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Heritable variation in needle spectral reflectance of Scots pine (*Pinus sylvestris* L.) peaks in red edge

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ABSTRACT

Foliar reflectance is readily used in evaluating physiological status of agricultural crops and forest stands. However, in the case of forest trees, underlying genetics of foliar spectral reflectance and pigment content have rarely been investigated. We studied a structured population of Scots pine, replicated on two sites, with the selected trees´ pedigree reconstructed via DNA markers. This allowed us to decompose phenotypic variance of pigment and reflectance traits into its causal genetic components, and to estimate narrow-sense heritability (h^2).

We found statistically significant h^2 ranging from 0.07 to 0.22 for most of the established reflectance indices. Additionally, we investigated the profile of heritable variation along the reflectance curve in 1 nm wavelength (WL) bands. We show that the maximum h^2 value (0.39; SE 0.13) across the 400 to 2500 nm spectral range corresponds to the red edge inflection point, in this case to 722 nm WL band. Resultant h^2 distribution indicates that additive gene effects fluctuate along the reflectance curve.

Furthermore, h^2 of the most widely used formats of reflectance indices, i.e. the simple ratio and the normalized difference, was estimated for all WL bands combined along the observed reflectance spectrum. The highest h^2 estimates for both formats were obtained by combining WL bands of the red edge spectrum.

These new genetically driven pigment- and spectral reflectance- based markers (proxies of adaptive traits) may facilitate selection of stress resistant plant genotypes. Recent development of high-resolution spectral sensors carried by airborne and spaceborn devices make foliage spectral traits a viable technology for mass phenotyping in forest trees.

1. Introduction

Foliage content of photosynthetic pigments (chlorophylls and carotenoids) responds readily to environmental conditions; thus, it is frequently used as a stress indicator. Photosynthetic pigments are also the main biochemical compounds that determine the leaf optical properties (reflectance, transmittance and absorbance) in the visible region of the electromagnetic spectrum. Pigment contents can be estimated from reflectance spectra acquired by a spectroradiometer either in a laboratory (Croft et al., 2014) or by remote sensing techniques (Ustin and Gamon, 2010) using empirical methods or radiative transfer models. In several current studies reflectance indices are used as a proxy for pigment content without any training and validation of a particular index-pigment retrieval model on a corresponding reflectance and biochemistry dataset (Mõttus et al., 2014; Cavender-Bares et al., 2016; Flood et al., 2016). Airborne or spaceborne hyperspectral data provide information on larger spatial scales, which is advantageous in the case of forest stands.

At present, there is a limited knowledge on the genetic variability and control of photosynthetic pigment contents and spectral reflectance properties in forest trees. Thus, it is fundamental to decompose the observed variability of these indices into the underlying genetic and environmental factors and their respective interaction. Knowledge of pigment content and pigment-related spectral signatures narrow-sense

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heritability (h^2) is critical to breeding programs, as these traits could be utilized as indirect proxies of desired phenotypes (e.g. to identify genotypes with drought-resistance, stress tolerance, etc.).

Relationship among the content of photosynthetic pigments, water status, other physiological features, and foliage spectral properties can be modeled by quantitative spectroscopic methods (e.g. Hernández-Clemente et al., 2012; Lhotáková et al., 2013). Needle characteristics derived from reflectance spectra (quantified by vegetation indices, e.g. the normalized difference vegetation index, NDVI) then approximate the physiological status of an individual tree or a population at a stand level (Campbell et al., 2004).

The red edge corresponds to a wavelength, which is defined mathematically as the inflection point position on the slope connecting the reflectance in the red and the NIR spectral regions (Horler et al., 1983). The red edge is very sensitive with regards to plant condition and it shifts to a shorter wavelength when the chlorophyll (Rock et al., 1988) or nitrogen (Mutanga and Skidmore, 2007) content decreases. Thus, the position of the red edge provides an indication of altered plant physiological condition due to air pollution (Campbell et al., 2004) or nutrient content (Mutanga and Skidmore, 2007). In a recent study, Feng et al. (2017) identified candidate genes controlling chlorophyll content in a thorough genome-wide association study of > 1500 hyperspectral indices in rice. They demonstrated that the red edge (680–760 nm) is vital to phenotypic and genetic insights into rice research.

Leaf spectra can also provide tools for elucidating genetic differences among populations. As shown by Cavender-Bares et al. (2016), full leaf spectral reflectance provides accurate models for differentiating among individual oak species within the genus or even different populations of a single oak species. Madritch et al. (2014) discriminated genotypic identity within the species of trembling aspen (*Populus tremuloides* Michx) using imaging spectroscopy and concluded that canopy spectra better described the genetic distance among genotypes than foliar traits. Spectral reflectance of dried and ground needles was used to distinguish various species of genus *Pinus* (Espinoza et al., 2012) and their hybrids (Meder et al., 2014). Thus, leaf spectral data appear to be relevant and have potential for high-throughput phenotyping approaches in forest tree breeding. Foliar spectral reflectance can be used as a predictor in phenomic selection, reducing high phenotyping and genotyping costs in breeding programs (Rincent et al., 2018).

As far as we know, no previous study has focused on spectral reflectance h^2 in conifers. Our study was based on two experimental plantations of Scots pine (*Pinus sylvestris* L.). Plantations were comprised of half-sib progenies of two seed orchards that were later converted into full-sib progenies through the marker-based pedigree reconstruction in accordance with the concept of Breeding Without Breeding (El-Kassaby et al., 2007; El-Kassaby and Lstibůrek, 2009). The reconstructed pedigree information facilitates conventional genetic evaluation (primarily estimation of h^2 and precision of additive genetic values). Progeny trials of forest trees are commonly used for evaluating production traits (such as height or volume), but they can also reveal information on traits indirectly influenced by environmental acclimation such as chlorophyll fluorescence (Čepl et al., 2016) or photosynthetic pigment content and spectral reflectance traits as shown in the current study.

The main aim of the present study was to investigate the existence and extent of heritable variation in needle spectral reflectance of Scots pine. Our method comprised of 1) the analysis of pigment- and water-related reflectance indices; 2) the assessment of biochemically determined contents of photosynthetic pigments and their ratios; 3) the gravimetrical estimation of water content in needles. The next aim of our study was to estimate h^2 in 1 nm wavelength bands along the wide range of the reflectance spectrum (400–2500 nm), which has not been previously published. Additionally, we explored the most widely used reflectance indices (normalized difference indices with special emphasis to NDVI and simple ratio indices) in terms of their heritable variation.

Table 1
Description of research sites.

Characteristics	Study sites	
	Skelná Huť	Nepomuk
Geographic coordinates	49°55′53.489″N, 13°6′43.268″E	49°29′40.735″N, 13°33′5.702″E
Altitude	610 m	490 m
Soil type	Planosol (PL)	Stagnosol (ST) Dystric Cambisol (CMdy)
LAI – hemisurface	5.2 (SE 0.1)	6.9 (SE 0.1)
Age of trees during measurement [years]	20	23
Approximate tree height [m][a]	12	14
Date of measurements	August 4–6, 2014	July 14–18, 2014
Number of measured trees	208	315

LAI – Leaf area index, SE – standard error.
[a] Last accurate measurement of height was conducted in 2007, giving 7.88 m (SD 1.59 m) and 10.02 m (SD 0.88 m) for Skelná Huť site and Nepomuk site, respectively.

2. Material and methods

2.1. Site description

The study was conducted on a Scots pine population originating from Western Bohemia, Czech Republic (Kaňák et al., 2009). Two sites were evaluated as being under no apparent environmental stress (for details see Čepl et al., 2016). Measurements were carried out on two half-sib progeny test plots planted as randomized incomplete block designs on two geographically distinct sites (Skelná Huť and Nepomuk) located in the western part of the Czech Republic (Western Bohemia; for specification, see Table 1). These test plots were grown from seeds originating from two separate seed orchards, each composed of selected plus-trees of Scots pine, all originating from the Western Bohemia provenance (Kaňák et al., 2009).

2.2. Sample collection and measurement setup

Sampling and measurements of needle reflectance, pigment and water content took place during the summer (July and August) of 2014 (Table 1). All trees included in our analysis possessed sun-exposed crowns and were previously genotyped (see section on Pedigree reconstruction). Only fully sun-exposed branches from the mid-to-upper part of a crown were cut using the combination of stepladder and telescopic pole-scissors generally from the southern crown side. However, as proven earlier, azimuth orientation of a branch does not play a role in variation of needle spectral, structural and biochemical parameters unless the branches are exposed to the full sunlight (Lhotáková et al., 2007). From each tree, a single branch was used for biochemical and spectral analyses: one sample for each analysis per branch was measured. In total 208 and 315 trees were sampled and processed biochemically and spectrally across the two test sites. Sampling was done on the two sites on three to four consecutive days from 10:00 am to 4:00 pm (Central European Summer Time). The length of collected branches was at least 100 cm to minimize desiccation; this was verified in a preliminary pilot experiment (Čepl et al., 2016). Branch stumps were wrapped in moistened towels and at the end of the day, they were transported to the laboratory to be processed the next day in the early morning. The collection time was recorded for each branch and the sample order was kept for spectral measurements so that all measurements were accomplished not later than 24 h after being cut. According to Richardson and Berlyn (2002), reflectance measurements in this setup are comparable to in-situ measurements.