Growth rate and survival: how much do short-term measurements underestimate lifetime growth?

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Background

In tropical forests, tree growth is routinely estimated by successive measurements of individual diameters over a few years, while growth-ring analyses spanning long lifetimes are rare (Rozendaal & Zuidema, 2011; Alfaro-Sánchez *et al.*, 2017). Unfortunately, there is a bias in growth measurements based on the two methods, because tree rings are based on the survivors, whereas repeated measurements in a forest plot include many that will die in the near future. Plot records have demonstrated the nature of this bias. In general, trees that grow more slowly are more likely to die than faster-growing neighbors, a pattern called growth-dependent survival (Russo *et al.*, 2020; Kobe & Coates, 1996; Kobe, 1996; Monserud, 1976; Pacala *et al.*, 1996; Camac *et al.*, 2018). Another way of describing the same phenomenon is that trees in poor condition suffer both in growth and in survival. This should be a general pattern across organisms.

In (Condit, 2022), tree lifespans in tropical forests in Panama were estimated from five-year growth taken from the 50-ha census plot at Barro Colorado Island. Do these substantially underestimate lifetime growth and thus the demographic potential of tree species? Because we now have 33 years of regular plot measurements, we can examine growth of long-term survivors and thus test how long the relationship between growth and future survival lasts.

We frame the question by considering the growth rates of trees during 1982-1985 relative to how long into the future they would survived. The difference in growth between those that died immediately after 1985 and those that survived 30 more years is the best estimate of the growth bias that plot measurements suffer. It will be better after we have observed the same trees even longer, but the 30-year record long for tropical plots, so it is the best comparison of plots to tree rings available.

Materials and methods

Plot and census

The 50 ha plot on Barro Colorado Island was first censused in 1981-1982, then every 5 years from 1985 through 2015. All stems ≥ 1 cm diameter-at-breast-height (dbh) were mapped, measured, and identified in each census (Hubbell & Foster, 1983; Condit *et al.*, 2012). We have tagged a total of 423,617 individual trees over 35 years, defining each genet – all stems from one base – as an individual. Though every stem is measured, here we only make use of the largest stem per individual. Stems were measured at breast height, 1.3 m above the ground, except where the stem was swollen or misshapen at that height. Growth rates are included here only when the same stem was measured at the same height in consecutive censuses; here, we refer to stem diameter by dbh (diameter-breast-height) or simply diameter (unless mentioned otherwise, stem diameter always mean at 1.37 m). Trees were considered dead when all stems died.

Species

Our main interest is the tree species that form the canopy of the Barro Colorado forest, so we restricted to the analysis to those species whose maximum height was ≥ 12 m. For every species in the forest, the five largest trees (by stem diameter) had their height measured to the top leaves with a laser range-finder (Wright *et al.*, 2015). From these, we selected those species with ≥ 500 individuals with a growth rate measured over 1982-1985, and having dbh ¡ 120 mm in 1982. Those 52 species represented 106003 of the 168928 growth measurements (62.7%) recorded in 1982-1985. Those 106003 individuals with a growth rate in 1982-1985 were the sample for all analyses.

Growth

In order to use the longest time interval, we need growth rates estimated during 1982-1985. In those two censuses, stems < 55 mm diameter were rounded downward to the nearest multiple of 5-mm, that is, any dbh ≥ 10 but < 15 was recorded as 10 mm, and likewise for every 5-mm up to 55. Condit *et al.* (1993b) discuss in detail growth estimates based on 5-mm precision, showing that the mean growth rate is slightly biased. In the present analysis, all our comparisons of growth are based on the same method, so the small bias is unimportant. The variance in growth when the precision is 5-mm is greatly altered, but that does not affect any of our tests.

We used growth estimates of saplings in three diameter categories – 10-20, 20-40, and 60-120 mm – deliberately defining diameter categories narrow enough that diameter could be excluded as a predictor from growth models. The smallest diameters offer the largest sample sizes, but we added the last group because trees above 60 mm were measured with millimeter precision. Growth rates of the ten common species, and of the entire forest combined, were calculated in each of the three categories.

Growth rate transformation

Each sapling for which a growth rate was estimated from 1982-1985 was included in our test. The survival variable was the census in which each was found dead, one of six possibilities: 1990, 1995, 2000, 2005, 2010, and 2015. Those still alive in 2015 formed a seventh survival category. Our question is whether growth rate in 1982-1985 was 'predicted' by future survival. This means 'predict' in a modeling sense, because in 1985, future survival could not be known. Wwe considered the survival groups as seven categorical variables. This allows us to test, for example, whether sapling growth in 1982-1985 differed between those that died in 2015 and those still alive in 2015. A regression between growth rate and future survival would not allow a comparison between specific survival categories. Much prior work has demonstrated this correlation. Our goal is determining whether the correlation lasts 30 years. We do not ask about growth over the entire 1982-2015 interval compared to the 1982-1985 interval, since that would confound effects of long-term fluctuations in growth (Condit *et al.*, 2020). The best test is to compare a group of saplings, all measured at the same time far in the past, relative to how much longer they lived.

The distribution of growth rates of saplings in the forest is highly skewed to the right. The vast majority of individuals grow little, but there are outliers with growth more than 10 times higher than the mean. In previous work, we have verified some of the highest growth rates while also carefully screening for errors. We follow previous methods and exclude from analysis any case where a stem shrank by more than 5% per year, or grew by more than 75 mm per year (Condit *et al.*, 1993a,b, 2006; Stephenson *et al.*, 2014). These extremes comprise very small number of records and generally have little impact on growth estimates in abundant species.

Highly skewed data require transformation to achieve quasi-normal distributions. A common approach is to use logarithms, which are effecting at eliminating the right skew. Unfortunately, this is impossible for negative growth rates, which commonly appear with 5-year measurements of saplings, where mean growth is often < 0.5 mm y^{-1}. In previous work, zeroes in growth were converted to the smallest positive growth rate that could be measured (1 mm dbh over 5 years), but the arbitrary nature of that smallest positive is a problem. When growth rates low, as in trees, the exact choice of a smallest positive has a large impact, because the logarithm varies rapidly at small numbers. In saplings, growth rates are typically ¡ 1 mm y-1, so arbitrarily convering 0 growth to 0.2 vs. 0.1 is a large difference and can affect model results.

Instead of log-transformation, we have used a cube-root transformation, or a power close to a cube root. This transformation allows negatives, assuming that transformed growth, T, is defined

$$T = \begin{cases} = g^k & g \geq 0 \\ = -[(-g)^k] & g < 0. \end{cases} \tag{1}$$

This is known as the modulus transformation (John & Draper, 1980). It reigns in negative growth outliers in the same way that it does for positive growth.

If k is an odd integer, the extra line is unnecessary, but with it included, any k is possible. We chose $k = 0.45$ because it reduces skewness toward zero in saplings (Kenfack *et al.* 2014; see histograms of untransformed and transformed growth in Appendix 1). The substantial advantage of the power transformation is that we can include small negative growth rates exactly as recorded; we do still exclude extreme negatives, just like extreme positives.

Modeling growth versus future lifespan

We calculated the mean and variance of transformed growth rate, T, in each of the survival categories: all trees found dead 5, 10, 15, 20, 25, or 30 years after the growth measurement, and finally in those trees still alive after 30 years. We did this for the entire sample, and for each individual species. In each category, whether one species or the full forest together, we report the mean of transformed growth, and use $1.96\sigma/\sqrt(N)$ as 95% credible intervals, where σ is the standard deviation of the sample and N the size.

Camac *et al.* (2018) found that most tree species at Barro Colorado had survival that increased with growth rate five years earlier. The converse of this observation is that 1982-1985 growth rates of trees that survive until 1990 were higher than those that died by 1990. Since we now have 33 years of censuses, we want to extend these observations to a longer scale. Was 1982-1985 growth higher in trees that survived to 1995 than those dying after 1990? Most interesting will be the growth of those trees living the longest – those still alive in 2015.

Since we anticipate that growth increases with future lifespan, we do not perform a simple regression between growth and the number of years of future survival. Instead, we compare growth in survival categories. How far in the future does survival still influence growth over 1982-1985? This requires a comparison of growth in discrete survival categories, so we rely on the 95% confidence limits of growth in each survival group.

Data Availability

A supplementary data archive includes the full species list with range sizes available for download (Condit *et al.*, 2019).

Results

Forest-wide growth rate vs. future lifetime

When all measurements for the 52 species were pooled into a single sample, the 1982-1985 growth rate increased steadily with increasing lifespan, across all survival categories (Fig. 1). In all three diameter categories, growth increased significantly with every additional 5 years of lifespan up to 20 years, and the longest-lived trees – those still alive after 30 years – had significantly higher growth than every other category (Fig. 1). Median growth rate of the longest survivors was higher than the overall average growth rate (dashed lines in Fig. 1) by 36%, 26%, and 21% in the three dbh categories (Table 1).

Species growth rates vs. future lifetime

In the three most abundant species, there was a broad trend for increasing growth with increasing future lifetime, though with fluctuations (Figs. 2-4). One result that held consistently, in all three dbh categories, was that the highest growth rate was always those trees still alive 30 years in the future. Another consistency was that the two slowest growth rates were always the two shortest lifetimes, meaning trees that died 5 or 10 years after growth was measuring in 1985. The growth bias, measured as the excess growth of the longest survivors relative to the average, was lowest in *F. occidentalis* at 13-18%, and highest in the other two species, reaching 45-52% in the smallest saplings (Table 1). Results for all 52 species considered are shown in the Appendix.

Considering all 52 species, growth rate in the longest survivors was higher than the overall median growth in all size categories and nearly every species (142 of 156 blue points are above the line, Fig. 5). On the other hand, growth rate of those dying at year 10 after growth was measured had lower than average growth (127 of 156 red points are below the line, Fig. 5). Slower growth in those that died held at 15 years in the future (Fig. 6a), but faded by 20-25 years (Fig. 6b). In the smaller size class, those that died 20 years ahead were divided around the line (Fig. 6b, 31 red points below the line and 21 above).

Discussion

Results across all species, and of the commonest species by themselves consistently showed growth rates increasing as a function of future survival out to 15 years in the future. For example, trees surviving 15 years had better growth than those surviving only 10 years. This means that in 1982, there were differences among the groups. Had we studied the detailed state of those trees, we would have seen some differences in fitness between the 15-year and 10-year groups: some had more leaves, fewer infections, deeper roots, better genes, and some of those traits led to longer survival.

In most species, the fastest growth rate was in the longest surviving group, those still alive 30 years later. Most important in the current context is how five-year compares to that maximum growth. That is the bias of a short-term measurement...

Conclusion

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Table 1: Effect of future survival on 1982-1985 growth rate in 54 species in the Barro Colorado 50-ha plot, and for all those species combined.One group of trees includes every individual surviving from 1982-1985. The second group includes the subset of those still alive in 2015.Growth columns show the ratio of growth rates in group 2 relative to group 1. Survival columns show the fraction of individuals in group 2.

	Growth ratio			Long-term survival		
Species	10-20	20-40	60-90	10-20	20-40	60-90
Species combined	1.26	1.21	1.23	0.52	0.52	0.49
Alseis blackiana	1.52	1.36	1.29	0.51	0.55	0.76
Beilschmiedia tovarensis	1.98	1.21	1.28	0.42	0.58	0.61
Brosimum alicastrum	1.30	1.16	1.08	0.76	0.75	0.85
Calophyllum longifolium	0.96	1.08	0.96	0.36	0.32	0.26
Cassipourea elliptica	1.07	1.23	0.90	0.72	0.78	0.73
Cordia bicolor	7.20	2.81	1.62	0.11	0.24	0.42
Cordia lasiocalyx	2.02	1.45	1.33	0.30	0.30	0.29
Coussarea curvigemmia	1.51	1.46	1.12	0.56	0.55	0.43
Cupania seemannii	1.12	0.99	0.96	0.86	0.92	0.84
Desmopsis panamensis	1.08	1.13	1.48	0.52	0.33	0.14
Drypetes standleyi	1.46	1.26	1.11	0.56	0.64	0.74
Eugenia coloradoensis	1.85	1.58	0.99	0.40	0.38	0.54
Eugenia galalonensis	1.07	1.37	0.78	0.60	0.45	0.23
Eugenia oerstediana	2.00	1.22	1.42	0.31	0.36	0.31
Faramea occidentalis	1.17	1.13	1.19	0.68	0.64	0.48
Garcinia recondita	1.09	1.10	1.12	0.69	0.66	0.57
Garcinia madruno	0.61	0.61	1.12	0.48	0.27	0.07
Guarea guidonia	1.37	1.33	1.27	0.44	0.55	0.71
Guarea bullata	1.76	1.83	2.34	0.24	0.26	0.32
Guatteria lucens	1.38	1.63	0.96	0.27	0.24	0.28
Hasseltia floribunda	2.97	1.69	1.59	0.17	0.28	0.40
Heisteria concinna	1.12	1.02	1.09	0.80	0.85	0.84
Hirtella triandra	1.57	1.29	1.12	0.54	0.64	0.75
Inga marginata	4.62	2.13	1.31	0.06	0.11	0.09
Inga nobilis	1.52	1.14	1.28	0.43	0.60	0.50
Inga umbellifera	1.44	1.27	1.33	0.54	0.48	0.16
Lacistema aggregatum	1.42	1.61	1.73	0.33	0.31	0.29

Table 1: cont.

	Growth ratio			Long-term survival		
Species	10-20	20-40	60-90	10-20	20-40	60-90
Lonchocarpus heptaphyllus	1.50	1.25	1.22	0.36	0.43	0.52
Maquira guianensis	1.16	1.13	1.21	0.73	0.72	0.63
Miconia argentea	4.55	2.80	1.92	0.02	0.07	0.07
Ocotea whitei	2.13	1.94	1.44	0.10	0.16	0.38
Ouratea lucens	1.33	1.10	0.19	0.61	0.57	0.40
Picramnia latifolia	1.59	1.40	0.85	0.34	0.32	0.33
Poulsenia armata	1.44	1.45	1.28	0.28	0.28	0.28
Pouteria reticulata	1.80	1.51	1.23	0.28	0.46	0.58
Prioria copaifera	1.32	1.19	1.21	0.70	0.76	0.76
Protium costaricense	1.55	1.08	0.98	0.40	0.42	0.41
Protium panamense	0.99	0.88	1.38	0.55	0.50	0.32
Protium tenuifolium	1.33	1.21	1.26	0.50	0.56	0.48
Pterocarpus hayesii	1.73	1.47	0.91	0.34	0.40	0.37
Quararibea asterolepis	1.64	1.34	1.16	0.59	0.64	0.74
Randia armata	2.13	1.32	1.02	0.44	0.62	0.71
Simarouba amara	1.64	1.62	0.99	0.09	0.20	0.26
Sorocea affinis	1.15	1.29	1.51	0.52	0.47	0.33
Swartzia simplex var. grandiflora	1.01	1.09	1.13	0.83	0.85	0.77
Swartzia simplex var. continentalis	1.01	0.96	1.10	0.90	0.85	0.79
Tabernaemontana arborea	1.73	1.52	0.94	0.50	0.57	0.75
Tachigali panamensis	1.59	1.68	1.25	0.16	0.17	0.35
Talisia croatii	1.03	1.12	1.20	0.72	0.81	0.55
Protium stevensonii	1.26	1.24	1.14	0.46	0.55	0.74
Trichilia tuberculata	1.45	1.35	1.50	0.44	0.43	0.46
Unonopsis pittieri	2.20	1.41	1.02	0.33	0.45	0.61
Virola sebifera	1.60	1.12	1.24	0.41	0.48	0.53
Xylopia macrantha	1.04	1.01	0.96	0.73	0.79	0.76

Figure legends

Figure 1. Growth rate (mm y^{-1}) during 1982-85 versus future survival for saplings in three diameter categories, all species pooled. The three panels are for sizes 10-20 mm, 20-40 mm, and 60-120 mm dbh saplings, as measured in 1982. Survival is expressed as the year in which trees were first observed dead, so lifespan increases from left to right. The rightmost category includes all trees still alive in 2015. The solid blue line connects the medians; the vertical red bars show 95% credible intervals. Dashed blue horizontal lines are the median, with upper and lower credible intervals, for lifespans combined. In the third panel, gray points are individual growth rates, each moved slightly to the left or right in order to reveal more. In smaller saplings, there are no points because growth was measured with 5 mm precision, meaning that individuals either grew 0 mm y^{-1}, 1 mm y^{-1}, or higher, so none appear near the average.

Figure 2. Growth rate (mm y^{-1}) during 1982-85 versus future survival for saplings in three diameter categories, species *Alseis blackiana*. See Figure 1 legend.

Figure 3. Growth rate (mm y^{-1}) during 1982-85 versus future survival for saplings in three diameter categories, species *Faramea occidentalis*. See Figure 1 legend.

Figure 4. Growth rate (mm y^{-1}) during 1982-85 versus future survival for saplings in three diameter categories, species *Trichilia tuberculata*. See Figure 1 legend.

Figure 5. Growth rate (mm y^{-1}) during 1982-85 across 52 species, comparing growth in two survival categories with mean growth in all survival categories combined.

Figure 6. Growth rate (mm y^{-1}) during 1982-85 across 52 species, comparing growth in four survival categories.

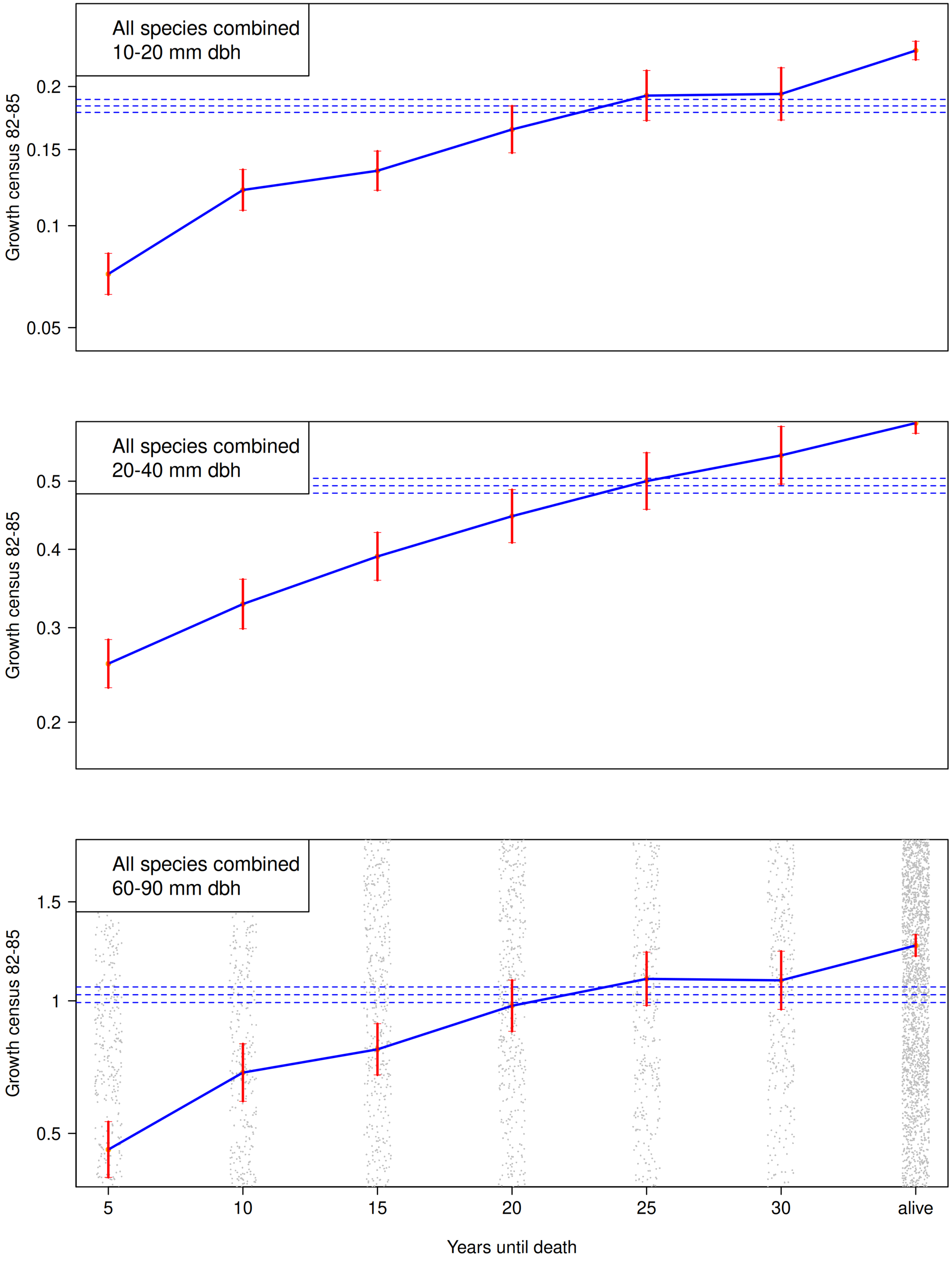

All species combined
10-20 mm dbh
Growth census 82-85
0.2
0.15
0.1
0.05
All species combined
20-40 mm dbh
Growth census 82-85
0.5
0.4
0.3
0.2
All species combined
60-90 mm dbh
Growth census 82-85
1.5
1
0.5
5
10
15
20
25
30
alive
Years until death

Figure 1

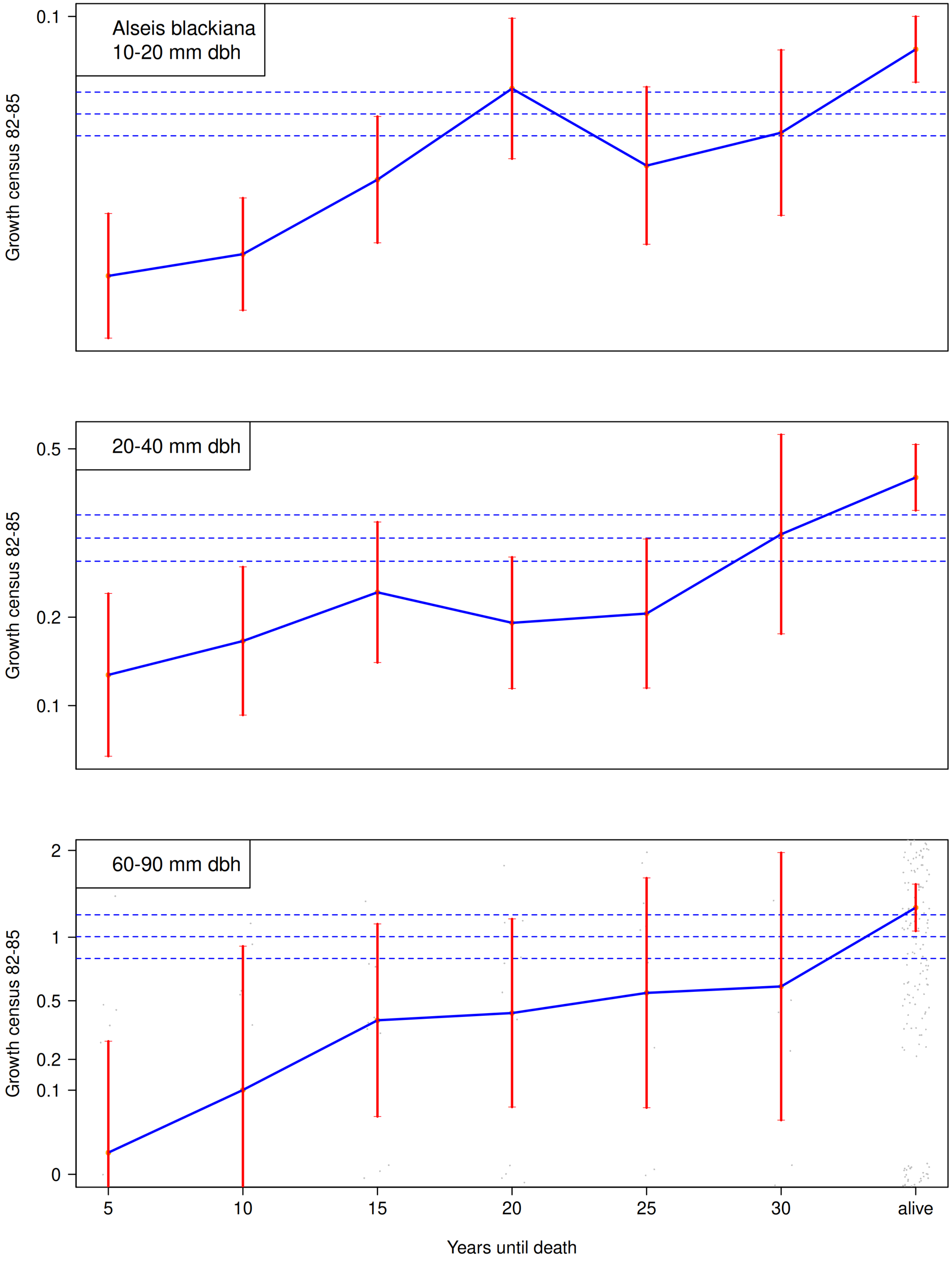
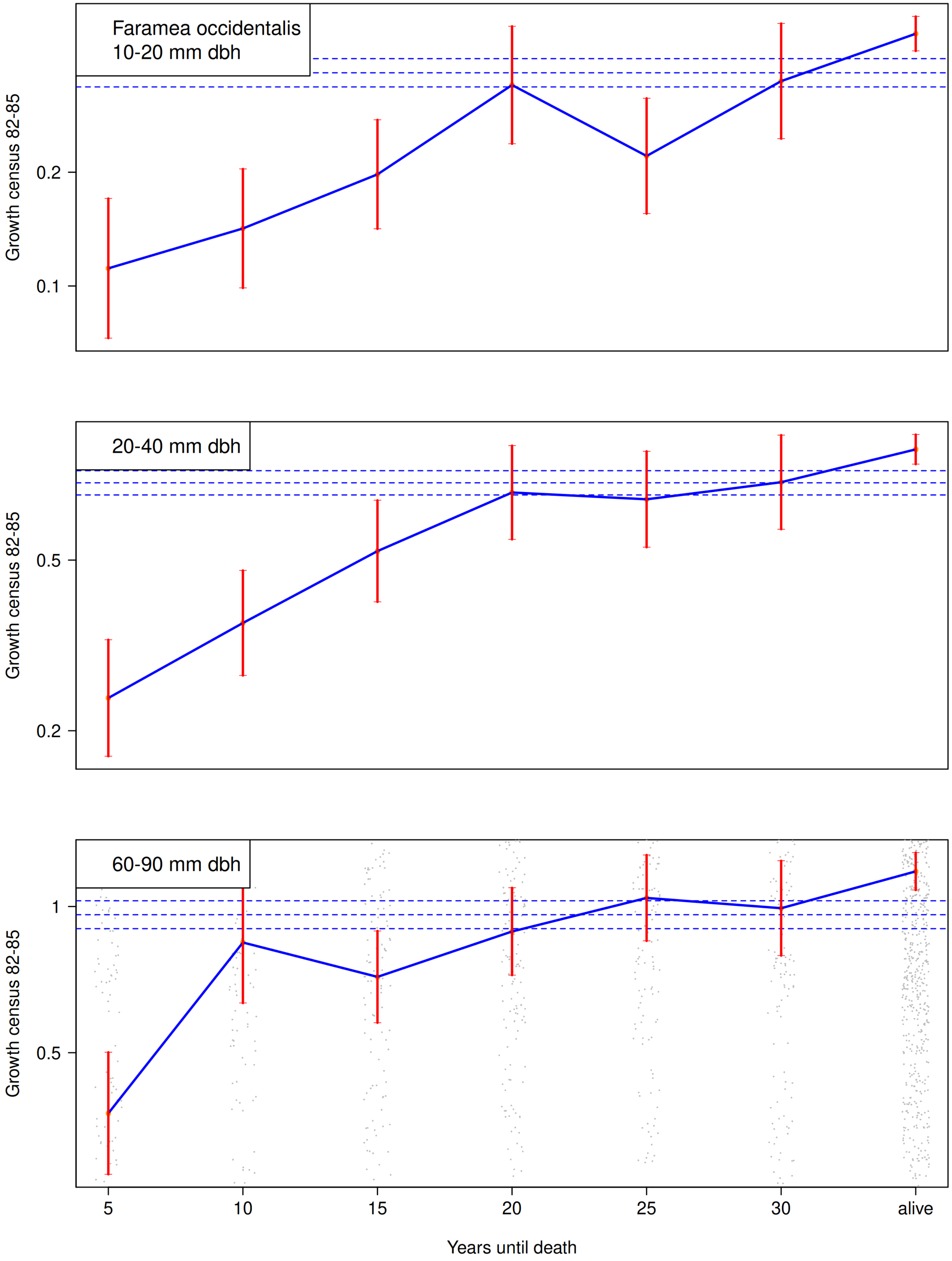

Alseis blackiana
10-20 mm dbh
20-40 mm dbh
60-90 mm dbh
Growth census 82-85
0.1
0.5
0.2
0.1
2
1
0.5
0.2
0.1
0
5
10
15
20
25
30
alive
Years until death

Figure 2



Faramea occidentalis
10-20 mm dbh
20-40 mm dbh
60-90 mm dbh
Growth census 82-85
0.1
0.2
0.2
0.5
0.5
1
5
10
15
20
25
30
alive
Years until death

Figure 3

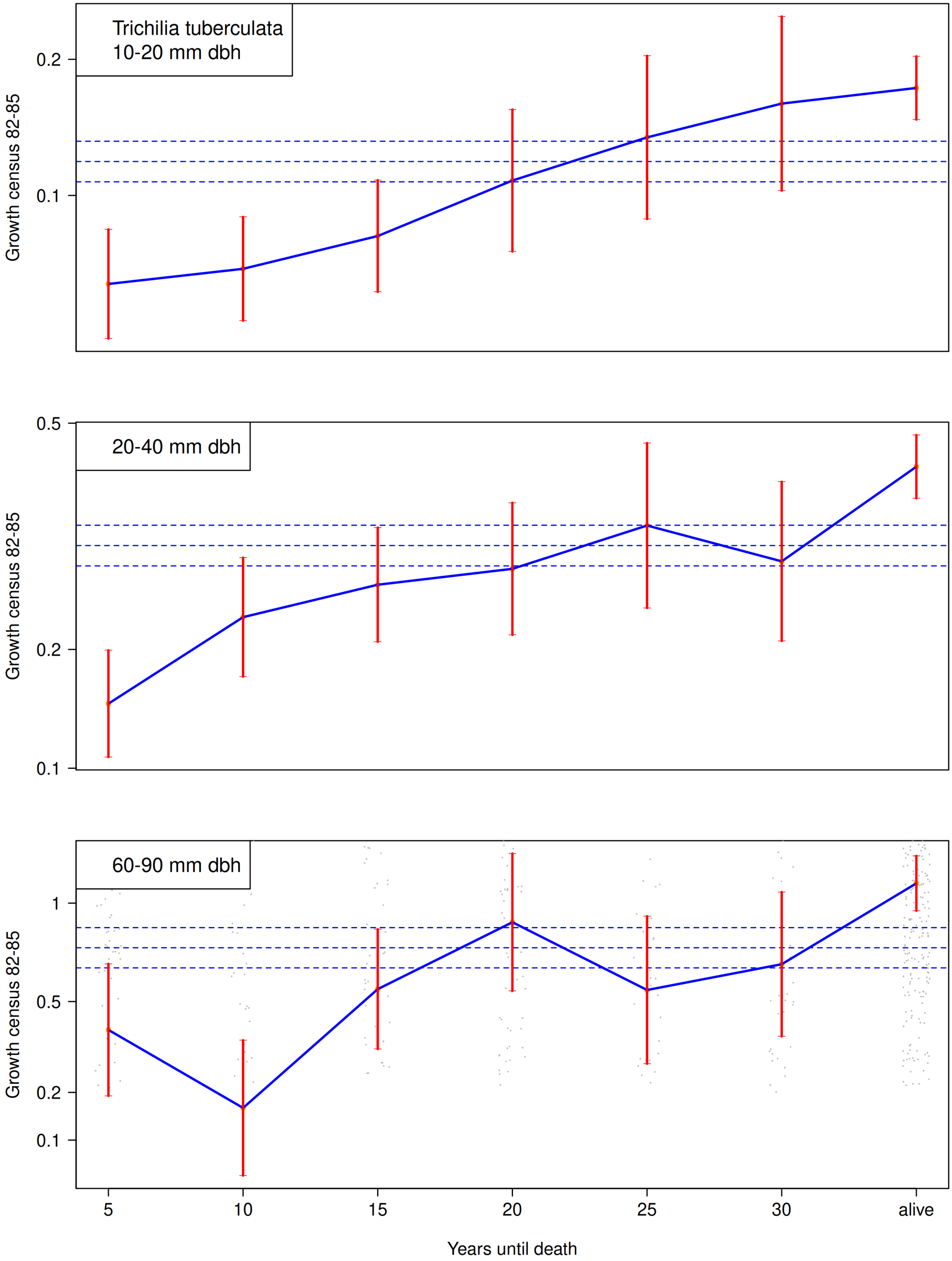

Trichilia tuberculata
10-20 mm dbh
20-40 mm dbh
60-90 mm dbh
Growth census 82-85
0.2
0.1
0.5
0.2
0.1
1
0.5
0.2
0.1
5
10
15
20
25
30
alive
Years until death

Figure 4

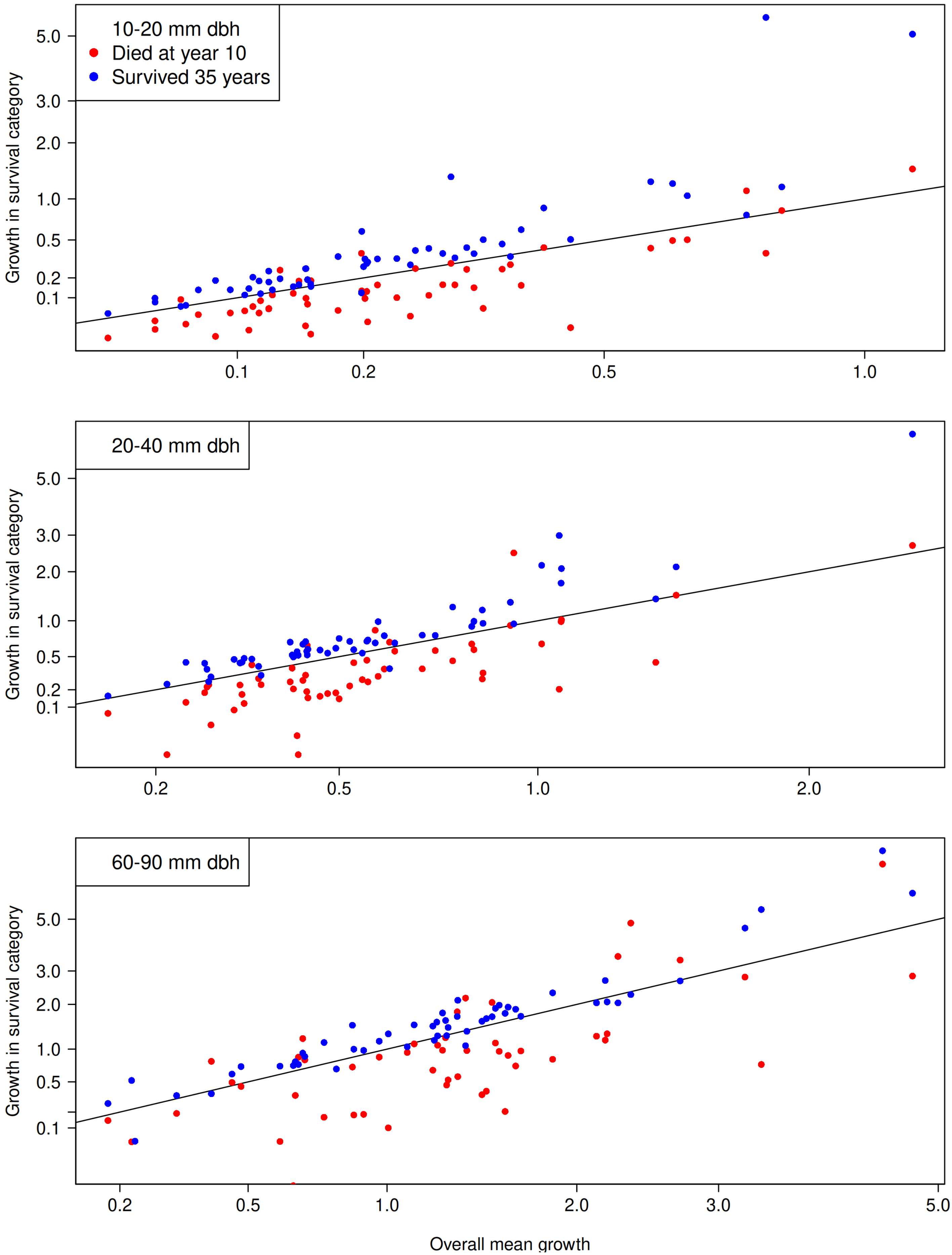

10-20 mm dbh
● Died at year 10
● Survived 35 years
20-40 mm dbh
60-90 mm dbh
Growth in survival category
Overall mean growth
0.1
0.2
0.5
1.0
2.0
3.0
5.0

Figure 5

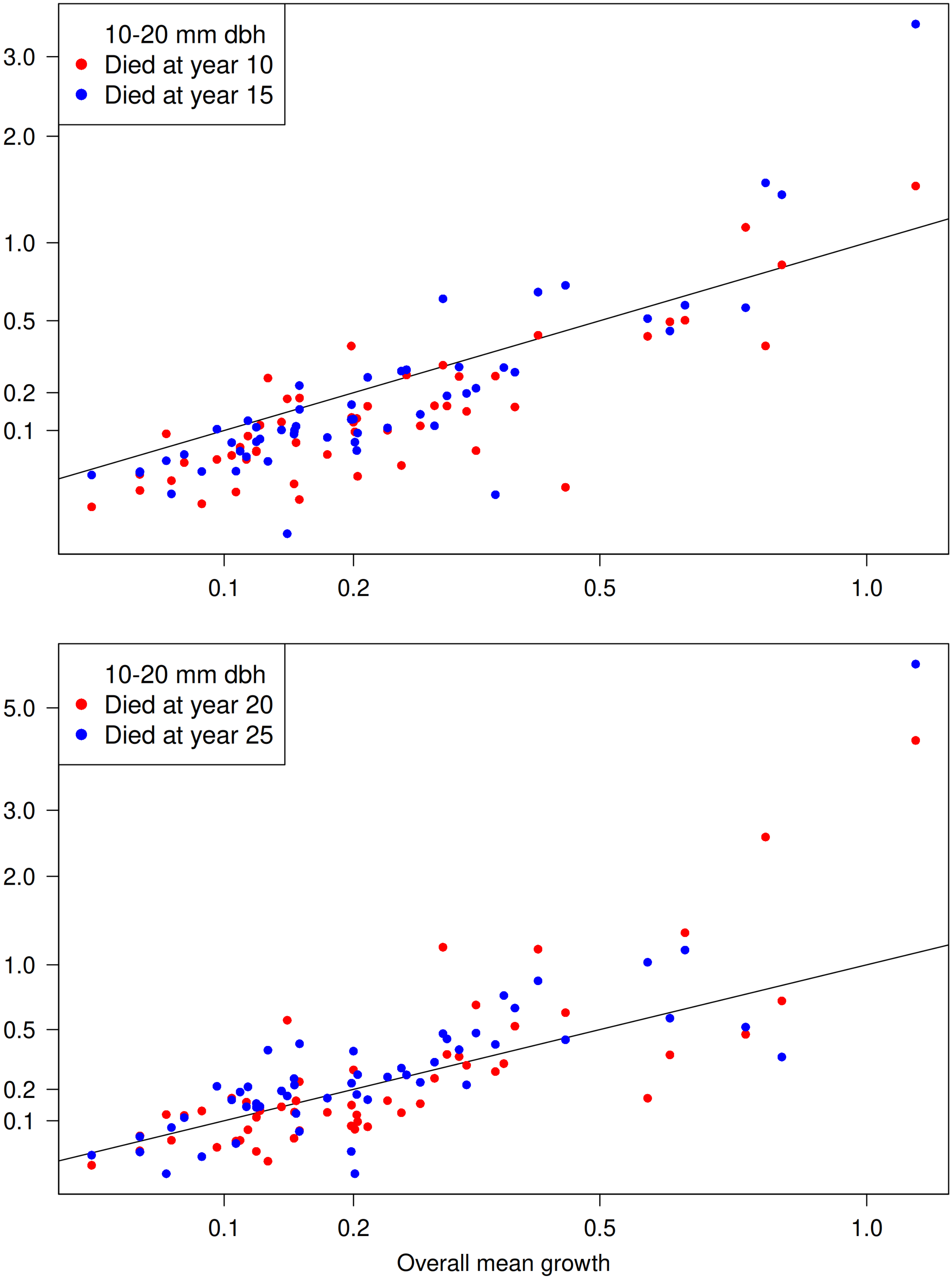

10-20 mm dbh
● Died at year 10
● Died at year 15
3.0
2.0
1.0
0.5
0.2
0.1
0.1
0.2
0.5
1.0
10-20 mm dbh
● Died at year 20
● Died at year 25
5.0
3.0
2.0
1.0
0.5
0.2
0.1
0.1
0.2
0.5
1.0
Overall mean growth

Figure 6

Appendix