

RESEARCH ARTICLE

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# Competition effects in an afrotemperate forest

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## Abstract

**Background:** Information about competition responses is mainly available for monospecific stands or mixed stands with a small number of species. Studies on complex multi-species and highly structured forest ecosystems are scarce. Accordingly, the objective of this study was to quantify competition effects and analyse competition responses in a species-diverse afrotemperate forest in South Africa, based on an observational study with mapped tree positions and long-term diameter increment records.

**Methods:** The sensitivity to competition was analysed for individual species and involved the calculation of the slope of the linear relation between the value of a competition index (CI) and diameter growth as a measure of sensitivity. In a next step different competition indices were combined and tree diameters were grouped in three classes as surrogates for canopy status and ontogenetic stage.

**Results:** Five competition indices were found to be effective in showing sensitivity to competition for a number of canopy and sub-canopy species. Significant linear regressions were fitted for 18 of a total of 25 species. Species reactions varied significantly in their sensitivity to the different CIs. The indices were classified as belonging to two groups, those that responded more to local crowding and those that are more sensitive to overtopping, which revealed species-specific sensitivities to both factors. The analysis based on diameter classes revealed that species clearly changed their sensitivity to crowding or overtopping depending on diameter. Canopy and sub-canopy species showed distinct differences in their reactions.

**Conclusions:** The application of multiple CIs brought novel insights relating to the dynamics of afrotemperate forests. The response patterns to different competition indices that focus on crowding and overtopping are varied and tree diameter dependent, indicating that oversimplified assumptions are not warranted in the interpretation of CI- growth relations.

**Keywords:** Observational study; Multi-species forest; Distance dependent competition indices; Simultaneous competition index approach; Tree-tree interaction; Ontogenetic effect

## Background

The natural world is to a great extent shaped by the interaction between organisms, in which the fitness of one is lowered by the presence of another (Begon et al. 1996). This interaction, known as *competition*, refers to the relationship between members of the same or different species in which individuals are adversely affected by those having similar resource requirements, such as moisture, nutrients or light. Competition is one of many interacting biotic and abiotic factors that affect the structure of a forest community (Sahney et al. 2010). Facilitation is another, but the focus of this study is on competition. In this

context, it is important to differentiate between competition effects and response to competition.

In a forest community, a competition effect is some measure of the aggregate “effect” on the performance of a specific tree by its competing neighbours. Competition effects can occur above and belowground ((Cahill 1999; Cahill 2002); (Song et al. 2012)) and involve a reduction in resource availability. A direct assessment of resource availability is usually very labour intensive and includes measurements of many variables such as light, water and nutrient availability under field conditions. For this reason, the aggregate effect is frequently estimated using a competition index (CI) instead, which may include a measure of density, the relative size or available growing space of a reference tree, the number and proximity of immediate neighbours, or estimates of shading and constriction.

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Possibly the earliest recorded index is the *available growing space* index (German: *Wachstraumzahl*) applied by (Seebach 1846)<sup>a</sup>, which is expressed by the observed crown diameter of a tree divided by its breast height diameter (dbh). The greater its value, the greater is the tree's potentially available growing space and the less is the competition effect. Various techniques for estimating available growing space have been proposed ((Green and Sibson 1977); (Lee 1980); (Nance et al. 1988)). A common approach involves the use of a *Voronoi* polygon, which contains the set of all points that are positioned closer to the centre tree in that *polygon* than to any other tree. (Pukkala 1989) describes a simulation study based on a mapped stand of *Pinus sylvestris* with an application of the *ecological field theory*, which is based on the assumption that each tree reduces the availability of radiation, water and nutrients by its roots, crown and stem. Each of these trees generates a *field* of resource use that can be described mathematically by a distribution function around each tree. The fields are then added up and in projected to the ground where they form the field map.

The most common forms of physical impediment within a group of trees interacting with each other are constriction of the growing space and shading. However, (Assmann 1953) pointed out that mechanical constriction by neighbouring trees limits the expansion of a tree crown and constitutes an element of competition. The available amount of light can have a similar limiting effect. So it is no surprise that CIs focussed on shading and overtopping have proven to be fairly reliable predictors when tree growth was simulated in light limited environments. Canham et al. (1999) for example developed a gap light index that takes into account the open areas of the sky where the tree crown can receive photon flux for mixed stands in North America. In extension of Canham's idea, hemispherical projections of neighbouring trees similar to *fish-eye*-photos were simulated to describe competition for trees ((Courbaud 1995); (Biber 1996)), and branches (Seifert 2003). A large body of distance dependent competition indices are typically making use of distance to neighbours and the proportion of the focus tree's dimension in relation to other trees (see (Biging and Dobbertin 1992) and (Bachmann 1998) for reviews). Prominent examples are the Hegyi index<sup>b</sup> (Hegyi 1974) basal area of the larger trees as proposed by (Wykoff et al. 1982), (see also (Coomes and Allen 2007)) or the cone based shading index used by (Pretzsch 1992). Despite not directly calculating shade they often emphasise the effect of larger trees and thus have a stronger focus on light related competition as experienced by overtopping.

However, also more local density related indices, describing local crowding, have been reported to provide good results for growth prediction, such as the local basal

area ((Steneker and Jarvis 1963); (Mailly et al. 2003); (Coomes and Allen 2007); (Seydack et al. 2011)).

An important step was the combination of light and crowding focussed CIs by (Canham et al. 2004), extended in (Coates et al. 2009), who applied a rigorous analysis to test the effects for different conifer species in British Columbia. Major outcomes of their study were that tree size is related to the sensitivity of a species to a CI and species display strongly different reactions to competition. Based on a CI study (Coomes and Allen 2007) also showed tree size dependent effects on competition. Whereas competition for nutrients affected trees of all sizes, competition for light was mainly affecting smaller trees in *Nothofagus* stands of New Zealand. (Coates et al. 2009) provided further evidence that competitive regimes might change during the lifetime of a tree.

Competition response is the degree to which the performance of a reference tree is reduced given the competition effect of the neighbours. Some trees are more sensitive to competition than others. The degree of indifference or sensitivity depends on the species, resource limitation and age. (Van Daalen 1993) was one of the first to provide quantitative proof on the influence of crown position on growth of trees in the mixed evergreen forests of the Knysna area at the southern coastline of South Africa. Light demanding trees, for example, may be less sensitive to shading at a young age, but they become gradually more sensitive with increasing age (cf. (Valladares and Niinemets 2008) for a review). Facilitation, which results in positive interactions between individuals, may significantly complicate the study of competition response. A typical example is that certain mixtures of tree species increase the nutrient availability, nutrient uptake or nutrient use efficiency ((Rothe and Binkley 2001); (Richards et al. 2010); (Forrester 2014)). However, isolating specific responses to different mixtures at varying levels of density is a challenging task.

Shifts in the root/shoot ratios reflect strategic allocation of plant biomass for resource acquisition and indicates specific response to competition (Casper et al. 1998). Numerous studies support the idea that resource availability influences biomass partitioning (Wilson 1988). (Bolte et al. 2004) reported that interspecific competition reduced the root/shoot ratio in the study of above- and below-ground biomass in mixed stands of European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*). Plants adjust their above- and below-ground biomass structure in response to environmental changes. Water and photo-active radiation are key resources that may affect the morphological response of individuals ((Seifert 2003); (Longuetaud et al. 2008); (Seifert et al. 2010); (Leuchner et al. 2012)) as well as the structural composition of a forest community (Sahney et al. 2010). (Bond-Lamberty et al. 2002) found that foliage production is highly sensitive

to light, water and nutrient conditions. Recent progress in explaining competition effects at the individual and stand level was achieved in simulation studies that could extend competition concepts in order to explain species-specific sensitivity to competition for resources and the interaction with stress (Rötzer et al. 2012).

The response to aboveground competition includes changes in the biomass structure and allometry of aboveground components ((Seifert 2003); (Wang et al. 2011); (Rötzer et al. 2012)). However, this may be insufficient to explain the response to belowground competition. Due to technical problems of sampling and measurement, belowground competition has been given little attention compared with aboveground competition in mature multi-species forests ((Casper and Jackson 1997); (Bauhus et al. 2000); (Curt & Prévosto 2003); (Bolte et al. 2004)). It has been reported that early-successional, fast-growing and light-demanding species are the most responsive to the removal of root competition and are capable of very rapid morphological adaptation ((Messier and Nikinmaa 2000); (Gunaratne et al. 2011)), but isolating the effects of aboveground vs. belowground competition is difficult.

Additional to considerations of above- and below-ground competition effects the inclusion of the spatial symmetry of competition might be desirable ((Pretzsch 1992); (Seifert 2003)). A sound argument for integrating such spatial effects is provided by the fact that there is not only a substantial effect on crown and branch development (Seifert 2003), but also first evidence that spatially irregular growing conditions reduce space-use efficiency (Ackerman et al. 2013).

Information about competition response patterns is mainly available for monospecific stands or mixed stands with a small number of species. Studies on complex multi-species and highly structured forest ecosystems are scarce ((Moravie et al. 1999); (Coates et al. 2009); (Seydack et al. 2011)). Accordingly, the objective of this study is to quantify competition effects and analyse competition response in a highly species-diverse afrotemperate forest in South Africa, based on spatial tree distribution data and long-term diameter increment records, obtained from a permanent observational study. The following specific questions are addressed:

- 1) **Are there species-specific differences in the correlation of diameter increment with distance-dependent competition indices?** The ecological question is whether the complex relationships of competitive tree-tree interactions in a sub-tropical afrotemperate stand can be captured by a rather simple index. With this question another one is addressed: is there a generic index that is useful for modelling competitive sensitivity equally well across species?

- 2) **Do tree species respond differently to crowding or overtopping in different ontogenetic stages?**

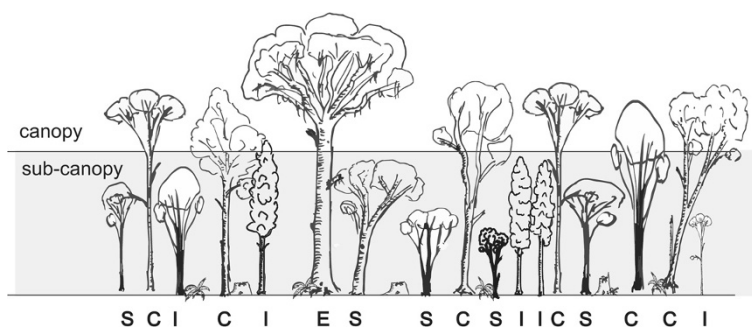
This includes the question whether the correlation of diameter increment with different indices allows conclusions on the specific ecological behaviour of a tree species and whether a general sensitivity of trees in different diameter classes has additional information value and takes cognisance of effects where CIs deliver complementary or redundant explanation values.

## Methods

The study area, known as Diepwalle Research Site (517 m a.s.l.) is part of the Southern Cape Forests, which are found on the coastal platform and foothill zone of the Outeniqua and Tsitsikamma mountains in South Africa between 190 and 520 m a.s.l. (Seydack et al. 2012). The average annual maximum temperature for the region is 19.2°C while the average minimum is 11.1°C. Rainfall occurs in all seasons and the climate can be considered transitional to the tropical/subtropical and temperate regions. The mean annual precipitation may vary between 700 and 1230 mm, subject to orographic influences and is increasing from west to east. The Southern Cape Forests, part of the afrotemperate group of forests (White 1978), are classified as Southern Cape Afrotemperate Forests (Geldenhuys and Mucina 2006). They are broadly tropical-type forests in terms of structure and function (Seydack et al. 2011; Seydack et al. 2012). The Diepwalle Research Site is located within the cool, moist upper foothill forest zone of these forests (Seydack et al. 2012).

## Canopy structure of the Diepwalle forest

Most forests display several reasonably well-defined layers of woody vegetation. The tallest trees, known as “emergents”, may rise well above the main canopy. “Canopy trees” intercept most of the radiation. Directly beneath the canopy there is another layer of woody vegetation, known as the sub-canopy layer (see Figure 1). The sub-canopy layer usually includes immature canopy trees and shade tolerant species that never reach canopy height. The shrub layer is formed by low woody plants, sometimes with multiple shoots or stems from the base, which attain only small heights at maturity. Canopy positions for individual species are indicated in Table 1. Canopy species with relatively high light responsiveness according to the crown position response index are *Pterocelastrus tricuspidatus*, *Podocarpus falcatius*, *Psyrax obovata* subsp. *obovata* and *Olea capensis* subsp. *macrocarpa*. *Podocarpus latifolius*, *Apodytes dimidiata*, *Curtisia dentata* and *Ocotea bullata* are comparatively shade-tolerant (Seydack et al. 2011). Derived from maximum negative water and negative osmotic potential values determined by (Mitlöhner 1998) we



**Figure 1** Schematic diagram showing typical layers in the afrotemperate forest of the Diepwalle observational study: Emergent (E) and canopy species (C) dominate the canopy layer, while the sub-canopy layer comprises of immature canopy species (I) and shade tolerant species (S) that never reach canopy height. The shrub layer is not shown in this diagram.

**Table 1** Species code, species names, number of measurements, and arithmetic mean and standard deviation (sd, cm) of diameter (dbh, cm) and diameter increment (id, cm/year) of the study site

| Species code | Scientific name                               | English name           | Canopy position* | N    | dbh       |      | id   |      |
|--------------|---|------------------------|------------------|------|-----------|------|------|------|
|              |   |                        |                  |      | Mean (cm) | Sd   | Mean | Sd   |
| Ass          | <i>Curtisia dentata</i>                       | Assegai                | c                | 2170 | 19.4      | 7.2  | 0.12 | 0.09 |
| BH           | <i>Rapanea melanophloeos</i>                  | Cape beech             | c                | 35   | 15.5      | 4.7  | 0.29 | 0.12 |
| BYH          | <i>Olea capensis</i> subsp. <i>macrocarpa</i> | False ironwood         | s(c)             | 35   | 20.8      | 7.7  | 0.07 | 0.06 |
| Btol         | <i>Diospyros whyteana</i>                     | Bladder-nut            | s                | 267  | 14.2      | 3.7  | 0.05 | 0.06 |
| Geel         | <i>Podocarpus latifolius</i>                  | Real yellowwood        | c                | 2539 | 27.1      | 14.4 | 0.13 | 0.09 |
| HP           | <i>Olinia ventosa</i>                         | Hard pear              | c(e)             | 9    | 33.1      | 26.2 | 0.43 | 0.22 |
| KE           | <i>Canthium mundianum</i>                     | Rock alder             | s                | 184  | 16.8      | 5.4  | 0.14 | 0.09 |
| KH           | <i>Lachnostylis hirta</i>                     | Coalwood               | s                | 189  | 15.9      | 4.9  | 0.13 | 0.08 |
| Kal          | <i>Podocarpus falcatus</i>                    | Outeniqua yellowwood   | e                | 209  | 22.5      | 14.5 | 0.17 | 0.12 |
| Kam          | <i>Gonioma kamassi</i>                        | Kamassi                | s                | 2573 | 15.1      | 3.5  | 0.09 | 0.08 |
| Kers         | <i>Pterocelastrus tricuspidatus</i>           | Candlewood             | c                | 1169 | 20.3      | 10.3 | 0.19 | 0.13 |
| Kw           | <i>Psydrax obovata</i> subsp. <i>obovata</i>  | Quar                   | c                | 323  | 28.6      | 11.1 | 0.14 | 0.12 |
| N            | <i>Halleria lucida</i>                        | Tree fuchsia           | s                | 155  | 16.7      | 6.0  | 0.07 | 0.10 |
| RH           | <i>Ochna arborea</i>                          | Cape plane             | s                | 58   | 11.9      | 1.4  | 0.05 | 0.07 |
| SH           | <i>Ocotea bullata</i>                         | Stinkwood              | c                | 491  | 27.1      | 12.2 | 0.12 | 0.12 |
| Saf          | <i>Elaeodendron croceum</i>                   | Common saffron         | s(c)             | 947  | 17.3      | 6.8  | 0.10 | 0.07 |
| Sw           | <i>Maytenus peduncularis</i>                  | Cape blackwood         | c                | 346  | 19.9      | 9.2  | 0.10 | 0.09 |
| Sy           | <i>Cassine eucliformis</i>                    | White silky bark       | s(c)             | 136  | 20.0      | 6.7  | 0.16 | 0.10 |
| V            | <i>Nuxia floribunda</i>                       | Forest elder           | c                | 422  | 19.7      | 8.0  | 0.10 | 0.10 |
| WE           | <i>Platylophus trifoliatus</i>                | White alder            | c                | 13   | 20.6      | 9.6  | 0.23 | 0.11 |
| WG           | <i>Burchellia bubalina</i>                    | Wild pomegranate       | s                | 31   | 11.3      | 1.3  | 0.07 | 0.05 |
| WH           | <i>Ilex mitis</i>                             | White wood, Cape Holly | c                | 12   | 24.8      | 5.9  | 0.46 | 0.14 |
| WP           | <i>Apodytes dimidiata</i>                     | White pear             | c                | 988  | 22.6      | 8.9  | 0.09 | 0.09 |
| YH           | <i>Olea capensis macrocarpa</i>               | Ironwood               | c                | 4204 | 30.3      | 14.3 | 0.17 | 0.13 |
| VRH          | <i>Kiggelaria africana</i>                    | Wild peach             | c                | 3    | 11.2      | 1.5  | 0.09 | 0.02 |

\*Canopy position indications (e: emergent; c: canopy; s: sub-canopy).

place canopy species into four perceived groups of declining tolerance to water deficits. 1) *Pterocelastrus tricuspidatus*; 2) *Podocarpus falcatus*, *Curtisia dentata*, *Psydrax obovata* subsp. *obovata*; 3) *Nuxia floribunda*, *Ocotea bullata* and 4) *Olea capensis* subsp. *macrocarpa*, *Apodytes dimidiata*, *Podocarpus latifolius*.

#### Data

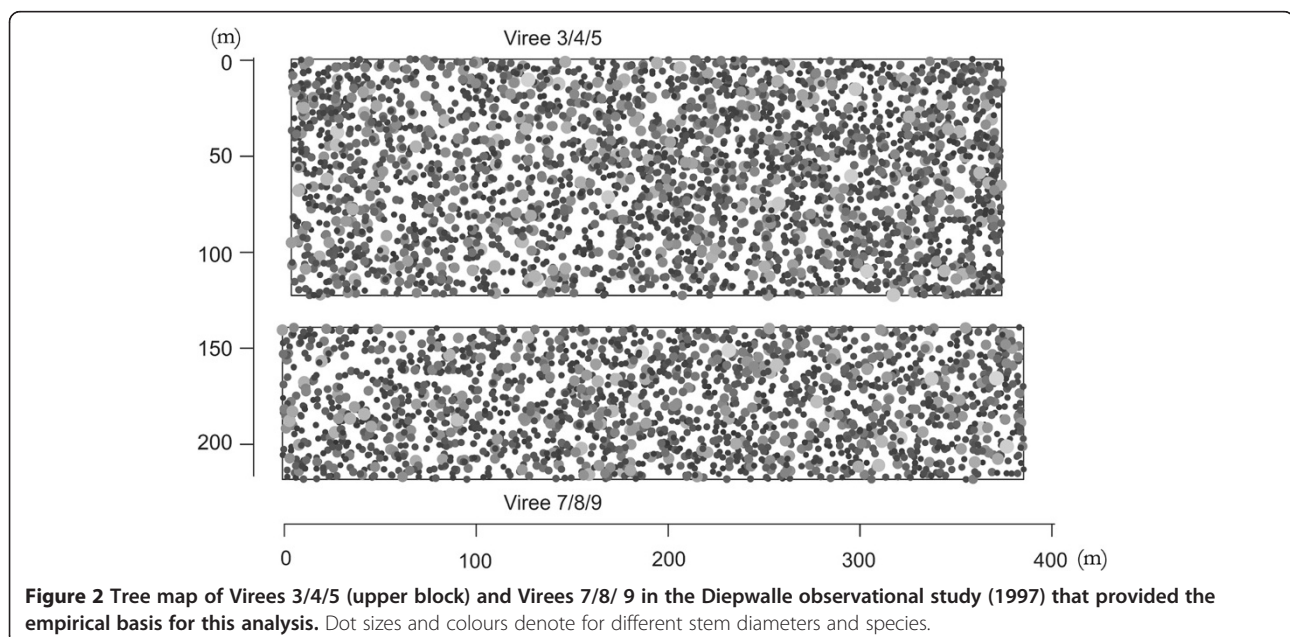
The data set for this study was obtained from the Diepwalle research area, which was established in 1937 on the Diepwalle State Forest. The study sites were established in their present form during 1972 by officers of the former Saasveld Forestry Research Centre (of the South African Forestry Research Institute) and were remeasured in 1978. Further remeasurements took place in 1987, 1997 and 2007 under the initiative and jurisdiction of the Scientific Services Section in Knysna (of the Department of Water Affairs and Forestry and of the South African National Parks since 2006). The research area is subdivided into strips (virees). The data used for the calculation of competition indices originated from Virees 3/4/ 5 and 7 (part), 8 and 9 (part), out of a total of 27 strips (total 44.4 ha). The selection of the virees was made based on the availability of spatial information on tree positions. The area used for the competition calculation was 60 m by 400 m since the total plot was slightly trapezoidal and the calculations of some CIs made an orthogonal shape necessary. Repeated dbh and a set of spatial tree coordinates were available for two distinct areas, separated by a strip without spatial information (Figure 2). The areas amounted to 4.55 ha (370 m × 123 m) with 760 trees · ha<sup>-1</sup> for the larger area and 3.86 ha (386 m × 79 m) with 652 trees · ha<sup>-1</sup> for the smaller.

#### Measuring competition effects

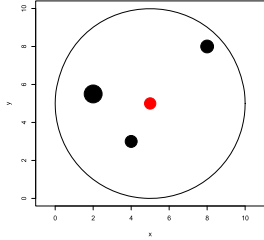
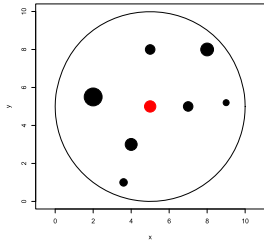
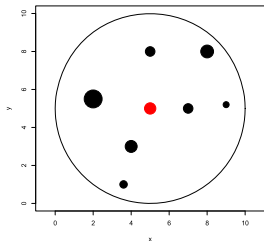
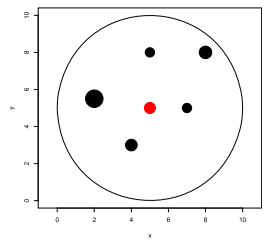
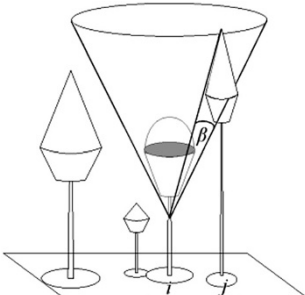
The literature on forest density and competition is extensive and covers a wide range from simple indices to complex models of light interception. Prominent above-ground density measures are basal area ((Assmann 1961); (Kramer 1988)), relative spacing and stand density index (Reineke 1933), leaf area index (Vose and Allen 1988) and crown competition factor (Krajicek et al. 1961). In forests where the spatial pattern is stationary across space, i.e., where the density of individuals  $\lambda(x)$  does not depend on the location  $x$ , the competition effects may be assessed by using a distance-independent measure of competition without requiring spatial information. A plausible distance-independent index should account simultaneously for the population attribute stand-density and the tree attribute of relative social class of the tree within the stand (Gadow 1996).

Numerous competition indices have been used in analysing forests with mapped trees. They include *overlapping zones of influence* (Gerrard 1969), *distance-weighted size ratios* ((Hegy 1974); Lee and Gadow (1997)), and *available growing space* ((Brown 1965); (Hessenmöller 2001)). The potential for developing new ones is boundless. Five distance-dependent measures of competition are being used in this study. They are briefly described in Table 2, using a simplified formula and a schematic diagram. Four of the five competition indices (BAL, LBA, CR13 and ITH) are based on direct observations in the field. The KKL-t index relies on quantities which have to be estimated.

The basal area of larger trees (BAL) is defined as the sum of the basal areas of all trees larger than the reference tree within a circular competition zone. In our study, the



**Table 2 The five measures of competition used in this study**

| Name                        | Formula  | Graph  | Reference                  |
|-----------------------------|--|--|----------------------------|
| Basal area of larger trees  | $BAL_{ij} = \sum_{j=1}^n BA_j,$ where $BA_j > BA_i$  |    | (Wykoff et al. 1982)       |
| Local basal area            | $lBA = \sum_{j=1}^n BA_j, \text{ where } i \neq j$   |    | (Steneker and Jarvis 1963) |
| Crowding index              | $CR13 = \sum_{j=1}^n DBH_j,$ where $10 \text{ cm} < DBH < 30 \text{ cm}$                                     |   | (Seydack et al. 2011)      |
| Iterative Hegyi             | $ITH = \sum_{j=1}^n \left( \frac{D_i}{D_j} \cdot \frac{1}{DIST_{ij}} \right), \text{ where } i \neq j$       |  | (Lee et al. 2004)          |
| Crown competition index KKL | $KKL = \sum_{j=1}^n \beta_{ij} \cdot \left( \frac{CCA_j}{CCA_i} \right) \cdot TM_j, \text{ where } i \neq j$ |  | (Pretzsch 2009)            |

Where  $i$  refers to the reference tree and  $j$  to the competitor; BA refers to basal area ( $\text{m}^2 \cdot \text{ha}^{-1}$ ), BA to basal area ( $\text{cm}^2$ );  $D$  to breast height diameter (cm),  $DIST_{ij}$  is the distance between tree  $i$  and its competitor tree  $j$ .  $\beta$  is the angle (in radians), CCA the cross sectional crown area and TM a species specific transmission factor. Further details may be obtained in the references listed in column 4.

reference tree is located at the centre of the circle with a radius equal to twice the mean distance between trees, calculated as the square root of 10000 divided by the number of trees per ha. The radius was 7.3 m for Virees 3/4/5 and 7.8 m for Virees 7/8/9 in the Diepwalle study area. The BAL index combines individual tree basal area percentiles with the density measure stand basal area (see (Wykoff et al. 1982) for details). It thus mainly estimates the effects of overtopping and radiation exclusion.

The local basal area (IBA) is defined as the basal area of all trees, excluding the reference tree, within a circle of influence (Steneker and Jarvis 1963). The reference tree is located at the centre of the circle and the circle radius is equal to two times the mean distance between trees as in the case of the BAL index. In a previous study (Coomes and Allen 2007) and (Seifert et al. 2011) used local basal area to describe crowding as a surrogate for below ground competition because a) it also includes the trees that are smaller than the reference tree and b) the circle of influence is not too big, so that close neighbours exert the crowding effect.

The crowding index CR13 (Seydack et al. 2011) represents the sum of all dbh values of trees between 10 to 30 cm in diameter within a given search radius. The use of dbh excludes a quadratic impact of bigger trees as found in the IBA and BAL indices and should thus give smaller trees a proportionally higher impact on the calculated CI value. For consistency the same search radius as for all previous CIs was chosen, which was considerably smaller than the one originally used by (Seydack et al. 2011), which was 11.3 m.

The iterative Hegyi index (ITH) proposed by (Lee et al. 2004) takes account of the size ratios and distances between the reference tree and its competitors within a circle of influence equal to that used for the BAL index. The ITH is thus related to the well-known Hegyi index (Hegyi 1974), but the important difference is that trees that are not directly facing the reference tree are not considered to be active competitors. Further details are presented in Gadaw and Hui (1999).

The KKL index ((Pretzsch 1992; Pretzsch 2009), p. 293) is the only CI applied in this analysis that requires information about tree height and crown dimensions. The search for potential competitors is based on a cone with an angle of 60° that is inserted with its tip at 60% of the tree height. The crown tips of all neighbouring trees that are presumed to reach inside that cone are considered to be competitors. For those the angle from the tree tip to the virtual cone mantle is calculated (angle  $\beta$  in Table 2). This is used as a measure of competition, which is additionally weighted by the cross-sectional crown area of the competitor in relation to the subject tree (CCA<sub>j</sub>/CCA<sub>i</sub>). A generalised modification of the KKL, called KKL-t further on, had to be used that ignored many species-specific

adaptations because the needed empirical data was not available. The light transmission factor (TM) was set constant to 0.8 since species-specific information was not available and no other of the applied CIs was modified at the species level. Crown diameters were calculated using the model for *Fagus sylvatica* (Pretzsch 1992) in the absence of species-specific models for afrotemperate forests. However, height and crown length were calculated using the locally developed parameters from (Seifert et al. 2011). Tree species without valid height-diameter models were assigned to corresponding species with available models.

A common challenge in the application of distance dependent CIs is the fact that typically no spatial and size information is available on trees outside the area of interest but that these trees de facto contribute to the competition. Ignoring the effect would thus mean a severe underestimation of competition at the edges. There are two possible generic solutions for this problem: one is to apply an edge correction algorithm to plausibly simulate competition from the edge-side dependent on the structure (see (Biber 1996); (Pommerening and Stoyan 2006); (Pretzsch 2009), p. 326–336). The other solution is to cut the size of the actual plot and limit inferences to trees that are unaffected by the edge. This may be effectively done by making use of the search radius of the respective CI. We applied both methods as it appeared appropriate. To prevent an edge bias, trees with distances to the border less than the circle of influence were excluded for BAL, IBA and ITH. As stated before, the two plots (Virees 3/4/5 and Virees 7/8/9) were treated as separate plots for the edge correction and competition calculation. Thus all trees near the edges were excluded. In the case of the KKL- index a simple exclusion is not possible because the potentially large search radius would exclude too many trees from the analysis. For the KKL-t we replicated the structure in the plot outside by shifting all trees by the width/length of the plot, thus replicating the entire plot as tiles, which is a proven method for edge correction in CI calculation procedures (Pretzsch 2009).

#### Data preparation

Data for the analysis of the correlation between CIs and tree increment were prepared in order to obtain the most accurate spatial representation of the stand for the CI calculations and to eliminate implausible increments from the calculation.

The first step was to obtain a valid and plausible dbh for each tree at each time period in order to compute the competition indices as accurately as possible. The second step was to exclude implausible increment measurements from the data for the increment response. Missing diameters of trees for certain dates were derived from a tree individual linear regression of the diameters over time, limiting the slope to positive numbers, i.e., not

allowing the tree diameter to shrink. This interpolation was exclusively applied to fill gaps for a few missing dbh values for competitors since excluding the trees would have significantly biased the competition calculation for focus trees. All trees with missing dbh records were excluded from the analysis of competition sensitivities.

Outliers were removed from further analysis if an overall increment of 20 cm in 40 years or an annual increment of 0.7 cm were exceeded in accordance with the empirically determined potential growth limits at the site. These growth limits were determined based on long term data from the site itself and long term inventories on permanent sample plots in a larger area. Additionally, all increment measurements smaller than  $-0.01$  cm per year and trees with diameters less than 10 cm were excluded from the calculation. The CI values were trimmed at the 99.9% percentile. The main characteristics of data set used in the analysis are presented in Table 1.

#### Steps of the analysis of the sensitivity to competition

The sensitivity to competition was analysed in two steps:

- 1) analysis of the sensitivity of the tree species to specific CIs, where one index at a time was used to quantify competition response using a linear regression;
- 2) analysis of the simultaneous contribution of different CIs in interaction with a multiple regression, where the data was differentiated in diameter classes in a second step to detect also changes in competitive sensitivity due to social position in the crown layer and ontogenetic development.

#### Specific sensitivity to competition

Sensitivity to competition was expressed by the slope of the linear relation between dbh increment and the different competition index values.

Strong negative correlations signify a substantial competitive sensitivity, whereas non-significant slope parameters indicate an insubstantial or no sensitivity to competition. The IBA and the CR13 indices are intuitively more suited to measuring local crowding, while the BAL and KKL-t indices emphasise overtopping effects and thus shading since they both exclude smaller trees in the selection of competitors. The ITH includes proximity and relative size of competitors and thus measures both shading as well as crowding but will focus more on overtopping when compared to the CR13 and IBA indices.

None of the indices clearly differentiates between crowding and shading effects and each index contains a measure of both. However, the mathematical formulation of the CIs allows for ranking according to their expected sensitivity to local crowding: CR13 > IBA > ITH > BAL & KKL-t.

#### Interaction of CIs and ontogenetic changes in competitive reaction

It is quite possible that competition effects are partly complementary or partly redundant. Hence a multi-CI approach was used in this step of the analysis where two indices that were intuitively more focussing on overtopping effects (KKL-t and ITH) entered in stepwise multiple linear regression with two indices that had a more pronounced focus on competition by local crowding (IBA and CR13). To trace potential influences of canopy position, the data was classified in three different classes to dbh (10–20 cm, 20–30 cm, >30 cm). The regression was initiated with the full model and used a stepwise exclusion algorithm, based on an optimal AIC value in the statistical modelling language R (R-Core Team 2012). Variance inflation factors (VIFs) were calculated to ensure that severe collinearity was excluded and all models with insignificant coefficients were discounted as well. All models that were not significant at the model level were excluded from further analysis as well as all models where no CI contributed significantly. All models which had less than 30 tree observations and a VIF > 5 were also discarded.

#### Results

##### Species-specific sensitivity to competition

As a result of the regression analysis, it became evident that 18 of the total of 25 species in the study area showed a significant sensitivity to at least one competition index (Table 3). Higher CI-values had a negative effect on increment for all species except for V and WH. For the BAL, IBA, CR13, ITH and KKL-t, respectively, 14, 11, 7, 14 and 13 sensitive species were identified.

The BAL and ITH indices were significant in 14 out of the 25 species. No single CI emerged from this analysis which had convincingly strong correlations to diameter increment in the majority of species.

In Figures 3 and 4 species-specific sensitivities to two indices are illustrated as an example for a more below-ground (IBA) and a more light oriented index (KKL-t). It is obvious from the two graphs that there is only a partial overlap in the sensitivities between the species regarding the two indices (see also Table 3). However, some indices seem to provide similar information. For example, tree species that reacted to the ITH-index were often also sensitive to the KKL-t index.

##### Interaction of CIs in multiple CI approach and ontogenetic changes in competitive reaction

While the above mentioned species-specific sensitivity was addressing the bulk reaction of all diameter classes under the assumption that every CI provides independent competition information, the multiple regression facilitated a differentiation between diameter classes and accounted



**Table 3 Species-specific sensitivity of diameter increment to a selection of distance dependent competition indices (CIs)**

| Species         | BAL         | IBA         | CR13           | ITH         | KKL-t       | N of 5 CIs |
|-----------------|-------------|-------------|----------------|-------------|-------------|------------|
| Ass             | -0.00093*** | -0.00079*** |                | -0.00863*** | -0.01016*** | 4          |
| BH              |             |             |                | -0.04100**  | -0.04251**  | 2          |
| Geel            | -0.00095*** | -0.00152*** | -3.8568E-06*** |             | -0.00799*** | 4          |
| Kal             | -0.00339*** | -0.00153*   |                | -0.01984*** | -0.02660*** | 4          |
| Kam             | -0.00048*** | -0.00044*** | -2.5260E-06*** | -0.00281*** | -0.00372*** | 5          |
| Kers            | -0.00141*** | -0.00120*** | -2.4227E-06*   | -0.00779*** | -0.01482*** | 5          |
| Kw              | -0.00177*** | -0.00235*** | -4.6099E-06*   | -0.01375*   | -0.01537**  | 5          |
| N               | -0.00167**  | -0.00160*   |                | -0.01048*   | -0.01292*   | 4          |
| RH              | -0.00239**  | -0.00193*   |                |             |             | 2          |
| Saf             | -0.00100*** | -0.00068*** | -2.1381E-06**  | -0.00428*** | -0.00852*** | 5          |
| SH              | -0.00138*** |             |                | -0.00616*   | -0.01067**  | 3          |
| Sw              | -0.00083*   |             |                | -0.00661*** | -0.00894*** | 3          |
| Sy              |             |             |                | -0.01130*   |             | 1          |
| V               |             |             |                | 0.00822**   |             | 1          |
| WG              | -0.00213*   |             |                |             |             | 1          |
| WH              |             |             | 3.6453E-05*    |             |             | 1          |
| WP              | -0.00074*** | -0.00075*** |                | -0.00523*** | -0.00649*** | 4          |
| YH              | -0.00251*** | -0.00199*** | -2.6044E-06*** | -0.01442*** | -0.02781*** | 5          |
| N of 18 species | <b>14</b>   | <b>11</b>   | <b>7</b>       | <b>14</b>   | <b>13</b>   | <b>Σ59</b> |

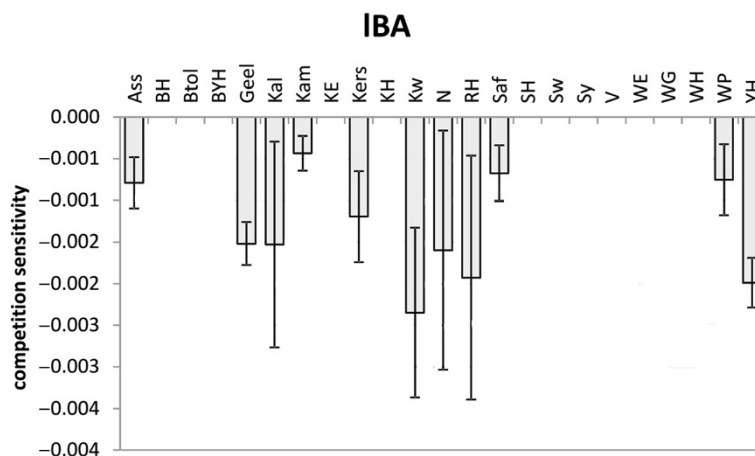
The significance level is indicated by \*\*\* ≤ 0.001, \*\* ≤ 0.01, \* ≤ 0.05.

Numbers in the body of the table are the slope parameters of the linear regression. Cells which did not have a significant slope parameter are left blank. The number of sensitive species per CI and the number of significant CIs for each species are presented in the last line and column respectively.

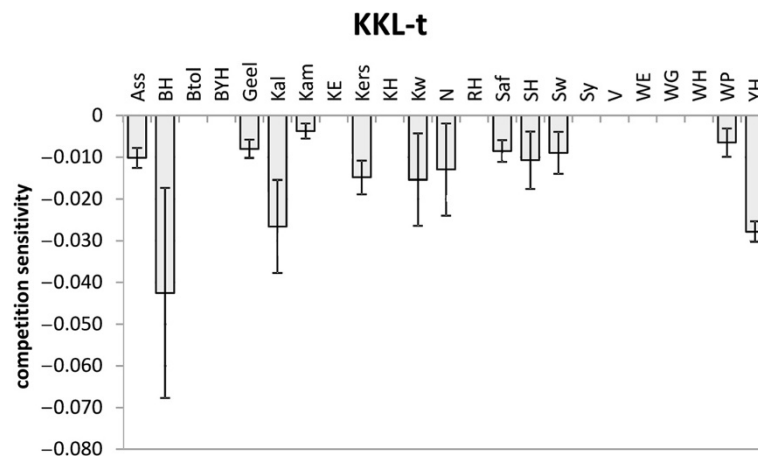
for the overlap of explanatory power among different CIs (Table 4). These results show an additional ontogenetic change in the species sensitivity to competition that is reflected in changes of the sensitivity to different CIs.

Looking at Table 4 it is obvious that most of the coefficients were negative but due to interaction effects between the CIs, several positive coefficients were found as well.

There is a species-specific change of competition sensitivity that was caused by different contributions of CIs in different diameter classes (Table 5). A proportion of the sub-canopy species was not sensitive to any CI at all. Comparing the change of sensitivity patterns over dbh-classes, marked differences within the canopy-forming species were evident, but also between canopy



**Figure 3** Competitive sensitivity of diameter growth of different afrotemperate tree species to the local basal area (IBA) slope parameter value is denoted by the bar, while the whiskers illustrate the 95% confidence intervals.



**Figure 4** Competitive sensitivity of diameter growth of different afrotemperate tree species to a modified KKL-t index (KKL-t). The slope parameter value is denoted by the bar, while the whiskers illustrate the 95% confidence intervals.

and sub-canopy species. Three main archetypes of changes in competitive reaction could be identified within the canopy species: i) the light demanding species (Kal, Kers), that showed a high sensitivity to light focused CIs throughout the diameter classes, ii) the species that changed from light sensitivity to edaphic sensitivity or non-responsiveness (SH, V, WP, YH), and iii) a species group that clearly changed response from mixed (light and edaphic) in the smaller dbh-class, to light focused in the middle diameter class and switched to a more edaphic response in the higher dbh-class (Ass, Geel, Sw). Kw could not be attributed to any of these groups, since it changed from an edaphic sensitivity in the lowest dbh-class to a mixed sensitivity in the highest.

The sub-canopy species, which were not represented in the upper diameter classes, displayed a response to edaphically focused CIs (RH) or mixed responses (Kam, Saf, Ke) or were entirely non-responsive to any CI (KH, N, Btol).

In total sub-canopy species behaved as expected and showed either no sensitivity or a more pronounced sensitivity to local crowding, expressed by the correlations with the CR13 and IBA indices. An exception was *Cassine eucliformis* that showed an increasing light sensitivity with larger diameters, marking it as a species that will have to wait opportunistically for disturbances of sufficient size to grow. The canopy species showed a distinct differentiation, following three main archetypical reactions. The first group comprising *Curtisia dentata*, *Maytenus peduncularis* and *Podocarpus latifolius* displayed a mixed reaction in the lower dbh-classes with a sensitivity to CIs with a light and edaphic focus, followed by a distinct light sensitive phase in the middle dbh class where trees are growing towards the canopy layer and, finally, in the phase when the trees had established in the canopy, an edaphic sensitivity.

A second group including *Podocarpus falcatus* and *Pterocelastrus tricuspidatus* showed an exclusive response to light focussed CIs, whereas species such as *Apodytes dimidiata*, *Nuxia floribunda*, *Ocotea bullata*, and *Olea capensis macrocarpa* changed from light-CI sensitivity to edaphic sensitivity or non-responsiveness with increasing DBH.

## Discussion

The main objective of this study was to analyse competition response patterns in a species-diverse afrotemperate forest in southern Africa, based on mapped tree positions and long-term diameter increment records within the context of a large observational study. One outcome was that the detailed analysis and comparison of competition indices within this study yielded a better understanding of the significance of CI indices for forest ecological research. The results revealed differentiated competition responses of the various tree species in terms of sensitivity to individual CIs, a different general sensitivity to a set of CIs and an ontogenetic change of sensitivity patterns. This confirmed previous results of (Canham et al. 2004), (Coomes and Allen 2007) and (Coates et al. 2009) obtained for species native to North America and New Zealand. Our study also confirmed the viability of the approach to classify CIs according to their focus on local crowding or overtopping and hence allows inference on light or edaphic competition. The obtained results based on the sensitivity to edaphic and light competition correspond well with expert knowledge on the species and create the expectation that a simultaneous CI approach, as proposed in this study, could be used to analyse similar competition effects in other forest communities and thus extend competition analysis studies based on a comparison of CIs (e.g. (Mailly et al. 2003); (Stadt et al. 2007)).

**Table 4 Results of the multiple regression of mean annual diameter increment depending on different competition indices (KKL-t, provided for three different dbh classes)**

| Species | dbh class | N    | Model p  | Intercept | CR13      | IBA      | ITH      | KKL-t    |
|---------|-----------|------|----------|-----------|-----------|----------|----------|----------|
| Ass     | 15        | 1125 | 3.38E-15 | 0.173699  | -2.95E-06 | n.s.     | n.s.     | -0.01095 |
| Ass     | 25        | 550  | 0.000696 | 0.160192  | n.s.      | n.s.     | n.s.     | -0.02517 |
| Ass     | 40        | 180  | 0.017064 | 0.075569  | 4.56E-06  | n.s.     | n.s.     | n.s.     |
| Btol    | 15        | 194  | NA       | 0.050504  | n.s.      | n.s.     | n.s.     | n.s.     |
| Geel    | 15        | 840  | 3.38E-21 | 0.205932  | -6.18E-06 | n.s.     | 0.004919 | -0.01496 |
| Geel    | 25        | 468  | 1.75E-11 | 0.188974  | n.s.      | n.s.     | n.s.     | -0.04412 |
| Geel    | 40        | 731  | 1.85E-08 | 0.178351  | n.s.      | -0.00154 | n.s.     | n.s.     |
| KE      | 15        | 91   | 0.000653 | 0.253622  | n.s.      | -0.00429 | 0.013454 | n.s.     |
| KH      | 15        | 83   | NA       | 0.122303  | n.s.      | n.s.     | n.s.     | n.s.     |
| Kal     | 15        | 111  | 0.009502 | 0.216795  | n.s.      | n.s.     | n.s.     | -0.01913 |
| Kal     | 40        | 51   | 1.15E-05 | 0.321026  | n.s.      | n.s.     | n.s.     | -0.17043 |
| Kam     | 15        | 1950 | 5.53E-11 | 0.116986  | -2.79E-06 | n.s.     | -0.00217 | n.s.     |
| Kam     | 25        | 203  | NA       | 0.099644  | n.s.      | n.s.     | n.s.     | n.s.     |
| Kers    | 15        | 625  | 1.45E-13 | 0.259641  | n.s.      | n.s.     | n.s.     | -0.02161 |
| Kers    | 25        | 241  | 0.035326 | 0.256824  | n.s.      | n.s.     | -0.02659 | n.s.     |
| Kers    | 40        | 160  | 0.021099 | 0.233276  | n.s.      | n.s.     | -0.0257  | n.s.     |
| Kw      | 15        | 70   | 0.000205 | 0.23613   | n.s.      | -0.00358 | n.s.     | n.s.     |
| Kw      | 25        | 59   | NA       | 0.11145   | n.s.      | n.s.     | n.s.     | n.s.     |
| Kw      | 40        | 108  | 0.017227 | 0.090819  | 7.46E-06  | n.s.     | -0.02707 | n.s.     |
| N       | 15        | 84   | NA       | 0.051058  | n.s.      | n.s.     | n.s.     | n.s.     |
| RH      | 15        | 47   | 0.008346 | 0.136467  | n.s.      | -0.00241 | n.s.     | n.s.     |
| SH      | 15        | 146  | 0.013018 | 0.133242  | n.s.      | n.s.     | n.s.     | -0.01251 |
| SH      | 25        | 120  | NA       | 0.120963  | n.s.      | n.s.     | n.s.     | n.s.     |
| SH      | 40        | 161  | NA       | 0.137281  | n.s.      | n.s.     | n.s.     | n.s.     |
| Saf     | 15        | 545  | 2.44E-07 | 0.135287  | -2.18E-06 | n.s.     | n.s.     | -0.00818 |
| Saf     | 25        | 165  | NA       | 0.121953  | n.s.      | n.s.     | n.s.     | n.s.     |
| Sw      | 15        | 185  | 4.99E-05 | 0.135873  | -5.61E-06 | 0.001362 | n.s.     | -0.01314 |
| Sw      | 25        | 64   | NA       | NA        | n.s.      | n.s.     | 0.046513 | n.s.     |
| Sw      | 40        | 31   | NA       | NA        | 1.40E-05  | n.s.     | n.s.     | n.s.     |
| Sy      | 15        | 70   | 1.28E-05 | 0.256883  | -6.14E-06 | n.s.     | -0.03055 | 0.036656 |
| Sy      | 25        | 35   | 0.008797 | 0.261282  | n.s.      | n.s.     | -0.04301 | n.s.     |
| V       | 15        | 220  | 0.000269 | 0.099427  | n.s.      | n.s.     | 0.027208 | -0.03165 |
| V       | 25        | 85   | NA       | 0.080784  | n.s.      | n.s.     | n.s.     | n.s.     |
| V       | 40        | 46   | NA       | NA        | 9.91E-06  | n.s.     | n.s.     | n.s.     |
| WP      | 15        | 355  | 0.00124  | 0.105007  | n.s.      | n.s.     | -0.00569 | n.s.     |
| WP      | 25        | 254  | 0.018489 | 0.137136  | n.s.      | -0.00123 | n.s.     | n.s.     |
| WP      | 40        | 182  | NA       | 0.086545  | n.s.      | n.s.     | n.s.     | n.s.     |
| YH      | 15        | 1021 | 3.96E-12 | 0.15323   | n.s.      | n.s.     | n.s.     | -0.01323 |
| YH      | 25        | 716  | 1.74E-09 | 0.217599  | n.s.      | n.s.     | 0.012894 | -0.0604  |
| YH      | 40        | 1655 | 4.65E-10 | 0.246719  | n.s.      | -0.00088 | n.s.     | -0.04353 |

The table presents the species code, dbh class (cm), number of increment observations used in the regression, significance level of the model (Model p, where n.s. is non significant), and the coefficients for intercept and the CIs.

**Table 5 Changing competition response of afrotemperate species with diameter class**

| Species | Canopy level     | Diameter class |    |    | Response in competition sensitivity |
|---------|------------------|----------------|----|----|-------------------------------------|
|         |                  | 15             | 25 | 40 |                                     |
| Ass     | Canopy           | le             | l  | e  | Changing response                   |
| Geel    | Canopy           | le             | l  | e  | Changing response                   |
| Kal     | Canopy           | l              |    | l  | Light demanding                     |
| Kers    | Canopy           | l              | l  | l  | Light demanding                     |
| Kw      | Canopy           | e              |    | le | Changing response                   |
| SH      | Canopy           | l              | n  | n  | Light to nonresponsive              |
| Sw      | Canopy           | le             | l  | e  | Changing response (CIs positive)    |
| V       | Canopy           | l              | n  | e  | Changing response                   |
| WP      | Canopy           | l              | e  | n  | Changing response                   |
| YH      | Canopy           | l              | l  | le | Light/changing response             |
| Kam     | Sub-canopy large | le             | n  |    | Mixed                               |
| KH      | Sub-canopy large | n              |    |    | Non responsive                      |
| N       | Sub-canopy large | n              |    |    | Non responsive                      |
| Saf     | Sub-canopy large | le             | n  |    | Mixed to non-responsive             |
| Btol    | Sub-canopy small | n              |    |    | Non responsive                      |
| KE      | Sub-canopy small | le             |    |    | Mixed                               |
| RH      | Sub-canopy small | e              |    |    | Edaphic                             |
| Sy      | Sub-canopy small | le             | l  |    | Mixed to light                      |

The species are sorted according to their status in the canopy hierarchy, the centroid of the diameter class with the predominant CIs (l: light focused CIs (ITH, KKL-t), e: edaphic focused CIs, le: mix of l and e, n: non-responsive to any index (intercept only model)). If no significant model could be found the corresponding cell was left blank.

### Sensitivity to competition

A fair amount of tree species (18 of 25) showed a significant influence of a CI to diameter increment. A share of non-significant regressions was obtained for immature trees of canopy species that typically grow in the understory and seem to be insensitive to the calculated CIs. This insensitivity suggests that the applied CIs did not sufficiently capture the resource availability of these species. For the remaining tree species with significant correlations, the reaction was rather variable, indicating a strong differentiation of the sensitivity to individual CIs between species. However, despite the fact that almost all relationships between diameter increment and single CIs were negative, no CI could be identified as a general best option to characterise the competition across all species in this evergreen mixed forest. In fact single species showed distinct sensitivities to particular CIs.

An aligned differentiation in crowding and overtopping focused CIs revealed clear sensitivities in some species for either one or another CI type but in the majority of species CIs regarding both aspects were represented in fair proportions. This might be a consequence of the fact that a true separation of edaphic and light competition in any of the CI is not possible. Each index contains edaphic as well as light competition effects. However, the more detailed analysis revealed another possible

explanation for the mixed response. Increasing the detail of differentiation in the analysis a step further by performing a multiple regressions involving three dbh-classes enabled conclusions on 1) ontogenetic changes of competitive sensitivity and 2) effects of redundancy or complementarity of the explanatory value of CIs.

The results of the multiple CI analysis over different dbh classes correspond well with the perceived light responsiveness of these species. The four most light responsive/demanding canopy species according to the crown position response index, *Podocarpus falcatus*, *Pterocelastrus tricuspidatus*, *Olea capensis macrocarpa* and *Psydrax obovata* subsp. *obovata* (Seydack et al. 2011) show competitive responses for light even in canopy positions (Table 5). An edaphic competitive response at the canopy level was absent in *Podocarpus falcatus* and *Pterocelastrus tricuspidatus*, the two species with greater water stress tolerance than the other canopy species (Mitlöhner (1998)). The pattern of changing competitive responsiveness indicating a need for light at the juvenile stage and moisture stress sensitivity in canopy positions as adults was observed in six canopy species (Table 5). These six canopy species (*Curtisia dentata*, *Podocarpus latifolius*, *Maytenus peduncularis*, *Nuxia floribunda*, *Apodytes dimidiata*, *Olea capensis macrocarpa*) with their characteristic pattern of changing competitive sensitivity pattern from light to

edaphic with increasing stem diameter make up more than 90% of canopy-level (trees >30 cm dbh) tree numbers. In canopy species, the effectiveness of the KKL-t index in capturing the light sensitivities of species is confirmed by congruence of their relative light sensitivities as indicated by the crown position response index (Seydack et al. 2011). *Podocarpus falcatus*, *Olea capensis* subsp. *macrocarpa*, *Pterocelastrus tricuspidatus*, and *Psydrax obovata* subsp. *obovata* have relatively high crown response indices, whereas *Podocarpus latifolius*, *Apodytes dimidiata* and *Ocotea bullata* have low index values (Seydack et al. 2011). These ratings concur with those of the KKL-t (Figure 4).

These results concur with growth analyses at the stand level by (Seydack et al. 2011) where sub-canopy cohorts of canopy species were identified as light resource sensitive and those at the canopy level as sensitive to water resource deficiencies. This is furthermore consistent with eco-physiological results obtained by (Mitlöhner 1998) who found the two light demanding species, *Podocarpus falcatus* and *Pterocelastrus tricuspidatus*, which did not show this pattern, being more water stress tolerant than the other six canopy species, which are apparently more prone to water stress when occupying canopy-level positions.

However, the common assumption that a small diameter is always correlated with a physiologically young tree does obviously not always hold true in multi-storey stands because old trees can persist over decades in the shade of the understory before their light conditions are improved. Such trees, although old, may show a physiologically very young behaviour in their growth patterns ((Pretzsch 1992); (Wright et al. 2000)). Referring to this physiological age one could thus indeed define smaller diameter canopy trees as young trees.

Further tests of multiple regressions with the inclusion of dbh as an independent variable showed complex interaction effects with competition indices, where the dbh was mostly taking over effects of the light focussed CIs. This is not unexpected since tree dbh is positively correlated with relative crown positions in the canopy. However, only trees with diameters exceeding 10 cm were used in the analysis. Thus an extrapolation of the results to smaller diameter trees is only possible with a high degree of uncertainty.

According to the competitive exclusion principle (Gause 1934), species less suited to compete for resources should either adapt or die out (Law and Watkinson 1989). The variability of the response to competition between species and ontogenetic stages within species are arguments for the existence of other effects that facilitate coexistence. The findings of this study suggest the existence of mechanisms of temporal and spatial niche differentiation as a form of ecological combining ability as postulated in the

theoretical works of (Aarssen 1983; Aarssen 1989). His second postulate for coexistence is that several species are equally competitive (competitive combining ability), which was not tested explicitly in this study but is probably the case since several canopy species showed very similar ontogenetic response patterns and would thus compete. The fact that they are co-occur might serve as an indication for an equal competitive ability of these species.

## Outlook

The analysis of various spatial competition effects in an afrotemperate multi-species forest provides some preliminary insights and an impetus for further research that should include nutrient and water effects. This requires an extension of assessment activities in the Diepwalle observational study area. However, how the competition effects vary with environmental conditions has not yet been generally understood. Some insight was provided by (Boyden et al. 2005) and (Forrester et al. 2011). (Forrester 2014) reviewed available articles and combined theoretic approaches with empirical examples on how environmental conditions modify competition. Hulme's theoretical base for coexistence that involves aspects of resource influence and aspects of niche differentiation ((Hulme 1996); (Schulze et al. 2005)) might prove a promising avenue for future analysis. Combining specific site effects (Seydack et al. 2011; Seydack et al. 2012) and spatially explicit responses to competition, as in the present study, may provide improved understanding of how individual trees compete for resources, including nutrients, water and light. This research depends on long term observational studies with mapped tree data.

Another research objective could involve the differentiation of competition effects in conspecific and interspecific competition components, which might shed further light on species mixing effects (e.g. (Pretzsch et al. 2012), (Forrester 2014)). Deciphering and separating facilitation and competition effects would add another level of complexity in to the analysis of these multi-species forests. However, such detailed research requires a more comprehensive data base.

## Conclusions

With the presented simultaneous-CI approach a significant proportion of the competition in complex South African multi-species forest can be captured in order to obtain an improved understanding of interactions between trees. Since most of the existing studies in this direction focus on light limited environments this extends the body of knowledge to more edaphically limited stands in Africa.

The differentiation in different dbh-classes as a surrogate for ontogenetic stages of a tree and at the same time also different social situations within a vertically structured canopy revealed different species-specific stages of sensitivity

to competition by crowding and/or overtopping, which changed during the lifetime of a tree. Here in particular differences between canopy and sub-canopy species were revealed.

The classification of CIs in crowding and light focussed indices confirmed existing results from other forest types and yielded ecologically relevant results regarding competitive tree-tree interactions in afrotemperate forests.

## Endnotes

<sup>a</sup>Sterba (1991), p. 41; see also the reference by Spiecker (1994) to applications by Kraft (1884).

<sup>b</sup>See also applications by Lorimer (1983); Martin and Ek (1984); Lee et al. (2004).

## Competing interests

The authors declare that they have no competing interests.

## Authors' contributions

T. Seifert conceptualized the article including large parts of the statistical analysis, wrote substantial parts of the manuscript and did most of the figures, S. Seifert was instrumental in conceptualising the analysis, programmed the R-code for the analysis, did most of the data handling and contributed to the text and figures. A. Seydack and G. Durrheim wrote parts of the text, provided data including the data plausibility checks and contributed with important sections to the manuscript, K. v. Gadow, was instrumental in conceptualising the analysis and contributed statistical techniques, as well as substantial parts of the text. All authors read and approved the final manuscript.

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