

**Competition in old growth *Pinus resinosa* in relation to basal area, growth rate, and biomass**

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**ABSTRACT**

This study focuses on relative growth rate, percent basal area, distance and biomass in relation to *Pinus resinosa* competition in the Pellston Plain, Northern Michigan. We ask how the proportion of tree basal area in an old growth *P. resinosa* plot affects growth rate, and how biomass changes over time. We measured these variables and compared to previous data collections from 1942-1999. *P. resinosa* RGRs are negatively correlated with basal area coverage at certain time intervals as a result of increased competitive stress with increased density. Total above ground biomass increases over time until 2011 as a result of high mortality. These findings contribute to the scientific understanding of the Pellston Plain, specifically regarding competitive interactions and their effects on biomass, relative growth rate, and proportion of basal area of a mature *P. resinosa* stand.

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## INTRODUCTION

### *Pinus resinosa* and Tree Competition

The Red pine (*Pinus resinosa*) is a coniferous tree native to Northern Michigan and the Great Lakes region at large (Hauser 2008). *P. resinosa* can live for 200 to 400 years and can grow up to 50m in height (Benzie 1977). It is characterized by a straight trunk and has an average diameter at breast height (DBH) of 30-60cm (Hauser 2008). It grows well in sandy, loamy soils (Li 1937). *P. resinosa* uses wind dispersal to deposit seeds at a radial distance equal to the height of the tree (Greene 1993 & Ahlgren 1976). The grow rate of *P. resinosa* increases over its lifetime, from 25cm per year during the first four years to 30-60cm per year for the next 10-20 years (Hauser 2008).

Intraspecific tree competition and its possible effects on tree growth rates are incompletely understood in the field of population ecology. Lormier (1983) argues that distances between trees are not a significant indicator for predicting growth of individual trees. Hara *et al.* (2009) showed that competitive interactions occur between adult trees greater than or equal to 4cm in DBH and only locally between a few species. They suggest that competition is almost entirely irrelevant to the variation in species coexistence. Getzin *et al.* (2006) conclude that spatial distribution and tree size are not independent of one another, but are affected by competition. If competition is an important indicator of tree size, there will be a significantly positive correlation between tree growth and size and distance from a tree to its nearest neighbor, and special distribution within a plot will become more regular over time due to self-thinning (Pielou 1962, Sterner *et al.* 1986, Duncan 1991, Shackleton 2002).

Growth rates of both individual trees and entire stands can be described by absolute growth rate (AGR), a measure of change in biomass over time, or relative growth rate (RGR), which measures the capacity of primary productivity (Larocque & Marshall 1993, Fitter & Hay 1987). If growth rate is in fact dependent on competition, RGR is believed to better consider the element of competition (Ford 1975). Larocque and Marshall's results support this observation in a *P. resinosa* stand (1993). They argue that RGR decreases as tree size increases before the onset of competition, and that a positive correlation between RGR and tree size indicates that mortality is strongly influenced by competitive stress (Larocque & Marshall 1993).

### *Natural History*

Approximately 12,000 years ago, glaciers covered Northern Michigan and as they retreated, they deposited sandy glacial till in low-lying areas called outwash plains (Lapin & Barnes 1995). Since the last ice age, the Pellston Plain near Pellston, Michigan, has experienced environmental and anthropogenic changes such as logging in the late Nineteenth Century (Vande Kopple 2011).

In 1942, the University of Michigan Forestry Department (UMFD) established a 0.813ha (~2 acres) plot called the Maple River West Stand to be studied and ultimately used as a lumber resource (Vande Kopple 2011). This plot consists of an old growth forest dominated by *P. resinosa* and has been undergoing secondary succession since a natural 1890s fire (Vande Kopple 2011). The UMFD, which later became the University of Michigan School of Natural Resources and Environment, tagged and pruned 421 trees of varying species in 1942 and measured DBH of the trees within the plot in 1942, 1947,

1953, 1957, 1962, 1980, and in 1999 (Maple River West Stand Summary 1953).

### ***Study Questions & Hypotheses***

In our study, we examined the relationships between basal area, competition, growth rate, and biomass. We first asked how the proportion of tree basal area in an old growth *P. resinosa* plot affects growth rate. We hypothesize that individual *P. resinosa* growth rate decreases with increased proportion of basal area due to intraspecific competition for resources. If this is true, then as distance between a target *P. resinosa* and the closest *P. resinosa* competitor increases, growth rate of the target tree will increase because a tree's nearest neighbor is a primary indicator of competition. Our second study question addresses the change in biomass and growth rate at the West Maple River Stand between 1942 and 2011. We hypothesize that total above ground biomass will increase over time because total growth rate remains positive as total proportion of basal area increases.

## **MATERIALS & METHODS**

### ***Study Site***

The Maple River West Stand is located in Northern Michigan, west of Douglas Lake on University of Michigan Biological Station (UMBS) property. The Pellston area has a temperate climate with an average annual rainfall of 80.09cm (Vande Kopple 2011 Records). The soil composition of the Pellston Plain is primarily sandy with low nutrient availability (Lapin & Barnes 1995). The total plot is 0.813ha in area and is mapped as three plots, A, B, and C, which run East to West. Plots A and C are unpruned and untagged. Our study site is restricted to the central area, Plot B, which is 0.203ha (201m East to West and 101m South to North). Plot B is pruned and contains 421 tagged trees, 403 of which are the dominant cover type *Pinus resinosa*. Small numbers of other stems are tagged on Plot B, including 13 White Pines (*Pinus strobus*), four White Spruce (*Picea glauca*) and one Northern White Cedar (*Thuja occidentalis*). *P. strobus* is the dominate sapling throughout the understory of Plot B.

### ***Data Collection***

In late May 2011, we marked the perimeter of Plot B with flags. Beginning with tree #1 in the Southeast corner, we measured the DBH of each tagged tree in order of tree tag number until we reached tree #421 in the Northwest corner. We recorded the DBH of 254 live, legibly tagged trees. We also marked 37 untagged or illegibly tagged *P. resinosa* stems within Plot B with flagging tape and labeled them alphabetically from A to Z and AA to KK and measured their DBHs. We also recorded the species and DBHs of dead trees within Plot B if their DBHs were greater than five cm.

We created a random stratified sample of DBH by sorting the live, tagged, *P. resinosa* trees in order of ascending DBH. Every eighth tree was selected to be a target tree. For each of the 30 target trees, we measured the distance to and the DBHs of the five closest live trees, or nearest neighbors. The including the target tree and its five closest competitors makes up one subplot. We also noted distance to and DBHs of dead trees within that radius, as well as their tree species.

## Data Analysis

Species distribution and DBH of tagged trees in the Maple River West Stand for the years 1942, 1947, 1953, 1957, 1962, 1980, and in 1999 were provided by UMBS (Maple River West Stand Summary 1953). Basal area of each tree for each year was calculated using the equation:

$$BA = \pi (DBH/2)^2$$

where  $BA$  ( $\text{cm}^2$ ) equals the surface area of the base of the bole (i.e. basal area). We calculated the proportion of BA by dividing the total tree BA by a given area. For calculating above ground tree biomass we used the equation:

$$M = a(DBH)^b$$

where  $M$  equals the over-dry weight of the biomass component of a tree (kg), and  $a$  and  $b$  are constant parameters which vary by tree species. We used the following species-specific equations (from Perala and Alban 1994) for the Upper Great Lakes region:

$$B. \text{ papyrifera}; M = 0.1182(DBH)^{2.4287}$$

$$P. \text{ glauca}; M = 0.1643(DBH)^{2.2480}$$

$$P. \text{ resinosa}; M = 0.0778(DBH)^{2.4171}$$

$$P. \text{ strobus}; M = 0.0755(DBH)^{2.3833}$$

$$T. \text{ canadensis}; M = 0.0991(DBH)^{2.3617}$$

$$T. \text{ occidentalis}; M = 0.0910(DBH)^{2.2340}$$

Relative Growth Rate (RGR) for all species was calculated using the equation:

$$RGR = [\text{LN}(DBH_2) - \text{LN}(DBH_1)] / T_2 - T_1$$

where  $RGR$  ( $\text{cm}/\text{year}/\text{cm}$ ) equals the increase in biomass adjusted by the accumulated biomass, or the increase in biomass per unit time per unit size (Hunt 1982).  $DBH$  is diameter at breast height and  $T$  is time. We also calculated the proportion of dead and live trees within the subplots of Plot B. We used Microsoft Excel and SPSS to analyze possible relationships between biomass, proportion of BA, RGR, DBH, and distance using  $\alpha \leq 0.05$  for linear regressions (Table 1). We also created bar graphs and scatter plots to explore trends exhibited in the data.

## RESULTS

The proportion of BA to total area within each subplot is negatively correlated with the overall (1942-2011) RGR of the target tree (Fig. 1;  $p=0.020$ ;  $R^2=0.178$ ;  $y=0.013-0.519x$ ), the RGR of the target tree between 1942 and 1947 (Fig. 2;  $p=0.031$ ;  $R^2=0.156$ ;  $y=0.12-0.467x$ ), and the RGR of the target tree between 1947 and 1953 (Fig. 3;  $p=0.000$ ;  $R^2=0.365$ ;  $y=0.024-1.03x$ ). Data from all three of these relationships met the assumptions of linear regression.

Total above ground biomass of live tagged trees within Plot B increased from 1942 to 1999 and then decreased in 2011 (Fig. 4). Within this trend, rate of total biomass changed between 1942 and 1962 and was much lower than that of 1962-1999. Mean biomass per tree increased exponentially over time with the largest change in mean biomass between 1980 and 1999 (Fig. 5). Proportion of BA increased linearly between 1942 and 1999 and decreased between 1999 and 2011 (Fig. 6).

The range of RGRs as well as median RGR of live tagged trees followed a negative trend as time progressed (Fig. 7). The mean RGR per tree decreased linearly

except during 1957-1962, where the value was lower than the observed trend (Fig. 8). The proportion of live to total tagged trees in Plot B showed a negatively logistic trend over time (Fig. 9). The proportion of dead to total *P. resinosa* stems increased exponentially while the proportion of dead to total non-*P. resinosa* followed a discontinuous increasing pattern (Fig. 10). Both proportions were comparable between 1942 and 1999; however, the proportion of dead *P. resinosa* was significantly higher than non-*P. resinosa* in 2011.

We found insignificant relationships in three additional linear regression tests. Overall RGR of the target trees was not significantly correlated with mean overall RGR of the target tree's three closest *P. resinosa* neighbors (p-value=0.953,  $R^2=0.000$ ), distance from a target tree to its closest competitor (p-value=0.397,  $R^2=0.026$ ), or the mean distance between a target tree and its five closest neighbors (p-value=0.397,  $R^2=0.026$ ).

## DISCUSSION

Proportion of BA coverage is a good indicator for overall RGR, and for the first two of seven time intervals, of the target tree (Fig. 1-3). RGR is most strongly affected by BA coverage for the first eleven years of the study. We can reject the null hypothesis that there is no relationship between RGR and BA coverage in the subplots for intervals 1942-2011, 1942-1947 and 1947-1953 because they are significantly negatively correlated in all three cases. Therefore, RGR of *P. resinosa* is dependent on tree spacing of Plot B for at least part of their lifespan. We assume that trees at high densities compete more strongly for a limited amount of resources than trees at low densities. As strength of competition increases, lower resource availability leads to higher rates of mortality. Due to the self-thinning of Plot B, stand density since 1953 is much lower than the stand density during the strongest period of competition.

The constant increase in total biomass between 1942 and 1999 can be explained by an extended period of weak competition, which in itself is defined by a low rate of self-thinning. The high proportion of dead trees we observed in 2011 (Fig. 9) explains the subsequent decrease in total above-ground biomass in the same year (Fig. 4). Thus, we can reject our second null hypothesis with the exception of year 2011. In 2011, mean RGR is positive, but proportion of BA decreases due to mortality, as a result of competition or low resource availability. In all other years, a decrease in stand density leads to lower levels of competition and higher net primary productivity.

The exponential increasing trend of mean biomass per tree can be explained by the increase in mean tree RGR at each time interval (Fig. 5). At this point in competition, good competitors are large in size and many poor competitors are deceased. Due to high stand biomass and a high proportion of dead tagged trees, a mean live tree in 2011 has a disproportionately high biomass. This explains why total stand biomass drops while mean biomass continues to increase throughout the study period. Total live BA and total live biomass follow the same trend over time because they are both dependent on DBH (Fig. 6); therefore, the decrease in BA in 2011 is also strongly linked to competition and mortality.

Since there are fewer remaining live trees in 2011 (Fig. 9), RGR is no longer a

good indicator of competition as it stabilizes to a narrow range throughout the study period (Fig. 7). This indicates that live trees may be allocating resources to things other than growth, such as reproduction, later in life. *P. resinosa* stems tend to reproduce at highest rates between ages 50 and 150 (McRae et al. 1994). A general decrease in median stand RGR by time interval supports the idea that *P. resinosa* RGR is strongest while the tree is young (Fig. 7). Mean RGR decreases with time due to increased competition for resources as the stand reaches stability (Fig. 8). The increase in number of *P. resinosa* and non-*P. resinosa* stems reflects mortality as a result of intraspecific and interspecific competition, respectively. Since there were only 18 tagged non-*P. resinosa* in 1942, the proportion of dead to total tagged non-*P. resinosa* stems does not follow a smooth curve (Fig. 10). The proportion of dead *P. resinosa* follows a predictable exponential curve; therefore, we can assume that there is a strong relationship between intraspecific competition and time.

That overall growth rate of a target tree is not strongly linked to distance between competitors lends strong evidence that in this study area, a tree's strongest source of competition is not its closest, or even several closest, neighbors. This indicates that distance between immediate competitors does not have a great effect on resource allocation during the study intervals.

Throughout this study, several factors limited our findings. The UMBS archives only had DBH, biomass, and BA data for Plot B as far back as 1942. We did not have access to this data during the years of highest growth rate and significant competition among *P. resinosa* individuals; therefore, we were unable to compare relationships between competition, RGR, biomass, and proportion of BA during that time. The DBH data was collected on infrequent intervals between 1942-2011; thus, we were unable to analyze data representative of the lifespan of the stand, specifically interactions during the early years of growth. Also, annual tree mortality was unknown, which means we were unable to recognize specific events such as drought or disease that occurred between measurements. We only measured the five nearest tree neighbors and not all of them were *P. resinosa*; thus we were unable to compare relative growth rate of all live trees within a given density. In addition, some of the trees were untagged or had unreadable tags. Therefore, it was unclear whether the trees we tagged as A-KK were part of the original 421 trees. If so, their volumes have not been included in the total live stand biomass since their tags were lost. However, we did include A-KK in our most recent total live biomass because they are significant carbon sinks. Furthermore, we did not test the soil for nutrient quality, which could be a limiting factor of RGR.

*P. resinosa* RGRs are negatively correlated with BA coverage at certain time intervals in Plot B as a result of increased competitive stress with increased density. Total above ground biomass increases over time until 2011 when a high level of mortality arose. Results of this study contribute to the scientific understanding of the Pellston Plain, specifically regarding competitive interactions and their effects on biomass, RGR, and BA coverage of a mature *P. resinosa* stand in the Upper Great Lakes region. Further studies could explore these concepts in younger, natural regenerated stands.

## ACKNOWLEDGMENTS

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## TABLES & FIGURES

Table 1. Non-correlated dependent vs. independent variables.

<b>Insignificant Relationships</b>
Total live biomass of Plot B (kg) vs. Year (1942, 1947, 1953, 1957, 1962, 1980, 1999, 2011)
Mean live biomass of Plot B (kg/tree) vs. Year
Proportion of live basal area (BA) to area of Plot B (cm <sup>2</sup> /ha) vs. Year
Total relative growth rate (RGR) in Plot B (cm/yr/cm) vs. Year
Mean RGR in Plot B (cm/yr/cm) vs. Year
Proportion of live trees in Plot B vs. Year
Proportion of dead <i>P. resinosa</i> and non- <i>P. resinosa</i> in Plot B vs. Year
Mean 1942-2011 (overall) RGR of three closest <i>P. resinosa</i> neighbors (cm/yr/cm) vs. Overall RGR of target tree (cm/yr/cm)
Overall RGR of target tree (cm/yr/cm) vs. Distance between target tree and nearest neighbor (m)
Overall RGR of target tree (cm/yr/cm) vs. Average distance between target tree and five nearest neighbors (m)
Mean DBH of dead trees (cm) vs. Mean DBH of live trees (cm) within the subplot
Overall RGR of target tree (cm/yr/cm) vs. Proportion of basal area to subplot area
1999-2011 RGR of target tree (cm/yr/cm) vs. Proportion of BA to subplot area
1962-1980 RGR of target tree (cm/yr/cm) vs. Proportion of BA to subplot area
1953-1957 RGR of target tree (cm/yr/cm) vs. Proportion of BA to subplot area
1947-1953 RGR of target tree (cm/yr/cm) vs. Proportion of BA to subplot area

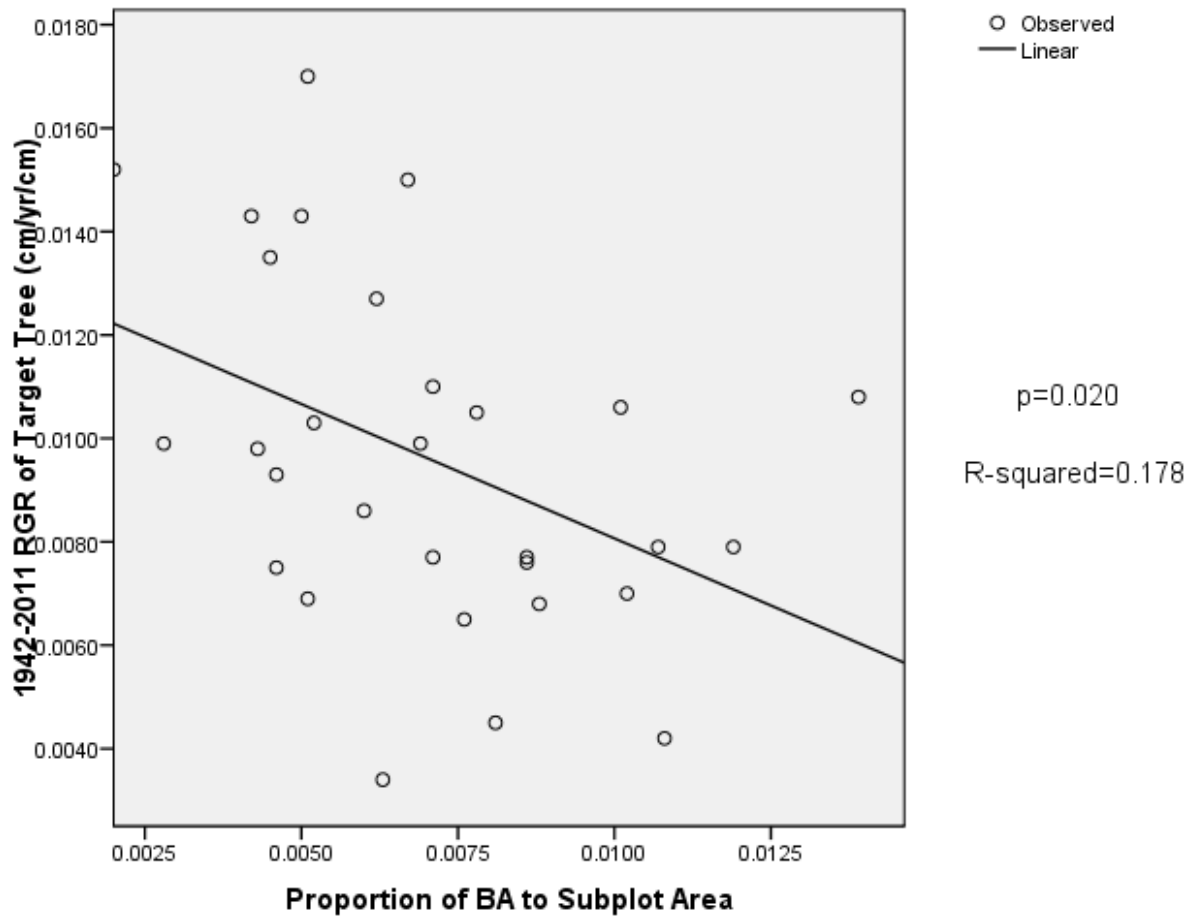


Fig. 1. The proportion of BA to total area within each subplot vs. target tree overall RGR.

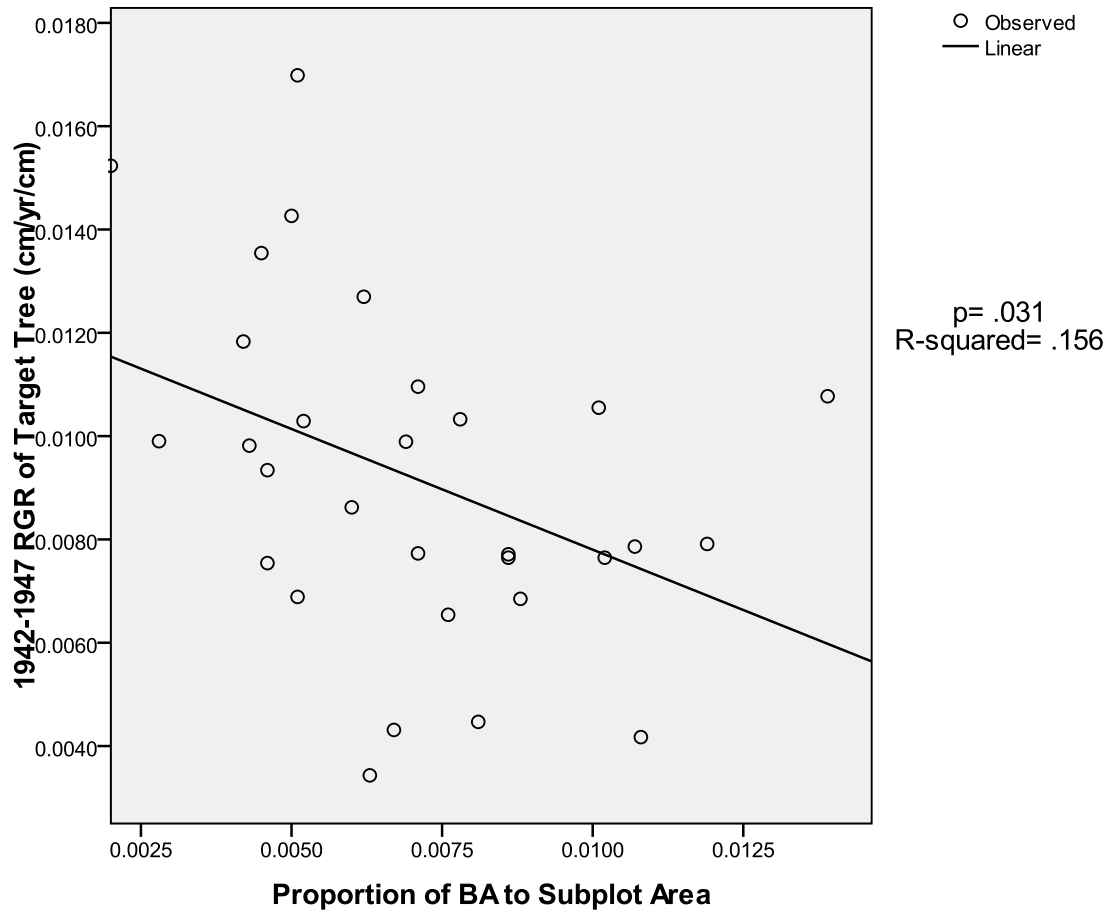


Fig. 2. The proportion of BA to total area within each subplot vs. target tree overall RGR.

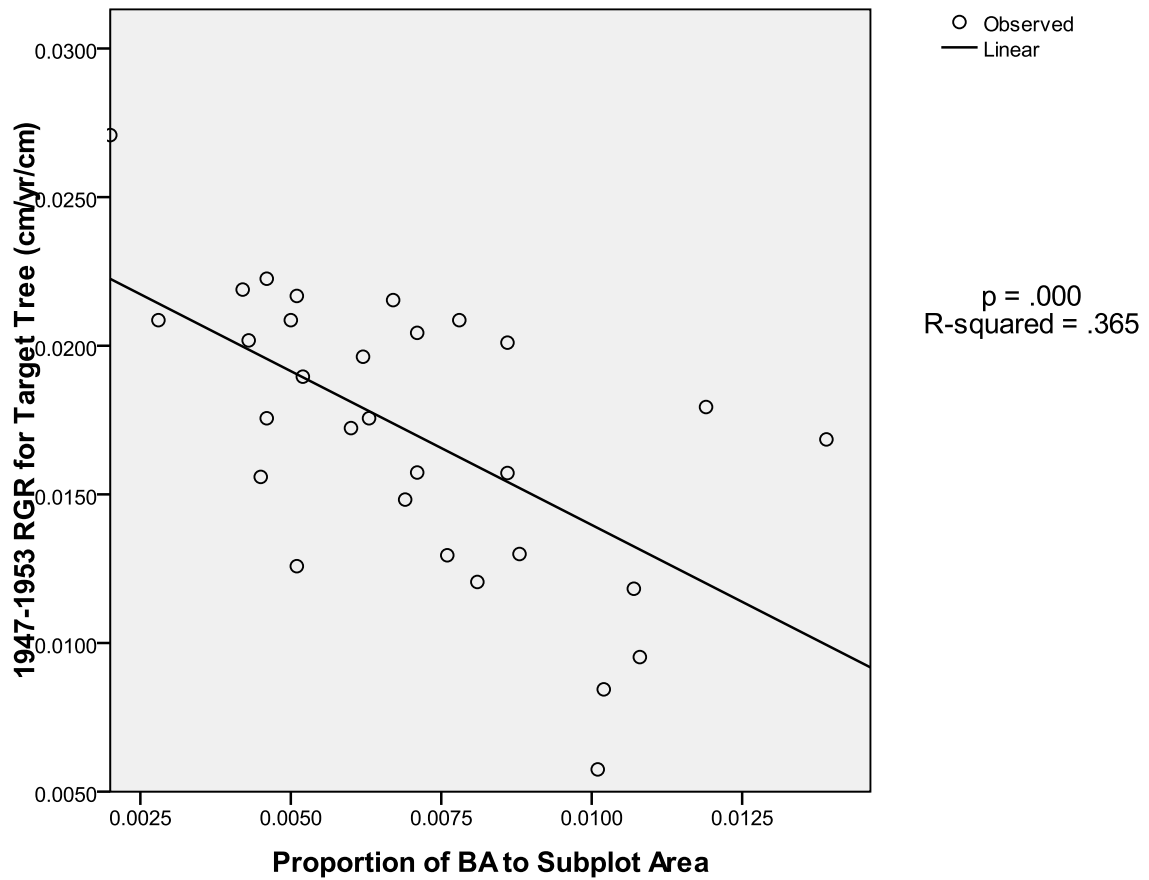


Fig. 3. The proportion of BA to total area within each subplot vs. target tree overall RGR.

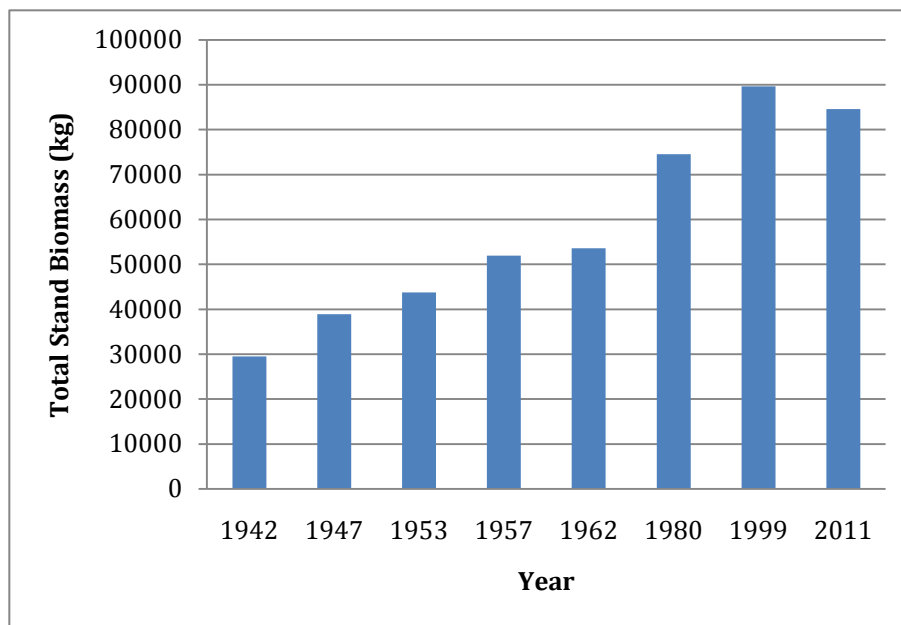


Fig. 4. Total above ground live biomass of Plot B per year measured.

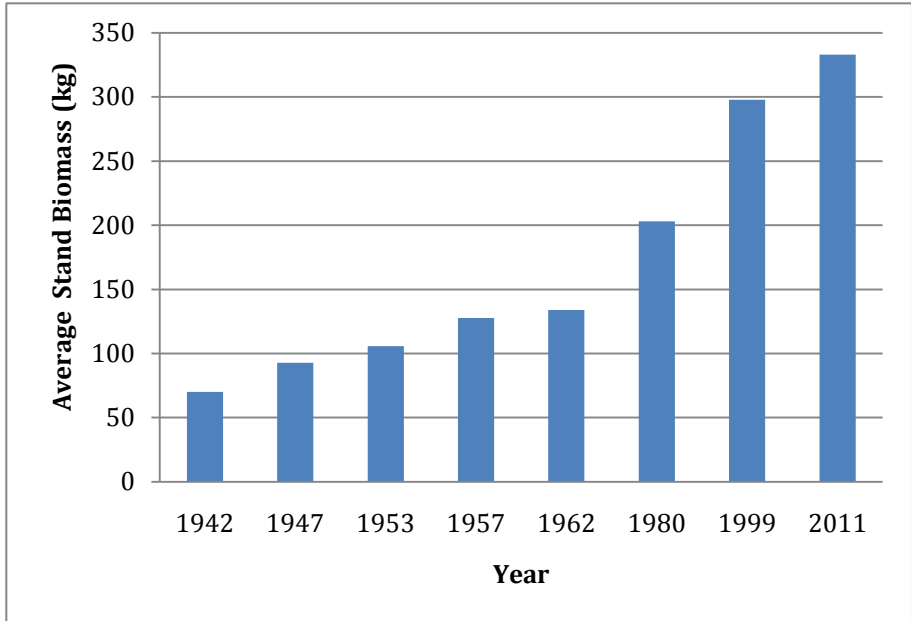


Fig. 5. Mean above ground live biomass of Plot B per year measured.

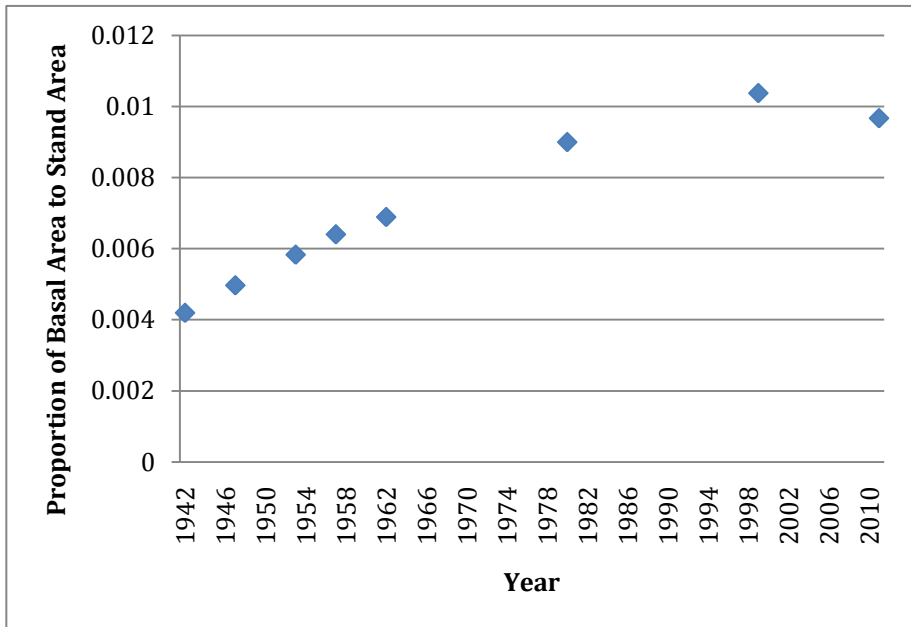


Fig. 6. Proportion of live BA to total area of Plot B per year measured.

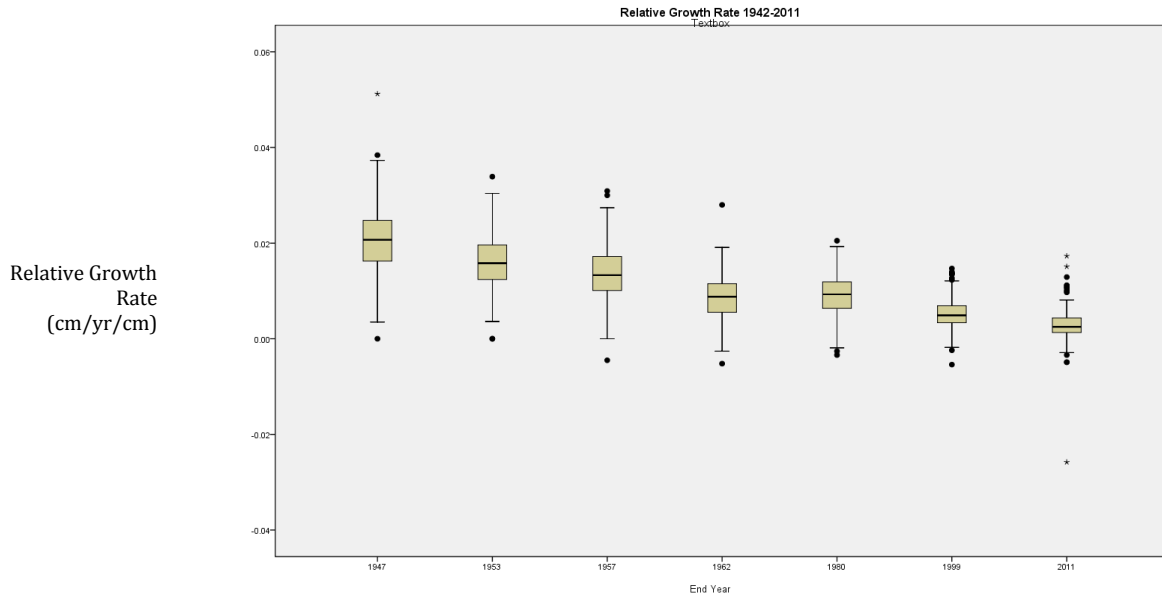


Fig. 7. Median RGR of Plot B for years measured.

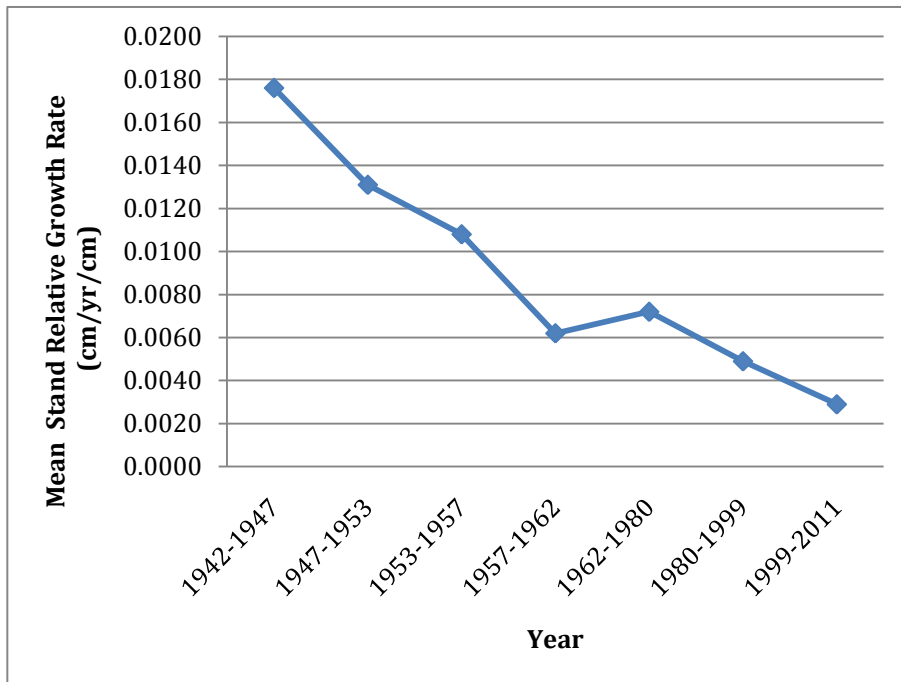


Fig. 8. Mean RGR of Plot B for time intervals measured.

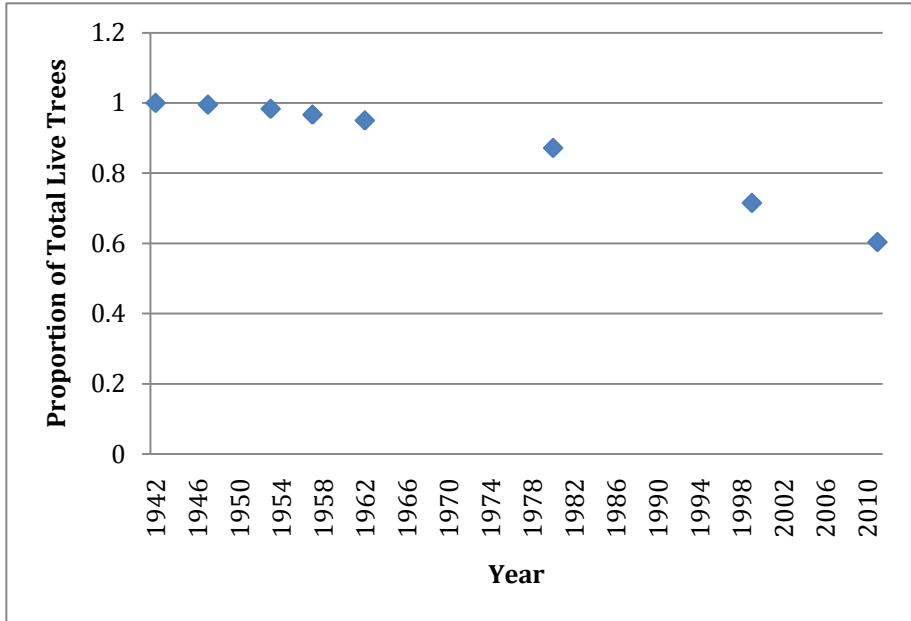


Fig. 9. Proportion of live trees to total trees in Plot B for years measured.

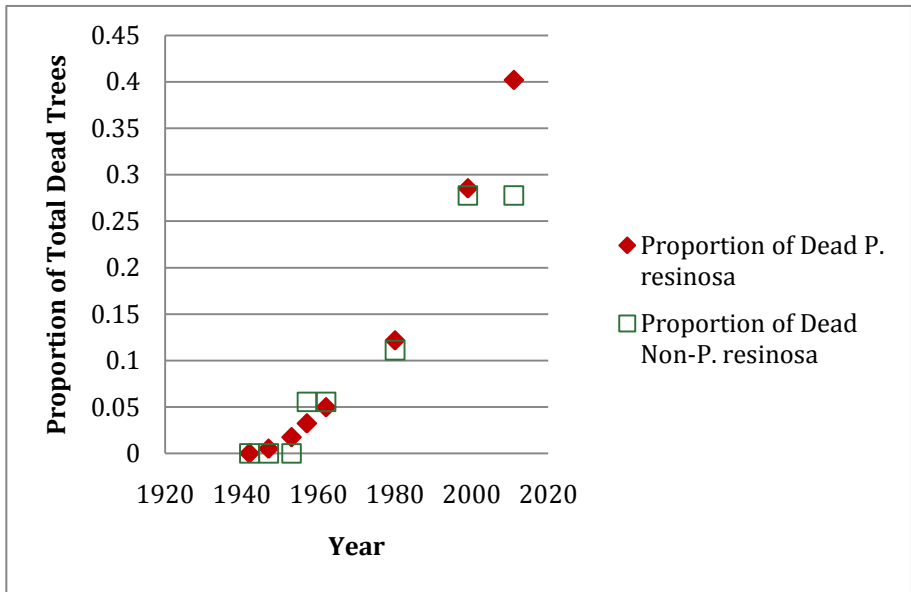


Fig. 10. Proportions of dead *P. resinosa* to total *P. resinosa* and of dead non-*P. resinosa* to total *P. resinosa* in Plot B for years measured.