

1 **Temporal dynamism of resource capture: a missing factor in ecology?**

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15 **Abstract**

16 Temporal dynamism of plant resource capture, and its impacts on plant-plant interactions, can
17 have important regulatory roles in multi-species communities. For example, by modifying
18 resource acquisition timing, plants might reduce competition and promote their coexistence.
19 But despite the potential wide ecological relevance of this topic, short-term (within-growing
20 season) temporal dynamism has been overlooked. This is partially a consequence of historic
21 reliance on measures made at single points in time. However, we propose that with current
22 technological advances this is a golden opportunity to study within-growing season temporal
23 dynamism of resource capture by plants in highly informative ways. Here, we set out an agenda
24 for future developments in this research field, and explore how new technologies can deliver
25 this agenda.

26

27 **What is temporal dynamism and why is it important?**

28 Understanding plant community composition and functioning are fundamental challenges in
29 ecology. It is not yet fully understood why specific communities exist at certain points in space
30 and time, why some communities are more diverse than others, and how diversity impacts
31 ecosystem function. In plant communities, many theories have been proposed to explain plant
32 coexistence including cyclical disturbance [1,2], different individual responses to species
33 interactions [3], multiple limiting resources [4,5], intraspecific trait variation [6], and facilitative
34 plant-plant interactions, particularly in extreme environments [7,8].

35 We argue that short-term (i.e. within-growing season) temporal dynamism (see
36 Glossary) in resource acquisition might be central to addressing these fundamental challenges.

37 Temporal dynamism can be described as a form of heterochrony (see Glossary), controlled by
38 intrinsic gene expression but also influenced by external environmental factors such as climatic
39 conditions [9]. However, apart from in a few cases, within-growing season temporal dynamism
40 in resource acquisition is rarely considered as a topic in its own right, in part because it has
41 historically proven hard to measure. This contrasts, for example, to our knowledge of other
42 temporally dynamic processes such as plant phenology, about which much more is known.

43 Phenological studies have shown the importance of the timing of key events in the
44 structure and functioning of plant communities [10]. Therefore, similar important
45 consequences for temporal dynamism in resource capture might be reasonably expected. For
46 example if different species temporally segregate (see Glossary) capture of common resources
47 to avoid competition, increased complementarity can promote plant coexistence [11] with
48 profound implications for fundamental processes such as biodiversity-ecosystem function
49 relationships. Importantly we propose that, due to the wealth of new analytical approaches
50 currently available, now is the time to address the historical oversight of within-growing season
51 temporal dynamism.

52 Before considering these new opportunities, we examine previous studies of temporal
53 dynamism, with a focus on resource capture. We discuss the limitations of, and lessons learned
54 from previous studies, and how they can form the basis of a future research agenda. We then
55 focus on new experimental approaches, considering how these can address current knowledge
56 gaps, and discussing the wider relevance of this subject area to ecology.

57

58 **Past studies of temporal dynamism in plant communities**

59 Previous research provides clear examples of how temporal dynamism of ecological
60 processes can regulate the structure and functioning of plant communities. Arguably one of the
61 most well studied examples is plant-pollinator interaction dynamics. Pollinators vary the plant
62 species visited inter-annually, which promotes coexistence in species rich communities [12,13].
63 Other examples involve temporally dynamic resource capture; in arid environments, temporal
64 dynamism has been found in the growth response of plants to erratic inputs of water [14],
65 depending on both the timing of the water input in the growing season and the time since the
66 previous water input [15]. In alpine systems, nutrient turnover is temporally dynamic, with
67 mineralisation occurring throughout winter [16], and spring microbial turnover then providing
68 nutrients to plants [17].

69 Such temporal dynamics are not only of academic interest – they can play a central role
70 in regulating the impacts of key environmental change drivers. For example, one way non-
71 native species can become invasive is by occupying a vacant niche [18]. Occupying a temporal
72 niche left vacant by the native plant community could allow the invasive species to capture
73 nutrients at a time of reduced competition. It may appear that in some cases invasive species
74 take over a niche from native species. However, it is unclear whether invasive species
75 establishment depends on the exploitation of a temporal niche gap. Although phenological
76 differences between native and invasive species have been shown [16], the underlying role of
77 within-growing season temporal dynamism in nutrient capture is yet to be demonstrated (likely
78 for the reasons we discuss below). A similar example is the phenology of hemi-parasitic plants.
79 The lifecycle of many hemi-parasites is shortened relative to its hosts, influencing nitrogen
80 cycling with earlier leaf fall than the host community [19,20]. Early leaf fall provides an input of

81 nitrogen to the host community when it is becoming limited [21]. Here the rate of water and
82 nitrogen uptake by *R. minor* parasitizing *Hordeum vulgare* (barley) has received attention [22]
83 but the temporal dynamics of this interaction have yet to be explored.

84 These examples, just a selection from the many that could be listed, demonstrate the
85 likely importance of temporal dynamism of resource capture by plants. Far fewer studies have
86 sought to measure this process directly. An important example is the work by Trinder *et al.*,
87 which used a series of destructive harvests to examine the temporal dynamics of nitrogen
88 capture and biomass accumulation of *Dactylis glomerata* (Cock's foot) and *Plantago lanceolata*
89 (Ribwort plantain). Trinder *et al.* found that in response to interspecific competition, both
90 species shifted the timing of the maximum rate of biomass accumulation and nitrogen capture
91 by up to 17 days [23]. The species diverged the timing of these resource capture processes, in
92 ways that possibly reduce direct competition. However, it is notable that this type of study,
93 looking explicitly at the temporal dynamism of resource capture, is to the best of our
94 knowledge, extremely rare.

95

96 **Why does it matter that temporal dynamism has been overlooked?**

97 Many of the fundamental processes and properties of terrestrial communities are governed by
98 the outcome of plant-plant interactions [24]. However, despite a huge amount of work on
99 plant-plant interactions, especially competition, there are still unanswered questions about the
100 role of plant-plant interactions in governing plant community composition.

101 For example, our current understanding of the niches available within plant
102 communities, which strongly regulates plant-plant interactions, cannot explain the level of
103 observed coexistence [25]. A better understanding of short-term temporal dynamism in
104 resource capture, and its consequences for plant-plant interactions, might help explain this
105 apparent paradox. Temporally dynamic resource capture processes, and the temporal niche
106 segregation which this could enable, could alter critical plant-plant interactions so as to have a
107 stabilising effect on communities. This would allow a higher diversity than would otherwise be
108 the case to be supported [26], at potentially both a species [27] and genotypic level [28], with
109 the community using a greater proportion of the available resources [29]. In this example,
110 temporal dynamism in resource capture can be considered as an unmeasured trait (Box 1).

111

112 **Why has temporal dynamism in resource capture been overlooked?**

113 Given the general importance of the temporal dynamism of ecological processes, and
114 the likelihood that in many cases this is related also to temporally dynamic resource capture
115 within a growing season, why have so few studies explicitly addressed this latter topic?

116 Plant ecology has traditionally relied on one final biomass measurement to assess the
117 consequences of plant-plant interactions. Biomass is a relatively cheap and easy measure of
118 plant response, making large-scale greenhouse and field studies possible [26]. However, there
119 are some drawbacks to using single time point measurements of biomass to assess plant-plant
120 interactions, and especially the short-term temporal dynamism of these processes. First, due to
121 the influence of other external environmental factors, the accumulation of biomass is rarely
122 influenced by competition alone [23]. This makes it an unreliable direct measure of the

123 outcome of competition. The use of only single harvesting to assess the outcome of plant-plant
124 interactions is clearly inappropriate for measuring short-term temporal dynamism in resource
125 capture. In addition, the precise timing of biomass harvest and measurement within a growing
126 season can influence the perceived outcome of the plant-plant interaction, as plants grow and
127 develop at different times throughout the year [26]. The same criticisms can also be made of
128 other common annual, single time-point measurements, for example flower production and
129 seed set. To understand the role of temporal dynamism of resource capture in regulating
130 community dynamics, repeated measures of *resource capture* are required. However, in order
131 to take this step we need first to realise and accept the limitations of single time point studies,
132 and move to more detailed studies of the competitive process itself.

133 Traditional approaches, for example plant biomass and tissue nutrient content analysis,
134 can be used to explore issues of temporal dynamism in plant-plant interactions. However, they
135 need to be coupled to multiple harvesting points through time, as used by Trinder *et al.* to
136 examine the temporal dynamics of resource capture in *Plantago lanceolata* and *Dactylis*
137 *glomerata* [23]. Although the multiple harvest approach is a valuable tool, it is destructive and
138 requires large-scale, labour intensive studies. The inclusion in a study of multiple harvests to
139 track temporal dynamism of resource capture and plant-plant interactions through time
140 increases the size and complexity of an experiment, and therefore reduces the complexity of
141 the questions that can be asked [11,29]. Also, multiple harvesting means responses are
142 averaged over many plants, potentially masking subtle dynamic individual-level responses in
143 resource capture and growth. Non-destructive methods, would instead allow the responses of
144 an individual plant to be studied over time.

145 Such drivers of the historical oversight support a case for the use of innovative new
146 technologies, particularly non-destructive, direct measures of resource capture, so that
147 temporal dynamism of resource capture can be given the attention it deserves.

148

149 **Setting and addressing a new research agenda**

150 From the above discussions, and consideration of well-known ecological concepts, a
151 series of questions can be presented (See Outstanding Questions box) in a clear research
152 agenda. If addressed, this agenda could advance the study of temporal dynamism of resource
153 capture. Importantly, this research agenda is not just of relevance to plant ecophysiologicals or
154 community ecologists. By influencing, for example, the temporal availability of resources to
155 other groups such as soil organisms, pollinators and herbivores, the study of temporal
156 dynamism in plant resource capture will likely have wide-reaching consequences for ecological
157 research.

158 As discussed, whilst temporal dynamism in resource capture can itself be detected using
159 destructive harvesting techniques [19], new technological approaches are required to look at
160 the complex series of processes involved in the dynamics of plant nutrient capture and its role
161 in community composition. Below, we provide examples of how these advances might enable
162 some of the key questions of the research agenda to be addressed.

163

164 *What is the interaction of temporal dynamism of resource capture with plant physiology and*
165 *morphology?*

166 The plasticity of plant root traits may facilitate the temporal dynamics of resource capture;
167 whilst at the same time, root physiology and morphology could be influenced by changes in the
168 temporal dynamics of nutrient uptake. Therefore, the relationship between temporal
169 dynamism of resource capture and root traits is a key topic, as roots are the organs of nutrient
170 uptake.

171 Microrhizotrons - small cameras inserted into the soil to record root foraging and fine
172 root developing [31,32] – allow the study of root foraging activity. However, they are limited in
173 not giving a view of the whole root system. Whole root system growth dynamics can be studied
174 with automated root phenotyping facilities, using high definition cameras to photograph root
175 development of plants grown in Perspex boxes [33]. Changes in root morphology and foraging
176 can then be related to the location of soil microbial activity (zymography – see below) and plant
177 nutrient capture.

178 For a 3D view of root growth dynamics, X-ray CT scanning can be used to visualise plant
179 roots grown in soil. Root architectural development can then be related to resource capture.
180 The development of specialist root tracking software and facilities [34] will allow much larger
181 and more complex experiments to be carried out into dynamic competition for soil resources
182 between the roots of multiple individuals. This approach has already been used to study root
183 growth in response to competition between *Populus tremuloides* (Quaking aspen) and *Picea*
184 *mariana* (Black spruce) seedlings. Both species increased rooting depth and altered root
185 architecture in response to a competitor [35], but this study did not simultaneously assess soil
186 resource capture. By combining successive scanning of root growth and successive destructive

187 harvesting to look at the temporal dynamics of nutrient uptake the relationship between root
188 growth and nutrient uptake can begin to be addressed.

189
190 *Is temporal dynamism in nutrient capture moderated in response to neighbours simply by*
191 *overlapping depletion zones or by more complex signalling pathways?*

192 Traditionally plant competitive responses to a neighbour have been thought to occur when the
193 zones of nutrient depletion in the soil overlap [36]. As the complexities of plant-plant
194 communication are revealed [37], it is becoming clear that plant-plant competitive interactions
195 might not occur solely based on nutrient availability. RNA sequencing, which enables us to
196 examine the genes upregulated in specific circumstances from tissue samples, is one way to
197 look at dynamic plant responses to the presence of a neighbour.

198 Studies in *Arabidopsis thaliana* have identified that common stress response pathways
199 such as jasmonate production are activated in response to a competitor [38]. Detection of the
200 upregulation of stress associated genes can indicate when a target plant detects the presence
201 of a neighbour, whether the response is different depending on the identity of the neighbour,
202 and the length of time between neighbour detection and any form of additional physiological
203 response by the target plant (e.g. priming of soil microbes – see below).

204 A key question is whether upregulation of gene expression occurs before the nutrient
205 depletion zones of neighbouring plants overlap. Such an effect would indicate that responses to
206 neighbouring plants are more complex than simply a response to the overlap of soil depletion
207 zones as a consequence of developing root systems. The question of whether plants start
208 responding to neighbours and the threat of potential competition long before they come into

209 close physical contact can then be addressed. This approach, therefore, provides a unique
210 opportunity to understand temporal dynamism and competition at a molecular level, and to
211 determine how temporal dynamism of resource capture is moderated in response to
212 competition through a cascade of molecular responses in the target plant.

213

214 *How does the activity of the soil microbial community influence temporal dynamism in resource*
215 *capture?*

216 Throughout the year, soil microbial communities mineralise and immobilise nutrients
217 from soil organic matter (SOM), driving nutrient cycles that mobilise organic nutrient stocks
218 into plant available forms during the growing season [39,40]. Plants can influence these
219 processes through the rhizodeposition of labile carbon and amino acids to influence microbial
220 process rates (rhizosphere priming effects, RPE [41,42]), with rhizodeposition varying with
221 plant development, species and genotype [43–45].

222 One method to examine the influence of plants on the dynamics of SOM mineralisation
223 is to study the timing of rhizosphere priming effects for plants in competition vs. isolated plants.
224 Stable isotope labelling ($^{15}\text{N}/^{13}\text{C}$) can allow plant impacts on soil nutrient cycles to be quantified
225 [46]. This can be done non-destructively and dynamically through isotopic partitioning of soil
226 CO_2 efflux into plant and SOM-derived components [47], or tracing ^{15}N fluxes (derived from
227 labelled organic matter) in soil solution [48–50]. This approach allows the timing and magnitude
228 of soil community priming to be measured over time, and compared relative to other
229 temporally dynamic measurements including RNA expression (see above) and resource capture.

230 Further information about specific soil microbial activities can then be provided through
231 soil zymography (see Glossary), allowing the location and intensity of enzyme activity in soil to
232 be quantified over time [51]. This methodology has already been used to identify 'hot
233 moments' when microbial activity is higher than background levels [52]. Such 'moments' can be
234 occasional or occur periodically with events like spring growth and autumn leaf fall [53]. Using
235 these techniques, it can be assessed for example, whether periods of greater microbial activity
236 precede plant nutrient capture or whether they are themselves dependent on priming activities
237 by the plant.

238

239 *How are the temporal dynamics of soil microbial community composition influenced by plant*
240 *temporal dynamics?*

241 A critical factor regulating the functional capacity of soil communities to mediate
242 nutrient cycling is their composition. The soil community is known to be temporally dynamic
243 seasonally and with plant developmental stage [24]. Shi *et al.* used a 16S ribosomal RNA
244 approach to produce a network representation of microbial diversity over two growing seasons,
245 comparing bulk and rhizosphere soil (Figure II) [54]. The decreasing cost, increasing throughput
246 capacity and analysis speed of genomics creates an opportunity to study temporal dynamism in
247 the soil community over the growing season [55]. When compositional studies are combined
248 with studies of soil microbial activity (e.g. using metatranscriptomics), it can be assessed how
249 changes in the dynamism of plant resource capture are associated with either short-term (i.e.
250 more activity-based) or long-term (i.e. more community-composition based) changes in the soil
251 community.

252

253 **What is the future strategy to study temporal dynamism?**

254 Temporal dynamism is an overlooked factor in ecology and could be a vital central mechanism
255 by which plants coexist in complex communities. Although studying temporal dynamism of
256 resource capture is not going to be straight forward, the potential benefit to the understanding
257 of ecosystem functioning is likely to be considerable. There is now an ideal opportunity to
258 understand the within-growing season temporal dynamics of resource capture as part of
259 broader ecological system dynamics.

260 In order to understand the role of temporal dynamism of resource capture in plant
261 coexistence it needs to be understood how plants coordinate temporally dynamic responses,
262 the intermediary role of the soil microbial community, and the consequences at the individual
263 plant and plant community level. Therefore, to study these distinct, but interconnected
264 processes, an integrated approach is required [56]. From the examples we have discussed
265 above it is clear that a vast amount of knowledge can be gained about temporal dynamism in
266 resource capture from using these cutting edge technologies. Once the fundamental questions
267 about temporal dynamism of resource capture have been addressed, the wider community
268 level consequences can then be considered, building upon these fundamental studies.

269 The ultimate goal of this research should be to integrate temporal dynamism as a factor
270 in existing models, to define new niche space and aid the explanation of coexistence in complex
271 communities. Only then can the question of whether temporal dynamism in resource capture
272 leads to coexistence of neighbouring plants can begin to be addressed. This approach can then

273 be applied to other temporally dynamic processes, answering other fundamental questions
274 about ecosystem functioning.

275

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281

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408

410 **Box 1. Theory of temporal dynamism of nutrient capture**

411 Plants do not uniformly take up nutrients throughout the growing season. Instead, nutrient
412 capture is regulated based on the nutrient requirements and growth stage of the plant [57].
413 When plants are grown in isolation, nutrients are taken up at the optimum time (Figure I,
414 panels A and B show two individuals grown in isolation). However, when plants are grown
415 together the timing of nutrient capture might change, perhaps to minimise competition (panel
416 C shows the two individuals grown together). This can then promote coexistence of competing
417 individuals [11], and might be an important factor in communities such as tropical rainforests
418 and grasslands, with multiple species timing key processes differently to minimise competition
419 (panel D shows a hypothetical multispecies community with each line representing a different
420 species).

421

422 **Schofield et al.**

423 **Glossary**

424 **Heterochrony:** a change in the timing and rate of a developmental process within an organism
425 compared to an ancestral species, including the onset and duration of flowering, leaf
426 production and internodal length [9].

427 **Temporal segregation:** a shift in the timing of a process in response to a neighbouring
428 individual. Commonly observed in animal feeding, it limits niche overlap and promotes
429 coexistence. Some niche overlap is still to be expected, but direct resource competition is
430 reduced.

431 **Resource capture:** the acquisition of resources, including nutrient, water and light, by a plant.
432 This is commonly expressed as a rate, i.e. units of resource capture over a period of time.

433 **Soil zymography:** non-destructive method to measure chitinase, cellulase or nitrogen
434 mineralisation hotspots at a fine spatial resolution in the soil. Useful for studying changes in the
435 location and intensity of enzymatic activity over time.

436 **Temporal dynamism:** variation through time in the rate or effect of a particular process. For
437 example, this could be variation in the per unit biomass capture by a plant of soil nutrients or
438 water, or the extent to which neighbouring plants are competing with each other (which might
439 itself result from temporal dynamism in resource capture by individuals). Such temporal
440 dynamism can be driven by external factors (changes through time in climate or resource
441 availability) or intrinsic factors (e.g. plant developmental stage).

442 **Within-season temporal dynamism:** variation through time, but within a given growing season,
443 in the rate or effect of a particular process. Such variation is distinct from inter-annual variation,
444 which might be caused by factors such as variation in climate between growing seasons.

445 **Schofield et al - Figure legends**

446 **Figure I. Theoretical role of temporal dynamism in plant coexistence**

447 In isolation (panels A and B) plants take up nutrients in a specific profile over the growing
448 season. But when grown together (panel C) the two plants offset the period of maximum
449 nutrient capture to limit competition. In a multispecies community (panel D) this might could
450 lead to species occupying distinct temporal niches, leading to coexistence.

451

452 **Figure II. Temporal dynamics of plant associated soil community**

453 Figure showing the potential role of soil community characterisation and network analysis to
454 study the temporal dynamics of soil community associated with resource capture. The
455 difference in the rhizosphere and bulk soil community of *Avena fatua* was compared over two
456 growing seasons. Samples were taken every three weeks for two seasons. Shi *et al.* looked at
457 the difference in the diversity and level of interconnection between bulk and rhizosphere soil.
458 Nodes represent operational taxonomic units (OTUs) and lines the linkages between them. The
459 rhizosphere soil becomes more interconnected but less diverse over time as the plant exerted a
460 selection pressure on the soil community [54].

461

462 **Figure III. The potential role of soil zymography in studying temporal dynamism in soil**
463 **community activity**

464 The potential role soil zymography analysis can play in studying the temporal dynamics of soil
465 functions. The cellulase activity surrounding roots of *Lupinus polyphyllus* (Large-leaved Lupin)

466 was analysed 18 days after sowing (a), and 10 days (b), 20 days (c) and 30 days (d) after cutting
467 shoots [51].