



## Leaf temperatures: dynamics and controls across a range of forest ecosystems

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Temperature strongly affects enzymatic reactions, ecosystem biogeochemistry, and species distributions. Although most focus is on air temperature, the radiative temperature of plant leaves is more relevant. Numerous studies suggest that plants in a variety of ecosystems are operating at or near thermal thresholds for carbon metabolism. Critical to this question is leaf temperature, as numerous leaf properties and processes influence its variations relative to air temperature. Leaf temperature dynamics reflect biophysical, physiological, and anatomical characteristics and interactions with the environment, and can be used to examine plant responses to droughts and heat waves. Reports of apparent leaf homeothermy, whereby leaves are warmer than air below an 'equality temperature', and cooler than air above this threshold, date back several decades. The hypothesis of homeothermy implies that plants regulate their temperature, especially at high air temperatures, to avoid overheating and sustain high rates of photosynthesis. This hypothesis implies that increasing air temperatures driven by warming – and attendant impacts on leaf metabolism and function – might be mitigated by leaves warming at a slower rate. Critically, these reports and associated analyses are largely based on short-term spot measurements using thermocouples, often in artificial settings like greenhouses, and thus the leaf homeothermy hypothesis remains largely untested in natural settings across a range of forest ecosystems.

Thermal infrared (TIR) imaging allows for extensive temporal and spatial monitoring of leaf temperatures, particularly compared to thermocouple measurements. In this work we present an unprecedented dataset of canopy leaf temperature data collected with thermal imaging at multiple well-instrumented forest sites in North and Central America, ranging from old- and second growth temperate conifer forests to a deciduous broadleaf forest to a semi-deciduous tropical forest. Our data do not support the homeothermy hypothesis, as leaves rarely cooled below air temperature, particularly at higher temperatures. Leaf temperatures at all forest sites were fairly well coupled to air temperature but displayed frequent departures from air temperature. This was particularly evident during clear sky conditions, when leaf temperatures were elevated compared to air temperature. During cloudy conditions leaves were at or below air temperature. In general, the relationship between leaf and air temperature is hysteretic rather than linear. Our empirical findings are buttressed by leaf energy balance modeling that incorporates realistic stomatal behavior in response to varying temperature and vapor pressure deficit. This modeling illuminates the drivers of the hysteretic behavior and highlights the critical influence of stomatal and leaf boundary layer conductance on leaf temperature dynamics.