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Finders keepers, losers weepers – drought as a modifier of competition between European beech and Norway spruce –

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Mixed stands of European beech (Fagus sylvatica L.) and Norway spruce (Picea abies (L.) Karst.) frequently reflect over-yielding, when compared to respective monospecific stands. Over-yielding is attributed to enhanced resource uptake efficiency through niche complementarity alleviating species competition. Under climate change, however, with severe and frequent summer drought, water limitation may become crucial in modifying the competitive interaction between neighboring beech and spruce trees. In view of the demands by silvicultural practice, basic knowledge from experimental field work about competitive versus facilitative interaction in maturing mixed beech-spruce forests is scarce. To this end, we investigate species-specific drought response including underlying mechanisms of species interaction in a maturing group-wise mixed beech-spruce forest, amongst 60 and 53 adult trees of beech and spruce, respectively (spruce 65 $\pm$ 2, beech 85 $\pm$ 4 years old). Severe and repeated experimental drought is being induced over several years through a stand-scale approach of rain throughfall exclusion (Kranzberg Forest Roof Experiment, KROOF). The experimental design comprises 6 roofed (E, automated, closing only during rain) and 6 control (C) plots with a total area of almost 1800 square meters.
In 2015 minimum predawn potentials of -2.16 MPa and -2.26 MPa were reached in E for beech and spruce respectively. At the leaf level, spruce displayed high drought susceptibility reflected by a distinct decrease in both stomatal conductance and net CO_2 uptake rate by more than 80% each, suggesting isohydric response. Beech rather displayed anisohydry indicated by less pronounced yet significant reduction of stomatal conductance and net CO_2 uptake rate by more than 55% and 45%, respectively. Under the C regime, a negative species interaction effect on stomatal conductance was found in beech, contrasting with a positive effect in spruce. However, drought reversed the effect of species interaction on stomatal conductance, suggesting competition release in beech and by contrast, a shift from facilitation to competition in spruce, if both species grew in mixture. Based on fine root distribution and soil moisture assessments, we interpret this reversed interaction effect as a consequence of different spatio-temporal patterns of soil water use in combination with enhanced root stratification between neighboring beech and spruce trees. Under humid climate conditions (i.e. with only short drought) the rather conservative strategy of spruce (isohydric response, root dominance in upper soil) appears to be advantageous, facilitating pre-emption of nutrients from litter mineralization and water from precipitation. During extended periods of drought, however, shallow rooting and early stomatal closure limits the accessibility to deep soil water and, hence, photosynthetic carbon assimilation, eventually constraining competitiveness of spruce. Beech rather benefits from reduced water consumption of its drought stressed competitor spruce. Regarding stomatal conductance, positive effects of beech-spruce interaction are overridden under extended periods of drought.