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Is climate warming advantageous for plants with untoothed leaves?

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Abstract

The percentage of dicotyledonous species with untoothed leaf margins is positively correlated with mean annual temperature across different continents and biomes. Paleobotanists commonly use this relationship as an index for inferring temperature in the past. However, leaf margin analysis often estimates cooler temperatures than alternative methods. Therefore, the following research hypothesis was stated: due to the observed climate warming, species with untoothed leaves are in better ecological status than species with toothed leaves. Responses of flora to global warming were studied for species with toothed vs. untoothed leaf margins after assigning species to the following categories based on data in the literature: (1) frequency; (2) population trends; (3) degree of endangerment; and (4) protected plants. A total of 2388 dicotyledonous woody and herbaceous plant species of Central Europe (separately from Germany and Poland) were analysed. The results were very similar in both analysed countries and for herbaceous and woody species. Contrary to assumptions, it was found that untoothed species clearly dominate in rare, disappearing, endangered, and protected plant groups. In contrast, plants with toothed leaf margins dominate in frequent and widespread species. The possible explanation is a delay in the response of local flora to climate change. This suggests a post-glacial relict nature of many species with untoothed leaves exists, persisting in local flora from the time of warmer periods. The constant error of underestimating past temperatures using the leaf margin method may explain the impact of today's flora in the models used because modern flora have more species with toothed leaves than expected. Taking into account the delayed reaction of flora to climate change may increase the accuracy of models predicting the climate in the past and in the future.

Zusammenfassung

Über verschiedene Kontinente und Biome hinweg ist bei dikotylen Pflanzen der Prozentsatz von Arten mit ungezähnten Blatträndern positiv mit der mittleren Jahrestemperatur korreliert. Paläobotaniker nutzen diese Beziehung als einen Indikator für Temperaturen in der Vergangenheit. Indessen ergeben sich mit der Blattrandanalyse häufig kühlere Temperaturen als mit anderen Methoden. Wir stellten deshalb diese Hypothese auf: Infolge der klimatischen Erwärmung ist der ökologische Status von Arten mit ungezähnten Blättern besser als der von Arten mit gezähnten Blättern. Basierend auf Literaturdaten wurden die Reaktionen der Flora auf die globale Erwärmung für Arten mit gezähnten und ungezähnten Blatträndern in den folgenden Kategorien analysiert: 1) Frequenz, 2) Populationsentwicklung, 3) Gefährdungsgrad und 4) Schutzstatus. Insgesamt wurden 2388 mitteleuropäische dikotyle Gehölz- und Krautarten (getrennt für Deutschland und Polen) analysiert. Die Ergebnisse

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waren sowohl für die beiden untersuchten Länder als auch für die Gehölz- und Krautarten sehr ähnlich. Im Gegensatz zu den Annahmen dominierten ungezähnte Arten eindeutig bei den seltenen, verschwindenden, gefährdeten und geschützten Pflanzen. Dagegen dominieren Pflanzen mit gezähnten Blatträndern bei den häufigen und weit verbreiteten Arten. Dies legt nahe, dass viele Arten mit ungezähnten Blättern eine postglaziale Relikteigenschaft aufweisen, die in der lokalen Flora aus Zeiten wärmerer Perioden überdauert. Der beständige Fehler, Temperaturen in der Vergangenheit nach der Blattrand-Methode zu unterschätzen, könnte mit dem Einfluss der heutigen Flora bei der Modellbildung erklärt werden, weil moderne Floren mehr Arten mit gezähnten Blättern enthalten als erwartet. Wenn man die verzögerte Reaktion der Flora auf den Klimawandel berücksichtigt, könnte dies die Genauigkeit von Modellen, die das Klima in Vergangenheit und Zukunft vorhersagen, steigern.

Keywords: Global warming; Endangered plants; Leaf margin analysis; Paleoclimate; Temperature

Introduction

Morphological characteristics of leaves often correlate with specific habitats (Givnish, 1979; Bragg & Westoby, 2002; Maciejewska-Rutkowska, Antkowiak, Jagodzinski, Bylka, & Witkowska-Banaszczak, 2007; Uslu & Bakış, 2013; Zanne et al., 2013; Cornwell et al., 2014). In the beginning of the 20th century, it was noticed that plant communities from regions with low mean annual temperatures have a higher number of dicotyledonous species with toothed leaves (Bailey & Sinnott, 1915, 1916). The relationship between mean average temperature and the proportions of toothed and untoothed woody species has been quantified across different continents and biomes (Wolfe, 1979; Wing & Greenwood, 1993; Wolfe, 1995; Wilf, 1997; Traiser, Klotz, Uhl, & Mosbrugger, 2005; Peppe et al., 2011). Paleobotanists commonly use this relationship as an index for inferring temperature in the past (Wing & Greenwood, 1993; Wilf, 2000; Kowalski & Dilcher, 2003; Peppe et al., 2011; Breedlovestrout, Evraets, & Parrish, 2013). The ecophysiological link between leaf and climate is often explained by the gas-exchange hypothesis (Baker-Brosh & Peet, 1997; Royer & Wilf, 2006). It has been shown that the intensity of gas exchange in leaf teeth is considerably higher than that in the central part of the leaf blade (Baker-Brosh & Peet, 1997; Royer & Wilf, 2006). The proportion of toothed area relative to the whole leaf blade is greater in young leaves (Baker-Brosh & Peet, 1997; Feild, Sage, Czerniak, & Iles, 2005). Greater efficiency of gas exchange is important in a cold climate, where the growing season is limited, and plants must grow in a short period of intensive vegetation. The function of teeth is to increase sap flow and delivery of nutrients to young leaves. It increases carbon gain and growth early in the spring. More carbon gain results in unavoidable water cost, which, in regions with a longer and warmer growing season, may be unprofitable (Royer & Wilf, 2006; Peppe et al., 2011).

However, phylogenetic influences on leaf form are very significant (Little, Kembel, & Wilf, 2010; Schmerler et al., 2012; Cornwell et al., 2014). It is known that leaf margins with teeth or multiple lobes have evolved numerous times in unrelated plant groups. Repeated evolution in unrelated plant groups suggests that toothed and lobed margins represent adaptive traits responding to climate and also suggests that some taxa do not respond to changing climate by changing their morphology (Baker-Brosh & Peet, 1997; Jones, Bakker, Schlichting, & Nicotra, 2009).

Toothed and lobed leaves are sometimes considered more advanced characteristics in the evolution of angiosperms and are associated with angiosperm radiation during the Cretaceous (Hickey & Wolfe, 1975). Nevertheless, more recent studies found that early angiosperms were commonly lobed and toothed (Little et al., 2010). Studies on the genus *Viburnum* support repeated evolutionary adaptation as a major determinant of the global correlation between leaf form and mean annual temperature. This means that changes in the leaf margin could proceed from untoothed ancestors to toothed in a cold climate and from toothed to untoothed in a warm climate (Schmerler et al., 2012). The effect of temperature on the irregularity of the leaf margin also has been demonstrated in experimental studies (Royer, McElwain, Adams, & Wilf, 2008). Therefore, the type of leaf margin may be evolutionarily labile (Jones et al., 2013) and respond plastically to climate, and, in particular, temperature (Royer, McElwain, Adams, & Wilf, 2008; Royer, Meyerson, Robertson, & Adams, 2009).

Due to the observed climate warming (IPCC, 2013), the following question is raised: can these changes significantly influence the ratio of toothed to untoothed species? It was demonstrated that an increase in temperature threatened many groups of organisms, including plants (Thuiller, Lavorel, Araújo, Sykes, & Prentice, 2005; Peñuelas et al., 2013). Therefore, the following research hypothesis was tested: due to the observed climate warming, species with untoothed leaves are in better ecological status than species with toothed leaves.

Materials and methods

Polish and German dicotyledonous species divided into woody and herbaceous species were analysed based on the following sources: Ellenberg, Weber, Düll, Wirth, and Werner (2001); Zając and Zając (2001); and Zarzycki et al. (2002). Data were supplemented by species from the German