

MECHANISMS OF PLANT COMPETITION

Plant ecology's guilty little secret: understanding the dynamics of plant competition

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Summary

1. Plant competition has been studied for decades. Yet, it is still an elusive concept that means different things to different people, is resistant to direct study and is shrouded in semantic and statistical complexity. We still lack basic information about many competitive mechanisms, processes and outcomes and their relationship to other ecological processes, and about how local interactions between individuals are propagated through communities. We suggest here that two critical issues have been overlooked in previous studies.

2. First, there is a need for direct measurements of the process of competition as opposed to indirect mechanisms of competitive outcomes. Biomass has become the 'industry standard' for measuring competition, but we suggest that biomass cannot provide unambiguous insights into plant competition because it is the product of too great a range of factors and processes.

3. Second, the use of a single measure of competition at an arbitrarily assigned end point of an experiment misses much of the complexity of dynamic interactions between competing plants and can lead to erroneous interpretations. Here, we suggest approaches to handle these difficulties, using new techniques or the application of well-known methods in a novel way. We also provide examples of systems or questions where the improved understanding these approaches could bring would be of particular benefit.

4. Ultimately, we suggest the need for a major shift in the way in which we consider and measure plant competition to identify broadly agreed rules for variation in its importance, its role in different communities and habitats, and how and whether it influences or drives patterns of species diversity and abundance.

Key-words: biomass, direct measurements, mechanism, multiple harvests, processes, scaling-up, short-term dynamics, trade-offs

Introduction

Plant ecology in the 21st century is concerned largely with understanding how communities assemble, function and respond to environmental challenges and how populations evolve spatially and temporally. It is almost axiomatic that a significant influence on those processes is competition between individuals. But close inspection reveals 'plant competition' to be an elusive concept that, despite decades of research, means different things to different people, is resistant to direct study and is shrouded in semantic and statistical complexity. Since Tansley's classic study in 1917, the literature has been replete with 'plant competition' experiments, but many of these give only partial, indirect

or weak information about the ecological and evolutionary role of competition. Yet, such experiments provide much of the empirical bedrock on which the prevailing theories of plant ecology rest and in which competition plays central but contrasting roles in relation to other ecological processes and environmental factors (Grime 1977; Tilman 1982). For example, there is substantial ongoing debate about the extent to which biotic interactions such as competition influence macroscale ecological patterns (Ricklefs 2008, 2009; Brooker *et al.* 2009).

Many mechanisms of plant competition are of course well known: shading of small plants by taller neighbours; aggressive growth of finely branched roots to exploit nutrient-rich soil; exudation of allelochemicals to suppress the growth of a neighbour; and so on. Surprisingly, however, we still lack basic information about many competitive

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mechanisms, their relationship to ecological processes (e.g. reproduction, dispersal, colonization) and, crucially, about how local interactions between individuals are propagated through communities. Until we understand and resolve these issues, we believe that the competition controversy (Craine 2005) will continue and the potentially powerful application of competition theory to address immediate and future problems of habitat conservation, ecosystem resilience and community responses to climate will continue to be hampered.

Here, we discuss two key issues that we consider have received insufficient consideration in investigations of the mechanistic bases, occurrence and ecological significance of plant competition. These are: (i) direct measurements of the process of competition as opposed to indirect measurements of the outcomes of competition; (ii) limitations to understanding imposed by conventional experimental approaches. These are linked by the idea that competition among neighbouring plants is *dynamic*, even though it is rarely investigated on that basis. This is something of which many plant ecologists are probably well aware, but tend to ignore, hence the title of this paper. We argue also that treating competition as a dynamic process, regulated via the mechanisms discussed in detail elsewhere in this Special Feature, could help resolve many enduring uncertainties. But first we need to be clear on the definition of 'plant competition' that we will be using in this paper.

Defining plant competition

Everything is vague to a degree you do not realize till you have tried to make it precise.

Bertrand Russell

Pleas for better ways to define and measure plant competition and to evaluate its true ecological role appear periodically. For example, Harper (1961), Grime (1973), Tilman (1982), Newman (1983), Welden & Slausen (1986), Thompson (1987), Grace (1995) and Craine (2005), and the many responses to them, have highlighted important aspects of this problem. They have all stimulated considerable discussion; some have sparked controversy, affirming the central importance of the idea of competition to ecological theory, the strong need to understand it properly and the continuing frustration at our inability to do so. It is worth noting that similar critical irruptions are also familiar in animal ecology (Diamond & Gilpin 1982; Simberloff 1983; Connor & Simberloff 1986). The current position is one in which 'competition' is as much a part of the plant ecology furniture as it is of ecology generally (Loreau 2010), not because it is fully understood, but because it is a useful concept.

But it is not news that a substantial part of the enduring difficulties with usefully applying the concept of 'competition' in ecology originates with semantic confusion (Harper 1977; Grace 1990). That is not necessarily a problem provided that the term is defined explicitly with respect

to a given study, and it is not assumed that the meaning of any definition is universally applied (or, indeed, accepted). Greater clarity is achieved if definitions are as unambiguous and precise as possible. Here, we define 'plant competition' as the capture of essential resources from a common, finite pool by neighbouring individuals (Grime 1979; Trinder *et al.* 2012a). This definition includes both the direct use of common resources by neighbours and also the indirect effect of one plant on the availability of a resource to its neighbour, a distinction noted by Goldberg (1990). Our definition implies that competition is a process. This automatically defines biomass or seed production by neighbouring individuals (the most usual indirect estimates of 'competition': see below) as *outcomes* of competition (but, importantly, of other processes too). This is a logical distinction. There is also a substantial difference between identifying a *mechanism* and understanding in detail how it operates to influence a *process*. Perhaps less obviously, our definition means that the production, functioning and maintenance of leaves, stems and roots (and their almost ubiquitous microbial symbionts) are considered mechanisms by which the process of competition can operate. This deliberately narrow definition allows mechanisms to be separated from the process, but does not preclude other ecologically useful definitions to suit other purposes. For example, 'capture' can be defined as instantaneous fluxes of resources – water, solar radiation, carbon, nutrients or their energetic equivalents – into individuals (such fluxes are shown as the broken arrows in Fig. 1) via growing roots and leaves, or as the resources accumulated by individuals over a certain period (Trinder *et al.* 2012b). In terms of Fig. 1, we are interested here in the measurement of the instantaneous resource fluxes indicated by the broken arrows, their mechanisms (including how they influence, and are influenced by, biomass production), their cumulative products and their temporal dynamics. Quantifying the effects of competition on subsequent demographic processes (seed production, dispersal and seedling recruitment: Fig. 1) is an ultimate but still-distant goal.

Direct vs. indirect measurements of plant competition

The use of resources to produce seeds and other propagules links competitive resource capture to fecundity (Fig. 1). Consequently, there are likely to be cause-and-effect relationships between resource capture and growth and, ultimately, with reproductive output and the potential demographic successes or failures of plants growing with their neighbours. Even so, measurements of neither competitive outcomes (seed production, for example) nor competitive mechanisms (root and leaf growth; release of allelochemicals) are *direct* measurements of the competitive process itself (resource capture). By measuring competition directly, we can test the justification for long-held assumptions about causal relationships between the process and either the mechanisms by which that process operates or

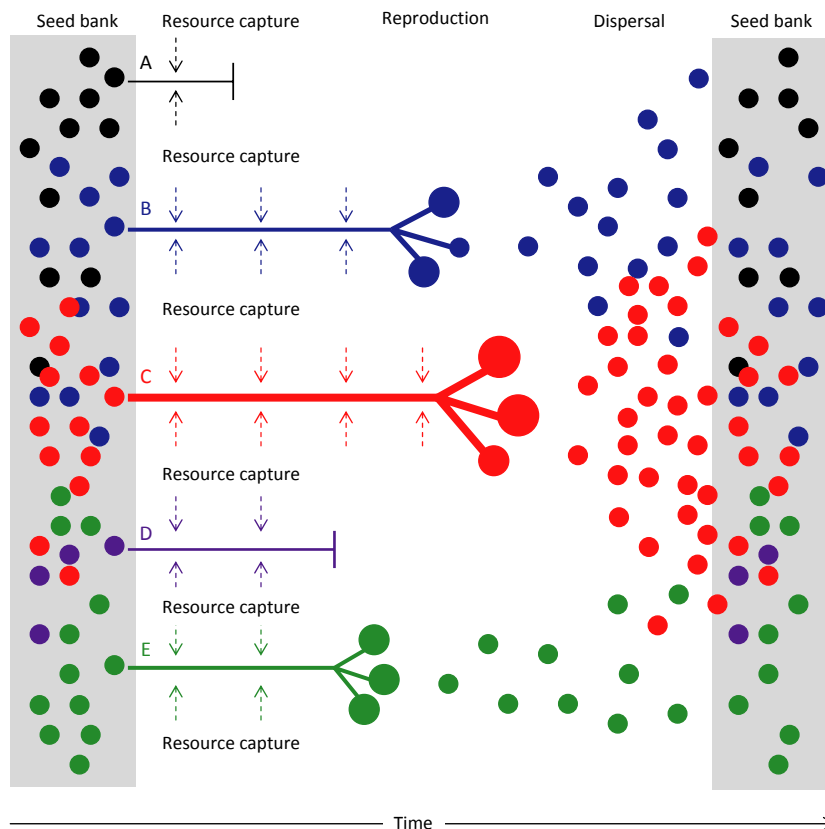


Fig. 1. Schematic relationships among five neighbouring plants (A–E) between competitive resource capture (broken arrows), biomass production (proportional to line thickness), survival and fecundity (seed production). Of the five individuals that recruit successfully from the seed bank, only three (B, C, E) capture sufficient resources and survive long enough to convert resources into seeds. Competition occurs while individuals survive and resources are available for capture. Of the seeds produced and dispersed, some enter the seed bank; others are predated. No distinction is made between intra- and interspecific interactions between neighbours. For simplicity, plants are shown as reproducing monocarpically and to compete within a single growing season. But with suitable elaboration, an analogous scheme can be developed for polycarpic individuals and which also includes competitive interactions across seasons. Modified from Harper (1977, p. 29).

might be regulated, or of its short- or long-term outcomes. For example, the attribution of functional significance to phenotypic traits has long been a preoccupation of plant ecologists (e.g. Grime 1979; Grace 1990) and, in particular, how specific traits contribute to ‘competitiveness’. The narrow definition of competition we use here is intended to improve the robustness of such attributions.

To apply our definition of plant competition, therefore, it is clearly necessary to measure resource capture by neighbouring individuals, and it is sensible to also measure their sizes (i.e. biomass, height, extent of root system and leaf canopy) and relevant environmental variables at the same time. Doing so quantifies how competition (i.e. *per capita* resource capture) depends on physiological mechanisms (e.g. root growth) or external drivers (e.g. soil nutrient availability). It also allows the functional interactions between resource capture and growth to be characterized and, by so doing, enables competitive resource capture to be attributed to the expression of specific traits. It also identifies which individuals in a community are succeeding and which are failing in the competitive contest.

However, while we can readily measure some of the mechanisms by which plants compete (e.g. superior root growth or leaf expansion), it is notoriously difficult to measure the process of competition (resource capture: the broken arrows in Fig. 1) directly and reliably. The outcome of the process often has to be inferred after the event (sometimes long afterwards) and estimated indirectly from crude proxies. And relating the outcome of competitive processes to demographic consequences – fitness – is even more uncertain and fraught with practical and theoretical difficulties, as is characterizing the roles of trade-offs between resource capture, growth, survival and fecundity (Aarssen & Keogh 2002). We argue, though, that these difficulties must be overcome if the significance of plants’ competitive interactions – their consequent population, community or evolutionary impacts – is ever to be understood.

Plant competition as a temporally dynamic process

Towards the end of the growing season, both annual and perennial plants divert resources from vegetative to

reproductive growth, and consequently, some vegetative tissues show signs of senescence. This should be a first indication that the time at which competition experiments are harvested could affect their results. Furthermore, if such experiments are focused exclusively on measuring biomass, and if not all acquired resources are being used in older plants to produce vegetative biomass but are stored for future use, simple estimates of biomass (as discussed above) become even less direct measures of competition. Nevertheless, the standard approach in competition experiments is to grow a mixture of plants or species together, and to then compare their 'final' biomass with that of plants of the same species growing in isolation. Analysing these differences assumes that the plants are at the same developmental point at the time of harvest and that differences in biomass between the competing plant and its isolated counterpart are constant through time. In other words, the apparent advantage indicated by the difference in biomass at the time of harvesting has remained constant throughout their development. Competition experiments in which multiple harvests are made illustrate the potential weaknesses in these substantial assumptions.

Figure 2a illustrates a situation where the difference in *per capita* biomass between competing and isolated plants is more-or-less constant. Harvesting at any time after 60 days in this example would give a similar picture of the effect of neighbours on an individual's growth. In contrast, in Fig. 2b the timing of harvest is critical to interpretation of the results. The difference in biomass between competing and isolated plants becomes progressively smaller until 74 days, after which competing plants are bigger. One interpretation might then be that facilitation, not competition, is somehow occurring in the later stages of the experiment. An alternative interpretation might be that the competing plant continued to invest resources in vegetative growth, while the growth rate of the isolated plant became progressively limited by early exhaustion of nutrients and consequently it had started to divert resources into reproductive growth. Alternative scenarios could also apply if we were measuring the competitive process directly. For example, if Fig. 2b showed N acquisition rather than biomass production and we made our uptake measurements only at the end of the growing season, we might conclude that the competing plant was actually taking up more N, whereas in reality the isolated plant could simply have reached a particular developmental stage and so started accumulation of nutrients in perennial storage organs such as roots or rhizomes (Clark 1977). In either case, it would be difficult to accurately interpret the results without the more detailed understanding provided by temporal information.

In the example in Fig. 2c, the competing plant takes longer to achieve its ultimate biomass than its isolated counterpart. The presence of a neighbour clearly influences biomass production during the middle of the experiment, but that effect would be undetectable if only one harvest was carried out at about 120 days when the two plants

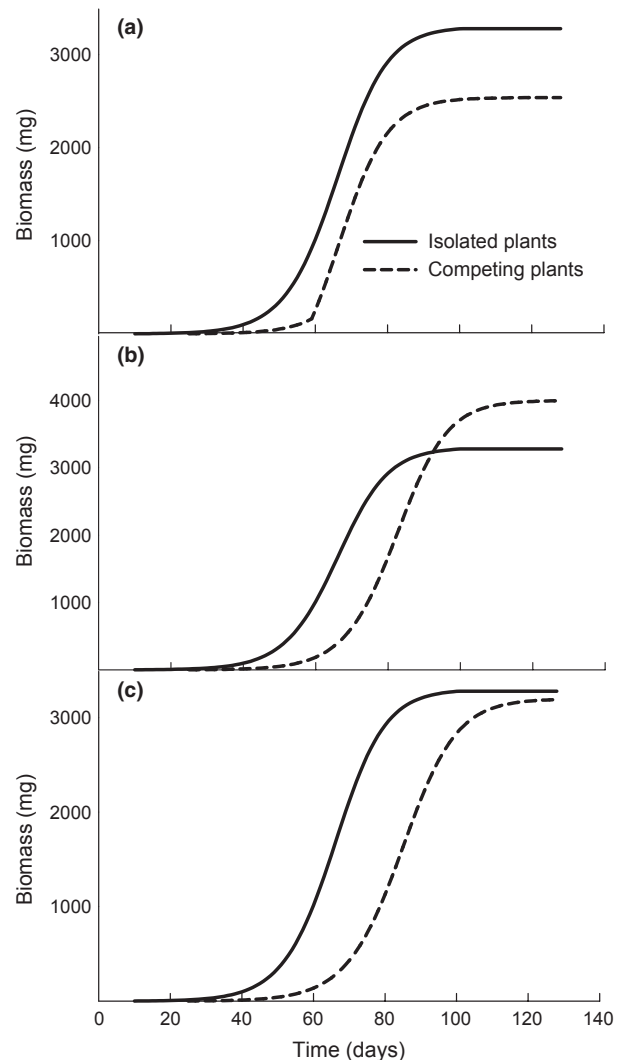


Fig. 2. Schematic trajectories of growth by competing and isolated plants. (a–c) Hypothetical dynamic relationships between competing and isolated plants. For simplicity and comparison with Fig. 3, trajectories are assumed to be logistic functions of time.

have almost identical biomass. Although it might be argued that there is then no impact of competition, this misses the important effect of the delay in development induced by a neighbour. In a pot experiment which is able to run until plant senescence, this probably represents no 'problem' for the plant (i.e. no ultimate negative impact on success), because ultimately the two plants will achieve identical biomass. However, in natural communities, especially those with relatively short growing seasons where rapid maturation and seed set are vital even for perennial species, for example, semi-arid or arctic/alpine environments, such changes in developmental rates can be demographically significant. Perhaps, in practice, this might not be a serious problem if we harvest anyway at peak biomass? This 'work-around' might be particularly effective if interannual variation in climatic conditions influences the extent to which phenological processes can move towards their 'final' state, in that using peak biomass as our end

point accounts for this interannual climatic variation. But assuming that, for example, peak biomass always represents the same end point along this temporal progression is unwise. Peak biomass may simply indicate the maximum developmental stage that a community has reached in a given year, and this may in truth be different on a year-to-year basis.

An additional complication is that at any time, a plant community will comprise a range of plants that germinated at different times and are inevitably at different developmental stages. Consequently, competitive effects early in the growing season such as resource or space pre-emption could have major impacts on the outcome of competition. If two species competed strongly, and these early effects determined, for example, which individuals first established or reached a critical size threshold for reproduction, this would not be apparent from one final harvest. Instead, we would see some cases where one species appeared to 'win' and some where another species would apparently do so, with no real understanding of the reasons why.

Such hypothetical arguments are easy to make, however, and it could be argued that in reality transient temporal interactions between competitors are probably weak and would not influence the ecological conclusions drawn from final biomass data anyway. In some cases, that would certainly be true, but it is impossible to know *a priori* which cases would fall into that category. Nor can we know, without making repeated measurements through time, when two or more competitors reach any kind of equilibrium with respect to one another such that differences between them in resource capture or biomass remain constant, the only situation for which single-harvest measurements can have any relevance. The critical point is that we just do not know how big an effect temporal dynamics have on apparent competitive outcomes. It is difficult to demonstrate the potential impact of something when very few studies have even examined it.

But we can use those experimental data that are available to illustrate that temporal dynamics can influence how competition experiments are interpreted. Figure 3a shows growth trajectories derived from multiple harvests of *Dactylis glomerata* growing with *Plantago lanceolata* and both plants growing in isolation (Trinder *et al.* 2012b). Although *Plantago* produced more biomass than *Dactylis* until around 65 days, *Dactylis* then overtook *Plantago*. If the plants had been harvested before 65 days, we would have concluded that *Plantago*, not *Dactylis*, was the dominant species in this contest; after 65 days, our conclusion would have been the opposite. The shifting balance between competing *Plantago* and *Dactylis* revealed by studying their interactions dynamically leads one to predict (albeit cautiously) that in the field these species do not have the capacity to drive each other to extinction by means of competitive superiority, but will probably coexist (a prediction considered further below). Sixty-five days might seem a short time to run a plant competition experiment, but this is not unusually brief (e.g. Cahill, Kembel &

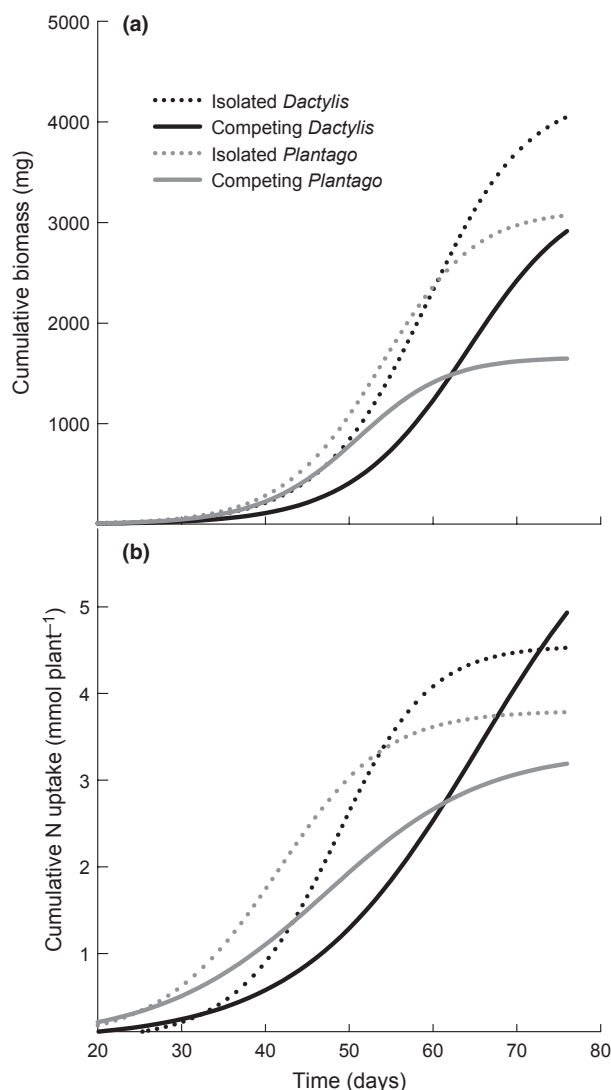


Fig. 3. Biomass and N capture trajectories for competing and isolated glasshouse-grown *Dactylis glomerata* (cocksfoot) and *Plantago lanceolata* (ribwort plantain), adapted from Trinder *et al.* (2012b). (a) Cumulative biomass; (b) cumulative N uptake. Curves are fitted two-parameter logistic models to experimental data (omitted for clarity) collected by destructively sampling replicate plants every 3 or 4 days.

Gustafson 2005; Ramseier & Weiner 2006; Damgaard & Kjør 2009) and is clearly adequate to reveal temporal dynamics of competitive interactions.

To emphasize one of our key points: we are not saying that all studies based on final harvest data are useless. Rather, we suspect that the impact of temporal dynamics on the interpretation of plant competition experiments *might* be substantial. What limited data we have support this suspicion, but obviously, far more effort should be invested in testing it more rigorously. If our suspicion proves to be incorrect, then we can continue to measure, think and argue about competition as we have done for the last 100 years. But if we are right, we then have to ask some hard questions about the ecological relevance of final harvest studies of plant competition. Either way, we

cannot simply ignore the problem or discount it on the basis of our current understanding.

The examples in Figs 2 and 3a refer to biomass, but we have argued above that biomass is only indirectly associated with the process of competition. This is shown to be true with respect to competitive dynamics. For example, the timing of certain stages within the process of competitive nutrient capture can be partly uncoupled from that of biomass production, despite any underlying stoichiometric constraints. Figure 3b shows the progression of cumulative *per capita* N capture by the plants in the same experiment as the biomass data in Fig. 3a. There are superficial similarities between the biomass and N capture trajectories, but they do not coincide. We suggested that the presence of a neighbour somehow changes the way in which plants use N following its acquisition (Trinder *et al.* 2012b). It is also worth considering that the biomass outcome shown in Fig. 3a may be only partly a consequence of the N competition dynamics shown in Fig. 3b. Other factors such as competition for light, water or other nutrients could also influence biomass production by the competitors. Incidentally, the trajectories of N capture by competing plants in Fig. 3b are rare examples of competition occurring *in real time*, and not, as is usual, its occurrence being inferred after the event.

This example demonstrates not only the need to characterize the temporal dynamics of competition, but also the need to remember the distinction between the process and the outcome of competition, and that multiple processes might influence any outcome. Taken together, these examples demonstrate that trying to understand plants' competitive mechanisms in ignorance of their temporal dynamics is like trying to understand why an animal population fluctuates in size by conducting only a single census of that population.

Importantly, there are approaches to directly estimate competitive resource capture, and which provide alternatives to indirect biomass estimates; some of these are summarized in Table 1. Most of these approaches are undoubtedly unattractive in terms of logistics and cost compared with the ease of measuring biomass, but the payoff in terms of the greater quality and quantity of information that they produce cannot be overestimated. For example, in our own work (Trinder *et al.* 2012a), we could interpret the measured patterns of the simultaneous uptake of soil nitrate and ammonium by competing individuals of *Dactylis glomerata* and *Plantago lanceolata* only by assuming the existence of strong temporal dependence in competitive resource capture, growth and how these interacted with factors such as climate and soil fertility. The measurement of such dependencies could not be included in those experiments, constrained as they were by the demands of the ^{15}N pool-dilution method, but they were revealed later in separate studies (Trinder *et al.* 2012b). These experiments showed that approaches that measure plant competition statically and indirectly at only one time and in terms of crude biomass production miss some of the most vital information about competition: its temporal dynamics.

Why have we continued to measure competition in the same way for so long?

So if the measurement of the dynamic process of competition, rather than indirect measures of its outcome, is both highly informative and possible, why do we continue to focus so strongly in experimental studies on single harvests and indirect proxies? Single-harvest biomass measurements provide an excellent case in point. By our definition of competition, biomass production (*per capita* or per unit area) is an outcome of resource capture, and so biomass is related to competition only indirectly. Yet biomass, usually above-ground and measured at a single harvest, is probably the most popular measurement reported in plant competition studies. This is understandable for a number of reasons, not least historical precedent. Early, now-classic, studies of how neighbours influenced one another's growth focused on interactions between annual crops and weeds, each grown from seed in small pots of soil (e.g. Donald 1958). That experimental design is appropriate because it is the impact of a weed on the yield of a crop at the time of harvest that matters to a farmer; how or why that impact occurs – the process of competition – is usually of less practical interest. Because such experiments are easy to do (if not necessarily easy to interpret: Harper 1977, p. 345), they became the industry standard for subsequent studies of interspecific (and intraspecific) competition: the familiar single-harvest experiment with its 'big plant–little plant' comparisons.

This is not to dismiss the utility of that approach. Such experiments have provided a wealth of data about some of the features of how neighbouring plants interact. But it must be acknowledged that they have also struggled to provide the kind of information needed to allow mechanisms and impacts of neighbour interactions to be understood in real communities and at temporal and spatial scales relevant to the demography of plants in those communities. This is not surprising given that they usually (with some exceptions: Ross & Harper 1970; Connolly, Wayne & Murray 1990; Anderson *et al.* 2007; Robinson *et al.* 2010; Trinder *et al.* 2012b; and the many studies of size–density relationships in artificial plant communities: Harper 1977; Deng *et al.* 2012) comprise measurements of above-ground biomass of plants made at only one, arbitrarily chosen time after a relatively short period of growth. This limitation was roundly criticized by Gibson *et al.* (1999) as '...possibly the single most neglected and important issue in current practice'. Gibson *et al.* referred specifically to greenhouse experiments, but we argue that the same problem applies to field studies. As we have shown, it is difficult to judge whether an 'end point' of a competition experiment, however it is chosen, can be truly informative if no measurements have been made to reveal how the plants arrived at that end point. Most researchers take care not to overextrapolate the results of short-term experiments to make broader community-scale predictions. But given the shortage of alternative data, there is clearly

Table 1. Methods for measuring competition for different resources, their strengths and weaknesses, with examples of where they have been used

Resource	Measurements required	Strengths	Weaknesses	Example
Light	Flux of PAR above canopy height, within canopies and at ground level, using quantum sensors or photodiodes. Partitioning of intercepted PAR among neighbouring plants. Information about canopy structure and leaf photosynthetic physiology of each neighbour. Leaf energy balance	Competition for light is often thought to be the decisive process in dense plant communities, including closed-canopy forests. Direct measurements of light competition are immediately relevant to understanding mechanisms of neighbour interaction in such communities. Nondestructive	Logistically demanding. PAR partitioning depends on the assumptions embedded in analytical models used	<i>Triticum aestivum</i> competing with <i>Avena fatua</i> (Ryel <i>et al.</i> 1990)
Water	Sap-flow rates of neighbouring individuals. Simultaneous leaf or canopy gas exchange measurements. Soil water balance during the measurement period	Relatively little is known about rates of competitive water capture and any direct measurements are potentially valuable. Nondestructive	Usually restricted to time periods much shorter than an entire annual cycle. Longer-term indicators of different water-use strategies among coexisting plants (e.g. measurements of the natural abundances of $^{13}\text{C}/^{12}\text{C}$ and $^{18}\text{O}/^{16}\text{O}$ in cellulose and leaf water, respectively; Moreno-Gutiérrez <i>et al.</i> 2012) can say nothing about <i>per capita</i> capture	<i>Pseudotsuga menziesii</i> competing with <i>Alnus rubra</i> (Moore, Bond & Jones 2011)
Nutrients generally	Nutrient contents of above- and below-ground tissues, preferably measured over an extended period of time. Soil nutrient concentrations during the measurement period. Root distributions	Straightforward if analytical facilities are available. Can, with suitable replication, be extended over long periods of time	Can measure only net nutrient capture: losses by exudation or senescence are ignored. Cannot distinguish between the capture of chemically distinct forms of the same element. Destructive	<i>Dactylis glomerata</i> competing with <i>Plantago lanceolata</i> (Robinson <i>et al.</i> 2010; Trinder <i>et al.</i> 2012b)
Nitrogen	Soil NH_4^+ and NO_3^- concentrations, assuming these are the only plant-available N forms of interest. Background ^{15}N abundance in soil, NO_3^- and plant N. Changes in ^{15}N enrichment of soil NH_4^+ and NO_3^- between 5 and 14 days after adding ^{15}N -enriched tracer ($^{15}\text{NH}_4^+$ or $^{15}\text{NO}_3^-$) to the soil containing the competing plants	Uses isotope pool-dilution models (Barracough 1991) to distinguish between the capture of different N sources that are available simultaneously to the competitors. Also estimates rates of gross N mineralization and nitrification that are indicative of N supply features of the soil. Can be used in both glasshouse experiments (pots) and in the field (plots). Estimates the capture of soil N pools, not just of ^{15}N -enriched tracer. Soil N supply often has a major effect on plant productivity. Competition for alternative N sources in different communities could be an important mechanism determining <i>per capita</i> rates of biomass production	^{15}N -enriched tracers and analyses are expensive. Experiments must be four times larger than a conventional competition experiment to accommodate all the comparisons required to derive NH_4^+ and NO_3^- uptake rates from ^{15}N analyses. Restricted to the relatively narrow temporal window (5–14 days) following addition of ^{15}N -enriched tracer. Destructive	<i>Dactylis glomerata</i> competing with <i>Plantago lanceolata</i> (Trinder <i>et al.</i> 2012a)

(continued)

Table 1 (continued)

Resource	Measurements required	Strengths	Weaknesses	Example
Phosphorus	Concentrations of radioactive P isotopes (e.g. ^{32}P , ^{33}P) following the injection of labelled P sources into soil adjacent to the competing plants. Root distributions and densities. Assessment of mycorrhizal presence and extent	The relatively poor diffusive mobility of plant-available P ions in soil suggests that competition for P is likely to occur only when roots or mycorrhizal hyphae of neighbouring plants are in close proximity. Introducing P isotopes to discrete soil zones rather than the whole rooting volume allows this possibility to be tested at fine spatial scales. Soil P supply is often inadequate to meet plant demands, so measurements of competition for P are important in elucidating the role of that process in P-limited communities	Radio-isotopes are now not recommended for use in the field because of health and safety considerations. P capture by only those fractions of the root systems close to soil to which isotopes has been added can be estimated. P capture can be evaluated only in relative, not absolute, terms. Limited to time periods compatible with the half-life of each P isotope. Destructive	<i>Agropyron desertorum</i> and <i>A. spicatum</i> competing with <i>Artemisia tridentata</i> (Caldwell <i>et al.</i> 1985)

a temptation to make this extrapolation. Problems could arise if the results of numerous relatively short-term experiments are then used to infer generalized competitive relationships among long-lived polycarpic species whose interactions extend across seasons, and the ecological and evolutionary impacts of which involve more than a measurement of yield at a single point in time.

Although at first glance it may seem baffling that an experimental approach so limited in what it can reveal about mechanisms of interspecific interactions has persisted for so long, perhaps it is really not so surprising. Biomass is cheap and easy to measure, and ecologists are often resource limited; pretty much any ecologist can use biomass as a response variable, and alternative approaches might be rejected simply on the basis of expense. Additionally, ecologists are usually pragmatic, often being forced by the complexity of the subject to ignore inconvenient truths for the sake of making some progress. We cannot be the first plant ecologists to have wondered about the inherent – but usually hidden – limitations of competition experiments based exclusively on a few biomass measurements. But, as long as no one measures the truly important processes directly, the scale of the problem remains hidden and we can convince ourselves that is probably not that substantial. Finally, the decision to continue to use biomass as the response variable can be rationalized by arguing that there is no alternative. Above, and in Table 1, we describe techniques that do allow competition, including its dynamics, to be measured directly. Perhaps only the new insights that will be provided by such techniques can reveal the scale of the potential pitfalls of relying solely on single biomass measurements or other proxy outcomes of competition, and so convince plant ecologists of the need to grapple with the complexity and cost of moving away from single time-point biomass-based studies.

So what?

Do short-term competitive dynamics have any larger-scale significance? Does knowing the relationship between the temporal trajectories of resource capture and biomass help us to understand plant community composition and the dynamics of coexistence? The experimental work to test this has not yet been undertaken, so the community-level significance of the temporal dynamics of competing species is difficult to assess at this point. But it is dangerous to assume that we currently know all that we need to about plant competition, and that current methods to study its occurrence and ecological significance are adequate: they clearly are not. To emphasize this point, we provide here some specific examples where detailed knowledge of the temporal dynamics of plant–plant interactions have improved, or could improve, understanding of ecological processes in particular contexts.

TEMPORAL DYNAMICS IN MYCORRHIZAL NETWORKS

Simard *et al.* (2012) discussed the current (if limited) state of knowledge of temporal changes in C flow through mycorrhizal networks and identified the need for models to take account of changes in nutrient exchange over the growing season. One of the few studies to consider this showed that C flow between Douglas fir and paper birch (via various belowground pathways, including mycorrhizal networks) apparently changed direction several times through the growing season (Philip 2006, as cited in Simard *et al.* 2012). Although entirely predictable given that the growth of plants and associated fungi are unlikely to be synchronized so closely that resource flow through the hyphal network will always be unidirectional, the quantification of such temporal variations in the trafficking of C

(and, possibly, other elements) between plants connected by common mycorrhizal networks could provide new insights into the subtleties of how mycorrhizal symbioses function at the community level. Whether this function includes a significant influence on how neighbouring plants interact with one another, either competitively or otherwise, still remains to be seen (Robinson & Fitter 1999).

LOCALIZED ROOT PROLIFERATION AND SOIL HETEROGENEITY

The localized proliferation response of roots when they encounter a nutrient-rich patch of soil is well known (Robinson 1994). It is such a spectacular and ubiquitous response that its actual contribution to nutrient capture in specific cases is rarely questioned. This can lead to incorrect attributions of the functional significance of that response. In the experiment reported by Van Vuuren, Robinson & Griffiths (1996), the roots of isolated *Triticum aestivum* (wheat) plants were forced to grow through a small patch of ^{15}N -enriched organic matter. At the end of the experiment, after 34 days growth, the root length density in the patch was about four times greater than the densities elsewhere in the soil. 'Obviously', the root proliferation response seen at 34 days must have been the main cause of N capture from the patch of organic matter. However, measurements of temporal dynamics of root growth and N uptake throughout the experiment revealed that most of the patch-derived N had, in fact, already been captured by 22 days, well before the root proliferation response was fully expressed. Localized N capture occurred mainly by means of rapid and transient local up-regulation of N inflow systems in root cells. The point is that the 'obvious' explanation was not the correct one.

These kinds of dynamic interactions could resolve some of the contradictions in the literature that root proliferation can have a decisive influence (or not) on the outcome of competition. For example, Robinson *et al.* (1999) dem-

onstrated that greater localized root proliferation by *Lolium perenne* was consistent with it capturing more N than neighbouring *Poa pratensis* over 56 days, providing the former species with a competitive advantage over that short time-scale. In contrast, Cahill & Casper (1999) detected no influence of root proliferation by competing *Ambrosia artemisiifolia* and *Phytolacca americana* on their *per capita* biomass production after 9 weeks' growth on patchy soil. Bliss *et al.* (2002) found that competitive responses to soil heterogeneity after 3.5 months' growth were sometimes statistically significant, but not always; responses depended on community composition and, in particular, the apparent precision with which different species foraged for nutrients. These, and other, conflicting reports suggest an incomplete understanding of the ecological significance of localized root proliferation over both long and short time-scales. Much of the missing information would be provided by extending the duration of competition experiments to encompass a wider range of time-scales and measuring key variables to reveal how above- and below-ground interactions between neighbours and resource availability develop.

PLANT COMMUNITY COMPOSITION

Earlier, we discussed an example of short-term competition between *Dactylis glomerata* and *Plantago lanceolata* to illustrate their competitive dynamics (Fig. 3). In that experiment, *Plantago* was initially superior, but was eventually overtaken by *Dactylis*. The question remains whether such short-term experiments carried out under artificial conditions could possibly have any bearing on the abundance of species in real communities. Table 2 indicates that they might. Across many sites of intermediate fertility, *Dactylis* and *Plantago* coexist and, one can imagine, compete. As sites become more fertile, the abundance of *Dactylis* increases and that of *Plantago* decreases until the latter is excluded from the most productive habitats

Table 2. Differences in mean fertility of sites containing different relative abundances of *Plantago lanceolata* and *Dactylis glomerata*. Data and analyses courtesy of J.G. Hodgson (unpublished data)

Site category with respect to the relative abundances of <i>Plantago lanceolata</i> and <i>Dactylis glomerata</i> *	Mean site fertility (Ellenberg units) [†]	95% Confidence limits	Number of quadrats
<i>Plantago</i> only	4.69	4.59–4.79	629
<i>Plantago</i> > <i>Dactylis</i>	4.46	4.35–4.57	336
<i>Plantago</i> = <i>Dactylis</i>	5.03	4.90–5.16	296
<i>Dactylis</i> > <i>Plantago</i>	5.16	5.03–5.29	193
<i>Dactylis</i> only	5.70	5.63–5.77	1133
ANOVA $F_{4,2582}$	120.5		
<i>P</i>	<0.001		

*Abundances were estimated visually as percentage frequencies of rooted plants of each species in 1-m² quadrats as described in Grime, Hodgson & Hunt (1988).

[†]Site fertility was quantified in terms of Ellenberg values (the larger the value, the more fertile the site: Ellenberg 1974). For these data, there was a positive correlation between Ellenberg value and the mean height of the canopy ($r = 0.62$, $n = 2587$, $P < 0.001$).

Data were collected in vegetation surveys conducted in the north of England by the Unit of Comparative Plant Ecology, University of Sheffield, UK, from the 1960s to the 1980s.

(Table 2). By contrast, as site fertility declines, *Plantago* becomes more abundant and *Dactylis* less, until the grass disappears from the sites with low fertility.

These large-scale, long-term ecological patterns would be inexplicable in terms of competitive mechanisms had only the standard single harvest, final biomass, competition experiments been carried out, for the reasons given above. But by characterizing even the small-scale, short-term competitive dynamics of these species (Fig. 3; Trinder *et al.* 2012b) and the range of competitive interactions that are revealed when the process is measured directly (Trinder *et al.* 2012a), we can begin to understand at least one of the mechanisms for the habitat-dependent shifts in relative abundance shown in Table 2.

Another example is the often-discussed relationship between community composition and ecosystem productivity. Thompson *et al.* (2005) rightly criticized the weaknesses in the BIODDEPTH experiment (Hector *et al.* 1999), mainly on the basis that the communities used in it were immature and individual plants had insufficient time for their competitive interactions to be fully expressed. By contrast, in the mature herbaceous community described by Thompson *et al.* (at Bibury, in SW England), competitively dominant plants have been able to suppress subordinate neighbours, the result of which is an absence of a strong relationship between species diversity and productivity. Would it not be of the greatest importance to test this possibility directly by measuring plants' competitive interactions as they occur and as a community evolves from an immature state to maturity? That would make quite a research project.

INTERCROPPING

Ironically, given the role of agricultural studies in emphasizing the utility of final harvest experiments, an improved understanding of temporal dynamics also has a direct application to major environmental challenges such as food security. Intercropping systems are mixed species crop production systems where two or more crops grow simultaneously on the same field for periods that include an overlapping vegetative stage (Gomez & Gomez 1983), and where the annual net yield relative to production of component species as monocultures – the land equivalent ratio, LER (Willey 1979) – is (sometimes very substantially) enhanced. Intercropping systems deliver food stuffs to a large proportion of the global population and are critical to food production in certain regions, especially those with relatively less agricultural mechanization. More than 20 million hectares of intercrop are sown annually in China, and intercrops are also common in India, Southeast Asia, Africa and Latin America (Li *et al.* 2007). Understanding in detail and optimizing the processes that drive enhanced yield in intercropping systems is therefore essential, especially given that intercropping can be a relatively sustainable form of food production involving reduced agro-chemical inputs.

Many different mechanisms have been implicated in the beneficial interactions that occur within intercrops to enhance the LER, including niche differentiation, the mobilization of P on P-deficient soils (Li *et al.* 2007) and compensatory growth (Lithourgidis *et al.* 2011). Many intercropping systems, for example maize–faba bean systems, involve the staggered planting of the crop, such that the second crop benefits from the above- and below-ground environmental conditions generated by the first crop. However, the net interaction between intercrops, as within natural plant communities (Bertness & Callaway 1994; Brooker & Callaghan 1998), is a balance between positive and negative plant–plant interactions. The exact nature of this balance depends on the temporal dynamics of the interactions occurring between the two crops. To maximize the benefits from intercropping systems and also to tailor these systems to regional variations in climate or soil conditions, it is essential to understand in detail the dynamic patterns in the key interaction processes, especially competition for soil nutrients.

Synthesis

The challenge is to integrate top-down, trait-based approaches to plant competition with the emerging understanding of smaller-scale, temporal dynamics. Where do we want to go with plant competition? Thousands of experiments, both in pots and the field, have been performed over the last 100 or so years, and yet, we seem no nearer to reaching broadly agreed rules on its importance, its role in different communities and habitats or how (indeed whether) it influences or drives patterns of species diversity and abundance. If we all carry on doing the same types of pot experiments, taking a single measure of final biomass for another 100 years, we fear that we may still be no closer to a better understanding of competition. Pot experiments have been hugely valuable in allowing us to look at some of the detail of simplified plant interactions, but were never intended to be a replicate of conditions in the field. They tell us what to look for in the otherwise chaotic noise of natural systems and we now need to start searching for these elusive signals.

Ultimately, does any of it really matter? Do these intricate temporal variations in the process of competition really impinge on final outcomes, however those are defined? Historically, ecologists have probably argued that it does not matter, but in reality, this could simply represent retrospective justification based on the practical limitation of being unable to measure the important factors very easily. The truth is, it might matter, but we just do not know. When we address plant ecology's guilty little secret, we might discover it to be a great big secret, and dealing with it will teach us a lot of things. Perhaps at least a few of us should spend some time trying to find out whether this is true.

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