



## Tamm review

## Tamm review: Tree interactions between myth and reality

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## ARTICLE INFO

## Keywords:

Interaction  
Facilitation  
Competition  
Mode of interaction  
Tree mechanics  
Stress-gradient hypothesis  
Niche theory  
Self thinning  
Janzen-Connell  
Herd immunity theories  
Overyielding  
Competition indices  
Ecological field theory  
Interaction kernels  
Point process statistics

## ABSTRACT

For a long time, interaction between plants in both general plant and forest science has been somewhat limited to competition, although an intuitive, non-scientific understanding of facilitation has influenced the development of a wide range of forest management techniques including silvicultural systems. Despite this, competition has dominated many ecological theories and the interpretation of density effects. Ongoing research in tree mechanics and in verifying the stress-gradient hypothesis reveal that our understanding of tree interactions is still incomplete. Promising research is currently underway attempting to uncover the physiological receptors and processes related to interaction whilst in the past largely plant performance, e.g. plant size and growth rates, was used for verifying competition. We give an overview of quantification methods and suggest a standardisation by common construction principles. Plant performance has been much used for providing empirical evidence of interactions, but when used in isolation it can be a confounding criterion leading to misinterpretations despite promising new developments in quantifying tree interaction. We therefore suggest using pattern-oriented modelling in analyses of tree interactions, where several plant traits are applied simultaneously.

## 1. Introduction

Interactions between plants is central to plant community ecology and is one of the fundamental ecological forces that shape dynamics in space and time at all organisation levels (Armas et al., 2004; Seifan and Seifan, 2015). Competition, as one possible type of interaction, is among the oldest notions in biology and ecology. The term can be traced back to Darwin's "struggle for existence" (Darwin, 1859) and has received many different definitions over the years, some of them leading more to confusion than clarification (Grime, 1977). For plants, the central part of this struggle is to find, harvest, transport and retain possession of resources (Keddy, 2017). Perry et al. (2008) noted that mathematical models and – in more general terms – any attempt to quantify competition have much influenced the traditional thinking of ecologists about this concept to an extent that one might think this is a human concept imposed on nature (Keddy, 1989). This relates to the fact that the physiological implications of competition processes only recently have started to be better understood including stress signal perceptions and genetic and metabolic responses (Atkinson and Urwin, 2012; Pierik et al., 2013). However, what ecologists typically observe are actually the effects of competition, i.e. a *reduction in the life performance of plants due to stress, where stress is related to sharing limited*

*resources at close proximity* (Begon et al., 2006). Burton (1993) described competition as an interference from a localized subset of other plants whilst Keddy (2017) generalised *reduction in performance to negative effects* that one organism has upon another. Indeed, competition and other forms of interaction are typically inferred from observed negative or positive effects of neighbouring plants without knowing in detail what resources the plants were sharing (Damgaard, 2011). This lack of more direct evidence has therefore given rise to conceptual theories and much speculation.

Grime (1977) pointed out that we can always expect interaction effects, wherever plants grow in close proximity, whether they are of the same or of different species. Perry et al. (2008) refer to this as "the struggle for space". Not all of these effects, however, can be attributed to competition or even to plant interaction. It is also indicative that competition is often defined in terms of its effects rather than its mechanisms (Grime, 1977), since we are still not always clear about them.

Bertness and Callaway (1994) and Keddy (2017) pointed out that ecologists for a long time were preoccupied and fascinated with negative interactions between individuals whilst positive ones received little attention and were largely ignored in models. This understanding of interactions has gradually given way to a new mindset where competition is only one possible type of interaction. Cooperation is part of the

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**Table 1**

Plant interactions (modified from Perry et al. (2008)). The + symbol means that the respective plant benefits, the – symbol indicates inhibition and 0 stands for no effect.

Type of interaction	Plant 1	Plant 2
Predation	+	–
Parasitism	+	–
Competition	–	–
Amensalism	–	0
Mutualism	+	+
Commensalism	+	0
Neutralism	0	0

struggle for survival (Keddy, 2017). More specifically one could describe species and plant interactions as including negative (competition), neutral and positive (facilitation) relationships on a continuous scale (Díaz-Sierra et al., 2012). Plant facilitation emerges as the moderation of biotic and abiotic stress, enrichment of resources or the increased access to resources. Facilitation leads to an increase in the survivorship, growth and/or reproduction of at least one of the interacting individuals and can occur simultaneously with competition. Particularly in harsh physical environments, positive interactions during succession and recruitment as well as among established adults are very common. Perry et al. (2008, see Table 1) further detailed interactions by suggesting a continuum that includes *predation*, *parasitism*, *competition*, *amensalism*, *mutualism*, *commensalism* and *neutralism*, where the concept of a superorganism is an extreme form of mutualism (Oliver and Larson, 1996). Facilitation in this context includes mutualism and commensalism. Symbiosis, for example, can be either mutualistic or parasitic (Perry et al., 2008).

The story of plant interactions is even more complex, considering that environmental changes can cause stress factors to change. The type, strength and importance of interaction depend on space and time, and as a consequence negative interactions can become positive and vice versa (as described by the stress-gradient hypothesis, SGH), i.e. plant interactions are context dependent.

## 2. Definitions and concepts

### 2.1. Terms and definitions

Very basic and traditional definitions include the terms *intra-* and *interspecific* competition, which sometimes are also referred to as *con-* and *heterospecific* competition, see for example Vogt et al. (2014). Intra- or conspecific competition describes a shared demand for limited resources within the same species population whereas inter- or heterospecific competition refers to this process between two different species (Kimmins, 2004; Begon et al., 2006). Tilman (1982) coined the term resource-competition theory in this context. Competition typically leads to decreased performance (in terms of survivorship, growth and reproduction) and this leads to decreased fitness (i.e. number of offspring that survive to reproductive age). Because they share the same niche, others of the same species are generally the strongest potential competitors with a given individual (Perry et al., 2008). More generally speaking the *competition-trait similarity hypothesis* predicts that competitive interactions between species increase with decreasing niche distance (Kunstler et al., 2012).

Intraspecific competition was and still often is expressed in terms of *density*, i.e. number of individuals divided by land area (as a proxy for the amount of resource). The importance of density lies in the fact that increased density reduces resource availability while increasing stress predisposes to mortality agents such as insects and disease. However, density of the population as a whole is a rather crude measure of competition, since the effect on an individual is rather determined by local density and particularly by the extent to which it is *crowded* or

inhibited by its immediate neighbours (Begon et al., 2006).

One cannot discuss an individual's interactions with its neighbours without a brief detour into *niche theory* (Hutchinson, 1957), where a species' niche is essentially defined as its ecological role given a set of necessary conditions, resources and interactions. For example, a tree species' niche might be defined partly by ranges of temperature, resource availability (e.g. light, moisture), frequency and severity of disturbance, and minimal number of growing season days it can tolerate, as well as the types of interactions it can abide. This inevitably leads one to fundamental concepts such as the *competitive exclusion* principle (also called Gause's Law; Gause, 1934; Connell, 1961), which says that two species cannot coexist if they occupy exactly the same niche (i.e. competing for identical resources) and *resource partitioning* (MacArthur, 1965; Schoener, 1974), where two or more species whose niches substantially overlap may evolve by natural selection to have more distinct niches (i.e. use different resources, occupy a different area of habitat, or grow during a different season).

Another important definition relates to the question of how individuals share resources. *Symmetric* competition is regarded as an equal sharing of resources amongst individuals, whilst *asymmetric* competition describes an unequal sharing, where large plants have a *disproportionate* advantage (for their relative size) in competition with smaller plants (Weiner et al., 2001) leading to pre-emption effects. As a consequence of the latter process, larger individuals have a competitive advantage over smaller ones. The word “disproportionate” plays a key role here and Weiner (1990) defined it in such a way: For competition to be asymmetric, an individual that is twice as large as another must have more than twice the competitive effect or obtain more than twice the amount of resources as its smaller neighbour. Selecting a suitable and meaningful size variable is obviously crucial in this context, as defining competitive effects in terms of different size variables of the same plant can potentially lead to different results. Asymmetric competition may arise, for example, as a consequence of variation in emergence times within a population (Freckleton and Watkinson, 2001) and leads to competitive dominance or suppression of some individuals over others (Keddy, 2017). The terms symmetric and asymmetric competition are collectively referred to by the “*mode of competition*”. Lin et al. (2013) concluded from the literature that above-ground competition tends to be size-asymmetric, while below-ground competition is more size-symmetric, see also the discussion in Weiner (1990) and in Weiner et al. (1997). Symmetric competition is argued to produce coexistence whilst asymmetric competition leads to competitive exclusion, where the weaker species or individuals manage to disperse into gaps not yet occupied by the dominant. In the extreme case of asymmetric competition, the subordinate species or individuals are driven to evolve away from the niche of the dominant (Keddy, 1989; Keddy, 2017). More subtle variants of these terms including “perfect/complete/partial a/symmetry” are summarised in Fernández-Tschieder and Binkley (2018).

A related, older definition is that of *one-* and *two-sided* competition (Freckleton and Watkinson, 2001; Begon et al., 2006). In a context of two species the former implies that one species is completely dominant over another. One-sided competition can therefore be regarded as an extreme form of asymmetric competition. Competition for light is often one-sided, because light comes directionally from above so that taller plants can shade shorter ones but not *vice versa* (Kikuzawa and Umeki, 1996; Falster and Westoby, 2003). Weiner (1990), however, has used one-sided competition as a synonym of asymmetric competition and equates two-sided competition with symmetric competition.

Lin et al. (2012) and Keddy (2017) have argued that the concept of “mode” universally applies to plant interactions regardless of position along the continuum or point in time it is observed. Accordingly there is not only a mode of competition but also a mode of facilitation. Moreover, different modes of competition and facilitation can act simultaneously. When for example facilitation among plants is asymmetric, smaller plants receive disproportionately more benefits from larger

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