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Towards making willows potential bio-resources in the South: Northern *Salix* hybrids can cope with warm and dry climate when irrigated

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ABSTRACT

Willow (*Salix* spp.) is an attractive biomass resource for many regions, but is today grown commercially mainly in cool-temperate areas. It is unclear whether modern willow hybrids bred for cool-temperate climate are capable of regulating strong water losses when exposed to warm and/or dry climate. The objective was to assess leaf scale water relations (evapotranspiration, *E*; and stomatal conductance, *GS*) and corresponding leaf traits in six wild and hybrid willows field-grown in Central Sweden (cool and well-watered), Northern Portugal (warm and dry), and Northern Italy (warm and well-watered). Diurnal courses of *E*, *GS* and leaf temperature were recorded, plant heights measured, and leaves sampled for assessment of specific leaf area (*SLA*) and area-based leaf N content (N_a). Height growth, *GS*, *SLA* and N_a varied between the genotypes, but genotype environment interaction was important only for plant height and GS. Thus, genotypic variation in leaf scale *E* was mostly caused by stomatal (*GS*) and not by non-stomatal (leaf temperature) genotypic variation. Leaf scale *E* was positively correlated with N_a when assessed across the drought gradient. It is concluded that the willow hybrids bred for cool-temperate climate (in Scandinavia) are capable of regulating strong water losses when exposed to warm and/or dry climate (in Southern Europe), provided that water supply is good. The ability to regulate water losses under warm and dry conditions in the short term is a pre-condition to high water use efficiency and improved growth in warm and dry environments also in the long term.

1. Introduction

Species and genotypes of the genera *Salix* and *Populus* are attractive biomass resources throughout Europe. Whereas *Populus* plantations are common in Central and Southern Europe, commercial *Salix* plantations, grown for biomass for energy, are today mostly restricted to cold-temperate regions of Northern Europe [1]. The *Salix* hybrids used in Scandinavian climates could also be promising crops for biomass production under different climate, for example in Southern Europe, provided they can cope with the corresponding drier and warmer conditions. In addition, many countries today exposed to cool-temperate climate might face warmer and drier summers in the future [2], requiring plant material to be adapted to changed climate. Similar to many other species currently grown in cool-temperate regions, biomass willows

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are sensitive to heat and drought stress [3,4], and *Salix* breeding programs have started to focus on the production of hybrids with increased growth performance under heat and drought, suitable for biomass plantations in regions with warm and dry summers such as in Southern Europe.

An immediate consequence of drought is a water deficit within plant organs, which then brings along an impairment of photosynthetic activity [5,6]. To counteract plant-internal water deficit, plants can regulate the water that evaporates from the leaf through evapotranspiration (*E*). Plant structural and physiological traits associated with regulation of transpiration include stomatal characteristics and responsiveness to atmospheric moisture [7,8].

Plants avoid excessive transpiration during periods of high vapor pressure deficit by regulating stomatal conductance (*GS*). Evapotranspiration increases with vapor pressure deficit (i.e. drought), as was reported for field-grown *Populus* grown under different water availabilities [9]. Drought-induced stomata closure causes evapotranspiration to cease, which in turn leads to an increase in leaf temperature [10]. The changes in leaf temperature are thus intimately related to the variation of air temperature and vapor pressure deficit, but the relationship can vary between plant species and genotypes [10]. For example, leaf temperature and its response to water stress was affected by genotype in maize [11]. In a greenhouse experiment, willow genotypes exposed to drought varied in leaf temperature [12]. We therefore expect that genotypic variation in leaf temperature contributes to genotypic variation in leaf-level evapotranspiration. Evidence for such a relationship could have implications for plant breeding, but first needs confirmation under field conditions.

A common effect of limited water supply is a reduced leaf area to lower whole plant evapotranspiration, and plants adapted to drought are able to raise the concentration of nitrogen (N) in leaves [13,14]. Thus, in a modeling approach, optimization of N economy under drought was predicted to be accomplished by increased leaf N content per area [15]. Under controlled conditions, also experimental evidence was found that increased leaf N is an acclimation to drought stress in various tree species [13,16,17], but field-based evidence is lacking. The expectation is that leaf N of a given genotype is greater in drier environments, and increased leaf scale evapotranspiration (caused by increased vapor pressure deficit) goes along with enhanced leaf N content per area when assessed in a drought contrast.

A typical feature of plants grown in drought-prone environments is a midday depression in *GS* and *E* [18]. There is great variation among different willow species in the diurnal course and development of such a midday depression [19]. As the midday depression is an acclimation to reduce water loss under drought, it is, in a plant breeding context, interesting to investigate whether biomass willows adapted to cold climates exhibit genotypic variation in midday depression when grown in warm and dry climate.

The objective was to assess leaf scale water relations (*E* and *GS*) together with corresponding leaf traits in various willow genotypes field-grown in contrasting climate with respect to temperature and water supply. An underlying question was whether modern willow hybrids bred for cool-temperate climate in Scandinavia are capable of regulating strong water losses when exposed to warm and/or dry climate in Southern Europe. We explored the hypotheses that (a) height growth, leaf water relations (*E* and *GS*) and other leaf traits vary between willow genotypes originating from, or bred for different environments across Europe, and interact with the environment (i.e., genotype rankings change between sites); (b) genotypic variation in leaf scale *E* is caused by stomatal (*GS*) and non-stomatal (leaf temperature) genotypic variation; and (c) leaf scale *E* is positively correlated with leaf N content per area when assessed under different drought stress. To address the objectives and hypotheses, wild willow genotypes originating from Northern and Southern Europe, and commercial hybrid *Salix* genotypes bred for the growth conditions in Northern Europe, were assessed in a young growth stage (<1 yr old plants) at three European sites with different climate and growth conditions: Central Sweden (cool and well-watered), Northern Portugal (warm and dry), and Northern Italy (warm and well-watered).

2. Materials and methods

2.1. Plant material and experimental sites

In total 18 *Salix* genotypes including Swedish hybrids bred for improved growth under cold-temperate or drier conditions, and wild genotypes native to Sweden and Portugal were planted in 2009 at three European sites with different climate (Table 2): Cavallermaggiore (North-Western Italy), Bragança (North-Eastern Portugal), and Uppsala (Central Sweden). Six out of the 18 genotypes were studied here (Table 1). The hybrid 'Björn' and a natural common osier (*Salix viminalis* L.) from Sweden (variety 78183) were selected because they are the parents of an intensively studied pedigree for which a dense genetic linkage map as well as a large amount of phenotypic and genomic information is available [16,21–24]. The other four genotypes in this study were three commercial hybrids ('Tora', 'Terra Nova', 'Dimitrios') selected in a Swedish

Table 1 – The *Salix* genotypes used in the study.

Genotype	Species/parentage [Geographical origin]
Björn[H]	*S. schwerinii* E. Wolf × *S. viminalis* L. [Siberia] [Southern Sweden]
Dimitrios[H]	(*S. schwerinii* × *S. viminalis*) × *S. aegyptiaca* L. [Siberia] [Sweden] [Southwest Asia, UK national willow collection]
78183[W]	*S. viminalis* L. [Southern Sweden]
Portugal1[W]	*S. alba* L. [North-Eastern Portugal]
Terra Nova[H]	(*S. viminalis* × *S. triandra* L. = *Salix* × *mollissima* Hoffm) × *S. miyabeana* Seemen [Sweden] [Northern Japan]
Tora[H]	*S. schwerinii* × *S. viminalis* [Siberia] [Southern Sweden]

H = Hybrid genotype obtained through artificial crossing. W = Wild genotype. All plant material was kindly provided by Lantmännen SW Seed AB, Sweden.