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Resin flow in conifers

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ABSTRACT

Resins are plant exudates of economic importance used by plants as defence. They flow out of resin ducts, open and long tube-like intercellular spaces lined by a layer of specialized parenchyma cells, called the epithelium, which secrete resin into the duct lumen. A model that describes resin flow in conifers is presented to investigate how duct structure, resin loading, crystallisation, and viscosity affect flow and could explain differences between species. Considering resin viscosity, the structure of resin ducts, and a pressure-driven resin loading through the duct wall, the unsteady Stokes equation was applied. There is an increase in flow towards the open end that is favoured by the duct geometry. Both flow and pressure depend on the loading mechanism and on the duct resistance, which depends on the duct geometry, viscosity and duct wall permeability to resin. These results confirm previous measurements and observations made on Pinaceae and seem to be physiologically advantageous for the defence role of resin. Understanding of how these physiological and morphological parameters affect resin flow might be useful for selecting varieties and species having a high resin yielding capacity. The model presented in this paper is also applicable to other external secretory systems in plants.

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1. Introduction

Resin ducts (or resin canals) are open, long tube-like intercellular spaces bordered by a layer of specialized parenchyma cells, called epithelial cells, which compose the epithelium and secrete resin into the duct lumen. The epithelium consists of varying proportions of thin- and thick-walled, living and dead cells depending on age, organ of the plant and species. In some species, epithelial cells become non-functional, while in others these cells remain thin-walled, unlignified and functional for longer periods of time (Evert, 2006). Surrounding the epithelium, there is one or more layers of specialized parenchyma cells with relatively thick unlignified cell walls called subsidiary cells that may become crushed as the duct develops and enlarges (Esteban et al., 2005; Fahn, 1990; Wiedenhoft and Miller, 2002). Resin ducts are mostly formed schizogenously (i.e. by separation of cells) and can be very branched, so when one branch is tapped or wounded, resin can flow from the wounded area from long distances. They occur in vascular and ground tissues of all plant organs and can be vertically or horizontally oriented. Resin ducts are a normal feature of gymnosperms Pinaceae and Araucariaceae and some species of tropical angiosperms belonging to: Anacardiaceae; Apiaceae; Asteraceae; Brassicaceae; Burseraceae; Dipterocarpaceae; Fabaceae; Griseliniaceae; Hypericaceae; Nitrariaceae; Rhabdodendraceae; Rousseoideae; and Simaroubaceae (Metcalfe and Chalk, 1988; Stevens, 2001; Watson and Dallwitz, 1992, 2008). Horizontal (radial) resin ducts occur in relatively few wood rays (fusiform rays) only; sometimes connecting vertical ducts and making, in some cases, an extensive three-dimensional system or network (Fahn, 1990; LaPasha and Wheller, 1990; Tolera et al., 2013; Werker and Fahn, 1969). Comparative studies show that there are clear differences in size, density, age and growth of ducts of different genera, while apparent differences do not exist among different species of the same genus (Romberger et al., 2004; Stark, 1965; Wu and Hu, 1997). Duct dimensions may range more than 1 m in length (e.g. *Pinus taeda* L. (LaPasha and Wheller, 1990)) and more than 200 μm in diameter (e.g. *Boswellia papyrifera* (Tolera et al., 2013); *Pinus canariensis* C.Smith (Esteban et al., 2005)). Vertical ducts are commonly three or four times wider than horizontal ducts (Koch, 1972). Traumatic resin ducts caused by wounding (mechanical or pathogenic) may occur together with normal resin ducts, but they can also appear in species that do not normally have resin ducts (e.g. *Abies, Cedrus, Juniperus, Pseudolarix, Sequoia, Taxus*, and *Tsuga*) (Metcalfe and Chalk, 1988; Stevens, 2001; Watson and Dallwitz, 2008). Usually, traumatic resin ducts are longer than the normal vertical ducts and often scattered, becoming further dispersed at a distance from the wound.

Resin is a plant exudate composed of a heterogeneous mixture of resin acids ($C_{19}H_{29}COOH$), fatty acids, esters of these acids, sterols, alcohols, waxes and resenes (mixtures of neutral alkali-resistant compounds containing carbon, hydrogen and oxygen),

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varying among plant species. Although it is believed that resin is not used as reserve food, its physiological role is not yet fully understood. Nevertheless, resin, which is also found in cell interiors and cell walls, makes wood resistant to decay; thus playing an important role in defence against insects, fungi and bacteria in conifers and many angiosperms. In addition, resin is a highly sought substance with many uses in different cultures since several millennia. Typically, resin yields are greater in conifers than in angiosperms and within conifers higher yields are observed in Pinaceae. The most important commercial resin is oleoresin obtained from pines. It consists of approximately 66% resin acids, 25% turpentine (an essential oil that is a mixture of terpenes), 7% non-volatile neutral compounds, and 2% water (Wise and Jahn, 1952). However, the composition of oleoresin may differ significantly between species and even individuals (Bäck et al., 2012).

Resin is synthesized in the epithelium from which it passes into the lumen of the duct or cyst where it collects. Most authors favour a granulocrine method of resin secretion, either by exocytosis or by plasma membrane invaginations, which surround the resin droplets and detach them from the protoplast (Beck, 2010). Epithelial cells lose their secretory function progressively as they age. However, they can be induced to increase resin synthesis by wounding, infestation by insects, bacteria, fungi, or treatment with specific chemicals, e.g. paraquat (an herbicide) (Kozlowski and Pallardy, 2007), sulphuric acid (Lorio Jr., 1994), which are often used in the harvest of resin. The regulation and factors determining resin synthesis are still unknown.

The model most currently accepted as typical of resin loading into the resin duct was first proposed by Ernst Münch by studying the exudation of oleoresin from Scots pine (*Pinus sylvestris* L) (Büsgen and Münch, 1929). Accordingly, when the amount of oleoresin in the duct increases, pressure builds up in the duct compressing the epithelial cells. Consequently and due to the reduction of their size, the epithelial cells osmotic potential decreases. Therefore, water is drawn into the epithelial cells from the neighbouring subsidiary cells, increasing their size and exerting pressure on the oleoresin in the duct towards equilibrium. If the duct is ruptured oleoresin is forced out, thus causing a decrease in the pressure within it, and the epithelium may then produce more oleoresin into the duct. Reaching the wound, oleoresin is exposed to air which causes turpentine and other volatile components to evaporate and the non-volatile rosins to crystallize sealing the wound eventually. Obviously, and accordingly to this model, this emptying and refilling of the duct can be best performed in ducts lined by thin-walled cells. But, unfortunately, this model has not been tested in other species although most authors consider it valid given the similarity of the structure of the resin ducts in many species. However, not all epithelial cells have the same wall thickness. For example, some species of *Pinus* have thick cell walls, some are lignified, and they can be differently surrounded by subsidiary cells (Wu and Hu, 1997), while other species are typically surrounded by a thin-walled epithelium (e.g. *Pinus canariensis* C.Smith (Esteban et al., 2005), *Pinus krempfii* Lecomte (Ickert-Bond, 2001), *Pinus caribaea* var. *hondurensis* (Ferreira and Tomazello-Filho, 2012)). Therefore, the ability of the duct and epithelium to change their volumes inversely according to Münch's model can differ greatly between species.

From the very few quantitative studies done on resin synthesis, it has been observed that the amount of resin exuded when a duct is ruptured can be influenced by the size of the duct and viscosity of the resin (Bourdeau and Schopmeyer, 1958; Schopmeyer et al., 1954). Differences in resin viscosity imply differences in the resin chemical composition that in turn may suggest different loading mechanisms among species. It has been observed, although on a limited number of species, that pressure in the resin duct varies diurnally, with the highest values occurring about dawn and the lowest in the afternoon when the water content of the trunk is lowest; thus in phase with the changes in stem diameter (Lorio Jr., 1994; Neher, 1993; Schopmeyer et al., 1954; Vité, 1961). Transpiration rate, as well as the moisture content of air and soil, has been observed to influence resin duct pressure in pines (Neher, 1993; Vité, 1961). However, Rissanen et al. (2015) observed that the diurnal changes in the pressure of Scots pine resin ducts were positively correlated with temperature and transpiration rate. Pressure in the resin ducts was lowest at the top part of the stem, where water potential was also more negative, and often closely linked to ambient temperature. Seasonal variations in resin flow seem to be appreciably influenced by soil moisture and atmospheric conditions (Blanche et al., 1992; Rissanen et al., 2015).

Despite the wide acceptance of the model first suggested by Münch for resin flow in pines (Büsgen and Münch, 1929), it has seldom been tested experimentally or used to explain differences among species. However, the collection of more quantitative data about resin flow in other species, including angiosperms, e.g. *Boswellia papyrifera* (Tolera et al., 2013), will certainly contribute to a clearer picture. The capacity to produce high resin yields has been demonstrated to be inherited in Pinaceae (Schopmeyer et al., 1954) while being also attributable to several internal (physiological and anatomical) and external (environmental) factors. Therefore, the measurement of these factors could be used not only to give a clearer picture of resin synthesis, how it relates to anatomy and explain differences observed among species but also to select individuals for crossing. Unfortunately, the number of studies with quantitative data on these issues on a reasonable number of species is lacking. The identification of such measureable physiological and anatomical factors is the main purpose of this study. In this paper, a model that describes flow in resin ducts is discussed with the goal of serving as basis to investigate how factors such as duct size, loading, crystallization, and viscosity of resin affect its flow and could contribute to explain differences between species.

2. The hydrodynamic model

Consider a resin duct of constant radius R open at the end of its length L through a wound (Fig. 1). Resin of constant viscosity μ and density ρ (i.e. a homogeneous Newtonian fluid) flows out of it. However, due to the subsequent crystallization of resin, upon exposure to air, resin flow decreases with time as the wound is closed eventually. Due to the long and narrow structure of resin ducts (Beck, 2010; Evert, 2006; LaPasha and Wheller, 1990; Wu and Hu, 1997), the very small velocity of the flow inside them, and the viscous nature of resin (Hodges et al., 1977, 1981; Schopmeyer et al., 1954) the Reynolds number, *Re*, (Kundu and Cohen, 2008) for resin flow in plants is very small, of about 10^{-2} to 10^{-1}. This range of Reynolds number values is thus indicative of what is called Stokes flow or creeping flow, where the advective inertial forces are small compared with the viscous forces. This is a typical situation in flows where the fluid velocities are very slow, the viscosities are very large, or the length-scales of the flow are very small. In these conditions, the advective term of Navier–Stokes equation can be neglected giving the unsteady Stokes Eq. (1) (Venkatlaxmi et al., 2004) that describes the dynamics of resin flow, with velocity $\vec{u}$, within resin ducts:

$$\frac{\partial \vec{u}}{\partial t} = -\frac{1}{\rho}\vec{\nabla} p + \nu \nabla^2 \vec{u} \tag{1}$$

where $\nu = \mu/\rho$ is the resin kinematic viscosity. Pressure p includes the gravitational effect; i.e. $p = p' + \rho g h$, where: p' is termed the hydrodynamic pressure inside the resin duct; g the local acceleration of gravity; and h is the vertical coordinate above a standard reference plane. As an incompressible fluid, the continuity equation

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