

## RESEARCH ARTICLE

# Species traits interact with stress level to determine intraspecific facilitation and competition

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## Funding information

Universiteit Utrecht; Vetenskapsrådet, Grant/Award Number: 2019-05099

**Co-ordinating Editor:** Andrew Tanentzap

## Abstract

**Questions:** Flooding and drought stress are expected to increase significantly across the world and plant responses to these abiotic changes may be mediated by plant–plant interactions. Stress tolerance and recovery often require a biomass investment that may have consequences for these plant–plant interactions. Therefore, we questioned whether phenotypic plasticity in response to flooding and drought affected the balance between competition and facilitation for species with specific adaptations to drought or flooding.

**Location:** Utrecht University.

**Methods:** Stem elongation, root porosity, root:shoot ratio and biomass production were measured for six species during drought, well-drained and submerged conditions when grown alone or together with conspecifics. We quantified competition and facilitation as the ‘neighbour intensity effect’ directly after the 10-day treatment and again after a seven-day recovery period in well-drained conditions.

**Results:** Water stress, planting density and species identity interactively affected standardized stem elongation in a way that could lead to facilitation during submergence for species that preferably grow in wet soils. Root porosity was affected by the interaction between neighbour presence and time-step. Plant traits were only slightly affected during drought. The calculated neighbour interaction effect indicated facilitation for wetland species during submerged conditions and, after a period to recover from flooding, for species that prefer dry habitats.

**Conclusions:** Our results imply that changing plant–plant interactions in response to submergence and to a lesser extent to drought should be considered when predicting vegetation dynamics due to changing hydroclimatic regimes. Moreover, facilitation during a recovery period may enable species maladapted to flooding to persist.

## KEYWORDS

neighbour intensity effect, plant–plant interactions, recovery period, riparian vegetation, stress gradient hypothesis, water stress

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## 1 | INTRODUCTION

Understanding how abiotic conditions set the stage for plant–plant interactions is critical to predicting species shifts, invasions and biodiversity patterns in a changing climate (Callaway & Maron, 2006; Schob et al., 2014; Sarneel, Hefting, et al., 2019). Plant–plant interactions can range from negative (competition) to positive (facilitation) and are mediated by plant traits. The relative importance of competition and facilitation is often hypothesized to depend on the stress level (Bertness & Callaway, 1994). More specifically, the stress gradient hypothesis traditionally predicts that plant–plant interactions shift from competition in benign environments towards facilitation in stressful (but not too harsh) environments (Bertness & Callaway, 1994; Michalet et al., 2006). The stress gradient hypothesis was found to explain plant species interactions for resources (nutrients, light) as well as non-resources (wind, temperature) and for interspecific interactions as well as intraspecific interactions (Saccone et al., 2010; Fajardo & McIntire, 2011). After the proof-of-concept across ecosystems and specific species, more focus has been placed on the relative role of environmental settings (Michalet et al., 2006; Gross et al., 2010; Holmgren & Scheffer, 2010). This proved that facilitation occurs under many abiotic environmental settings often not related to stress (Michalet et al., 2006; Maestre et al., 2009; Holmgren & Scheffer, 2010; Liancourt et al., 2020). From a plant perspective, however, 'stress level' is an ambiguous term that may depend on species-specific traits to deal with the specific conditions (Gross et al., 2010; Liancourt et al., 2020). For example, flood-tolerant plants close rivers may experience flooding as less stressful compared to species that may be more resistant to drought growing at locations flooded less often, further away from rivers (van Eck et al., 2006; Sarneel, Hefting, et al., 2019). Indeed, Liancourt et al. (2005) found that among three grass species in the field, facilitation was largest for the most drought sensitive one. It is still poorly understood how plant adaptations and traits determine facilitative or competitive interactions along water stress gradients.

Riparian systems along rivers are excellent model systems to disentangle the relative roles of abiotic conditions and plant–plant interactions, as these biodiverse hotspots harbour a strong flooding gradient along which facilitation occurs (Luo et al., 2010; Saccone et al., 2010; Doua et al., 2018). Besides, many rivers of the world are predicted to drastically alter their flooding regimes (Hirabayashi et al., 2013). Understanding what drives changes in riparian plant community composition therefore has relevance for biodiversity, restoration and climate change mitigation. The main drivers of species distributions along the riparian gradient from the channel to upland are soil moisture and flooding frequency (van Eck et al., 2004; Bornette & Puijalon, 2011; Sarneel, Bejarano, et al., 2019) and a suite of traits are found to help survive submergence. In a meta-analysis including 33 species, Garssen et al. (2015) concluded that the ability to elongate above the water column was the most crucial

trait that enabled plants to survive periods of submergence, while van Eck et al. (2004) found that capacity to recover was important for shorter floods. Surviving drought has been less intensively investigated for riparian plants, but is likely to be associated with root growth (Garssen et al., 2014), and may result in facilitation for grasses (Liancourt et al., 2005; Doua et al., 2018). Phenotypic plasticity in response to both drought and submergence may induce environmental changes (e.g. gas concentration in the water, shading) affecting not only plant performance but also plant interactions. Alternatively, plant interactions may affect the ability to allocate resources to responding to environmental stress, hence affecting survival of that stress. It is therefore of much relevance to study how plant–plant interactions can modify responses to stress. Strikingly, most studies included in the two meta-analyses mentioned before were experiments with only a single plant per pot. This means that we have limited information on how plant traits mediate plant–plant interactions under flooding or drought stress. This is an important knowledge gap that limits our ability to apply the knowledge of such controlled studies to the field situation, where plants usually grow together in intra- and interspecific communities. Moreover, to understand community composition in the field, intra- and interspecific interactions (via plastic trait responses) immediately after the stress release may also be of significant importance and are systematically understudied (van Eck et al., 2004; Striker, 2012). Yet, they could be of importance in explaining why certain maladapted species persist for long times after changes in flooding regimes (Sarneel, Hefting, et al., 2019).

In this study, we tested how plant–plant interactions change the response of plants to abiotic stress and the recovery from it, and tested if these interactions depend on species habitat preferences for moisture. Due to the high degree of clonality among riparian species, we focussed on intraspecific interactions. We therefore selected six species and measured their traits and performance when growing alone or together with conspecifics *during* and *after* two types of water stress (drought or submerged conditions), and compared this with well-drained control conditions. The measured traits were related to surviving floods and droughts (stem elongation, root porosity, root:shoot ratio). We chose a deep but relatively short flood as this represents typical summer flooding conditions that are the most influential for species' distributions along riverine altitudinal gradients (van Eck et al., 2004).

Following the stress gradient hypothesis, we expect that facilitation will occur during stress. For conspecifics, facilitation may occur when species are maladapted to the conditions, either during the stress or directly after. For this line of reasoning, we first hypothesized that water regime, plant density and recovery period will induce phenotypic changes (stem elongation, root porosity and relative investment in roots, regrowth capacity). Second, since plant–plant interactions depend on traits, we hypothesize different responses to neighbours (facilitation or competition) depending on the availability of water and the ability of species to deal with water-related stress.

## 2 | METHODS

### 2.1 | Species selection

Six forb species were selected to represent a wide gradient of habitat preferences from adapted to growing under wet, frequently submerged conditions to adapted to dry growing conditions (Table 1). We choose three plant families and selected one species adapted to dry and one to wet habitats from each family (Table 1). In this way we obtained a species selection that minimizes the risk of phylogenetic relations driving the patterns, yet still represents more diversity than only one phylogenetic family would (Tanentzap & Lee, 2017). We used the recalculated Ellenberg moisture values from the Synbiosys database (Hennekens et al., 2010). Since the difference in moisture value was not constant between the species within each plant family, and our species selection limited, we did not focus on phylogeny explicitly in the statistical analysis. Nomenclature follows Van der Meijden (2005).

### 2.2 | Experimental setup

Seeds were germinated on a layer of polyethylene terephthalate (PET) grains (Elf Atochem, Marseille, France) floating on tap water in a growth chamber (12 h light; 25°C). When the seedlings were 1–2 cm tall, they were transplanted to a pot (10 cm × 11 cm × 15 cm) filled with a mixture of 5:5:2 (volume) river sand, quartz sand and river clay and watered from the bottom by placing them in a bigger tray in a greenhouse. The seedlings were planted in two densities, with either one plant in the middle of the pot (referred to as 'alone'), or with six plants per pot (referred to as 'neighbours'), which were

**TABLE 1** Species in the experiment: Phylogenetic pairs with their Ellenberg moisture values (Ell.) obtained from the Synbiosys database (Hennekens et al., 2010), with 1 indicating very dry and 12 indicating aquatic habitat preferences

Pair	Name	Ell.
1	<i>Chamerion angustifolium</i> (L.) Holub <sup>a</sup>	5.7
1	<i>Epilobium hirsutum</i> L. <sup>a</sup>	7.6
2	<i>Rumex acetosa</i> L. <sup>b</sup>	6.2
2	<i>Rumex palustris</i> Sm. <sup>c</sup>	7.8
3	<i>Arabidopsis thaliana</i> (L.) Heynh. <sup>c</sup>	4.6
3	<i>Nasturtium officinale</i> R.Br. <sup>a</sup>	8.9

Note: The Synbiosys database contains about 500,000 vegetation surveys of the Netherlands and for each vegetation survey, the mean Ellenberg moisture value was calculated. A species-specific Ellenberg moisture value was calculated as the mean Ellenberg moisture value of all the vegetation surveys where this species occurred. Seed sources are indicated with superscript numbers. Nomenclature following Van der Meijden (2005).

<sup>a</sup>Jelitto Staudensamen GmbH (Schwarmstedt, Germany).

<sup>b</sup>Collected from the field in a floodplain along the river Waal near the city of Nijmegen (the Netherlands).

<sup>c</sup>From seed stocks at Utrecht University (UU).

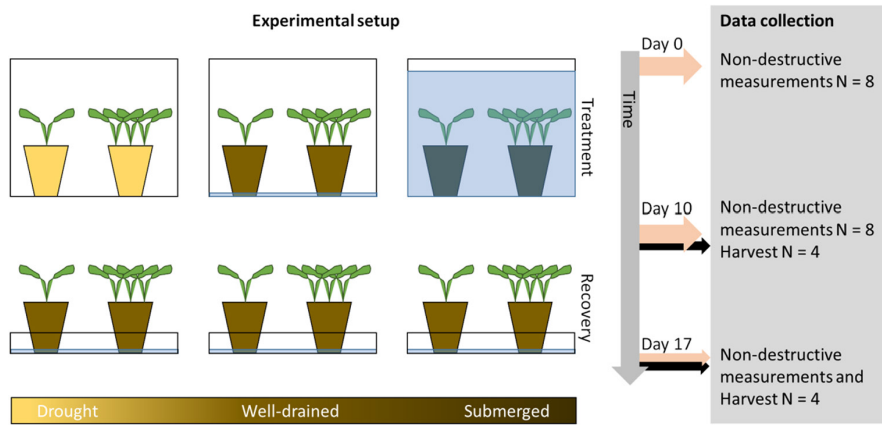
arranged such that one central plant was surrounded by five conspecific plants. One litre of modified Hoagland solution (7.50 mM  $[\text{NH}_4]_2\text{SO}_4$ , 15.00 mM  $\text{KH}_2\text{PO}_4$ , 15.0 mM  $\text{KNO}_3$ , 86  $\mu\text{M}$  Fe-EDTA, 0.80  $\mu\text{M}$   $\text{MnSO}_4$ , 0.34  $\mu\text{M}$   $\text{ZnSO}_4$ , 0.06  $\mu\text{M}$   $\text{CuSO}_4$ , 8.0  $\mu\text{M}$   $\text{H}_3\text{BO}_3$ , and 0.11  $\mu\text{M}$   $\text{Na}_2\text{MoO}_4$ ) was added to one tray of plants (containing an equal mixture of 'alone' and 'neighbour' pots) two times during the pre-experimental growing period to prevent nutrient limitation. The soil pH was  $6.8 \pm 0.08\text{SE}$ . When plants were on average 7 cm tall (or wide, in case of rosettes), and the leaves of the plants with neighbours were touching each other, three treatments were imposed on both planting densities, each with eight replicates. Half of the replicates was harvested directly after the experimental period, while the other four replicates were left to recover for one week under well-drained control conditions.

At the start of the experiment, all pots were placed in large glass aquaria of 30 cm height, with four pots per aquarium subjected to one of three treatments (Figure 1). In the 'Drought' treatment, moisture content was decreased to the wilting point (5%–10% soil moisture by weight) by extracting excess soil moisture with rhizons (Eijkelkamp Soil & Water, Giesbeek, the Netherlands) attached to a vacuum (typically overnight). After water extraction to the wilting point, pot were kept at a constant weight, and tap water was added every other day when necessary. In the second treatment, 'Well-Drained', water was kept at field capacity (20%–23% soil moisture) by keeping the water level at 1 cm in the aquaria. In the submerged treatment, tap water was added to 15 cm above the average plant height, and plants never reached the water surface during the experiment. When necessary, algae were removed from the water surface every other day. All experimental treatments lasted 10 days, which mimics average summer flood duration and is already impacting most sensitive species (van Eck et al., 2004).

After the experimental period (Figure 1), all plants were taken from the aquaria and those that were not harvested were placed in large trays where the water level was kept at 1 cm. Plants growing alone in a pot were prevented from interacting with plants in other pots by maintaining enough distance throughout the whole experiment and recovery period (van Eck et al., 2004).

### 2.3 | Measurements

Non-destructive measurements were conducted at the start of the experiment, after 10 days of treatment and after the recovery period that lasted seven days (Figure 1). Measurements were conducted at the central plant in a pot and included plant size (stem height or rosette diameter), number of leaves and leaf length of the two but youngest leaves at the start of the water treatments (marked with tiny plastic bands). At the end of the treatment and recovery period, four plants of each treatment were harvested, roots and shoots were separated, dried (70°C, 48 h) and weighed. We determined the root porosity directly after harvesting on a subsample of 0.5 g using the buoyancy-based method (Raskin, 1983; Thomson et al., 1990; Visser & Bogemann, 2003).



**FIGURE 1** Experimental setup, water availability, planting density and measurements taken during the course of the experiment. The shading of the pots indicates water availability in the pots. Density 1 or 6 plants per pot. Timing, amount and type of measurements are indicated with orange arrows for non-destructive measurements while black arrows indicate destructive measuring. Arrow size indicates number of replicates.

The buoyance-based method measures the relative volume of internal gas spaces by determining the loss in upward buoyant force before and after infiltrating the roots by water under a vacuum for five minutes (Visser & Bogemann, 2003). This is done by using below-balance weighing of the sample while being submerged in water. Weighing in water allows for more precise measurements because errors due to water clinging to the roots do not interfere, as it would in normal balance weighing. This buoyancy-based measure of root porosity provides a functional measure of aerenchym content.

## 2.4 | Calculations

To quantify the overall species-specific reaction to the treatment and recovery period, we calculated the response ratio (RR) of the species-specific total biomass by dividing the total biomass under drought or submergence ( $M_t$ ) by the biomass in the well-drained treatment ( $M_c$ ) and taking the logarithm ( $RR = \ln[M_t/M_c]$ ). Elongation was standardized to overcome differences in growth forms. Standardized elongation ( $E_t$ ) was quantified by calculating the relative increase in length ( $L_{t1}-L_{t2}$ ) per initial length ( $L_{t1}$ )  $\Delta L = (L_{t1} - L_{t2})/L_{t1}$  and standardized by subtracting the average observed in the well-drained treatment ( $\Delta L_c$ ). Standardized elongation ( $E_t = [(L_{t1} - L_{t2})/L_{t1}] - \Delta L_c$ ) can thus be interpreted as the absolute additional increase in length (or loss in length) per cm of plant height.

We calculated competitive strength as the neighbour-effect Intensity index with additive symmetry ( $NInt_A$ , Diaz-Sierra et al., 2017). It quantifies the degree to which the presence of neighbours influences the performance on a standardized, symmetric scale from  $-1$  (competitive exclusion) to  $+2$  (obligate facilitation). The neighbour-effect Intensity index was calculated as  $2 \cdot \Delta P / (P_A + |\Delta P|)$  where  $\Delta P = P_N - P_A$ , and  $P_N$  and  $P_A$  are the total biomass productivity in the 'Neighbours' and 'Alone' treatment, respectively. Because we did not pair our 'alone' and 'neighbour' pots, but randomized them in space, we calculated the  $NInt_A$  for all possible pairs of replicas of the alone and neighbours treatments per species after the treatment and recovery period separately

(time-step), and took the average per species, treatment and time-step combination (for a comparison with other approaches see Appendix S1). The  $NInt_A$  after the recovery period should be interpreted as integrating both the effect of the treatment and of the recovery period. We chose this approach because: (1) all experimental replicas were sampled individually and contributed to the error of the index; and (2) all the combinations among data are equally valid, with a large risk of bias when they would be assigned to pairs randomly. The errors of the indices were estimated by bootstrapping these values 1000 times and calculating the 95% confidence intervals using the BCa method. This method is recommended to correct for skewness as well as bias in the bootstrap distribution common for ratios (Silverman et al., 2004; Puth et al., 2015).

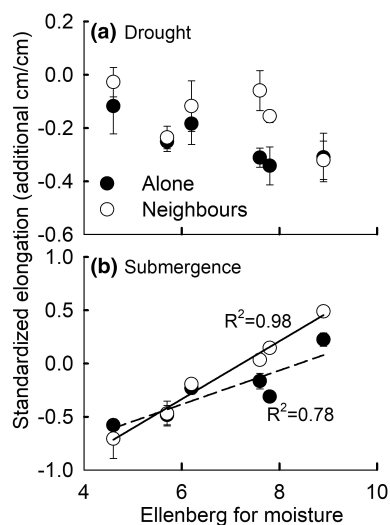
## 2.5 | Statistics

We used linear models to test the effects of the fixed variables planting density, treatment, time (before or after recovery period) and Ellenberg moisture (F) value in R3.5.1 (R Core Team, 2021). The dependent variables root porosity, root:shoot ratio and biomass were tested including all predictor variables. For standardized elongation, however, we focussed on the measurements directly after the treatment and did not analyse the changes after the recovery period. Standardized elongation under drought merely reflects the relative growth with respect to the well-drained treatment. For this reason, we ran separate linear models for the drought and the submerged treatment. These models included planting density and Ellenberg moisture value and excluded the well-drained treatment due to standardized elongation being defined as zero there. Treatment effects on plant biomass were also tested for each species separately. Due to our way of calculating  $NInt_A$ , we did not test differences between treatments within species. Instead, we used the R-package *ezanova* (Lawrence, 2016) and performed a repeated-measures ANOVA where the average  $NInt_A$  per species was the dependent variable, with treatment and time-step as fixed, within-subjects factors, and Ellenberg moisture values as between-subjects factor.

### 3 | RESULTS

#### 3.1 | Effects on plant traits

The examined plant traits responded differently to the imposed treatment, planting density and Ellenberg moisture values. In our experiment, shoot elongation was not solely determined by treatment ( $F_{1,82} = 0.506$ ,  $p = 0.479$ ), since we observed a three-way interaction between Ellenberg moisture value, treatment and planting density ( $F_{1,82} = 59.51$ ,  $p < 0.001$ ; other statistics in Appendix S2, Table S2.1). To understand this interaction, we separated the analysis per individual treatment. During drought, standardized elongation was generally negative and not affected by plant density ( $F_{1,40} = 1.57$ ,  $p = 0.218$ ; Figure 2). It tended to decrease with higher Ellenberg moisture values ( $F_{1,40} = 2.94$ ,  $p = 0.094$ ). This was especially clear when plants were grown alone (Figure 2a), but the interaction between Ellenberg moisture value and planting density was not significant ( $F_{1,40} = 0.297$ ,  $p = 0.589$ ). Under submerged conditions on the other hand, the species that typically occur in wet habitats had clear elongation responses (Figure 2). Hence, we found a strong positive relation between Ellenberg moisture values and elongation ( $F_{1,42} = 73.68$ ,  $p < 0.001$ ). The interaction between Ellenberg moisture values and planting density was also significant ( $F_{1,42} = 7.20$ ,  $p = 0.010$ ). This indicates that wetland species with high Ellenberg moisture values elongated more when grown with neighbours, whereas species from dryer habitats generally had a low level of elongation, which decreased even further when grown with neighbours (Figure 2b).



**FIGURE 2** Standardized elongation for plants grown alone in a pot and with conspecific neighbours under (a) drought and (b) submergence. Each point is a different combination of water stress treatment and species at the end of the water stress period ( $n = 8$ ). Error bars represent SE. Lines indicate significant relations with solid and dashed lines for the treatment with neighbour and alone respectively.

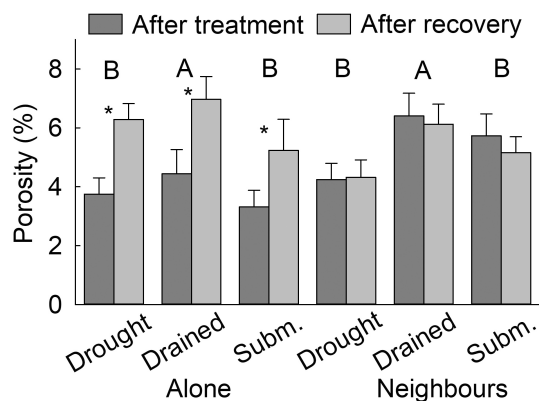
Root porosity was significantly affected by treatment ( $F_{2,244} = 4.88$ ,  $p = 0.008$ ), with higher values under well-drained control conditions (Figure 3). Species with higher Ellenberg moisture values had significantly higher root porosity ( $F_{1,244} = 12.75$ ,  $p < 0.001$ ), but this relationship was only visible in the well-drained controls, with a significant interaction between Ellenberg moisture value and treatment ( $F_{2,244} = 9.05$ ,  $p < 0.001$ , Appendix S2, Figure S2.1). Although root porosity was lowest for the plants grown alone for the measurements directly after the water treatments, planting density did not have an overall effect on root porosity ( $F_{1,244} = 0.955$ ,  $p = 0.329$ ). However, it interacted with time-step ( $F_{1,244} = 10.92$ ,  $p = 0.001$ , Figure 3) in such a way that root porosity of plants standing alone in a pot increased after the recovery period, whereas it remained unchanged, and relatively high, for the plants with neighbours. Other interactions were not significant (Appendix S2, Table S2.1).

Plant root:shoot ratio was highest under drought and decreased towards the well-drained and submerged treatments, indicating a relatively larger investment in roots in dryer soils ( $F_{2,233} = 9.96$ ,  $p < 0.001$ ; Appendix S2, Figure S2.2). The difference in root:shoot ratio between the drought and well-drained treatments was mostly driven by a change in shoot biomass. That is, root biomass barely differed between those treatments whereas in the submerged treatment, both shoot and root biomass were strongly affected. There was a trend towards higher root:shoot ratios when plants were grown with neighbours ( $F_{1,233} = 3.42$ ,  $p = 0.066$ ) and for species with higher Ellenberg moisture values ( $F_{1,233} = 3.60$ ,  $p = 0.059$ ). There was no significant change in root:shoot ratio after the recovery period, nor were any of the interactions significant (Appendix S2, Table S2.1).

#### 3.2 | Effects on plant–plant interactions

In all species, plant biomass was highest in the well-drained treatment and decreased by submergence (treatment:  $p < 0.001$  for all species, Appendix S2, Tables S2.2 and S2). Although wilting was observed in the drought treatment, the difference with the well-drained treatment was generally small, but the log response ratio decreased for species with higher Ellenberg moisture values (Appendix S2, Figure S2.2). After the recovery period, this pattern was less strong. The overall effect of plant density on total biomass was significant for *Rumex acetosa*, ( $F_{1,29} = 7.49$ ,  $p = 0.01$ ), *Rumex palustris* ( $F_{1,36} = 40.85$ ,  $p < 0.001$ ) and *Nasturtium officinale* ( $F_{1,36} = 23.02$ ,  $p < 0.001$ ) and nearly significant for *Epilobium hirsutum* ( $F_{1,38} = 3.307$ ,  $p = 0.077$ ). For *Rumex palustris*, we found a significant interaction between treatment and density ( $F_{2,36} = 16.52$ ,  $p < 0.001$ ). Plants increased in biomass during the recovery period ( $p \leq 0.008$  for all species), irrespective of their treatment or planting density, and none of the interactions with time-step were significant (Appendix S2, Table S2.3).

Calculated from the differences in biomass between the plants grown alone or together with neighbours, the neighbour interaction

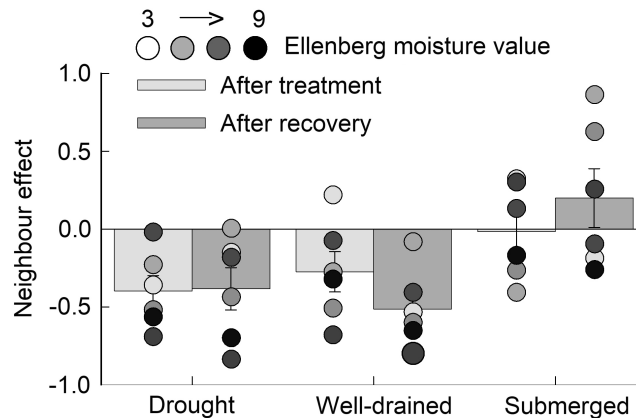


**FIGURE 3** Mean root porosity of the six species in the water stress treatments (drought, well-drained or submerged) when grown alone and together with neighbours ( $n = 4$  per species). Bars represent the mean ( $\pm$ SE) values across species directly after water stress treatments and after the recovery period. Different letters above the pairs of bars indicate a significant effect of water treatment, and an asterisk reflects a significant interaction of planting density and time, indicating when the root porosity changed over time.

effect ( $NInt_A$ ) was mostly negative in the drought and well-drained treatments, indicating competition. It was significantly higher in the submergence treatment compared to the other treatments (Moisture,  $M$ ;  $F_{2,8} = 10.56$ ,  $p = 0.006$ ) and indicated facilitation directly after submergence treatment for *Arabidopsis thaliana*, *Epilobium hirsutum* and *Rumex palustris* and after the recovery period for *Chamerion angustifolium* and both *Rumex* species (Figure 4). After the recovery period,  $NInt_A$  had decreased in the well-drained treatments and increased after submerged treatments. However, the effect of recovery period nor its interaction with treatment were significant (Time,  $T$ ;  $F_{1,4} < 0.01$ ,  $p = 0.98$ ;  $M \times T$ ,  $F_{2,8} = 0.57$ ,  $p = 0.16$ ).  $NInt_A$  decreased with Ellenberg moisture value (Ellenberg,  $E$ ;  $F_{1,4} = 4.12$ ,  $p = 0.11$ ), and this was clearest in the drought and well-drained control treatments. In the submergence treatment, more complicated patterns were found, where  $NInt_A$  decreased with Ellenberg moisture value only after the recovery period, except in *Arabidopsis thaliana*. However, neither the interaction effect, nor the three-way interaction were significant ( $M \times E$ ,  $F_{2,8} = 0.14$ ,  $p = 0.87$ ;  $E \times T$ ,  $F_{1,4} = 0.28$ ,  $p = 0.63$ ;  $M \times E \times T$ ;  $F_{2,8} = 0.57$ ,  $p = 0.58$ ).

## 4 | DISCUSSION

Our hypothesis of facilitation depending on the interaction between species identity and stress level was supported by phenotypic changes and to some extent by the calculated neighbour interaction effects. Yet, we saw some evidence of facilitation during stress for well-adapted and maladapted species we saw facilitation during different conditions (during stress and the recovery period respectively). That is, neighbours enhanced elongation for plants with high Ellenberg moisture values during submergence, while they decreased elongation for plants with low Ellenberg moisture values. In addition,



**FIGURE 4** The mean neighbour interaction effect (bars) across species (dots) in the different water treatments directly after treatment and after a week of recovery under well-drained control conditions. Each point is the average of one species (with  $NInt_A$  calculated from all alone-neighbour combinations), with shades of grey reflecting the Ellenberg moisture value. Error bars indicate SE.

planting density affected the plasticity to change root porosity during the recovery period. The calculated neighbour effect indicated that facilitation predominantly occurred during the recovery period after submerged conditions. This underlines the importance of plant interactions during a recovery period and these interactions should be considered when predicting vegetation dynamics due to changing hydroclimatic regimes (van Eck et al., 2004).

### 4.1 | Plant traits during drought and submergence

Both water regime and neighbours affected plant traits in ways that could enhance stress tolerance and potentially result in facilitation. This was especially clear for elongation where submergence induced a stronger response in obligate wetland species compared to species from dryer habitats. Stem elongation leads to enhanced gas transport to supply photosynthesis (Voisenek & Blom, 1989; Fenster, 1997; Voisenek et al., 2004; Mommer et al., 2007). We now show that in obligate wetland species, neighbours facilitated this elongation, whereas for species with lower Ellenberg moisture values, neighbours reduced additional growth in length. This implies that whether facilitation of growth in length may occur is determined by species identity and stress level of the environment.

To enhance water uptake, plants often allocate more biomass towards roots during drought (Farooq et al., 2009), while submergence creates oxygen deficits and reductions in root biomass (Voisenek et al., 2006) and increases root porosity (Jackson & Armstrong, 1999). Both mechanisms can explain the observed response in root:shoot ratio to water stress treatment in our study and the species with higher Ellenberg moisture values tended to have higher porosities. However, our porosities were overall quite low (Tanentzap & Lee, 2017), which may be associated to the young age of the plants and the short time span of our submergence treatment that may have prevented the formation of specific aerenchymatous



roots (Zhang et al., 2017; Yang et al., 2018). Root porosity was lowest during drought, which is in line with water conservation strategies during drought (van der Knaap et al., 2014; Gao et al., 2019) and increased gas exchange during wetter conditions (Garssen et al., 2015; Wright et al., 2017). However, it remains unclear why the root porosity responded to the recovery period only when plants were grown alone.

## 4.2 | Role of neighbours

The few previous studies that specifically tested the effect of plant density during submergence or drought have found indications for facilitation (Araya et al., 2010; Luo et al., 2010; Li et al., 2014; Douda et al., 2018; Li et al., 2018), neutral effects (Davis et al., 2009; Chauhan & Abugho, 2013; Hong & Kim, 2016) and competition (Grace & Wetzel, 1981). Results tend to vary depending on the species used (Davis et al., 2009; Luo et al., 2010) and elements of the experimental design such as flooding depth (Grace & Wetzel, 1981; Luo et al., 2010), intensity of drought (Douda et al., 2018; Gao et al., 2019) or soil type (Li et al., 2018).

For drought, facilitation is thought to be associated with water conservation (Li et al., 2014; van der Knaap et al., 2014). In arid and semiarid ecosystems, neighbours are reported to decrease soil evaporation (Aguar & Sala, 1994), provide shielding from bright sunlight and increase water infiltration (Navarro-Cano et al., 2019), for example due to reducing soil bulk density. In line with this, we observed that the little water added in the drought treatment was generally taken up more easily in pots with more plants, and that those tended to dry out less compared to the pots with one plant. Although this points towards better water conservation for plants grown together, we cannot prove this statistically.

During submergence, facilitation is hypothesized to be associated with increased gas exchange in shoots and roots. The results indicate a potential role for shoots that elongate above the water and enhance gas transfer. Luo et al. (2010) and Wright et al. (2017) however, found strong indications that root porosity leading to increased soil aeration may be beneficial. As this is something that any type of neighbour could benefit from, it can be speculated that maladapted species may benefit more from this than the well-adapted species when grown in mixtures. Our results do suggest some role for root porosity as it responded on water treatment and planting density. Despite the observed interactions of neighbours, water stress treatment and species traits, the relationships between the neighbour intensity and Ellenberg values were complicated and reflected unclear benefits of plastic responses to neighbours or stress level. This is in line with the work of Mommer et al. (2007), who showed that despite drastic changes in leaf morphology of flood-tolerant and intolerant species in response to submergence, the internal oxygen pressure was the same across species. However, we did observe that facilitation occurred most frequently during and directly after submergence, and elongation accompanied this treatment. Nevertheless, direct correlations of

traits with the magnitude of the neighbour effect were indistinct (Appendix S2, Figure S2.4), because a lack of statistical power. We hypothesize that in our experiment, increased elongation may have resulted in increased shading by neighbours, which may have balanced out some of the potential benefits from elongation in surviving submergence. In addition, we observed that *Arabidopsis* had a much higher  $NInt_A$  than was expected based on the elongation measurements. The relatively high root porosity of this species may have provided compensation. Different traits that can be used to compensate and survive submergence (Mommer et al., 2007) and counteract the lack of adaptations in other traits may have further obscured a direct relation between stem elongation and  $NInt_A$ .

## 4.3 | Role of recovery period

It has generally been assumed that extreme events like floods and droughts may cause changes in community composition due to direct, selective pressure during the stress. However, the capacity to regrow after stress events can be equally important (Colmer & Voisenek, 2009; Striker, 2012). Along that line, plant-plant interactions may also be important during recovery from drought and flooding (Striker, 2012). During the recovery period in our experiment, we observed that most of the measured traits were rather plastic and reacted directly to the changed moisture conditions in the recovery period. That plant-plant interactions can play a role during the recovery period is indicated by a quite drastic change in  $NInt_A$  during the recovery period. During well-drained control conditions,  $NInt_A$  merely decreased, indicating stronger competition for older plants. However, we did not observe this in the recovery periods following the other water treatments. Since  $NInt_A$  integrates the effect of both the treatment and the response in the subsequent recovery period, this indicates that these changes were not merely due to increased age, but that they were co-determined by past (soil moisture) conditions (historical contingency). It is worth noting that strong changes towards facilitation were found after the recovery period for *Chamerion angustifolium* and *Rumex acetosa* that have relatively low Ellenberg moisture values. Although yet poorly understood, such interactions during a recovery period could enable certain species to persist after short to intermediately long flooding events and thereby contribute to the high biodiversity of riparian zones (Doudová & Douda, 2020). In addition, this advocates further investigation of plant interactions during recovery periods in studies that address stress tolerance (Striker, 2012; Sasidharan et al., 2017).

## 4.4 | Stress and biodiversity

The stress gradient hypothesis predicts that facilitation occurs mostly in stressful habitats. For both drought and submergence, we found reasonable indications that facilitation (or at least release from competitive pressure) occurs in species that are well adapted

to these conditions as long as the conditions prevail. However, the highest absolute values for facilitation were found after the recovery period following submergence, which adds to the rapidly growing body of evidence that facilitation also occurs in mild or benign environments (Holmgren & Scheffer, 2010), and could play an important role for species composition and in stabilizing vegetation diversity (Doudová & Douda, 2020).

Many riparian species are clonal and as a result intraspecific competition is common in this habitat. Luo et al. (2010) showed that for three wetland species intra- and interspecific competition change in similar directions along a flooding gradient. When other species are able to benefit from the conditions created by the facilitating species (e.g. less evapotranspiration during drought or higher soil aeration during submergence), diversity can increase (Schob et al., 2014; Navarro-Cano et al., 2019; Liancourt & Dolezal, 2021). Indirect evidence for the role of facilitative interactions comes from the observation that, except for legumes, biomass was less negatively affected by flooding in higher-diversity treatments (Luo et al., 2016; Wright et al., 2017). Douda et al. (2018) further observed a positive relation between facilitation and subordinate species' stability during drought stress, but Doudová and Douda (2020) found a rather complex relation to functional traits in the same experiment. Taken together, it is starting to resonate in the literature that it is important to consider whether plants (or other organisms) are adapted to the conditions when evaluating facilitation or the effect of the stress level of the environment (Holmgren & Scheffer, 2010; Doudová & Douda, 2020; Liancourt et al., 2020). This is important when predicting changes in a world facing global changes.

#### AUTHOR CONTRIBUTIONS

Judith Sarneel was involved in all parts of the work, Mariet Hefting, Eric Visser, Rens Voeselek and George Kowalchuk substantially contributed to designing the experimental setup and writing the paper. Rubén Díaz-Sierra was involved in analyses and interpretation of the neighbour intensity effect and in writing. All authors agree with the final version of this document, and are accountable for the aspects of the work they conducted and ensure that questions related to the accuracy or integrity of any part of their work are appropriately investigated and resolved.

#### ACKNOWLEDGEMENTS

We thank B. Verduijn, G. Rouwenhorst, P. Veenhuizen, A. Ammerlaan, E. Reinen and R. Welschen for practical help during the experiment.

#### FUNDING INFORMATION

Judith M. Sarneel conducted the work within (1) the strategic theme Sustainability of Utrecht University, subtheme Water, Climate, and Ecosystems and (2) the Swedish Research Council Vetenskapsrådet (2019-05099).

#### DATA AVAILABILITY STATEMENT

Data is attached as Appendix S3.


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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Justification of calculating  $NInt_A$  in non-paired designs

**Appendix S2.** Additional results

**Appendix S3.** Data of the plants in the experiment

**How to cite this article:** Sarneel, J.M., Hefting, M.M., Visser, E.J.W., Díaz-Sierra, R., Voeselek, L.A.C.J. & Kowalchuk, G.A. (2022) Species traits interact with stress level to determine intraspecific facilitation and competition. *Journal of Vegetation Science*, 33, e13145. Available from: <https://doi.org/10.1111/jvs.13145>