintering through buds more than 50 cm above the soil, pink cluster) were not detected by the MRT. Based on low shares in hemicryptophytes, the MRT analysis only separated two of the excavated plots from the other plots based on their high extra fine sand fraction.

2.4 Discussion

In line with earlier studies (e.g. Grime, 1977; Schläpfer et al., 1996; Weiher et al., 1999), soil moisture and nutrient gradients together with the geographical location were identified as the most important filters for plant species composition. The analyses of plant strategy composition supported these findings but also added the effect of excavation and summer inundation (see Figure 2.6 for a schematic representation). Our results indicated the importance of the nature of disturbance for strategy class composition. Excavation led to more diverse strategy classes, like a mixed life span, onset of flowering and groundwater dependence class composition, while summer inundation led to a monopoly of the herbaceous perennial life span. As excavation removes any history of filters leading to a specific strategy class composition, species that can germinate and grow will do so, but how vital a species strategy is, is not yet tested in terms of establishment and propagation. For example, the share of annuals is expected to dwindle, as space becomes occupied by perennials (Crawley and May, 1987). Inundation of the vegetation during summer is likely to have removed any annuals and biennials which were not able to resprout from below ground organs. Even though the timing of the vegetation survey (about six weeks after the flooding event) could have exaggerated the effect of summer inundation, the results are corroborated by Van Eck et al. (2004; 2006). They identified summer inundation as an important filter in floodplains of heavily modified rivers. The spatial varying duration of inundation during the growing season shapes vegetation patterns which can be observed for several years after a summer flood. Remarkably, grazing did not show as a controlling filter.

The analyses of leaf economic spectrum of species shed light on where nutrients and water availability selected for more conservative (nutrient saving) or acquisitive (competitive) plant strategies. The higher the leaf nitrogen and the thinner the leaves the more plant composition is steered by light competition. Vice versa, the lower the leaf nitrogen and the sturdier the leaves the more plant composition is governed by nutrient availability. The findings of this study are therefore in line with general theory on the leaf economic spectrum of plant species (Wright et al., 2004; Diaz et al., 2016).

The two plant strategies for soil water availability, ‘Anatomy’ and ‘Groundwater dependence’, indicated the importance of the soil water gradient and how this gradient give rise to niche differentiation (Silvertown et al., 1999). However, the information provided by the two strategies differ. The 'Groundwater dependence' strategy focusses more on how groundwater dynamics lead to increased nutrient availability and cue germination and flowering of species (Londo, 1975). The 'Anatomy' strategy focusses on a broader soil-water gradient and includes some aspects of competition strength (the class "hydromorphs"). Nevertheless, both strategies indicate roughly the tipping points for shifts in plant strategy composition governed by soil water or nutrient availability, and hence for the ecological functioning of floodplains. The findings of resource gradients steering vegetation dynamics in terms of plant trait and strategy composition was also confirmed in several other studies (Bornette et al. 2008; Hodgson et al. 2011; Violle et al. 2011; Baastrup-Spohr et al. 2015).

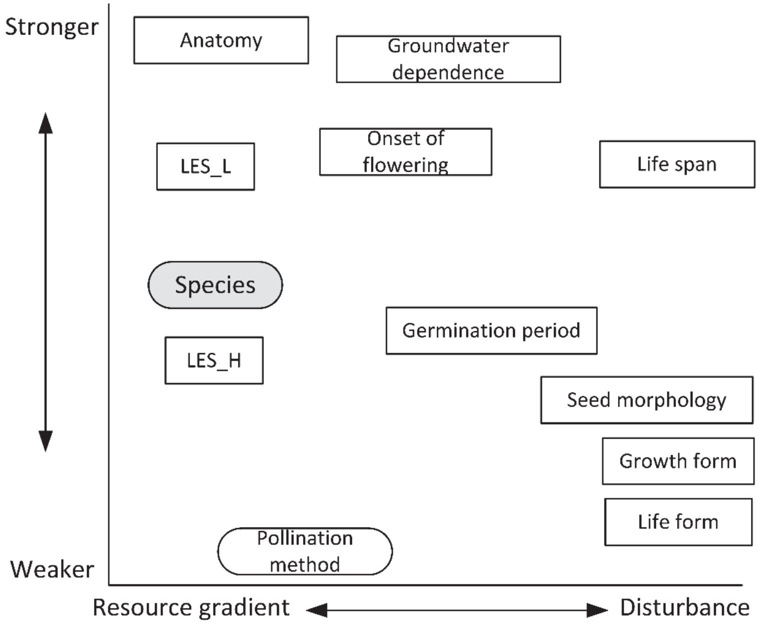

Figure 2.6: *Schematic representation of how strong various plant strategies linked to the resource and disturbance gradients. The position of these strategies was based on the explanation power of the multivariate regression trees and how well the clustering of the multivariate regression trees was in line with the clustering of the fuzzy clustering (Figure 2.5). The result of 'Species' is emphasized by a grey box. An oval box indicates that the geographical location was an important filter as well.*

The link between filters and strategies was not always clear-cut. This may have been caused by the proxy approach, use of strategies instead of plant physiology, missing filters and intraspecific variation. The proxy approach and use of strategies followed from the study set-up: a quick-scan approach using the trait concept to explore whether this concept is an easy amendment or substitution for species composition. Possible missing filters should not have a profound effect on all plots. Therefore, candidates for missing filters could be variation in grazing intensity (Díaz et al. 2007; Hodgson et al. 2011), other than the rosette form anti-grazing traits like spines and toxins, (Klimešová et al., 2008) different starting conditions caused by for example previous land use (Douma et al. 2012b) and subsequent colonization (Fukami et al., 2005), and winter floods (van Eck et al., 2005). Intraspecific variation could have led to weaker fitting of filter – strategy relations. As plants can withstand periods of unfavorable conditions, a poorly fitting of filter – plant strategy relations could have been found. Moreover, mechanistic explanations are still lacking for some relations, like the soil organic content for 'Pollination method' and the extra fine sand fraction for 'Germination period'.

Nonetheless, the filter-plant strategy approach could be of added value to daily floodplain management by disclosing additional information. For example, the leaf economic spectrum was coupled to a water and nutrient gradient. The leaf economic spectrum can also be used as an estimation of biomass production (Niklas et al. 2005; Reich 2014) and therefore is an useful estimate for changes in hydraulic roughness of floodplain vegetation. From a nature point of view, excavation indicated to promote a more diverse strategy composition. Hence, sequential excavations (i.e. cyclic rejuvenation) of floodplains may lead to different succession stages, which, in its turn, may host a variety of plant and animal species (Baptist et al. 2004; Geerling et al. 2013). The filter-plant strategy approach could be used as indicator for the level of impairment of a river, thereby revealing the potential of a floodplain in relation to specific rehabilitation measures (Barbour 1991).

Our results may also contribute to extend identified zones with specific hydrogeo-morphological processes and vegetation strategies (Gurnell et al. 2016) , as most of today's rivers are no longer in a pristine state. The model extension would be primarily based upon resource availability, but other processes like summer inundation (Van Eck et al. 2006), excavation (Geerling et al. 2008), grazing intensity (Díaz et al. 2007; Hodgson et al. 2011), starting conditions (Douma et al. 2012b), and time in terms of competition (Garnier et al. 2004), would interfere with the resource dominated strategy compositions.

2.5 Conclusion

Using analyses of plant strategy composition to supplement species surveys benefited the mechanical understanding of local assembly of species by environmental filters and tipping points for establishment of plants with specific strategies for coping with natural and anthropogenic disturbances in floodplain systems. This adds to analyzing species composition only, as species assemblages differ from location to location and species may resemble each other in how to deal with certain environmental conditions. The filter-plant strategy concept can support decision making on floodplain management, as it allows for spatial mapping of environmental filters and concurrent plant strategies, potentially optimizing different floodplain functions. Subsequently, the filters and strategies can be linked to functional diversity, biomass production and changes in hydraulic roughness.

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S2.A Proxy database

Table S2.A: *Overview of filter values. SoilM: soil moisture (%), CSoil, NSoil and Ca: soil carbon, nitrogen and Ca content (mg/mg), LOI550: organic matter ignited at 550 ^{0}C (%), EF, VF and F sand: fractions of extra fine , very fine and fine sand (%), EC, VC and CSand: fractions of extra coarse, very coarse and coarse sand (%), Flood: duration of summer flood (1: not flooded; 2: short period; 3: longer period; 4:long period), Stype: soil type (1: steep pf curve; 2: medium pf curve; 3: flat pf curve), Exc: excavated (yes or no).*

	SoilM (%)	**Csoil (mg/mg)l**	**Nsoil (mg/mg)**	**Ca (mg/mg)**	**LOI550 (%)**	**Lutum (%)**	**Silt (%)**	**EFSand (%)**	**VFSand (%)**	**FSand (%)**	**CSand (%)**	**VCSand (%)**	**ECSand (%)**	**Flood (-)**	**Stype (-)**	**Exc (y/n)**	**Grazed (y/n)**
EW01	46.0	59.9	4.8	2.9	2.3	12.7	80.9	3.7	0.8	0.3	0.4	0.6	0.6	4	3	no	no
EW02	44.4	58.1	4.4	2.9	2.3	13.3	76.9	4.3	1.5	0.9	0.9	1.0	1.1	4	3	no	no
EW03	39.2	56.5	4.0	2.8	2.2	10.0	71.9	6.5	3.7	2.9	2.5	1.6	0.9	4	3	no	no
EW04	33.5	55.8	3.5	3.1	1.8	7.4	49.2	17.0	11.9	7.7	3.9	1.4	1.4	3	3	no	no
EW05	25.9	43.5	2.5	3.2	1.6	5.7	41.4	19.3	14.7	10.5	6.0	2.0	0.4	1	3	no	no
EW06	16.4	39.1	2.3	2.3	1.0	2.8	24.2	11.1	14.0	16.8	16.9	10.5	3.7	1	3	no	no
EW07	3.7	7.8	0.5	1.0	0.2	0.2	6.8	0.0	3.0	15.9	33.3	28.3	12.4	1	1	no	no
EW08	6.7	10.3	0.5	1.4	0.4	1.0	13.3	4.5	9.1	17.5	24.8	19.7	10.2	1	1	no	no
EW09	10.7	29.4	1.4	2.6	1.0	1.9	16.1	9.1	15.4	20.8	21.4	12.4	2.9	1	2	no	no
EW10	6.0	11.9	0.5	1.5	0.4	0.8	11.3	4.3	9.6	18.3	25.6	20.1	10.1	1	1	no	no
MW01	25.4	25.6	0.4	7.0	0.5	3.1	42.0	29.1	15.8	7.5	2.3	0.2	0.0	4	3	yes	no
MW02	23.1	24.1	0.5	6.3	0.5	3.5	36.5	25.3	16.5	9.6	4.3	1.7	2.5	4	3	yes	no
MW03	22.0	23.4	0.6	6.1	0.6	3.6	44.7	27.6	14.6	6.6	2.0	0.4	0.5	4	3	yes	no

Table S2.A (continued)

	SoilM (%)	Csoil (mg/mg)l	Nsoil (mg/mg)	Ca (mg/mg)	LOI550 (%)	Lutum (%)	Silt (%)	EFSand (%)	VFSand (%)	FSand (%)	CSand (%)	VCSand (%)	ECSand (%)	Flood (-)	Stype (-)	Exc (y/n)	Grazed (y/n)
MW04	7.3	19.9	1.1	1.4	0.4	0.3	7.8	1.8	7.0	16.8	27.3	24.4	14.8	1	1	no	no
MW05	14.6	29.4	2.0	1.5	0.6	2.0	15.5	4.6	10.7	18.4	23.5	17.3	7.9	1	1	no	no
MW06	10.8	29.2	1.6	2.3	0.7	1.7	16.2	7.7	13.6	19.9	22.3	14.2	4.5	1	2	no	no
MW07	16.3	36.2	1.9	2.1	0.9	2.3	19.4	7.2	12.4	18.5	21.3	13.9	4.9	1	2	no	no
MW08	4.6	4.9	0.4	0.6	0.2	0.0	4.7	0.2	0.4	7.5	26.7	34.2	26.4	1	1	no	no
MW09	6.2	4.5	0.4	0.7	0.2	1.4	11.9	1.9	8.5	18.5	26.6	20.9	10.3	1	1	no	no
MW10	5.4	15.5	0.8	1.8	0.6	0.0	6.0	0.5	1.5	10.8	27.5	30.6	23.1	1	1	no	no
DW01	15.3	30.6	2.4	2.1	0.5	2.2	20.4	7.0	11.0	17.2	21.1	15.0	6.3	1	1	no	yes
DW02	14.8	27.5	2.0	2.1	0.5	1.6	14.0	4.0	10.5	19.3	25.2	18.0	7.5	1	1	no	no
DW03	14.9	20.8	1.4	2.1	0.4	1.5	11.5	2.0	8.5	18.7	27.0	21.1	9.6	1	1	no	yes
DW04	15.4	30.4	2.3	1.5	0.4	0.7	9.0	0.5	6.5	19.0	30.6	23.8	9.9	1	1	no	no
DW05	9.8	24.8	1.2	2.9	0.3	0.8	10.8	4.3	11.1	20.1	26.0	18.8	8.1	3	1	no	no
DW06	14.2	26.1	1.4	2.9	0.5	2.2	13.4	5.0	12.6	20.7	24.5	16.1	5.5	2	1	no	no
DW07	21.0	38.1	2.5	2.6	0.7	2.5	14.9	8.5	16.4	22.2	21.8	11.6	2.1	1	2	no	no
DW08	31.0	47.9	3.9	1.7	1.1	5.3	35.1	4.7	10.2	15.6	16.9	9.9	2.3	3	3	no	no
DW09	34.2	48.1	4.1	1.8	1.0	4.5	23.5	7.1	11.9	17.4	19.6	12.4	3.6	4	3	no	no
DW10	48.7	58.8	5.0	1.8	1.2	7.4	42.8	5.3	8.9	12.6	13.4	7.8	1.8	4	3	no	no

S2.B Classes of the plant strategies

***Table S2.B:** Overview of the classes within each strategy. If found necessary, a short explanation is given to elucidate the class.*

Strategy	Class	Explanation
Life span	Annual	
	Biannual	
	Herbaceous perennial	
	Woody perennial	
Life form	Herbaceous chamaephyte	Buds on overwintering shoots near soil surface
	Woody chamaephyte	Buds on overwintering shoots near soil surface
	Geophyte	Subterranean resting buds
	Helophyte	Buds resting in moist/wet soil
	Hemicryptophyte	Buds are at or near soil surface
	Liana	Use structures for support, rooted in soil
	Parasite	Derive its nutritional requirements from other living plant
	Phanerophyte	Buds more than 50 cm above soil
	Therophyte	Annuals
Growth form	Gras	
	Non rosette forb	
	Rosette forb	
	Species with no leaves.	

Table S2.B *(continued)*

Strategy	Class	Explanation
Groundwater dependence	Local phreatophyte	Groundwater only required on certain locations
	Non obligatory phreatophyte	Occasionally growing without groundwater influence
	Aphreatophyte	Not ground water dependent
	Obligatory phreatophyte	requires groundwater dynamics
	Wet phreatophyte	Require ground water dynamics for part of the year
Anatomy	Helomorphes	Fit to survive longer periods of water logging conditions
	Hygropmorphes	Flimsy built plants living in shadow and semi shadow
	Mesomorphes	No special adaptations
	Scleromorphes	Thick cuticula, fortified shoots
	Succulents	Parts of plants are fit to store water.
Pollination method	Wind pollinated	
	Insect pollinated	
Seed morphology	None	
	Active dispatch	
	Nuts	
	Glandular structure	
	Hooks or spikes	
	Myrmecochory	Dispersion by ants
	Special protection of seed	
Onset of flowering	Months	
Germination of flowering	Period of year/month	

S2.C Vegetation mappings

Table S2.C1: *Overview of the mapped species and their used abbreviations*

Species	Abbreviation
Achillea millefolium	Ac_mi
Achillea ptarmica	Ac_pt
Agrostis capillaris	Ag_ca
Agrimonia eupatoria	Ag_eu
Agrostis stolonifera	Ag_st
Arrhenatherum elatius	Ar_el
Arenaria serpyllifolia	Ar_se
Arctium species	Ar_sp
Artemisia vulgaris	Ar_vu
Carex arenaria	Ca_ar
Calamagrostis epigejos	Ca_ep
Carex hirta	Ca_hi
Carex spicata	Ca_sp
Cerastium arvense	Ce_ar
Cerastium fontanum	Ce_fo
Centaurea jacea	Ce_ja
Cirsium arvense	Ci_ar
Cirsium species	Ci_sp
Convolvulus arvensis	Co_ar
Cynodon dactylon	Cy_da
Daucus carota	Da_ca
Dactylis glomerata	Da_gl
Elytrigia repens	El_re
Equisetum arvense	Eq_ar
Erigeron annuus	Er_an
Eryngium campestre	Er_ca
Euphorbia cyparissias	Eu_cy
Euphorbia esula	Eu_es

Table S2.C1 (continued)

Species	Abbreviation
Festuca arundinacea	Fe_ar
Festuca pratensis	Fe_pr
Festuca rubra	Fe_ru
Galium aparine	Ga_ap
Galium mollugo	Ga_mo
Galium verum	Ga_ve
Geranium molle	Ge_mo
Glechoma hederacea	Gl_he
Helictotrichon pubescens	He_pu
Holcus lanatus	Ho_la
Hypericum perforatum	Hy_pe
Iris pseudacorus	Ir_ps
Jacobaea erucifolia	Ja_er
Jacobaea vulgaris	Ja_vu
Lepidium latifolium	Le_la
Lolium perenne	Lo_pe
Lotus pedunculatus	Lot_pe
Lysimachia nummularia	Ly_nu
Medicago falcata	Me_fa
Medicago lupulina	Me_lu
Odontites vernus s. serotinus	Od_se
Odontites vernus	Od_ve
Oenothera biennis + O. x fallax	Oe_fa
Ononis repens s. spinosa	On_sp
Origanum vulgare	Or_vu
Phalaris arundinacea	Ph_ar
Phleum pratense	Ph_pr
Pimpinella saxifraga	Pi_sa
Plantago arenaria	Pl_ar
Plantago lanceolata	Pl_la
Plantago major	Pl_ma

Table S2.C1 *(continued)*

Species	Abbreviation
Potentilla anserina	Po_an
Populus nigra	Po_ni
Poa pratensis	Po_pr
Potentilla reptans	Po_re
Poa trivialis	Po_tr
Ranunculus acris	Ra_ac
Ranunculus repens	Ra_re
Rumex acetosa	Ru_ac
Rubus caesius	Ru_ca
Rumex crispus	Ru_cr
Rumex hydrolapathum	Ru_hy
Rumex thyrsiflorus	Ru_th
Salix alba	Sa_al
Saponaria officinalis	Sa_of
Salix purpurea	Sa_pu
Senecio inaequidens	Se_in
Solidago canadensis	So_ca
Taraxacum species	Ta_sp
Tanacetum vulgare	Ta_vu
Thalictrum minus	Th_mi
Torilis japonica	To_ja
Trifolium campestre	Tr_ca
Trifolium dubium	Tr_du
Trisetum flavescens	Tr_fl
Trifolium pratense	Tr_pr
Trifolium repens	Tr_re
Urtica dioica	Ur_di
Veronica chamaedrys	Ve_ch
Veronica austriaca s. teucrium	Ve_te
Vicia cracca	Vi_cr

Table S2.C2: Overview of plant mapping coverages (%) per plot. Plant name abbreviations are listed in table S2.C1. Table continues on following pages.

	Ph_ar	Po_re	Ru_cr	Ar_sp	Ci_sp	Ci_ar	Fe_pr	Ga_ap	Gl_he	Le_la	Po_tr	Ta_vu	Ur_di	Ar_sp	Ac_mi	Ag_st	Da_gl	El_re	Ga_mo	Lo_pe
EW01	38	38	2	2	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
EW02	88	1	...	3	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
EW03	3	88	2	3	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
EW04	...	...	...	...	...	1	2	1	8	38	3	1	4	1	...	...	...	...	...	...
EW05	...	...	...	1	...	8	...	...	...	...	38	...	...	...	1	2	1	2	1	2
EW06	...	...	...	...	...	...	...	...	...	...	8	8	...	...	2	...	2	...	2	...
EW07	...	...	...	...	...	...	...	...	...	...	2	...	...	...	...	...	...	...	2	...
EW08	...	...	...	...	...	...	...	...	...	...	...	2	...	...	2	...	...	...	2	2
EW09	...	...	...	...	...	...	...	...	...	...	2	2	...	...	2	...	...	...	...	...
EW10	...	...	...	...	...	...	...	...	...	...	3	...	...	2	2	...	2	...	8	2
MW01	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...
MW02	...	1	...	...	...	...	...	...	...	...	2	...	...	...	...	...	...	...	...	...
MW03	...	1	...	...	...	...	...	...	...	...	...	...	...	2	...	...	...	...	...	...
MW04	...	...	...	...	...	1	...	...	...	...	3	8	...	...	...	...	...	3	...	...
MW05	...	...	...	...	...	...	...	...	2	...	3	1	1	...	...	...	...	2	38	...
MW06	...	2	...	...	...	1	...	...	2	...	...	...	2	...	...	...	2	2	...	...

Table continues from previous pages. Overview of plant mapping coverages (%) per plot. Plant name abbreviations are listed in table S2.C1. Table continues on following page.

	Ph_ar	Po_re	Ru_cr	Ar_sp	Ci_sp	Ci_ar	Fe_pr	Ga_ap	Gl_he	Le_la	Po_tr	Ta_vu	Ur_di	Ar_sp	Ac_mi	Ag_st	Da_gl	El_re	Ga_mo	Lo_pe
MW07	...	2	...	...	...	2	...	...	2	...	...	...	...	...	...	...	2	...	8	...
MW08	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...
MW09	...	2	...	...	...	...	2	...	2	...	3	...	...	...	...	...	2	...	...	...
MW10	...	1	...	...	...	...	...	1	...	...	2	8	...	...	...	...	...	2	...	...
DW01	...	2	...	...	...	1	...	...	2	...	...	...	...	...	...	...	...	...	...	...
DW02	...	...	...	...	...	...	2	...	...	...	...	...	...	...	2	2	...	...	...	38
DW03	...	...	...	...	...	...	...	...	8	...	2	...	38	...	...	...	...	...	...	...
DW04	...	...	...	...	...	...	3	...	...	...	...	...	...	...	...	...	...	...	...	38
DW05	...	3	...	...	...	...	...	...	...	...	...	2	...	...	3	38	...	...	...	38
DW06	...	...	...	...	...	2	3	...	2	...	...	...	...	...	...	...	2	...	...	...
DW07	...	...	...	...	...	1	2	...	2	...	3	...	...	...	...	...	2	...	...	38
DW08	...	2	...	...	...	3	38	...	...	...	...	...	...	...	...	...	...	...	...	...
DW09	...	3	...	...	...	...	...	...	...	...	...	...	...	...	...	3	...	...	...	...
DW10	...	2	...	...	...	...	...	...	...	...	...	...	...	...	...	2	...	...	...	...

Table continues from previous pages. Overview of plant mapping coverages (%) per plot. Plant name abbreviations are listed in table S2.C1. Table continues on following page.

	Pl_la	Tr_re	Ve_ch	Ja_vu	Ta_sp	Ag_ca	Ca_ep	Er_ca	Fe_ru	Hy_pe	Or_vu	Er_an	Ce_fo	Oe_fa	Ru_th	Sa_of	Se_in	Da_ca	Ge_mo	Ar_se
EW01	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
EW02	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
EW03	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
EW04	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
EW05	2	8	2	38	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
EW06	2	...	...	8	...	3	2	1	38	2	38	2	1	...	...	...	...	...	...	...
EW07	...	...	...	1	...	...	88	1	38	...	...	...	...	1	8	2	2	...	...	...
EW08	...	...	...	...	...	...	8	1	38	...	...	...	...	...	8	38	...	...	...	...
EW09	3	...	...	...	...	3	3	38	8	...	...	1	...	...		2	...	...	...	...
EW10	3	...	...	1	1	38	...	...	8	...	...	1	...	...	2	2	...	...	...	...
MW01	...	...	...	...	2	...	...	...	...	...	...	...	1	...	...	...	...	2	...	...
MW02	...	...	...	...	1	...	8	...	...	...	...	...	2	...	...	...	...	2	...	
MW03	...	...	...	...	1	...	...	...	...	...	...	2	...	...	...	...	...	1	...	2
MW04	...	...	...	...	...	...	...	38	38	...	...	...	...	...	...	...	...	...	...	...
MW05	...	...	...		...	2	2	38	...	...	...	...	...	...	2	3	...	...	...	...
MW06	...	...	...	1	...	...	4	1	8	...	...	...	...	...	2	38	...	...	...	...
MW07	...	...	...	1	...	...	38	38	8	...	...	...	...	...	...	8	...	...	...	...

Table continues from previous pages. Overview of plant mapping coverages (%) per plot. Plant name abbreviations are listed in table S2.C1. Table continues on following page.

	Pl_la	Tr_re	Ve_ch	Ja_vu	Ta_sp	Ag_ca	Ca_ep	Er_ca	Fe_ru	Hy_pe	Or_vu	Er_an	Ce_fo	Oe_fa	Ru_th	Sa_of	Se_in	Da_ca	Ge_mo	Ar_se
MW08	...	...	...	...	...	...	88	8	...	...	...	...	...	...	...	...	...	...	...	...
MW09	...	...	...	...	...	...	...	1	38	...	...	...	...	...	8	...	...	...	...	...
MW10	...	...	...	...	...	...	...	...	8	...	...	...	...	...	2	1	...	...	...	...
DW01		...	...	...	...	3	...	...	38	...	...	...		...	8	...	...	...	...	...
DW02	2	...	...	1	...	...	...	8	38	...	...	...	2	...	2	...	...	...	...	...
DW03	...	...	...	...	...	...	...		4	...	...	...	...	...	...	...	...	...	...	...
DW04	...	...	...	...	...	...	...	2	38	...	...	...	...	...	...	...	...	...	...	...
DW05	3	2	...	...	...	...	...	...	38	...	...	...	...	...	...	...	...	...	...	...
DW06	...	...	...	...	...	2	...	...	8	...	...	...	...	...	...	...	...	...	...	...
DW07	...	...	...	...	...	38	...	1	8	...	...	...	...	...	8	...	...	...	...	...
DW08	...	...	...	...	...	4	2	...	...	...	...	...	...	...	...	...	...	...	...	...
DW09	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
DW10	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...

Table continues from previous pages. Overview of plant mapping coverages (%) per plot. Plant name abbreviations are listed in table S2.C1. Table continues on following page.

	Eu_cy	Tr_du	Pl_ar	Eu_es	Ar_vu	Ca_hi	Ru_ca	Sa_pu	Ja_er	Tr_fl	So_ca	Od_ve	Ce_ar	Ar_el	To_ja	Co_ar	Me_fa	Ve_te	Th_mi	Ca_ar
EW01	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
EW02	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
EW03	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
EW04	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
EW05	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
EW06	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
EW07	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
EW08	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
EW09	2	2	8	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
EW10	...	2	...	...	1	2	1	38	1	3	1	1	...	...	...	...		...	...	...
MW01	...	...	...	...	...	...	...	...	2	...	2	1	...	...	...	...		...	...	...
MW02	...	...	...	...	...	2	8	...	...	...	38	...	...	...	...	...	2	...	...	...
MW03	...	3	...	...	...	...	8	...	...	...	3	...	...	...	...	...	...	...	...	...
MW04	...	...	...	2	...	1	...	...	...	2	...	...	...	3	1	...	...	...	...	...
MW05	...	...	...	...	...	2	...	...	...	2	...	...	...	3	1	...	...	...	...	...
MW06	...	...	...	...	...	8	...	...	...	3		...	2	3	2	1	1	2	1	...
MW07	...	...	...	...	...	2	8	...	...	...	2	...	...	...	...	...	...	...	...	...

Table continues from previous pages. Overview of plant mapping coverages (%) per plot. Plant name abbreviations are listed in table S2.C1. Table continues on following page.

	Eu_cy	Tr_du	Pl_ar	Eu_es	Ar_vu	Ca_hi	Ru_ca	Sa_pu	Ja_er	Tr_fl	So_ca	Od_ve	Ce_ar	Ar_el	To_ja	Co_ar	Me_fa	Ve_te	Th_mi	Ca_ar
MW08	...	...	...	1	...	3	...	...	1	3	...	...	1	...	...	...	...	...	...	...
MW09	...	...	...	...	8	38	...	...	...	...	...	...	2	3	2	...	...	...	...	...
MW10	...	...	...	...	...	...	2	...	...	...	...	...	...	...	...	...	...	...	...	3
DW01	...	...	...	...	...	3	...	...	...		...	...	...	38	1	2	...	...	8	...
DW02	...	...	...	...	...	...	...	...	...	3	...	...	...	...	2	...	2	...	...	...
DW03	...	...	...	...	...	2	1	...	...	...	...	...	...	3	1	2	...	...	...	...
DW04	...	...	...	...	...	3	...	...	...	...	...	...	...	3	...	1	2	...	...	...
DW05	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
DW06	...	...	...	...	...	8	...	...	...	...	...	...	...	2	...	2	1	...	...	...
DW07	...	...	...	...	...	3	...	...	...	...	...	...	...	8	...	...	2	...	...	...
DW08	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	8	...	...	...	...
DW09	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
DW10	...	...	...	...	...	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...

Table continues from previous pages. Overview of plant mapping coverages (%) per plot. Plant name abbreviations are listed in table S2.C1. Table continues on following page.

	Eq_ar	On_sp	Fe_ar	Lot_pe	Po_ni	Ra_re	Sa_al	Tr_pr	Od_se	Ho_la	Tr_ca	Pl_ma	Pi_sa	Po_pr	Ra_ac	Ce_ja	Ph_pr	Cy_da	Ga_ve	He_pu
EW01	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
EW02	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
EW03	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
EW04	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
EW05	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
EW06	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
EW07	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
EW08	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
EW09	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
EW10	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
MW01	2	…	…	1	2	2	2	1	…	…	…	…	…	…	…	…	…	…	…	…
MW02	8	…	2	…	…	2	1	1	3	2	2	…	…	…	…	…	…	…	…	…
MW03	2	…	…	…	2	…	2	…	…	…	…	1	…	…	…	…	…	…	…	…
MW04	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
MW05	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
MW06	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
MW07	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…	…

Table continues from previous pages. Overview of plant mapping coverages (%) per plot. Plant name abbreviations are listed in table S2.C1. Table continues on following page.

	Eq_ar	On_sp	Fe_ar	Lot_pe	Po_ni	Ra_re	Sa_al	Tr_pr	Od_se	Ho_la	Tr_ca	Pl_ma	Pi_sa	Po_pr	Ra_ac	Ce_ja	Ph_pr	Cy_da	Ga_ve	He_pu
MW08	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
MW09	...	...	3	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
MW10	2	38	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
DW01	...	...	3	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
DW02	...	...	...	...	...	...	...	38	...	...	...	1	3	2	8	2	3	...	...	...
DW03	...	...	...	...	...	...	...		...	...	...	...	...	...	...	...		...	...	...
DW04	...	...	...	...	...	...	...	38	...	...	...	...	...	...	38	...	2	2	8	2
DW05	...	...	...	2		2	...	...	...	...	...	...	...	...	...	...	1	...	...	...
DW06	...	...	...	...	...	...	...	...	...	...	...	...	1	...	2	...	88	...	...	...
DW07	...	...	...	...	...	...	...	2	...	...	...	...		...	3	...	38	...	3	...
DW08	...	...	2	...	...	3	...	...	...	...	...	...	...	...	...	...	...	...	...	...
DW09	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
DW10	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...

Table continues from previous pages. Overview of plant mapping coverages (%) per plot. Plant name abbreviations are listed in table S2.C1. Table continues on following page.

	Ru_ac	Ac_pt	Ag_eu	Ru_hy	Vi_cr	Ca_sp	Me_lu	Ly_nu	Ir_ps	Po_an
EW01	...	...	...	...	...	...	...	...	...	...
EW02	...	...	...	...	...	...	...	...	...	...
EW03	...	...	...	...	...	...	...	...	...	...
EW04	...	...	...	...	...	...	...	...	...	...
EW05	...	...	...	...	...	...	...	...	...	...
EW06	...	...	...	...	...	...	...	...	...	...
EW07	...	...	...	...	...	...	...	...	...	...
EW08	...	...	...	...	...	...	...	...	...	...
EW09	...	...	...	...	...	...	...	...	...	...
EW10	...	...	...	...	...	...	...	...	...	...
MW01	...	...	...	...	...	...	...	...	...	...
MW02	...	...	...	...	...	...	...	...	...	...
MW03	...	...	...	...	...	...	...	...	...	...
MW04	...	...	...	...	...	...	...	...	...	...
MW05	...	...	...	...	...	...	...	...	...	...
MW06	...	...	...	...	...	...	...	...	...	...
MW07	...	...	...	...	...	...	...	...	...	...

Table continues from previous pages. Overview of plant mapping coverages (%) per plot. Plant name abbreviations are listed in table S2.C1.

	Ru_ac	Ac_pt	Ag_eu	Ru_hy	Vi_cr	Ca_sp	Me_lu	Ly_nu	Ir_ps	Po_an
MW08	...	...	...	...	...	...	...	...	...	...
MW09	...	...	...	...	...	...	...	...	...	...
MW10	...	...	...	...	...	...	...	...	...	...
DW01	...	...	...	...	...	...	...	...	...	...
DW02	...	...	...	...	...	...	...	...	...	...
DW03	...	...	...	...	...	...	...	...	...	...
DW04	...	...	...	...	...	...	...	...	...	...
DW05	2	...	...	...	...	...	...	...	...	...
DW06	...	2	1	8	2	...	...	...	...	...
DW07	...	...	2	...	...	2	3	...	...	...
DW08	...	...	1	...	...	...	...	2	...	...
DW09	...	...	...	...	...	...	...	...	...	...
DW10	...	...	...	...	...	...	...	1	8	3

S2.D Species strategies

Table S2.D1: *Overview of the measured leaf traits of the dominant species (plot coverage >8%). LA means leaf area, LMA leaf mass per area and Nleaf N per leaf.*

	Species	**Dry weight** (g/leaf)	**LA** (m^2/leaf)	**LMA** (g/m^2)	**Nleaf** (%)
EW01	*Potentilla reptans*	5.73E-02	1.75E-03	32.68	39.23
EW01	*Phalaris arundinacea*	7.27E-02	1.83E-03	39.82	38.93
EW02	*Phalaris arundinacea*	5.39E-02	1.51E-03	35.65	35.22
EW03	*Phalaris arundinacea*	5.89E-02	1.68E-03	35.07	40.16
EW03	*Potentilla reptans*	4.55E-02	1.46E-03	31.13	42.42
EW04	*Urtica doica*	3.98E-02	9.91E-04	40.10	32.92
EW04	*Lepidium latifolium*	3.98E-02	9.58E-04	41.57	55.57
EW05	*Jacobaea vulgaris*	4.99E-02	6.03E-04	82.76	28.98
EW06	*Festuca rubra*	2.03E-01	2.09E-03	97.12	15.54
EW06	*Origanum vulgare*	1.46E-02	2.12E-04	69.03	15.61
EW07	*Festuca rubra*	1.59E-01	1.67E-03	94.99	25.54
EW08	*Saponaria officinalis*	3.14E-02	4.39E-04	71.61	19.99
EW08	*Festuca rubra*	1.27E-01	1.88E-03	67.77	20.10
EW09	*Eryngium campestre*	6.86E-02	3.79E-04	181.0	19.98
EW10	*Salix purpurea*	2.36E-02	3.51E-04	67.24	27.25
EW10	*Galium mollugo*	7.75E-03	1.54E-04	50.40	33.85
MW01	*Solidago canadensis*	2.61E-02	5.03E-04	52.00	18.70
MW02	*Solidago canadensis*	2.55E-02	3.74E-04	68.10	14.76
MW03	*Solidago canadensis*	3.86E-02	8.03E-04	48.11	19.12
MW04	*Eryngium campestre*	6.53E-02	4.33E-04	150.8	23.39
MW04	*Festuca rubra*	1.93E-01	2.20E-03	87.66	15.59
MW05	*Galium mollugo*	5.58E-03	9.78E-05	57.03	25.13
MW05	*Eryngium campestre*	3.60E-02	3.08E-04	116.8	25.90
MW06	*Saponaria officinalis*	5.90E-02	8.94E-04	66.00	25.29
MW06	*Calamagrostis epigejos*	2.55E-01	2.99E-03	85.47	19.72

Table S2.D1 *(continued)*

	Species	**Dry weight** (g/leaf)	**LA** (m^2/leaf)	**LMA** (g/m^2)	**Nleaf** (%)
MW07	*Calamagrostis epigejos*	1.36E-01	2.14E-03	63.34	20.48
MW10	*Ononis repens s. spinosa*	1.33E-03	3.25E-05	41.01	41.02
MW10	*Calamagrostis epigejos*	2.46E-01	2.59E-03	95.06	20.85
DW02	*Ranunculus acris*	8.39E-02	1.87E-03	44.87	23.35
DW02	*Trifolium pratense*	1.14E-02	3.23E-04	35.34	45.04
DW03	*Urtica dioica*	4.07E-02	6.49E-04	62.62	20.74
DW03	*Festuca rubra*	3.59E-02	9.96E-04	36.05	34.06
DW04	*Ranunculus acris*	9.71E-02	1.87E-03	51.95	33.46
DW04	*Trifolium pratense*	1.48E-02	4.10E-04	35.99	40.96
DW08	*Festuca pratensis*	1.01E-01	1.87E-03	53.87	24.20
DW08	*Agrostis capillaris*	5.58E-03	2.64E-04	21.15	35.10
DW09	*Potentilla reptans*	5.53E-02	1.65E-03	33.51	41.32
DW09	*Agrostis stolonifera*	1.63E-02	6.46E-04	25.17	50.79
DW10	*Iris pseudacorus*	3.56E-01	4.80E-03	74.04	19.04
DW10	*Potentilla reptans*	2.83E-02	8.25E-04	34.26	29.13

Table S2.D2: *Overview of the non-LES strategies per species (retrieved from TurboVeg (Hennekens and Schaminée, 2001)). Species are represented by abbreviation (Table S3.1). Only for the strategies using abbreviations for their categories an explanation in this caption is given. Life span: 'Ann': Annual, 'Bian': Biannual, 'Per": Perennial. Life form: 'ChamH': Herbaceous chamaephyte, 'ChamW': Woody chamaephyte, 'Geo': Geophyte, 'Helo': Helophyte, 'Hemi': Hemicryptophyte, 'Lia': Liana, 'Par': Parasite, "Phan": Phanerophyte, 'Thero': Therophyte. Growth form: 'Gras': Gras, 'NR forb': Non rosette forb, 'R forb': Rosette forb, 'No leaves': Species with no leaves. Grwtrdep (Groundwater dependence):'LPhr': Groundwater only required on certain locations, 'Non ObPhr': Occasionally growing without groundwater influ-ence, 'NoPhr': Not ground water dependent, "OblPhr": requires groundwater dynamics, 'WPhr': Require ground water dynamics for part of the year. Anatomy: 'Helo': Helomorphes, 'Hygro': Hygropmorphes, 'Meso': Mesomorphes, 'Sclero': Scleromorphes and 'Succ' = Succulents. Table continues on following pages.*

Species	Life span	Life form	Growth form	Grwtrdep	Anatomy	Seed Morph	Germ period	Onset of flowering	Poll method
Ac_mi	Per	Hemi	NR forb	NoPhr	Meso, Sclero	None	Winter, Spring	June	Insects
Ac_pt	Per	Hemi	NR forb	OblPhr	Helo, Meso	None	Spring	July	Diptera, Hymen
Ag_eu	Per	Hemi	NR forb	NoPhr	Meso	Hooks	Spring	June	Diptera, Hymen
Ag_ca	Per	Hemi	Gras	NoPhr	Meso	None	Direct	June	Wind
Ag_st	Per	Hemi	Gras	LPhr	Meso, Helo	None	Direct	June	Wind
Ar_sp	...	...	Forb	...	...	...	Autumn, Summer	...	...
Ar_se	Ann	Thero	NR forb	NoPhr	Sclero,	None	Direct	May	Insects
Ar_el	Per	Hemi, Geo	Gras	NoPhr	Meso	None	Direct	May	Wind
Ar_vu	Per	Hemi	NR forb	NoPhr	Meso, Sclero	None	Spring	July	Hymen, Wind
Ca_ep	Per	Hemi	Gras	NoPhr	Sclero	None	Direct	June	Wind

Table S2.D2 (continued)

Species	Life span	Life form	Growth form	Grwtrdep	Anatomy	Seed Morph	Germ period	Onset of flowering	Poll method
Ca_ar	Per	Geo, Hemi	Gras	NoPhr	Sclero	None	LSpring	April	Wind
Ca_hi	Per	Geo, Hemi	Gras	NoPhr	Meso	None	Summer	May	Wind
Ca_sp	Per	Hemi	Gras	NoPhr	...	None	Summer	May	Wind
Ce_ja	Per	Hemi	NR forb	NoPhr	Sclero, Meso	None	Lsummer, Autumn	June	Insects
Ce_ar	Per	ChamH	NR forb	NoPhr	Sclero, Meso	None	Spring	April	Diptera, Hymen, Cleis
Ce_fo	Per	ChamH	NR forb	...	...	...	Spring	April	
Ci_ar	Per	Geo	R forb	NoPhr	Meso, Sclero	Feather	LSpring	June	Insects
Ci_sp	...	...	Forb	...	...	...	...	...	...
Co_ar	Per	Geo, Hemi, Lia	Climb, NR forb	NoPhr	Meso	None	Autumn	June	Diptera, Hymen
Cy_da	Per	Hemi	Gras	NoPhr	Sclero, Meso	None	Spring	July	Wind
Da_gl	Per	Hemi	Gras	NoPhr	Meso	None	Direct	May	Wind
Da_ca	Ann, Bian	Hemi	NR forb	NoPhr	Meso	Hooks	Spring, Summer	June	Coleo, Diptera

Table S2.D2 (continued)

Species	Life span	Life form	Growth form	Grwtrdep	Anatomy	Seed Morph	Germ period	Onset of flowering	Poll method
El_re	Per	Hemi, Geo	Gras	NoPhr	Meso, Sclero	None	Direct	June	Wind
Eq_ar	Per	Geo	No leaves	LPhr	Sclero, Helo	Covered	…	April	Wind
Er_an	Bian, Per	Thero, Hemi	NR forb	NoPhr	…	Feather	Spring	July	Insects
Er_ca	Per	Hemi	NR forb	NoPhr	Sclero	None	Spring	July	Insects
Eu_cy	Per	Hemi, ChamH	NR forb	NoPhr	Meso	Active	Spring	April	Insects
Eu_es	Per	Hemi	NR forb	NoPhr	Meso	Active	Direct, Spring	May	Insects
Fe_ar	Per	Hemi	Gras	Non ObPhr	Sclero, Meso	None	Direct	June	Wind
Fe_pr	Per	Hemi	Gras	NoPhr	Meso	None	Direct	June	Wind
Fe_ru	Per	Hemi	Gras	NoPhr	Meso, Succ	None		May	
Ga_ap	Ann	Thero, Lia	Climb	NoPhr	Meso, Hygro	Hooks	Winter, Espring	June	Coleo, Diptera
Ga_mo	Per	Hemi, ChamH	Climb	NoPhr	Meso	None	Autumn, Spring	May	Coleo, Diptera
Ga_ve	Per	Hemi	NR forb	NoPhr	Sclero, Meso	None	Autumn	June	Coleo, Diptera

Table S2.D2 (continued)

Species	Life span	Life form	Growth form	Grwtrdep	Anatomy	Seed Morph	Germ period	Onset of flowering	Poll method
Ge_mo	Ann	Thero	R forb	NoPhr	Meso	None	Direct	May	Hymen
Gl_he	Per	Hemi	NR_Forb	NoPhr	Meso	None	Spring, Summer	April	Diptera, Hymen
He_pu	Per	Hemi	Gras	NoPhr	Meso	None	Lsummer, Eautumn	May	Wind
Ho_la	Per	Hemi	Gras	LPhr	Meso, Hygro	None	Direct	May	Wind
Hy_pe	Per	Hemi	NR forb	NoPhr	Meso, Sclero	None	Spring	June	Diptera, Hymen
Ir_ps	Per	Geo, Helo	NR forb	WPhr	Helo, Meso	None	ESummer	May	Hymen
Ja_er	Per	Hemi	NR forb	NoPhr	Sclero, Meso	Feather	Spring	July	Diptera, Hymen
Ja_vu	Bian, Per	Hemi	R forb	NoPhr	Meso	Feather	Spring	June	Insects
Le_la	Per	Hemi	NR forb	NoPhr	…	None	Spring	June	Insects
Lo_pe	Per	Hemi	Gras	NoPhr	Meso	None	Direct	June	Wind
Lot_pe	Per	Hemi, Helo	NR_Forb	Non ObPhr	Meso, Helo	None	Spring	June	Hymen
Ly_nu	Per	ChamH, Hemi	NR_Forb	Non ObPhr	Hygro	None	…	June	Diptera, Hymen

Table S2.D2 (continued)

Species	Life span	Life form	Growth form	Grwtrdep	Anatomy	Seed Morph	Germ period	Onset of flowering	Poll method
Me_fa	Per	Hemi	NR_Forb	NoPhr	Meso, Sclero	None	...	May	...
Me_lu	Bian, Per	Thero, Hemi	NR forb	NoPhr	Meso	None	Summer, Autumn	April	Hymen
Od_ve	Ann	Thero, Par	NR forb	NoPhr	Meso	None	Lspring, Esummer	June	Hymen
Od_se	Ann	Thero, Par	NR forb	NoPhr	Meso	None	...	July	...
Oe_fa	Ann, Bian	Hemi	R forb	NoPhr	Meso, Sclero	None	Spring	June	Insects
On_sp	Per	ChamW, Hemi	Shrub	NoPhr	Meso	None	Autumn, Spring	June	Hymen
Or_vu	Per	Hemi, ChamH	NR forb	NoPhr	Sclero, Meso	None	Eautumn, Esummer	July	Insects
Ph_ar	Per	Hemi, Helo	Gras	Non ObPhr	Helo	None	Direct	June	Wind
Ph_pr	Per	Hemi	Gras	NoPhr	Meso	None	Direct	June	Wind
Pi_sa	Per	Hemi	NR forb	NoPhr	Meso, Sclero	None	Spring	July	Hymen
Pl_ar	Ann	Thero	NR forb	NoPhr	Sclero, Meso	...	...	June	Wind

Table S2.D2 (continued)

Species	Life span	Life form	Growth form	Grwtrdep	Anatomy	Seed Morph	Germ period	Onset of flowering	Poll method
Pl_la	Per	Hemi	R_forb	NoPhr	Meso, Sclero	None	Autumn, Spring	May	Coleo, Diptera, Wind
Pl_ma	Per	Hemi	R_forb	LPhr	Sclero, Meso	None	Spring	May	Wind
Po_pr	Per	Hemi	Gras	NoPhr	Meso	None	Direct	May	Wind
Po_tr	Per	Hemi	Gras	NoPhr	Hygro, Meso	None	Direct	May	Wind
Po_ni	Per	Phan	Tree	Non ObPhr	Meso	Feather	…	April	Wind
Po_an	Per	Hemi	R_forb	LPhr	Hygro, Helo	None	ESummer	May	Insects
Po_re	Per	Hemi	R forb	NoPhr	Meso, Hygro	Elai	Summer, Autumn	June	Diptera, Hymen
Ra_ac	Per	Hemi	R forb	LPhr	Meso	None	Summer	April	Insects
Ra_re	Per	Hemi, ChamH, Helo	R forb	LPhr	Helo, Hygro	…	Summer	May	Insects
Po_ni	Per	Phan	Tree	Non ObPhr	Meso	Feather	…	April	Wind
Ru_ca	Per	ChamW, Hemi	Shrub	NoPhr	Meso	Nuts	Autumn, Espring	May	Insects
Ru_ac	Per	Hemi	R forb	NoPhr	Meso	None	Spring	May	Wind

Table S2.D2 (continued)

Species	**Life span**	**Life form**	**Growth form**	**Grwtrdep**	**Anatomy**	**Seed Morph**	**Germ period**	**Onset of flowering**	**Poll method**
Ru_cr	Per	Hemi, Helo	NR forb	NoPhr	Meso	None	Spring	May	Wind
Ru_hy	Per	Helo	NR forb	WPhr	Helo	None	Spring	July	Wind
Ru_th	Per	Hemi	NR forb	NoPhr	Meso	None	Spring	June	Wind
Sa_al	Per	Phan	Tree	WPhr	Meso, Helo	Feather	Direct	April	Insects
Sa_pu	Per	Phan	Shrub	WPhr	Meso, Helo	Feather	Direct	April	Insects
Sa_of	Per	Hemi	NR forb	NoPhr	Meso	None	Direct	July	Insects
Se_in	Per	ChamH	NR forb	NoPhr	…	Feather	…	June	Insects
So_ca	Per	Hemi	NR forb	NoPhr	Meso	None	Spring	August	Diptera, Hymen
Ta_vu	Per	Hemi	NR forb	NoPhr	Sclero	None	Spring	July	Insects
Ta_sp	…	…	Forb	…	…	…	…	…	…
Th_mi	Per	Hemi	NR forb	NoPhr	Meso	None	Autumn	June	Diptera, Wind, Apo
To_ja	Ann, Bian	Thero	NR forb	NoPhr	Meso	Hooks	Spring	June	Diptera
Tr_ca	Ann	Thero	NR_Forb	NoPhr	Meso	None	Spring	May	Insects
Tr_du	Ann	Thero	NR forb	NoPhr	Meso	None	Autumn	May	Hymen

Table S2.D2 (continued)

Species	Life span	Life form	Growth form	Grwtrdep	Anatomy	Seed Morph	Germ period	Onset of flowering	Poll method
Tr_pr	Bian, Per	Hemi	NR forb	NoPhr	Meso	None	Autumn, Spring	May	Hymen
Tr_pe	Per	Hemi	NR_Forb	NoPhr	Hygro, Meso	None	Lspring, Eautumn	May	Hymen
Tr_fl	Per	Hemi	Gras	NoPhr	Meso	None	Direct	June	Wind
Ur_di	Per	Geo, Hemi	NR forb	NoPhr	Hygro, Meso	None	Direct, Delayed	June	Wind
Ve_te	Per	ChamH	NR forb	NoPhr	Sclero, Meso	None	…	May	Diptera
Ve_ch	Per	ChamH	NR forb	NoPhr	Meso	None	Autumn, Spring	April	Diptera, Hymen
Vi_cr	Per	Hemi, Lia	Climb	NoPhr	Meso	None	Direct	June	Diptera, Hymen

S2.E Ranges of the filter and frequency analyses of the plant strategy classes

Table S2.E: *The minimum and maximum values of the filters (raw data) over all the studied plots.*

Filter	**Range**
SoilM	3.7 – 48.7 %
L550	0.2 – 2.3 %
CSoil	4.5 – 59.9 mg/g
NSoil	0.4 – 5.0 mg/g
Ca	0.6-7.0 mg/g
Grain size – Lutum	0.0 – 13.3%
Grain size – Silt	4.7 – 80.9 %
Grain size – extra fine sand	0.0 – 29.1%
Grain size – very fine sand	0.4 – 16.5%
Grain size – fine sand	0.3 – 22.2%
Grain size – coarse sand	0.4 – 33.3%
Grain size – very coarse sand	0.2 – 34.2%
Grain size – extra coarse sand	0.0 – 26.4%

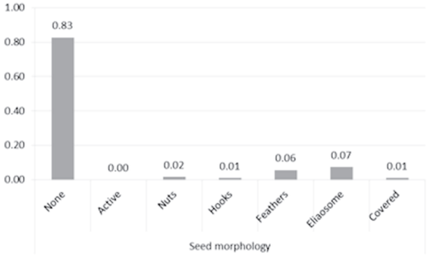

Figure S2.E1: *Weighted averaged fractions of "lifespan" and "lifeform" categories of all the identified species.*

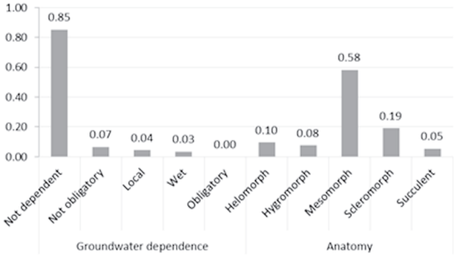

Figure S2.E2: *Weighted averaged fractions of "groundwater dependence" and "Anatomy" classes of all the identified species.*

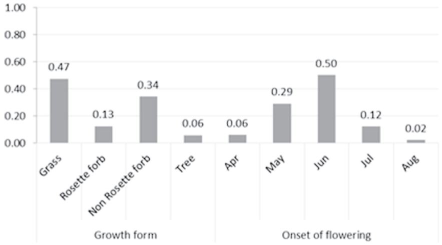

Figure S2.E3: *Weighted averaged fraction of "growth form" and "onset of flowering" for the identified species.*

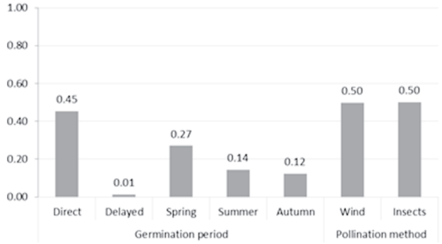

Figure S2.E4: *Weighted averaged fraction of "germination period" and "pollination method" for the identified species. For 'Pollination method' the insect categories are grouped into 'Insects'.*

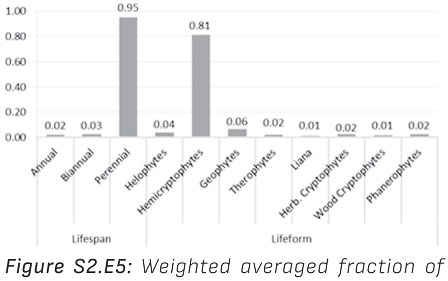

Figure S2.E5: *Weighted averaged fraction of "seed morphology" for the identified species.*

S2.F FC clustering

Table S2.F: *Overview of the FC analyses per plot. The value indicates to which cluster the plot belonged for each of the FC analysis. 1 = red, 2 = green, 3 = blue, 4 = turquoise, 5 = pink, 6 = yellow and 7 = grey. The colors are the same as in Figure 2.4. Sp = Species, Ana = Anatomy, Pol = Pollination method, Glow = Onset of flowering, Grwat = Groundwater dependence, Germ = Germination period, Lsp = Lifespan, Smor = Seed morphology, Grf = Growth form, Lff = Life form.*

	Sp	Ana	LES_H	LES_L	Pol	Flow	Grwat	Germ	Lsp	Smor	Grf	Lff
D01	2	3			2	3	2	2	2	2	2	2
D02	6	3	5	3	1	3	2	3	3	2	4	4
D03	2	1	6	2	2	2	2	2	2	2	6	2
D04	6	3	5	1	1	3	2	1	3	3	4	1
D05	3	3			2	2	1	3	1	1	2	1
D06	2	4			2	4	2	2	1	2	2	2
D07	6	2			2	2	2	2	2	3	2	3
D08	2	2	5	3	2	1	1	2	1	3	1	2
D09	7	1	2	1	1	1	1	1	1	1	1	1
D10	7	1	6	3	4	3	1	1	1	1	4	3
E01	1	1	1	1	1	1	1	1	1	1	1	1
E02	1	1	1		2	1	1	2	1	1	2	1
E03	1	1	1	1	4	1	2	1	1	1	3	1
E04	2	2	2	1	4	2	2	3	2	2	3	2
E05	3	2		2	1	3	2	3	3	3	4	3
E06	3	3	3	3	3	4	2	3	3	3	4	4
E07	4	4		3	2	2	2	2	2	3	2	4
E08	3	3	4	2	3	4	2	3	2	2	4	4
E09	3	4		2	4	4	2	3	2	3	3	4
E10	3	2	5	2	1	5	1	3	4	3	5	5
M01	5	2		2	3	5	3	1	4	4	6	5
M02	5	2		2	3	5	3	1	4	4	6	6
M03	5	2		2	4	5	3	1	4	4	5	7
M04	4	4	3	3	3	4	2	2	2	2	1	3
M05	4	2	3	2	4	4	2	1	2	2	3	6
M06	2	3	6	3	3	4	2	2	2	2	4	6
M07	4	4		3	3	4	2	2	2	3	6	3
M08	4	4			2	2	2	2	1	3	2	4
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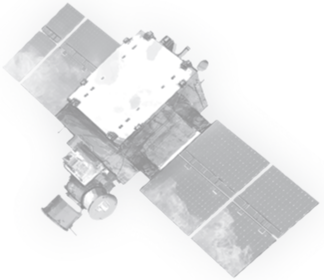
M10	4	4	5	3	1	2	2	3	2	2	5	7



Chapter 3

Revealing 35 years of landcover dynamics in floodplains of trained lowland rivers using satellite data

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Abstract

Lacking substantial erosive and sedimentation forces, regulated rivers allow their floodplains to become overgrown with forest, increasing the flood risk of the hinterland. In the Netherlands floodplains have therefore been subjected to interventions, like clear cutting, lowering and creation of side channels, and management, consisting of grazing and mowing. However, the comprehension of how those activities influence landcover dynamics is lacking. The aim of this study is therefore to investigate long-term landcover dynamics of a regulated river system through the lens of remote sensing. What transitions between landcover classes can be observed? And how (if) do management and interventions impact succession and retrogression? The study area comprised the upstream part of the Dutch Rhine river, its three branches and five adjacent floodplains. Satellite data (LandSat 5 and 8), encompassing a 35-year period (1984-2018), were used for studying landcover dynamics. Landcover classification was based on seven classes: water, built-up area, bare substrate, grass, herbaceous vegetation, shrubs and forest. Retrogression was highest for the landcover classes obstructing water flow (shrubs, forest and herbaceous vegetation), succession was most frequent on bare substrate, and water and grass were the most stable landcover classes. The regulated nature of the system became apparent from the spatial and temporal cacophony of landcover dynamics which differ from those of natural meandering rivers. This study showed that satellite data are useful for analyzing the impact of human activities within floodplains of regulated rivers and may assist in floodplain management aimed at combining water safety and nature policies.

3.1 Introduction

Floodplains of natural rivers are one of the world's most distinct ecosystems (Tockner and Stanford, 2002). These rivers actively shape the vegetation composition of their floodplains by meandering through the landscape in which erosion removes vegetation and sedimentation provides areas with bare substrate to restart vegetation succession (Geerling et al., 2006; Corenblit et al., 2009a; Corenblit et al., 2009b). These landscaping processes create a diverse landscape with a variety of successional stages (Nanson and Beach, 1977). When rivers become channelized, fixed, or dammed riverine forces cease and floodplain vegetation composition is shaped more dominantly by biological processes (Bornette et al., 2008; Geerling et al., 2008; Garofano-Gomez et al., 2017), potentially leading to floodplains overgrown with forests (Ward et al., 2002).

The disruption of the floodplain – river interaction and hence the massive development of shrubs and forests in floodplains may jeopardize flood safety by hampering water flow, which, during periods of high-water discharges, results in decreased water discharge capacity and therefore increased flood levels (Baptist et al., 2004). In the Netherlands, flood risk is reduced by actively managing vegetation development. However, as many of the Dutch floodplains are listed as natural areas with a legal status, the active management of vegetation may conflict with nature policies, as flood safety demands smooth areas, while natural areas thrive under high variety of vegetation structures brought about by different development stages. As such, both the river manager and various authorities responsible for nature have a keen interest in understanding large-scale dynamics of floodplain vegetation (Geerling et al., 2013).

Various management and intervention activities have been executed and have focused on flood safety and/or nature policies (Figure 3.1). The activities can be divided in two types: there are small-scale management activities which mostly affect the rate of succession and larger scale interventions, which have a more disruptive character. The small-scale management activities are often ad hoc, have various forms and have remained largely undocumented. Examples of types of small-scale management are sowing bare sediments with seed mixtures to create 'natural' grasslands to cut-off direct succession from bare soil to forest (softwood); grazing by horses and cattle at higher intensities to halt or limit succession and at lower densities for semi-natural landscaping; and beavers were reintroduced to enhance diversity in vegetation structure of woody vegetation

(Pelsma et al., 2003; Sluiter, 2003). The larger-scale (1-5 kms) interventions have been aimed at sand and clay extraction and have been deployed for nature rehabilitation purposes (Buijse et al., 2002). Examples are the removal of trees, shrubs and reed (Oosterloo and Otermann, 2016) and floodplain lowering (Geerling et al., 2008; Simons et al., 2001; Vuren et al., 2002).

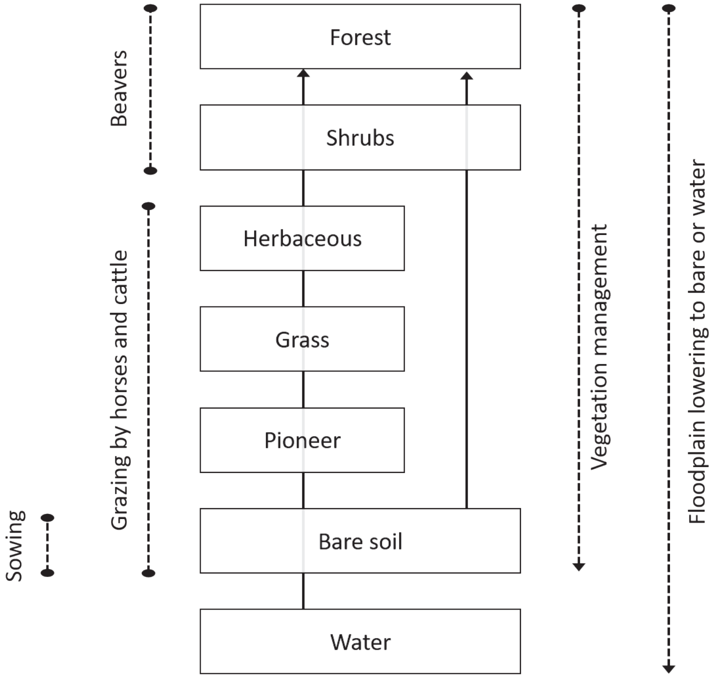

Figure 3.1: *Vegetation succession and human management and interventions practiced in the Dutch Rhine system. Succession to floodplain forest is simplified along two main pathways via intermediate stages (pioneer, grass, herbaceous) and straight from bare soil to shrubs and forest. Management and interventions consist of halting or slowing succession (sowing grass, various forms and intensities of grazing, reintroduction of beavers) and setting back succession by vegetation management or large-scale floodplain lowering (excavation). Adapted from Geerling et al. (2006).*

The various management activities and interventions produced a patchwork of land covers of which the long-term (> 10 years) large-scale dynamics in terms of succession, retrogression, and their spatial patterns are unknown. Therefore, the aim of this study is to investigate long-term landcover dynamics of a regulated river system through the lens of remote sensing. What transitions between landcover classes can be observed? And how (if) do management and interventions impact succession and retrogression? We show large scale pattern dynamics and selected smaller scale examples of management and interventions related to succession and retrogression. In the discussion we focus on linking the observed pattern dynamics to known management policies and activities. As method we use the time series of Landsat 5 and 8 as available in Google Earth Engine which has been applied to river landscape changes (Donchyts et al., 2016; Gorelick et al., 2017; Zurqani et al., 2018).

3.2 Data and method

The Rhine river enters the Netherlands with an average discharge of 2217 m^2/s (100 year averaged, www.waterinfo.rws.nl). Shortly after entering the Netherlands, the Rhine river splits into the Waal river and the Nederrijn river. A few kilometers downstream the first split, the IJssel river branches off from the Nederrijn river. The discharge is roughly divided in a ratio of 6:2:1 between the Waal, Nederrijn and IJssel, respectively (ten Brinke, 2005). The Nederrijn is the only impounded branch. Since the late 1980's the use of floodplains has shifted from mainly agriculture to more nature conservation (Baptist et al., 2004). This study encompassed three scales: the river scale, the branch scale and the floodplain scale (Figure 3.2). On floodplain scale, five floodplains were selected to cover a range of management intensities and interventions (Table 3.1). The branch scale comprises the floodplains adjacent to those branches and the river scale comprises all the floodplains.

The availability of ground truth data is a major challenge, but of high importance for vegetation and landcover classification by satellites and other remote sensing techniques. It is needed for training and validating the selected classification algorithm. In the Netherlands, floodplain vegetation surveys for the Rhine took place in 1997, 2005, 2008, 2012 and 2017. The maps are based on manual interpretation of 25 cm ground resolution stereographic true color airborne images (Geerling et al., 2009). In these maps floodplain land cover is grouped into 29 classes, like natural and production grasslands, orchards, natural and production forests, pioneer vegetation and several more classes. The automatic classification of satellite images allows for identification of a limited set of vegetation classes. Therefore the 29 detailed landcover classes were lumped together into seven classes: water, built-up area, bare substrate, grass, herbaceous vegetation, shrubs and forest (Supplementary Material S1). Landcover changes in (part of) this sequence are referred to as succession, changes in the reverse order are referred to as retrogression. These lumped classes were used as ground truth data in the classification procedure.

Figure 3.2: *Overview of the study area. In blue the study area, of which the lowest branch is the Waal river, the middle branch the Nederrijn river and the vertical branch the IJssel river. The red pins indicate the location of the five floodplains used as case studies: Blauwe Kamer (BK), Duursche Waarden (DW), Gamerensche Waarden (GW), Klompenwaard (KW), and IJsseloordsche Polder (IJP). Satellite image: Googe Earth (2018).*

On Google Earth Engine, data from LandSat 5 and 8, with a spatial resolution of 30*30 m, were used to study the period 1984–2018. All cloud free images were used. For each year, a composite image was produced by creating a seasonal median of each band and subsequently those bands were stacked. Using multiple images allowed for a better distinction between classes because of class specific spectral changes caused by differences in seasonal growth of (agricultural) management. Next, areas on the vegetation mappings were selected that remained the same between 1997 and 2017. The selected areas were used for training and validation, for which stratified sampling was used: 1000 pixels were selected, of which 700 were randomly selected for training and 300 for validation. The training pixels of the seven landcover classes were used to train a random forest classifier algorithm. This classifier was chosen because of its accuracy for classifications (Belgiu and Drăgu, 2016). The algorithm was based on 50 decision trees per class. This classification was then applied to the whole composite image.

The accuracy across each landcover class was expressed in precision and sensitivity. Precision was defined as the true positives compared to the sum of the true positives and the false positives for a class. Sensitivity was defined as the true positives compared to the sum of true positives and false negatives for a class. The training and validation of the LandSat data resulted in an average accuracy of 77%. The accuracy differed between the landcover classes, where water was classified with the highest precision and sensitivity and herbaceous, shrubs and forest were classified with the least precision and sensitivity (Supplementary Material S2 and Supplementary Material S3). The overall kappa coefficient, to correct for chance, amounted to 72%, with a minimum value of 60% in 2002 and a maximum value of 81% in 2018.

To reduce noise of year to year fluctuations due to misclassification or short-term vegetation changes all data points were clustered into seven equal cohorts of five years. The clustering was based on the five-year median value per data point. The clustering obviously masked dynamics on smaller time scales but allowed for a general impression of the landcover dynamics. The data were then used to compile an overview of the net changes in landcover composition on the three scales, the age composition of today's vegetation (defined as the time a pixel solidly belonged to its present-day class) to deduce the turnover rate of the landcovers, and subsequently, each pixel was tracked to obtain information on how frequent pixels changed into another landcover class to quantify the degree of change. Note that a forest pixel may counter-intuitively show succession, as it may start as forest, changes into bare substrate (retrogression) and returns to forest again (succession). For water it is similar, but then for retrogression as a water pixel may start as water, change into bare substrate (succession) and return to water again (retrogression). Additionally, per pixel a trendline was fitted through the seven cohorts as indication for the rate of succession and retrogression.

Table 3.1: Information on the selected floodplains: their river, area, date of function conversion, former use, date of excavation and the current intensity of grazing or mowing.

Floodplain	River	Area (ha)	Conversion to nature	Former use	Excavation	Current grazing intensity (animal/ ha)
Blauwe Kamer (B)	Nederrijn	229	1984	Clay extraction, grass and hay fields	1991/1992	3.0, year round
Duursche Waarden (D)	IJssel	406	1987	Clay extraction	1989, 2007	1.3 year round
Gamerensche Waarden (G)	Waal	98	1996	Farmland, clay extraction	1996-1999, 2005/2006, 2009/2010, entire area	1.0, summer half year
Klompen-waard (K)	Nederrijn and Waal	93	1999	Grass fields	1999, entire area	0.3, year-round
IJsseloordse Polder (IJP)	IJssel	65	Not converted	Still agriculture		Mowing

3.3 Results

3.3.1 Changes in landcover

In all three branches grass was the most dominant landcover (> 50% on average), followed by water (> 10% on average). Subsequent shares of landcover differed between the branches (Figure 3.3). Over the period 1984-2018 the area of grass decreased in all branches (1859 ha on river scale). Also, the area with forest (182 ha) and built-up (40 ha) decreased on river and branch scale with the exception of built-up area in the Waal branch. On river scale, the landcovers of herbaceous vegetation, water bare substrate and shrubs all increased, 1012, 941, 91 and 36 ha respectively. The Nederrijn and Waal branches showed, however, a decrease in shrub landcover.

Landcover composition was more diverse and dynamic on floodplain scale (Figure 3.3). Considering the 35-year period, grass dominated in IJsseloordsche Polder, Duursche Waarden, Klopmenwaard and Gamerensche Waarden, while herbaceous vegetation dominated Blauwe Kamer (but only just). The decreasing trend in grass area found on river and branch scale was also apparent on floodplain level, except for IJsseloordsche Polder were all landcover classes were rather stable. For the four other floodplains, the area with water increased, as did the herbaceous vegetation and bare substrate. Shrubs decreased only in Gamerensche Waarden and forest in Blauwe Kamer and Duursche Waarden. Built-up area decreased only in Blauwe Kamer and Gamerensche Waarden.

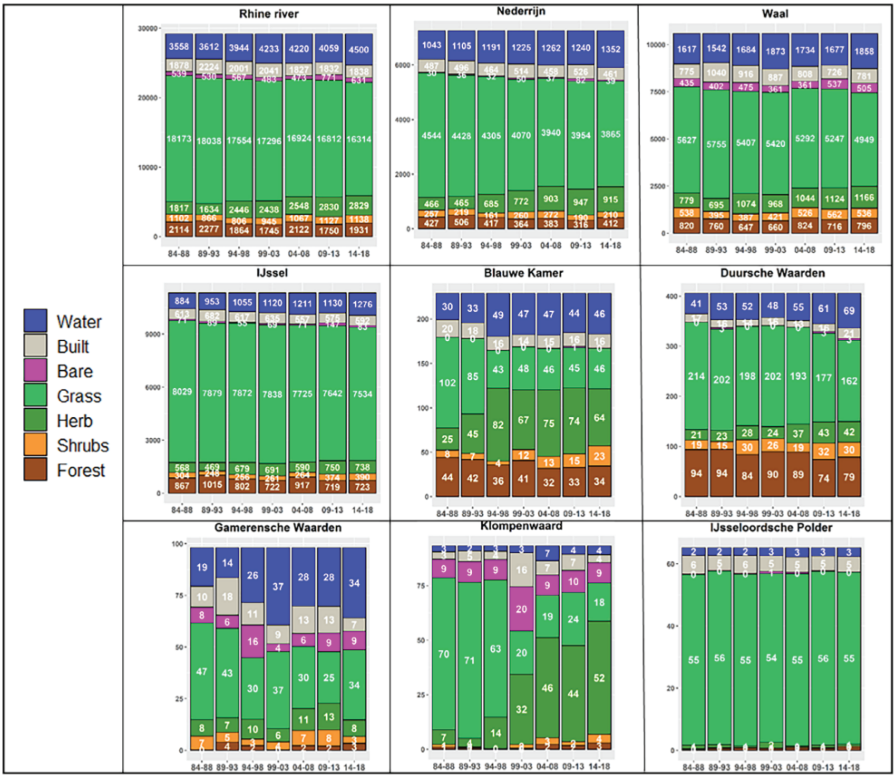

***Figure 3.3:** Mean land cover composition (hectare) on all three scales and in 5-year median cohorts of landcover composition (hectare) for the five floodplains over the period 1984-2018.*

3.3.2 Age composition

The changes in landcover composition were temporally non-equidistant on any of the three scales (Figure 3.4). Grass, water, built- up and forest were the oldest (most stable) landcovers, while shrubs, herbaceous vegetation and bare substrate were younger. For example, in general around 70% of today's grass landcover has been present since 1984-1988. The shrub landcover existed mostly (ca 80%) of vegetation younger than 15 years. On floodplain scale, the age composition of the landcover classes was more variable than on river and branch scale.

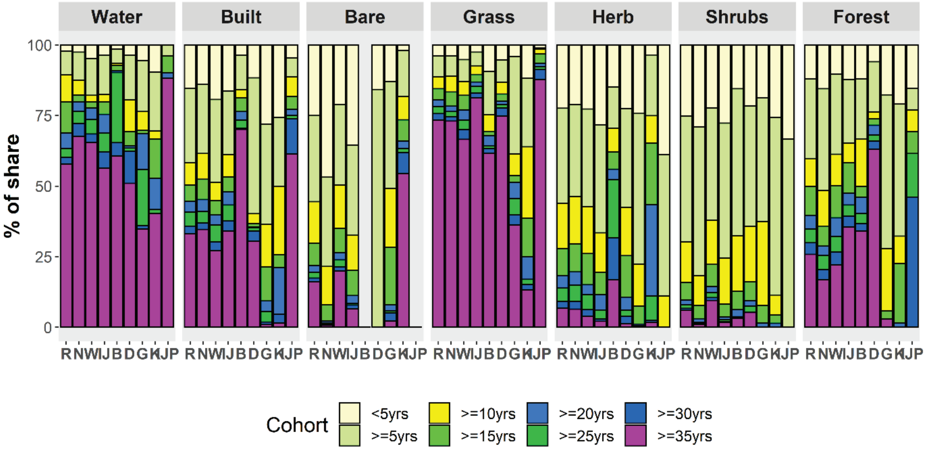

Figure 3.4: *Age composition of the present-day land cover composition for the classes "water", "built", "bare substrate", "grass", "herbaceous vegetation", "shrubs" and "forest" for the river (R), its three branches (N, W and IJ) and the five floodplains (B, D, G, K, IJP).*

3.3.3 Succession, retrogression and stability

On all levels, retrogression was higher than succession and stability for herbaceous vegetation, shrubs and forest (Figure 3.5). On floodplain level there were two exceptions. Herbaceous vegetation did show higher stability than retrogression in Blauwe Kamer and in Duursche Waarden forest dynamics were dominated by stability instead of retrogression. On all levels, stability was highest for water and grass. Again, two exceptions were observed on floodplain level: retrogression of grass instead of stability dominated Blauwe Kamer and succession of grass dominated stability in Gamerensche Waarden. Succession was, on all levels, highest for built-up landcover as it started to become overgrown, expect for Blauwe Kamer and IJsseloordsche Polder where built up area remained mostly stable. Bare substrate showed mixed dynamics: succession was most dominant on river scale, for the Waal and IJssel branches and in Gamerensche Waard and IJsseloordsche Polder. In Duursche Waarden retrogression and succession were balanced and in Klompenwaard stability dominated over retrogression and succession dynamics.

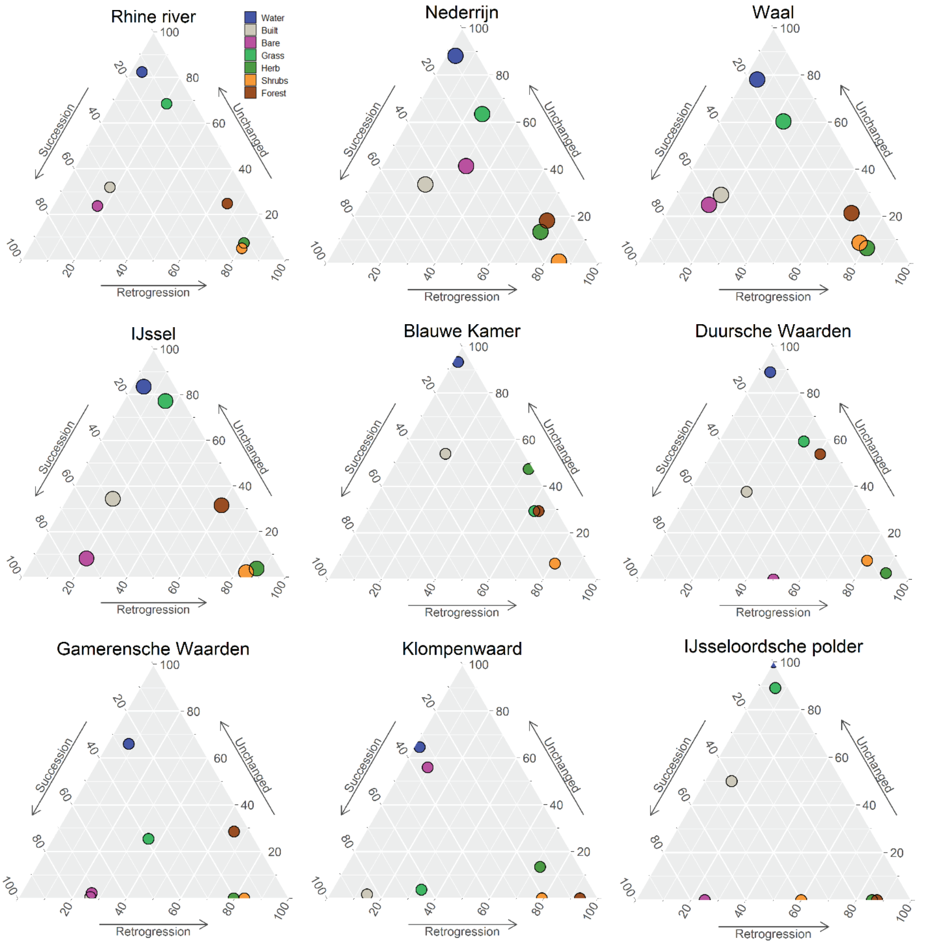

Figure 3.5: Ternary graphs of the share of each landcover class that progressed, retrogressed and remained stable for all three scales. For each pixel and per five-year cohort it was scored how often a pixel remained the same or changed along the succession or retrogression pathway. Starting point for the pixels was the landcover class they adhered to in the 1984-1988 cohort. The text direction of numbers along the axes indicates the gridlines connected to a specific axis.

3.3.4 Landcover dynamics

Changes in landcover were brought about by a variety of transitions. For example, grass could develop into shrub and subsequently retrogress into herbaceous vegetation, or it could develop into herbaceous vegetation and then into forest (Supplementary Material S4, database is available by contacting the first author). Even though numerous potential changes were observed, principal links between landcovers could be identified. On river and branch scale, bare substrate developed mostly into grass and herbaceous vegetation, grass into herbaceous vegetation and bare substrate, herbaceous vegetation into grass and shrubs, shrubs into herbaceous vegetation and forest, and forest into shrubs and herbaceous vegetation (Supplementary Material S5). These changes between landcovers were also identified on floodplain scale, but there were differences. The more rigorously excavated floodplains (Gamerensche Waarden and Klompenwaard) showed a strong tendency of the vegetated landcover classes turning into bare substrate. In IJsseloordsche Polder grass could change into another vegetation class, but most of the initial grass landcover returned back to grass.

3.3.5 Spatial dynamics

Seen on an aerial view, areas could be highlighted with high rates of succession and retrogression and areas with stable land cover dynamics over the 35-year study period. For some floodplains, like Klompenwaard, high succession rates are present in the whole floodplain, while in others those higher succession and retrogression rates are only present in some areas of the floodplains, like in Duursche Waarden, Blauwe Kamer and Gamerensche Waard. In those three floodplains, and the whole of IJsseloordsche Polder, there are also areas with almost stable to stable land covers (Figure 3.6).

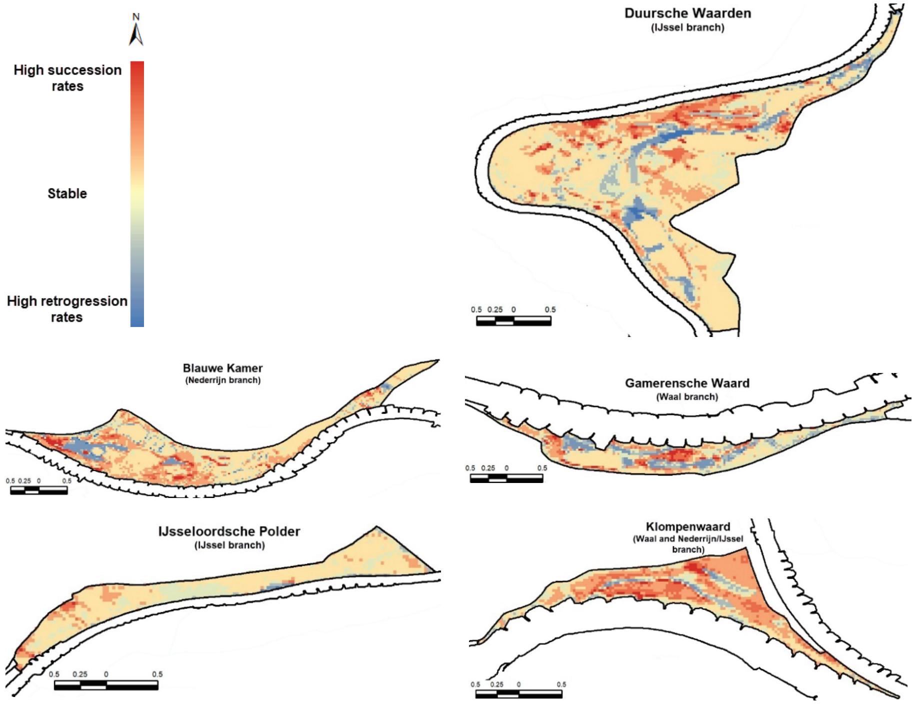

Figure 3.6: *Aerial view of succession, retrogression and stability of the landcovers of the five floodplains. Areas with high rates of succession are indicated with red, those with high rates of retrogression with blue and the more stable areas as yellow. The white tube-like shape is a river branch of which the name is mentioned in the titles of the figures.*

3.4 Discussion

When comparing age composition (Figure 3.4) and landcover dynamics (Figure 3.5) to natural flowing rivers (e.g. Marston et al., 1995; Geerling et al., 2006), the regulated nature of the floodplains of the branches of the Dutch Rhine river is illustrated clearly. The studies of Marston et al. (1995) and Geerling et al. (2006) showed that water, bare substrate and grass landcovers are the most dynamic landcovers due to active alluvial processes. Shrub and forest landcovers were shown to be the most stable because those landcover classes are typically located in less active areas. In contrast, in the floodplains of the regulated Dutch Rhine river, water, grass and forest landcovers were the most stable landcovers and shrubs the least stable, signaling the absence of alluvial landscaping forces and the presence of other landscaping forces, like human management and interventions. In addition, clues on the presence of management and interventions were also given by the rates of succession and retrogression: the rate of succession was in general lower and the rate of retrogression higher than observed in the natural meandering Allier river (Geerling et al., 2006)

The strong retrogression found in our study may be linked to the creation of side channels and/or floodplain lakes in Blauwe Kamer (Demon and Van Bussel, 1994), Duursche Waarden (Rijkswaterstaat, 1994), Gamerensche Waarden (Jans, 2004) and Klompenwaard (Schoor et al., 2011). And, although being speculation, the relative high rate of succession in those four floodplains, compared to the rate of succession in IJsseloordsche Polder, which is still under an agricultural management regime, could be caused by the transition from agricultural to nature-oriented management. Interesting though, is the effect of grazing intensity in the non-agricultural managed floodplains. Landcovers appeared more stable under lower grazing intensity than under higher grazing intensity. This is unexpected as in general higher grazing regimes are used to control vegetation development: fixating the landscape (Vulink, 2001). However, the actual effect of grazing on landscape dynamics may be more complex, as vegetation structure and how the landscape is used by grazers may play a role (Gill, 2006). Additionally, landscape characteristics such as soil moisture and vegetation productivity are found to interact with land cover changes and grazing intensities (Adler et al., 2001; Zheng et al., 2015).

To balance vegetation management between flood safety and nature policies, the information in Figure 3.6 could be helpful to managers by revealing how management and interventions spatially and temporally steer landcover dynamics. Nowadays practice is to allow for as much natural landcover dynamics as possible. To do so, models on landscape dynamics (Baptist et al. 2004) and a real-time monitoring system of landcover composition based on satellite imagery have been used (Geerling et al., in prep). However, the success of allowing as much space to landcover dynamics as possible for conserving riparian vegetation is to be questioned, as the habitat template of the floodplains has changed by regulation of the Dutch Rhine river and the continuous human-disturbance (Stella et al., 2013). Under those changed environmental conditions, competition between riparian and terrestrial species become more important, altering the composition and the ecological functioning of those floodplains (Corenblit et al., 2007).

Note that the accuracy of the classified images could have led to overestimation of landcover dynamics, especially between grass and herbaceous landcover and shrub and forest landcover. This effect was partly overcome by using five-year cohorts. Although being in agreement with accuracies of other studies (Mitchell et al., 2016; Azzari and Lobell, 2017; Huang et al., 2017), the accuracy may be increased by adding radar data as input to the classifier (Joshi et al., 2016). Also, adding satellite data with higher spatial and temporal resolution improves accuracy, like Sentinel2 data, with a resolution of 10*10 meter, or even commercially available higher accuracy satellites, like Spot, Triple Sat or Worldview 3.

3.5 Conclusion

Satellite images proved useful in researching how long-term vegetation development is impacted by river regulation and human activities aimed at guaranteeing water safety and meet nature goals. The satellite imagery revealed that human management and interventions resulted in a cacophony of landcover dynamics. In natural flowing rivers, there are distinct areas of higher and lower landcover dynamics which can be explained by the course of the river. In the studied regulated river system, higher and lower landcover dynamics resulted from spatially diverse management and interventions, obstructing disclosure of large scale natural landcover developments.

Compared to natural flowing rivers, management and interventions slowed down succession rates and increased retrogression rates for the more water obstructing landcover classes (shrubs, forest and herbaceous vegetation). The smoother landcover classes (water and grass) displayed slower rates of both succession and retrogression. The presented aerial views of dynamic and stable areas could be an aid in streamlining management and interventions to allow vegetation to develop as natural as possible on its current habitat template without jeopardizing water safety.

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S3.A Landcover classes

Table S3.A: *Description and characteristic species (if applicable) of the used landcover classes (based on Van Velzen et al., 2003, and Geerling et al., 2008).*

Landcover class	Description/characteristic species
Water	Several types of water bodies: river, side gullies, lakes
Built	Buildings and roads
Bare	Bare soil and soil with sparse vegetation (coverage by vegetation < 25%)
Fields and grass	Arable land Grazed grass, characteristic species: Perennial ryegrass (*Lolium perenne)* and Meadow grass (*Poa trivialis*) Open grassland, characteristic species: Bentgrass (*Agrostis stolonifera*), Couch grass (*Elytrigia repens*), Creeping cinquefoil (*Potentilla reptans*), Silver weed (*Potentilla anserine*), British fleabane (*Inula Britannica*), and Curled dock (*Rumex crispus*)
Herbaceous	Characteristic species: Field eryngo (*Eryngium campestre*), Red fescue (*Festuca rubra*); Yarrow (*Achillea millefolium*), Greater plantain (*Plantago lancealata*), Jewel weed (*Impatiens glandulifera*), Stinging nettle (*Urtica dioica*), Spotted dead-nettle (*Lamium maculatum*), Creeping thistle (*Cirsium arvense*), Common tansy (*Tanacetum vulgare*), Black mustard (*Brassica nigra*)
Shrubs	Characteristic species: Hawthorn (*Crataegus monogyna* and *Crataegus laevigata*), and young specimens of White willow *(Salix alba)*; Crack willow (*Salix fragilis*); Black poplar (*Populus nigra*), Wild Cherry (*Prunus avium* (Wild cherry) and several species of Oak (*Quercus)* and Elm (*Ulmus)*
Forest	Softwood forest, characteristic species: White willow *(Salix alba)*, Crack willow (*Salix fragilis*); Black poplar (*Populus nigra*) Hardwood forest, characteristic species Wild Cherry (*Prunus avium* (Wild cherry) and several species of Oak (*Quercus)* and Elm (*Ulmus)* Orchards.

S3.B Precision and sensitivity satellite data

Table S3.B: *Overview of the 10th and 90th percentile and mean of the precision (P) and sensitivity (S) per landcover class for the 35-year period.*

	Water		Built		Bare		Grass		Herb		Shrub		Forest	
	P	S	P	S	P	S	P	S	P	S	P	S	P	S
10 percentile	0.89	0.88	0.70	0.77	0.83	0.76	0.69	0.75	0.61	0.53	0.61	0.57	0.60	0.61
Average	0.92	0.92	0.78	0.84	0.89	0.83	0.78	0.80	0.69	0.65	0.68	0.65	0.69	0.70
90 percentile	0.96	0.97	0.86	0.92	0.94	0.90	0.85	0.86	0.77	0.74	0.74	0.72	0.78	0.79

S3.C Error matrices

Table S3.C: *Error matrices of the years with ground truth, except for 2012. Satellite data for 2012 was not available due to damage of LandSat 7 images, error matrices for 2011 and 2013 are given instead.*

Year	Real class	Classified class						
		Water	Built	Bare	Grass	Herb	Shrub	Forest
1997	Water	295	5	2	0	6	1	1
	Built	11	270	6	6	5	12	2
	Bare	2	15	130	0	1	0	0
	Grass	0	14	4	261	18	7	4
	Herb	6	11	2	36	181	13	36
	Shrub	7	9	0	8	23	206	43
	Forest	2	11	0	7	34	32	204
	True positives	0.95	0.87	0.88	0.85	0.64	0.70	0.70
		Water	Built	Bare	Grass	Herb	Shrub	Forest
2005	Water	291	1	0	1	4	4	1
	Built	2	252	6	2	0	8	12
	Bare	3	15	117	1	0	0	0
	Grass	0	5	1	257	21	2	7
	Herb	5	3	0	27	224	18	36
	Shrub	3	8	0	5	10	222	31
	Forest	2	19	0	11	32	42	203
	True positives	0.96	0.89	0.86	0.88	0.72	0.80	0.66

Table S3.C (continued)

Year	**Real class**	**Classified class**						
		Water	Built	Bare	Grass	Herb	Shrub	Forest
2008	Water	256	27	0	3	4	3	5
	Built	6	234	8	1	16	9	13
	Bare	2	33	103	1	5	0	0
	Grass	1	10	1	235	58	10	10
	Herb	2	10	0	25	198	24	34
	Shrub	3	15	0	8	31	197	58
	Forest	2	8	4	10	51	51	158
	True positives	0.86	0.82	0.72	0.72	0.68	0.63	0.56
		Water	Built	Bare	Grass	Herb	Shrub	Forest
2011	Water	266	6	0	0	2	10	2
	Built	2	264	7	0	4	5	1
	Bare	1	15	121	1	1	0	0
	Grass	0	15	1	238	28	11	8
	Herb	2	8	1	32	236	15	21
	Shrub	4	9	0	2	12	229	39
	Forest	3	9	1	6	24	43	193
	True positives	0.93	0.93	0.87	0.79	0.75	0.78	0.69

Table S3.C *(continued)*

Year	Real class	Classified class						
		Water	Built	Bare	Grass	Herb	Shrub	Forest
2013	Water	280	7	1	1	3	7	2
	Built	5	280	9	6	4	5	2
	Bare	1	23	102	9	0	0	1
	Grass	0	14	5	223	25	8	7
	Herb	4	6	0	38	205	29	27
	Shrub	3	9	0	12	22	212	41
	Forest	1	3	0	6	19	42	208
	True positives	0.93	0.90	0.75	0.79	0.66	0.71	0.75
		Water	Built	Bare	Grass	Herb	Shrub	Forest
2017	Water	290	12	0	0	4	5	0
	Built	6	252	11	15	11	7	0
	Bare	1	23	109	3	5	0	0
	Grass	2	18	1	223	29	10	7
	Herb	6	10	0	38	219	31	17
	Shrub	2	10	0	6	16	229	30
	Forest	0	2	0	12	25	35	207
	True positives	0.93	0.83	0.77	0.77	0.68	0.78	0.74

S3.D Landcover change matrix

Table S3.D: *Overview of changes in land cover (hectare) for the period 1984–2018 for the river, the branches and the five floodplains. 'Area (Ha)' represents the area as it for the 1984–1988 cohort and 'Stable (Ha)' refers to the area that remained stable during the 1984–2018 period. The part of the table with the landcover classes in the heading, reads as follows: from the class listed in the row to the class listed in the column. Note that the summed areas per landcover class per row are in general higher than the changed area, as changing data points tended to change more than one time.*

Location	Class	Area (Ha)	Stable (Ha)	Water	Built	Bare	Grass	Herb	Shrub	Forest
Rhine	Overall	29181	16805							
	Water	3558	2933	453	513	88	68	173	158	281
	Built	1878	599	299	691	411	856	526	258	326
	Bare	539	128	122	406	229	233	130	57	48
	Grass	18173	12432	857	1745	905	3506	4393	959	805
	Herb	1817	135	227	396	117	1723	1267	695	558
	Shrub	1102	56	243	259	41	510	855	679	891
	Forest	2114	522	346	408	65	706	1094	1166	911
Nederrijn	Overall	7255	4118							
	Water	1043	921	104	98	4	9	43	21	53
	Built	487	163	110	170	63	186	160	67	97
	Bare	30	12	21	40	8	20	11	6	4
	Grass	4544	2880	259	468	128	994	1404	287	235
	Herb	466	62	76	132	21	381	354	182	122
	Shrub	257	2	55	68	6	146	250	151	195
	Forest	427	77	74	86	10	159	289	250	198

Table S3.D (continued)

Location	Class	Area (Ha)	Stable (Ha)	Water	Built	Bare	Grass	Herb	Shrub	Forest
Waal	Overall	10590	5263							
	Water	1617	1264	244	300	68	41	90	100	155
	Built	775	225	99	313	254	381	231	105	102
	Bare	435	108	80	307	200	174	99	41	32
	Grass	5627	3395	304	727	568	1339	1674	350	249
	Herb	779	50	77	160	70	773	510	261	188
	Shrub	538	47	102	118	25	218	371	331	387
	Forest	820	174	136	174	35	260	451	478	350
IJssel	Overall	11336	7450							
	Water	884	737	103	112	15	18	39	36	72
	Built	613	210	89	207	93	287	133	86	127
	Bare	71	6	20	55	19	37	18	9	11
	Grass	8029	6196	294	546	204	1167	1303	320	321
	Herb	568	21	74	103	25	566	401	252	249
	Shrub	304	6	85	72	9	144	231	195	307
	Forest	867	273	136	147	20	286	351	439	363
Blauwe Kamer	Overall	229	94							
	Water	30.0	28.0	0.9	1.1	0.1	0.1	0.5	0.6	0.9
	Built	19.8	10.7	2.2	5.0	0.7	5.7	5.7	2.3	2.2
	Bare	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Grass	101.9	29.9	13.0	3.4	0.2	23.5	79.1	16.4	13.0
	Herb	25.1	11.9	1.7	0.8	0.1	10.0	11.6	5.7	1.7
	Shrub	8.2	0.6	3.0	0.9	0.1	1.2	5.7	4.2	3.0
	Forest	44.1	12.9	7.3	3.7	0.7	4.2	25.4	24.3	7.3

Table S3.D (continued)

Location	Class	Area (Ha)	Stable (Ha)	Water	Built	Bare	Grass	Herb	Shrub	Forest
Duursche Waarden	Overall	406	222							
	Water	40.9	36.4	3.9	1.5	0.2	0.6	0.9	2.1	3.9
	Built	17.1	6.4	0.3	4.5	1.0	10.8	6.4	3.6	0.3
	Bare	0.1	0.0	0.0	0.1	0.0	0.1	0.1	0.0	0.0
	Grass	214.0	126.6	13.1	21.3	5.6	35.3	69.4	29.1	13.1
	Herb	20.9	0.6	3.7	2.6	0.8	16.4	11.8	11.7	3.7
	Shrub	19.2	1.5	6.3	2.5	0.4	3.5	8.7	14.0	6.3
	Forest	93.7	50.4	17.3	6.6	0.7	11.2	16.4	34.4	17.3
Gamerensche Waarden	Overall	98	25							
	Water	18.7	12.3	7.0	6.7	1.0	0.9	2.2	2.1	7.0
	Built	10.1	0.1	4.5	4.0	6.5	6.1	3.6	3.0	4.5
	Bare	7.6	0.2	2.9	8.2	5.2	3.3	2.4	1.4	2.9
	Grass	46.8	11.9	15.5	18.3	16.2	22.2	21.6	6.1	15.5
	Herb	8.0	0.0	2.9	4.0	1.1	8.6	5.6	4.1	2.9
	Shrub	6.5	0.0	3.0	2.5	0.6	4.1	5.5	3.5	3.0
	Forest	0.4	0.1	0.0	0.1	0.0	0.3	0.3	0.2	0.0
Klompenwaard	Overall	93	10							
	Water	2.7	1.7	0.6	1.5	0.6	0.1	0.1	0.1	0.6
	Built	3.5	0.1	0.5	1.2	2.9	2.5	2.2	0.1	0.5
	Bare	8.5	4.8	0.1	2.5	2.1	2.8	2.1	1.2	0.1
	Grass	69.6	2.6	5.3	18.0	16.2	22.6	61.9	5.8	5.3
	Herb	6.7	0.9	0.0	1.8	0.7	8.5	5.6	1.0	0.0
	Shrub	1.3	0.0	0.0	0.7	0.1	1.6	1.6	0.4	0.0
	Forest	1.0	0.0	0.1	0.2	0.1	0.8	1.6	1.0	0.1

Table S3.D (continued)

Location	Class	Area (Ha)	Stable (Ha)	Water	Built	Bare	Grass	Herb	Shrub	Forest
IJsel-oordsche Polder	Overall	65	54							
	Water	2.5	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Built	6.0	3.0	0.3	1.3	0.1	2.8	0.6	0.4	0.3
	Bare	0.2	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0
	Grass	54.8	48.9	0.4	2.9	1.1	4.7	3.5	0.6	0.4
	Herb	1.2	0.0	0.0	0.2	0.2	0.9	0.1	0.1	0.0
	Shrub	0.2	0.0	0.0	0.1	0.1	0.2	0.1	0.0	0.0
	Forest	0.3	0.0	0.0	0.3	0.0	0.1	0.1	0.1	0.0

S3.E Dominant pathways

***Table S3.E:** Overview of the most dominant pathways found for each of the three branches. 'Starting class' lists the class to which the pixels belonged in the 1984-1988 cohort, 'Total changed' lists the summed number of hectares that switched landcover over the 1984-2018 period. Note that this differs from Supplementary material S3.D 'Stable' column, where only the area is considered comprising changing pixels. 'Succession 1' and 'Succession 2' list the dominant and second dominant change in landcover together with the number of hectares. The same is depicted for 'Retrogression 1'and Retrogression 2'. W →F means that water (W) changed into forest (F). The other classes are abbreviated as B (Bare), G (Grass), H (herb) and S (Shrub).*

Location	Starting class	Total changed	Succession 1	Succession 2	Retrogression 1	Retrogression 2
Nederrijn	Water	162	**W → F** 36	**W → H** 24	**F → W** 20	**H → W** 16
	Bare	48	**B → G** 7	**G → H** 2	**H → G** 6	**B → W** 6
	Grass	2946	**G → H** 1173	**H → F** 118	**H → G** 660	**G → W** 162
	Herb	1034	**G → H** 170	**H → S** 128	**H → G** 307	**S → H** 90
	Shrub	752	**S → F** 141	**H → S** 63	**S → H** 129	**F → S** 61
	Forest	923	**S → F** 90	**H → F** 65	**F → S** 169	**F → H** 155
Waal	Water	457	**W → F** 86	**W → S** 44	**F → S** 31	**F → W** 30
	Bare	374	**B → G** 108	**G → H** 37	**G → B** 39	**H → G** 30
	Grass	3949	**G → H** 1453	**B → G** 205	**H → G** 770	**G → B** 466
	Herb	1756	**G → H** 332	**H → S** 165	**H → G** 664	**S → H** 90
	Shrub	1339	**S → F** 308	**H → S** 115	**S → H** 199	**F → S** 158
	Forest	1573	**S → F** 195	**H → S** 102	**F → S** 327	**F → H** 227

Table S3.E (continued)

Location	**Starting class**	**Total changed**	**Succession 1**	**Succession 2**	**Retrogression 1**	**Retrogression 2**
IJssel	Water	205	**W → F** 46	**W → H** 20	**F → W** 22	**H → W** 13
	Bare	73	**B → G** 19	**G → H** 6	**B → W** 9	**H → G** 5
	Grass	3205	**G → H** 1125	**G → F** 167	**H → G** 676	**G → W** 173
	Herb	1485	**G → H** 206	**H → F** 165	**H → G** 452	**S → H** 86
	Shrub	915	**S → F** 230	**H → S** 54	**F → S** 111	**S → H** 96
	Forest	1492	**S → F** 178	**H → F** 88	**F → S** 313	**F → H** 190

Chapter 4

Linear Programming as a tool for understanding plant trait strategies interactions

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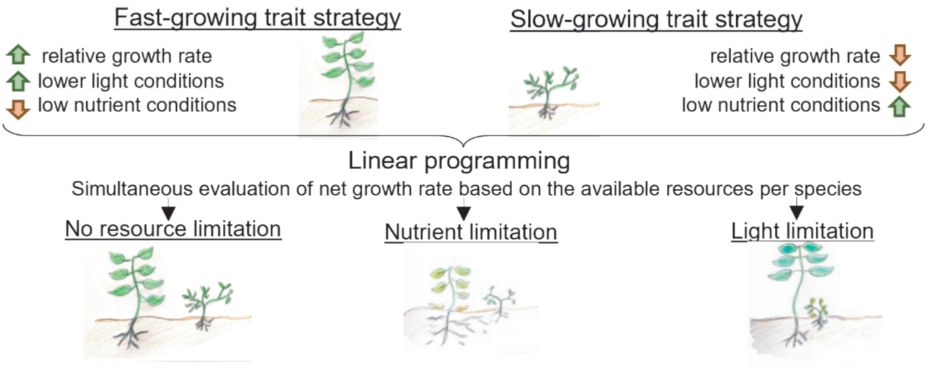
Abstract

For many years, researchers have been striving to understand and predict how environmental processes steer vegetation dynamics and vice versa. Amongst others, deterministic models have been used to explore and simulate this interaction. However, within this type of models, simulating plant competition remains challenging. Linear programming could, as a modelling technique, aid in this challenge, as it may aid in solving these challenges and thereby enhancing deterministic vegetation models. The aim of this research is therefore to demonstrate how linear programming can be used to model vegetation dynamics. The developed model comprised a fast- and a slow-growing plant trait strategy competing over a light and nutrient gradient. The model results showed that the fast-growing trait strategy outcompeted the slow-growing trait strategy under low light or high nutrient availability, while the slow-growing trait strategy outcompeted the fast-growing trait strategy under low nutrient availability. Co-existence occurred when resources were sufficiently available. These results are consistent with theory and show that linear programming could be a useful technique in solving plant competition within deterministic models. Additionally, the developed model also illustrated how linear programming allows for intraspecific variation and conveys clear information on the limiting resources steering competition.

Graphical abstract



4.1 Introduction

Predicting vegetation dynamics and concurrent vegetation composition from a system's understanding has long been one of the major objectives within the field of ecology (Laughlin et al., 2012). Being able to predict vegetation dynamics, the effects of climate change, nature restoration, or other (human) interventions on the interaction between vegetation dynamics and biogeochemical cycles as well as the resilience of vegetation composition against disturbances can be explored and perhaps even quantified. However, for this, vegetation composition, interaction between the environment, plant trait strategies and among plant trait strategies must be understood (Lavorel and Garnier, 2002).

Already in 1872 research was documented on how environmental conditions filter (sensu Keddy, 1992) species characteristics (i.e. trait strategies) that match these conditions best (Darwin, 1872). Since then, scientists have made steady progress in illuminating the mechanisms behind environmental and biological filters and the floral and faunal trait strategies they select. For example, certain physiological and morphological plant trait compositions have been associated with specific parts of gradients in soil moisture, flooding intensity or grazing pressure (Keddy, 1992; McGill et al., 2006). Additionally, despite that the process of filtering selects similar strategies (Shipley, 2010), competition among trait strategies (i.e. biological filters) fuels strategy diversity within these local trait strategy pools (Silvertown, 2004).

Spatial and temporal variability in resources or disturbances is also found to be an important filter for plant species composition, in which intraspecific variation is essential for plant species to thrive in these altering environments (Weiner, 2004). Environmental intraspecific variation enables stress reduction and increases plant species' niche breadth by adapting their physiological, morphological and demographic traits (Siefert et al., 2015, Hart et al., 2016) as well as their biomass allocation (optimal partitioning theory, Garnier 1992; Enquist, Brown, and West 1998; McCarthy et al., 2007). Yet, the range of intraspecific variation is bound by physical constraints and subjected to trade-offs and as such curbing a plant species' occurrence in specific environments (Tilman, 1990).

Based on the existing knowledge of the interactions between filters and trait strategies, several models have been developed to predict vegetation dynamics and concurrent trait strategy composition. Popular statistical models include CATS

(Shipley et al., 2006) and Traitspace (Laughlin et al., 2012). These models test the concept of environmental filtering of traits but do not offer mechanistic links between environmental conditions and traits or trait strategies. Deterministic models, on the other hand, may provide for this mechanistic link. An example of a deterministic model predicting trait strategy composition is the Gemini model (Soussana et al., 2012). This model includes intraspecific variation and describes the dynamics between filters and plant species and concurrent trait strategy composition. However, the description of nutrient competition between plant trait strategies is for many such models a challenge and nutrient competition is solved by either a first come, first served principle in terms of code (e.g. Kiniry et al., 1992) or a biomass volume ratio (e.g Soussana et al., 2012; DeMalach et al., 2016).

Linear programming (LP, Dantzig, 1963) could be a useful addition in modelling vegetation dynamics, as it can combine the mechanisms of filtering with the selection of plant species or trait strategies that are most fit for the prevailing filters. Additionally, by strictly applying Liebig's law of the minimum, LP not only reveals information on the limiting filter(s) for trait strategies growth but also allows for co-existence of plant species or trait strategies. The latter has proven difficult to achieve using deterministic models (Los, 2009). Even though the origin of LP is in the optimization of mathematics, transportation and business-like operations (Dantzig, 2002), it has been used in various ecological contexts before: for example, to simulate biomass allocation in individual plants (Cohen, 1971; Iwasa, 2000: Mironchenko & Kozlowski, 2014), crop yields (Racsko and Semenov, 1989), food web fluxes (Diffendorfer et al., 2001) and phytoplankton competition (Los, 2009). While the concept of LP (maximizing profits (biomass gain) and minimizing costs (use of resources)) fits ecosystem functioning (Craine, 2009), LP has, to our knowledge, never been applied to simulate plant trait strategy competition and composition within an ecosystem setting.

Contributing to the desire to predict vegetation dynamics and concurrent vegetation composition, the aim of this article is to demonstrate LP as an approach to model plant trait strategy competition leaning on the filter-trait concept. To this end, a model has been developed that has LP as its main calculation core. The model includes intraspecific variation to cater for the niche breadth of trait strategies and comprises two herbaceous trait strategies that compete over a light and nutrient gradient. Section 2 describes the method and section 3 presents the results. In section 4 the results are discussed together with possible model applications and developments.

4.2 Modelling framework and description

In this section, first, the conceptual framework is explained after which the modelling approach is described.

4.2.1 Conceptual framework

The backbone of environmental filtering of plant trait strategies and their competition is the fast-slow growth continuum, in which the relative growth rate of trait strategies takes centre stage (e.g. Grime, 1977; Westoby, 1998; Wright et al., 2004). The key difference between the two strategies is how the strategies handle their photosynthates and nutrients. Fast-growing trait strategies invest their photosynthates more in biomass growth, while slow-growing trait strategies invest it in enforcing their organ structures and the maintenance of these structures (Reich et al, 1992; Westoby, 1998). This difference leads to a lower photosynthetic rate (on mass base) for slow-growing trait strategies (Lambers et al., 2008). However, this strategy also leads to increased longevity of the leaves, stems and roots, as those organs are better protected against wear and tear, and additionally increases nutrient use efficiency (Lambers et al., 2008; Reich et al., 2008).

Whether a trait strategy is at an advantage or disadvantage compared to another trait strategy in a certain environment is a combination of a strategy’s resource-capturing capabilities within a specific environment and how these resources are used. Fast-growing trait strategies are well suited for competition: with their high relative growth rate and often tall stature they have good access to light and simultaneously block light for slower-growing trait strategies. Also, fast-growing trait strategies obtain nutrients faster per unit of root dry weight than slow-growing trait strategies (Lambers and Poorter, 1992). However, when nutrients are scarce, the ongoing high nutrient demand of fast-growing trait strategies causes nutrient deficiencies in those strategies and allows slow-growing trait strategies to outcompete the fast-growing trait strategies (Lambers et al., 2008).

An important feature of plant strategies is the ability to change some trait values (e.g. the rate of nutrient uptake, leaf angle) to obtain as much of the required resources within ever-changing environments (Lambers and Poorter, 1992). The type of resource limitation controls how trait strategies adapt. Under light limitation, morphological adjustments aim to improve light harvesting: thinner leaves to increase leaf area and flatten the leaf angle. Under nutrient limitation biomass allocation to roots is increased, roots thin and nutrient uptake rates are enhanced (Poorter et al., 2012). Adaptation, therefore, increases competitive strength.

4.2.2 Model description

The model was kept as simple as possible to be able to demonstrate the use of LP in simulating trait strategy competition. Therefore, the model only comprised two resources (light and nitrogen) and two plant trait strategies. The two model trait strategies were based on the relatively fast-growing trait strategies *Urtica dioica* (stinging nettle) and the relatively slow-growing trait strategies *Eryngium campestre* (field eryngo). Those trait strategies are known to be abundant under different light and nutrient availabilities but are found together in some trait strategies associations (Schaminée et al., 2007). The two trait strategies were simulated by including roots, stems, and leaves only. A whole growing season was simulated by reducing biomass allocation to roots, stems and leaves when flowering and seed production would have started. Storage organs were not included as only one growing season was considered.

The model simulates competition by including just one individual per trait strategy, however, duplicate bookkeeping is used to represent competition between more than two individuals. This latter is done by populating a certain number of individuals on one square meter, the spatial unit of the model. All those individuals are assumed to be identical to the modelled ones and compete for light and nutrients too. The maximum number of individuals on the spatial modelling unit is biomass dependent as it the number is based on the combined leaf area of the individuals per trait strategies. When the plot becomes overpopulated, the excess individuals die, and their plant material is converted to soil organic matter.

The model is comprised of three parts, each covering a different aspect of plant dynamics:

- The first part concerns mortality and respiration of the three plant parts of both trait strategies as well as the mineralization rates of dead organic material. For all rates, first order linear differential equations are used (S4.A). The mortality rate for the leaves of the fast-growing strategy is extended to resemble the shedding of leaves of the fast-growing trait strategy when a certain leaf-biomass is reached (Lambers et al., 2008). This was done by adding a critical biomass level of the leaves above which mortality rate of leaves increases. Mortality rates were used for calibration, as gross growth (see third bullet) and respiration rates were based on literature and field data (S4.B). The mineralization rate of soil differs between the two strategies: it is assumed that the mineralization of the soil on which the fast-strategy grows is higher than that of the slow-growing strategy, as material of fast-growing strategies is more degradable (Lambers et al., 2008). The soil organic content comprises the initial organic material concentration in combination with dead plant material that is added throughout the simulation. Within each time step of the first order linear differential equations, also one time step of the other two model parts is simulated.
- In the phenology part, the onset of different plant phases is simulated (flowering, seed production, senescence) by counting the number of degree days until a threshold value is reached. The degree days are based on measured temperatures of the year 2017 (www.knmi.nl) and are kept the same for both trait strategies.
- The competition part first calculates the available resources per trait strategy and subsequently simulates the competition among plant trait strategies using the LP approach. The outcome of the competition is the amount of photosynthetic produce that is acquired per trait strategy, i.e. the gross growth rate of the two strategies. Next, the photosynthetic produce is divided between the three plant parts according to a fixed ratio (based on Poorter et al., 2012). The competition approach and resource availability is explained in more detail below.

The model was built in R (R Core Team, 2019, using the 'deSolve' and 'lpSolve' packages).

4.2.2.1 Optimization

LP uses an objective function to define the goal that should be maximized (like profit) or minimized (like costs) within a set of given constraints. Within this model, the LP part maximizes the combined net growth rate (Pn, [gC d^{-1}]; gross growth rate – respiration – mortality) of the trait strategies to represent an ecosystem's tendency to strive for the highest efficiency of resource use under specific environmental conditions (Craine, 2009):

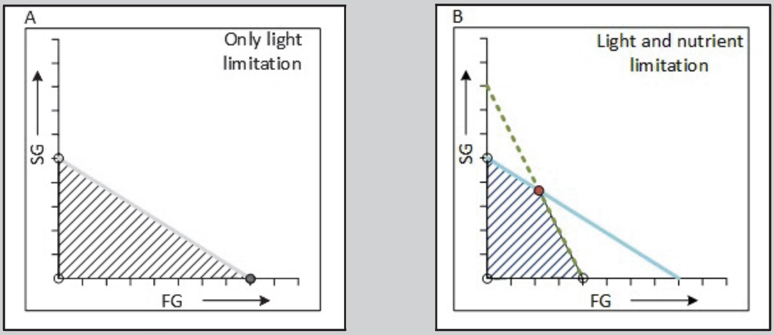
$$\text{Maximize } \sum Pn_s \tag{1}$$

Where Pn_s represents the net growth rate for each of the trait strategies (g), and *s* indicates the trait strategy.

4.2.2.2 Adaptation

In the model, adaptation (intraspecific variation) was included by defining three different phenotypes (in short 'types') per trait strategies. Analogous to the defined types in the phytoplankton competition model of Los (2009), those three types are either growth (G), light (L) or nutrient (N) limited. Each type represents morphological and/or physiological adaptations triggered when encountering light or nutrient limitation. The G-type reflects growth under optimal conditions and is limited by a trait strategy's inherent maximum growth rate. The L-type has a flattened leaf angle and higher light absorptance and therefore captures more light than the G-type. However, the L-type has a lower maximum photosynthetic rate, as this type reflects growth in the shade, meaning photosynthesis is light-limited. The N-type has, compared to the G-type, higher nutrient uptake rates, thicker leaves, and higher root mortality and respiration rates. It also allocates more biomass to its roots compared to the other types. Furthermore, the three types differ in their N:C ratio to represent differences in stoichiometry, which is used for translating nutrient uptake to biomass gain (Poorter et al., 1990; Reich et al., 1997, 2008; Table 4.1). Parameter settings are listed in S1. See Box 1 for more background on linear programming.

Box 1: Optimization of plant trait strategies and types



The two model trait strategies (fast-growing: FG [g], slow-growing: SG [g]) compete over two potentially limiting resources: light and nutrients. In figure A the light constraint (light blue line) is depicted: the shaded area indicates the feasible combinations of FG and SG that can be achieved based on the light climate and satisfies the assumption that the biomass of both strategies cannot be smaller than zero. An LP solution always results in stable equilibrium (Dantzig, 1963). Those equilibria are indicated with circles, in which the red circle indicates the optimum (highest net growth rate) solution. Figure B illustrates the effect of added nutrient limitation (nutrient constraint indicated by the dashed green line). Under nutrient limitation, the net growth rate of FG is more affected than the net growth rate of SG (hence the steep slope of the dashed line) and, in this case, co-existence between the two trait strategies occurs. When nutrient limitation increases, fewer nutrients are to be allocated to FG until only SG can still achieve net growth rate.

The three phenotypes are represented within the same individual: when environmental conditions change, the trait strategies' phenotype switches to the most profitable one continuing from the already existing plant biomass, like the ratio between roots, stems and leaves, height, and leaf area. The simulated plant individual may therefore represent a mix of its characteristic phenotypes.

Table 4.1: Overview of some typical trait strategy characteristics and how they relate between the two trait strategies and three phenotypes. FG and SG indicate the fast and slow-growing trait strategies, respectively. G, L and N stand for the G-type, L-type and N-type (taken from Lambers et al., 2008 and Poorter et al., 2012). The values are relative to give a general idea of how fast- and slow-growing trait strategies and their types differ. The terms are to be interpreted as comparisons between either the trait strategies or the types.

Characteristic	**plant part**	**unit**	**Trait strategy**		**Type**		
			FG	**SG**	**G**	**L**	**N**
Gross growth rate		gC d^{-1}	Slightly higher	slightly lower	same	same	same
Respiration	leaves	gC d^{-1}	lower	higher	medium	higher	lower
	stem	gC d^{-1}	lower	higher	medium	higher	lower
	roots	gC d^{-1}	lower	higher	lower	lower	higher
Partitioning	leaves	-	higher	lower	medium	higher	lower
	stem	-	lower	higher	medium	higher	lower
	roots	-	lower	higher	medium	lower	higher
Mortality		gC d^{-1}	higher	lower	lower	medium	higher
N/C ratio		-	higher	lower	medium	higher	lower
Leaf thickness		cm	thinner	thicker	medium	thinner	thicker
Leaf angle		-	flatter	steeper	medium	flatter	steeper
Stem density		gC m^{-1}	less	more	medium	lower	Higher
Root thickness		gC m^{-1}	thinner	thicker	medium	medium	thinner
Nutrient uptake		gC d^{-1}	higher	lower	medium	medium	higher

4.2.2.3 Growth

A trait strategy's net growth rate results from its gross growth rate [gC d^{-1}] minus its respiration and mortality rates for roots, stems, and leaves [gC d^{-1}]. A trait strategy's potential growth rate is the maximum growth rate that can be achieved in an environment with ample resources. The potential growth rate was assumed to depend on temperature. Rates for growth and root, stem and leaf respiration are scaled to temperature, as were mortality rates. Below a trait strategy's specific optimum temperature, growth, respiration, and mortality rates are scaled using the temperature coefficient Q10. Above the optimum temperature, these rates are scaled with a factor lower than the Q10 ratio, as plants are capable to adapt their growth: respiration ratio to higher temperatures (Lambers et al., 2008). Thus, the maximum net growth rate depends on a trait strategy's inherent gross growth rate, respiration and mortality rates, which are governed by temperature.

The net growth constraint (Gr_c, [gC d^{-1}]) per trait strategies type is formulated as:

$$Gr_c \leq e^{TI_{G_{sn}\Delta t}} * BM_{sn} - BM_{sn} \tag{2}$$

Where BM_{sn} represents the biomass of trait strategy *s* and type *n* [gC], TI_G_{sn} the temperature and insolation corrected growth rate [-].

4.2.2.4 Nutrients

The nutrient gradient is a simplified nitrogen gradient: it does not consider nitrogen dynamics in the environment, but the impact of nutrient abundance or shortage on the photosynthetic capacity of the trait strategies reflects nitrogen dynamics and is based on the work of Lambers et al. (2008) and Reich et al. (2010). Uptake of and competition for nutrients is described by partitioning a trait strategy's root biomass into four fractions: existing root biomass not in competition, new root biomass not in competition, existing root biomass in competition, and new root biomass that competes. The latter fraction is split in two: a fraction of existing non-competing biomass that competes because of invading roots, and a fraction that is encroaching into the root zone of other plant individuals (Figure 4.1).

When roots compete, their maximum nutrient uptake rates are lower than for roots not in competition. The degree of competition is based on two assumptions: how full-grown the trait strategy is, based on its leaf layers (derived from data of Harezlak et al., 2020) and plant density. The fuller grown and the higher the plant density, the higher the degree of competition. This relation is assumed to increase logistically on a scale from 0 (no competition) to 1 (full competition) and increases faster for the fast-growing trait strategy than for the slow-growing trait strategy. The potential uptake rate per root fraction per trait strategy's type (N_upt_{sn}, [gN/gC_{root}]) is calculated according to Michaelis-Menten kinetics:

$$N\_upt_{sn} = \sum_{compartments}(1 - Comp) * \frac{(Umax_{sn} * NConc_c)}{(K_{sn} + Nconc_c)} * BM_{sn_r} \qquad [3]$$

Where *Comp* represents the degree of competition [-], $Umax_{sn}$ the maximum nutrient uptake rate of a trait strategy's type [gN], $NConc_c$ the nutrient concentration within one of the three specific compartment (gN, see figure 4.1),

K_{sn} a trait strategy's type specific half-saturation constant [gN], and he root biomass per trait strategy's type within a certain compartment [gC_{root}].

The nutrient constraint ($N_{c,}$ [–]) for nutrient uptake is then as follows:

$$N_c \leq \sum N\_upt_{sn} \tag{4}$$

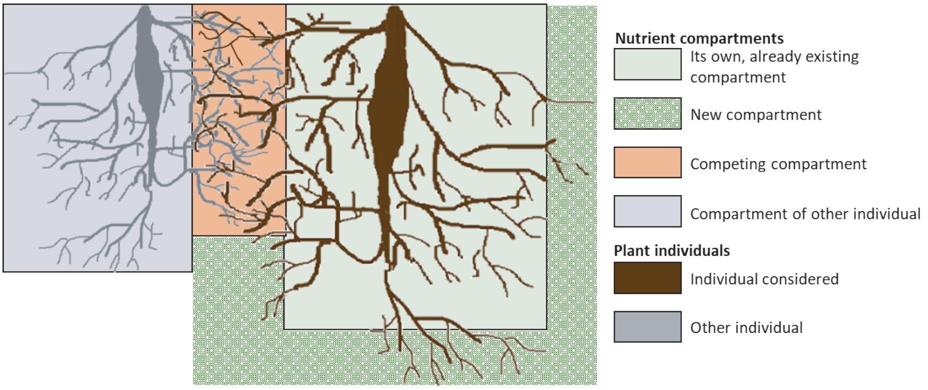


Figure 4.1: *Schematic representation of nutrient competition and hence availability.*

4.2.2.5 Light

A higher-statured trait strategy's type directly affects a shorter-statured trait strategy's type's access to light and as such light competition is asymmetrical. In the model, a trait strategy's type's influence on the light climate is reflected through five characteristics: its height (H_{sn}, [m]), the number of ground covering leaf layers (LL_{sn}, [gC leaf m^{-2}]), the thickness per leaf layer (LT_{sn}, [m]), plant density (PD, [individuals m^{-2}]), and leaf angle (k_{sn}, [–]). The height of each trait strategy's type is based on the combination of its stem biomass (SB_{sn}, [gC]) and its specific stem density (SD_{sn}, [m gC^{-1}]). The leaf layers are calculated based on leaf biomass per fully ground covering layer. The layer thickness is related to the leaf layer, and plant density is calculated by the actual number of individuals divided by the theoretical maximum, which is deduced from the ground covering area per individual. The leaf angle is represented by a value between 0 (vertically oriented) and 1 (horizontally oriented). Parameter values stem from literature (Kleyer et al., 2019; Poorter et al., 2012; Siebenkäs et al., 2015; Tjoelker et al., 2005) and collected field data from the first author (Harezlak et al., 2020).

In the model, the light was expressed in daily quantum input (I_0, [mol m^{-2} d^{-1}], ranging from 0 to 37.5, the latter being the maximum daily quantum input at the top of canopies during the growing season in Western Europe (Poorter and Van der Werf, 1998). The light extinction was calculated in intervals of one cm from top to bottom of a trait strategy, taking into account the effect of the other trait strategy's types on light extinction. Light extinction in the canopy was calculated according to Monsi et al. (2005):

$$I_{sn} = I_0 e^{-k_{sn}\, LL_{sa}} \tag{5}$$

Where I_{sn} represents the daily light quantum input at a certain depth within the canopy [mol m^{-2} d^{-1}], I_0 the daily light quantum input at the top of the canopy [mol m^{-2} d^{-1}], k_{sn} the leaf angle of a trait strategy's type [-] and LL_{sa} the sum of all leaf biomass above the depth of I_0 expressed in ground covering leaf layers [gC leaf m^{-2}]. The biomass above a specific depth within the canopy was calculated using the realized height of a trait strategy's type [m] and the leaf biomass expressed in ground covering leaf layer [LL$_{sn}$, [gC leaf m^{-2}]) of all present trait strategy types, using the specific trait strategy's type leaf layer thickness to calculate the actual amount of leaf biomass above a certain point and hence the available quantum input at that depth. Plant density was incorporated as a correction factor within the exponent of equation 5.

As light extinction is related to the light efficiency of photosynthesis, a look-up table has been created to translate the received light within the canopy to the trait strategies' photosynthetic efficiency (eff$_{sn}$, [-]). The curve of the assumed values is comparable to Lambers et al. (2008). Subsequently, and following Los (2009), the light constraint is based on the light climate and a trait strategy's type maximum extinction coefficient (Kmax$_{sn}$, [m^{-1}]), which is controlled by its photosynthetic efficiency and light compensation point (LCP$_{sn}$, [gC]). When the calculated extinction is higher than the maximum extinction needed to satisfy a trait strategy's LCP$_{sn}$, that trait strategy type has no light available for growth and is therefore not considered within the optimization. When a trait strategy type cannot sustain its LCP, its biomass gradually decreases. The light constraint (K$_{sn}$, [m^{-1}]) is as follows:

$$\int_{ground}^{top\ canopy} eff_{sn} * I_{sn_{min}} \geq \int_{ground}^{top\ canopy} eff_{sn} * I_{sn_{act}} \tag{6}$$

Where eff_{sn} is the photosynthetic efficiency of a trait strategy's type, the minimum required light climate to sustain a strategy's type LCP, and the actual light climate.

4.2.3 Scenarios

The functioning of the linear programming approach for plant trait strategies composition is demonstrated through various scenarios. These scenarios were developed specifically to illustrate the effect of unlimited resources and limitation of light and/or nutrients for trait strategies grown in isolation and in competition. For the isolation runs, typically one individual is simulated, however, to demonstrate light limitation, multiple individuals of the same trait strategies are used to assure light is reduced for the lower leaf layers (Table 4.2).

Table 4.2: Scenarios for model runs, reflecting plant density (number of individuals) and resource settings (FG: Fast-growing trait strategies, SG: Slow-growing trait strategies). The lowercase 'c' in a scenario's name refers to a high number of individuals.

Scenario	**Number of individuals**		**Light at top of canopy ([mol/m²/day])**	**Initial nutrient concentrations in root compartment ([gN])**
	FG	SG		
FG_No	1	0	37.5	2.5
FG_N	1	0	37.5	0.03
FG_L	50	0	20	2.5
SG_No	0	1	37.5	2.5
SG_N	0	1	37.5	0.03
SG_L	0	50	20	2.5
C_No	1	1	37.5	2.5
C_cNo	50	50	37.5	2.5
C_N	1	1	37.5	0.03
C_cN	50	50	37.5	0.03
C_L	1	1	20	2.5
C_cL	50	50	20	2.5
C_NL	1	1	20	0.03
C_cNL	50	50	20	0.03

4.3 Results

This chapter first presents the results of the scenarios in which trait strategies grow separately, to demonstrate how resource limitation control shifts between trait strategy types. Subsequently, the results of the scenarios in which multiple trait strategies grow together are presented.

4.3.1 Shifts between trait strategy types

When resources are abundant (scenarios FG_No and SG_No) the growth of both the fast- and slow-growing trait strategies is solely limited by the trait strategies' inherent growth rate (GRR, [gC/gC]) and as such the G-type is selected for both trait strategies. Under ample resources, the fast-growing trait strategy has a higher net growth rate and hence accumulates more biomass in a given period than the slow-growing trait strategy (Figure 4.2A). The biomass gain for both trait strategies slows down around mid-July and about a month later, the biomass of both trait strategies starts to drop.

When nutrients are scarce (scenarios FG_N and SG_N), the fast-growing trait strategy is immediately limited by the available nutrients, while the slow-growing trait strategy experiences nutrient limitation after a few weeks. This results in the fast-growing trait strategy consisting solely of the N-type. In contrast, the slow-growing trait strategy consists of a mixture of the G- and N-type: at the start, it consists solely of the G-type, but switches to a mixture of the G- and N-type when nutrients become scarcer. Eventually, the slow-growing species switches to the N-type completely, as indicated by the flattening of the G-type biomass curve (Figure 4.2B). For both species, the accumulated biomass is lower than without nutrient limitation, being reduced the most for the fast-growing trait strategy.

The effect of poor light conditions (scenarios FG_L and SG_L) differs between the fast- and slow-growing trait strategies. The fast-growing trait strategy selects for the L-type throughout the course of the simulation, while the slow-growing trait strategy switches mid-June from the G- to the L-type. Note that albeit the G-type is selected, this type is also light-limited (Figure 4.2C). Again, biomass accumulation is lower than without resource limitation, and most for the fast-growing trait strategy due to its closer canopy, leading to self-shading.

The maximum gross growth rate and resource uptake differ between the trait strategies. The maximum gross growth rate is trait strategy type-specific and depends on temperature (Figure 4.2D). The nutrient uptake differs per scenario (No, N and L) and reflects not only the biomass accumulation under limitation of the gross growth rate and light, in the case of nutrient limitation it signals increasing nutrient limitation, as the nutrient uptake rate is going down (Figure 4.2E). The effect of light limitation (Figure 4.2F) shows no decrease in light efficiency for the No and N scenarios but does for the L scenario. The light efficiency is steadily decreasing for the fast-growing trait strategy, keeping pace with biomass increase and hence indicates increasing light limitation through self-shading. The slow-growing trait strategy has a much more open canopy structure than the fast-growing trait strategy and hence, light efficiency remains rather stable with increasing biomass. However, increased biomass does lead to a bit of self-shading, forcing the slow-growing trait strategy to switch back and forth between the G-type and L-type light efficiency.

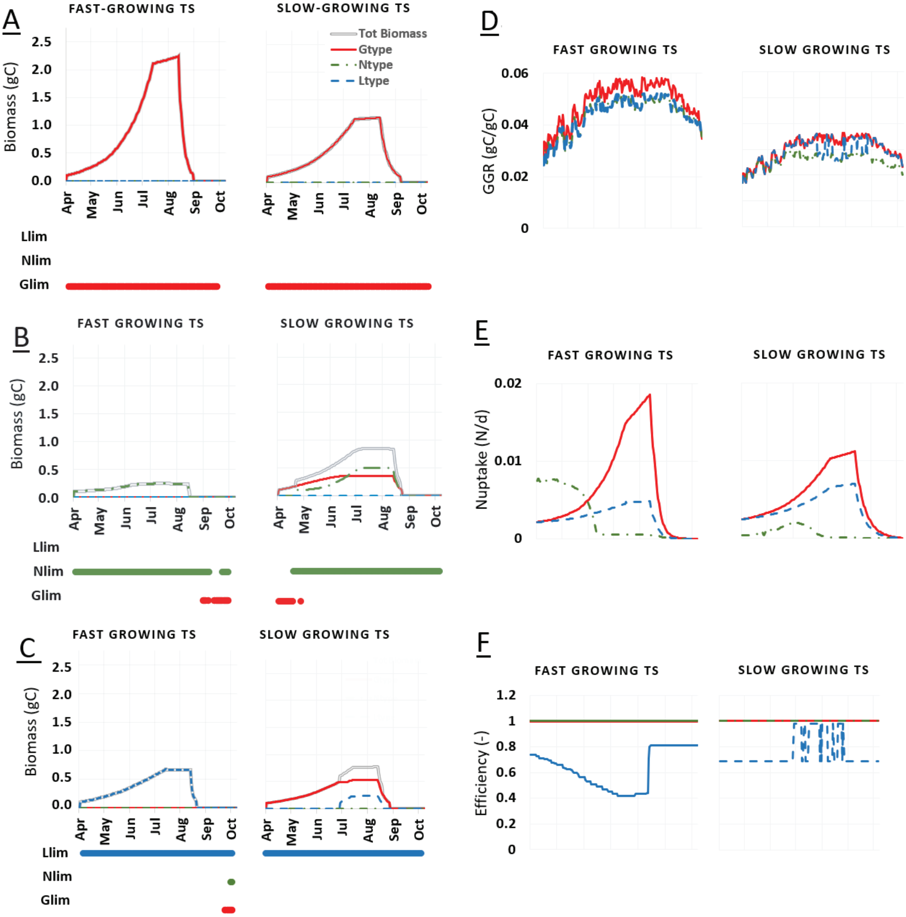


Figure 4.2: *Biomass development and limitations (left column) and resources (right column) over time for the six scenarios. The columns are ordered as follows: panel A represent the scenarios with ample resources (FG_No and SG_No), panel B the scenarios with scarce nutrient availability (FG_N and SG_N) and panel C the scenarios with low light availability (FG_L and SG_L, pane C). The left sub-column of each of the three panels represents the fast-growing trait strategy (TS) and the right sub-column the slow-growing trait strategy. Biomass development of the trait strategy types is indicated as the red solid line is the G-type of either the fast- or slow-growing trait strategy, the green stripe-dot line the N-type and the blue dotted line the L-type. The open grey line represents the total biomass per trait strategy. The limitations panes indicate the type of limitation, regardless of the trait strategy type. Panel D indicates the maximum gross growth rate for the fast- (left) and slow-growing (right) trait strategies for all six scenarios, with the red solid line indicating the G-type, the green stripe-dot line the N-type and the blue dotted line the L-type. Panel E shows the results for nutrient uptake for the six scenarios (again: fast-growing trait strategies at the left, slow-growing trait strategies at the right) and panel F for light efficiency.*

4.3.2 Competition between trait strategies

Growing together may cause competition for nutrients and light between trait strategies' individuals as the density of the vegetation contributes to the intensity of the competition. When nutrients and light are amply available (scenarios C_No and C_cNo), low plant density has no impact on the net growth rates of both trait strategies (Figure 4.3A). However, when plant density is substantial, the fast-growing trait strategy burdens the slow-growing trait strategy by increasingly blocking the light, as illustrated by the slow-growing trait strategy eventually switching from the G- to the L-type (Figure 4.3B).

Under nutrient limitation (scenarios C_N and C_cN), low vegetation density leads to the fast-growing trait strategy being constrained by nutrient availability from the start of the simulation and the slow-growing trait strategy a couple of weeks later. The slow-growing trait strategy accumulates more biomass than the fast-growing trait strategy. At the end of the simulation, the fast-growing trait strategy becomes partly limited by its inherent growth rate, as nutrients become available due to mineralization of soil organic matter (Figure 4.3C). As the fast-growing trait strategy is strictly curbed by the nutrient limitation, it does not affect the slow-growing trait strategy by light limitation when plant density is high (Figure 4.3D)

A poor light climate (scenarios C_L and C_cL) causes the fast-growing trait strategy to outcompete the slow-growing trait strategy, albeit both trait strategies experience reduced net growth rates (Figure 4.3E). Low plant densities allow for co-existence of the two trait strategies, in which both trait strategies start as G-type but switch to the L-type in mid-June (fast-growing trait strategy) and at the beginning of June (slow-growing trait strategy). High plant density decreases light availability, causing both trait strategies to start the simulation with the L-type instead of the G-type. The decreased light availability causes the slow-growing trait strategy to die prematurely (Figure 4.3F).

When both nutrients and light are scarce (scenarios C_NL and C_cNL), nutrient availability overrules light limitation: the fast-growing trait strategy is immediately limited by nutrient limitation, and the slow-growing trait strategy first by light and from mid-May by nutrient availability as well. Because of the multiple limitations, the slow-growing trait strategy selects firstly for the G-type and switches later to the N-type. The fast-growing trait strategy plant strategy co-exists with the G- and N-type. As nutrients are overruling, plant density has a minimal effect (Figure 4.3G and H).

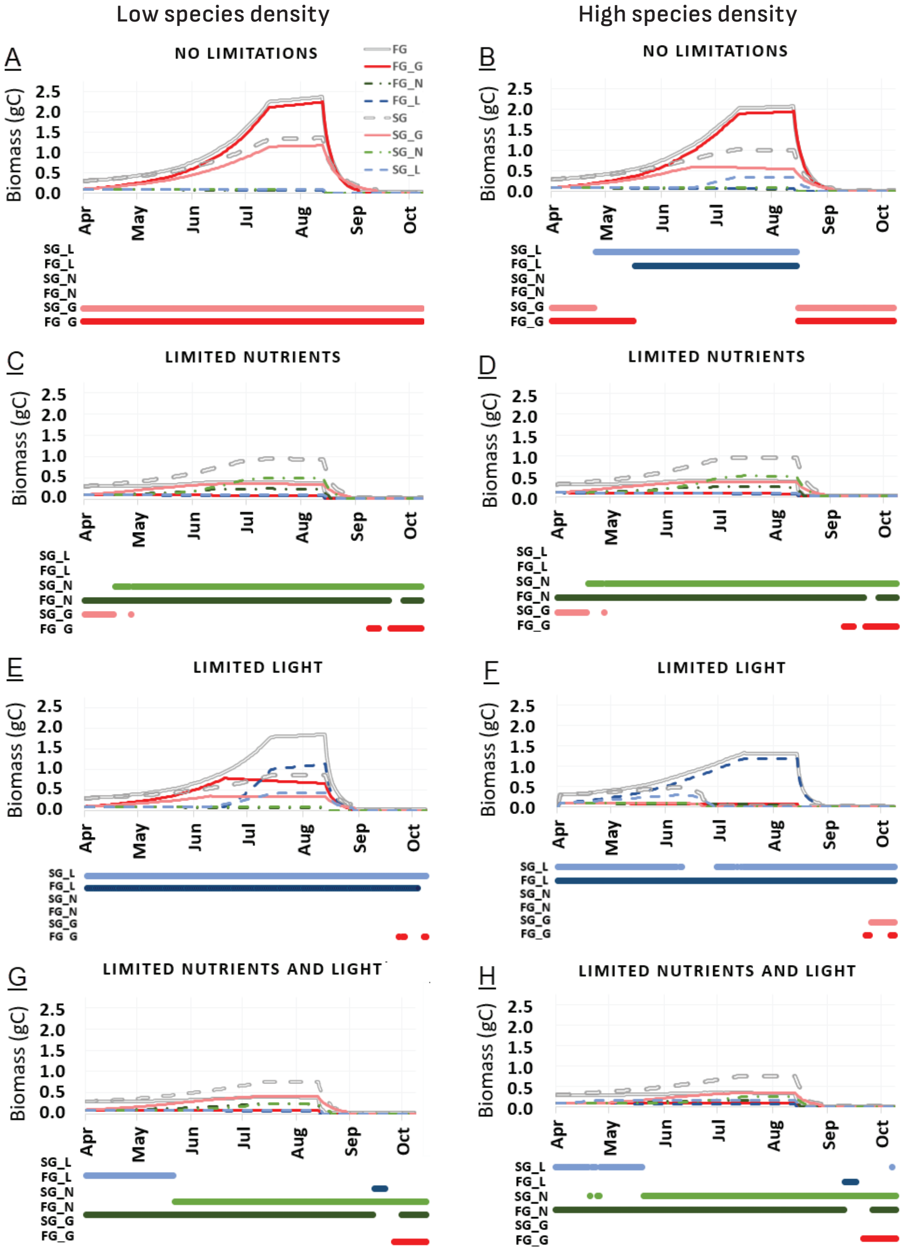


Figure 4.3: *Biomass development and limitations for the fast- (FG) and slow (SG) growing trait strategies for the eight competition scenarios. The left column reflects competition scenarios with low plant density and the right column the scenarios with high plant density. Panels A en B are the scenarios with no limitations (C_No and C_cNo). Panels C and D show the scenarios with scarce nutrients (C_N and C_cN). Panels E and F show the scenarios with low light availability (C_L and C_cL) and panels G and H the scenarios with both scarce nutrients and low light availability (C_NL and C_cNL). In each of the panels, the top figure depicts the biomass development of the types of the two trait strategies and the bottom figure the type of limitation. The fast-growing trait strategy is depicted in dark colors and the slow-growing trait strategy in light colors. Red represents the G-type and growth limitation, green the N-type and nutrient limitation and blue the L-type and light limitation. The grey lines in de biomass developments figures represent the total biomass for the fast- (solid line) and slow-growing (dotted line) trait strategies.*

4.4 Discussion

The model results captured several empirical phenomena regarding the growth of fast and slow growing species as well as the competition between them. For example, when resources are in ample supply and remain so during the growing season, both trait strategies are only limited by their inherent relative growth rate (Figure 4.2A, Figure 4.3A). However, higher plant densities cause the slow-growing trait strategy to become shaded by the fast-growing trait strategy, allowing for less accumulation of biomass. Over the years, this may lead to the fast-growing trait strategy outcompeting the slow-growing trait strategy. As storage organs are not included in the presented model, this statement cannot be supported by the modelling results, and so, the model results cannot be validated by prevailing theory on this part of the competition (e.g. Grime, 1977; Westoby, 1998; Wright et al., 2004).

The model also showed that nutrient scarcity, whether plant density was low or high, results in the slow-growing strategy becoming dominant (Figure 4.3, panels C, D, G and H). This result stems from the difference in nutrient handling of the two trait strategies. The fast-growing strategy encounters nutrient scarcity earlier than the slow-growing strategy, as the fast-growing trait strategy takes up more nutrients per root unit (Poorter et al., 1990), but also loses more nutrients than the slow-growing strategy. These features are amplified for the N-type and therefore the N-type is especially expensive in terms of respiration and mortality for the fast-growing trait strategy compared to the slow-growing trait strategy (Van der Werf et al., 1993). In the model, this behavior is simulated through the higher biomass accumulation during prolonged nutrient limitation of the slow-growing strategy compared to the fast-growing one, which is in line with theory, which states that albeit the fast-growing trait may have the advantage of scavenging more soil volume, its lavish use of nutrients is not sustainable in the long run (Lambers et al., 2008; Van der Werf et al., 1993).

As light competition is more asymmetrical than nutrient competition (e.g. Newbery and Newman, 1978; Weiner and Thomas, 1986; Rasmussen et al., 2019), the competition process and hence the outcome of competition over light between the two trait strategy is different. Under light limitation, the fast-growing trait strategy outcompetes the slow-growing trait strategy (Figure 4.3, panels E and F), illustrating the race for light as a driving mechanism for succession (Westoby, 1998). The outcompeting of slow-growing trait strategies by the fast-growing ones is caused by slow-growing trait strategies having sturdier leaves than fast-growing trait ones, resulting in lower photosynthesis per unit leaf mass. Additionally, fast-growing trait strategies have a more gradual reduction in their photosynthetic rate than slow-growing trait strategies when light is limited. Note, however, that slow-growing shade strategies are generally fit to survive in these low-light conditions (Lambers et al., 2008). However, this is not the case for the model's slow-growing trait strategy, as it was based on *Campestre Eryngium*, a slow(er)-growing species fitted to nutrient-poor conditions.

When both nutrients and light are scarce (Figure 4.3G and H), the low nutrient availability restrained the fast-growing trait strategy from out-competing the slow-growing trait strategy through shading, under both low and high plant densities. An interesting outcome of the model is that when both nutrients and light are limiting, the slow-growing trait strategy selects for the G-type, as the resources are either not sufficient to support the N-type (light limitation) or the L-type (nutrient limitation). The model results stem from the balance between the two resource limitations. When nutrients are less limiting for the fast-growing trait strategy than for the slow-growing trait strategy, the fast-growing trait strategy may outcompete the slow-growing trait strategy or at least co-exist (Figure 4.4), which is in line with the found co-existence in the field of the two species on which the trait strategies' parameterization is based (Schaminée et al., 2007).

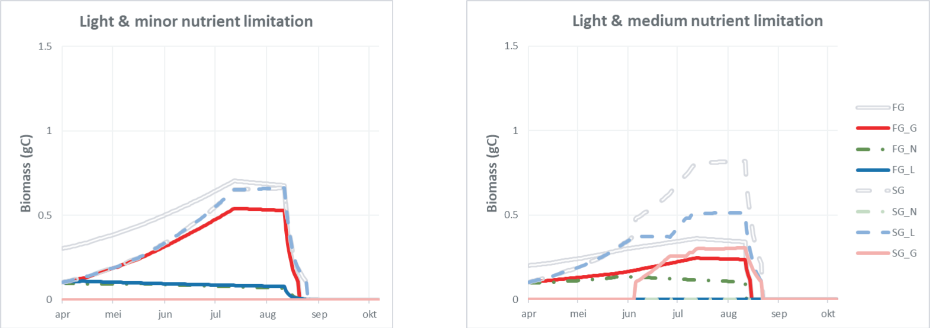


Figure 4.4: *The effect of changes in nutrient limitations: the left pane shows the results with light and minor nutrient limitation and the right pane with light and medium nutrient limitation. Be aware that the y-axis is enlarged compared to figures 4.2 and 4.3 for readability purposes. Legend as in Figure 4.3.*

4.4.1 Model simplifications

The model results led to some findings that at first sight may cause doubts about how well the model can simulate trait strategy competition. The first one is the abrupt changes in biomass: a slowing down of biomass accumulation around mid-

July and a decrease in biomass around mid-August (Figures 4.2 and 4.3). The slowing down in biomass accumulation represents the phase when biomass allocation to leaves, roots and stems switches to flowers and seeds, which is not explicitly simulated by the model. The decrease in biomass is the onset of senescence. In the model both the switch of biomass allocation and senescence is based on days since germination. However, this simplification of reality does not affect the aim of the model: demonstrating how the LP approach can be used to simulate plant strategy competition.

Another finding is the gradual shift to G and N-types and the crisp switches to and from the L-type (e.g. compare the slow-growing trait strategy in Figure 4.2B and C). In theory, the L-type switches should also be gradual, but the rather coarse approach in which light (in DQI) is translated to photosynthetic efficiency results in a very small range where types of the same strategy can grow together. The last finding concerns the growth limitation at the end of several simulations (fast-growing trait strategy in Figures 4.2B and C, several in Figure 4.3). This model artefact is due to senescence, as the limitations that are indicated depend solely on the available resources and the possible biomass gain, regardless of senescence. When biomass decreases, fewer resources are required and a poor light climate due to self-shading improves, allowing an individual to grow with its inherent relative growth rate if it wasn't for the overruling process of senescence.

4.4.2 LP as competition solving core

The model results show that trait strategies are able to adapt to changed environmental conditions: trade-offs are made in response to resource limitation, just like what is described in literature (e.g. Tilman, 1990; Weiner, 2004). This demonstrates that the LP approach is suitable for simulating plant strategy competition. Compared to purely deterministic vegetation competition models, the integration of LP into these models provides some advantages. For example, deterministic models often require small time steps to assure a stable simulation, while LP can integrate resource availability over longer time steps. This is because LP never reaches a negative solution as it solves for a mathematical optimum (maximization in case of plant biomass). This decreases the computational burden of the often calculation-intensive deterministic models, and allows for separation in time scales between model components. This separation decreases the calculation burden even further, supporting the addition of more trait strategies or spatial upscaling.

Another advantage of LP is that it solves competition between trait strategies simultaneously. This allows for the instantaneous evaluation of growth based on the resources available to each of the trait strategies, thus avoiding the model artefacts caused by the 'first come first serve' principle applied in deterministic models. As a result, LP allows for the simulation of co-existence of species, which is often a hard feat in Monod-based competition models (Los, 2009). However, in the case of nutrient availability, simulating resource availability remains cumbersome. In this research, the soil was compartmented to allow for differentiation in levels of nutrient competition, but as such, LP does not ease the challenges of competition in capturing nutrients (e.g. DeMalach et al., 2016). This differs from the application of LP to phytoplankton, in which, with a large enough time step to assure switches in phytoplankton community composition, a total nutrient pool is available that can be divided amongst phytoplankton trait strategies based on their suitability for prevailing conditions (Los, 2009).

A third advantage of LP is that it provides a clear indication of what is limiting specific trait strategies: LP has a straightforward way of seeking an optimum distribution of resources over different strategies, in which eventually one resource is the limiting resource. As such, Liebig's law of the minimum is strictly applied. This is not the case when, for example, a Monod approach is used to calculate resource availability, assumptions have to be made on how to weigh the results of the different resources (Los, 2009). Insight into limiting resources could be useful for the development of measures for nature conservation or management as it highlights what resources or processes may hamper specific trait strategies.

4.4.3 Model recommendations

Albeit the model results are in line with theory, the use of LP as a tool to simulate plant trait strategy competition should ideally be validated quantitatively instead of qualitatively. For that field data that reports on both environmental and trait strategy parameter values are required. Examples of such reported data are found in Baastrup-Spohr et al., (2015), Garnier et al. (2007), Harezlak et al. (2020), and Ordoñez et al. (2010). To be able to apply the model to a more realistic situation, additional filters and trait strategies are also required. Such filters and traits could encompass grazing (Díaz et al. 2007; Hodgson et al. 2011), trampling (Kobayashi et al., 1997; Hill and Pickering, 2009), wildfires (Russel-Smith and Stanton, 2002; Johnsen and Cochrane, 2003), soil water (Douma et al., 2012; Baastrup-Spohr et al., 2015), or flooding (van Eck et al., 2005; Colmer and Voesenek, 2009).

Second, the current model does not take into account several plant organs, like seeds, flowers and storage. Including seeds and flowers are important when strategies for early and late bloomers are considered. However, the creation of a storage organ appears to be a more crucial development as it not only enables multiple-year simulations but also, and perhaps most importantly, enables trait strategies to survive longer under adverse conditions because of the below-ground storage of carbohydrates (Chapin, 1980) and therefore allows also for the inclusion of space occupation as a filter. Also, storage organs enable differentiation between life spans: annual, biannual and perennial. This differentiation is not only a prerequisite for simulating primary and secondary succession, but it also aids in understanding how disturbances may impact spatiotemporal trait strategy composition. This knowledge could be used in nature restoration in for example floodplains (Geerling et al., 2008), fens (Hedberg et al., 2013), or grasslands (Gilhaus et al., 2014).

Third, the current model comprises characteristics and processes that influence intraspecific variation, like resource gradients (Keddy, 1992; McGill et al., 2006), competition (Poorter et al., 2012), and growth form (Husáková et al., 2018 and references therein), but does not consider ontogenetic drift. When including ontogenetic drift, the early stage of vegetation dynamics is included more realistically, as younger plants have a larger leaf fraction compared to older plants. Especially when densely populated, the light climate is affected earlier, favouring the fast-growing trait strategy at the start of the growing season, which may result in different competition results. However, the work of Iwasa (2000), Ioslovich and Gutman (2005) and Mironchenko and Kozlowski (2014), which apply LP to plant development processes, are more appropriate for in-depth analyses of the impacts of ontogenetic drift on intraspecific variation.

So, by using linear programming, an ecosystem's strive for optimal use of resources in terms of production can be simulated. The presented model, based on LP, is promising, and could be further developed and integrated in a full plant competition model.

4.5 References

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S4.A First order linear differential equations

The mortality of leaves, stems and roots per trait strategy type was calculated as follows:

$$\frac{dMort_{sn}}{dt} = \sum_{l,s,r} mort_{sn} * BM_{sn} \tag{S4.A1}$$

Where $\frac{dMort_{sn}}{dt}$ is the calculated biomass mortality per time step per trait strategy's type (g/d), $mort_{sn}$ the specific mortality rate per trait strategy's type (d^{-1}) and BM the biomass of each trait strategy's type (g). *l, s,* and r indicate the three different plant parts: leaves, stems and roots (g). Note that for the fast growing trait strategy the leaf mortality is increased after reaching a certain biomass matching the leaves' net growth rate to resemble the shedding of the lower leaves upon reaching a certain total leaf biomass.

Loss of biomass through respiration was calculation as follows:

$$\frac{dR_{sn}}{dt} = \sum_{l,s,r} resp_{sn} * BM_{sn} \tag{S4.A2}$$

Where $\frac{dR_{sn}}{dt}$ is the respiration loss per time step per trait strategy's type (g/s), $resp_{sn}$ the respiration rate for each trait strategy's type's plant part (l, s, and r, [d^{-1}]) and BM_{sn} the biomass of each of the trait strategy's type plant part (g).

The mineralization rate of nutrients in the soil was calculated as follows:

$$\frac{dN_s}{dt} = degr_{soil} + \sum_{s} ratNC_{n_{l,s,r}} * degr_{n_{l,s,r}} * Mort_{n_{l,s,r}} \tag{S4.A3}$$

Where $\frac{dN_s}{dt}$ is the amount of nutrients becoming available each time step in the root zone of each of the trait strategies (g/d), $degr_{soil}$ a constant fraction of organic material that mineralizes each time step (g/d), $ratNC_n$ a conversion factor from carbon to nutrient (–), $degr_n$ the instant mineralization (leakage) rate (d^{-1}) of just shed biomass per trait strategy (g).

S4.B Parameters

Table S4.B1: *an overview of the used parameter values for the two simulated trait strategies, and the key references. As exact data for the trait strategy types are not available, the references have been used as an indicator of the range of realistic values and were calibrated within that range.*

		Fast-growing trait strategies (Urtica dioica)			***Slow-growing trait strategies (Eryngium campestre)***			
Parameter	**Unit**	G	N	L	G	N	L	**References**
Growth rate	gC/d	0.058	0.052	0.052	0.036	0.029	0.029	Lambers et al., 2008; Reich et al., 2008; Harezlak et al., 2020
Leaf respiration	/d	0.0058	0.0042	0.0052	0.0064	0.0023	0.0052	Lambers and Poorter, 1992; Reich et al., 2008
Stem respiration	/d	0.0046	0.0031	0.0042	0.0025	0.0011	0.0020	Lambers and Poorter, 1992; Reich et al., 2008
Root respiration	/d	0.0070	0.0182	0.0035	0.0054	0.0072	0.0043	Lambers and Poorter, 1992; Reich et al., 2008
Mortality leaves	/d	0.0041	0.0052	0.0036	0.0011	0.0012	0.0009	Calibrated
Mortality stems	/d	0	0	0	0	0	0	Calibrated
Mortality roots	/d	0.0058	0.0078	0.0052	0.0011	0.0012	0.0009	Calibrated
N:C ratio	g/g	0.088	0.079	0.091	0.054	0.043	0.061	Harezlak et al., 2020*

Table S4.B1 (continued)

Parameter	Unit	*Fast-growing trait strategies (Urtica dioica)*			*Slow-growing trait strategies (Eryngium campestre)*			References
		G	N	L	G	N	L	
Leaf layer thickness	m	0.2	0.2	0.20	0.3	0.3	0.3	Unpublished data first author
Leaf weight/ layer	gC	0.332	0.349	0.306	5.780	6.18	5.51	Harezlak et al., 2020
Leaf angle	–	0.60	0.60	0.70	0.20	0.20	0.22	Calibrated
Specific stem length	m/gC	1.35	1.30	1.40	0.18	0.15	0.21	Kleyer et al., 2019
Specific root length	m/gC	39	41	36	39	41	36	Siebenkäs et al., 2015
Max N uptake rate	gN/gC	0.025	0.150	0.025	0.025	0.080	0.025	Lainé et al., 1995; Volder et al., 2009
Half saturation constant N uptake	g/m3	0.50	0.02	0.50	0.15	0.06	0.15	Calibrated
Leaf fraction	–	0.35	0.34	0.39	0.36	0.31	0.37	Poorter et al., 2012
Stem fraction	–	0.30	0.29	0.31	0.31	0.30	0.32	Poorter et al., 2012
Root fraction	–	0.35	0.37	0.30	0.33	0.39	0.31	Poorter et al., 2012

*: leaf values, but translated to the whole plant for simplicity reasons

Chapter 5

Synthesis, conclusion and recommendations

5.1 Synthesis

Regulated rivers differ from natural flowing lowland rivers in, amongst others, how they interact with their floodplains. Within their active meandering plane, natural flowing rivers have a strong interaction with their floodplains through the hydro-morphological filter (i.e. discharge dynamics, and erosion and sedimentation), selecting plant trait strategies able to thrive within this highly dynamic, and biodiverse, zone. In regulated rivers, this hydro-morphological filter is largely missing, and other filters, like inundation depth and duration, nutrient and soil water content, and plant trait strategy competition, are essential for trait strategy selection. In natural flowing rivers, these filters are only dominant further away from the main river channel (Bornette et al., 2008; Gurnell et al., 2016; Merritt et al., 2010).

Because the hydro-morphological filter is largely missing in floodplains of regulated rivers, those floodplains are, without interventions, overgrown with shrubs and forests, resulting in an impoverished biodiversity compared to natural flowing rivers. Additionally, as regulated rivers often flow through densely populated areas, water safety is a main concern, in which floodplains overgrown with shrubs and forests may jeopardize water safety. Therefore, understanding how filters are steering plant trait strategy dynamics, composition, and the resulting spatial pattern in floodplains of regulated rivers, is important for floodplain management (Baptist et al., 2004; Geerling et al., 2008). To further insight into the relations between filters and plant trait strategy composition and dynamics, this thesis posed the following main research question:

> *What are the main steering processes shaping vegetation patterns in floodplains of regulated lowland rivers and how can this knowledge be used in floodplain management?*

With the following sub-questions:

1. What does the filter-trait concept add to the understanding of vegetation composition in floodplains of regulated lowland rivers?
2. What are the main filters that govern the vegetation dynamics in floodplains of regulated lowland rivers and are those filters scale-independent?

3. How can the knowledge of the filter-trait concept, as underpinning for the dynamics of plant trait strategies in floodplains of regulated rivers, be translated into a modelling approach?

Chapter 2 focused on the presumption the filter-trait concept holds compared to a species approach: providing a more generic and mechanical link between filters and the presence and absence of trait strategies (sub-question 1). Chapters 2 and 3 focused on answering sub-question 2 by unravelling the filters steering vegetation composition on a small spatial scale (Chapter 2) and landcover composition and dynamics on a large(r) spatial scale (Chapter 3). Sub-question 3 was researched in Chapter 4. This chapter used data and knowledge gathered in Chapter 2 and from literature to set up a model based on linear optimization to allow for insightful modelling of competition of trait strategies. The first part of underlying Chapter (5.1.1) delves further into the connection between the three sub-questions to explore usages of the found insights on different spatial and temporal scales and answers the main steering processes part of the main research question. The second part of this Chapter (5.1.2) answers the main research question by reflecting on how the knowledge of this research may contribute to floodplain management on different temporal and spatial scales.

5.1.1 Floodplains of regulated rivers: traits, filters, scales and models

The theme of this thesis is the filter-trait concept and how it could be used to further the insight into landcover and plant trait strategy dynamics and composition in floodplains of regulated rivers. As Dutch floodplains of the larger rivers are missing the hydro-morphological filter, as illustrated by the massive growth of shrubs and forests following 'Plan Ooievaar' (De Bruin et al., 1987), those floodplains are good examples for researching what is steering floodplain plant strategies dynamics and composition, as in many floodplains of regulated rivers this filter is also missing (Tockner et al., 2008).

5.1.1.1 The filter-trait concept

In the floodplains of regulated rivers, the filter-trait concept has been scarcely applied, and the applicability of the concept was mixed (Baastrup-Spohr et al., 2015; Baattrup-Pedersen et al., 2015; Douma et al., 2012; Ordoñez et al., 2010). In the research presented in Chapter 2, the findings show that the filter-trait concept on grass and herbaceous vegetation did give insight into the filters steering plant trait strategy composition and ranked the dominance of those filters for the trait strategy composition. The filter-trait concept, therefore, disclosed more information than the species approach (Figure 2.5 in Chapter 2) and holds, at least for grass and herbaceous vegetation in the floodplains of regulated rivers, its premise.

The dominant filters for the trait strategy composition were disturbances (excavation and summer flooding) and resource gradients in which the disturbance filters overruled the resource filters. The species approach only revealed soil moisture and geographical location as filters. The geographical filter was absent for the trait strategy approach, seconding the hypothesis that trait strategies are, unlike species, location independent. These findings answer sub-question 1 by confirming that the trait strategy approach adds additional knowledge to what steers vegetation composition in floodplains of regulated rivers compared to the species approach.

The filter-trait approach also highlighted an important mechanistic characteristic of ecosystem dynamics: self-organization. Because of the interplay between resources (gradients in for example nutrient and soil moisture availability) and trait strategies, natural ecosystems tend to show gradients in structure (like distinct bands of vegetation). Through time, and without disturbances, those structure gradients become more complex, as they are fueled by, amongst others, biological interaction (Müller and Kroll, 2011). The gradients in structure, due to self-organization, were identified in terms of differences in trait strategy composition (Chapter 2), and these findings are corroborated by, amongst others, van Eck et al. (2004, 2006).

The resilience of the trait strategy composition to natural or anthropogenic filters is relevant knowledge for floodplain management, as insight into resilience aids in understanding when and why trait strategy composition may change. How and when (tipping points) does the trait strategy composition of free-flowing rivers change when those rivers become regulated? How may climate change alter trait strategy competition and hence composition? Even though desirable, quantifying resilience of trait strategy composition is challenging because connected traits may not react in sync (Auer et al., 2014) to changes in covariation between processes, nonlinear biotic responses and historical influences (Allan, 2004). However, the work of Sterk et al. (2013) offers a framework on how to assess the resilience of trait strategies to disturbances on small and large spatiotemporal scales, by identifying traits with strong resistance (i.e., resilient) to system-specific environmental disturbances.

The work of Sterk et al. (2013) could be developed by reflecting on the six major traits that are identified by Diaz et al. (2016) and are linked to the survival, growth and reproduction of plants across the globe. The work of the latter is a large step towards understanding the crucial trade- and spin-offs within plant trait strategies caused by filters, reducing uncertainties brought about by trait covariance. The filter-trait concept as such bears not only additional information on filters compared to a species approach, but it is also valuable considering resilience given river regulation and a changing climate. However, care should be taken considering its spatiotemporal scale. The work of Diaz et al. (2016) did present a global plant trait spectrum that is suitable on small to large spatial scales. The temporal scale was not explicitly included, but the global spectrum does distinguish between fast and slow-growing traits. This insight can be useful for floodplain management: for water safety areas of fast-growing vegetation are to be monitored meticulously, and for biodiversity, a diverse pallet of fast- and slow-growing strategies are favoured. Together with the framework of Sterk et al. (2013) the use of the global trait spectrum could be used to develop insight into resilience, which may help floodplain management in exploring the effects of for example climate change or envisaged measures (e.g. water safety, nature conservation) through the resilience of certain traits against change.

5.1.1.2 Scale dependency of filters for landcover and trait strategy composition

The trait compositions in the researched Dutch floodplains showed that on a small scale trait strategies of grass and herbaceous vegetation were filtered by resource gradients, summer flooding, and excavation (Chapter 2), and on larger spatial and time scales, landcover types were filtered by interventions and management (Chapter 3). This disagreement in filters stems from the differences in temporal and spatial scales and the object of study (plant trait strategy versus land cover). In the field study, time was not included as a factor as the samples were collected just once. The satellite data comprised 35 years, revealing information on long-term trends of land cover dynamics: succession and retrogression. Furthermore, the determination techniques also differed: in the field study individual plants were identified by hand on a meter scale, while spectral bands were used to identify different land covers on the satellite images covering 30*30 meters. The combination of the different spatial scales identified that (answering sub-question 2) on a larger scale, the filters of management and intervention set the boundaries in which processes present in the floodplains of regulated rivers differentiate trait strategy composition further.

The combination of more detailed research on plot level and large-scale satellite data, or other remote sensing techniques, could eventually lead to more insight into trait strategy composition and dynamics. For example, Van Iersel et al. (2018a, 2018b) showed promising progress in bridging the gap between large spatial scale, low-resolution satellite data and small spatial scale, high-resolution fieldwork. By developing techniques to classify floodplain vegetation based on remote sensing images obtained through UAV (Unmanned Airborne Vehicles), the seasonal development of the height of specified vegetation classes can be followed. This type of remote sensing information, in which the remote sensing data is less coarse compared to satellite data, allows, for example, for analyzing the influence of grazers on trait strategy composition by combining information on landscape and inundation characteristics, the seasonal development of vegetation classes, and grazing (Figure 5.1). The combination of different data sources could therefore aid in quantifying the impact of larger scale, like floodplain excavation, and smaller scale, like grazing, processes on trait strategy dynamics and hence composition.

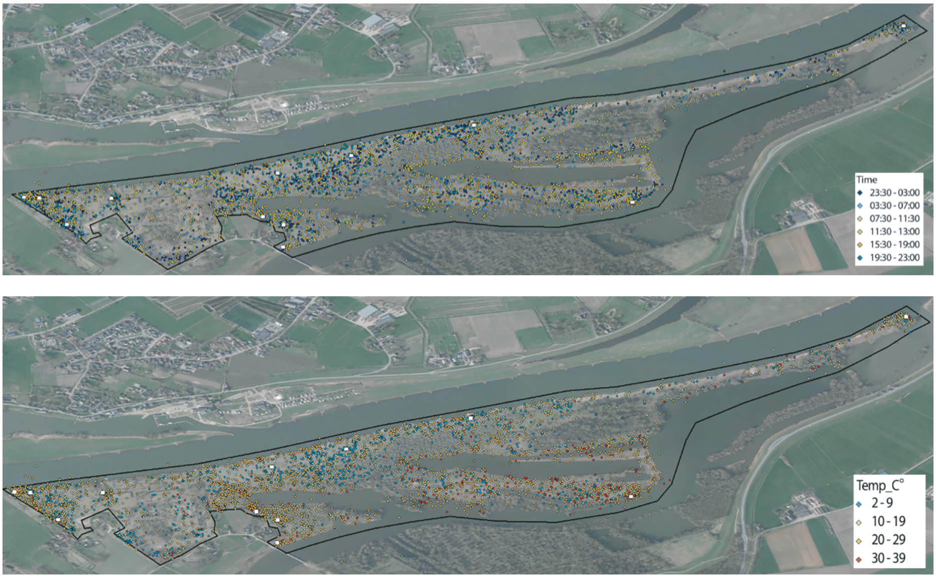

Figure 5.1: *Aerial view of floodplain te Duursche Waarden, where horses and cows were tagged. Their movement through the floodplain was coupled to vegetation class, management, time, date and temperature. The upper pane shows the use of the floodplain of the horses during day and night. The lower pane shows their movement coupled with temperature (Melman, 2020).*

One important aspect to overcome to use the filter-trait concept in combination with remote sensing techniques is the information on environmental conditions, like soil moisture and nutrient concentrations. That information is only available on larger scales than the scale on which trait strategy compositions may change (in the order of several meters, Chapter 2). For example, soil moisture is reported to be mapped at a 3*3 km grid (NASA, 2023). A higher resolution is reached for total nitrogen, where spatial resolution comes down to 100*100 m, but with a rather low Pearson correlation coefficient of around 0.45 (Song et al., 2018). The 100*100 m resolution comes within reach of the resolution required for linking it to land cover gradients observed in Dutch floodplains. However, the accuracy of the results is not (yet) sufficient to rely upon. When the resolution of trait strategy composition and environmental conditions become matching, a wealth of knowledge on the interaction between filters and trait strategies may become disclosed, not only in the Dutch regulated floodplains but in floodplains of natural flowing and regulated rivers all around the world.

5.1.1.3 Simulating the filter-trait concept

To answer the third sub-question, a model was developed (Chapter 4). The model used five of the six traits of the global trait spectrum (Diaz et al., 2016) to define two trait strategies: a fast- and a slow-growing herbaceous strategy. Values for four traits (leaf nitrogen content per unit leaf area, leaf area, leaf mass and adult height) were based on field data (Chapter 2). Based on the leaf nitrogen content per unit leaf area, ranges for relative growth rate were deduced (Niklas et al., 2005). Values for the fifth trait, specific stem density, were taken from literature. The model did not consider the sixth trait: diaspore mass, as the reproduction stage was not included in the model. By including five traits of the globals trait spectrum the model proved able to simulate trait strategy competition over a light and a (simplified) nutrient gradient.

Based on linear programming, the model was able to simulate the self-organization character of ecosystems. The model allowed, due to the linear programming technique, a more in-depth analyses of resilience and intra-specific variation of plant trait strategies than process-based (i.e. deterministic) models because the model solved the competition of the two different trait strategies and their intra-specific variation simultaneously and revealed the limiting factor for competition, which is cumbersome for deterministic models (Los, 2009). Therefore, the developed model not only allowed for exploring how filters impact competition, but also what the niche breadth of a strategy is under different (combinations of) filters. When further developed, the model could also be used to explore the fitness of a trait strategy in the longer run: by including a storage organ, estimations could be made on how long a trait strategy can survive under less favourable conditions, i.e. how resilient a trait strategy is to changes in filters.

The required knowledge to use the developed modelling approach as a means to explore resilience and trait strategy competition, boils down to quantified relations between fluvial processes and trait strategy composition. For example, if inundation frequency decreases, how fast would a more competitive trait strategy take over the flood-tolerant trait strategy? And how long a drought could a competitive trait strategy undergo before giving way to a more drought-resistant trait strategy? An important aspect of these questions is the fitness of a strategy under different environmental conditions (Figure 5.2). This kind of knowledge is very difficult to retrieve, but some relations are already thoroughly studied, albeit often the effect of changing environmental conditions on trait strategies is studied per environmental condition (Baastrup-Spohr et al., 2015; Douma et al., 2012; Lambers et al., 2008; Poorter et al., 2019, 2012). While this knowledge is gathered by field and lab studies and remote sensing, models can be developed further by assuming quantitative relations between changing environmental conditions and trait strategies, and subsequently, testing hypotheses of those relations.

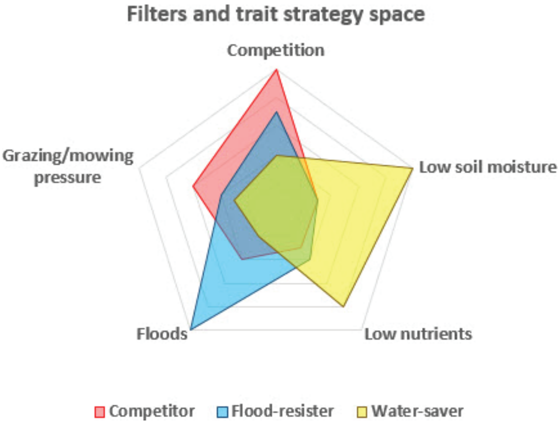

Figure 5.2: *Conceptual representation of how well three trait strategies (competitor, flood resister, and water saver) suit different environmental conditions, like competition (i.e. high nutrient concentrations and light availability), low soil moisture, low nutrients, floods and grazing or mowing. The figure shows the trade-offs between the three trait strategies: the competitor is well suited to thrive under high nutrients and light availability but cannot cope well with low nutrient concentrations or dry soil. The flood resister is tailored to survive frequent floods but at the expense of being outcompeted when water and nutrients are scarce or when nutrient concentrations are high. The water-saver trait strategy is not able to allocate energy to height growth to compete under luscious resource availability or withstand additional pressure from grazing/mowing or floods but can cope with low nutrient and water availability.*

5.1.2 Knowledge and tools for floodplain management

The management of floodplains of regulated rivers is a demanding task: it is not only about balancing ecosystem services like flood safety and biodiversity, but it is also about quantifying those ecosystem services and reaching agreement on intended management between involved stakeholders. Tools available for ecosystem services and stakeholder involvement are amongst others BIO-SAFE (Lenders et al., 2001), which evaluates biodiversity based on policy and legal criteria, a quantification method for floodplain services (Koopman et al., 2018), a hybrid serious game (combining a physical board game with computer models) to explore the complexity of river management together with stakeholders (Den Haan et al., 2020), and scenario explorations based on trade-offs between measures to compensate for an increase in river discharge and sea-level rise (Straatsma et al., 2019). The underlying thesis may support floodplain management by giving more insight into the spatiotemporal dynamics in filters steering vegetation competition and hence how those dynamics shape the distinct vegetation patterns in floodplains of regulated rivers. Below some examples are given that illustrate how the insights obtained in this thesis could be condensed into potentially useful tools and models for floodplain management.

5.1.2.1 Using satellite data

Satellite data is a useful source of information: it is cheap, covers a large spatial scale and has a high temporal resolution. The classification of satellite data into landcover classes allows for tracking landcover changes on a weekly to monthly basis. Knowing the current-day land cover composition of floodplains is valuable for flood protection: where are, or develop, rough land covers jeopardizing water safety? This information is in use by the Dutch national water authority (RWS) via the 'VegetatieMonitor'[1] for vegetation management (Geerling et al., *in prep*).

Besides near real-time information on landcover composition, satellite data could also aid in analyzing large-scale (i.e. multiple floodplains, river stretches, river catchment) trade-offs between flood protection and nature development: it might be more efficient to manage some floodplains principally as areas for flood control and other floodplains as nature areas instead of mixing both aims. Adding this option to the work of Straatsma et al. (2019), which quantifies the trade-offs

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[1] https://www.openearth.nl/vegetatiemonitor/

between measures that can be implemented for water safety, may enlarge the trade-off scope for floodplain management.

Landcover classes derived from satellite data can also improve existing models. For example, a year-round series of classified images could be incorporated into hydrodynamic models. This could improve model results as often year-round fixed roughness of floodplain vegetation is assumed (e.g. Baptist et al., 2004; Benjankar et al., 2011). Furthermore, a series of historic year-to-year changes in landcover composition of floodplain vegetation (and hence roughness), allows for lifelike sensitivity analyses of the effects of measures or discharges on water safety, as satellite images reflect actual rates of vegetation development. A simplified version of this, but still valuable, would be to include only information on slow and fast-developing areas of land cover in terms of roughness into hydrodynamic models (Figure 3.6 in Chapter 3).

5.1.2.2 Models as knowledge carrier

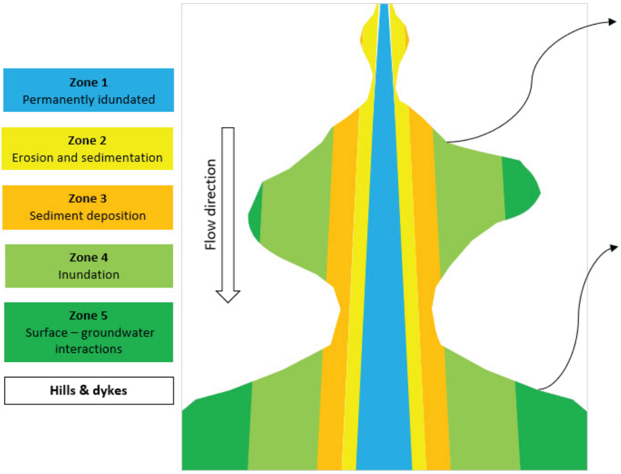
Models may range from simple to complex and from black box to deterministic. Whether a model is 'good' depends on the question. In floodplain management static habitat suitability models, like BIO-SAFE (Lenders et al., 2001) or CASiMiR (Benjankar et al., 2011), are often used. But more complex models are also used, which are often hydrodynamic models in 2 or 3D. Also for vegetated-oriented questions, deterministic models are available, like the model of van Oorschot et al. (2015), which uses life-stage dependent plant height, age, rigidity and mortality to simulate the initial recruitment and interaction between flow and vegetation development. Plant trait models (not specifically fluvial oriented) also exist and include stati(sti)c (Laughlin et al., 2012; Shipley et al., 2006) and deterministic (DeMalach et al., 2016; Kiniry et al., 1992; Soussana et al., 2012) approaches. The knowledge disclosed in this thesis would allow best for improvements of static habitat and deterministic models.

5.1.2.1.2 Static habitat model development

The conceptual model of Gurnell et al. (2016; and Figure 1.4 in Chapter 1), which is based on a vast knowledge of the interaction between vegetation and fluvial processes in freely flowing rivers, would be suited to convert to a static habitat simulation model. The conceptual model discerns five zones of interaction between fluvial processes (i.e. filters) and trait strategies, and those different zones can be translated into quantified relations (i.e. knowledge rules) between the filters as results of those processes and trait strategies. When the values of the steering filters are available (field, observation and/or model data, or through assumptions), the knowledge rules can be used to simulate the spatial arrangement of the different trait strategies. How good the model result is, depends on both the input data (filters) and how well the knowledge rules can be quantified.

Field data, like the data gathered in Chapter 2, is essential input to develop and quantify links between filters and trait strategies for the zones defined in Gurnell et al.'s (2016) model. Defining and quantifying these links are the first step in the operationalization of the model. Based on the field data of Chapter 2, zones 4 and 5 could be detailed further in terms of knowledge rules, making the model more suitable for the floodplains of regulated rivers (Figure 5.3). If knowledge is available on the succession trait strategies, the model could also be developed into a semi-static model by incorporating a time component that reflects succession and retrogression in trait strategies, depending on natural and anthropogenic processes. Information on such succession and retrogression schemes may come from satellite data (Chapter 3) or already established schemes (Benjankar et al., 2011).

(Semi-) Static habitat models are not very calculation intensive in terms of both memory and simulation time, which make them not only suitable on a small scale (floodplain or smaller) but also for a whole river catchment. However, those types of models do (partially) miss a temporal scale, preventing to simulate the interaction between floodplain vegetation and fluvial filters, rendering a snapshot in time of the spatial trait strategy arrangement based on static filters. Such results show floodplain managers the spatial trait strategy arrangement (e.g. fast- or slow-growing) and allow them to explore how changes in filters through measures or natural processes would impact this spatial arrangement.



Inundation & trait strategies

Duration of inundation discriminates within the following trait strategies:

- Groundwater dependence
- Life span
- Germination period
- Onset of flowering

Surface-groundwater interaction & trait strategies

Example for soil moisture

Trait strategy	Split at
Anatomy	33.8 & 21.5%
Leaf economic spectrum	32.2%
Onset of flowering	28.4%

Figure 5.3: *The potential contribution of the fieldwork results presented in Chapter 2. The data gathered in Chapter 2 could be used to link trait strategies to filters and quantify these links within the defined zones in Gurnell et al.'s (2016) conceptual model. The duration of inundation, the fourth zone, could be linked to different strategies concerning groundwater dependence, life span, germination period and the onset of flowering. Quantification within a zone between the dominant filter(s) and trait strategies is illustrated by soil moisture availability (see table part of the figure): soil moisture availability refines the fifth zone as around 30% of soil moisture availability leads to significantly different anatomy, leaf economic spectrum values and different timing of flowering (see Chapter 2).*

5.1.2.2.2 Deterministic model development

Knowledge of trait strategy composition could also be added to deterministic models, such as the model described in Chapter 4. The advantage of deterministic models over static models is the ability to mimic a part of the real world: time is incorporated through process rates and changes in mass are accounted for. Deterministic models can therefore give insight into how changes in floodplain filters impact trait strategy composition on shorter and longer periods. Using such models, insight is gained into how (dynamic) vegetation patterns are formed: how do filters change or interact, and how robust are trait strategies to change?

The model presented in Chapter 4 could be a starting point for a model able to simulate vegetation dynamics in floodplains of regulated rivers, but further development is required. For example, the model should be converted from a 1D to a 2D or 3D model, and fluvial filters and trait strategies should be added. Adding spatial dimensions allow for researching the effects of filter gradients on trait strategy competition and composition (2D) and how trait strategy patterns are formed spatially (3D). For floodplain management, a 3D model would be most useful, however, a 2D model on trait-strategy competition and composition is the first step as it aids in developing insights into the interaction between filters and trait strategies. When these insights are established, a 3D model could be developed by translating the interactions between filters and trait strategies onto a floodplain layout.

To develop the model from Chapter 4 into a floodplain vegetation model for regulated rivers, more filters and trait strategies should be added. Required filters would be inundation and soil moisture dynamics (Gurnell et al., 2016), and grazing and mowing (Baptist et al. 2004; Geerling et al. 2008). The trait strategies to add should be sensitive to those filters, like investment in aerenchyma formation and stem elongation to survive inundation (Van der Werf et al., 1993), and growth forms to withstand grazing and mowing (Siebenkäs et al., 2015). These developments render a model capable of simulating self-organization and resilience of trait strategies. However, how realistic such a dynamic model is, depends on the available knowledge and thus requires tying together knowledge obtained by field, lab and remote sensing.

A deterministic model is much more memory and calculation intensive than a (semi-) static model. And even though linear programming simulates trait strategy competition faster than deterministic models (Los, 2009), the adding of time comes at the expense of the spatial scale as calculation times increase greatly compared to (semi-) static models. Therefore, the spatial scale to explore the dynamics of the filter trait concept by a dynamic model may be limited to for example a river stretch. Nonetheless, such a dynamic model may support floodplain management in providing insight into the processes shaping trait strategy patterns and especially at what rate natural and anthropogenic processes may impact trait strategy patterns.

5.2 Conclusions

Floodplains of regulated rivers serve several ecosystem services, of which water safety and biodiversity are two important and often colliding ones as floodplain vegetation is both the pillar of floodplain roughness and of potentially high riparian biodiversity. This thesis focused on unravelling the interaction between filters and observed vegetation patterns in those floodplains to support floodplain management. To do so, three sub-questions were formulated that focused on identifying the main filters steering trait strategy composition, the scale (in-)

dependency of the filter–trait approach, and how the filter–trait interaction can be simulated in a simple model concept.

Chapter 2 showed that the filter–trait concept applied to grass and herbaceous vegetation revealed useful information on the filters for trait strategy composition. It added information on disturbance filters (excavation and summer flooding) and resource filters and their relative importance, which was not retrieved when solely species mappings were used. The absence of a geographical filter in the trait approach seconds the hypothesis of traits being more generic than species. So, the filter–trait approach has an added value compared to using species mappings for understanding the dominant filters for vegetation composition and may therefore be useful for floodplain management.

Chapters 2 and 3 identified different filters. On small scale (i.e. field plot scale) excavation, summer flooding and resource gradients proved the most dominant steering filters, while on large scale (i.e. floodplain, river branch and river scale) management and interventions were the most important. The combination of data from the field study and satellites thus identified the spatial nesting of filters: the filters identified during the field study function within the boundaries of the large-scale filters of management and interventions. The combination of the two data sources was therefore valuable for a more into depth understanding of the main filters and their scale of influence. Additionally, the time series available through satellite data highlighted that filters may change over time and in space.

Chapter 4 showed how resource availability (light and nutrients) steers trait strategy composition through competition. An important aspect of the developed model was the ability to transparently simulate intra-specific variation by using linear programming. Furthermore, linear programming provided a means to solve competition between trait strategies based on maximum net growth: the key to survival and the essence of floral ecosystem functioning. The model results were deemed realistic, as they were in line with findings in literature.

The insights gained during this research using the filter–trait concept on plant trait strategy composition and dynamics in floodplains of regulated rivers can be embedded in models to explore these insights further. An example has been given by the development of the linear programming model. However, more types of models can be of use: the required simplicity or complexity depends on the questions to be answered. However, models are a part of the means of furthering the comprehension and the management of safe and biodiverse floodplains of regulated rivers: data is a much-needed source of information as well. For example, data may be used for tracking changes in land cover and identifying potential water safety threats due to roughening of the vegetation.

To conclude, the combination of field and satellite data identified interventions and management as being the main steering processes for vegetation patterns in the floodplains of the large regulated Dutch rivers. The data also demonstrated that natural disturbances by floods and resource gradients are dominant filters within the boundaries set by interventions and management. These insights can be included in models to disclose them for floodplain management. Furthermore, the usefulness of the trait-strategy concept for identifying the most dominant steering filters for floodplain vegetation is a valuable finding on its own, since it adds more generic insight into the dominant filters for trait strategy composition than species composition. And it is this insight in dominant steering filters that is essential for effective floodplain management.

5.3 Recommendations

Based on the undertaken work, several recommendations can be made to better support floodplain management. The recommendations can be split into four groups: field data, satellite data, models and management. Field data on the filter-trait interaction should be extended to other landcover classes (bare sediment, shrubs and tree) to not only test the filter-trait interaction on those classes but also as a compare for satellite data. The field data should be gathered along transects, to encompass gradients in filters and trait strategies, and to minimize costs in terms of budget and time compared to randomized field plots. When using permanent plots for several years, insight into the stability in filters and trait strategy is gained, which can be compared to satellite data as well. It is recommended that the plots are mapped at least twice a year, as unpublished data from the author suggest that trait strategy composition changes within in growing season.

LandSat data was used for the long-term analyses of succession and retrogression of landcover classes. This data has a spatial resolution of 30*30 meters. Since 2015 Sentinel data has also become available and has a higher spatial resolution of 10*10 meters. By adding Sentinel data as a data source, the spatial accuracy of landcover classes is likely to increase, and with that the confidence in signalled landcover changes. In this thesis, the satellite data was analysed to see whether the effect of grazing could be retrieved (which was not the case, see Chapter 3). The same type of analysis could be done to see whether the satellite data holds information on the effects of flooding frequency, historic land use, and topography related to landcover classes and their rates of change. This type of information could perhaps be easier retrieved by combining satellite data with spatial data from other sources (e.g. mappings, models). Finally, more into depth analyses could be made on whether the combination of small-scale dynamics on trait strategy composition can be linked to remote sensing data (not satellite data per se) to estimate for example the level of biodiversity within (areas of) a floodplain.

To allow for exploring how trait strategy patterns are shaped by filters, the linear programming model could be extended by including more filters and trait strategies. By also including reproduction and storage as part of trait strategies, the model can be developed into a floodplain-tailored model to support floodplain management by providing insight into the dynamics of filters and trait strategies. For this to happen, the model should be developed in at least a 2D model to develop insight into how filter gradients impact trait strategy composition.

In the floodplains of the Dutch large rivers, cyclic rejuvenation is applied straightforwardly: once every so many years (part of the) floodplain vegetation is reset. However, with the availability of satellite data, insight is provided into how fast vegetation develops on a 10*10 meter spatial resolution. This information can be used to apply tailor-made management of floodplain vegetation, possibly allowing for more vegetation development and hence enriched biodiversity while still meeting water safety targets. Also, more information can be revealed that may support floodplain management by using the data of vegetation species mappings (which are executed regularly) to retrieve information on actual trait strategy composition. This allows for identification of the dominant filters steering vegetation composition and may add not only to system understanding but also allows for the development of efficient measures for floodplain management.

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About the Author

Valesca Harezlak was born on March 20, 1982, in Breda, the Netherlands. She received her basic and secondary education in Breda, first at the 'Vrije School' and then transferring to the Nassau Scholengemeenschap. She received her diploma in 2001. Having been rejected by lottery for several times to study veterinary medicine in Utrecht, she enrolled one year of biology coursework at Utrecht University and one year veterinary medicine coursework at Ghent University, Belgium. In 2003 she started her bachelor's degree in environmental sciences at the Utrecht University. In 2008, she earned her master's degree in sustainable development with a focus on land use, environment and biodiversity from Utrecht University. Her thesis focused on how Heinrich Events drove plant competition in the last 20.000 years in Florida, USA.

After graduating, she worked for 8 months as a trainee innovation management at TransForum, a research program that supported more sustainable agriculture. She began working at Deltares in 2009 as a junior researcher and consultant on water quality and ecology, focusing mostly on lakes. In 2014 the chance arose to start a PhD position at the University of Twente. The PhD position focused on how vegetation patterns are formed in floodplains of regulated rivers, and was part of the RiverCare program. During the PhD she remained working at Deltares for one day a week. She returned to Deltares when her PhD contract expired at the end of 2019. Her work at Deltares is focused on the development of a quick global ecological assessment tool for lotic waters (REACT), the WFD explorer, tool development of nationwide assessments of habitat suitability of aquatic organisms and the impact of aquathermia on the ecological functioning of water bodies.

List of publications

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Harezlak, V., Augustijn, D.C.M., Geerling, G.W., Van Geest, G.J., Leuven, R.S.E.W., 2020. Linking plant strategies to environmental processes in floodplains of lowland rivers. Journal of Hydro-environment Research 30, 45–62, doi.org/10.1016/j.jher.2020.01.002

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