



## Growth ring analysis of multiple dicotyledonous herb species—A novel community-wide approach

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### Abstract

Longevity is a key demographic characteristic of herbaceous plants, but often unknown. While root or rhizome growth ring analysis may allow assessment plant longevity directly and conveniently, so far it has only been used in a few case studies of herbaceous dicotyledonous species. To evaluate whether growth ring analysis is applicable to a large spectrum of herbaceous dicotyledonous plant species, we used plant communities of varying species richness in a 12-year-old grassland biodiversity experiment (Jena Experiment). Cross-sections of the oldest available part of the plants were analysed for all available dicotyledonous perennial herb species ( $S = 37$ ), which represented three functional groups: legumes, small herbs and tall herbs. We studied 1664 individuals representing the genet in clearly distinguishable plant individuals, and the ramet in clonally growing plant species.

Roots of eleven species with permanent primary root were harvested. They showed clearly visible growth rings. Longevity was extended with a mean age of 4.0 years ( $SE = 0.3$ ). Seven species, which also had a permanent primary root, showed less distinct growth rings. They were shorter-lived (mean age 3.0 years ( $SE = 0.3$ )). In six species with obligate clonal growth mostly rhizomes were sampled, but individuals were still identifiable due to their growth habit. For these species growth rings were clearly visible. Longevity of rhizomes was extended (mean age 3.3 years ( $SE = 0.5$ )). In 13 species with obligate clonal growth also rhizomes were sampled, but plant individuals were not identifiable. For these species longevity was low (mean age 2.1 years ( $SE = 0.2$ )). Community mean age was significantly lower when small herbs were present and higher when tall herbs were present, while legumes had no effect on community mean age. In summary, anatomical analysis of roots and rhizomes is a suitable tool to study the population age structure of a large spectrum of perennial dicotyledonous herbaceous species and therefore opens new perspectives for demographic studies at the community level.

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## Introduction

Plant community assembly is driven by the dynamics of plant populations. One important mechanism is demographic storage. It describes the buffering of populations against adverse environmental conditions by forming less sensitive life stages (Warner & Chesson 1985). Seeds stored in the soil and well established adults are more likely than other demographic stages to persist during harsh environmental conditions and may ensure the survival of a plant population. Methods of seed bank analysis are well established (Thompson, Bakker, & Bekker 1997). In contrast, less is known about the longevity of adult individuals in perennial herbaceous plant species. While wood-anatomical methods are well established to determine the age of tree species in temperate regions (Schweingruber 2007), it is a challenge to determine the longevity of herbaceous dicotyledonous species. This is reflected in a wide range of methods applied for age determination in different case studies (see review in de Witte & Stöcklin 2010), while systematic studies on the age structure of populations of a larger number of herbaceous dicotyledonous species are still lacking.

Methods used for plant age determination can be classified into direct and indirect methods (Schweingruber & Poschlod 2005, de Witte & Stöcklin 2010). Direct methods observe the fate of plant individuals for a prolonged time in permanent plots or by marking plant individuals (Tamm 1948, Roach 2012). These methods are reliable, but very laborious and not feasible in dense vegetation and in studies with many species. In some species it is also possible to use morphological growth markers like shoot scars (Klimešová & de Bello 2009, Štastná, Klimešová & Doležal 2012, Klimešová, Doležal & Štastná 2013). Indirect methods include the size-stage approach (Gatsuk, Smirnova, Vorontzova, Zaugolnova, & Zhukova 1980) and the use of population matrices (e.g. Caswell & Salguero-Gómez 2013), whereby the latter method can only be used for populations and is not suitable to determine the age of individuals.

More recently, the application of growth ring analysis has been extended from tree species to herbaceous species, which may also form annual growth rings (Landolt 2010). Annual growth rings are caused by the formation of large vessels during fast growth in spring, while smaller vessels are formed later in the growing season during slower growth. Dietz and Ullmann (1997) showed that 31 species form annual growth rings, and Landolt (2010) and the Xylem database (<https://www.wsl.ch/dendropro/xylemdb/>) (Accessed 27 October 2016) confirmed the formation of annual growth rings for many additional dicotyledonous species. These studies indicate that actually the majority of dicotyledonous species in non-tropical regions form growth rings. It was also demonstrated by seeding experiments that growth rings are robust markers of annual growth (Schweingruber & Poschlod 2005, von Arx & Dietz 2006).

Stem anatomical traits may also archive variation in growth conditions caused by the environment. So far, the indicative value of plasticity in stem anatomical characteristics has only rarely been explored in ecological studies of herbaceous plants. Only recently, plasticity in xylem anatomy in response to environmental variation such as soil moisture availability, temperature constraints or fertilization has been studied in selected perennial forb species (von Arx, Archer, & Hughes 2013; Olano, Almería, Eugenio, & von Arx, 2012; Dee & Palmer 2016).

One major drawback of growth ring analysis, however, is that sampling is destructive. For herbaceous species the oldest preserved tissue is located in the root crown. Therefore, plants have to be excavated for anatomical analysis. Another challenge is that many herbaceous species grow clonally and do not have a long-lived primary root (Harper 1977). In clonally growing plants, the genet comprises a series of ramets, which are partly or completely independent from each other. Essentially, longevity of a plant genet and life span of a ramet are independent from each other. Especially in clonal plants the primary root often dies off or is undiscoverable. In these cases not the genet age but the ramet age is determined. Thus, information on the age of ramets only provides limited information on the life history of a genet.

Case studies with selected species compared the age structures of *Helianthemum nummularium* (Čelak) Holub. and *Lotus corniculatus* L. in differently managed calcareous grasslands (Poschlod, Hoffmann, & Bernhardt-Römermann 2011), of *Lupinus laxiflorus* Dougl., *Penstemon venustus* Dougl. and *Rudbeckia occidentalis* Nutt. along altitudinal gradients (von Arx et al. 2006), between the native *Rumex crispus* L. and the invasive *Bunias orientalis* L. (Dietz & Ullmann 1998) and the invasive *Heracleum mantegazzianum* Sommier et Levier in native and invaded ranges (Pergl, Perglová, Pyšek, & Dietz 2006). Nobis and Schweingruber (2013) used ring counts from three individuals per species to derive mean adult ages for 708 herbaceous species and related these data to environmental factors. These studies showed that growth ring analysis may be valuable for ecological research. The usefulness of growth ring analysis for ecological studies at the community level, however, requires the applicability of this method to a major proportion of species within a community. All preceding studies used carefully selected species or data of many species were assembled from different case studies. Therefore, it is uncertain to which extent growth ring analysis can be applied in a community-wide approach, for example, if too many species or a larger portion of individuals of particular species within a community do not show growth rings.

To test the applicability of growth ring analysis in the context of community ecology, we used 12-year-old experimental grasslands of varying species richness and composition (Jena Experiment, Roscher et al. 2004) and applied growth ring analysis to all available perennial herb species, which represented three plant functional groups (legumes, small herbs and tall herbs). The major goal of our study was

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