

Seedling survival of riparian plants during summer drought

Master Thesis: A literature review

By Peter Zomer

under supervision of Annemarie Garssen

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Introduction

Riparian plant communities

Rivers and running waters in general are of vital importance for humans. We depend on them for drinking water, irrigation of croplands, transport, energy and multiple other reasons including the joy of their esthetical and recreational aspects (Malanson. 1993). The term riparian is defined by the American Heritage Dictionary of the English Language as an adjective describing 'Of, on, or relating to the banks of a natural course of water'. Ecologists describe it as the link or interface between aquatic and terrestrial ecosystems (Malanson. 1993, Richardson *et al.* 2007). Their importance as an ecosystems is acknowledged by numerous authors (Malanson. 1993, Decamps. 1993, Naiman and Decamps. 1997, Perry *et al.* 2012). For socio-economic reasons as the riparian vegetation functioning as a nutrient filter (Decamps. 1993) and playing an important role in erosion control (Yu *et al.* 2012).

Also for ecological reasons the riparian habitats are considered as special, because of their highly diverse, dynamic and complex properties. These properties all facilitate plant diversity on a broad temporal and spatial scale. (Naiman and Decamps. 1997). Its role for animal biodiversity is seen in species conservation both in water (Naiman and Decamps. 1997) and on land and furthermore in its function as a migration corridor (Malanson. 1993, Decamps. 1993, Naiman *et al.* 1993). The protection of these ecosystems is also important in the implementation of the EU Water Framework Directive, the EU Habitats Directive, the RAMSAR Convention and the Convention on Biological Diversity (REFRESH. November 2011).

European lowland system

The European lowland streams are of special interest for this research in the framework of REFRESH, a European project to develop knowledge for efficient management of freshwater ecosystems (REFRESH. November 2011). Dominant features in these European systems are hydrology, soil composition, pH, lime content and nutrient loading. Sand, clay, loam or peat form the ground layer of rivers and floodplains and wet and drier valleys can be found. (Higler. 1993) Along the longitude of a stream several sections can be defined. The high section which is not in the focus of this thesis and the mid and the lower sections, all with other energy levels (Brown and Peet. 2003). Streams in the mid sections have a fairly consistent base flow and are additionally fed by ground water. Periodic flooding occurs together with meandering and sediment deposition. The lower sections are characterised by their drainage function, some ground water is still fed, flooding occurs normally, discharge is higher and the nutrient loading less. Hydrological inflow overall is diverse and so are nutrients and quantity.(Higler. 1993)

Higler (1993) furthermore describes how 15.000 years of human impacts together with climate changes have formed this river system to its present state. Human activities on land have replaced original riparian vegetation by arable land borders, buildings, etc. (Higler. 1993, Brown and Peet. 2003). The local historical ecosystems were diverse and specific for the area and restoration would thus facilitate formation of new, plant rich vegetation types (Brown and Peet. 2003).

Increasing summer drought

In all riparian ecosystems water is the central feature and changes in water flow are the primary factor affecting soil properties, flora and indirectly fauna (Cooper *et al.* 2003). Most riparian zones normally experience increased flow in early spring through melt water and a reducing flow through the warmer summertime (Rood *et al.* 2008). This thesis focuses specifically on consequences of summer drought. Summer drought is already increasing and is expected to increase even more in the future (Strom *et al.* 2012), it is driven by human impact and climate change (Higler. 1993). Human impact is causing decreased water flows through irrigation, regulation of stream flows by dams, flood control and other human activities (Salinas and Casas. 2007, Lytle and Poff. 2004). Climate change is showing to have a large impact on riparian ecosystems (Naiman and Decamps. 1997). Based on climate scenarios, earlier spring flows and reduced summer flows are expected for the European region (Strom *et al.* 2012). According to scenario's from the IPCC overall precipitation is expected to increase in North Europe and decrease in South Europe, in both summer and winter. Furthermore temperatures are expected to increase especially for the northern regions. (IPCC *et al.* 2007) Projections based on this lead to increased floods in North Europe. Central and South Europe are expected to experience increased evapotranspiration in the summer, reduced river discharge and an increased variation in discharge, finally leading to decrease soil moisture in summer time. (Decamps. 1993) Within the project REFRESH climate change is especially expected to affect small water bodies, influence from temperature will be highest there together with other factors like nutrient loading and hydrological changes (Website REFRESH).

Seedling survival

Increasing summer droughts are affecting plant ecology, in which seedlings are expected to be most sensitive (Rood *et al.* 2008). This sensitivity is based on availability of water (and light) as the most important factor for seedling survival (Dixon and Turner. 2006, Kussner. 2003), more important than for example grazing (McDonald. 2001). The seedling stage is seen as vital for the reproduction and succession of vegetation, the survival of seedlings might be the limiting step in plant reproduction (Stella and Battles. 2010). Mortality of seedlings can affect regeneration of forests, but also has effects on species composition. Species-specific adaptations will lead to selection for survival of species within a short time span (Kussner. 2003) and in the climate projections to possible drier vegetation type.

Thesis outline

This thesis has the purpose to facilitate management practitioners with knowledge about seedling survival and future development of plant communities subjected to summer droughts. The main research question will be: 'How do increased summer droughts affect seedling survival for riparian plant communities in the European temperate lowland region?' To answer this research question and to reach conclusions useful for management we will answer several research questions. First we will zoom in on coping mechanisms available to plants. Secondly we zoom out to the effect on individual plants distinguishing trees and herbaceous plants. Thirdly our even larger focus will be on a community level also distinguishing trees from herbs. Fourthly we will look at the effects on seedlings along the elevation gradient relative to the water level, also called stream riparian gradient. The fifth and final research question will review the role of invasive species related to

seedling survival during summer droughts. This leads to a conclusion which will also incorporate the appropriate measurements to be taken by management.

1. What coping mechanisms do riparian seedlings use to survive summer drought?

Plants differ in their ability to withstand drought, since coping mechanisms can differ between plants. Pallardy (2008) makes a general comparison of coping mechanisms (figure 1), based on the water potential of elongating tissues (Ψ_w) and relative water content (RWC) of the plant. The scheme suggests stress avoidance or tolerance on three levels of drought severance: Drought, desiccation and dehydration. From this scheme four classes of plants can be defined: three classes avoiding respectively drought, desiccation and dehydration; and a class that tolerates dehydration. These classes are not strict, plant species may choose for a different coping mechanism in a specific situation or season (Pallardy. 2008).

For this research we will look at the drought tolerant plants, because these plants will have mechanisms to cope with drought. It must be admitted that some herbs can finish their life cycle in a few weeks and avoid drought, but most perennials can't (Pallardy. 2008, Kramer and Boyer. 1995). Some woody plant species that are drought tolerant can be classified as dehydration avoiders. But most species will try to avoid desiccation by maintaining high water levels (Kozlowski and Pallardy. 2002), for example via increased water uptake via roots. In a relative moist ecosystem like the European low land river systems it is also more likely to find plants that avoid desiccation. Species that are desiccation tolerant are more often specialists adapted to the arid regions of this world (Pallardy. 2008).

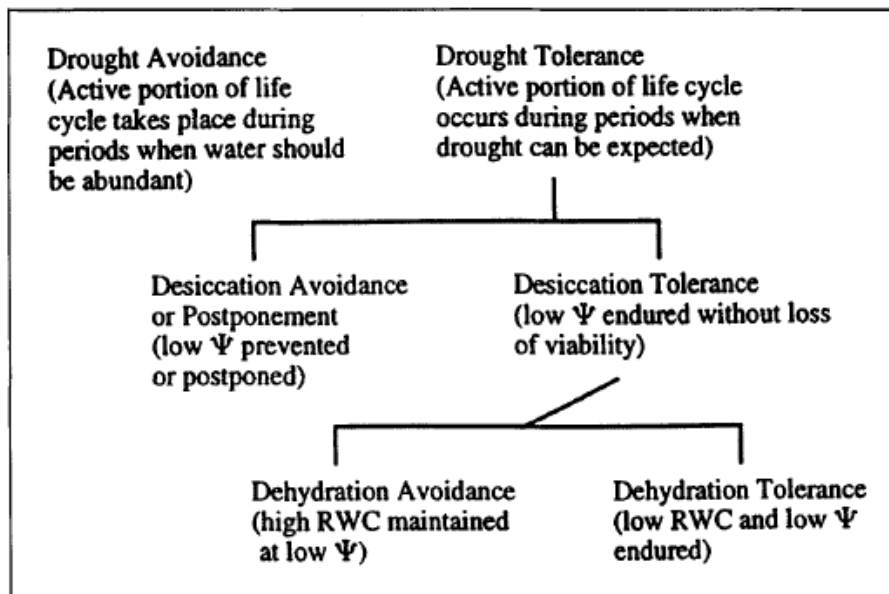


Figure 1: General overview of different coping mechanisms to survive drought, Source: (Pallardy. 2008)

Most times drought tolerant plants avoid a low Ψ from happening, coping mechanisms are either increasing water uptake or decreasing water loss (Pallardy. 2008). Next to this RWC will be kept high with internal mechanisms to use water efficiently. In this chapter we will separately

review increased water uptake, decreased water loss and internal coping mechanisms like increased water use efficiency.

Increased water uptake

In plants water is mainly taken up by roots, the size and depth of roots networks are related to the ability of water uptake (Pallardy. 2008, Kramer and Boyer. 1995, Kozłowski and Pallardy. 2002). Increased root growth is also observed when water (or nutrient) deficiencies are present (Pallardy. 2008, Kozłowski and Pallardy. 2002) this is seen from carbon allocation and increased partitioning of roots (Kleczewski *et al.* 2012). In drought experiments specifically, changed biomass allocation is benefitting roots for shoots (Stella and Battles. 2010) for example by allocation of saccharides (Elcan and Pezeshki. 2002).

Survival of specific species is also related to root size of seedlings. During drought experiments pendunculate oak (*Quercus robur*) for example showed a four times higher root to shoot biomass than common linden (*Tilia cordata*) or red ash (*Fraxinus pennsylvanica*) and had higher survival rates (Kussner. 2003). This was also seen in similar experiments for four species of salicaceae seedlings, where *Populus Nigra* had a higher root to leaf area ratio than *Salix alba*, *S. triandra* and *S. viminalis* (Splunder *et al.* 1996). In experiments simulating a water table decline differences in root growth could also be observed. Foremost, water table decline should not exceed root growth rate in dry areas for seedlings to survive in sufficient amounts. (Lytle and Merritt. 2004) Initial seed size and respiratory reserves are possibly related to this ability to keep up with a declining water table. Willow (*Salix exigua* and *S. drummondiana*) seeds for example are smaller than cottonwood (*Populus angustifolia* and *P. balsamifera*) seeds and are less likely to keep up with a water table decline in experiments (Amlin and Rood. 2002).

Other mechanisms to survive drought are based on the cooperation with ectomycorrhiza which can facilitate water (and nutrient) uptake (Kleczewski *et al.* 2012). Furthermore the xylem structure and function can be adapted to reduce flow resistance to increase inflow (Pallardy. 2008). These symbioses with ectomycorrhiza and xylem structure and functioning can also make the species specific difference in survival between seedlings.

Reduced water loss

Transpiration is the most important way in which plants lose water (Pallardy. 2008). Consequently, coping mechanism are in place to reduce this transpiration, often focused on leaves. A reduction in leaf size and altered morphology lead to reduced specific leaf area (Stella and Battles. 2010, Pallardy. 2008) and less transpiration. To save water from evaporation conductance of stomata for water may also be reduced, for example by closing them (Pallardy. 2008, Amlin and Rood. 2002). Closed stomata will in turn lead to reduced CO₂ availability and consequently reduced photosynthetic activity, what will lead to an extra reduce in water use (Elcan and Pezeshki. 2002). Changes in the cuticle properties can also take place, reducing the transpiration rate from the leaf (Pallardy. 2008). Severe drought can even activate relative resource-expensive mechanisms that lead to leaf abscission (Pallardy. 2008), branch abscission and crown dieback (Stella and Battles. 2010).

These coping mechanisms were also found in experiments. Comparison of willow saplings (*Salix exigua* and *S. drummondiana*) and cottonwood saplings (*Populus angustifolia* and *P. balsamifera*) showed willows to be less able to reduce water loss via stomata closure or other

responses (Amlin and Rood. 2002). This was also found for *Populus nigra* seedlings compared with seedlings from *Salix alba*, *S. triandra* and *S. viminalis*, all had different water-loss characteristics. Specific leaf area for example differed and *P. Nigra* eventually had the lowest transpiration rates and was found able to survive drought experiments better. (Splunder *et al.* 1996)

Internal coping mechanisms

Internal adaptations and mechanisms to cope with drought are based on optimising water use; to prevent damage from happening and even ensure growth. Prevention of damage largely takes place by maintaining turgor at an acceptable level. Osmoregulation can be used to increase diffusion to certain cells and keep turgor and relative water content high. The osmoregulation in roots can increase osmotic values to heights which even increase the water uptake by the root cells. (Kozłowski and Pallardy. 2002) When osmoregulation is not present or possible, the elasticity of cells can be used to maintain turgor (Kozłowski and Pallardy. 2002).

Certain proteins can also reduce damage to important macromolecules and membranes. When dehydration is severe, these proteins will be newly synthesised or produced in larger quantities during drought stress. (Kozłowski and Pallardy. 2002) Photosynthetic activity and growth capacity will also reduce through limited water availability (Pallardy. 2008) this can be caused directly by reduced turgor and indirectly through reduced carbon availability because of closed stomata (Elcan and Pezeshki. 2002).

Recovery after drought stress

Recovery from stress is often strong and relatively fast, this can be seen when increased gas exchange is measured (Amlin and Rood. 2002). This may benefit certain species in the future competition, quickly recovering species can then take their place in space and dominate the vegetation. A willow like *Salix goodingii* for example has a better physiological recovery to drought stress than *Populus fremotii* and may have an advantage after stress (Stella *et al.* 2010).

Drought stress and other types of stress are in tree plantations also seen as hardening of seedlings for their future life. Many mild and/or slowly increasing types of stress may have beneficial effects for plants. To adjust to stress before it becomes really severe but also because stress at certain moments in a plants life may benefit growth (Kozłowski and Pallardy. 2002). A specific example is found in the increased defense capacities of cuticle after earlier stress (Pallardy. 2008).

Summary

Most plants need to withstand or cope with drought to survive all year round. Different mechanisms can promote survival, increased uptake and reduced loss of water will lead to a postponed and reduced impact of water shortage. Several internal mechanisms also add to this like increased water use efficiency; other internal mechanisms will even help to prevent damage from happening by for example maintaining turgor. These different coping mechanisms of seedlings, but also the mechanisms for the recovery after drought will determine which plant or species will perform better in the community.

2. What are the effects of summer drought on herbs and trees specific?

Although herbs and trees were found similarly dependent on environmental factors in the Mediterranean area (Salinas and Casas. 2007). Normally woody and herbaceous species of plants are differently affected by environmental factors (Lite *et al.* 2005). Partly because they depend on other factors, trees for example can be subject to a higher diversity of light availability than herbs (Sagers and Lyon. 1997). But Sagers and Lyon (1997) also describe the difference in recovery rate. The shorter lifespan of herbaceous species, their higher colonisation rates and ability to spread vegetatively all lead to a faster adaptation to environmental conditions (Salinas and Casas. 2007, Sagers and Lyon. 1997).

For water conditions the smaller herbs are also more sensitive to changes in environment, because of their dependency on subsurface soil moisture or flooding (Higler. 1993, Sagers and Lyon. 1997). Trees in contrast reach the steadier ground water levels (Higler. 1993). These differences between reactions to soil moisture heterogeneity are also seen in researches after soil drainage related to occurrence of trees, shrubs and herbs (Nichols *et al.* 1998).

General effects on herbs

Because herbs are depending on subsurface soil moisture, they are also less affected by ground water table decline (Higler. 1993). This is also seen for species diversity which is found to be high in places with shallow subsurface moisture (Tiegs *et al.* 2005). The subsurface soil moisture may be more related to precipitation than to water table (Sagers and Lyon. 1997).

Water table and stream flow decline affecting herbaceous species is also observed though. In a specific research in an arid region of North America a more intermittent stream flow led to a decline in diversity and cover of herbaceous species (Stromberg *et al.* 2007). In another research in a Mediterranean area effects of reduced flood duration were seen to be negative for hydric herbs, but not for mesic and xeric herbs (Salinas and Casas. 2007). The outcome of these last two researches could possibly be linked to the dry areas where they were conducted.

General effects on trees

In general more literature can be found for the research on trees and individual species of trees. Chapter one already described some examples of tree species that were differently affected by drought, as coping mechanisms (*e.g.* root:shoot ratio) to survive drought differed (Kussner. 2003, Stella and Battles. 2010). The difference between trees was also studied in a broad research conducted after a severe drought in the USA. Results showed three general effects: the effects of drought were affecting all dominant species of the different ecosystems; average mortality differed between species; and all species showed local levels of high mortality consistent with the drought gradient. (Gitlin *et al.* 2006) These effects on trees were also found for differing flood durations, caused either by summer drought or flow control through dams (Johnson. 1994). Different species do not always differ in their response though, Salinas *et al.* (2007) demonstrated that forest cover of three functional groups of species (hydric, mesic and xeric) was negatively affected for all groups with reduced flood duration. Species diversity was also found to decline for all of the groups in this Mediterranean area.

For a drier area in the USA effects were seen related to a reduced ground water table. Diversity of riparian woody species (*Salix* and *Populus*) declined and species composition shifted

from wetland pioneer species to drought tolerant shrubs. (Stromberg *et al.* 2007) The changes in stream flow are especially expected to affect species with small regeneration windows (Stromberg *et al.* 2007). These species like poplar (*Populus*) and willow (*Salix*) have small seeds and are adapted to a specific moisture level in a specific time frame (Stella and Battles. 2010, Gonzalez *et al.* 2010). Complete communities of these trees might be adapted to a specific flow regime and have optimised their moment of seed release to increase germination chances (Rood *et al.* 2008). Changed flow regimes are expected to provide these species of trees, often pioneers, with a smaller window for reproduction (Stella and Battles. 2010, Stromberg *et al.* 2007, Gonzalez *et al.* 2010), thereby affecting colonisation success.

Summary

Woody and herbaceous species of plants are differently affected by environmental factors. Herbaceous species are also expected to be more sensitive to these environmental factors. This is also applicable for summer droughts. Groundwater table is more important for tree species and subsurface soil moisture is more important to herbaceous species. Differences in coping mechanisms furthermore drive the difference between and within herb and tree species.

3. What are the specific differences between open and forested plant communities, looking at (seedling) survival and responses to drought?

This chapter gives a more general overview of riparian plant communities with a separated look at the difference between tree and herbaceous communities. If possible, seedling survival specific will be highlighted. Important is the assumption that plant communities are defined in occurrence considerably by the success of seedlings. Seedlings have such an important role for the whole plant community because of their importance for plant reproduction (Stella and Battles. 2010).

Naturally the riparian plant community is highly diverse and dynamic. Normal development would occur via succession, starting with an open vegetated area with small pioneers and developing into the climax state of a forest. (Malanson. 1993, Brown and Peet. 2003) Riparian vegetation in managed ecosystems might not always be able to develop into a forest state because of management practices focusing on maintaining low herbaceous vegetation by for example mowing or grazing. This is also the common practice in floodplains in for example the Netherlands (Grootjans *et al.* 2002).

Tree and herbaceous types of vegetation do not always have to be linked to each other (Sagers and Lyon. 1997). Trees and herbs are namely differing in sensitivity and adaption to environmental factors, as seen in chapter two. But Sagers and Lyon (1997) add another possible causation namely: the possibility of biased species inventories. The last explanation for a higher diversity seen between herbaceous communities might be because there are just more herbaceous species, which could bias inventories (Nichols *et al.* 1998).

It is again important to mention that these differences between differently sized plants as trees, shrubs and herbs might partly not apply for (small) seedlings. But we assume that natural communities in a further state of succession will consist of individuals in all stages of the lifecycle of plants. So environmental factors shaping communities may affect communities in all lifecycle stages, but sensitive stages like seedlings will be more vulnerable to conditions and thus have a stronger effect on community formation. It is thus important to look in more detail to the way

plants and communities affect each other. This will also provide information about how woody species and herbaceous species interact. These interactions will now be described for periods of summer drought and related to water for the competition between seedlings and the advantages woody cover can offer seedlings.

Competition for light between plant communities

Competition between herb and tree communities is based on light availability, because it is one of the most important factors for seedling performance (Kussner. 2003). For example when trees start replacing grasses in succession (Naiman and Decamps. 1997, Pollock *et al.* 1998). Competition for light between herbs and trees might be changed through increased summer droughts. The examples for this in the next paragraph are describing trees but will also be applicable for herbs because of similar differences between species specific coping mechanisms.

The pendunculate oak (*Quercus robur*) can better compete with other trees for light because it is better able to reach water tables during droughts than competitors like common linden (*Tilia cordata*) and red ash (*Fraxinus pennsylvanica*) (Kussner. 2003). Another example is Fremont Cottonwood (*Populus deltoides*) which will be better able to compete for light with the more drought tolerant tamarisk (*Tamarix ramosissima*) when water is available (Cooper *et al.* 1999). Another natural phenomenon affecting competition for light is (summer) flooding. Regeneration and occurrence of seedlings is often limited by tall herbs. But when (summer) floods regularly take place competition for light might become less and (tree) seedlings establishment following floods will be more abundant. (Kussner. 2003, Siebel and Bouwma. 1998)

Advantages of woody cover

Advantages from specifically woody cover for seedlings are described here, because trees and shrubs form more important landscape elements than herbs. Trees can control more environmental factors that affect seedlings, for example light, erosion or nutrients and the impact of herbs on these factors is just smaller. Woody riparian vegetation can regulate temperature, light and water flow and provides nourishment and woody debris (Naiman and Decamps. 1997, Lite *et al.* 2005). Temperature and overall climate regulation for water and air is provided through leaves blocking the intensity of the sun, maintaining humidity and blocking wind (Higler. 1993, Vasicek and pivec, 1991 in Malanson. 1993). This makes riparian forest reacting slowly to temperature and moisture shifts (Malanson. 1993). These effects do though differ from season to season, but are depending on the presence of leaves (Higler. 1993, Lite *et al.* 2005) and will thus have an effect in mitigating summer droughts.

Light regulation by woody cover is in most cases negatively affecting tall herbs, grasses and grass-like species, limiting occurrence in heavily shaded places (Pollock *et al.* 1998, Siebel and Bouwma. 1998). This limited occurrence of tall herbs will leave room for other plants, the occurrence of hardwood floodplain species for example is related to a reduced light transmission during summer (Siebel and Bouwma. 1998). The reduced light availability might thus not always affect occurrence of plants and depend on light intensity. In some sites seedling diversity and density are even found to be uncorrelated to understory light intensity (Naiman and Decamps. 1997). This is also confirmed by the studies that do not find relations between forest and herbaceous assemblages (Sagers and Lyon. 1997, Lyon and Sagers. 1998).

The regulation of water flow through woody debris and stems can provide higher floodplain surfaces with finer sediment and higher soil organic matter (Nakamura *et al.* 1997). Trees are also known to initiate sandbar formation in some rivers (Erskine *et al.* 2009, Lisle, 1989 in Malanson. 1993). These woody debris and trunks of trees resisting floods (*e.g. Salix*) can thus accumulate sediments at their base and here seedlings will establish (Malanson. 1993).

Plants in general provide nourishment for all kinds of organisms in the riparian ecosystems, whether aquatic or on land (Naiman and Decamps. 1997). Litter can also provide positive effects during summer droughts because it maintains soil humidity which seedlings need under dry conditions (Eckstein and Donath. 2005). However, litter can also have a negative effect because it blocks light for germination (Lite *et al.* 2005, Eckstein and Donath. 2005).

Summary

The direct focus of this chapter was on plant communities and not the specific seedling stage, but description of communities also indirectly describes seedling survival because of its importance in the reproductive cycle. Herbaceous and tree communities are differently affected by environmental factors like drought, because they depend and adapt differently to soil moisture. Herbaceous and tree communities do thus not have to be related to each other but do affect each other. Especially in the seedlings stage trees can be negatively affected by herbs, but trees affecting herbs is also common. This is related with drought because some plant species seem better able to compete for light when water is sufficiently present. The advantages of a woody cover were also described for seedlings and these depend on the control of temperature, light and water flow, but also on nourishment and woody debris

4. How are seedlings affected by summer drought over the elevation gradient relative to the water level?

Factors related with elevation

Plant species richness and cover can differ along the elevation gradient from the water level to higher areas, also called the stream riparian gradient. Lyon and Sagers (1998) found that woody species richness was significantly correlated with organic matter, slope, water retention capacity and elevation. In another research occurrence of hardwood flood plain forest specifically was found positively correlated to elevation (Siebel and Bouwma. 1998). For herbaceous plants this elevation gradient was also found correlated with the species richness, but only in a few studies (Lyon and Sagers. 1998). Normally herbaceous species are expected to be more dependent on subsurface soil moisture (Higler. 1993, Sagers and Lyon. 1997). This in turn may be dependent on elevation, because of slopes and soil water retention capacity (Lyon and Sagers. 1998).

Factors determining species occurrence in the above researches may be related to elevation, but the mechanisms controlling this occurrence are still not clear. According to Lyon and Sagers (1998) these mechanisms depend on slopes; water retention capacity of soil; and organic matter. Seedling survival during summer droughts and low water tables specifically will then be dependent on the water retention capacity of the soil; the depth of the ground water table; and availability of extra water by for example precipitation (Gonzalez *et al.* 2010). Ground water table is determined by seasonal changes like melt water and summer drought. This leads to a decrease in flow from spring to summer, the exact time seedlings emerge and develop their first growth. (Rood *et al.* 2008) This

depth of the ground water is relative to the elevation, higher elevations will have less water. But this can thus be compensated by water retention capacity of soils through the capillary fringe and precipitation (Gonzalez *et al.* 2010).

Importance of floods

A large amount of research into water table decline is related to the research concerning floods (especially in dam controlled rivers in North America) and the effects of reducing summer drought might be impossible to review when flooding is not taken into account. An example of this is the survival of poplar (*Populus*) seedlings which must be positioned high enough to survive floods - causing sediment burying or submergence stress- and low enough for roots to keep contact with the decreasing water level and related soil moisture level (Gonzalez *et al.* 2010). This is an example of not only mean (low) flow making the difference, but also the variation between maximum and minimum flow. (Strom *et al.* 2012) Furthermore, floods can also determine substrate properties like sediment size and organic matter. An extreme example comes from floodplain forests studied on a mountain slope, which show strong differences in current and height of floods. Sediment there is found to be smaller and organic matter content to be higher on the higher surfaces, because on the lower surfaces everything flushes away (Nakamura *et al.* 1997), this also led to higher soil moisture levels on higher surfaces. This is an extreme example and probably not the case for lowland rivers where particle size can be found to be smaller at low elevation (Lyon and Sagers. 1998).

Different vegetation belts

Different experiments have already been carried out to assess effects of low water table on vegetation shifts along the elevation gradient. Some experiments show strong limiting effects of water levels, cottonwood (*Populus deltoides*) seedlings were in one experiment found to survive summer drought only in sites elevated less than 1 meter (Cooper *et al.* 1999). Cooper *et al.* (2003) furthermore describe how seedling mortality will increase in the mid and high elevation floodplains surfaces. At the same time establishment will be promoted on low surfaces because of the newly exposed bare grounds (Johnson. 1994, Gonzalez *et al.* 2010). These different levels in riparian vegetation are also described with different vegetation belts in Strom *et al.* (2012), where plant species are restricted by their hydrological niches. Based on climate scenarios they expect that especially in the higher belts –the riparian forest and willow shrub belts- a lowered water table will lead to species loss. Species will not be completely lost, the belts are not strictly exclusive and species can occur in more than one belt, and will shift to lower belts –the graminoid and amphibious belts. (Strom *et al.* 2012)

This strict difference between different vegetation levels along an elevation gradient was not found by all studies in this field though. Other researches point at the heterogeneity of substrates in the riparian areas. Differences between plant communities are still found to be led by water availability but on a more local scale. For example, in one study soil drainage heterogeneity explains 65% of the variance in plant diversities (Nichols *et al.* 1998). Heterogeneity can also be found on a large scale for other factors like pH, elevation, slope, sand, clay and organic matter (Lyon and Sagers. 1998). Several studies also point at the importance of sediment type in drought experiments (Gonzalez *et al.* 2010, Nakamura *et al.* 1997).

Summary

Tree communities are more dependent on the depth of the ground water and thus on elevation than herbaceous communities. Herbaceous communities are more dependent on the specific substrates, and these can differ over a wide range of gradients related to elevation. But even for these substrates, their most important property seems to be soil moisture. Furthermore, variation between low and high river levels and the occurrence of floods were also found to be significantly affecting seedling survival. The importance of seedlings is seen from poplar seedlings and their dependency on the relative elevation to water level, as an example for most woody seedlings.

5. What role do invasive species have related to seedling survival during summer droughts?

Exotic species invading ecosystems is common and is often observed (Aslan *et al.* 2012). Normally only a few non-native species can successfully invade long time established plant communities (Rejmánek *et al.* 2005). But changes in environmental conditions like nutrient enrichment or high physical impact can favor exotic species (Salinas and Casas. 2007). Other drivers for invasion are precipitation, temperature and rising CO₂ (Bradley *et al.* 2010). Higher temperatures can move species populations up the longitude of rivers (Perry *et al.* 2012). In riparian ecosystems drought can also lead to the establishment of more drought tolerant invaders (Dixon and Turner. 2006).

Vulnerability of riparian ecosystems

Riparian ecosystems in general and European lowland rivers specifically, are more sensitive to invasion (Salinas and Casas. 2007) than other ecosystems, like extreme terrestrial environments (Tabacchi *et al.* 1996). More biodiverse communities already have the highest amount of exotics (Naiman and Decamps. 1997). The riparian zones are also especially threatened because trees can easily invade from more inland forests or plantations (Tabacchi *et al.* 1996). This mechanism together with the presence of densely populated areas with horticulture in Europe will provide an enormous pool of potential invasive species (Aslan *et al.* 2012). Furthermore, riparian zones are mentioned to act as corridors for invasion of exotics (Salinas and Casas. 2007), and exotic plants are expected to move easier up and down rivers than over land (Naiman and Decamps. 1997).

Impact of invasive species

Examples of invasion of species can be found in the Northern American riparian ecosystems. The sand bar willow (*Salix exigua*) is the most common woody plant species along rivers in the Western United states of America, second is cottonwood (*Populus*), third tamarisk (*Tamarix*), and Russian olive (*Elaeagnus angustifolia*) is fourth. Both tamarisk and Russian olive are non-native and considered invasive species. (Friedman *et al.* 2005) A lot of research has been done on this invasion of tamarisk (Cooper *et al.* 2003, Stromberg *et al.* 2007, Cooper *et al.* 1999, Reynolds and Cooper. 2010) and on the invasion of Russian olive (Reynolds and Cooper. 2010). Competition between cottonwood and tamarisk are related to floods and to droughts, with tamarisk being more drought tolerant, better able to survive without ground water and more resilient against severe floods (Cooper *et al.* 2003). But tamarisk is not expected to overgrow poplar or willow when water is available in sufficient amounts (Stromberg *et al.* 2007, Cooper *et al.* 1999). Russian olive is able to

establish under much severe conditions than poplar or tamarisk is, and can tolerate deep shade and drought (Reynolds and Cooper. 2010).

Summary

Invasive species are expected to occur more often with the expected change in climate and facilitated by drought. In riparian ecosystems invasive species especially are a real threat, because these systems are easy to invade and can function as a corridor. The impact of invasive species is already strongly visible in North America and expected to form a major threat for European lowland ecosystems.

Management approach and Conclusion

To give appropriate measurements for management the research questions will be recalled in the following text. Suggestions for management from literature will also be mentioned related to these research questions.

Research questions and management approach

The first research question ‘What coping mechanisms do riparian seedlings use to survive summer drought?’ showed that plants use different mechanisms to survive droughts. Increased uptake, reduced loss of water and internal mechanisms were all in place to reduce impact from water shortage. These coping mechanisms and the speed of recovery differed per species, which will through time affect the species composition of communities after stress.

Management could make use of this response to stress. As described in chapter one hardening by stress takes place in seedlings. In plantations it is thus important to ‘train’ seedlings to stress by exposing them to mild and regular stresses in their first life stages before replanting them in nature (Kozłowski. 2002). Further attention for coping mechanisms is concerning fertilisation in replanting of seedlings. Over fertilisation is common in managed settings and this may increase susceptibility of seedlings to drought injury. Plants on nutrient rich soils will invest less in root formation because nutrient deficiency as a motivator for root growth is not applicable. Symbioses with ectomycorrhiza will also be similarly affected. (Kleczewski *et al.* 2012)

The second research question ‘What are the effects of summer drought on herbs and trees specific?’ was mainly answered by the different way plants obtain water, either from subsurface soil moisture or from the groundwater table. Furthermore, herbaceous species are expected to be more sensitive and adaptive to environmental factors. Differences between and within herb and tree species are also related to their individual mechanisms to cope with stress. Concluding from this chapter, management should not focus on the restoration of specific herbaceous communities but on the restoration of the substrate and environmental conditions which normally facilitate high species diversity (Lyon and Sagers. 1998).

The third research question was ‘What are the specific differences between open and forested plant communities, looking at (seedling) survival and responses to drought?’ The focus of this chapter on plant communities is related to the seedling stage, because it is the limiting step in the reproductive cycle and thereby community formation. Drought affects herbaceous and tree communities in separate ways because the communities depend and adapt differently to soil moisture. Communities do thus not have to be related to each other based on environmental

conditions, but can affect each other related to drought. For example in the competition for light. The outcome of this competition can be affected by water shortage. The advantages of a woody cover are related to the control of temperature, light and water flow, but also on nourishment and woody debris. These advantages may also be important for management because woody cover can buffer effects of increased temperature and light intensity. Of herbaceous plants the perennial species are in turn important because their consistent presence in all seasons will provide an habitat for wildlife (Lite *et al.* 2005).

The fourth research question was 'How are seedlings affected by summer drought over the elevation gradient relative to the water level?' Because herbs depend more on subsurface soil moisture they are less related stream riparian gradient than tree communities. Specific substrates with different water retention capacities will be more important for herb communities. Floods proved to be important as major shaping events for seedling establishment.

The management of stream flows by dams should be strictly organised with respect to the downstream vegetation types. Perennial and active flood regimes will facilitate high biodiversity in ecosystems. (Lite *et al.* 2005). Good management of flows may even have a mitigating effect on the impact of climate change on this vegetation (Perry *et al.* 2012). Another approach for management is related the narrowing of riparian vegetation belts along the stream riparian gradient. The higher belts are expected to be affected most severely by drought and at the same time extreme floods may shift vegetation zones up the elevation gradient (Strom *et al.* 2012, Kramer *et al.* 2008). To maintain the same size of riparian area land management should create new areas suitable for riparian vegetation (Strom *et al.* 2012).

The fifth research question was 'What role do invasive species have related to seedling survival during summer droughts?' Exotic species react to changes in environmental conditions, like drought. Riparian ecosystems are especially susceptible to these invasive species and may in turn function as corridors for further spread of invaders. In North America the impact of invasion is already clear and the European lowland rivers are also expected to be highly susceptible.

For management riparian ecosystems might prove to be flexible because vegetation shifts according to the elevation gradient might happen. Species which are pushed out of their original habitats might be able to survive as invasive species in higher elevated areas along the longitudinal gradient. This would only shift the problem upwards. A complete management approach should thus incorporate low and higher elevated areas (Lite *et al.* 2005).

Conclusion

Restoration and management of riparian vegetation prove to be of major importance in the modern projections on climate. Together with the effects of human practices riparian vegetation might in the future undergo shifts in plant communities. This will be driven by the differences in coping mechanisms and strongly visible for and affected by seedling survival. The specific effects on vegetation are not easy to predict and will differ between tree and herbaceous communities and vary along the stream riparian gradient. Invasive species will also be even more present in these future vegetation types. In the end restoration of ecosystems -riparian or not- should be based not solely on a historical context but especially on future projections of climate and human activity.

References

1. G. P. Malanson, *Riparian landscapes* (Cambridge Univ. Press, Cambridge, 1993).
2. D. M. Richardson *et al.*, "Riparian vegetation: degradation, alien plant invasions, and restoration prospects," *Divers. Distrib.* **13**(2007).
3. H. Decamps, "River Margins and Environmental-Change," *Ecol. Appl.* **3**(1993).
4. R. J. Naiman, H. Decamps, "The ecology of interfaces: Riparian zones," *Annu. Rev. Ecol. Syst.* **28**(1997).
5. L. G. Perry, D. C. Andersen, L. V. Reynolds, S. M. Nelson, P. B. Shafroth, "Vulnerability of riparian ecosystems to elevated CO₂ and climate change in arid and semiarid western North America," *Global Change Biol.* **18**(2012).
6. G. Yu, H. Q. Huang, Z. Wang, G. Brierley, K. Zhang, "Rehabilitation of a debris-flow prone mountain stream in southwestern China - Strategies, effects and implications," *Journal of Hydrology* **414**(2012).
7. R. J. Naiman, H. Decamps, M. Pollock, "The Role of Riparian Corridors in Maintaining Regional Biodiversity," *Ecol. Appl.* **3**(1993).
8. REFRESH, "EU FP7 – REFRESH Project Number 24412, Adaptive strategies to Mitigate the Impacts of Climate Change on European Freshwater Ecosystems," *SEVENTH FRAMEWORK PROGRAMME, THEME 6: Environment (Including Climate Change)*(November 2011).
9. L. W. G. Higler, "The Riparian Community of North-West European Lowland Streams," *Freshwat. Biol.* **29**(1993).
10. R. L. Brown, R. K. Peet, "Diversity and invasibility of southern Appalachian plant communities," *Ecology* **84**(2003).
11. D. J. Cooper, D. C. Andersen, R. A. Chimner, "Multiple pathways for woody plant establishment on floodplains at local to regional scales," *J. Ecol.* **91**(2003).
12. S. B. Rood *et al.*, "Declining summer flows of Rocky Mountain rivers: Changing seasonal hydrology and probable impacts on floodplain forests," *Journal of Hydrology* **349**(2008).
13. L. Strom, R. Jansson, C. Nilsson, "Projected changes in plant species richness and extent of riparian vegetation belts as a result of climate-driven hydrological change along the Vindel River in Sweden," *Freshwat. Biol.* **57**(2012).
14. M. J. Salinas, J. J. Casas, "Riparian vegetation of two semi-arid Mediterranean rivers: Basin-scale responses of woody and herbaceous plants to environmental gradients," *Wetlands* **27**, 831 (2007).
15. D. A. Lytle, N. L. Poff, "Adaptation to natural flow regimes," *Trends in Ecology & Evolution* **19**(2004).

16. Regional Climate Projections. in *Climate Change 2007: The Physical Science Basis*. (Cambridge University Press, New York, 2007).
17. "www.refresh.ucl.ac.uk".
18. M. D. Dixon, M. G. Turner, "Simulated recruitment of riparian trees and shrubs under natural and regulated flow regimes on the Wisconsin River, USA," *River Research and Applications* **22**(2006).
19. R. Kussner, "Mortality patterns of *Quercus*, *Tilia*, and *Fraxinus* germinants in a floodplain forest on the river Elbe, Germany," *For. Ecol. Manage.* **173**, PII S0378-1127(01)00818-0 (2003).
20. A. W. McDonald, "Succession during the re-creation of a flood-meadow 1985-1999," *Applied Vegetation Science* **4**(2001).
21. J. C. Stella, J. J. Battles, "How do riparian woody seedlings survive seasonal drought?" *Oecologia* **164**(2010).
22. S. G. Pallardy, in *Physiology of woody plants* (Academic press, Elsevier, <http://www.scribd.com/doc/5015386/Physiology-of-woody-plants>, ed. 3, 2008), pp. 355-356-364.
23. P. J. Kramer, J. S. Boyer, *Water relations of plants and soils* (Academic press, , 1995).
24. T. T. Kozlowski, S. G. Pallardy, "Acclimation and adaptive responses of woody plants to environmental stresses," *Bot. Rev.* **68**(2002).
25. N. M. Kleczewski, D. A. Herms, P. Bonello, "Nutrient and water availability alter belowground patterns of biomass allocation, carbon partitioning, and ectomycorrhizal abundance in *Betula nigra*," *Trees-Structure and Function* **26**(2012).
26. J. M. Elcan, S. R. Pezeshki, "Effects of flooding on susceptibility of *Taxodium distichum* L. seedlings to drought," *Photosynthetica* **40**(2002).
27. I. v. Splunder, L. A. C. J. Voesenek, H. Coops, X. J. A. DeVries, C. W. P. M. Blom, "Morphological responses of seedlings of four species of Salicaceae to drought," *Canadian Journal of Botany-Revue Canadienne De Botanique* **74**(1996).
28. D. A. Lytle, D. M. Merritt, "Hydrologic regimes and riparian forests: A structured population model for cottonwood," *Ecology* **85**(2004).
29. N. M. Amlin, S. B. Rood, "Comparative tolerances of riparian willows and cottonwoods to water-table decline," *Wetlands* **22**(2002).
30. J. C. Stella, J. J. Battles, J. R. McBride, B. K. Orr, "Riparian Seedling Mortality from Simulated Water Table Recession, and the Design of Sustainable Flow Regimes on Regulated Rivers," *Restor. Ecol.* **18**(2010).

31. S. J. Lite, K. J. Bagstad, J. C. Stromberg, "Riparian plant species richness along lateral and longitudinal gradients of water stress and flood disturbance, San Pedro River, Arizona, USA," *J. Arid Environ.* **63**(2005).
32. C. L. Sagers, J. Lyon, "Gradient analysis in a riparian landscape: contrasts among forest layers," *For. Ecol. Manage.* **96**(1997).
33. W. F. Nichols, K. T. Killingbeck, P. V. August, "The influence of geomorphological heterogeneity on biodiversity II. A landscape perspective," *Conserv. Biol.* **12**(1998).
34. S. D. Tiegs, J. F. O'Leary, M. M. Pohl, C. L. Munill, "Flood disturbance and riparian species diversity on the Colorado River Delta," *Biodivers. Conserv.* **14**(2005).
35. J. C. Stromberg, V. B. Beauchamp, M. D. Dixon, S. J. Lite, C. Paradzick, "Importance of low-flow and high-flow characteristics to restoration of riparian vegetation along rivers in and south-western United States," *Freshwat. Biol.* **52**(2007).
36. A. R. Gitlin *et al.*, "Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought," *Conserv. Biol.* **20**(2006).
37. W. C. Johnson, "Woodland Expansion in the Platte River, Nebraska - Patterns and Causes," *Ecol. Monogr.* **64**(1994).
38. E. Gonzalez, F. Antonio Comin, E. Muller, "Seed dispersal, germination and early seedling establishment of *Populus alba* L. under simulated water table declines in different substrates," *Trees-Structure and Function* **24**(2010).
39. A. P. Grootjans, J. P. Bakker, A. J. M. Jansen, R. H. Kemmers, "Restoration of brook valley meadows in the Netherlands," *Hydrobiologia* **478**, 149 (2002).
40. M. M. Pollock, R. J. Naiman, T. A. Hanley, "Plant species richness in riparian wetlands - A test of biodiversity theory," *Ecology* **79**(1998).
41. D. J. Cooper, D. M. Merritt, D. C. Andersen, R. A. Chimner, "Factors controlling the establishment of Fremont cottonwood seedlings on the upper Green River, USA," *Regulated Rivers-Research & Management* **15**(1999).
42. H. N. Siebel, I. M. Bouwma, "The occurrence of herbs and woody juveniles in a hardwood floodplain forest in relation to flooding and light," *Journal of Vegetation Science* **9**(1998).
43. J. Lyon, C. L. Sagers, "Structure of herbaceous plant assemblages in a forested riparian landscape," *Plant Ecol.* **138**(1998).
44. F. Nakamura, T. Yajima, S. Kikuchi, "Structure and composition of riparian forests with special reference to geomorphic site conditions along the Tokachi River, northern Japan," *Plant Ecol.* **133**(1997).
45. W. Erskine, A. Chalmers, A. Keene, M. Cheetham, R. Bush, "Role of a rheophyte in bench development on a sand-bed river in southeast Australia," *Earth Surf. Process. Landforms* **34**(2009).

46. R. L. Eckstein, T. W. Donath, "Interactions between litter and water availability affect seedling emergence in four familial pairs of floodplain species," *J. Ecol.* **93**(2005).
47. C. E. Aslan, M. Rejmanek, R. Klinger, "Combining efficient methods to detect spread of woody invaders in urban-rural matrix landscapes: an exploration using two species of Oleaceae," *J. Appl. Ecol.* **49**, 331 (2012).
48. M. Rejmánek, D. M. Richardson, P. Pyšek, in *Vegetation Ecology*, E. van der Maarel, Ed. (Blackwell, Oxford, 2005), pp. 332-333-355.
49. B. A. Bradley, D. M. Blumenthal, D. S. Wilcove, L. H. Ziska, "Predicting plant invasions in an era of global change," *Trends in Ecology & Evolution* **25**(2010).
50. E. Tabacchi, A. M. PlantyTabacchi, M. J. Salinas, H. Decamps, "Landscape structure and diversity in riparian plant communities: A longitudinal comparative study," *Regulated Rivers-Research & Management* **12**(1996).
51. J. M. Friedman *et al.*, "Dominance of non-native riparian trees in western USA," *Biol. Invasions* **7**(2005).
52. L. V. Reynolds, D. J. Cooper, "Environmental tolerance of an invasive riparian tree and its potential for continued spread in the southwestern US," *Journal of Vegetation Science* **21**(2010).
53. T. T. Kozłowski, "Physiological-ecological impacts of flooding on riparian forest ecosystems," *Wetlands* **22**(2002).
54. K. Kramer, S. J. Vreugdenhil, D. C. van der Werf, "Effects of flooding on the recruitment, damage and mortality of riparian tree species: A field and simulation study on the Rhine floodplain," *For. Ecol. Manage.* **255**, 3893 (2008).