

Competition theory — science and application in mixed forest stands: review of experimental and modelling methods and suggestions for future research

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Abstract: Competition in forest stands has long been of interest to researchers. However, much of the knowledge originates from empirical studies that examined the effects of competition. For instance, many studies were focused on the effects of the presence of herbaceous species on the development of tree seedlings or the decrease in individual tree growth with increases in stand density. Several models that incorporate competitive effects have been developed to predict tree and stand growth, but with simplified representations of competitive interactions. While these studies provided guidance useful for forest management, they contributed only partially to furthering our understanding of competitive mechanisms. Also, most competition studies were conducted in single-species stands. As competitive interactions occurring in mixed stands are characterized by a higher degree of complexity than those in single-species stands, a better understanding of these mechanisms can contribute to developing optimal management scenarios. The dynamics of forest stands with at least two species may be affected not only by competition, but also by facilitation or complementarity mechanisms. Thus, knowledge of the mechanisms may provide insight into the relative importance of intra- versus inter-specific competition and whether competition is symmetric or asymmetric. Special attention to the implementation of field experimental designs is warranted for mixed stands. While traditional spacing trials are appropriate for single-species stands, the examination of competitive interactions in mixed stands requires more complex experimental designs to examine the relative importance of species combinations. Forest productivity models allow resource managers to test different management scenarios, but again most of these models were developed for single-species stands. As competitive interactions are more complex in mixed stands, models developed to predict their dynamics will need to include more mechanistic representations of competition.

Key words: competition, facilitation, complementarity, experimental designs, site resources, modelling.

Résumé : Les chercheurs s'intéressent depuis longtemps à la compétition dans les peuplements forestiers. Cependant, la majeure partie des connaissances provient d'études empiriques n'examinant que les effets de la compétition. Par exemple, plusieurs études se sont concentrées sur les effets de la présence d'espèces herbacées sur le développement des plantules d'arbres ou sur la diminution de la croissance des arbres individuels avec l'augmentation de la densité. Plusieurs modèles incorporant les effets de la compétition ont été développés pour prédire la croissance des arbres et des peuplements, avec cependant des représentations simplifiées des interactions compétitives. Bien que ces études fournissent des pistes utiles pour l'aménagement forestier, elles contribuent seulement partiellement à améliorer notre compréhension des mécanismes compétitifs. De plus, la plupart des études sur la compétition ont été conduites dans des peuplements monospécifiques. Puisque les interactions compétitives survenant dans les peuplements mixtes se caractérisent par un degré de complexité plus élevé que celles des peuplements monospécifiques, une meilleure compréhension de ces mécanismes pourra contribuer au développement de scénarios d'aménagement optimisés. La dynamique des peuplements comportant au moins deux essences peut se voir affectée non seulement par la compétition, mais aussi par des mécanismes de facilitation ou de complémentarité. Ainsi, la connaissance des mécanismes peut jeter un nouvel éclairage sur l'importance relative de la compétition intra- vs inter-spécifique et déterminer s'il s'agit de compétition symétrique ou asymétrique. Une attention spéciale lors de la conception de plans expérimentaux est essentielle pour les peuplements mélangés. Alors que les essais d'espacement traditionnels conviennent pour les peuplements monospécifiques, l'examen des compétitions interactives nécessite des plans expérimentaux plus complexes pour évaluer l'importance relative des combinaisons d'espèces. Les modèles de productivité forestière permettent à l'aménagiste des ressources de vérifier divers scénarios d'aménagement, mais encore une fois la plupart de ces modèles ont été développés pour des peuplements monospécifiques. Les interactions compétitives étant plus complexes dans les peuplements mixtes, les modèles développés pour prédire leur dynamique devront désormais inclure de plus fortes représentations des mécanismes de compétition. [Traduit par la Rédaction]

Mots-clés : compétition, facilitation, complémentarité, plans expérimentaux, ressources des sites, modélisation.

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Introduction

Although competition is a widespread phenomena [sic] exhibited by organisms from microbes to mammals, empirical evidence is elusive. Controlled laboratory experiments usually involve simplified competitive systems whose results cannot be applied to the complexity obtained in natural ecosystems; and the complexity of variables operating in natural ecosystems confounds the interpretation of results, making alternate plausible explanations possible. [E.J. Kormondy, *Concepts of Ecology* (4th ed.), 1996]

Forest resource managers deal with the challenges of ecological complexity on a daily basis. In theory, their goal is to realize optimum wood production while maintaining biodiversity and ecosystem processes (Lieffers et al. 2008; Canadian Forest Service 2011). In practice, the key to achieving these goals lies in the successful management of competition. To accomplish this, resource managers must not only understand the general principles of competition, one of the most difficult interactions to study in ecology (Kormondy 1969), but must also apply these principles to a highly variable landscape and do so within procedural and economic constraints that often limit their management options. More than ever before, resource managers and the public are expressing their preference for mixed-species stands, as these are viewed as better emulating the dynamics of natural forests (McCarthy 2001; Puettmann et al. 2008). However, our knowledge of mixed-species dynamics and therefore our ability to predict outcomes from management interventions in mixed stands remain limited.

Although competition was once seen as the major organizing force in nature, that view is now considered overly simplistic by most ecologists (Perry and Millington 2008). This perspective may be linked to the fact that much of our theoretical understanding of competition, and hence productivity, is built on work with simplified systems, short-term studies, and relatively short-lived, often herbaceous, species. In reality, the study of productivity assumes additional complexity when applied to forests that include woody and herbaceous individuals of different ages, sizes, structures, physiological characteristics, and life histories. The task of resource managers is further complicated when effective silvicultural interventions, applied at various times in stand development, must be crafted to account for both the future and the past. Because forests are long-lived complex systems, they often move from monoculture to polyculture and back again over time and space. This is true for stands of both natural (e.g., fire) and anthropogenic (e.g., plantation or following harvest) origin. In the boreal region of Canada, often only a single species is planted and managers may expend considerable resources (e.g., vegetation control using herbicides) to promote that species to the dominant position. However, few if any forests remain single species (e.g., Dampier et al. 2007). Ingrowth almost always results in mixed-species stands early in the course of succession (see Burgess et al. 2001; Gordon et al. 2001), while autogenic processes, such as soil acidification, can lead to simplification as stands age (see Falkengren-Grerup 1989; Nordin et al. 2005).

The merits of mixed-species versus single-species stands have been debated since the beginning of organized forest management (see Kelty 2006; Del Rio and Sterba 2009; Pretzsch et al. 2010). Considerations have included resistance to pests (Brockerhoff et al. 2006), ability to provide habitat and ecosystem services (Burton et al. 2006), and productivity (Zavala and Bravo de la Parra 2005). No consensus has been reached. Clearly, when making choices about stand composition, resource managers must recognize a range of values — economic, ecological, and social — and apply the best science and practices available. Resource managers have long recognized the futility of policy-driven mandates to maintain simplified young forests, especially on landscapes characterized by extensive management and stochastic disturbance

events. At the same time, external factors such as public scrutiny and dwindling silviculture budgets have forced stand interventions that, on one hand, promote mixed-species stands, and on the other, discourage them. So it appears that resource managers are already implementing treatments that result in mixed-species stands (Puettmann et al. 2008). Unfortunately, these actions are not usually informed by appropriate theory and therefore the outcomes are unpredictable and probably less than optimal. In other words, practice has preceded science and leaves researchers scrambling to catch up.

In forestry, most of the experimental work on competition has been conducted in single-species stands. For instance, Evert (1973, 1984) identified close to 900 documents reporting initial tree-spacing studies between 1920 and 1984, and most referred to single-species stands. Relatively few attempts have been made to better understand the full range of interactions in mixed stands using well replicated experimental designs. The reasons for this are many (e.g., expenses, time), but the lack of evidence limits resource managers' ability to design the most appropriate interventions and researchers' ability to develop productivity models for application to mixed stands. While we cannot fully address these knowledge gaps in this synthesis, we can identify the key questions and make recommendations for their resolution. Progress in addressing the operational concerns of resource managers, the scientific questions of ecologists and the socio-economic interests of the public with respect to complexity and productivity in forest systems will require the development and application of appropriate theory, experimentation, and modelling. The objectives of this synthesis are to (1) review the current evidence on competitive interactions in coniferous-deciduous mixtures in temperate and boreal forests, (2) summarize current experimentation and modelling approaches used to study competition, and (3) recommend productive research strategies.

Critical terms and key concepts

As the starting point for our review, we define healthy forest systems as exhibiting a range of processes resulting in structures that promote productivity and diversity. Ecologists would argue that key processes involve interactions between species and competition theory provides a basis for the discussion. To begin, we define the key terms and challenges associated with competition, which relate to plant interactions and their effects on productivity.

Terminology

The language of competition theory — even the use of the word “competition” — is confusing and may, in itself, impede research progress. This situation was noted by Odum (1953) in a statement about competition not necessarily being “harmful” and reiterated later (Odum 1971) when he specifically recommended using the word “competition” in the broadest sense. Grace and Tilman (1990) began their book on plant competition by acknowledging confusion with the term and, like Odum (1971), observed that “a more profitable approach [to a narrow definition], may be to define competition broadly, but to study specific kinds of competition such as resource competition or interference competition.”

The term “competition” has been defined in many ways (Connell 1983), depending on the context and the relative degree of emphasis on the mechanism (e.g., individuals compete for a common resource in short supply) or the outcome of the interaction (e.g., one or both competitors suffer due to the act of competing). Grime (1973) defined competition as “the tendency of neighbouring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space.” Begon et al. (1996) included the result of this interaction: Competition is “an interaction between individuals, brought about by a shared requirement for a resource in limited supply, leading to a reduction in the survivorship, growth and (or) reproduction of at least some of the competing individuals concerned.” These two definitions illustrate a

common problem in that one refers to the action — to compete — while the other includes an outcome (reduction in survivorship). Both definitions require extrapolation of the circumstances surrounding the interaction of individuals and the latter reflects the commonly held view that competition must lead to negative outcomes. The language of competition becomes further complicated when terms such as competitive production are introduced to counter the implied negative. Because of the potential for confusion in the terminology, we have adopted a nomenclature (Table 1) first adapted to plants by Burkholder (1952), promoted by Odum (1971), and simplified by Perry (1994).

These terms (Table 1) directly reflect the net responses of two individuals without reference to the specific mechanism responsible. In the case of competition, both individuals “lose”; in commensalism, one individual “gains” while the other remains unaffected, and so on. For example, two intolerant individuals trying to capture the same quantum of light may both lose (that is, over the long run neither gets enough light to prosper) while a tolerant species in the shade of an intolerant may actually benefit from changes in light quality and (or) quantity created by the latter. Burkholder's scheme assumes that the individuals are physically close enough to interact and the response (i.e., gain or loss) can be ascertained (Burkholder 1952). In addition to naming the interaction based on the outcome, we are interested in identifying the mechanisms that lead to them and this language has also been complicated by the introduction and adoption of various terms. For the purposes of this paper, we use the terms complementarity and facilitation to describe mechanisms that promote interactions with a positive outcome and interference and exploitation to describe mechanisms leading to negative outcomes.

Complementarity requires niche differentiation that results in the combination of species using site resources more efficiently than when each grows alone. Plants are said to complement one another when species differences give rise to a better overall use of available resources in intercrops rather than in sole crops (Vandermeer 1989). Vandermeer (1989) termed this interaction “competitive production” and identified the land equivalent ratio (LER) as a way of identifying its occurrence. For example, a stand with 1000 stems of trembling aspen (*Populus tremuloides* Michx.) and 1000 stems of white spruce (*Picea glauca* (Moench) Voss) might be more productive ($LER > 1$) than one with 2000 stems of either species alone ($LER = 1$). Complementarity may result from reductions in crown or root interference due to physical or temporal stratification, improved nutrient conditions due to exploitation of larger soil volumes or improved physical conditions such as increased wind stability. Complementarity could lead to commensalism or proto cooperation. Facilitation occurs when the growth of one species is dependent upon the presence of a second species or “facilitator”. Facilitators (also referred to as ecosystem engineers) are defined as species that directly or indirectly modulate the availability of resources (apart from themselves) to other species. They cause physical state changes in biotic or abiotic materials and thereby modify, maintain, and (or) create habitats and resources for other organisms. Facilitation could support commensalism or mutualism.

We use the terms interference and exploitation to describe “real” competition, as defined by Grace and Tilman (1990) and others. Interference is a direct interaction between two individuals where one physically excludes the other from a portion of the habitat and therefore from the associated resources. For this type of interaction to occur, the resource supply must not be limited (Begon et al. 1996). For instance, two species may compete for light, but sunlight is never limited. Exploitation occurs indirectly through a common limiting resource that acts as an intermediary. The use of the resource by any one species or individual depletes the amount available to others. The end result may be that all competitors suffer (competition) or one obtains resources while another does not (amensalism).

Table 1. Different types of interactions between two species (adapted from Burkholder 1952, Odum 1971, and Perry 1994).

Interaction	Species		General nature of interaction
	1	2	
Competition	–	–	Both species lose
Amensalism	–	0	One species loses, the other is unaffected
Mutualism	+	+	Interaction favourable to both species and obligatory
Symbiosis			A special case of mutualism; implies an intimate physical relationship
Proto cooperation*	+	+	Positive interaction between both species but not obligatory
Commensalism	+	0	The “commensal” species gains, the other (sometimes known as the “host”) is unaffected
Neutralism	0	0	Absence of interaction between both species

Note: +, beneficial; –, detrimental; 0, neutral.

*From Odum 1971.

The process of competition is often classified based on symmetry, expressed as either asymmetric or symmetric competition (Weiner 1990; Weiner et al. 1997). The idea is that, if organisms acquire resources relative to their own size in a competitive environment, then the competition is symmetric (Weiner et al. 1997); if the acquisition is not relative to size, that is, large individuals have a multiplicative competitive effect on resource acquisition of small individuals, then it is asymmetric. The concept of the symmetric nature of competition may be helpful to better understanding how competing organisms share resources. However, it should not be extended to suggest some kind of value. That is, either symmetric or asymmetric competition is inherently “good” or “bad”. We contend that conceptual and logistical problems occur when these terms are applied to trees, particularly for mixed stands, as discussed later in this review.

Intra- and inter-specific competitive interactions

Debate continues as to the mechanisms and outcomes associated with interactions between and among species. Much has been written about the relative intensity of intra- or inter-specific competition between trees, but it is well recognized that both types of competition are important in species co-existence (Connell 1983). The key difference seems to be that competing individuals of the same species (i.e., intra-specific competition) must acquire the same resources, in the same quantities per unit biomass and at the same time. This situation is magnified when the individuals are even aged and at the same stage of development. Competing individuals of different species (i.e., inter-specific competition) may avoid some resource use conflicts by stratifying their use in time (e.g., different times of bud break and (or) foliage expansion) or space (e.g., vertical and (or) horizontal heterogeneity). They might also require resources, such as nutrients, in different ratios or forms. The likelihood of negative outcomes for one or both individuals or species is increased under both competition scenarios when densities are higher and (or) resources are scarce (Huston and Smith 1987).

The most common case in natural systems is for two or more species to occur in the same space. Clearly, co-existence is normal and is both a product of and a reason for interactions between individuals. As noted previously, competition (i.e., where both individuals/species lose) is only one possible outcome from such interactions. Individuals and populations of different species will experience a range of interactions with the outcome determined by the net effect of those interactions. However, as equilibrium or

uniform states are rare in nature, the net effect (loss or gain) will change with time (Huston 1979; Cavard et al. 2011). This is because change is always occurring due to small- and large-scale disturbances (Connell 1978; White 1979; White and Pickett 1985; Reice 1994), predation, or density-independent mortality (Huston 1979). For example, white spruce seedlings under a trembling aspen canopy may grow more slowly than their counterparts in the open (Pitt et al. 2010), but they may also be more likely to survive frost events (Groot and Carlson 1996) and develop higher quality fibre due to earlier self-pruning (Pitt and Bell 2004). In this case, the net effect of the interaction is positive for the spruce. If the aspen is not affected by the spruce, then the relationship is commensal.

In young, managed boreal forests, the likelihood of intra- or inter-specific competition is related to the mode of stand establishment. For example, in a stand regenerated by planting with a single species, seedlings are rarely closer than 2 m and intra-specific competition can be delayed many years. Given that “acceptable” stocking levels can be as low as 40% or 1000 stems per hectare (sph) (Lieffers et al. 2008), the onset of intra-specific competition is even further delayed. However, under certain circumstances such as postfire or where coppicing or seeding is used, high densities of stems (e.g., >10 000 sph; Teste and Lieffers 2011; Landhäusser 2009; Bell et al. 1997; Van Damme and McKee 1997) are possible and intra-specific competition will largely determine which individuals will survive. In some cases, density is so high that no individuals can dominate and the outcome is stagnation. Thinning by machine or brushsaw at an early age (i.e., precommercial thinning) has been used to change access to resources and promote growth.

The more likely situation is that crop trees are established at the same time that other species are regenerating or present; hence, resource managers are more often concerned with inter-specific competition, especially in the early stages of stand establishment. Unfortunately, the naturally occurring, less desirable shrubs/trees may be better suited for the existing site conditions (e.g., high light levels); so the manager is put in the difficult position of trying to defend the less competitive trees. Ideally, deliberate combinations of crop and noncrop species can be used to achieve the identified management goals.

Both facilitation and complementarity are possible when two or more tree species are growing together. In practice, it is sometimes difficult to distinguish between the two. For example, a classic case involves the argument that the litter of a deciduous species can improve nutrient availability for a coniferous species, thus positively affecting survival or productivity. This could happen in at least two ways. In the first, the simple presence of the deciduous litter, which theoretically has lower C:N and fewer recalcitrant components, improves the quality of the soil organic matter and enhances mineralization. This would be facilitation, especially if the conifer is not growing well without the deciduous litter. In the second, the deciduous trees actually exploit a different (perhaps deeper) portion of the soil profile, thus accessing resources (water, nutrients) that would not otherwise be available. This would be complementarity. Clearly, both mechanisms could be happening simultaneously. Chapin et al. (1994) found the facilitative effect of two nitrogen fixers, *Alnus sinuata* (mid-successional species) and *Dryas drummondii* (early successional species), on the growth of Sitka spruce (*Picea sitchensis*), a late-successional species at Glacier Bay, Alaska. In their study, Sitka spruce planted in spruce forests had one-half the biomass of those planted among alders. Seed germination and survivorship were reduced due to the thicket of vegetation. Despite a net facilitative effect, spruce seedlings were also found to be inhibited due to competition with alder roots. Several factors, including facilitation, affected the final stage of community composition and productivity.

Characteristics such as shade tolerance, height growth, crown structure or leaf area density, and foliar and root phenology can

lead to complementarity (Kelty 2006). Variations among species in their ability to capture the limiting resources also result from different physiological needs and acclimation (Cannell et al. 1996; Jose et al. 2000a, 2000b). For example, vertical stratification of canopies divides the available space and creates a range of light conditions that may increase productivity and biodiversity. In the early stages of even-aged aspen – white spruce forests, aspen crowns occupy the upper layers where they are exposed to full sunlight (Man and Lieffers 1999). With attributes such as vertical leaf placement and petioles that encourage leaf fluttering and high photosynthetic rates, aspen is well adapted to these conditions. It, in turn, modifies the light environment of species in the subcanopy. As long as the reduction in photosynthetic active radiation is not excessive, shade tolerant or mid-tolerant species, such as spruce, can exhibit good photosynthetic efficiencies based on lower compensation points, greater specific leaf area, and higher chlorophyll concentrations than those in the open (Man and Lieffers 1999). Complementarity can also be based on phenology. For example, spruces are physiologically able to respond to suitable light and temperature conditions before aspen leaves develop in the spring and after they abscise in the fall (see Cannell et al. 1996; Jose et al. 2000a, 2000b). In a way, the growing season is longer for the spruces than for aspen.

Theoretically, under very specific conditions where resources are limited and two species inhabit exactly the same ecological niche, one species will eventually eliminate the other. Known as the competitive exclusion principle (Gause 1934), this phenomenon has rarely been demonstrated in situ or with native species. This may be because organisms, by definition, exhibit completely unique niches and the balance between them changes due to small- and large-scale disturbances (Connell 1978; White 1979; White and Pickett 1985; Reice 1994) that redistribute resources and shift the advantage from one species to another. An alternate explanation, Tilman's resource-ratio hypothesis, suggests that “stable coexistence is possible for species that are competitively superior at different ratios of essential resources” (Tilman 1982, 1985, 1990). A species' competitive ability will change as conditions change (Huston and Smith 1987). For example, planted conifer seedlings may not show signs of competition until the assart effect has passed and site resources become limiting. Nonetheless, it is widely recognized that forest tree species occupy similar enough niches so that certain combinations can lead to economically significant reductions in size and survival of desirable individuals. There is abundant literature that indicates potential productivity increases when noncrop species are prevented from acquiring site resources (Wiensczyk et al. 2011). An equally large body of research confirms the benefits of allowing resources to be spread among many species (Wagner et al. 2001). These benefits often include biodiversity, greater wood quality, soil stabilization, and carbon sequestration, among others. Forest stands that are managed for fibre must deliver products of a quality and size that justify these investments. The challenge for resource managers is to adjust their approach to recognize the critical interactions and trade-offs and design silvicultural interventions that take advantage of positive species interactions. The challenge for researchers is to tease out the interactions so they can be quantified to better inform management decisions.

Methods for studying competitive plant interactions

The study of plant interactions has evolved since Harper (1977), but this book remains a valuable source of information on plant population biology, including the description of different types of experimental methods. Plant interactions can be studied using observational or manipulative approaches. To be effective, these approaches should account for the relative importance of biological (e.g., symbiots and parasites), environmental (e.g., soil moisture and nutrients), proximity (e.g., plant density, species proportion, and spa-

tial arrangement among individuals), and idiosyncratic factors and their interactions (Harper 1977; Radosevich 1987; Gibson et al. 1999; Freckleton and Watkinson 2000; Keddy 2001; Radosevich et al. 2007). Four types of competition studies are routinely conducted by applied and basic plant ecologists (Table 2). Interrelationships between types of interactions that occur in plant associations can be revealed or masked by a particular design (Table 2).

Manipulative designs are a form of bioassay in which the response of one species (e.g., total or individual plant yield, plant growth rate or plant survival) is used to describe the influence of the other in the mixture. The requirements for these studies include (i) manipulating composition, density and (or) spatial arrangement of individuals, (ii) measuring plant responses (e.g., short-term physiological responses or long-term changes in size, weight or area), (iii) comparing with controls, and (iv) measuring resource level, i.e., evaluating an environmental factor such as a resource in both a treatment and a control may make it possible to determine which resources are affected and how (Keddy 2001). Manipulative designs involve the application of randomly allocated treatments (composition, density and (or) arrangement of crop and noncrop species) and controls to plots while keeping environmental conditions as constant as possible. Partial cut treatments may be used in forests to establish one of the experimental designs listed in Table 2, but this approach may be fraught with difficulty, such as the control of species mixture. For the efficient control of density, species composition, and variation in soil characteristics, it is preferable to plant trees. Plantations facilitate the implementation of replicated experimental designs, particularly for substitutive designs based on replacement series or Nelder or Diallel trials.

Observational studies (also termed sample surveys or comparative studies) can be used to document relationships between a dependent variable such as a crop response (e.g., biomass) and independent variables such as the presence, density, proportion or spatial arrangement of neighbouring species. They can be established in unmanaged forests by sampling stands of different densities and species composition. Retrospective observational studies often consider the question of successional dominance, that is, what species will assume a dominant role on a site or landscape over time or as a result of a management treatment. Since it is highly unlikely researchers can begin studies to investigate competition between trees and assess them through to climax conditions, a common approach is to examine sites at various stages of successional development within a region (Radosevich et al. 2007). Gradient studies involve quantifying species occurrence along environmental gradients that exist in most habitats. Gradients such as climate (e.g., solar radiation, precipitation, and temperature), soil types (and underlying substrate), and soil depth exist in most habitats. In general, observational studies cannot be used to identify cause-effect relationships of the underlying mechanisms of competition (Caspersen and Pacala 2001). For this reason, observational studies that capitalize on the power of regression analysis to characterize under field conditions species' proximity and their interactions with biological and (or) environmental factors should be considered (Freckleton and Watkinson 2000).

Clearly, there is no "optimum" design for competition studies. To select an appropriate design, researchers need to clearly define their aim, objectives, and practical constraints (Freckleton and Watkinson 2000), be mindful of the abundance-composition model that is appropriate for the ecosystem of interest, and even consider using a combination of observational and manipulative approaches. Many abundance-composition models of forest ecosystems follow a geometric series or log-series model (e.g., boreal forests) or a log-normal model (e.g., temperate mixedwood forests) (Magurran 2004). As a consequence, it might simply be too complex to establish replicated simple randomized complete block experiments, particularly when researchers wish to study

competitive interactions in ecosystems containing more than two species. The dimensions of the experimental unit also need to be carefully considered. Tilman (1989) reviewed several hundred studies of plant competition and found that nearly half of all studies were on a spatial scale of a square metre or less and three quarters were carried out in plots of less than 10 m × 10 m. Only 15% of the studies lasted longer than 3 years. Considering that tree root systems may overlap on very large areas around individual trees (e.g., Stiel 1970), relatively large sample plots are required. For trees that are to be grown to maturity, plots greater than 40 m × 40 m may be necessary. However, as plot size increases, uniformity of experimental areas with respect to species distribution generally decreases. The solution may be to focus on individual trees ("subject trees") surrounded by competitors rather than considering all the trees within sample plots, which are usually considered as experimental units. In this way, it is possible to better control species distribution. For instance, trees of a particular species can be removed to obtain desirable densities and species proportions. A major drawback of this type of solution is that the area required to implement a well-replicated experiment can increase considerably.

Researchers wishing to explore the effects of a large number of treatments could consider fractional factorial or response surface designs. As the number of combinations of species, densities, and species proportions increases, the number of potential treatment combinations increases exponentially. Experiments using only a fractional replication of the factorial arrangement (i.e., one half, one quarter, or even smaller fractions of the 2nd level of treatment combinations) are proposed as a means to reduce the number of treatment combinations that have to be evaluated, while ensuring sufficient data are available for statistical analyses, resulting in a carefully controlled set of "treatments" to consider (Kuehl 2000).

As far as analyzing the observational and manipulative data is concerned, structural equation modeling (SEM) has recently been proposed as a technique that permits us to test hypothesized patterns of directional and nondirectional relationships among a set of observed (measured) and unobserved (latent) variables. Since its inception in 1995 (Hoyle 1995), SEM has rapidly become one of the primary statistical means to address issues related to complexity. SEM allows the direct analysis of the network of causal relationships among variables, including complex interactions such as feedback cycles (Grace and Pugsek 1997; Shipley 2000; Grace 2006; Shipley et al. 2006). SEM has recently been applied to competition studies in grasslands and agricultural systems (Lamb and Cahill 2008; Lamb et al. 2011); but to our knowledge, it has not been applied in forest systems.

The first stage of every analysis using the SEM approach is a formal test of existing theory followed, if necessary, by an ordered search for empirical relationships that may represent unidentified ecological mechanisms. Unexpected pathways in other studies have led to the postulation of new ecological mechanisms in past studies (Grace and Pugsek 1997; Shipley et al. 2006). Such an analytical framework provides direct tests of current theory and frequently gives rise to new theoretical insights because few other analytical approaches can accommodate the range of processes and interactions that can be included in a SEM (Grace 2006). SEM has two key advantages over multiple regression models: (1) correlations between observed variables increase explanatory power; and (2) the paths in the structural model can represent specific ecological mechanisms, allowing the relative strengths of mechanisms to be compared.

Detection of asymmetric versus symmetric competition

The consensus that seems to emerge from the literature is that plants compete asymmetrically for light and symmetrically for

Table 2. Overview of four types of manipulative designs (sources: Harper 1977; Radosevich 1987; Gibson et al. 1999; Freckleton and Watkinson 2000; Radosevich et al. 2007).

Manipulative design	Composition	Density	Spatial arrangement	Pros and cons	Comments
Additive	More than two species can be grown together in an additive experiment, but most studies are conducted with only two species, for example, a crop and a weed or a desirable tree and a shrub species.	The density of one species, such as the crop, is always held constant while the density of the other is varied, usually by removal or addition. Total plant density always varies among treatments.	Assumed to be uniform, since the crop is usually planted in a grid pattern; and the influence of intraspecific competition is assumed to be constant.	The <i>simple additive design</i> where plants are grown “with” and “without” competition is commonly employed when large numbers of species and (or) other factors (such as nutrient levels, symbionts, and parasites) are manipulated, as it allows the size of the experiment to be minimized. The most complete design, the <i>response surface method</i> , allows complete quantification of the effects of competition within the range of densities explored in the experiment, but at the expense of very large designs.	Fully additive designs are the most labour-intensive. The additive approach is also criticized on the grounds that it confounds density and proportion and because the results may be biased by initial or final size. Proportion among species changes simultaneously with total plant density; thus, these two factors covary, making it impossible to evaluate the effect of either factor alone.
Substitutive (replacement series, Nelder and Diallel)	Species proportions are varied. Replacement series include pure stands as well as mixtures in which the proportion of species studied is varied. Nelder designs are usually restricted to a single species. A second species can be introduced by sowing the entire area with the second species or by alternating the placement of the species along an arc or spoke, so that differing ratios or species proportions result. Diallel designs combine individuals of each species under study into all possible pairs to examine their interactions.	Total plant density is held constant. In replacement series, total plant density is a constant over all treatments; thus, they must be conducted at sufficiently high densities and (or) for a long enough period to fall within the range of constant final yield. Several monoculture densities can be included in the design. In Nelder designs, the area per plant or the amount of space available to each plant changes in a consistent manner over the different parts of the grid.	Arrangement among individual plants is usually nonrandom. In replacement series, a nonrandom grid is used. Nelder designs consist of a grid of plants often planted in an arc or circle — alternating bigger and smaller plants along a spoke or arc is an artifact of the planting scheme and can produce a “wave” of size differences as the experiment proceeds through time.	The premise of substitutive designs is that the yield of a mixed stand can be determined relative to the yield of a monoculture.	In replacement series, four models are used to interpret negative, neutral or positive effects between species. An assumption of the replacement series is that each species has equal ability to interfere with the other. Replacement series may yield more information than a simple additive approach, since the components of the mixture are varied through a continuous range, but it confounds the effects of intra- and inter-specific competition and there are problems with the analysis and interpretation of the resulting coefficients. With Nelder designs, an array of densities can be studied without changing the pattern of plant arrangement and only a small area is required to examine the effect of many densities. Nelder designs have several disadvantages: (i) only individual plants can be measured, causing difficulty in obtaining the “stand” effect; (ii) they do not allow for partitioning of density and proportion effects unless more than one species proportion is used; (iii) intraspecific competition effects cannot be separated readily from inter-specific competition effects; and (iv) arcs are often difficult to plant. Diallel designs have simple layouts that allow examination of both intra- (compare A with AA or B with BB) and inter-specific (compare AB with either A or BB) interaction. Diallel designs have several disadvantages: (i) they are restricted when working with individual plants and pot or plot size is critical; (ii) resources may be relatively unlimited in a system that uses only one or two individual plants; and (iii) the influence of density from more than a single neighbour cannot be determined.

Table 2 (concluded).

Manipulative design	Composition	Density	Spatial arrangement	Pros and cons	Comments
Systematic (addition series, additive series or factorial designs)	Can be expanded to include up to four species.	Addition series are a combination of several replacement series over a range of total densities that encompass a triangular portion of a matrix of density combination. Additive series or factorial designs are a combination of additive experiments at different total densities that include all possible combinations of several densities of each species.	Either the addition series or the additive series method accounts for spatial arrangement.	A range of monoculture densities, total densities, and proportions can be varied systematically throughout the experiment, in terms of both total and relative plant densities (proportion).	
Neighbourhood	Target species either grown alone or surrounded by individuals of the neighbouring species. Proportions among species vary systematically throughout the design.	Varies systematically throughout the design.	Systematic grid that varies by density among target and neighbouring species.	May be appropriate when individual response to the proximity of other plants is of primary interest. Performance of a target individual is recorded as a function of the number, biomass, cover, aggregation or distance from its neighbours. Generalized equations have been developed to represent the relationship of target individual species performance to the proximity of neighbouring plants.	

water and nutrient resources (see Weiner 1988, 1990; Cannell and Grace 1993; Kikuzawa and Umeki 1996; Weiner et al. 1997; Blair 2001; Stoll et al. 2002; Rewald and Leuschner 2009). According to Nye and Tinker (1977) and Raynaud and Leadley (2005), differences in the symmetry of competition between resource types would be related to the specific mechanisms involved. Light penetrates within canopies from specific directions. As a consequence, when leaves overlap, those in the upper sections of the canopy intercept considerably more light than those in the lower sections. On the other hand, competing roots occupy a homogeneous medium composed of soil particles, nutrients, and water and have the same capacity per unit area to reduce the flow of nutrients and water among adjacent roots.

The detection of asymmetry in competition is not straightforward because direct measurement of the amount of different types of resources that individuals use is both complex and difficult. For this reason, indirect methods that are based on analyzing tree-size distribution were developed (Cannell and Grace 1993; Weiner 1990). Weiner and Thomas (1986) concluded that competition not only decreases the overall growth rate of individual plants but also increases the variability in growth rate. Thus, competition becomes asymmetric when larger plants are able to acquire a disproportionate share of resources and also suppress smaller ones.

Size inequality represents the degree to which most of the biomass of the population is concentrated in a few larger trees versus many smaller trees (Weiner and Solbrig 1984; Weiner and Thomas 1986). The Lorenz curve and Gini coefficient (G) were suggested for evaluating the inequality in plant populations where G is the deviation from the state of perfect equality.

$$G = \frac{\sum_{i=1}^n \sum_{j=1}^n |x_i - x_j|}{2n(n-1)\bar{x}}$$

where x is an attribute, such as size or biomass, of individual i or j , and n is the number of individuals.

Growth efficiency measures, such as relative growth rate, can be used to examine the symmetry of competition. The approach used by Schwinning (1996) is based on the decomposition of relative growth rates:

$$S = RAC$$

where S is the relative rate of resource uptake, R is the resource availability factor; A is the allometry factor, and C is the resource capture efficiency factor. The symmetry index, s , is then computed as

$$\ln s = \ln S_1 - \ln S_2$$

where S_1 and S_2 are the relative resource uptake rates of plants 1 and 2, respectively, where plant 1 is larger than plant 2. If $\ln s > 0$, the larger plant captures more resources per unit biomass than the smaller plant (positively asymmetric competition). If $\ln s = 0$, then large and small plants capture equal amounts of resources per unit biomass (relative symmetric competition). If $\ln s < 0$, the smaller plant captures more resources per unit biomass than the larger plant (negatively asymmetric competition).

Many questions remain to better understand the symmetry of competition, particularly for mixed stands. In particular, the methods based on the analysis of size distribution or variation in relative growth rate have mostly been applied in single-species stands. Few examples exist for mixed stands or plant communities (e.g., Peterson and Squiers 1995). Freckleton and Watkinson

(2001) used an approach based on the shape of yield-density response functions of mean biomass to examine the symmetry of competition in mixed conditions, but their work was limited to wheat and weed species. Rewald and Leuschner (2009) used a root coring technique in a growth chamber to estimate root biomass and distribution in a mixed *Carpinus-Quercus-Fagus-Tilia* forest. They concluded that root competition was asymmetric. However, this type of experimentation is not sufficient to provide conclusive evidence on the symmetry of competition. Differences in root biomass and distribution may differ among species but are not necessarily directly related to water and nutrient uptake rates.

Single-tree models are a very effective tool to explore the symmetry of competition (Cannell et al. 1984; Cannell and Grace 1993; Weiner 1990; Freckleton and Watkinson 2001; Alswais and Deussen 2005; Weiner and Damgaard 2006). If the representation of competitive interactions, which commonly consists in deriving competition indices, is realistic (see later in the paper), it is logical to expect that single-tree models can be effectively used to explore competition asymmetry in mixed stands. Asymmetric competition may be detected when the effect of larger competitors of the same or different species on the subject plant is represented by a significant nonlinear relationship in a model. In several cases, competition indices have been used to draw conclusions about the symmetry of competition in mixed stands. Good examples can be found in Peterson and Squiers (1995), Weiner et al. (2001), Pretzsch and Biber (2010), and Pierce and Taylor (2010). However, these indices must also be used with caution. Weiner et al. (2001) examined the role of spatial pattern, density, and competitive asymmetry on size variation in a crowded population. They found that size inequalities were sometimes due to spatial pattern or structure. In the early stages of stand development, the effect of spatial pattern on size inequality was more important than symmetric competitive interactions. However, as plants matured, size asymmetry became a more important source of size variation or inequality.

Even though the study of size distribution and derivation of single-tree models has contributed to increasing knowledge on asymmetric competition, the most logical step to strengthen the evidence for both single-species and mixed stands would be to directly measure how competing trees deplete resources by implementing experimental designs where water, nutrients, and light supplies vary, coupled with indirect methods based on the use of light interception and photosynthesis models (Cannell and Grace 1993). This is important particularly for mixed stands, as species exhibit different levels of efficiency in resource uptake. Despite the difficulties, different experimental approaches can be considered (see earlier in the paper). For light competition, the analysis of different patterns of interception within different configurations of branch and foliage interlock among trees differing in size can be performed. For root competition, the problem becomes more complex because of the difficulties in assessing root systems, but field assessment can be combined with measurements of water and nutrient uptake rates using appropriate instruments, such as sap flow systems.

Modelling methods

Modelling is a general term used to describe the process of deriving mathematical models. In forestry, the models used can be classified in two general groups: (1) analytical models and (2) dynamic models. Analytical models consist of mathematical relationships that relate a dependent variable to one or several independent variables. Good examples are growth and yield tables, allometric relationships or stem taper functions. Dynamic models include groups of interactive equations to simulate tree or forest growth over time. For their development, the basic principles of systems analysis are used and their mathematical structure gener-

ally consists of differential or difference equations that represent the dynamic nature of forest ecosystems, that is, the rate of change.

Analytical modelling of competition effect on individual-tree variables and their relationships

A detailed review of different types of analytical models is beyond the scope of this paper, but height–diameter relationships and stem taper functions are discussed because these variables are directly used in calculating product recovery and are affected by competition. In general, the more intra-specific competition (more trees per hectare in single-species stands), the better the stem form. That said, very little information is available on the stem form of trees in different stands with the same number of trees but varied species composition. Indeed, considering stem quality through appropriate crown stratification may improve individual-tree growth and stem form in both pure and mixed stands (Kelty 2006).

For single-species stands, Sharma et al. (2002) looked at possible asymmetric effects, which they called spacing rectangularity effects, on the growth of loblolly pine trees established at nominal (3:4) and greater (1:3) rectangular spacings that resulted in the same initial planting density of 2240 trees/ha. Spacing rectangularity was defined as the ratio of tree distances within and between rows. They reported that at age 17 the crown size was significantly affected by asymmetry effects, but height and diameter growth were not. In another study, Amateis et al. (2004) evaluated the asymmetric effect on tree stem quality of the same trees at age 19. They also reported no asymmetric effect on overall stem quality. For mixed stands, Larson et al. (1998) found that asymmetric shapes in crowns in mixed stands of red and white pines did not result in asymmetric bole growth.

The competition effect on the height–diameter relationship has been investigated by several researchers. López Sánchez et al. (2003) listed studies of stand density effects on the height–diameter relationship. They hypothesized that, for a particular height, trees that grow in high density stands would have smaller diameters than those growing in less dense stands as a result of greater competition among individuals. They examined several height–diameter models that included a variety of stand variables, such as dominant diameter, dominant height, age, stand density (basal area per hectare and trees per hectare), and site index, to account for the competition effect.

Sharma and Zhang (2004a) assumed that the height–diameter relationship of a tree species varies among environments and stand conditions (trees per hectare, basal area, etc.). They along with others (e.g., Ferguson and Leech 1978; Krumland and Wensel 1988; Harrison et al. 1986; Larsen and Hann 1987; Zakrzewski and Bella 1988; Parresol 1992; Soares and Tomé 2002; Eerikainen 2003; Calama and Montero 2004; Sharma and Parton 2007) used stand variables to explain the competition effect on the height–diameter relationship.

In contrast to the wealth of studies published on the competition/stand density effect on height–diameter relationships, little information is available about the competition effect on stem taper. It is well known that the shape of a tree is influenced by stand density (Gray 1956; Larson 1963; Sharma and Zhang 2004b). Wang et al. (1998) reported that the slenderness coefficient of a tree defined as the ratio of total height to outside bark diameter at breast height is related to tree taper and is positively correlated with stand density, species composition, and site index values.

Larson (1963) stated “tree growth and stem form development follow certain general laws or patterns of growth that are inherited. But the basic patterns may be modified by many environmental factors and by silvicultural practices.” He further stated “most variations in stem form may be traced to changes in the size and distribution of the live crown on the stem and to length of the branch-free bole.” Obviously, the size and distribution of the live crown on the stem and the length of the branch-free bole are affected by competition/stand density. Recently, Sharma and Parton (2009)

examined the competition/stand density effect on the taper of plantation-grown jack pine and black spruce trees and incorporated a stand variable (basal area per hectare) into their taper equations to account for the competition effect of stand density.

A literature search on species composition effect on the height–diameter relationship and tree taper indicated that this question remains to be investigated. The only significant study was conducted by Wang et al. (1998) for some North American mixed-species forest types. As mentioned earlier, patterns of crown recession rate and branch structure vary significantly among species and these patterns affect both height–diameter relationship and stem taper. Therefore, it is logical to expect that species composition may have an effect on both height–diameter relationships and stem taper.

Dynamic models

Forest productivity is the final outcome of competitive interactions and the majority of forest productivity models are based on the modelling of this process. Models can be classified in several ways (Munro 1974; Shugart 1984; Porté and Bartelink 2002; Larocque 2008). While Munro (1974) focused on empirical growth and yield models; Shugart (1984), Porté and Bartelink (2002), and Larocque (2008) distinguished between statistical and mechanistic models. Larocque (2008) suggested three broad categories of models: (1) growth and yield, (2) gap, and (3) process-based.

Growth and yield models

Growth and yield models, also known as empirical models, are derived using statistical analyses of stand inventory data. This category of model does not explain the underlying mechanisms of tree and stand growth, but rather derives relationships that best fit the data. There are two large well-recognized subcategories: whole-stand models and single-tree models (Munro 1974; Groot et al. 2004).

Whole-stand models predict growth based on stand attributes, such as basal area, total bole volume or stand density. The representation of the effect of competition in whole-stand models is quantified directly through the use of independent variables, such as basal area or stand density. Stand-level models generally have been constructed for single-species stands with examples for mixed stands being rare. Payandeh (1988) developed yield functions for boreal spruce–fir stands to estimate separate yield components for conifers and hardwoods. Payandeh and Wang (1996) also developed yield functions for boreal mixedwood stands (mixed conifer–hardwood stands) but did not separate yield estimates by species. Penner (2008) developed yield models for mixed-species stands in boreal forests but found that their accuracy varied with forest type. In their current state, stand-level yield models for mixed-species boreal stands cannot be used to analyze the effect of species proportion on stand growth and yield. Stand density management diagrams (SDMDs), which are based on self-thinning theory, constitute another form of stand-level model that has mainly been applied to even-aged, single-species stands (Newton 1997). Some progress has been made in developing mixed-species SDMDs for boreal and temperate forests. For example, Smith (1996) added species proportion to a boreal mixedwood SDMD as a third dimension, permitting analysis of the effect of species on size–density relationships, but noted that verification was required. Despite the fact that, compared with single-tree models, whole-stand models have a long history of development and use, they have limited use for representing competitive interactions as competition occurs locally among plants and results in increasing size variation within a forest stand (Weiner 1984; Berger and Hildenbrandt 2000; Berger et al. 2008).

Single-tree models predict the growth of individual trees by deriving mathematical representations of the effect of the presence of neighbouring competitors. They may or may not be spatially explicit. Commonly used terms according to Munro's (1974) classification sys-

Table 3. Five categories of spatial competition indices used to model competitive interactions among trees within a stand.

Competition index categories	Basic concept in the computation of the intensity of competition	Examples
Zone of influence	Degree or amount of overlap between zones of influence	Newnham (1966); Bella (1971); Wyszomirski et al. (1999)
Size and (or) distance of competitors	Size of each competitor adjusted by distance between trees	Hegyi (1974); Vettenranta (1999)
Area potentially available	Area of a polygon with a dimension that is a function of the number of competitors	Brown (1965); Moore et al. (1973); Nance et al. (1988)
Open-sky view and (or) exposed crown area	Sky proportion that is not obstructed by neighbouring crowns	Hatch et al. (1975); Chan et al. (1986); Kuuluvainen and Pukkala (1989); Wyckoff and Clark (2005)
Crown interference	Degree to which crown overlap reduces growth	Larocque (2002); Pretzsch (2009)

tem are distance-independent (not spatially explicit) or distance-dependent (spatially explicit) single-tree models.

The intensity of competition in non-spatially explicit models may be quantified using stand variables, such as basal area, stand density, number of neighbouring trees, basal area of trees greater than the subject tree or size of individual trees relative to mean tree size (Weiner 1984; Larocque 2008). Many non-spatially explicit models were developed for single-species stands. Relatively fewer examples exist for mixed stands, such as those by Biging and Dobbertin (1995), McRoberts et al. (2002), Lacerte et al. (2006), Stadt et al. (2007) or Diggins et al. (2010). In such models, growth and mortality equations are calibrated for each species, but the coefficients of stand-level independent variables (e.g., basal area) or competition indices do not necessarily represent well the effects of species-specific ecological differences. Even if a model includes the basal areas of different species as independent variables, it implicitly assumes that a unit of basal area of all species has the same competitive effect on the growth of a tree, which is unlikely, since species vary in their resource needs/uses. A major difficulty for mixed stands is the considerable amount of data required for their calibration, as species composition may vary considerably, particularly when there are more than two species.

Spatially explicit models are based on the computation of competition indices with formulations that include inter-tree distances. Examples of five types of competition indices are presented in Table 3. For the zone of influence type, which is based on the concept of crown competition factor (Krajicek et al. 1961), the intensity of competition is a function of the amount of overlap in the zones of influence between subject trees and competitors within a stand. The zone of influence represents the area within which trees compete for site resources and is estimated from the expected maximum crown width of an open-grown tree of the same species and diameter. Competition indices based on the sizes and distances between subject trees and competitors are the most simplified representations of competitive interaction. The category area potentially available consists of the derivation of a polygon that delimits the area available for each tree. The number of sides of the polygon depends on the number of perpendicular intersected lines between a subject tree and competitors. The last two indices in Table 3 are based on crown interactions. For the open-sky view/exposed crown, several indices were developed, but they all share the same basic feature with respect to neighbouring crown obstruction. The crown interference category represents the effects that the crowns of competitors have on the growth of subject trees. Spatially explicit models have a long history of development and use. Many studies that developed or compared competition indices showed mixed results (e.g., Pukkala 1989; Gourlet-Fleury 1998; Soares and Tomé 1999). For the majority of competition indices, the strength of the relationships varied, but most were poor. In fact, most models that successfully predicted individual-tree growth were based on relationships that included initial tree size and a competition index; but in many cases, the competition indices contributed little to the significance of the relationships.

This raises questions about whether existing competition indices adequately represent the complexity of competitive interactions. For instance, very few competition indices account for the symmetry of competition.

Many spatially explicit models have been derived or used for single-species stands. Research work on competition indices for mixed-species stands has been on-going (Burkhart and Tomé 2012) and the literature has been increasing steadily. Good examples can be found in Holmes and Reed (1991), Biging and Dobbertin (1995), Berger and Hildenbrandt (2000), Canham et al. (2004), Zhao et al. (2006), and Stadt et al. (2007). However, few of them accounted for differences in species ecological characteristics. Holmes and Reed (1991) raised this issue when they concluded that the degree of significance of some competition indices varied with species-specific shade tolerance. Burton (1993) associated the shade tolerance effect on competition index performance with species-specific physiological and morphological properties. Zhao et al. (2006) separated the statistical effect of different species groups in the neighbouring effect but highlighted data limitations for effective species functional stratification. Pretzsch et al. (2002) developed their competition index by considering differences in light transmission capacity and crown surface area among species. Despite some successful results in the integration of the representation of species differences, more work is needed for the development of competition indices for mixed-species stands, beyond the application of different statistical approaches. In particular, the representation of species-specific ecological characteristics with respect to soil resource use must be integrated; and the symmetry of competition, the importance of which may be more important in inter- than intra-specific competitive interactions (Zhao et al. 2006) must be taken into account.

Growth and yield models have been used extensively for growth prediction. One of the assumptions in these models is that species composition and site conditions (soil characteristics and climate) do not change over time (Canham et al. 2004; Grant 1994; Kimmins et al. 2008). These assumptions are reasonable for short-term predictions that span two or three decades. However, when predictions are needed to answer questions on the course of succession or the effects of climate change, growth and yield models have severe limitations. Gap or process-based models are better equipped to deal with both issues, but their ability to represent competitive interactions still needs to be assessed, particularly for mixed stands.

Gap models

Gap models belong to the category of single-tree models that are non-spatially explicit. Compared with the single-tree growth models discussed earlier in the paper, they may be considered as semimechanistic because they include basic theoretical representations of biotic and abiotic processes occurring in forest stands, including the effects of light interception, site fertility, and temperature on tree growth. They are considered flexible enough to predict the development of mixed, uneven-aged stands with com-

plex structures (Larocque 2008). In gap models such as FORET (Shugart 1984), ZELIG (Urban et al. 1991) or PIEDMONT (Druckenbrod et al. 2005), each species is classified into growth sensitive response classes for shade tolerance and soil fertility and moisture, and the growth of each tree is constrained by the rate of crown recession, which is influenced by the amount of light intercepted by all the trees within a stand and the species-specific shade tolerance class. According to DeAngelis and Mooij (2005), gap models integrate the effects of phenotypic variations among individual trees. However, despite the fact that they still need further development with respect to some of their assumptions, including competitive interactions (Liu and Ashton 1995; Larocque et al. 2006), they have potential for application in mixed stands because they lack the limitations associated with growth and yield models.

In gap models, one of the features that needs further refinement is the integration of crown plasticity (Strigul et al. 2008). For instance, assumptions, such as representation of crown structure by a cylinder or horizontally uniform crown distribution, need to be challenged. These refinements are essential not only to better characterize differences in competitive ability among species, but also to better formulate how crowns interact (Vincent and Harja 2008). As far as can be evaluated from the literature, the modelling of competitive interactions has not been considered in the light of the symmetry of competition. According to Toda et al. (2009), both crown shape and foliage profile of individual trees are two key factors that affect the intensity of competitive asymmetry.

Process-based models

Process-based models simulate the ecophysiological processes and flows of energy, carbon, water or nutrients that govern tree and stand growth. They are commonly used to predict the effects of disturbances, such as climate change, and have been used mostly to simulate stand- or landscape-level changes. Relatively few examples exist at the tree level (e.g., Gayler et al. 2006; Host et al. 2008; Brotsma et al. 2010a, 2010b). Despite significant progress in testing various approaches, along with their assumptions and limitations, the major challenge remaining is modelling competitive interactions. For instance, Brotsma et al. (2010a, 2010b) simulated competition for light and water using a model that included photosynthesis, transpiration, respiration, and water flow components. Light interception was modelled at the tree level, but they used the big leaf approach to represent variation in crown characteristics, which limited the possibility of examining different scenarios of asymmetric competition for light. Gayler et al. (2006, 2008) developed the PLATHO model to simulate mechanisms of inter-tree competition, including radiation absorption, leaf photosynthesis, and shading by neighbours. PLATHO also includes detailed model components to account for the effects of external factors on growth. However, the intensity of competition is computed using the traditional concept of overlap between zones of influence between crowns and root systems, similar to competition indices. As such, the potential effects of asymmetric competition are not factored in. However, the model has the flexibility to take into account differences in plant morphology and, therefore, has potential for mixed-species stands.

Adding more mechanistic details to single-tree process-based models may prove very useful to better understand competitive interactions. By simulating carbon partitioning and nutrient allocation at the tree level, it becomes possible to examine the different conditions that may define the symmetry of competition in depth and detailed descriptions of tree architecture may prove useful for application in heterogeneous stands (Letort et al. 2008). Toda et al. (2009) pointed out that the degree of competitive asymmetry may be closely associated with changes in microclimatic conditions, affecting physiological factors, such as maximum carboxylation velocity, within a forest stand. Some mechanistic models simulate detailed crown architecture reconstruction at both the branch and foliage levels and physiological processes (e.g.,

Host et al. 2008; Letort et al. 2008). One of the best examples is the ECOPHYS model (Rauscher et al. 1990), which is used to simulate different scenarios of light interception at both the leaf and branch levels, allowing users to examine different questions on asymmetric competition for light among crowns of different sizes and morphological characteristics within both single-species and mixed stands.

Concluding remarks

Much has been accomplished in the study of competitive interactions in tree and plant communities, and the knowledge has contributed to developing management scenarios for mixed forests and provided guidance for suitable species mixtures for plantations. However, many research questions remain, particularly about competitive interactions in mixed forest ecosystems. It is not evident from the literature whether intra-specific competition affects individual-tree growth more or less than inter-specific competition. Within single-species stands, reduced growth of individual trees with increases in competitive stress has been observed in many spacing trials and thinning experiments and the associated effects of intra-specific competition can be quantified. For mixed stands, the situation is more complex. While competitive interactions between two or more species can reduce tree growth for some species mixtures, the occurrence of facilitation or complementarity mechanisms may benefit other species mixtures. The issue of species mixture must be considered by examining several characteristics, such as stand structure, species variation or development stage, to shed more light on the mechanisms involved. For instance, while two species might compete severely at specific development stages, at other development stages they may not. As well, the occurrence of inter-specific competition must be considered beyond tree and stand productivity, as mixed stands may provide several ecosystem services, including wood quality, biodiversity issues, soil stabilization or carbon sequestration.

Future research in competition should be based on a mechanistic approach by studying the processes involved, including light interception and water and nutrient uptake. Most studies that examined processes have been conducted for single-species stands, as the study of processes in mixed stands is much more complex. For both single-species and mixed stands, improving understanding of competition for site resources requires acknowledging that crowns and roots are closely interlinked. Crowns intercept light for photosynthesis, but the photosynthetic machinery requires both water and nutrients to reach an adequate level of efficiency, and underground processes and root systems warrant more attention. The study of processes can also contribute to better understanding the symmetry of competition.

The implementation of state-of-the-art experimental design methods is also required to improve the understanding of competitive interactions. In forestry, most competition studies involve spacing trials containing one species. Several designs have been suggested for species mixtures but were applied mostly to evaluating the effect of herbaceous species on seedling development. For mature mixed stands, it is more difficult to implement appropriate experimental designs because of the extensive spatial variability in terms of species distribution and structure, which may restrict the establishment of statistically replicated designs.

Despite all the models that have been developed, the modelling of competitive interactions remains a challenge. Not only is there a need to develop models for mixed stands, but also to improve the modelling of competitive interactions, which is not a trivial task given the complexities involved. For instance, existing spatial models that incorporate competition indices are based on fairly simple assumptions. Future investigations should focus on the development of more mechanistic models that include realistic representations of competition.

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