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Estimating root longevity at sites with long periods of low root mortality

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Abstract

Minirhizotron technique is capable of providing median root longevity. The use of the median longevity might overestimate root longevity if the distribution of survival times is very skewed or irregular, as is the case at sites where root mortality is very low during the long winter. In this paper we illustrate the case theoretically and compare that with field observation in northern Sweden to show an alternative procedure for such sites. Hypothetical root cohorts were constructed to investigate and show some technical problems with estimating median root longevity at a Swedish northern site where root mortality is very low during long winter time (8 months), and to investigate whether these problems could be overcome by discarding winter time from the survival analysis and include only the growing season in which the roots are at risk of mortality. Authentic root data, gathered in a minirhizotron study at such a site, were analysed on a whole year basis and on season basis. By analysing longevity based only on the season when there is a risk for root death, the median longevity became a more reliable estimate of the true mean longevity. When this method was applied to root data from northern Sweden, the estimated root longevity in different treatments became between 17% lower and 8% higher compared to the longevity estimated on a whole year basis. We conclude that the reliability of the median longevity as an estimate of the true mean longevity can be increased by basing the survival analysis only on the parts of the year when fine roots are at risk of mortality at sites with long winter and low root mortality.

Introduction

Fine root turnover is of vital importance when assessing nutrient and carbon fluxes in a plant-soil system, as the fluxes below ground might be higher than those above ground (Vogt et al., 1986; Fahey and Hughes, 1994). Our insight into root dynamics, i.e., root production, mortality and longevity, has increased dramatically due to the development of the minirhizotron technique (Hendrick and Pregitzer, 1993; Majdi and Kangas, 1997; Wells and Eissenstat, 2001; Johnson et al., 2001; Tierney and Fahey, 2001). Transparent plastic tubes (minirhizotrons), into which fits a camera, are inserted into the soil. Through repeated observations of fixed areas outside the minirhizotron, individual roots can be followed from birth to death. Computer software, e.g., RooTracker (Craine and Tremmel, 1995), makes it possible to keep track of length, width, type, order and age at death for

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thousands of individual roots. From these data it is possible to calculate fine root turnover (yr^{-1}) either as root length production ($cm\ yr^{-1}$) divided by observed root length (cm) (c.f. Hendrick and Pregitzer, 1993) or by a direct evaluation of recorded ages at death of individual roots (c.f. Tierney and Fahey, 2001), as root turnover is the inverse of mean root longevity.

To calculate the mean longevity one must follow all roots until they die and calculate the mean value of these roots' ages at death. As there are often some roots that live a long time, the study times need to be equally long. All new roots that can be observed meanwhile are of no use unless we wait for all these to die as well. A common way (c.f. Tierney and Fahey, 2001) of estimating the mean longevity without knowing the exact age at death for all roots is to use the median age at death, i.e., the time by which 50% (by number, length or weight) of the roots have died. This is possible as long as at least 50% of the roots have known values of age at death. A Kaplan-Meier survival analysis results in a root survival probability plot, where the ages of roots still alive at the last observation date (censored values) also are taken into consideration (Kaplan and Meier, 1959; Altman, 1991; Fox, 1993). The median longevity is a satisfactory estimate of the mean longevity as long as the mortality of roots is not variable over time, i.e. the distribution of age at death must not be too skewed or irregular.

In the following, we first illustrate problems associated with the use of the median longevity at sites where there are long periods of very low mortality by discussing simple hypothetical root cohorts. We also suggest an alternative procedure to overcome this problem, and we apply the procedure to authentic root data from a site in northern Sweden that has very low root mortality during the eight-month long winter.

Materials and methods

Hypothetical root cohorts

In order to illustrate problems associated with the use of the median root longevity, purely hypothetical root cohorts were used as examples. These cohorts were given a constant mortality (constant number of roots per week) during specified parts of the year, contrasting to a zero-mortality for other parts of the year.

Authentic root data

We used the minirhizotron technique to gather information on root dynamics in the mineral soil of a spruce forest in Flakaliden, Northern Sweden. This site (64°07′ N, 19°27′ E) is characterised by cool summers and long cold winters. The growing season lasts approximately 120 days and more than one third of the annual precipitation of 600 mm falls as snow. An optimum fertilisation experiment was started in 1987, and we investigated root dynamics in control (C) plots, irrigated (I) plots (irrigation supplied as needed to maintain a soil water potential above −100 kPa) and irrigation plus liquid fertilisation (IL) plots (irrigation with a complete nutrient solution added to the irrigation water). A further description of the site is given by Linder (1995). Five minirhizotrons per plot were installed in the mineral soil of three plots per treatment in 1994, and data were recorded during May–September 1997 and 1998. In total, 3345 individual roots were followed and analysed by applying a Kaplan-Meier survival analysis. A further description of the rhizotron set-up and the results is given by Majdi (2001). Relevant in this context is that the mortality during the 8-month long winter between our recordings in September and May was very low. Of the roots present at the beginning of the winter, 98% (C), 97% (I) and 92% (IL) were still alive in the spring, making the use of the median longevity problematic.

Data evaluation

The data evaluation procedure suggested here means that only parts of the year when roots are at a reasonable risk of dying are included in the data analysis. This means that if root mortality is restricted to the four-month long growing season, root longevity should be counted as number of 'growing season months' (GSM) survived rather than total number of months survived.

Results and discussion

Hypothetical root cohorts

Looking at single hypothetical cohorts of roots, it is obvious that the median might be problematic to use when there is a long period of low mortality (Figure 1a–b). The median longevity of a cohort born early in the season, of which just over 50% die before winter, would greatly underestimate the mean longevity, whereas the opposite is true for a somewhat later cohort of which just over 50% survive until and over the winter (Figure 1a). The same effect can be seen for cohorts with marginally contrasting mortality. If the mortality during the growing season for the early cohort decreased by 17%, the mean longevity would increase by 28345% (Figure 1b). This is of course an extreme case, but the possibility of such effects should be enough to merit extreme caution. When all root cohorts observed at a site are analysed together regardless of birthdate, the problem appears to be smaller. If the inactive period is not too long, death ages of the early cohort overlap those of late cohorts, so that overall mortality becomes more or less constant (Figure 1c). However, if the period of very low mortality is 8 months, the overall mortality is still not constant over time (Figure 1c). The median again presumably overestimates or underestimates the mean depending on the relative location of the inactive period compared to when the median time is reached (c.f. Figure 1a and 1b). In order to estimate mean longevity at such sites, it is evidently not sufficient to hope that early and late cohorts together will result in a constant-slope survival curve.

If median longevity is to be used as an estimate of the mean longevity, the data clearly need to be adjusted in some way in order to achieve a constant mortality. If low winter mortality is the problem, the obvious solution would appear to be to take away the winter. Just as mean production over the year can be calculated from mean biomass over the year and longevity in years, the production during the growing season can be calculated from the mean biomass and longevity based on the same season. For simplicity single cohorts were considered again (Table 1). If a single cohort with a given mortality is produced each year in the same way, it would result in a standing biomass that is variable within the year but not between years. Considering a June cohort as in Table 1, standing biomass is highest in

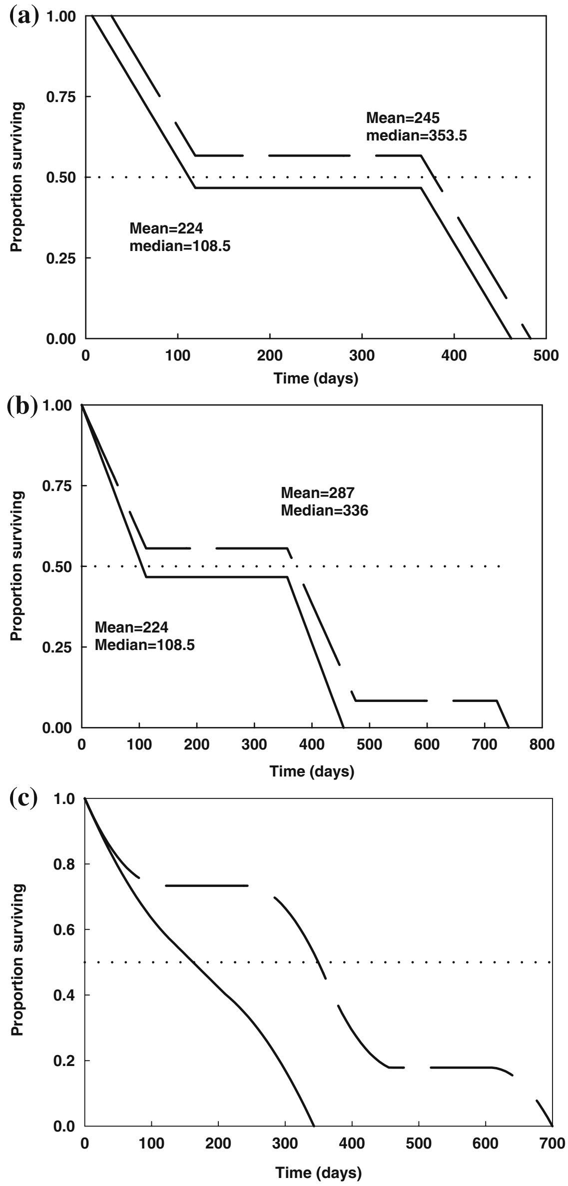

Figure 1. Fine root survival plots of hypothetical root cohorts. Mean and median values of longevity was calculated from age at death for all roots in the cohort. (a) single cohorts of 30 roots born at the beginning (solid line) or end (broken line) of June. Mortality is constantly 1 root week^{-1} June-September. (b) Solid line as in Figure 1a, broken line shows a similar cohort with a lower mortality (0.83 roots week^{-1}). (c) Multiple root cohorts (1 cohort week^{-1}) of the same sort as in Figure 1a. Root production and mortality between March and October (solid line) or between June and September (broken line). Dotted line at 50% survivorship.

Table 1. Living biomass (mm cm^{-2}) and age (months or ''growing season months'' (GSM)) for two hypothetical root cohorts followed from cohort birth until all roots of the cohort were dead after 25 months. Root production: 9 mm cm^{-2} yr^{-1} (in June or August), root mortality: 1 mm cm^{-2} $month^{-1}$ (from June to September). † denotes the death of 1 mm cm^{-2}. Total standing biomass at each month was calculated assuming the same root production and mortality as in previous years. Seasonal basis means that only the four growing season months are considered and winter time is discarded.

Yearly basis							Seasonal basis						
	June-cohort			August-cohort				June-cohort			August-cohort		
	Cohort living biomass	Cohort age	Total standing biomass	Cohort living biomass	Cohort age	Total standing biomass		Cohort living biomass	Cohort age (GSM)	Total standing biomass	Cohort living biomass	Cohort age (GSM)	Total standing biomass
June	9		15			10	June	9		15			10
July	8	1†	12			8	July	8	1†	12			8
Aug	7	2†	10	9		15	Aug	7	2†	10	9		15
Sep	6	3†	8	8	1†	12	Sep	6	3†	8	8	1†	12
Oct	6	4	8	8	2	12	June	5	4†		7	2†	
Nov	6	5	8	8	3	12	July	4	5†		6	3†	
Dec	6	6	8	8	4	12	Aug	3	6†		5	4†	
Jan	6	7	8	8	5	12	Sep	2	7†		4	5†	
Feb	6	8	8	8	6	12	June	1	8†		3	6†	
Mar	6	9	8	8	7	12	July	0	9†		2	7†	
Apr	6	10	8	8	8	12	Aug				1	8†	
May	6	11	8	8	9	12	Sep				0	9†	
June	5	12†		7	10†								
July	4	13†		6	11†								
Aug	3	14†		5	12†								
Sep	2	15†		4	13†								
Oct	2	16		4	14								
Nov	2	17		4	15								
Dec	2	18		4	16								
Jan	2	19		4	17								
Feb	2	20		4	18								
Mar	2	21		4	19								
Apr	2	22		4	20								
May	2	23		4	21								
June	1	24†		3	22†								
July	0	25†		2	23†								
Aug				1	24†								
Sep				0	25†								

June (15 mm cm^{-2}; simply add all biomass values for June in Table 1, i.e. the biomass from the current year cohort + the biomass from earlier years' cohorts that would still be alive if they behaved similarly to the current cohort), and gradually decreases in July (12), August (10) and September (8), and finally stays constant over winter (8) as there is no winter mortality in this case.

For the August cohort, the peak is in August and the biomass during wintertime is higher, leading to a higher mean biomass (Table 2). As the longevity is also higher due to the greater proportion of roots living over the winter, the calculated production is in agreement with the stipulated production in both cases (Table 2). However the median longevity underestimates or overestimates the mean longevity quite substantially (7–18%) for the reasons discussed previously (Figure 1). Table 2 also illustrates that when only months of the growing season (June–September) are considered, the calculated pro-

Table 2. Mean values of longevity and standing biomass, and mean root production calculated from these values. Median longevity is given for comparison with the true mean longevity. All values are based on Table 1. Mean longevity is the mean value of root ages at death as denoted by † in Table 1 and mean standing biomass is the mean value of monthly standing biomass in Table 2. Calculated production is mean standing biomass divided by mean longevity. For the calculations on a yearly basis, a year is considered to consist of 12 months. For the calculations on a seasonal basis, a year is considered to consist of 4 growing season months (GSM). Median value of longevity is the median death age in Table 2 (the age of the fifth death denoted by † in this case).

	Yearly basis		Seasonal basis	
	June-cohort	August-cohort	June-cohort	August-cohort
Mean values				
Longevity (months or GSM)	12.1	15.7	5	5
Longevity (years)	1.009	1.305	1.25	1.25
Standing biomass (mm cm^{-2})	9.08	11.75	11.25	11.25
Calculated production (mm cm^{-2} year^{-1})	9	9	9	9
Median value				
Longevity (months or GSM)	13	13	5	5
Longevity (years)	1.08	1.08	1.25	1.25

duction based on seasonal mean values is still correct. The longevity measured as "growing season months" (GSM) survived is naturally shorter, but the mean biomass during these months is correspondingly higher. This hypothetical example shows that when correct mean values are known, calculations based on only parts of the year give the same results as calculations on a whole year basis. In this case, this also makes the median a more reliable estimate of the mean, as the distribution of ages at death is now more symmetrical. It is important to remember that the reason for "overlooking" inactive parts of the year is just to adjust data in order to achieve a symmetrical distribution of death ages. The adjusted data might not be suitable for further statistical testing among strata.

Authentic root data

The very low winter mortality in Flakaliden (results not shown) resulted in a Kaplan-Meier survival probability plot with a long flat portion (Figure 2a) similar to the plots in Figure 1. Obviously the median longevity in this case may overestimate or underestimate the true mean longevity, similarly to the example shown in Figure 1.

When we disregarded the inactive period between the last autumn observation and the first spring observation (230 days) in accordance with

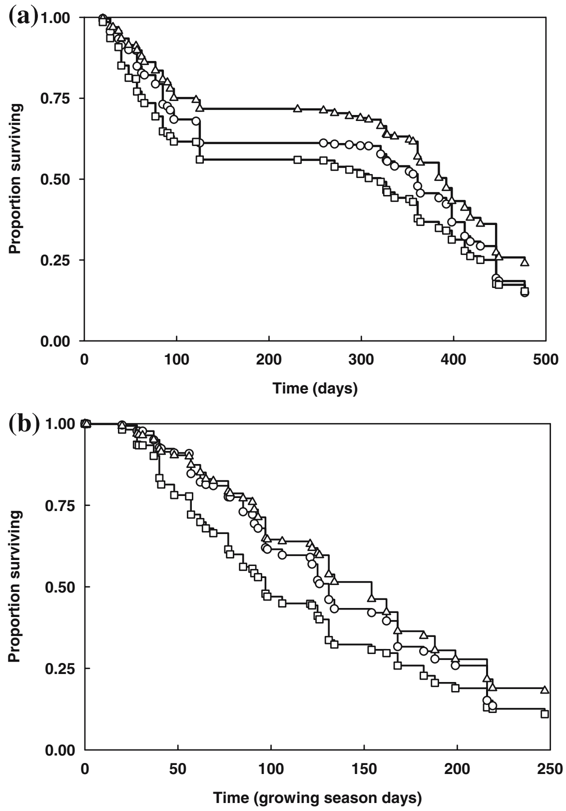

Figure 2. Survival probability plots for roots in the mineral soil in Flakaliden, northern Sweden. Control plots (circles), irrigated plots (triangles) and fertilised plots (squares). (a) Original data, age at death based on real age. (b) adjusted data, age at death as growing season days (GSD) when ignoring the winter period (230 days) for roots surviving the winter.

Table 3. Median longevity calculated on a whole year basis and seasonal (135 "growing season days" (GSD) yr^{-1}) basis for fine roots in the mineral soil in Flakaliden site. C = control plots, I = irrigated plots, IL = irrigated and fertilised plots.

	C		I		IL	
	Year	Season	Year	Season	Year	Season
Longevity (days or GSD)	361	131	392	154	321	97
Longevity (years)	0.99	0.97	1.07	1.14	0.88	0.72
Difference	−2%		+ 7%		−18%	

the suggested season-based calculations proposed above, the resulting survival probability plot became one of constant mortality (Figure 2b). Note that the flat part was not simply cut out from the curve, but that the curve was the result of a completely new survival analysis. The resulting shift in the median value depended on the relative location of the flat portion of the curve in Figure 2a (c.f. Figure 1a and 1b). In control plots there was no difference between the methods, whereas in I and IL there was a rather large difference (Table 3). Any difference in longevity would result in the same relative difference in calculated root production. We believe that the season-based estimate is the better of the two in this case.

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