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Frankincense tapping reduced photosynthetic carbon gain in *Boswellia papyrifera* (Burseraceae) trees

Tefera Mengistu [a,b,*], Frank J. Sterck [a], Niels P.R. Anten [c], Frans Bongers [a]

[a] Wageningen University, Centre for Ecosystem Studies, Forest Ecology and Forest Management, PO Box 47, 6700AA Wageningen, The Netherlands
[b] Hawassa University, Wondo Genet College of Forestry and Natural Resources, PO Box 128, Shashemene, Ethiopia
[c] Wageningen University, Centre for Crop Systems Analysis, PO Box 430, 6700AK, The Netherlands

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ABSTRACT

Whole-crown carbon gain depends on environmental variables and functional traits, and in turn sets limits to growth sinks of trees. We estimated the annual whole-crown carbon gain of trees of the species *Boswellia papyrifera*, which are tapped for frankincense, by integrating leaf photosynthetic rates over the total leaf area and leaf life span. We examined the effect of tapping on total leaf area and leaf photosynthesis and, in turn, on carbon gain and resin yield for trees of a dry highland population and a wetter lowland population. Highland and lowland trees had similar total leaf area, but highland trees had higher photosynthetic rates per unit leaf area than lowland trees since they received more light and had higher photosynthetic capacities. Highland trees therefore achieved a higher annual carbon gain than lowland trees, despite a shorter rainy season and shorter leaf lifespan. Intensive tapping reduced crown leaf area and the carbon gain in the lowland trees, but not in highland trees. These results highlight how the interplay between local conditions and functional traits determine regional variation in tree productivity. However, such differences in productivity and carbon gain did not influence frankincense yield across sites. We conclude that tapping *B. papyrifera* trees reduces annual carbon gain but the extent differs among different populations.

1. Introduction

Several tree species in the plant families of the Pinaceae (e.g. pines), Euphorbiaceae (e.g. rubber tree), Mimosaceae (e.g. Acacia) and Burseraceae (e.g. Boswellia) produce gum and resin upon bark wounding or tapping. Boswellia trees of the Burseraceae family dominate large areas of dry woodlands in eastern and central Africa and elsewhere, and produce frankincense which is tapped by local communities for local or international markets (Ogbazghi et al., 2006; Tadesse et al., 2007; Mertens et al., 2009). Tapping creates a carbon sink that may be at the cost of growth sinks, including vegetative growth and reproduction (Cannell and Dewar, 1994; Rijkers et al., 2006; Silpi et al., 2006; Chantuma et al., 2009). Moreover, dry woodland trees may suffer from irregular rainfall patterns, thus creating more limiting growth conditions during some years than others (Murphy and Lugo, 1986; Bullock et al., 1995; Vanacker et al., 2005). Climate change may affect rainfall patterns and reduce the ability of trees to acquire and supply carbon to the different carbon sinks (Lacointe, 2000; Hély et al., 2006; Bolte et al., 2010). It is a major challenge to understand how resin tapping will affect the ability of trees to maintain their vegetative status and photosynthetic capacity and, in turn, their ability to acquire carbon and produce more resin in the future.

For resin producing trees, the whole-crown carbon gain depends on a number of functional plant traits, environmental conditions and tapping intensity. Functional traits that affect crown carbon gain include leaf photosynthetic rates, total leaf area and average leaf lifespan (Kikuzawa and Lechowicz, 2006; Selaya and Anten, 2010). However, it is not clear how they scale-up to crown carbon gain in the field (Poorter and Bongers, 2006) and *vise versa*. This information is especially limited for tropical dry forests and dry woodland trees (Yoshifugi et al., 2006; Kushwaha et al., 2010). In such systems, the seasonality in rainfall is expected to impact the annual carbon gain strongly, particularly when trees lose leaves during a long dry season (Kikuzawa and Lechowicz, 2006). Moreover, the intensive tapping of resin may create a major carbon sink to the system. This carbon drain down tunes the production of seeds (Rijkers et al., 2006), and thus potentially also the production of leaves or the maintenance of proteins that are required for photosynthesis. In turn, such a reduction in growth sink may also impact the future carbon gain and resin yield, as has been

* Corresponding author at: Hawassa University, Wondo Genet College of Forestry and Natural Resources, PO Box 128, Shashemene, Ethiopia. Tel.: +251 0912021945; fax: +251 0461191499.

E-mail addresses: teferamengistu@yahoo.com (T. Mengistu), Frank.sterck@wur.nl (F.J. Sterck), N.P.R.Anten@uu.nl (N.P.R. Anten), Frans.bongers@wur.nl (F. Bongers).

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suggested for the frankincense producing trees (Rijkers et al., 2006).

In the present study, we present an experiment that links frankincense tapping and crown functional traits to carbon gain and resin yield for frankincense trees from two populations. One population occurred at a lower altitude (810–900 masl) with a longer and wetter rainy season than the population at higher altitude (1400–1650 masl). These two populations represent the climatic extremes of this species in Ethiopia. The objective of this study was to determine the effects of frankincense tapping on crown carbon gain and resin yield and the underlying functional traits. Our intention, however, is to assess the impact of tapping on leaf and crown traits and on photosynthetic carbon gain, and not to make exact predictions of carbon gain. Moreover, we evaluated how the environmental conditions differed between both populations, and set different constraint on carbon gain and resin yield. Because frankincense, like most resins, is rich in carbon (Hamm et al., 2005; Mertens et al., 2009), tapping is expected to drain carbon reserves limiting the carbon availability for leaf formation. We thus expect a higher tapping intensity to reduce crown leaf area and hence canopy carbon gain. We also expect that trees in the drier highland area, with a shorter rainy season, will be restricted in the crown carbon gain by a limited leaf lifespan, and thus be more affected by tapping compared to lowland trees. To test these hypotheses, we measured leaf and canopy traits of *Boswellia papyrifera* trees in contrasting sites under different tapping intensities.

2. Materials and methods

2.1. Description of the study sites

We studied leaf and crown traits and their impact on carbon gain in *B. papyrifera* of the family Burseraceae in two contrasting woodlands in northern Ethiopia. Abergelle is at an altitude of 1400–1650 masl (hence referred to as "highland" site) and Metema is at a lower altitude of 810–900 masl (referred to as "lowland" site). The highland site is drier and has erratic rainfall with a shorter wet season than the lowland site (Fig. 1). The highland site is dominated by hills, and compared to the lowland and is characterized by soils that are similar in texture, but shallower (on average 15.3 cm versus 27.7 cm) and poorer in cation exchange capacity (CEC 39 versus 48 meq/100 g soil) (Eshete et al., 2011) thus limiting plants to form deep roots. The two sites have similar phosphorus and potassium contents in the soil (Birhane et al., 2010), but the highland site has a higher nitrogen content in the soil (0.29% versus 0.19% soil mass, Eshete et al., 2011). The vegetation at the highland site is categorized as *Combretum–Terminalia* and *Acacia–Commiphora* woodlands dominated by *B. papyrifera*, *Acacia etbaica*, *Terminalia brownii* and *Lannea fruticosa*. The vegetation of the lowland site is categorized as *Combretum–Terminalia* woodland where *Acacia spp*., *Balanites aegyptiaca*, *B. papyrifera*, *Combretum spp*., *Stereospermum kunthianum* and *Terminalia brownii* are the dominant species.

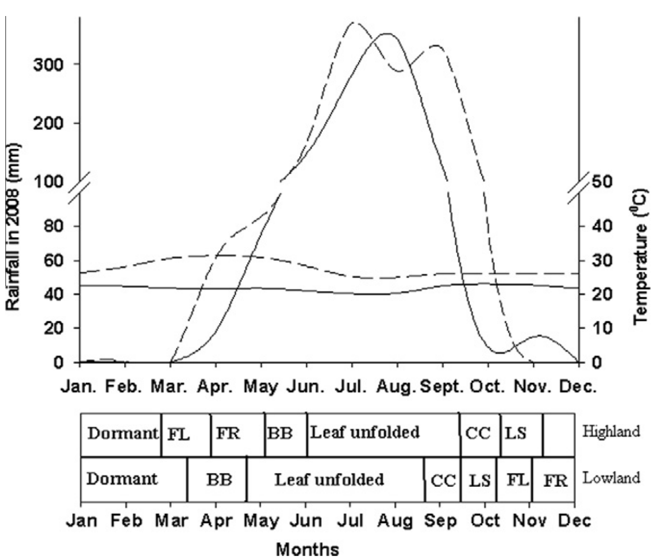

Fig. 1. Phenological patterns of *Boswellia papyrifera* in relation to rainfall and temperature in Metema (lowland, dashed line) and Abergelle (highland, solid line) sites in Ethiopia. The horizontal lines are temperature curves (axis on the right side) and vertical lines are rainfall curves (axis on the left). Codes for successive phenological periods include: FL = flowering, FR = fruiting, BB = leaf bud breaking, CC = pre-leaf fall color change and LS = leaf shedding. Meteorological data is average over a period of 20 years.

2.2. Tapping and data collection

We selected trees with a DBH of 20 ± 3 cm for the experiment. For each site, the experimental trees were randomly allocated to one of three treatments, i.e. 0 incisions (control), 6 incisions (low tapping intensity) and 12 incisions (high tapping intensity), following traditional tapping techniques. Such tapping starts with a superficial cut of the bark at different locations along the stem. The number of locations is here referred to as the number of incisions. With every resin collection round during the dry season, the incisions are deepened and/or enlarged to open the resin ducts and thus stimulate resin production. The incision on the bark triggers sink stimulation similar to what has been shown in rubber production (Chantuma et al., 2009) and drains the resin (frankincense) to exude (Plate 2). Tapping starts early in October and lasts till the beginning of June and is thus practiced during the dry season (Fig. 1), when trees of this species carry no leaves. While the same locations on the stem are used during a given dry season, different locations are selected in the next dry season. Traditionally, tappers wound the bark with a small hand axe such that the frankincense exudes. Tappers decide the number of cuts usually ranging from 3 to 15 incisions depending on tree size. Six and 12 incisions thus represent the lower and higher tapping intensities, respectively for the selected diameter class in our study area. The tapping treatments were applied over two successive dry seasons, but with seven collection rounds in 2007–2008 and 14 collection rounds in 2008–2009. In the highland, we established one plot and selected 10 trees per tapping treatment for gas exchange out of which five from each tapping treatment were also used for estimating total leaf area. In the lowland, we established four plots with *a priori* assumption of local variation and five trees were selected per tapping treatment in each plot for both gas exchange and total leaf area.

Boswellia is a tree up to 13 m height with leaf and floral buds protruding on the apices along the branches. The tree is monoecious and has compound leaves that contain 9–20 pinnate, veined, leaflets supported by petioles (Plate 1). To estimate the total leaf area of a tree, we counted the total number of apices per tree, the number of leaves per apex (on a sample of three apices per tree), the number of leaflets per leaf (on a sample of three leaves per tree), and measured leaflet area (on five randomly selected leaflets per tree) using ADC model AM 100 leaf area meter (ADC, Bioscientific, Hoddesdon, UK). For each tree, total leaf area was calculated as the product of the number of apices, the number of leaves per apex, the number of leaflets per leaf and the average leaflet area after full expansion.

To estimate the leaf lifespan and crown leaf area over the wet season (trees were without leaves during the dry season), we counted leaves and measured leaf size weekly on three apices on