Small differences in arrival time influence composition and productivity of plant communities

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Summary

‘Who comes first’ is decisive for plant community assembly and ecosystem properties. Early arrival or faster initial development of a species leads to space occupancy both above and below ground and contributes to species success. However, regular disturbance (e.g. biomass removal) might permit later-arriving or slower-developing species to catch up.

Here, artificial communities of grassland species belonging to the plant functional types (PFTs) herb, grass and legume were used to test the effect of stepwise arrival (sowing) of PFTs.

Dramatic effects were found as a result of a 3 wk arrival difference on composition and above-ground biomass that persisted over four harvests and two seasons. Priority effects, such as unequal germination time (arrival), and thus differences in community age structure, had lasting effects on PFT biomass contribution and associated ecosystem functioning. These effects were robust against above-ground disturbance. Benefits of earlier root formation outweighed above-ground species interaction.

Earlier space occupancy and bigger reserve pools are the likely causes. Natural populations commonly exhibit age diversity and asynchrony of development among taxa. In experiments, artificial synchrony of arrival (sowing) may thus induce assembly routes favouring faster-establishing taxa, with consequences for ecosystem functioning (e.g. productivity). Founder effects, such as those observed here, could be even greater in communities of slow-growing species or forests, given their longer generation time and minor disturbance.

Key words: biodiversity, biomass production, competition, germination, population, priority effect.

Introduction

Community composition is largely determined by assembly rules (Diamond, 1975; Weiher & Keddy, 1999). Arrival time of species and their developmental speed and state are key components of these rules. A perennial grassland community is composed of plant species that differ in seed dormancy, seasonal timing of germination, duration to first reproduction, timing of flowering and seed maturation, significance of clonal spreading, and total reproductive life span (Rabotnov, 1966, 1992; Harper, 1977; Rychnovska, 1993). One net result of the influence of these time-dependent traits is the coexistence of several characteristic life stages, such as dormant seed, viable seed, germling, seedling, juvenile, adult, and senescent. The presence or abundance of any of these seven life stages may have a profound influence on ‘ecosystem functioning’, either through the actual biomass contribution of a given species or through robustness and performance, when it comes to disturbance (cutting, grazing, fire) or extreme events (drought, frost). Age diversity thus contributes to the insurance effects of species diversity (Loreau, 2000).
When new land opens or when a given community is eradicated by an extreme event (flooding, fire, landslide, etc.) the early-arriving and faster-developing species are likely to control (dominate) the founder community. As time progresses, initial synchrony will diminish, but the ‘founder effects’ might be propagated for quite some time. There is clear evidence that arrival time of taxa may cause communities to develop into quite different steady-state assemblages. In aquatic model ecosystems, assemblage differences as a result of stepwise arrival of species persisted over as many as 100 generations (Robinson & Dickerson, 1987; Drake, 1991; Fukami, 2004) and final biomass in such systems was found to depend more on arrival time than on initial species diversity (Matthiessen & Hillebrand, 2006). For the outcome of 200 yr of succession under boreal conditions, first arrival of certain (N-fixing) pioneers was found to drive the later forest structure (Chapin et al., 1994). In long-lived trees, founder effects were shown to overrule other environmental influences on later tree species dominance so that only 10% of the compositional variation was attributable to site factors and 90% reflected other, mostly historical, influences.

For grassland, there is circumstantial evidence in the older community ecology literature (Lawton, 1987; Ellenberg, 1996) that ‘priority effects’ may drive succession along different trajectories and a number of studies concerned with invasion and invasibility (VanderPutten et al., 2000; Fukami et al., 2005; Ejrnaes et al., 2006) underpinned the significance of ‘who comes first’. As in aquatic systems (Drake, 1991), different assembly routes (often addressed as ‘assembly rules’) produced vast differences in community structure and biomass. The dominance of certain taxa in mature communities may be the result of priority effects (founder effects, sensu Grime, 1998) as well, and similar to initial differences in nutrient availability, they may affect community composition for a series of years (Inouye & Tilman, 1995; Chase, 2003). Sequential effects in plant communities play a powerful role in channelling community-assembly and also deserve great attention in experiments exploring biodiversity effects on ecosystem functioning.

In recent years, a number of experiments have aimed to test the influence of plant species diversity on ecosystem processes, such as light ‘harvesting’ (Spehn et al., 2000), nutrient retention (Niklaus et al., 2001) and biomass production (Tilman et al., 1997; Hector et al., 1999). Such tests were performed with grassland species for practical reasons. While these experiments have established a firm link between biodiversity and ecosystem processes (Loreau et al., 2001; Naeem, 2002; Hooper et al., 2005), they have also caused considerable controversy (Aarssen, 1999; Huston, 1997; Naeem & Li, 1997; Grime, 1998; Wardle, 1999). The practice of sowing seed mixtures (or planting seedlings) on empty ground represents a potential bias in such experiments. Since this type of experiment will remain of interest for testing biodiversity theory, it is important to know what magnitude of effect species or plant functional type arrival may have.

A central question then is, what effect it has if viable seeds of several species are sown at one date, compared with a variable diaspore release/arrival and germination, as is the case in nature. In naturally assembled communities, variability in timing of arrival and germination influences the assembly path, and thus species establishment. Most of this variability is (at least initially) ironed out for all species used in a common sowing date. Differences in the rate of development among species or plant functional types (PFTs) will create a very particular competitive situation, which differs from that under steady-state community dynamics. If germination happened at one common date, species-specific regeneration waves may cause oscillating species abundance, depending on life history. Synchronous populations may even become extinct by environmental singularities or disturbance, which are affecting one specific life stage but not others (e.g. drought soon after germination, freezing during flowering).

Experiments with grassland systems can be seen as models for systems such as forests that develop too slowly to match convenient experimentation periods. A week in grassland may translate into a year in forest growth, and 50 wk may resemble the development over 50 yr in a forest. Age synchrony and founder effects by unequal, or at least not ‘natural’, starting conditions are thus a general problem in experimental plant communities and deserve more attention. In grassland communities we can test such effects; in forests this would be quite difficult.

Here we offer a test of the influence of one component of community assembly, namely a lag of germination among plant functional types. In naturally assembled communities, a suite of other time-dependent processes may come into play as explained earlier. The test presented here simply mimics a certain delay in arrival (3 wk) of species, for whatever reason such a delay might occur. Variation in time to germination may differ much more in nature. While arrival effects may disappear over many years and lead to steady-state assemblages of populations of diverse ages, such effects are unlikely to disappear in experimental communities observed for a few years.

In the experiment reported here, we first tested the hypothesis that total biomass and functional group biomass contribution at full canopy development are unaffected by a 3-wk earlier arrival of one out of three plant functional groups of plants. The second hypothesis tested is that effects of early arrival, should they occur initially, would disappear during several cutting events over two growing seasons.

Materials and Methods

Experimental design

The effect of species arrival was tested by stepwise sowing of calcareous grassland species, which were selected for their common ecology, similar phenology, vigour and adult size.
The experiment was conducted in a glasshouse (the first 8 wk), and in a common garden (the rest of the time and over winter) using containers. We selected nine species, three belonging to each of one of the three commonly used PFTs in perennial grassland studies: nonlegume herbs, grasses and legumes (in the following nonlegume herbs are referred to as ‘herbs’).

Seeds were obtained from a wild plant seed company (Fenaco, Winterthur, Switzerland), hence the plants, including *Trifolium pratense*, originate from wild populations. Viability of seeds was tested before the start of the experiment, and was 70–100% except for *Anthyllis*, which had only 20% viability, which was accounted for by appropriate seeding density. Six out of nine species were selected to form five different types of communities, so that the number of representatives per functional group was always two species.

Growth conditions

We aimed for a low fertility substrate. Soils were a sieved (5 mm mesh) 2 : 2 : 1 mix of calcareous silt, calcareous sand and garden compost, steam-sterilized before use, and inoculated with 100 ml of a slurry made of 3 kg of rhizosphere soil collected in a seminatural calcareous grassland near Basel where the species used in the experiment occur. The slurry was sieved through a 0.3 mm mesh ‘mycorrhiza-sieve’ (eliminating seeds). Water extracts of the 2 mm soil fraction (1 : 2, field capacity soil : water) revealed the intended low N (570 µmol l⁻¹), normal K (660 µmol l⁻¹), but above-average P (129 µmol l⁻¹, normal range 30–70) concentration. Humus concentration was c. 4% and pH was 7.9, reflecting the calcareous nature of the substrate.

Test containers (27 × 17 × 22 cm, length × width × height) had a 3 cm drainage mat and were filled to 1 cm below the rim with soil (gently compressed). After seeding (in June 2003, see details later), the seedbed was covered with a 3 mm layer of fine soil. Watering until seedling emergence was done carefully with a spray can to avoid washing out of seeds. During the establishing phase (until first harvest), containers were on roll-on tables in a glasshouse, the position of treatment categories was randomized per table and table positions in the glasshouse were randomized weekly. Plants were constrained to grow within the periphery of the containers (constant ground area) by a transparent ‘fly mesh’ net mounted on four corner sticks. Water was always nonlimiting. A fungicide (Hortosan Z, Maag Dielsdorf, Switzerland) was needed once in July to stop mildew on *Trifolium*, and an insecticide (Karate Zeon, Syngenta, Basel, Switzerland) had to be applied to defeat glasshouse whiteflies (*Trialeurodes vaporariorum*), when sticky traps were insufficient during the first 6 wk. The temperature in the glasshouse during July and August reached 25–30°C during the early afternoon, despite full cooling power, because we encountered the hottest summer on record. After the first harvest on 14 September, containers were moved into the botanical garden (under a bird net) for the rest of the time.

<table>
<thead>
<tr>
<th>Mixture</th>
<th>Nonlegume herbs</th>
<th>Grasses</th>
<th>Legumes</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td><em>Centaurea jacea</em> L.</td>
<td><em>Festuca pratensis</em> Hudson</td>
<td><em>Anthyllis vulneraria</em> L.</td>
</tr>
<tr>
<td>B</td>
<td><em>Salvia pratensis</em> L.</td>
<td><em>Holcus lanatus</em> L.</td>
<td><em>Lotus corniculatus</em> L.</td>
</tr>
<tr>
<td>C</td>
<td><em>Centaurea jacea</em></td>
<td><em>Dactylis glomerata</em> L.</td>
<td><em>Anthyllis vulneraria</em></td>
</tr>
<tr>
<td>D</td>
<td><em>Salvia pratensis</em></td>
<td><em>Holcus lanatus</em></td>
<td><em>Trifolium pratense</em> L.</td>
</tr>
<tr>
<td>E</td>
<td><em>Centaurea jacea</em></td>
<td><em>Festuca pratensis</em></td>
<td><em>Trifolium pratense</em></td>
</tr>
</tbody>
</table>

Six species out of nine were randomly selected to form each of five types of communities, so that the number of representatives per functional group was always two species.
Time schedule and harvests
The first cohort of seeds (the founder group) was sown on 28 June 2003, and the second cohort followed on 18 July. Canopies reached closure in the second half of August and were harvested to 5 cm above ground only (in order to avoid any damage) on 12/13 September. This is the only harvest where species could be separated. At later harvests only functional groups were separated. On 14 September all units were moved to the garden and showed rapid regrowth. The second harvest was done on 5–9 November. At that time, the standard 5 cm harvest was complemented with a 1 cm above-ground harvest (harvesting stubble), as plants became robust enough and should enter winter with little above-ground remains. The third harvest in spring 2004 was on 10–11 June (to 5 cm above ground) and the last on 20–23 July (to 5 cm plus total above ground). At the final harvest, we cut a 5.7 cm vertical slice of 17 × 18 cm of the monoliths and washed roots from the upper 9 cm and lower 9 cm separately to calculate total biomass and check for pot bounding effects (accumulation of roots at the bottom, which was not the case). All biomass was dried for 48 h at 80°C.

Statistics
Above-ground biomass of herbs, grasses, legumes, all plants together, and roots was used to test for the effect of ‘species mixtures’ (five levels) and the effect of ‘stepwise sowing’ (three levels). We used ANOVA, when the assumptions of ANOVA (normally distributed residuals and variance homogeneity) could be achieved. Otherwise we used Kruskal–Wallis tests, which was the case when biomass of PFTs was analysed. Students t was used to test for differences between pairs of treatments. Data from the four harvests were tested independently from each other. Taking into consideration stubbles from the second harvest (1–5 cm) did not affect the outcome of the statistical tests. Therefore, and for the sake of comparison and simplicity, we present above-ground biomass data > 5 cm from all four harvests (Fig. 1), and total biomass including root biomass from the final harvest (Fig. 2). Because the assumptions of ANOVA were mostly not met, we did not perform interaction tests or repeated-measures analysis. All statistical tests were done with JMP 3.1. (SAS, Cary, NC, USA).

Results
Stepwise sowing had dramatic effects on biomass of herbs, grasses and legumes at the first harvest when canopies were fully developed and had reached c. 300 g m⁻² in the above-5 cm biomass fraction (Fig. 1, Table 2). Depending on which PFT was the founder group, the biomass composition of the resulting communities was very different: when made a founder group, legume species reached 70%, herbs 98% and grasses 94% of above-5 cm biomass, respectively. Biomass of all plants per treatment group together was also affected significantly by stepwise sowing (Table 2). Total biomass was higher when herbs were the founder group, but also when all species were sown at the same time compared with when legumes or grasses were the founder group (P < 0.05, t-tests).

In the synchronous mixtures, the contribution of functional groups to above-ground biomass differed dramatically from the three stepwise sowing treatments. Herbs dominated the synchronous mixtures as in the herb-founder group, but grasses and legumes were strongly suppressed compared with the legume-start and grass-start group.

This picture did not generally change with the second harvest in November (53, 90 and 90% for legumes, herbs and grasses in the respective start-groups), although the total harvested biomass reached only about one-third of the September biomass, because of shorter duration since the last cutting, shorter day-length and cool weather during growth in the garden plots at that time of the year (Fig. 1). Remarkably, total biomass was lowest at this harvest, when herbs were the founder group (P < 0.05, t-test, Fig. 1), so we expected a suppression of herbs in the next growing season.

After outdoor overwintering and normal spring development, the third harvest yielded some gradual adjustments, but herb- and grass-start communities still retained the first growing season patterns, and differed significantly in their functional group biomass contribution from that in synchronous mixtures. In contrast, legume-start communities were now similar to synchronous mixtures, in terms of both the legume fraction and total biomass (Fig. 1). Stepwise sowing still affected total biomass, but differences among stepwise sowing treatments were now smaller and no longer significant (Fig. 1, Table 2). The data illustrate that grasses could catch up when legumes had an early start, but not when nonlegume herbs had an early start. These latter, herb-dominated communities were still almost grass-free and the grass-start communities were almost herb-free.

At the final harvest after two seasons and four cuts in July 2004, the communities still differed as a consequence of stepwise sowing in their herb and grass fractions, but not in their legume fraction (Fig. 1, Table 2). Biomass of all plants together was significantly lower when herbs or grasses were the founder group (P < 0.05, t-tests). When legumes were the founder group and in the synchronous communities, total community biomass was similar and higher than in the other two groups. Grass-start communities still had hardly any herbs, and herb-start communities had hardly any grasses, as a result of the 3-wk delay of germination of the now suppressed groups. The most pronounced change compared with harvests in the first year is the general recovery of the formerly suppressed legumes in the herb- and grass-start communities. By July 2004, the legume fraction had arrived at a similar share in all community types (of c. 50–58%).
The stubble fraction (0–5 cm) from the final harvest added 60–70 g m\(^{-2}\) biomass to total above-ground biomass in all communities but this changed neither the general picture with respect to community composition (data not shown) nor the difference in above-ground biomass (Table 2). Together with below-ground biomass, communities arrived at c. 560–600 g m\(^{-2}\) biomass at the final harvest (Fig. 2). Legume-start communities had significantly less below-ground biomass than all other communities (\(P < 0.05\), \(t\)-tests). At the final harvest total above-ground biomass (including stubble or not) and below-ground biomass tested separately showed significant effects of both stepwise sowing and type of mixture. However, when above- and below-ground biomasses are pooled, these effects are balanced and disappear.

The effect of species mixtures, that is, of the five different communities of six species that we had randomly chosen from a pool of nine species, showed an interesting trend. Initially (the two harvests in 2003), the presence or absence of a certain species in any of the functional groups did not matter, but the mixture effect became significant in June 2004, but only for legume biomass, and highly significant at the final harvest for legume and total biomass (Table 2). This effect results from
the presence or absence of *T. pratense* in the legume group. The presence of this species caused the biomass of legumes to increase considerably, thereby causing the mixture effect in the second year of the study. Hence our randomization had not completely removed species effects within functional groups, at least not for legumes.

Accumulated over the complete experimental period, the above-ground (> 5 cm) biomass production was highest (900 g m\(^{-2}\)) in synchronous sowing, lower (850 g m\(^{-2}\)) in the legume-start communities, and lowest in the grass-start (774 g m\(^{-2}\)) and herb-start (778 g m\(^{-2}\)) communities (*P* = 0.045). Thus, even when legumes were a start group, the above-ground biomass was lower than in synchronously sown communities, with a balanced PFT presence. That difference became enhanced when roots were included (means for synchronous 1210 g m\(^{-2}\) vs 1050, 1065 and 1080 g m\(^{-2}\) for the grass-, herb- and legume-start treatments; including final stubble the corresponding numbers were 1280, 1158, 1136, and 1131 g m\(^{-2}\)), but because of the low replication in synchronous communities, these differences were not significant.

**Discussion**

A 3 wk difference in initial germination can cause lasting differences in community composition and biomass even after four harvests and two seasons of growth. Our first hypothesis was falsified and we need to conclude that differences in founder species are significant for community composition and final biomass even when species and functional group diversity are identical. At our final harvest, the contribution of herbs still varied between 4 and 44% of total above-ground biomass, that is, 11-fold. In competition with grasses, which were given a 3 wk advantage at the start, herbs were sustainably suppressed, almost eradicated and vice versa for grasses in herb-start mixtures. Given the only 3 wk difference in arrival under otherwise identical growth conditions, these effects were far more dramatic than we had expected and illustrate the importance of timing effects for community assembly. Using similar microcosms, Ejrnæs *et al.* (2006) tested 5 month to 1 yr delayed arrival effects in specialist vs opportunist taxa (a total of 24) across a monthly vs no cutting and 18-fold N-addition treatment. These treatments created large differences in final species assembly, with the fastest-growing opportunist-start group in fertile soil arriving at 31 times the biomass of the slowest-growing, small size specialist-start group in very poor soil. Their experiment showed that soil fertility and disturbance controlled the assembly process in a way that made final diversity predictable.

The fact that synchronous and legume-start communities arrived at similar final functional group composition and above-ground biomass comes as another surprise. For legume-start mixtures, our hypothesis that priority effects would disappear within a growing season was not falsified, perhaps because of the high phosphate, but rather moderate nitrogen, availability in our soil and the positive effects of N-fixation on the N-limited companion PFTs. Legumes were the only functional group that did not perpetuate its initial advantage; hence the priority effect disappeared after the first season. For grass and herb-start communities, it seems that a lot more time is required for priority effects to disappear.

Some of these effects might have emerged so clear-cut because of the high standardization and replication we used, and we cannot exclude the possibility that some species effects, that is, special behaviour of a single taxon, had some influence on our results, given that we only sampled from a pool of nine species. This was the case for *T. pratense*, the presence of which caused mixtures to become more productive after a year. In a natural setting, priority effects, such as the one observed in our study, are likely to matter as well, but may not become so obvious because of greater variability of population demography (age distribution).
Table 2 P-values from tests of the effects of ‘species mixtures’ and ‘stepwise sowing’ on biomass above 5 cm of herbs, grasses, legumes and their sum in four consecutive harvests, as well as on total above- and below-ground biomass at the final harvest

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Harvest after 8 wk</th>
<th>Harvest after 16 wk</th>
<th>Harvest after 50 wk</th>
<th>Harvest after 56 wk</th>
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<tbody>
<tr>
<td>Species mixtures</td>
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<td>Stepwise sowing</td>
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<tr>
<td>Harvest after 8 wk</td>
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<td>Species mixtures</td>
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<td>Harvest after 16 wk</td>
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<td>Species mixtures</td>
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The five different ‘species mixtures’ contained six out of nine species, so that the three functional groups, herbs, grasses and legumes, were represented by two out of three available species. ‘Stepwise sowing’ (three levels) consisted of sowing one functional group (two species) 3 wk before the two other functional groups. Each combination of ‘species mixtures’ × ‘stepwise sowing’ was represented by four replicates (n = 60). Significance levels are from ANOVA, when their assumptions were met, otherwise they are from Kruskal–Wallis tests. ***, P < 0.001; **, P < 0.01; *, P < 0.05; ns, not significant.

*Measured only at the final harvest after 56 wk.

From the persistence of priority effects after repeated severe above-ground disturbance (harvesting), we must conclude that what we observe strongly reflects below-ground effects. Initial soil exploration and root biomass formation during the establishment phase seems to determine the competitive status of plants, and the regular resetting of leaf area index to low values does not negate differences in starting conditions. Root system development needs photo-assimilates in the first place, but once established, the root : shoot ratio seems to be conservative (Brouwer, 1983), except for legumes which recovered fastest from suppression as a result of late arrival. High phosphate availability in the current experiment, known to favour legumes’ competitiveness in calcareous grassland, may have facilitated this fast recovery (Stöcklin & Körner, 1999).

The strong influence of arrival sequence found in this experiment is not necessarily in conflict with the major outcome from standardized (synchronous) species diversity – ecosystem functioning experiments, which successfully tested hypotheses for a given composition and diversity of designed plant communities. However, the initial absence of a natural variation in age structure may have contributed to a very specific biomass fractionation among species and PFTs and, thereby, may have influenced the results (e.g. harvestable biomass). In contrast to what is seen in nature (Al-Mufti et al., 1977; Kahmen et al., 2005; Grace et al., 2007), these experiments have shown greater productivity in mixtures with higher species number, which was explained by complementarity or sampling effects (Tilman et al., 1997; Hector et al., 1999). Early arrival represents a quasi-sampling effect (giving priority to certain species or PFTs), whereas late arrival represents a quasi-depletion of effective diversity, because later-arriving species contribute less to community biomass. In other words, only slight differences in arrival or onset of development can mimic both a sampling and a complementarity effect. The role certain species or PFTs play in a community is thus strongly affected by such initial timing issues. Randomization of species from a large pool may mitigate such effects to some degree, as may long duration of observation. However, such phenomena may still contribute to the obvious discrepancy between results of designed (initially synchronous) experiments and natural grassland, simply by unintentionally giving priority to faster-developing taxa, of which there may be more in more diverse communities (sampling).

Presumably, the fast life cycles in grassland communities are diminishing arrival effects with time, and repeated seeding into existing communities is a wise precaution. However, self-perpetuation of timing phenomena during early community establishment in longer-lived plants such as trees would inevitably have far more dramatic consequences and need to be taken into account in the planning of such long-term experiments. Just imagine planting seedlings of poplars and oaks, or alder and spruce, on the same day – to mention two extreme examples. Providing unequals with equal starting conditions always causes some bias, as does the neglect of timing and development in any experiment with plants.

References


