Competition in the Knysna Forest: is GIS suitable for the analysis of spatial patterns?

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Abstract:

Competition was analysed in the Lilyvlei Nature Reserve of the Knysna Forest. GIS was used to spatially map and then create Thiessen polygons for each of the individual trees within 33 plots. Thereafter, regression analyses were performed to test the relationships between the diameter at breast height (dbh) and the area of the Thiessen polygons, and the growth and area of the Thiessen polygons for each individual. None of the regressions were significant, and all showed very poor correlations and relationships between the variables. This study therefore does not support the hypothesis that there is competition in the Knysna Forest. However, it was concluded that GIS is not a useful tool to demonstrate competition, and could have been the reason for the insignificance of the results.

Introduction:

Very few studies in indigenous forests have reported results indicative of competition. This could be because competition is indeed weak, or because it is difficult to unambiguously prove that competition is the driving force behind certain patterns observed (van Daalen, 1993). There are several types of competition and various resources that individuals could be competing for (Yodzis, 1986) and the spatial dynamics of a community should reflect these competitive interactions between the individuals. The aim of this study was to test this in the Lilyvlei Nature Reserve using GIS as a tool.

There are many different indices for measuring competition, incorporating many different variables. Several tests have attempted to determine which index shows more reliability when determining competition in a community. Lorimer (1983) concluded that the "essentially equal predictive ability of the different indices suggests that it may be desirable to focus greater attention on the simpler diameter-distance indices". Diameter-distance indices involve the use of the relative diameters and distances between the subject tree and the competing trees. The diameter of the base, stem or crown of the tree could be used in this type of index. An advantage of the diameter-distance indices is that they are easy to measure in the field, and relatively easy to compute (Lorimer, 1983). The major limitation of this type of index, however, is that over time competition appears to decrease in a plot because the number of stems per unit area decreases, and the distance between trees increases (Lorimer, 1983). This lessens the effects that near-neighbours have on each individual, as the number and density of near-neighbours is predicted to be inversely proportional to the size of the subject tree, while the distance of the near-neighbours from the subject tree is directly proportional. However, the time-scale of this study is too short to worry about this temporal restriction on the index. Contrary to the results of Lorimer's (1983) study, Mugasha (1989) found that including all selected trees in a competition index gave better results than when only trees of an equal or greater height/size class than the subject tree were used.

Mugasha (1989) evaluated the ability of seven simple competition indices to predict the growth of an 8-year old jack pine and trembling aspen trees. This study was one of the first to look at competition in a mixed stand. The conclusion here was that inter-tree distances between the subject tree and the competitors should be taken into account, as well as the diameter at breast height (dbh) for all trees, in order to predict competition most accurately. Mugasha (1989) also highlighted the fact that different species respond differently to competition, and van Daalen (1993) added that the suppression of trees under competition varies with species and forest type. Lorimer (1983) also observed that different competition indices show varying strengths of correlations with growth, depending on the species. The shade tolerance of a particular species appeared to be influencing the strength of the correlations, i.e. those species that exhibited the lowest correlations between a particular competition index and the observed increment, were considered to be shade tolerant species. This proposes that shade-tolerance is an important consideration when trying to demonstrate competition.

Grace and Platt (1995) investigated the effect that larger trees had on the distribution of juveniles by altering their growth and survival. Their results demonstrated that at short distances the near-neighbours had a significant effect on the survival and growth of the juvenile trees. This was inversely correlated with the size and density of the competitive larger trees, and was positively correlated with distance. The influence of the larger near-neighbours on the size and survival of the juveniles extended up to 15 m and 18 m respectively (Grace and Platt, 1995). At closer distances the larger trees appeared to be able to induce death, or at least restrict the height and growth of the juveniles.

van Daalen (1993) investigated competition between certain combinations of tree species in the southern Cape forests, of which the Knysna Forest is a part. From a correlation analysis of the dbh and relative distances between each tree, it was found that interspecific competition played a significant role between most of the chosen combinations. Intraspecific competition appeared to be significant for only a few of the forest species. The results from this study also showed that the closer the subject trees were to a larger tree, the smaller the subject trees were in diameter. Larger trees were also spaced further apart in general than smaller trees (van Daalen, 1993). It therefore appears that interspecific and intraspecific competition could be affecting the growth of trees in the southern Cape forests, but the evidence is very limited and equivocal (van Daalen, 1993). The similarity of the average distances between competitive and non-competitive species could be due to the fact that most of the southern Cape species are shade-tolerant and can grow in close proximity to each other. This research by van Daalen (1993) is especially relevant to the present study on competition in the Knysna Forest, as both of the studies take place in the southern Cape indigenous forest, and both investigate the competitive interactions between most of the common tree species found here. A comparison between the results will therefore be useful.

Why the Knysna Forest is a good study site to investigate competition:

The variation in species richness between forests can be explained by a variation in dynamism (Phillips *et al.*, 1994). Dynamism, or turnover, is defined as the mean rate of mortality and recruitment. In rapidly growing tropical forests the turnover is high (Phillips *et al.*, 1994), whereas in the Knysna Forest the rates of turnover are relatively slow (Midgley *et al.*, 1995; Phillips *et al.*, 1994). Subsequently, competitive interactions are less important in a tropical forest community due to the more frequent and unpredictable small-scale disturbances

(Phillips *et al.*, 1994). The slower rates of turnover found in the Knysna Forest are likely to be attributed to the fact that most of the species are shade-tolerant and thus grow very slowly (Midgley *et al.*, 1990). The slower growth rates result in a lower production of gaps and disturbances, thus reducing openings in the canopy for individuals to colonise without repression by older and larger trees. This ought to increase the effects of competitive interactions (Phillips *et al.*, 1994). The Knysna Forest should therefore the be a good site to investigate the influence of competition.

Study area:

The afromontane Knysna Forest is situated on the south coast of South Africa (White, 1978) (Figure 1). The section known as the Lilyvlei Nature Reserve is about 30km from Knysna (33 57'S, 23 03'W). This part of the Knysna Forest has never been harvested and is therefore in as natural a state as possible (Midgley *et al.*, 1995). The height of the main canopy is 18 – 22 m, while the average understorey plant is 2 m tall (van Daalen, 1993). The climate is warm temperate subhumid to humid, with a mean annual rainfall of 1200 mm which has a relatively even distribution throughout the year (van Daalen, 1993). The underlying geology of the region is fine to coarse-grained brownish sandstone of the Goudini formation of the Table Mountain group.

The dominant overstorey tree species are *Podocarpus falcatus, Podocarpus latifolius, Faurea macnaughtonii, Ocotea bullata, Elaeodendron croceum, Apodytes dimidiata* subsp. *dimidiata, Ochna arborea, Curtisia dentata, Olea capensis* subsp. *macrocarpa, Gonioma kamassi* and *Psydrax obovata* subsp. *obovata*. *Trichocladus crinitus* is the dominant understorey species, and can be quite thick in places. There are many other less common, but still relatively abundant species in the region.

Figure 1: The position of the Lilyvlei Nature Reserve near Knysna, on the south coast of South Africa (inlay).

The Department of Water Affairs and Forestry in Knysna compiled data in 1985 for circular plots of 11.3 m each. Within each plot, for each individual tree with a diameter at breast height (dbh) 10 cm and bigger, the dbh, distance and bearing from the centre of the plot was measured, and tree species noted. In 1991 and 2001, these plots were re-measured, this time including all new individuals which had now reached a dbh of 10 cm or bigger. The existence of this data spanning 16 years is very useful for the study of competition in the Lilyvlei Nature Reserve.

Aims, assumptions and hypotheses:

There were two primary aims of this thesis. Firstly, to use spatial data to determine whether there is competition between trees of the Lilyvlei Nature Reserve. Secondly, if Arcview, the GIS program is useful for determining competition. In order to perform this study we are assuming that the measurements of dbh and growth, as well as Thiessen polygons, are accurate indicators of competitive interactions (see below).

The key hypothesis is that competition between trees of the Knysna Forest is affecting their size and growth. Within this, it is predicted that the area of the Thiessen polygon should be greater for trees with a larger dbh, as the larger the subject tree, the further away the near-neighbours are predicted to be. In the same way, the area of the Thiessen polygon of each individual will influence the growth of that individual, i.e. an individual with a smaller area will grow slower.

Methods:

Thirty three plots, each with a radius of 11.3 m, were sampled in the central regions of the Lilyvlei virgin forest. The position of each individual tree had been recorded in 1985 and 1991 in terms of bearing and distance from the centre point of the plot, and the diameter at breast height (dbh, which is conventionally measured at a height of 1.3 m) determined. Subsequently in 2001, each tree was then found using these coordinates, and the dbh was measured again for all previously recorded trees (in cm), as well as for any new young trees which had reached a dbh of at least 10 cm. A metal spike hammered into the base of each tree provided a constant position from which the 1.3 m was measured in order to determine dbh. The distance and bearing was recorded for these new trees for future use.

The trees for each of the 33 plots were plotted spatially in the GIS program, Arcview, using the distance and bearing coordinates from the measured data. An extension program was used to create Thiessen polygons around each individual tree in each plot (measured in meters). Thiessen polygons can be used to show the spatial distribution of sessile organisms, and are formed when polygon sides are drawn to connect the mid-points of lines joining the subject tree to each near-neighbour, i.e. the polygons sides are perpendicular bisectors of point connectors (Figure 2). We tried to weight the polygons, i.e. by bisecting the connecting lines proportionally closer to the tree with the smaller dbh, rather than half way between the two neighbours. Unfortunately we were unable to do this in the GIS Thiessen polygon program, but if we had succeeded, the sizes of the Thiessen polygons would have been a closer reflection on the competitive influence each tree is having on its near-neighbours. Another shortcoming of this program was that duplicate points had to be excluded, e.g. resprouters, which have the same coordinates.

These Thiessen polygons were created separately for 1985, 1991 and 2001 to observe and compare the changes throughout the years (Figure 3). The neighbours of the trees near the edge of the circular plots that were outside the measured plots were obviously not part of the data, and thus the number of near-neighbours around those trees will appear to be less than they are in reality. These trees will therefore seem to be under a greater influence by fewer competitors. We attempted to eliminate these edge effects by creating a buffer several meters (x) from the edge. This would mean that only trees more than x m away from the perimeter would be considered to be subject trees, thus ensuring that all the near-neighbours within a certain distance were included for each tree. Disappointingly, this was not possible either in the Arcview program. The nature of the data in GIS made it very difficult to analyse any other variables. For example, we wanted to be able to analyse the distances of the near-neighbours and sizes for each individual tree, but this would have required hours of time creating several programs.

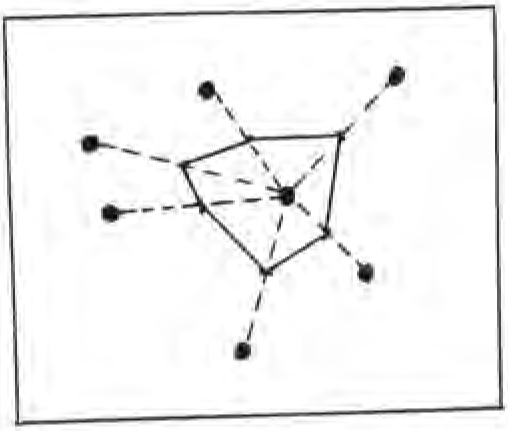

Figure 2: Thiessen polygon, with the polygon sides connecting the mid-points of the lines joining the subject tree and its near-neighbours.

The data was analysed in the statistics program, Statistica. Regression analyses were performed to test for correlations between every individual in each of the 33 plots. The correlation between diameter at breast height (dbh) and Thiessen polygon area was tested for 1985, 1991 and 2001. Both of these variables are

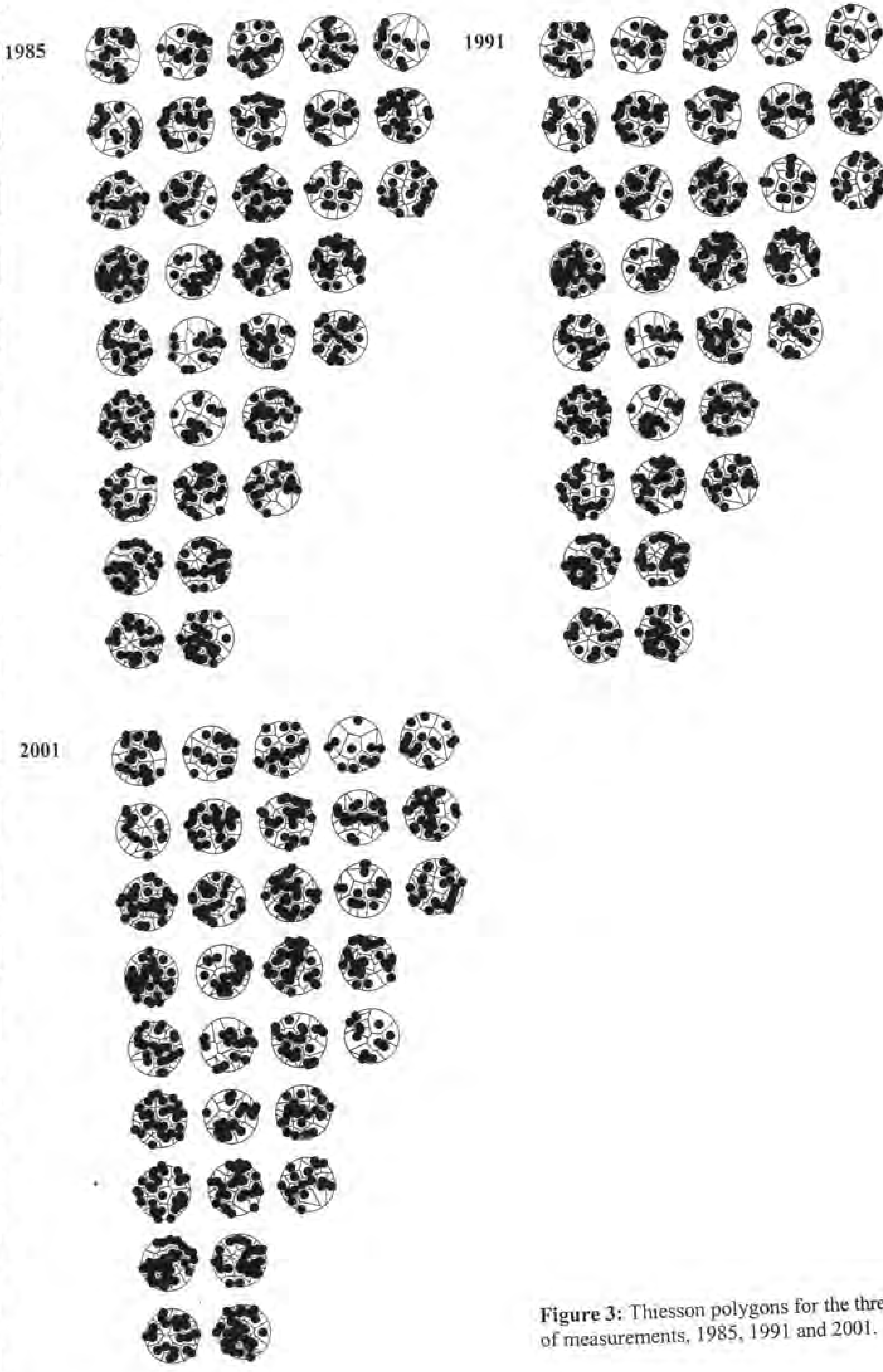

Figure 3: Thiesson polygons for the three years of measurements, 1985, 1991 and 2001.

expected to influence the other, it was decided that the control of the dbh on the area of the Thiessen polygon would be a better determination of competition than vice versa, and thus we made the dbh the independent variable. The relationship between growth and Thiessen polygon area was analysed, with area as the independent variable. Growth was determined for the 1985-1991 and 1991-2001 periods by subtracting the earlier dbh from the dbh recorded 6 and 10 years later, respectively, and the area used was that of the earlier measurement, i.e. 1985 and 1991 respectively.

Results:

The R values were extremely low for all the regression analyses performed, for example, the highest value was 0.2583. The coefficient of determination (R^2) values were also very low, and the amount of variability explained was never more than 0.14%. None of the regression analyses showed significant p-values. There is therefore not a significant correlation between the area of the Thiessen polygon and the diameter at breast height, or between the growth and Thiessen polygon area of the trees in the Lilyvlei Nature Reserve.

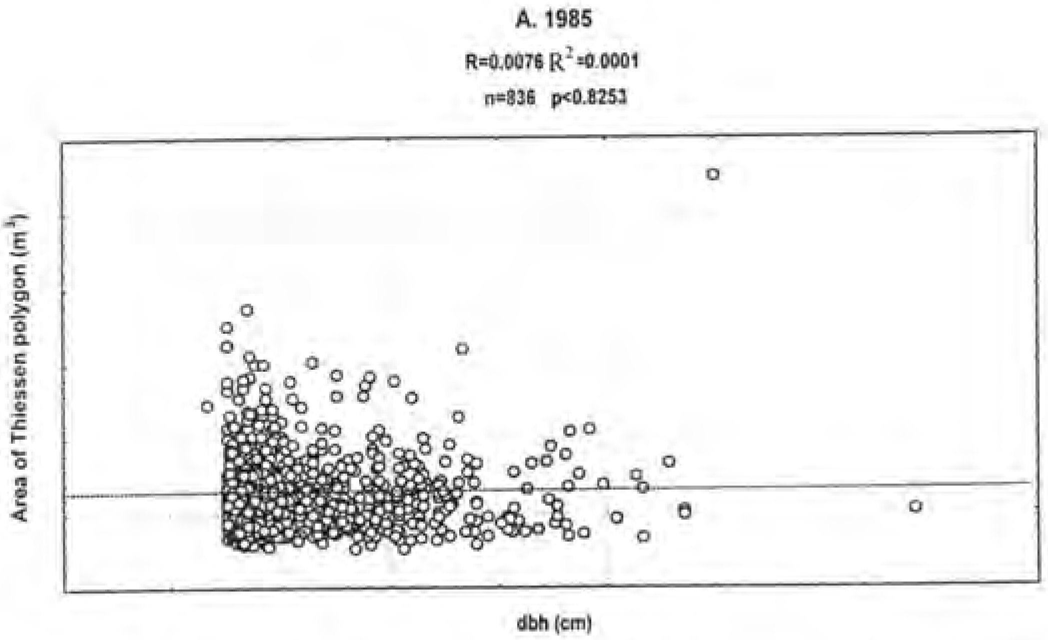

Figure 4: A. Regression analysis of the diameter at breast height (dbh) and the area of the Thiessen polygon for each tree in all of the 33 plots in 1985.

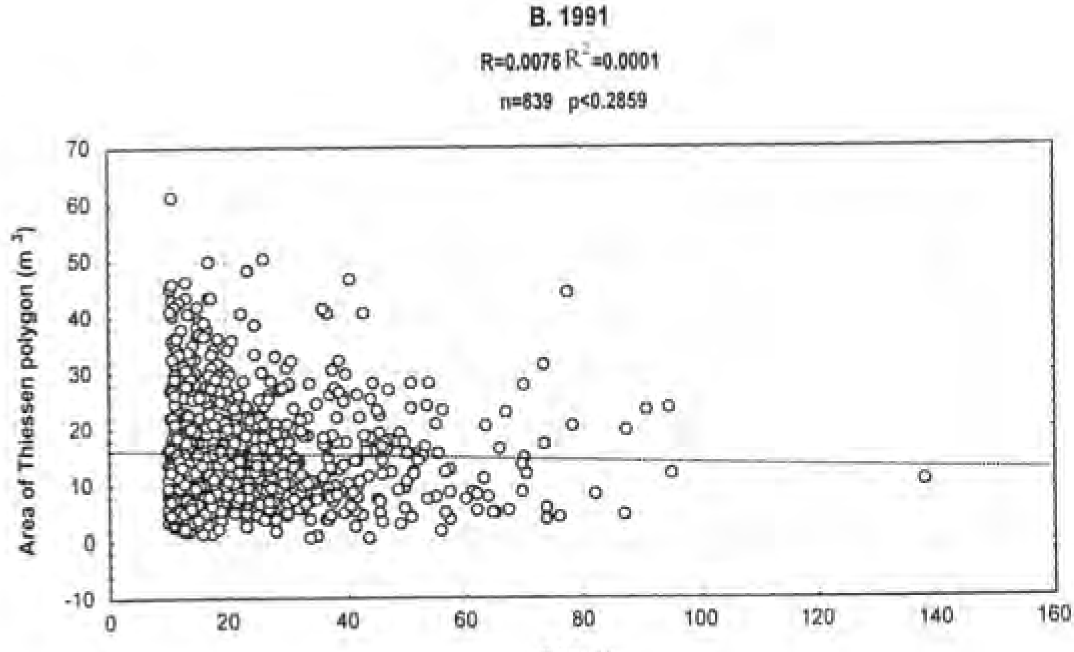

Figure 4: B. Regression analysis of the diameter at breast height (dbh) and the area of the Thiessen polygon for each tree in all of the 33 plots in 1991.

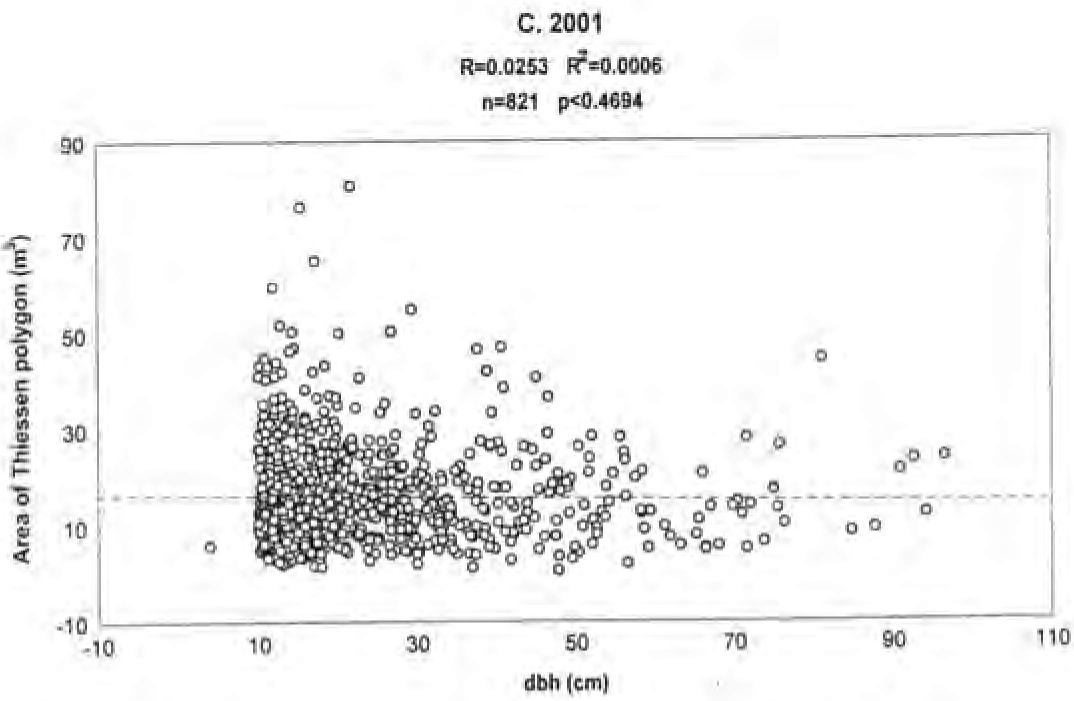

Figure 4: C. Regression analysis of the diameter at breast height (dbh) and the area of the Thiessen polygon for each tree in all of the 33 plots in 2001.

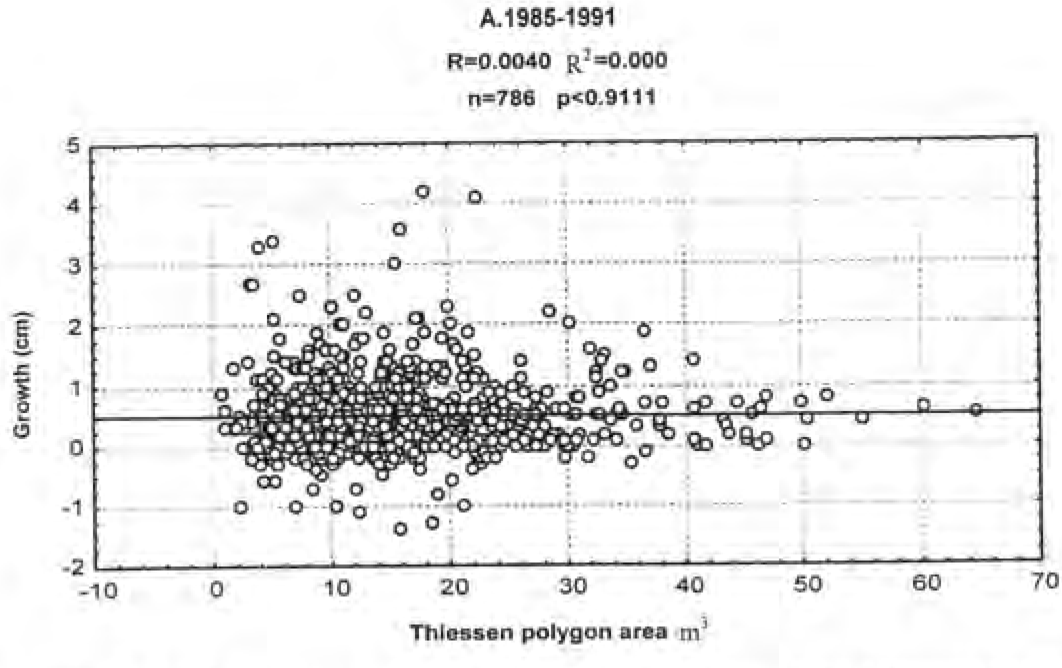

Figure 5: A. Regression analysis of the growth and area of the Thiessen polygon for each tree in all of the 33 plots, for the time period 1985-1991.

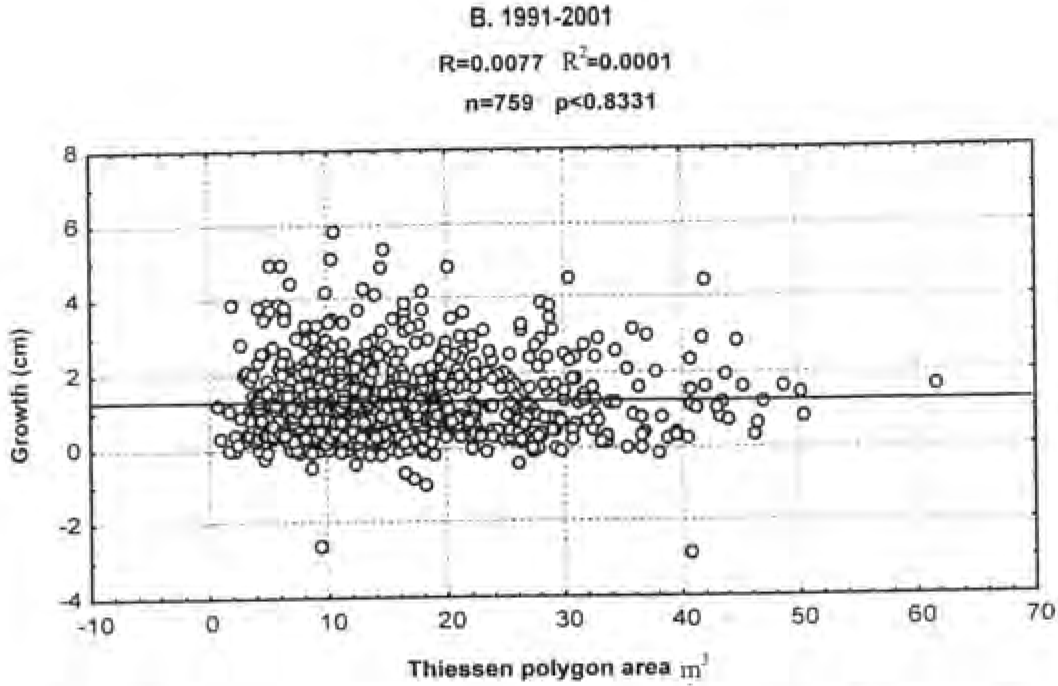

Figure 5: B. Regression analysis of the growth and area of the Thiessen polygon for each tree in all of the 33 plots, for the time period 1991-2001.

Discussion:

The evidence from this study for the absence of competition in the Lilyvlei Forest is overwhelming. All of the regression analyses performed were insignificant and showed almost no relationship between the variables. As mentioned before, there are three things, or combinations thereof, that these results could mean. Either that there is no competition in the Lilyvlei Nature Reserve, or that the influences of other variables and factors are clouding the visible effects of competition, or thirdly that the methods of determining competition were ineffective. Many of the variables and hypotheses we wanted to test within the GIS program, and from the data generated in Arcview, were not feasible. The result is that the analysis of competition in the Knysna Forest is incomplete, and may be one reason why the results were insignificant.

Competition may indeed be weak, or non-existent, as the results from Parker's (2000) study also suggested. If a forest is in equilibrium and at the final/optimal stage of succession, it will have reached carrying capacity and possess the full amount of biomass possible. If the Knysna Forest has reached equilibrium and carrying capacity, an increase in the basal area of one species will only be possible if another species undergoes a decrease in basal area, i.e. the carrying capacity remains constant (Parker, 2000). If this is the case, then that means that competition is at play. Parker (2000) showed that this is not the case, and so concluded that there is no competition, or very weak competition, in the Knysna Forest.

Indigenous forests are at various stages of recovery from ecological disturbances, such as windfalls (Midgley, 2001). The basal area of the Knysna Forest is very similar to that of the tropics, even though there is a reduced amount of disturbance (including less gaps) in the Knysna Forest compared to tropical forests (Midgley, pers. comment). Most of the Knysna Forest species are shade-tolerant, which reduces the effects of gaps in the forest canopy as shade-tolerant trees can regenerate and grow under a full canopy (Midgley *et al.*, 1990), and there appears to be no preference for which of the common species fills these gaps (Midgley *et al.*, 1995). The added characteristic of a very low turnover, and thus a low production of gaps available for regeneration, results in the apparent stability of composition found here (Midgley *et al.*, 1995). The high number of shade-tolerant tree species in the Knysna Forest makes it fair to assume that there is no strong competition for sunlight. This is due to the fact that most of the species do not need a gap to regenerate and grow, and thus sunlight is not a limited resource. It will therefore follow on that competition for space above and below the canopy will also be reduced as trees can grow in relatively close proximity (van Daalen, 1993).

As the Lilyvlei Nature Reserve is claimed to be the only part that has never been exploited or harvested (Midgley, 1995), it would be expected that the results from this area would reflect the difference in history. Interesting to note, is that the results from Parker's study (2000) were extremely similar to those from other sites within the Knysna Forest. Thus the results obtained in the Lilyvlei region could be extended to all the forests of the Southern Cape.

Conclusion:

None of the hypotheses of this study appear to be verified. Although van Daalen (1993) determined that there was probably competition between many of the species in the Knysna Forest, this research in Lilyvlei and Parker's (2000) results indicate that there is very weak, if any, competition. The apparent incompetence of GIS as a tool for determining competition may also have influenced the insignificance of the results. The characteristic shade-tolerance of the majority of the species is likely to have some effect, but this cannot be the sole reason behind what has been observed in this study.

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References:

Grace, S.L. and Platt, W.J. 1995. Neighbourhood effects on juveniles in an old-growth stand of longleaf pine, *Pinus palustris*. Oikos, **72**, 99-105.

Lorimer, C.G. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. Forest Ecology and Management, **6**, 343-360.

Midgley, J.J. 2001. Do mixed-species mixed-size indigenous forests also follow the self-thinning line? Trends in Ecology and Evolution, **16** (12), 6610662.

Midgley, J.J., Cameron, M.C. and Bond, W.J. 1995. Gap characteristics and replacement patterns in Knysna Forest, South Africa. Journal of Vegetation Science, **6**, 29-36.

Midgley, J.J., Seydack, A., Reynell, D and McKelly, D. 1990. Fine-grain pattern in Southern Cape plateau forests. Journal of Vegetation Science, **1**, 539-546.

Mugasha, A.G. 1989. Evaluation of simple competition indices for the prediction of volume increment of young jack pine and trembling aspen trees. Forest Ecology and Management, **26**, 227-235.

Parker, R. 2000. Additive basal area in Knysna Forest – myth or reality? Botany honours thesis, University of Cape Town.

Phillips, O.L., Hall, P., Gentry, A.H., Sawyer, S.A. and Vasquez, R. 1994. Dynamics and species richness of tropical rain forests. Proceedings of the National Academy of Science United States of America, **91**, 2805-2809.

Van Daalen, J.C. 1993. The effect of competition on timber growth in a mixed evergreen forest stand. South African Forestry Journal, **165**, 21-28.

White, F. 1978. The afromontane region. In: Werger, M.J.A (ed.) Biogeography and ecology in southern Africa. Dr W. Junk b.v. Publishers, The Hague, 463-513.

Yodzis, P. 1986. Competition, mortality, and community structure. In: Diamond, J and Case, T.J. (eds), Community Ecology, 480-491