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# Common leaf life span of co-dominant species in a continuously grazed temperate pasture

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## Abstract

Short leaf life span is thought to be associated with low construction costs and consequently short payback times. Frequent defoliation could decrease the available payback time and force individuals to decrease construction costs to maintain a positive carbon balance. Therefore, we hypothesize that dominant species of frequently grazed pastures show similar and short leaf life span. Leaf life span was measured on four co-dominant species, two grasses and two dicots, in a pasture that was intensively grazed by cattle for six years. Leaf life span was analysed in terms of its components: the phyllotherm and the number of live leaves. Phyllotherm and number of live leaves were determined in eight to 20 individuals of *Lolium perenne*, *Poa pratensis*, *Taraxacum officinale* and *Trifolium repens*, during autumn 2006 and autumn and spring 2007. Leaf life span was estimated as the product of phyllotherm and number of live leaves. After critically assessing five operational definitions of leaf death, a leaf was considered alive during the time elapsed between its appearance and the senescence of 25% of its area. In general, leaf life span did not differ between species nor was there clear evidence for seasonal effects. The leaf life span ranged between 400 and 520 growing degree days (base temperature: 4 °C). The similarity of leaf life span between species was based on different mechanisms: dicots had shorter phyllotherms and more live leaves than grasses. Observed leaf life spans were short when compared with data from plants growing in less disturbed habitats, but similar to the dominant species of grazed grasslands with a similar disturbance regime. The similarity of leaf life spans resulted in a common community-level leaf life span. It is suggested that this trait could control community-scale biogeochemical features, such as the residence time of carbon in the aboveground structural biomass of this leafy ecosystem.

## Zusammenfassung

Eine kurze Blattlebensdauer wird im Allgemeinen mit niedrigen Blatt-Konstruktionskosten und folglich auch kurzen Rückerstattungszeiten in Verbindung gebracht. Häufige Entblätterung könnte die vorhandene Rückerstattungszeit verkürzen und die Pflanzen dazu zwingen, ihre Blatt-Konstruktionskosten zu verringern, um einen positiven Kohlenstoffhaushalt zu erhalten. Daher stellen wir die Hypothese auf, dass dominante Arten häufig beweideten Graslands eine ähnliche und kurze Blattlebensdauer aufweisen. Die Blattlebensdauer von vier co-dominanten Arten, zwei Grasarten und zwei dikotylen Arten, wurde gemessen. Diese wuchsen auf einer Weide, die seit sechs Jahren intensiv von Rindern beweidet wurde. Die Blattlebensdauer wurde bezüglich ihrer Komponenten Phyllotherm und Anzahl der lebenden Blätter analysiert. An acht bis 20 Individuen der Arten *Lolium perenne*, *Poa pratensis*, *Taraxacum officinale* und *Trifolium repens* wurden das Phyllotherm und die Anzahl der lebenden Blätter im Herbst 2006 und im Frühjahr und Herbst 2007 bestimmt. Die Blattlebensdauer wurde als das Produkt von

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Phyllotherm und Anzahl der lebenden Blätter berechnet. Nachdem verschiedene operationale Definitionen der Blattlebensdauer kritisch geprüft wurden, wurde der Zeitraum zwischen dem Erscheinen des Blattes und der Seneszenz von 25% der Blattfläche als Blattlebensdauer festgelegt. Im Allgemeinen unterschied sich die Blattlebensdauer weder zwischen den Arten noch gab es deutliche Anzeichen für saisonale Effekte. Die Blattlebensdauer betrug 400 bis 520 Gradtage (Basistemperatur: 4 °C). Die Ähnlichkeit der Blattlebensdauer verschiedener Arten basierte auf unterschiedlichen Mechanismen: die beiden dikotylen Arten hatten ein kürzeres Phyllotherm und mehr lebende Blätter als die beiden Grasarten. Die beobachteten Blattlebensdauern waren kurz im Vergleich zu Beobachtungen anderer Autoren in weniger gestörten Habitaten, aber ähnlich denen dominanter Arten von beweidetem Grasland mit einem ähnlichen Störungsregime. Die Ähnlichkeit der Blattlebensdauern führte zu einer uniformen Blattlebensdauer auf Ebene der Pflanzengemeinschaft. Wir vermuten, dass dieser Sachverhalt auch biogeochemische Eigenschaften der Pflanzengemeinschaft bestimmen kann, wie zum Beispiel die Verweildauer von Kohlenstoff in der oberirdischen strukturellen Biomasse dieses blattreichen Ökosystems.


***Keywords:*** Leaf turnover; Grassland; Phyllotherm; Phyllochron; Leaf number; *Lolium perenne*; *Poa pratensis*; *Taraxacum officinale*; *Trifolium repens*

## Introduction

Leaf life span ($t_L$) is a trait of great ecological meaning (Chabot & Hicks 1982; Kikuzawa & Lechowicz 2011). Across species gradients, short leaf life span is associated with both low leaf mass per unit area and high photosynthetic capacity per unit leaf mass (Reich, Walters, & Ellsworth 1992; Wright et al. 2004). Conversely, long leaf life span is related to a longer payback time, defined as the relation of construction costs to daily photosynthesis (Williams, Field, & Mooney 1989; Navas et al. 2003; Coste, Roggy, Schimann, Epron, & Dreyer 2011). Leaf life span has therefore been considered indicative of the species' trade-off between productivity (rate of resource acquisition) and persistence (resource retention) (Westoby, Falster, Moles, Vesk, & Wright 2002; Hikosaka 2005). Further, long leaf life span is associated with a long residence time of nutrients in plants (Escudero, Arco, Sanz, & Ayala 1992; Eckstein, Karlsson, & Weih 1999; Kazakou, Garnier, & Gimenez 2007). Likewise, carbon residence time in aboveground biomass of 'leafy' communities may be controlled by leaf turnover, as most leaf carbon is structural and not recycled during senescence (Robson & Deacon 1978). In consequence, the leaf life span of the species that dominate a community has substantial implications for the biogeochemistry of the whole ecosystem, particularly in those dominated by herbaceous plants, such as grasslands.

Across species leaf life span can vary from weeks to years (Wright et al. 2004). Besides this interspecific variation, there is also evidence for phenotypic plasticity of leaf life span in response to ontogenetic effects (Duru & Ducroqc 2000a), seasonality (Vine 1983; Duru & Ducroqc 2000b), light regime (Vincent 2006; Hikosaka 2005), and nutrient availability (Duru & Ducroqc 2000b; Al Haj Khaled, Duru, Theau, Plantureux, & Cruz 2005; Kazakou et al. 2007). Conversely, the influence of the defoliation regime upon the leaf life span has received less attention. This is particularly important for grasslands, relatively disturbed habitats with major disturbances including grazing and mowing.

Ryser and Urbas (2000) found a negative correlation between leaf life span and ecological indices of disturbance frequency, across several grass species, noting that the nutrient conservation often associated with greater longevity was superimposed by the influence of disturbance frequency. This suggests that long-lived leaves would be disadvantageous when leaf survival is limited by regular disturbance, possibly because (parts of) leaves are lost from the plant before complete pay-back of construction costs. Accordingly Lemaire, Da Silva, Agnusdei, Wade, and Hodgson (2009) argue that long-lived leaves have a higher probability of defoliation than short-lived leaves under a given grazing intensity. Further, it is proposed that severe disturbance generally leads to lower functional diversity (*e.g.* intermediate disturbance theory: Grime 1973; Biswas & Malik 2010; Duru, Theau, & Cruz 2012). For these reasons, we hypothesize that the leaf life span of the dominant species in a habitat with frequent defoliation, such as intensively grazed grassland, lies in a narrow range and is rather short.

Many grassland species show a succeeding type of leaf production (Kikuzawa 1984) and progressive senescence (Leopold 1961), where plants, mainly consisting of leaves, have growing and senescing leaves at the same time. This mechanism keeps the morphology of plants in the vegetative state relatively unaltered and leads to a close interrelationship between the leaf life span, the phyllotherm ($t_{Phyll}$) – the delay between the appearance of successive leaves on a tiller expressed in thermal time – and the number of live leaves on the tiller ($n_L$). These dynamics have been thoroughly investigated in grass species (Lemaire & Chapman 1996; Matthew et al. 2001), and the equivalence $t_L = t_{Phyll} * n_L$ has been validated by Lemaire and Agnusdei (2000) for C3 and C4 grasses of a grazed community. For dicotyledonous plants with a succeeding type of leaf production/appearance and progressive senescence the same dynamics should be expected.

In this study, we tested the prediction of similar and short leaf life span for four co-dominant species, two perennial grasses and two dicots, which co-occurred in an intensively managed temperate humid grassland paddock. Some of these