FunDivEUROPE

Functional significance of forest biodiversity in Europe

Project number: 265171

Large scale integrating, collaborative project

SEVENTH FRAMEWORK PROGRAMME

Environment (including Climate Change)

Deliverable D3.7
Water Balance: Effects of tree species and functional diversity on the water balance of trees and forests

Due date of deliverable: M36

Actual submission date: M43

Start date of the project: October 1st, 2010 Duration: 48 months

Organisation name of lead contractor: ALU-FR

Revision: V1.0

Project co-funded by the European Commission within the Seventh Framework Programme (2007-2013)	
Dissemination Level	
PU Public	X
PP Restricted to other programme participants (including the Commission Services)	
RE Restricted to a group specified by the consortium (including the Commission Services)	
CO Confidential, only for members of the consortium (including the Commission Services)	

Water Balance: Effects of tree species and functional diversity on the water balance of trees and forests

V1.0

Date: 20/04/14

Abstract:

Forest ecosystems are affected by drivers of global changes, such as climate warming. Drought alters forest ecosystems with profound consequences for the functions and services they supply. On the other hand, tree diversity has beneficial impacts on ecosystem resistance and resilience to environmental stresses and provides compelling management options for conserving and adapting forests to future climatic conditions.

Along a North-South gradient in Europe within the exploratory and the experimental platforms of FunDivEUROPE, we show that tree diversity affects the water balance of trees and forest stands in various ways. We assessed the response of stand-level water-use efficiency (WUE_{plot}), which describes the time-integrated compromise between ecosystem carbon uptake and water loss, across the experimental platforms (and thus for the main forest types in Europe) under contrasting soil water conditions. Our results showed that most studied forests exhibited higher WUE_{plot} in years with highly limiting soil water conditions compared to wetter years, but the increase varied according to tree species diversity. For the majority of forest types in Europe, we interpret that higher biodiversity alleviates the negative effects of drought for the water balance of forest ecosystems. One considerable exception was however found: in the boreal forests, WUE_{plot} was higher in highly diverse stands in dry years, indicating increased drought stress as compared to pure stands. Lower drought exposure in most forest types in Europe could be the consequence of underlying complementary effects of biodiversity while higher drought exposure in northern forests could derive from the dominance of competition mechanisms among species. When assessing the direct interaction between different species we observed, in addition to such general stand-level trends, that particular tree species also compete or facilitate each other for water acquisition in dry Mediterranean regions and that drought alleviation will thus be modified depending on species identities. Furthermore, by estimating the soil water uptake depth in the experimental platform, we observed evidences for a below-ground complementarity for water use among different functional groups demonstrating the importance of functional diversity rather than species richness *per se* on ecosystem functions related to carbon and water relations.

Our results overall highlight the complexity and spatial variability of the relationship between ecosystem processes and tree species diversity at the continental scale. Both should be taken into account in global vegetation models that aim to predict the effects of future climate changes on carbon and water cycles. The results are also of major importance for forestry as the beneficial biodiversity effect on drought resistance of forest ecosystems might not hold true for the boreal region and for the mixture of particular species in other growth regions.

Authors: ARTHUR GESSLER, DAMIEN BONAL, ANDRÉ GRANIER, CHARLOTTE GROSSIORD

Version: V1.0

Validation process: Document prepared by ALU-FR and INRA in cooperation with the project Coordinator and workpackage leaders. They constitute the Executive Committee.

Update process: This document will not require further updates.

Table of Contents

1 The influence of tree species mixture on ecosystem-level carbon and water balance in young plantations

1.1 Boreal plantation

Context

Throughout the world, huge areas have been occupied by monospecific tree plantations in order to fulfil the increasing demand for industrial wood products. The use of mixed-species plantations has been advocated as a potential compromise between maintaining high-volume wood production and conserving other ecosystem services. Yet little is known about the impact of tree species mixture on species- and ecosystem-level carbon accumulation and water use in mixed plantations.

Material and Methods

We combined data on above-ground biomass, xylem sap flux density, and the carbon and oxygen isotope composition of leaves and needles in the FunDivEUROPE, boreal, experimental plantation (Satakunta plantation, Finland) to test whether different levels of species mixture would impact tree- and plot-level biomass production, transpiration (sap flux density) and water use efficiency (the ratio of carbon assimilation over transpiration). Data were recorded in 22 20-x-20-m plots (7 for transpiration) randomly allocated to either monocultures or to two-, three-, and five-species mixtures of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), Silver birch (*Betula pendula*), Common alder (*Alnus glutinosa*) and Siberian larch (*Larix sibirica*).

Results and Discussion

At tree level, for a given species, we found significant differences among mixtures in transpiration and water use efficiency, though species mixture had no impact on above-ground biomass. At plot level, a large variability in functioning among mixtures was observed, but increasing the number of species in the mixture did not enhance productivity, transpiration or water use efficiency. The presence in mixtures of a high performing species like birch brought about changes in the canopy structure which in turn may have led to changes in micro-environmental conditions. Such changes could have contributed to explain differences in transpiration and water use efficiency among mixtures.

We concluded that mixing locally-adapted species under non-limiting soil water conditions did not provide any benefit for ecosystem-level carbon accumulation and water use at this young ontogenic stage, but our study does not preclude that some benefits might arise at older stages.

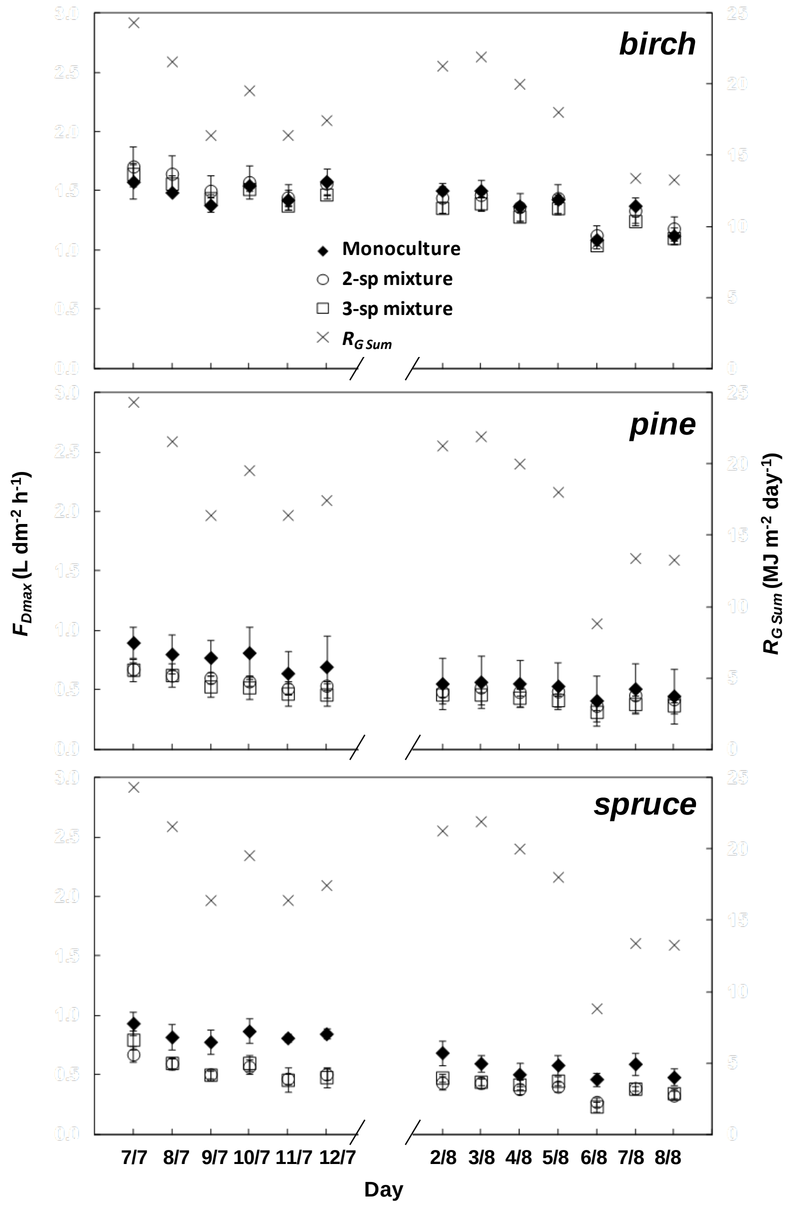
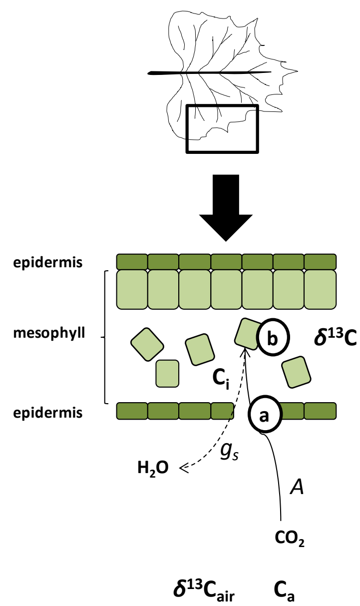


Figure 1: Mean of daily maximum sap flux density (F_{Dmax}, L dm^{-2} h^{-1}) of the measured trees by species (birch, pine and spruce) and for each level of mixture (monoculture, 2-sp mixture, 3-sp mixture) and daily sum of global radiation ($R_{G\,Sum}$, MJ m^{-2} day^{-1}) during the two measurement periods (7-12 July, 2011 and 2-8 August, 2011). Vertical bars are standard errors of the mean for n = 3-4 trees.

NOTE: Schematic representation of the processes involved in leaf carbon isotope discrimination during photosynthesis. The carbon isotope composition ($\delta^{13}C$) of total leaf organic matter is determined by the carbon isotope composition of CO_2 in the air ($\delta^{13}C_{air}$) and the CO_2 concentration in the air (C_a) and in the leaf intercellular spaces (C_i). Discrimination processes against $^{13}CO_2$ occur during photosynthetic CO_2 assimilation (A) when CO_2 passes through the stomata (g_s) from the outside air (fractionation factor a) and during the carboxylation process by the Rubisco enzyme inside the chloroplasts (fractionation factor b). The plain arrow represents A and the dotted arrow represents the transpiration flux. Leaf carbon isotope discrimination is negatively correlated with intrinsic water use efficiency (WUE_{int}), which is defined as the ratio of A over g_s.



1.2 Temperate plantation

Influence of tree diversity on ecosystem carbon and water balance

Context

A positive effect of species mixture on forest ecosystem productivity (Paquette & Messier 2011; Zhang et al. 2012) and transpiration (Forrester et al. 2010; Kunert et al. 2012) has previously been reported. Promoting a mixture of tree species to enhance the ratio of ecosystem-level productivity to transpiration (i.e. high water use efficiency, WUE) has been advocated for sustainable forest management (McCarthy et al. 2011), of particular importance in a context of climate change. To further investigate this relationship, we studied the impact of tree species mixtures on ecosystem-level water use efficiency (WUE_{plot}) in the BIOTREE, FunDivEUROPE, temperate, experimental plantation (Kaltenborn plantation, Germany).

This plantation is located on acidic sandy soils and includes four species: Fagus sylvatica (L.), Quercus petraea (Matt.), Picea abies (L.) Karst. and Pseudotsuga menziesii (Mirb.) Franco. In summer 2011, we sampled leaves and needles from four trees per species and per plot in monocultures (n = four plots), two-species mixtures (n = six), three-species mixtures (n = four) and four-species mixtures (n = one). In each plot, we only took samples from trees at the corners of the patches. The samples were oven-dried at 60°C for 48 hours, then finely ground. $\delta^{13}C$ analysis was carried out at the Stable Isotope Facility of UC Davis, USA. The $\delta^{13}C$ (‰) values are expressed relative to the Vienna Pee Dee Belemnite standard.

We found large differences in net biodiversity effect, complementarity effect, and selection effect among plots, with either positive or negative values. Positive or negative values confirmed that in this plantation, interactions among species influence the carbon and water balance at ecosystem-level (WUE_{plot}). Our findings point toward lower WUE_{plot} when several different species coexist. This result contrasts with previous patterns of enhanced water use efficiency found in species mixtures (Forrester et al. 2010; Kunert et al. 2012). The absence of a significant selection effect on WUE_{plot} indicates that the overall negative net biodiversity effect observed in the 2-species mixtures was primarily driven by a complementarity effect of resource use. Our interpretation is that the species coexisting in the mixed plots are in direct competition for the same resources because they still share the same ecological niche at the early establishment stage (7 years after planting, at the time of our measurements). This competition most likely caused a decrease in the ratio between carbon acquisition and transpiration at the ecosystem level in the two-species mixtures. As no overshading was observed, the competition among species is presumably occurring belowground. This assumption is consistent with the strong competition among fine roots observed by Lei et al. (2012) in this plantation.

In this young mixed temperate plantation, competition rather than facilitative effects were the substantial drivers of plot water use efficiency. As the plantation ages and taller trees with broader root systems begin to compete for light and soil resources, the facilitative effects might arise. It will thus be interesting to follow the changes in the relative importance of the two components of net biodiversity effects for a multitude of ecological processes and functions.

<u>Influence of tree diversity on soil water extraction depth</u>

Context

Interactions among tree species in forests can be beneficial to ecosystem functions and services related to the carbon and water cycles. However, we need to enhance our knowledge on below- and above-ground mechanisms leading to these positive effects. We tested whether stratification in soil water uptake depth occurred among tree species in a 10-year-old temperate mixed plantation.

Material and Methods

We selected dominant and co-dominant trees of European beech, Sessile oak, Douglas fir and Norway spruce in neighbourhoods with varying species diversity, competition intensity and where different plant functional types were present. We applied a deuterium labelling approach that consisted in spraying highly labelled water to the superficial soil layers in order to create a strong vertical gradient of the deuterium isotope composition in the soil water. The deuterium isotope composition of both the xylem sap and the soil water was measured before labelling, and then again three days after the labelling, to be able to estimate the soil water uptake depth through a simple modelling approach. We also sampled leaves and needles from selected trees to measure their carbon isotope composition (a proxy for water use efficiency) and total nitrogen content.

Results and Discussion

At the end of the summer, we found differences in the soil water uptake depth among plant functional types but not within types: on average, coniferous species extracted water from deeper horizons than did broadleaved species. Neither species diversity nor competition intensity had any influence on soil water uptake depth, foliar water use efficiency or nitrogen content in the species studied. However, when interacting with an increasing proportion of conifers, beech extracted water from progressively deeper soil layers.

We conclude that complementarity for water uptake could occur in this young plantation because of the inherent differences among functional groups (conifers and broadleaves). Furthermore, the water uptake depth of beech was already influenced at this young development stage by interspecific interactions whereas no clear niche differentiation occurred for the other species. This finding does not preclude that plasticity-mediated responses to species interactions could increase as the plantation ages, leading to the coexistence of these in adult forest stands.

2 Tree species mixture and ecosystem functioning across mature European forests under contrasted soil water conditions

2.1 Ecosystem Transpiration

Contrasting influence of local-neighbourhood diversity on transpiration of Mediterranean tree species during a summer drought

Context

Climate models forecast a decrease in annual mean precipitation in large areas in the northern hemisphere in the future, accompanied by an increase in air temperatures (IPCC 2013). As a result, the evaporative demand over these regions will increase and summer droughts will not only become more frequent but will also increase in severity and duration. These climatic changes will drastically affect those European regions located at the Southern part of Europe, i.e., the Mediterranean one. Such expected conditions may lead to gradually increasing tree mortality rates and rapid forest die-off events during the next century (Allen et al. 2010).

Since the early 19th century, ecologists have been trying to understand how ecosystem processes are influenced by community assembly and species interactions. Resource use complementarity among co-occurring species usually leads to a more effective use of available resources and may be a driver of higher productivity in species-diverse ecosystems (Loreau et al. 2001). Higher tree species diversity has been shown to increase transpiration in dry-climate mixed forests (Forrester et al. 2010; Kunert et al. 2012). According to the "stress-gradient" hypothesis (Bertness & Callaway 1994), the intensity and relative contribution of beneficial diversity effects on ecosystem functioning increases as climatic conditions become harsher. A shift between competition (negative interactions) and complementarity (positive ones) in resource use can therefore be expected when resources become limiting. Consequently, one would expect that, in ecosystems frequently subjected to extreme soil water conditions, like Mediterranean forests, higher tree species diversity is likely to have a beneficial effect on water availability and/or accessibility. We addressed here the question whether species diversity in the local neighbourhood of Mediterranean pine and oak species influence their transpiration response to drought?

Material and Methods

We measured the sap flux density of three tree species (*Quercus faginea*, *Pinus nigra* and *Pinus sylvestris*) along a gradient of neighbourhood species diversity during a summer drought in plots selected within the exploratory platform of FunDivEUROPE set up in central Spain (Alto Tajo National park, Mediterranean mixed forest). Measurements of foliar carbon isotopic composition ($\delta^{13}C$, a proxy for water-use efficiency) were also conducted on the same trees.

Results and Discussion

The decline in transpiration during drought was the greatest for *P. sylvestris* and the least pronounced for *Q. faginea*. For *P. nigra*, the decrease in transpiration as the drought progressed was not influenced by neighbourhood species diversity. In contrast, the decrease for *P. sylvestris* was higher, and the decrease for *Q. faginea* was lower, when diversity was increased. There was a negative relationship between $\delta^{13}C$ and neighbourhood diversity for *Q. faginea*, whereas there was no effect for the two conifer species.

We thus showed that community assembly of coexisting species with differing functional characteristics can influence water availability and water use in Mediterranean forest ecosystems during a summer drought. We assume that root stratification in the more diverse neighbourhoods was beneficial for the deepest-rooted species (*Q. faginea*) because competition for soil water was attenuated compared to pure *Q. faginea* neighbourhoods. The shallowest-rooted species (*P. sylvestris*) was disadvantaged by competition for water resources in the more diverse neighbourhoods, most likely as a result of more rapid water depletion in the superficial soil layers. Finally, we have shown that more diverse forest stands do not seem to be systematically beneficial in terms of soil water availability and water use for all the interacting species.

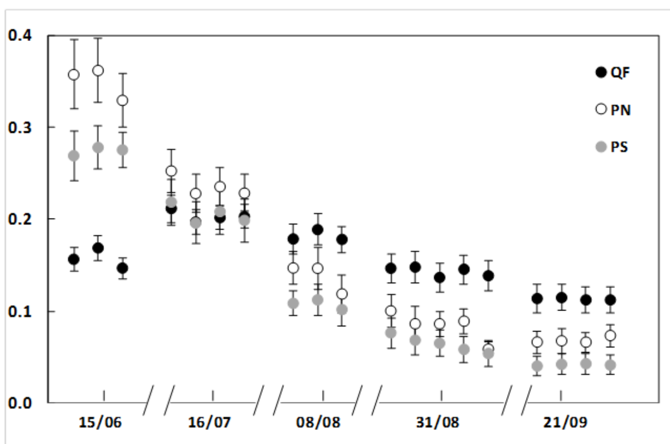


Figure 2. Seasonal pattern of sap flux density. Mean daily sap flux density (F_{Dmean}, L dm^{-2} h^{-1}) for *Quercus faginea* (QF), *Pinus nigra* (PN) and *Pinus sylvestris* (PS) for each day. Measurements were taken throughout the summer (from 14 Jun 2013 to 22 Sept 2013). Vertical bars represent the standard error of the mean for each species and each day.

Interspecific competition influences the response of oak transpiration to increasing drought stress in a mixed Mediterranean forest

Context

Increasingly severe droughts are expected to negatively impact forest functioning in the future, especially in the Mediterranean region. Favouring mixed species stands has been advocated as a compromise between wood production and biodiversity conservation, but whether such management practices would allow forest ecosystems to acclimate to future climate conditions remains to be addressed.

Material and Methods

We tested whether the transpiration of *Quercus cerris* (Qc) and *Quercus petraea* (Qp) during droughts differ when they grow in pure or mixed forests. We measured sap flux density (F_D) and leaf carbon isotope composition ($\delta^{13}C$), as a proxy for intrinsic water use efficiency (WUE_{int}), in pure and mixed Qc and/or Qp forest plots in Italy during the summer 2012.

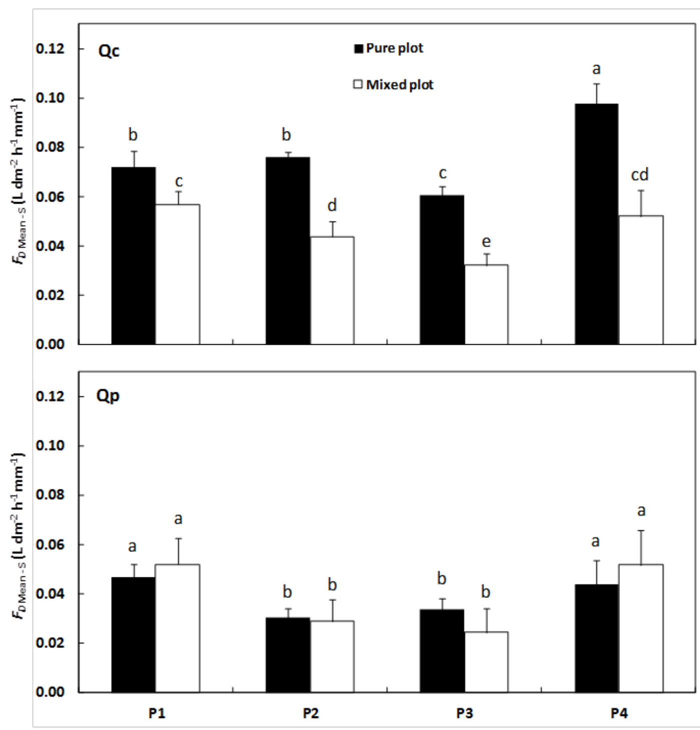


Figure 3. Mean of the daily mean sap flux densities standardized for potential evapotranspiration ($F_{D\ Mean-S}$, L dm^{-2} h^{-1} mm^{-1}) for each measurement period and for each study plot for turkey and sessile oak (QC and Qp respectively). Letters denote significant differences between plots and periods revealed by contrast tests for each species after mixed effect models had been applied.

Results and Discussion

Qc and Qp showed a drop in F_D of 41% and 52% respectively during the summer drought independently of the mixtures, but with different seasonal trends. Qp transpiration response to soil drought did not differ between pure and mixed plots. In contrast, Qc transpiration was reduced by 56% in mixed plots at the maximum of the drought and only by 31% in the pure plot. Furthermore, we observed higher WUE_{int} for Qc in the mixed plot and no change for Qp, supporting the higher water stress intensity in the mixed plot for Qc.

Our study illustrated the negative impact of Qp on Qc when these species compete for water resources. We suggest that managing for mixed stands in the Mediterranean region might, in some cases, increase the detrimental effect of drought on species functioning.

2.2 Ecosystem carbon and water balance

Context

Biodiversity can control ecosystem functioning through mechanistic processes directly under the influence of species interactions. Competition among species arising from niche overlap commonly leads to lower ecosystem performance. Conversely, complementarity for resources through niche partitioning or facilitation induces higher ecosystem performance since resources are better shared among interacting species and are thus potentially more available (Loreau and Hector 2001). According to the stress-gradient hypothesis, the intensity and relative contribution of these mechanisms are thought to be determined by environmental conditions with a shift from negative (competition) to positive (complementarity) effects of biodiversity on ecosystem functioning as environmental conditions become harsher (Bertness and Callaway 1994). Thus, more diverse ecosystems might be better adapted and/or more resilient when future unequivocal worldwide warming leads to more frequent and severe drought episodes in large areas of the world. More intense and frequent droughts will affect the carbon and water cycles of the terrestrial biosphere globally, which in turn will have drastic consequences for the maintenance of many vital ecosystem functions.

Forests, locally controlled by environmental conditions, play an important role in the global carbon and water balance as they release into (through respiration) and assimilate from (through photosynthesis) the atmosphere huge amounts of CO2 while losing water vapour through transpiration. When soil water supply is diminished, stomatal regulation adjusts leaf gas exchange levels in order to optimize the ratio of carbon uptake to water loss, i.e. water-use efficiency (Farquhar et al. 1989). Thus, during drought, an increase in water use efficiency is observed. However, plants differ strongly in the way they optimize the trade-off between carbon gain and water loss (Field et al. 1983). Consequently, one can expect that forest ecosystems with different species composition differ in the way these fluxes are controlled and in their response to environmental changes. If the pool of water resources available to coexisting species is increased or at least better shared among species in species-diverse ecosystems as compared to pure ones, one can hypothesize that ecosystem-scale stomatal down-regulation will be slower. Under this assumption, in species-diverse ecosystems, coexisting species will be able to use water resources for a longer period than in pure ecosystems as drought progresses. It will result in a lower decrease in ecosystem-scale transpiration in species-diverse ecosystems and therefore in a less important increase in ecosystem-level water-use efficiency.

Material and Methods

We analyzed the influence of drought on the relationship between tree species diversity and stand-level water-use efficiency (WUE_{plot}) using the carbon isotopic signature of tree rings, in the six exploratory platforms set-up within the FunDivEUROPE project. Using a water balance modelling approach, we examined the influence of drought by comparing two years with highly contrasting water availability (dry vs. wet year) between 1997 and 2010. Higher WUE_{plot} values in species-diverse stands as compared to pure ones during dry years could mainly be the consequence of less water available to the roots, because of interspecific competition in the species-diverse stands. Conversely, lower WUE_{plot} values in species-diverse stands would mainly point to higher water accessibility in species-diverse stands that could stem from a complementary water use strategy among the interacting species. In each stand (N = 300 in total), we extracted wood cores at breast height on a sub-sample of dominant and/or co-dominant trees from each species during the summers 2012 and 2013. From each core sample, we extracted the late wood of a year with high water-stress and a year with low water stress at each site. The late wood samples for each species in each stand were pooled and ground before being analyzed with a mass-spectrometer for carbon isotope composition. Stand-level carbon isotope composition was then calculated and converted into stand-level water use efficiency (WUE_{plot})

Results and Discussion

Under wet conditions, no significant effect of tree diversity on WUE_{plot} was observed in four out of six forest types (Fig. 4). For each of these four types, the large variations in ecosystem-level carbon and water balance under highly favourable soil water conditions thus cannot be explained by above and belowground interactions among species. However, for the two other types, species-diverse stands have a lower WUE_{plot} than pure stands during the wet year. Limiting soil water conditions cannot be evoked to explain these relationships. Other local stand conditions arising from species coexistence, which could not be controlled for when selecting the study stands, might account for the variability in WUE_{plot}. Indeed, although we mainly selected forest stands with single-layered canopies, differences in canopy structure between pure and species-diverse stands could have influenced variations in WUE_{plot} by changing radiation interception. Below-ground competition among tree species for nutrients (e.g. nitrogen, phosphorus) that affect carbon assimilation and thus WUE_{plot} may also have contributed to these effects.

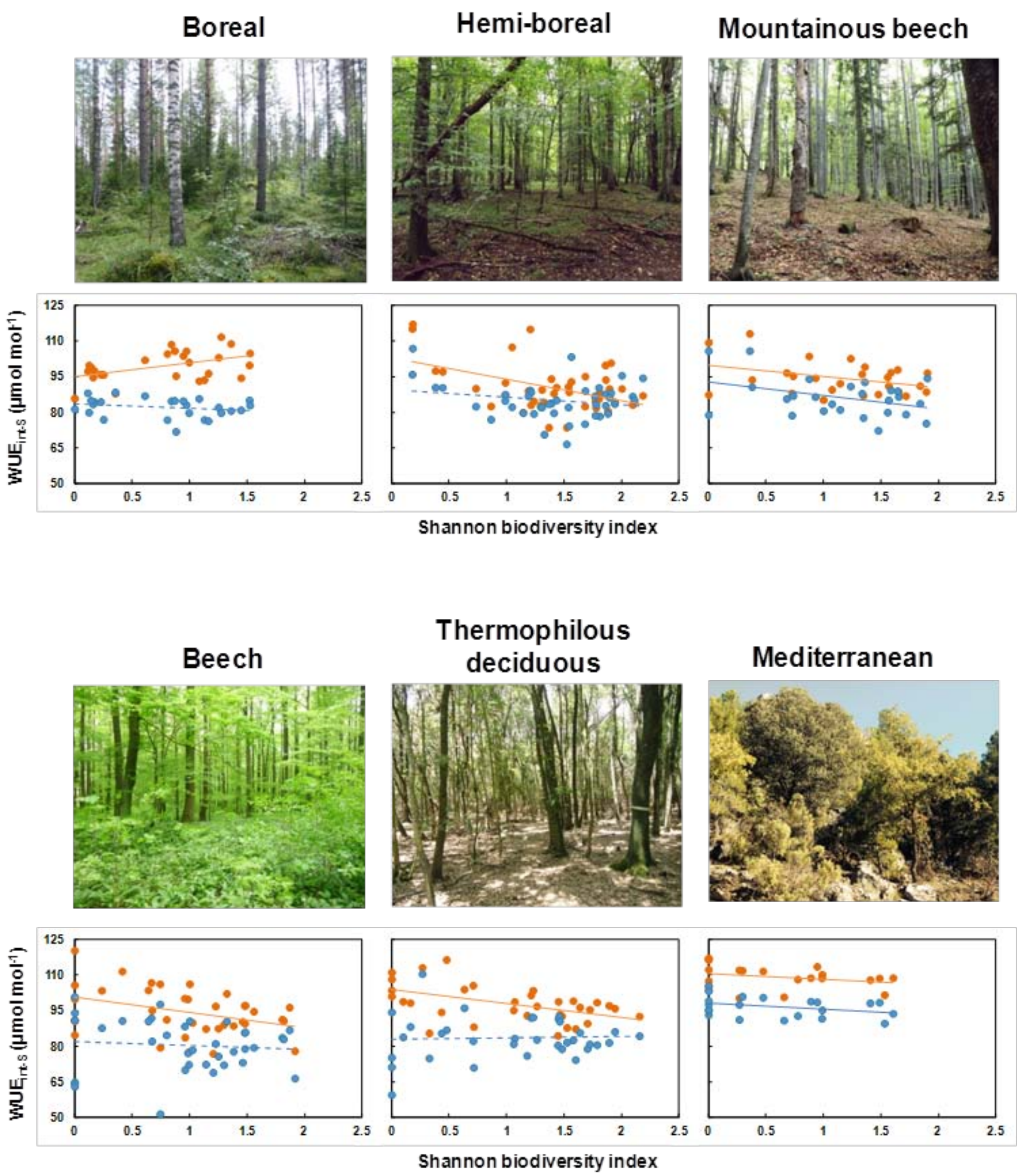


Figure 4. Relationship between stand-level intrinsic water-use efficiency (WUE_{plot}) and tree species diversity during one dry and one wet year in the 1997-2010 period for each forest type studied. Stand-level intrinsic water-use efficiency for each selected year (dry = orange, wet = blue) is shown as a function of the Shannon biodiversity index for each forest type studied. The Shannon biodiversity index expresses tree diversity and gives information not only on species richness but also on species evenness in the

community. This index ranges from zero for pure stands to the logarithm in base two of the total basal area of the species in the stand. Dashed lines show the fitted relationship between the Shannon biodiversity index and the stand-level water-use efficiency for a given year when the regression was not significant. Solid lines indicate statistically significant relationships.

Selecting a year with strong drought conditions further improved our understanding of the influence of climatic conditions on the role of species interactions in ecosystem carbon and water balance. We can affirm that species diversity effects on WUE_{plot} were mainly driven by water availability. Under dry soil water conditions, five out of the six forest types showed a negative relationship between species diversity and WUE_{plot} (Fig. 4). These relationships imply that water availability was higher in species-diverse stands than in pure ones during the dry year. Coexisting plants with different functional characteristics can better share a given amount of soil water and/or can extend their rooting system deeper towards wetter soil layers as they occupy different ecological niches in space and over time. Water resources available for the coexisting species are thus higher and can sustain tree functioning for a longer period during the drought. As a consequence, trees can invest the assimilated carbon into productivity for longer periods, which is consistent with the commonly observed over-yielding in species-diverse ecosystems. Results for the five forest types confirm such complementarity mechanisms of water use in species-diverse stands under dry conditions. In contrast, species-diverse stands in the boreal forest type had apparently lower soil water availability than pure stands as shown by the higher WUE_{plot} in the more diverse stands (Fig. 4). In these forests, we suspect that niche overlap among the interacting species at belowground level induces longer and more severe drought exposure in the species-diverse stands.

Overall, our study highlighted the complexity and spatial variability at a continental scale of the relations between tree species diversity and ecosystem processes related to the carbon and water balance. We conclude that, at least for non-boreal forest ecosystems, managing as pure stands reduces the chance of alleviating the water stress to which trees are subjected during dry years. Our findings should be taken into account when biodiversity conservation plans and forest management practices are prepared, particularly in the context of optimizing the acclimation of forest ecosystems to future climatic conditions.