Water stress interacts with early arrival to influence interspecific and intraspecific priority competition: a test using a greenhouse study

James E. Moore & Scott B. Franklin

Abstract

Questions: Do species arriving early (priority effect) to a site have a competitive advantage over species arriving later? Does early arrival aid in species ability to tolerate water stress? Is intra- and interspecific competition different for early and late arrivers?

Location: Greenhouse, University of Northern Colorado, Greeley, Colorado, USA.

Methods: A 1-mo ‘head start’ in the greenhouse was used to simulate early arrival of *Panicum capillare* and *Polygonum persicaria*. We used a completely randomized design to examine the effects of water stress (drained, drought, flood) and priority competition (interspecific and intraspecific) in relation to species’ cohort [older (established) and younger (novel) individuals planted in different combinations]. We calculated increases in root and shoot weights, total biomass, root/shoot ratios, height, leaf number and length of longest leaf. All dependent variables were analysed using MANOVA and individual GLM ANOVAs.

Results: Increases in shoot and root biomass were significantly affected by water stress but the effects were species- and priority level-specific. Root biomass for established individuals was significantly reduced after flooding and drought. Shoot biomass was least for drought and flood treatments of both older and younger *P. persicaria*, but older and younger *P. capillare* were unaffected. There were species-specific priority differences (i.e. greater for older individuals) for shoot height and increases in leaf number; however, the opposite was seen for increases in leaf length.

Conclusions: In terms of community assembly, neither species appears to have an advantage in relation to competition or water stress, as both seem plastic and are negatively affected by flood and drought stress. The greater impact of older *P. persicaria* on *P. capillare* is the only advantage *P. persicaria* seems to have in the greenhouse. Correlating this to natural conditions, it appears that chance in reaching a site first plays a major role in *P. persicaria*’s colonization success. This study provides evidence of the impacts of arrival time on subsequent physiological and competitive abilities of plants.

Introduction

Understanding the processes that govern plant community assembly has been a central theme in ecology since the first successional concepts (Gleason 1927; Samuels & Drake 1997; Weiher & Keddy 1999; Chase 2003). Recently, much attention has been given to the history of community assembly, examining the stochastic sequential arrival of species from a regional species pool of potential community members (Chase 2003; Fukami & Morin 2003; Körner et al. 2008). These historical effects are commonly referred to as ‘priority effects’, because they involve early colonists altering the performance of later colonists (Grace 1987; Kennedy et al. 2009). With the knowledge that communities are dynamic and often a function of chance (Hubbell 2001; Keppel et al. 2010), understanding how arrival...
Early arrival influences priority competition

J.E. Moore & S.B. Franklin

order affects interactions may increase predictability of community assembly.

Priority effects have been examined for a variety of organisms at both the micro- and macro-organism scale (Dix & Webster 1995; Morin 1999; Chase 2003; Fukami & Morin 2003; Fukami 2004; Fukami et al. 2007; Kennedy et al. 2009), with the most common empirical study systems being aquatic microcosms. For plants, the advantage of early arrival can be thought of as preemption, meaning that the first individuals to arrive inhibit invasion by others either through making sites unsuitable for germination or through interfering with subsequent growth (competitive advantage; Grace 1987). Numerous studies have shown that even the slightest difference in germination time (Moore & Lacey 2009) and seedling growth can have a strong impact on competitive outcomes (Mack & Harper 1977; Grace 1985, 1987). In addition to being ‘larger’, these first colonizers may act to alter the environment in numerous ways due to species-specific rooting space, water and nutrient uptake (Bergelson 1990; Chadwell & Engelhardt 2008) and litter decomposition rates, as well as alterations to the root microbial community (Mayer & Poljakoff-Mayber 1975). In communities prone to frequent disturbance, the order of arrival is important to secure space or some limiting resource. For this study, we assess how priority (i.e. the cohort status of the neighbour plant) affects competitive ability between older and younger cohorts; does order of arrival affect competitive interactions?

To understand how communities assemble, we must understand how order of arrival (priority) and subsequent competitive advantages interact with stresses such as disturbance to affect community composition. Disturbance has been shown to directly weaken competition effects (Wilson & Keddy 1986; Wilson & Tilman 1993; Turkington et al. 1993). Goldberg (1996) proposed that species segregate along a disturbance gradient and that species become excluded based on their competitive abilities, while Suding & Goldberg (2001) suggested some species increase their competitive ability along a disturbance gradient relative to other species (competitive change). Although species do not need constant disturbance to persist, weaker competitors rely strongly upon regular disturbances for some competitive release (Huston 1979).

Disturbance increases available sites for colonization, thus inducing a stronger dispersal limitation effect that acts as a filter restricting the rate at which similar species arrive in a community. A species must be able to survive physical rigours of an area (MacArthur 1972) and be near enough for dispersal and colonization (Gleason 1939; MacArthur & Wilson 1967). In turn, arrival or failure to arrive will influence the expression of assembly rules (Belyea & Lancaster 1999; Fukami 2004); i.e. communities are continuously invaded and the invasion rate itself may influence community assembly. For example, in marine intertidal systems, barnacle larval settlement rates are determined by oceanic circulation patterns; communities with high settlement rates may be structured by predators while communities with low settlement rates are structured more by dispersal and chance (Roughgarden et al. 1987). This suggests that a combination of both niche and neutral (chance) factors (Foster & Tilman 2003; Tilman 2004; Moore et al. 2011) affect community assembly. Since we cannot mimic natural flood disturbances that plants experience on islands, here we used water inundation time as the stress (flood disturbance).

To explicitly test the role of priority effects in competition and flood tolerance of plant species, the order of arrival was experimentally manipulated to quantify advantages for one species over another. Here, we measured the effects of arrival time (cohort) and inter- and intra-specific priority competition under three water stresses for two common ruderal species. Specifically, we examined the effects of a 1-mo ‘head start’ for each of the two study species to determine if this confers a competitive advantage and increases water stress tolerance. We hypothesized that growth measures of older individuals would be greater compared to younger individuals (cohort effect) regardless of water stress (stress effect). Furthermore, we hypothesized the effects of intraspecific priority competition would be greater than interspecific priority competition (priority (cohort) competition effect), regardless of stress treatment.

Methods

Study species

Panica capillare L. (witchgrass) is an annual C3 plant with a facultative indicator (FAC) status and extensive US distribution [USDA NRCS, 2010, The PLANTS Database (http://plants.usda.gov, accessed 28 November 2010). National Plant Data Center, Baton Rouge, LA, USA]. P. capillare is commonly found on roadsides and wasteland throughout its range (USDA NRCS, http://plants.usda.gov). Roots tend to be shallow and fibrous, but tillers can also root. Seed germination for P. capillare is typically high, with seed dispersal occurring in autumn (Baskin & Baskin 1998). Seed production typically averages approximately 11 400 seeds plant\(^{-1}\) (Stevens 1932) but can exceed 56 000 seeds plant\(^{-1}\) (Baskin & Baskin 1986).

Polygonum persicaria (L.) Small (spotted ladysthumb) is also an annual C3 plant with a facultative wetland (FAC-W) status and a wide distribution in the US, although commonly found in disturbed moist habitats (USDA NRCS, http://plants.usda.gov). Taproots are generally branched and secondary roots are fibrous. P. persicaria seed production
ranges from 200 to 800 nuts plant$^{-1}$ and seeds are often dispersed by animals. In water, nuts float for 1 d; thus, water dispersal is likely (Simmonds 1945).

Experimental design

The experiment was done in the Research Greenhouse at the University of Northern Colorado, Greeley, Colorado, USA. Greenhouse temperature was set at 23 °C (ranged from 20 to 37 °C) with no supplemental lighting. Ambient light conditions ranged, on average, from 370 to 1218 μmol·m$^{-2}$·s$^{-1}$ daily for the duration of the experiment.

Seeds of P. capillare and P. persicaria were collected in October 2009 from Dean Island in the lower Mississippi River at river mile 754 (1213 km) (35°25′54.9″ N, 90°0′28.0″ W). Seeds were collected for each species from a minimum of five plants located at least 20 m apart. All seeds were cold-stratified at 12 °C for 2 mo. For each species, seeds from all locations were mixed before sowing. Seeds of older (established) cohorts were sown on 26 March 2010 and the younger (novel) cohorts were sown on 23 April. Two weeks after germination of the younger cohort (6 wk post-germination for the older cohort), plants were transplanted into 2.5-L pots (15.24 cm opening, 13 cm base and 17.15 cm tall) containing a 70:30 Quikrete® (Quikrete Concrete Co., Atlanta, GA, US) play sand and Miracle-Gro® (The Scotts Miracle-Gro Company, Marysville, OH, US) Potting Mix mixture and fertilized with Ferti-lome 20-20-20 soluble plant food mixed to manufacturer’s specifications. Each species was planted as a younger or older cohort with the same species (intraspecific) or with a different species (interspecific), so there were two planting combinations for each species: older P. capillare with younger P. persicaria, and older P. capillare with younger P. capillare; older P. persicaria with younger P. capillare, and older P. persicaria with younger P. persicaria, resulting in two individuals pot$^{-1}$ for all pots in the study. Two weeks after transplanting seedlings, the pots were randomly placed into one of six 150-L tubs to be subjected to their respective water stress treatment.

For each species, three factors were examined in this study (cohort, water stress and priority competition). Each cohort level (older, younger) was replicated six times in three different water stress levels (drained, flood, drought) and two priority competition levels (interspecific, intraspecific). Thus, our experiment had a total of 72 pots (36 species$^{-1}$) (cohort (2) × water stress (3) × priority competition (2) × 6 replicates = 72).

Water stress

This experiment is part of a series of experiments examining community assembly patterns on riverine islands located within the Mississippi River (Moore & Franklin 2011; Moore et al. 2011). Thus, greenhouse water stress treatments were used to mimic fluctuations in water levels along a flooding gradient typical of the islands. Durations at intermediate elevations on islands range from 8 to 16 d, and for this experiment flooding lasted an average of 7 d (Fig. 1). The greenhouse water stress conditions did not mimic all factors of flooding created by river flow (i.e. removing sediment and vegetation); inundation times, however, were similar.

Water levels in flooding tub pots were kept at 5–10 cm above the soil surface, drained tub pots were watered every other day, and drought tub pots differed based on irrometer (Watermark®, Irrometer Company Inc., Riverside, CA, USA) readings (measured in kilopascal – kPa) due to species-specific water use in the greenhouse. Irrometers were randomly placed in six pots with established P. capillare individuals and five pots with established P. persicaria individuals, as well as in nine and ten random pots from the flooded and drained treatment tubs, respectively. Irrometer readings of 0–10 kPa represent soil field capacity, 10–30 kPa represents adequate moisture in soils except sands, 30–60 kPa represents time to water, and 60–100 kPa indicates plants are experiencing drought (Watermark® Irrometer). The average irrometer readings at the final day of drought treatments were 62 kPa for established P. capillare pots and 94 kPa for established P. persicaria pots; other treatments remained at soil field capacity or adequate moisture throughout the study. Wilting was used to assess when to stop drought treatments, and P. persicaria was noticeably more wilted than P. capillare each time the drought treatment was ended.

Biomass calculations

Prior to starting the experiment, ten individuals of each species and each cohort were randomly selected and
weighed to obtain shoot and root starting weights for comparison (Table 1). After 38 d of treatment, plants were extracted, separated into roots and shoots (roots of each species were easily distinguishable), dried for 48 h at 80 °C and weighed. Data were calculated as increases (ending—beginning) in root and shoot weights, total biomass and root/shoot ratios, along with height, leaf number and length of longest leaf.

Statistical analysis
The effects of cohort (older, younger; i.e. neighbour priority status), water stress (drained, drought, flood) and priority competition (interspecific, intraspecific) on the dependent variables (increased root and shoot biomass, total biomass, root/shoot ratio, height, number of leaves and length of longest leaf) were analysed with a general linear analysis of variance (ANOVA) and multiple analysis of variance (MANOVA) in SAS (SAS 9.1; SAS Institute Inc., Cary, NC, USA). Due to space limitations, we did not assess competition within cohorts, only among them. Species were analysed separately. Post-hoc comparisons were made using a Tukey’s adjustment for multiple comparisons. Prior to analysis, dependent variables were assessed for normality using PROC Univariate procedure in SAS to determine if transformations were needed; no variables were transformed.

Results
Biomass
MANOVA results showed three significant interactions on biomass (Table 2). *P. capillare* root weight was affected by an interaction between stress and cohort; stress effects were only seen in older individuals where root biomass was greater under drained conditions than flooding or drought (Fig. 2a). Priority competition and cohort also interacted to affect root weight increases (Table 2); root biomass was higher under interspecific priority competition for older individuals (Fig. 2a). *P. persicaria* root weight was affected by an interaction of stress and cohort; as with *P. capillare*, stress effects were also only seen in older individuals, where root biomass was higher under drained conditions than flooding or drought (Fig. 2b). Shoot weight for *P. capillare* was significantly affected by cohort (Table 2; Fig. 3a). *P. persicaria* shoot biomass was affected by an interaction of stress and cohort; stress effects were, again, only seen in older individuals, where shoot biomass was higher under drained conditions than under flooding or drought stress (Fig. 3b). Priority competition and cohort interacted to affect shoot weight increases; *P. persicaria* shoot biomass was higher under interspecific priority competition for older individuals (Fig. 3b). *P. capillare* total biomass increase was significantly affected by a stress × cohort interaction, having greater total biomass increases of older individuals in drained conditions (Fig. 4a). *P. persicaria* total biomass increase was significantly affected by two interactions (Table 2). An interaction of stress × cohort showed significant differences in older individuals as well as intraspecific younger individuals, with total biomass increases the greatest in drained conditions (Fig. 4a). *P. persicaria* showed significant differences in older individuals in drained conditions (not shown).

Increase in height, leaf number and leaf length
Priority competition and cohort interacted to affect *P. capillare* height increase; older individuals only grew more than younger individuals under interspecific competition (Fig. 5a). The interaction of stress and cohort affected *P. persicaria* height increases (Table 2). Intraspecific novel and interspecific older individuals showed pair-wise differences for height growth, with the greatest height increases in drained conditions and the least in drought (Fig. 5b). There were no significant interactions for root/shoot ratio for either species (Table 2). Stress significantly affected *P. capillare* root/shoot ratio, with the highest ratio found in drained conditions (not shown).

### Table 1. Mean (n = 10) initial measurements of established and novel Polygonum persicaria and Panicum capillare individuals.

<table>
<thead>
<tr>
<th>TAXA cohort</th>
<th>Average # leaves</th>
<th>Length of longest leaf (cm)</th>
<th>Stem height (cm)</th>
<th>Root biomass (g)</th>
<th>Shoot biomass (g)</th>
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<tr>
<td>Established <em>P. persicaria</em></td>
<td>8.4</td>
<td>59.2</td>
<td>155</td>
<td>85.34</td>
<td>278.44</td>
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<td>Novel <em>P. persicaria</em></td>
<td>4.6</td>
<td>24.8</td>
<td>51.4</td>
<td>20.56</td>
<td>31.96</td>
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<tr>
<td>Established <em>P. capillare</em></td>
<td>3</td>
<td>108.4</td>
<td>39.6</td>
<td>42.18</td>
<td>52.6</td>
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<tr>
<td>Novel <em>P. capillare</em></td>
<td>3.6</td>
<td>60.6</td>
<td>18.6</td>
<td>12.36</td>
<td>15.9</td>
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Table 2. General Linear Model (GLM) three-way ANOVA and MANOVA results for absolute values of increases in growth parameters for Panicum capillare and Polygonum persicaria in an experiment examining soil moisture (stress) effects (drained, drought and flood [three levels]), Priority Competition (Comp) [established or novel individuals of P. persicaria and P. capillare [two levels]], and Priority effects (Cohort) [same or different species as dominant [two levels]]. Values in bold are significant ($P < 0.05$); asterisks indicate significance at the 0.1 $\alpha$ level.

<table>
<thead>
<tr>
<th>Species</th>
<th>df</th>
<th>Root weight (g)</th>
<th>Shoot weight (g)</th>
<th>Total biomass (g)</th>
<th>Root: shoot ratio</th>
<th>Height (cm)</th>
<th>Leaf number</th>
<th>Longest leaf</th>
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<td>F-value</td>
<td>P</td>
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<td>&lt;0.001</td>
<td>0.55</td>
<td>0.582</td>
<td>4.30</td>
<td>&lt;0.001</td>
<td>0.125</td>
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<td>1.61</td>
<td>0.212</td>
<td>0.12</td>
<td>0.726</td>
<td>0.08</td>
<td>0.782</td>
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<td>54.71</td>
<td>&lt;0.001</td>
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<td>&lt;0.001</td>
<td>0.019</td>
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**Discussion**

To better understand how order of species arrival and species interactions affect community assembly on riverine islands, we conducted a greenhouse experiment on riverine islands to examine the effects of priority (1 mo growth head start) on subsequent competition in combination with stresses on (Table 2). Established $P$. capillare individuals had the longest leaves in drained conditions, and under interspecific competition, however, leaf length was affected by any interaction; length were not significantly affected by any interaction. Intraspecific competition (not shown). $P$. persicaria growth under three water stresses (drained, drought, flooded). Error bars represent ± 1 SE. Diagonal lines represent a significant species interaction; horizontal lines indicate no significant capital letters indicate significant competition. Capital letters indicate significant stress differences. Alpha levels for all comparisons = 0.05.
that mimicked hydrologic gradients experienced on Mississippi River islands (Moore et al. 2011). Early germination in plants (one type of priority effect) confers multiple advantages throughout their life cycle by enhancing subsequent competitive ability, primarily for water and light (Jones & Sharitz 1989; Jones et al. 1989; Moore & Lacey 2009). Plants colonizing sites earlier (as simulated in our study) are likely to benefit from reduced or absent competition and the ability to secure rooting space. Both species in this study were annuals, suggesting the potential to be the first invaders on islands following floods. The data clearly support that first arriviers ultimately grow more than later arrivers. The positive influence of priority has been shown in a variety of studies, ranging from aquatic microcosms and ponds (Drake 1991; Chase 2003), to floodplain plant communities (Jones & Sharitz 1989) and grasslands (Körner et al. 2008) to ectomycorrhizal fungi colonizing root tips (Kennedy et al. 2009).

Older individuals maintained their competitive advantage over younger individuals regardless of stress. Benefits of early arrival were more pronounced in drained (control) soil moisture conditions compared to drought or flood, but benefits clearly outweighed stress effects. Körner et al. (2007), who examined the effects of a 3-wk time lag of sowing grassland species, also found early arrival benefits regardless of disturbance. Early arrivers dominated founder communities.

Stress was a factor in this study, however, as shown by the decreased growth of most parameters for older individuals. Studies have shown that P. persicaria exhibits a high degree of root plasticity in various moisture conditions, but
affected by stress than *P. persicaria*, nor did *P. capillare* seem less plastic in its response to stress. For example, under stress treatments both species had more leaves than their younger control counterparts without stress, and both species had shorter leaves. Reduced leaf size is common in drought conditions (Raven et al. 1999); although some studies also found leaf elongation under flooded conditions (Jackson & Drew 1984; Banga et al. 1995).

Because we find these two species co-existing on Mississippi River islands, we expected stronger intraspecific competition effects than interspecific competition effects. Classic competition theories predict that under stable environmental conditions (absence of stress or disturbance), species co-exist when intraspecific competition is greater than interspecific competition (Goldberg & Barton 1992; Tilman & Pacala 1993). For below-ground growth, older *P. capillare* competitive intensity was greater when grown with younger conspecifics than heterospecifics, as would be expected for co-existence. In contrast, younger *P. capillare* was more impacted when grown with heterospecifics than conspecifics, suggesting late arrivers are under stronger interspecific competition. The results may be due to the different way in which these species acquire underground resources. *P. capillare* obviously had higher water use efficiency as expressed by the drought-ending irrometer readings that were approximately one-third less than in *P. persicaria*, as well as the noticeable wilting of *P. persicaria* when drought events ended. The efficiency may result in less intraspecific competition between *P. capillare* and greater interspecific competition between older *P. persicaria* and younger *P. capillare*. Chadwell & Engelhardt (2008) showed through a greenhouse study (which did not hold true in field experiments) that established native *Vallisneria americana* decreased the ability of the exotic *Hydrilla verticillata* to invade due the nutrient drawdown by *V. americana*. The intensity of the priority competition effect would require a comparison between two older individuals grown together and an older and younger individual grown together—a planned future study. We unfortunately did not have the space to include those levels of treatment in this study.

Studies have also shown that multiple disturbances (Vinebrooke et al. 2004), timing of disturbance events in relation to each other (Beckage et al. 2003) and the sequence of disturbances (Fukami 2001) play important roles in determining community outcomes, because species are affected differently by the physiological stresses of the disturbance. Stress regimes (due to disturbance) are likely to be tightly coupled with arrival sequence on riverine islands, in part due to the dispersal mechanisms of individual species. While our study only looked at one disturbance treatment, the treatment was periodically applied and younger individuals had to respond to the

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**Fig. 5.** Mean height (cm) increases for (a) *Panicum capillare* and (b) *Polygonum persicaria* grown under three water stresses (drained, drought, flooded). Error bars represent ± 1 SE. Capital letters indicate significant competition x cohort differences. Diagonal lines represent a significant stress x cohort interaction; horizontal lines indicate no significance. Alpha levels for all pair-wise comparisons = 0.05.
Early arrival influences priority competition

J.E. Moore & S.B. Franklin

One additional factor suggests *P. capillare* should be more common than *P. persicaria*, i.e. propagule pressure. Chance colonizations are likely on Mississippi River islands where periodic inundations occur throughout the growing season. *P. capillare* produces copious amounts of seed, much more than *P. persicaria*. Such repeated dispersal events should lead to more invasion success (e.g. Chadwell & Engelhardt 2008; Lockwood et al. 2009). Hence, *P. capillare* should be found at greater frequency on Mississippi River islands, which is also corroborated from field data (Moore et al. 2011).

Competition, on the other hand, did not appear to be a major factor determining community assembly in this greenhouse study. However, as evidenced by increased shoot height (Fig. 5), *P. persicaria* could be characterized as the dominant competitor between the two species in this study. The higher impact of older *P. persicaria* on *P. capillare* is one advantage that *P. persicaria* seems to have on the island, suggesting chance of reaching a site first plays a major role in its colonization success. Thus, the resulting community assembly involves niche-based physiological constraints that restrict the commonness of these species to middle elevations and continuous dispersal and chance of early arrival for their continued existence in areas more frequently flooded or drought-prone: the lower and upper ends of the disturbance gradient, respectively. The novelty of this study is that it takes into account arrival time and subsequent response to competition and disturbance regimes that are coupled on riverine islands. Only the interactions of these factors explain the natural distributions of these two species on Mississippi River islands. This study provides evidence for the importance of early arrival and establishment on the subsequent physiological and competitive abilities of plants.

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References


