

## Intraspecific variability in leaf traits strongly affects alder leaf decomposition in a stream

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### Abstract

This study assessed the intraspecific variability of senescent leaves of alder (*Alnus glutinosa* Gaertn.) and the effects of this variability on leaf decomposition in streams. Leaves were collected at five geographically distant locations in Europe. We analyzed 10 batches of leaf samples for seven quantitative leaf traits as well as leaf decomposition rate in coarse and fine mesh bags exposed in a single stream. The geographic origin of leaf samples largely explained the observed variation in litter quality and decomposition rate. Phosphorus (0.034–0.187%) and lignin (3.9–18.7%) concentrations in leaves varied widely. Together, these two traits accurately predicted leaf decomposition rate ( $r^2 = 84.1\%$ ). Intraspecific variation in leaf decomposition rate was within a range similar to that reported for interspecific variation among co-occurring riparian plant species in Europe. Our study demonstrates extensive intraspecific variability in leaf traits on a continental scale, which can have enormous effects on major ecosystem processes such as leaf decomposition.

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### Zusammenfassung

Die vorliegende Studie untersucht die Variabilität von Erlenfalllaub (*Alnus glutinosa* Gaertn.), das an fünf Orten von Schweden bis Portugal gesammelt wurde, und ihren Einfluss auf die Streuzersetzung. Wir analysierten zehn Blattproben in Hinblick auf sieben quantitative Blatteigenschaften und die Abbauraten in groben und feinen Netzbeuteln nach Ausbringung in einem Fluss. Die geographische Herkunft der Blattproben erklärte weitgehend die Variabilität der Streuqualität und Blattabbaurate. Die Konzentrationen von Phosphor (0.034–0.187%) und Lignin (3.9–18.7%) in den Blättern variierten stark. Zusammen bestimmten diese beiden Faktoren die Laubabbaurate sehr genau ( $r^2 = 84.1\%$ ). Der intraspezifische Variationsbereich der Blattabbaurate ähnelte dem interspezifischen Variationsbereich für gemeinsam auftretende europäische Ufergehölzarten. Unsere Untersuchung zeigte große intraspezifische Variabilität der Blatteigenschaften im kontinentalen Maßstab, was erhebliche Auswirkungen auf wichtige ökosystemare Prozesse wie die Streuzersetzung haben kann.

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## Introduction

Plant functional traits are relevant to examine how plants respond to their environment and conversely how they alter ecosystem properties (Lavorel & Garnier, 2002; Violle et al., 2007; Westoby & Wright, 2006). Since leaves play a central role in the exchange of energy and nutrients between plants and their environment, particular attention has been paid to the enormous interspecific differences in many leaf traits (Wright et al., 2004). Complementary issues on variability in leaf traits within species have been much less extensively addressed, conceivably because current evidence supports the general idea that intraspecific variations are generally much smaller than interspecific differences (Garnier et al., 2001; Roche, Díaz-Burlinson, & Gachet, 2004).

Intraspecific variability in leaf traits can alter organic matter dynamics in soil and streams. Some investigators have found that decomposition rate of senescent leaves varies among individual populations, plants, and leaves (Sariyildiz & Anderson, 2003; Silfver, Mikola, Rousi, Roininen, & Oksanen, 2007; Treseder & Vitousek, 2001). These variations were attributed to differences in litter quality, a notion encompassing a suite of physical and chemical traits, which affect leaf utilization by consumers (Cadish & Giller, 1997). Besides being controlled by litter consumers and abiotic factors, leaf decomposition rate is thus also regulated intrinsically by nutrient (N, P) content and concentration of refractory compounds such as lignin and phenolics (e.g., Enriquez, Duarte, & Sand-Jensen, 1993; Gessner & Chauvet, 1994; Ostrofsky, 1997; Valachovic, Caldwell, Cromack, & Griffiths, 2004).

While researchers have focused on genetic and environmental determinants of intraspecific variability in leaf traits (e.g. Cornelissen & Stiling, 2005; Koricheva, Larsson, Haukioja, & Keinänen, 1998; Madritch & Hunter, 2005; Whitham et al., 2006), only a few studies have investigated temporal and spatial variation patterns. Large variations may occur in widely distributed species, the rationale being that strong biogeographic, climatic and ecological gradients would promote genetic differentiation and phenotypic plasticity in plants (Cordell, Goldstein, Mueller-Dombois, Webb, & Vitousek, 1998). Since alder (*Alnus glutinosa* Gaertn.) is a major component of riparian vegetation in Europe (Prat, Leger, & Bojovic, 1992), it can be used to assess intraspecific variability at the continental scale. Alder supplies stream food webs with large amounts of deciduous leaves, a high quality substrate to microbial decomposers and detritivore invertebrates (Hieber & Gessner, 2002; Lecerf, Dobson, Dang, & Chauvet, 2005).

This study was designed to assess the extent of variation in quality and decomposition rate of senescent alder leaves across Europe. More specifically we

determined seven leaf traits in leaf samples originating from five geographically distant locations and examined the relationships between leaf traits and leaf decomposition rate in coarse and fine mesh bags exposed a single stream. Variation among locations was compared to local sources of variation assessed in each location; in addition, we compared intraspecific variation in alder leaf decomposition rate observed in this experiment to the interspecific variability reported in previous studies.

## Materials and methods

### Origin, selection and collection of leaf litter

Senescent leaves of alder were collected in European sites near the cities of Umeå (Sweden), Manchester (England), Lucerne (Switzerland), Toulouse (France) and Coimbra (Portugal). The five sampling sites were located far apart from each other (> 650 km) and encompassed a broad latitudinal gradient (40.3–64.1°N). All leaves were collected in autumn 2002, with the exception of France, where an additional collection was made in autumn 2003. Senescent leaves were either picked from trees or collected from the forest floor just after leaf fall. After air-drying to constant weight, the leaves collected in Umeå, Manchester, Lucerne, and Coimbra were sent to Toulouse, France, for determination of leaf traits in the laboratory and decomposition rates in a single stream.

Two contrasting batches of leaf samples were collected from a single area at each location with the aim to distinguish the intraspecific continental variability from the local sources of variation. We applied different criteria in each location for the leaf selection to increase the chances of encompassing all major sources of sampling-induced variability (Table 1). Outcomes from previous studies suggest that the date of leaf collection and discrimination among leaf types or tree habitats while sampling are important sources of intraspecific variation in leaf traits (Cornelissen et al., 2000; Cornelissen & Stiling, 2005; Gill, Amthor, & Bormann, 1998; Sariyildiz & Anderson, 2003; Tibbets & Molles, 2005; Treseder & Vitousek, 2001). In this experiment, two leaf samples were collected from a single alder stand in Sweden at a 1-month interval. In France, leaves collected in autumn of 2002 were compared to those from the same trees collected 1 year later, after an exceptional summer heat wave. The two leaf samples originating from the same sets of trees in England and Switzerland differed according to their physical traits (Table 1), with the sun leaves being smaller and thicker than the shade leaves (Sariyildiz & Anderson, 2003). In Portugal, the leaves were collected from two nearby alder stands growing in different habitats (streamside and floodplain) and hence may

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