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The intraspecific drought tolerance of *Betula pendula* Roth.

– Ecotypic aptitude as tree selection criteria for the urban landscape

Simon Hannus

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The intraspecific drought tolerance of *Betula pendula* Roth. – Ecotypic aptitude as tree selection criteria for the urban landscape

Torktålighetens variation inom Betula pendula Roth.
– Ekotypisk lämplighet som trädselektionskriterium för det urbana landskapet

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Abstract

The ecosystem services provided by urban trees are substantial contributors to the quality of urban living, and their environmentally regulating capabilities are increasingly regarded as integral in order to efficiently secure urban resilience, by ameliorating the human and material impacts of extreme weather events. However, current trends of urban development presents challenges of how to preserve urban greenery ecosystem functioning, particularly in light of the ongoing climate change; which also has brought forth the importance of taxonomically diverse urban forests, to mitigate risks of catastrophic tree loss associated with these conditions. The elevated temperatures and irregular water availability which generally characterizes the highly urbanized landscape thusly necessitates approaches that promotes usage of trees with corresponding adaptations which adequately facilitates survival in spite of such environmental stressors. Such adaptations have previously been studied in species native to similarly tough habitats. But granted the wide distribution of some cosmopolitan tree species, such as *Betula pendula* Roth., there's opportunity for significant differential ecotypic variations due to the locally distinct selective pressures, which could be expedient from an urban tree selection perspective and leveraged to further the goal of improved urban forest resilience.

To probe this opportunity, the leaf drought tolerance of 13 global *B. pendula s.l.* proveniences was investigated by measuring leaf osmotic potential at full turgor in order to estimate their hydrological limitations by its firm linear correlation with the turgor loss point (TLP). Local climatic selective pressure was investigated by characterization and statistical comparison of the local climates and atmospheric water balance. The group of European subspecies *ssp. pendula* was found to be significantly more drought tolerant than the Asiatic subspecies *ssp. mandshurica* and *ssp. szechuanica*, at a TLP of -2,75 MPa, compared with -2,28 MPa for both respectively. A linear correlation was found between the birch provenience's TLP and the local climatic potential evapotranspiration (PET). Though the relationship couldn't be fully established due to lack of conclusive data; the possible driving factors for this adaptive separation were however discussed, and besides currently acting pressures, the recent evolutionary history of *ssp. pendula* was highlighted as possibly contributing to the observed results. The modes and extent of drought adaptations in *B. pendula* were also discussed in the wider context of ecotypic differentiation of other deciduous temperate tree species, along the role of geography. Methods for enhancing the selection of fit ecotypes for the urban landscape were explored, e.g. by using analytical advantages provided by GIS-aided spatial analysis.

Keywords: Betula pendula, clinal variation, drought tolerance, ecosystem services, ecotypes, potential evapotranspiration, turgor loss point, urban forestry, urban resilience, urban tree selection

Sammanfattning

De ekosystemtjänster som urbana träd tillhandahåller bidrar väsentligt till livskvalitén i städer och dess klimatreglerande egenskaper betraktas allt mer som ett centralt verktyg för att säkra urban resiliens, genom att reglera de negativa effekterna av extremväder på människor och material. Nuvarande stadsutvecklingstrender presenterar emellertid utmaningar för hur man ska kunna bevara urban grönska och dess ekosystemtjänster, särskilt med hänsyn till pågående klimatförändringar. Dessa tendenser har belyst vikten av taxonomisk diversitet av träd i våra städer som en strategi för att mitigera de överhängande risker för katastrofal trädförlust som följer av de stadstypiska förhållandena. De förhållanden av förhöjda temperaturer och ojämn vattentillgänglighet –som generellt präglar det urbana landskapet– fordrar sålunda en kompetent trädanvändning som är observant på och främjar sorter som har motsvarande anpassningar för att överleva stressen av stadens extrema ståndorter. Anpassningar som dessa har tidigare studerats hos trädarter som växer under liknande växtbetingelser i det vilda. Men den vida, näst intill hemisfärt globala, utbredningen av somliga trädarter, som *Betula pendula* Roth., medför en möjlighet till märkbar ekotypisk differentiering som följd av lokalt evolutionärt distinkta selektionstryck, som i sin tur skulle kunna utnyttjas för att hitta nya genotyper inom en och samma art för att ytterligare förbättra den klimatmässiga resiliensen hos träden i våra städer.

För att utforska denna möjlighet undersöktes torktoleransen av 13 internationella provenienser av *B. pendula s.l.* Detta genom att mäta bladens osmotiska potential vid full turgor, för att utröna dess hydrologiska begränsningar genom ett linjärt samband till bladets vissningspunkt (TLP). Lokalt klimat och atmosfärisk vattenbalans karaktäriserades och jämfördes statistiskt för att undersöka dess potentiella inverkan på torkanpassning. Gruppen av den europeiska underarten *ssp. pendula* visade sig här vara betydligt mer tålig för torka än de asiatiska underarterna *ssp. mandshurica* och *ssp. szechuanica*, vid en TLP på -2,75 MPa, jämfört med -2,28 MPa för de båda. Linjärt korrelat fanns mellan björkproveniensernas TLP och den lokala potentiella evapotranspirationen (PET). Fast detta samband kunde inte säkerställas fullständigt, på grund av det begränsade antalet samplingsgrupper; de möjliga orsaksfaktorerna för den adaptiva separeringen diskuterades emellertid, och förutom rådande selektivt tryck av klimatfaktorer belystes den sentida evolutionärhistorian av *ssp. pendula* som möjligt bidragande till en högre torktolerans. Björkens olika drag av torkanpassningar och dess omfattningar diskuterades också i det bredare sammanhanget av ekotypisk differentiering hos lövträd, samt geografins betydelse. GIS diskuterades därför som viktigt verktyg för vidare studier och trädselektion.

Nyckelord: Betula pendula, ekosystemtjänster, ekotyper, klinal variation, potentiell evapotranspiration, torktolerans, urban resiliens, urban trädförvaltning, urban trädselektion, vissningspunkt

Preface

At last!
If you're reading this it means that I have managed to persevere the process of producing a master's thesis. A feat not to be underestimated really; I might even have generated something with legitimate scholarly value in the process, who knows? – What a trip

This thesis marks the conclusion of my studies of horticultural sciences at the Swedish University of Agricultural Sciences (SLU) and my master's degree in biology. As the name of the programme suggests, it's mainly geared toward teaching matters of horticultural crop production and related biotech, and whiled those subjects maintained a certain appeal to me for some time after I began my education, they became gradually supplanted by the increased curiosity for trees and their biology; surely because of the university's close proximity to Alnarpsparken and all its wonderful trees. Naturally the curiosity prompted me to pursue this interest further, by opting for courses that engaged in themes relating to trees and their utilization, such as landscape architecture, urban forestry, ecosystem services etc.

My interest in plant physiological processes lingered however, and was allowed to resurface and intermingle with landscape architectural subject matters for this thesis project, where I, along with my supervisor journeyed to Ness Botanic Gardens in England to study their collection of silver birches and investigate their variation in drought tolerance and how it could potentially be extrapolated to improve urban tree selection.

The topic for this thesis is therefore more or less a result of the motley lot of courses I've partaken in during the years, and my intent has been to approach it in a deliberately interdisciplinary matter that would bridge the two aforementioned aspects of my academic curiosity. So, as much as it has been a quest to fulfill the scientific objective of a thesis, it has also been my ambition to provide a collective theoretical foundation of '*interdisciplinary understanding*' by including a wide, but condensed overview of the multifaceted challenges associated with the maintenance of urban trees and greenery, including current understanding of tree drought adaptation in an urban- and climate change context. My hopes are therefore that potential readers from either academic domain can find something useful in the text and the references I've cited, to further build upon the understanding of the interconnectedness of our urban landscapes, the plants we use there and the people whom inhabit it.

Society grows great when old men plant trees
whose shade they know they shall never sit in.

-Greek proverb

Table of contents

List of tables 8

List of figures 10

Abbreviations and terminology 12

1 Introduction 13

1.1 Background 14

1.1.1 Global warming and its effect on trees 14

1.1.2 The urban environment, trees and resilience 14

1.1.3 Abiotic stress adaptation in trees 16

1.1.4 Urban tree selection 22

1.2 Aims and objectives 25

1.2.1 Implementation and delimitations 26

2 Materials and methods 27

2.1 Birches 27

2.1.1 Betula pendula 27

2.1.2 Fossil history and genus origin 28

2.1.3 Taxonomy of Betula 29

2.2 Plant material for investigation 31

2.3 Turgor loss point 33

2.4 Climate 34

2.4.1 Variables and indices 35

2.5 Statistical analysis 37

3 Results 38

3.1 Turgor loss point 38

3.2 Climate 39

3.3 Drought tolerance correlations 45

4 Discussion 47

4.1 Birch drought adaptations 47

4.2 Environmental gradients and drought adaptations 50

4.3 On refining urban tree selection 51

4.4 The effects of complexity and variability 54

4.4.1 Climate 54

  4.4.2 Genetics 55
  4.4.3 Trait plasticity 56
4.5 Urban resilience and drought tolerance 57

5 Conclusions 60

References 62

Acknowledgements 75

Appendix 1 – Osmometry readings 77

Appendix 2 – Climate data 78

Appendix 3 – Thermal Lapse Rates 89

Appendix 4 – Ness climate 93

List of tables

Table 1. Subdivision of the genus Betula 29

Table 2. Origin and assigned taxa of investigated birch specimens 31

Table 3. Summary of proveniences and corresponding weather station from which climate data was sourced. Weather station serial number corresponds to those assigned by WMO for their network, superscript letter corresponds with source reference. 35

Table 4. Yearly accumulated and averaged climate data. 40

Table 5. Linear regression analysis of TLP-climate interactions. 45

Table 6. Linear regression analysis of TLP-PET interactions for B. pendula subspecies. 46

Table 7. Osmometry readings (mmol kg^{-1}) from B. pendula s.l. Specimens were collected at Ness Botanic Gardens, UK. 77

Table 8. Normal temperatures for Irkutsk[1] (°C) 78

Table 9. Average temperatures for Nyingchi (1978-2007)[1] (°C) 78

Table 10. Normal temperatures for Juzhno-Kurilsk[1] (°C) 79

Table 11. Average temperatures for Asahikawa (1961-1990)[1] (°C) 79

Table 12. Normal temperatures for Montana[1] (°C) 79

Table 13. Average temperatures for Colle Belenda (2004-2016)[1] (°C) 80

Table 14. Normal temperatures for Ostrava[1] (°C) 80

Table 15. Average temperatures for Lahti (1981-2010)[1] (°C) 80

Table 16. Normal temperatures for Novosibirsk[1] (°C) 81

Table 17. Average temperatures for Jiulong (1978-2007)[1] (°C) 81

Table 18. Normal temperatures for Red Deer[1] (°C) 82

Table 19. Average temperatures for Kanding (1978-2007)[1] (°C) 82

Table 20. Average temperatures for Linguaglossa (1968-1997)[1] (°C) 82

Table 21. Normal precipitation for Irkutsk[1] (mm $month^{-1}$) 83

Table 22. Average precipitation for Nyingch (1978-2007)[1] (mm $month^{-1}$) 83

Table 23. Normal precipitation for Juzhno-Kurilsk[1] (mm $month^{-1}$) 84

Table 24. Average precipitation for Asahikawa (1961-1990)[1] (mm $month^{-1}$) 84

Table 25. Normal precipitation for Montana[1] (mm $month^{-1}$) 85

Table 26. Average precipitation for Colle Belenda (2004-2016)[1] (mm month^{-1}) 85
Table 27. Normal precipitation for Ostrava[1] (mm month^{-1}) 85
Table 28. Average precipitation for Lahti (1981-2010)[1] (mm month^{-1}) 86
Table 29. Normal precipitation for Novosibirsk[1] (mm month^{-1}) 86
Table 30. Average precipitation for Jiulong (1978-2007)[1] (mm month^{-1}) 86
Table 31. Normal precipitation for Red Deer[1] (mm month^{-1}) 87
Table 32. Average precipitation for Kanding (1978-2007)[1] (mm month^{-1}) 87
Table 33. Average precipitation for Lingualossa (1968-1997)[1] (mm month^{-1}) 88
Table 34. Seasonal temperatures of Sicily (°C) 89
Table 35. Lapse rates of Mt. Etna (°C km^{-1}) 90
Table 36. Seasonal temperatures of Carmolangan[1] (°C) 90
Table 37. Lapse rates for Carmolangan (°C km^{-1}) 91
Table 38. Lapse rates for China[1] (°C km^{-1}) 92
Table 39. Monthly average climate for Ness Botanic Gardens (2016)[1] 93

List of figures

Figure 1. Grime's CSR-Triangle, visualization of his theory of Universal Adaptive Strategies. Adapted from (Grime, 1977). 18

Figure 2. Conceptual model of drought tolerance strategies' role in mitigating fatal drought scenarios. Modified from (McDowell *et al.*, 2008). 20

Figure 3. Geographical distribution of *Betula pendula* s.l. 🟪: *Betula pendula ssp. pendula* 🟦: *Betula pendula ssp. szechuanica* 🟩: *Betula pendula ssp. mandshurica.* The area where the subspecies interface hosts intermediary forms of the species. (Ashburner & McAllister 2016). Used with permission: © RBG Kew. 30

Figure 4. Growing locales of the investigated birch proveniences. 32

Figure 5. Turgor loss point as predicted by osmometry of fully turgid birch leafs of 13 proveniences. Bars show SE, $F_{12,91}$ = 10,33, p <0.001 across the total dataset according to One-Way ANOVA. Superscript lettering indicate significance at a 95% confidence level as indicated by Tukey's Test. 39

Figure 6. Predicted turgor loss of *B. pendula* subspecies, using data pooled from the 13 proveniences. Bars show SE, $F_{3,100}$ = 26,06, p < 0.001. Letters indicate significance at a 95% confidence level as indicated by Tukey's Test. 39

Figure 7. Dendrogram illustrating grouping of birch proveniences according to cluster analysis of climatic variables. 42

Figure 8. Scatter plot from PCA for the birch proveniences, utilizing the same climatic variables as the cluster analysis (Figure 7). 42

Figure 9. Loading plot of eigenvectors for PCA (Figure 8), showing the vectorial weight of each climatic variable. 43

Figure 10. Climatic classification of loading plot, utilizing PC1- and PC2-scores for each quadrant (Figure 9). 🟥: -WB, summer 🟦: +WB, summer ⬜: -WB, winter ⬛: +WB, winter. Pie chart area is proportional to number of variables of that quadrant. 43

Figure 11. Contour plot of the monthly water balance (mm month^{-1}) for each birch provenience. Y-axis denotes hypothetical positive and negative watershed runoff. Dashed line represents zero runoff, and solid line indicate water balance equilibrium. Plots are grouped according to previously established

clustering (Figure 7) a: Western-Europe/North America, b: China, c: East Asia, d: Italy. 44

Figure 12. Relationship between drought tolerance (Ψ_{P0}) and potential evapotranspiration (PET). Solid line represents a significant ($R^2 = 0.53$, $F_{1,11} = 12.38$, $p = 0.005$) linear correlation. Blue and red dashed lines represents a 95% confidence- and prediction interval respectively. 45

Figure 13. Examples of spatial analysis approaches for urban tree selection, utilizing geoclimatic-, hydrological- and species distribution modelling: Annual geomorphological-dependent PET **(a)**, from (Dyer, 2009). Climatic-dependent probability of beech distribution in Switzerland **(b)**, from (Zimmermann *et al.*, 2009). Relative water presence from TWI in Lake District UK **(c)**, from (Gallay, 2013). Modelled urban radiant temperature, using ENVI_MET simulation **(d)**, from (Deak Sjöman, 2016). Used with permissions: © Springer Nature, © National Academy of Sciences, CC BY 4.0. 53

Figure 14. Water balance for Ness Botanic Gardens (2016) 93

Abbreviations and terminology

DEM	Digital elevation model
NBG	Ness Botanic Gardens
PET	Potential evapotranspiration
SDM	Species distribution modeling
SLA	Specific leaf area
s.l.	*Sensu lato* – 'in a broad sense'
sp.	Species
ssp.	Subspecies
TLP	Turgor loss point

Throughout the thesis I use certain terminology that's traditionally linked to the fields of ecology and genetics, with established definition within those disciplines. While they have similar definitions herein, I've chosen to attach them to a semi-hierarchical categorization to distinguish certain concepts and emphasize aspects of their original connotation. This is in order to aid the contextual understanding of population ecology and how it relates to tree selection sampling:

Genotype	Singular individual tree or its progeny, may represent sample of a specific ecotype
Ecotype	Collective reference to group of genotypes, signifies local adaptation
Phenotype	Collective reference to a set of genotypes, signifies specific traits

1 Introduction

Trees hold a nigh self-evident importance and value to people, as they are persistently treasured for their cultural and material significance all over the world (Konijnendijk, 2008). Beyond being objects for the intangible subjective esteem with which we as a culture might hold for them –as solitary trees or entire forests–, trees can provide tangible benefits that directly or indirectly enriches our society. These benefits are often referred to in literature as "ecosystem services" and encompasses the whole gamut of positive effects and materials provided by any ecological processes (De Groot *et al.*, 2002). The classification of ecosystem services that currently is the most widely recognized is the one formulated by the Millennium Ecosystem Assessment (2005), which includes four separate categories: *provisioning*-, *regulating*-, *supporting*- and *cultural ecosystem services*.

The utility of ecosystem services is especially pertinent to the urban landscape as cities are increasingly regarded as representations of the modern human habitat, where green infrastructure –or lack thereof– can have multifaceted implications for human health, social wellbeing and economic prosperity (Jansson *et al.*, 2013). The processes that grows cities can jeopardize the provision of ecosystem services, as urban sprawl is generally deleterious to natural ecosystems (Johnson, 2001), and urban densification often occurs at the expense of existing public green spaces (Haaland & Konijnendijk van den Bosch, 2015). Conscientious objective-oriented strategies and a subsequent steadfast execution for the conservation and development of green infrastructure and urban forests are thus necessary in order to guarantee the efficacy of trees as nature-based solutions and providers of critical ecosystem services (Roy *et al.*, 2017; Kabisch *et al.*, 2016; Mell, 2008).

It can however be quite nontrivial to introduce trees to highly urbanized areas as they are often characterized as being harsh environments for plants in regards to temperature and water availability, which can exacerbate problems with tree mortality and poor vitality due to physiological stress (Deak Sjöman *et al.*, 2015). Adequate knowledge of context-appropriate tree species, that are adapted to similar stressful conditions of irregular water availability, is therefore essential in order to build resilient urban forests that can still offer ecosystem services under hot and dry conditions (Sjöman, 2012; Roloff *et al.*, 2009).

1.1 Background

1.1.1 Global warming and its effect on trees

Global warming is part of the current anthropogenic climate change, which has affected local weather and global climate since the onset of the industrial revolution. Records shows that in the past century, global surface temperatures has increased by an average of 0,85 °C, at a rate which has been accelerating. The *Intergovernmental Panel on Climate Change* estimates that the global surface temperature will increase by an additional 2,6-4,8 °C in the coming century, if greenhouse gas emissions remains unchecked for (IPCC, 2014). This change in climate has led to more severe and frequent weather extremes in the form of heat waves and precipitation events (or lack thereof), something that's also predicted to increase alongside the continued rise of global temperatures (Fischer & Knutti, 2015; Donat *et al.*, 2013; Perkins *et al.*, 2012).

Drought from heat waves and erratic precipitation patterns exposes trees and forest vegetation to abnormally prolonged periods of thermal and hydraulic stress as an effect of the decreased water availability (Anderegg *et al.*, 2012b). Thusly overall tree mortality is predicted to increase due to the anthropogenic climate change, threatening the capacity of tree communities globally in providing crucial ecosystem services (Anderegg *et al.*, 2013; Allen *et al.*, 2010), as well as altering species compositions and successional ecosystem dynamics (Cavin *et al.*, 2013; Mueller *et al.*, 2005).

1.1.2 The urban environment, trees and resilience

By virtue of being artificial man-made habitats, cities are designed and formed by the utilitarian need to facilitate the functions of a society and to house its population, and not necessarily the preservation of natural processes and ecosystems. Cities are therefore associated with a particular set of environmental challenges to the establishment and maintenance of urban vegetation, which mainly includes challenges of aberrant temperatures and water availability (Sieghardt *et al.*, 2005).

Cities are to varying degrees, depending on structure and size, characterized by generally having higher temperatures when compared to adjacent rural and peri-urban areas. This phenomena of meso-/macroclimatic discrepancy is known as the *urban heat island* (Oke, 1973). While several factors contribute to the urban heat island, the core causes are the thermal properties and albedo of a city's paved and built surfaces, which yields higher absorption and retention of solar energy, causing locally elevated temperatures as the materials re-emit the stored heat (Taha, 1997). This effect may be mitigated locally by moderating factors such as the shading and evaporative cooling provided by urban vegetation, likewise it can be exacerbated by its absence (Orlandini *et al.*, 2017).

Urban heating has several inhibitory effects on the physiological processes in trees, which stems from increased transpiration due to the inverse influence of temperature on local atmospheric water balance (Thornthwaite, 1948). The decreased water potential drives primary stress responses to halt foliar desiccation and wilting, such as reduced stomatal aperture to minimize loss of extracellular water (Taiz & Zeiger, 2010). This process impairs CO_2 diffusion –and in turn photosynthesis– as well as evaporative heat dissipation, resulting in eventual carbon starvation and increased susceptibility to photo-oxidative stress (Rennenberg *et al.*, 2006; Flexas *et al.*, 2004). The water balance pertaining to the urban vegetation is also affected by circumstances below ground, such as limitations imposed by paved surfaces and subterranean utility infrastructure; these installations diminishes rainwater infiltration and root-available water due to excessive surface runoff, as well as insufficient soil volumes to adequately allow for satisfactory root proliferation and retention of water (Jim, 2017; Sanders & Grabosky, 2014; Nielsen *et al.*, 2007). The climate and periodic droughts that most urban trees are faced with are thus causal factors to significant water stress, that can irrevocably disrupt a tree's hydraulic functions (Savi *et al.*, 2015). Leaf functioning may be similarly affected by severe droughts, as permanent wilting can occur when leaf transpiration exceeds water uptake, lowering leaf water potential to the critical point where the deficit causes the cells to collapse from lost turgor pressure, a point also known as the leaf's turgor loss point (TLP) (Schulze *et al.*, 2005a). Thus the establishment and development of urban trees may be put at significant risk of becoming considerably compromised, unless these factors are controlled for, e.g. by means of management, improvement of site specific growth conditions and tree selections. If not, ever increasing instances of poor vitality, tree decline and subsequent mortality is to be expected as a prevailing trend in the urban landscape as consequence (Sjöman, 2012; Bühler *et al.*, 2007; Nowak *et al.*, 2004; Clark & Kjelgren, 1990).

Drought-induced stress has also been noted to cause an increased susceptibility of urban trees to various biotic stressors in the form of diseases and pests, particularly in conjunction with impervious, paved surfaces (Östergren, 2017; Dale *et al.*, 2016; Raupp *et al.*, 2010). The overall detrimental load of diseases and pests on urban trees is also likely to increase with the global climate change, as the warming is predicted to aid in the proliferation of numerous pathogenic species, including improved survival of exotic pests which would contribute to the increasing risks of eventual geo-ecological range extensions (Tubby & Webber, 2010; Tello *et al.*, 2005). Additionally compounding factors are global trade and communications, which are constant sources of concern as they have historically acted as vectors facilitating the introduction of exotic diseases and pests, including the devastating chestnut blight that spread throughout the eastern U.S. in the early 20th century (Anagnostakis, 1987), and more recently, outbreaks of xylophagous beetles such as the Emerald ash borer (*Agrilus planipennis*) and Asian long-horned beetles (*Anoplophora sp.*), whose presence can inflict considerable damage on host trees and decimate urban forests (Herms & McCullough, 2014; Nowak *et al.*, 2001).

Urban forests are contributors to urban resilience through the provision of ecosystem services, meaning the environmentally regulating properties of trees can act as capable buffers to extreme weather events and urban heating which otherwise would cause significant discomfort and distress to urban dwellers, and by extension also cause disturbance to the city's social and economic functioning (McPhearson *et al.*, 2015; Akbari *et al.*, 2001). This is however contingent of the extent of the urban forest's maturity and health status, as tree size and vitality are known requisites to the trees' individual ability to fully deliver on potential ecosystem services (Gomez-Muñoz *et al.*, 2010).

As urban trees face elevated mortality rates from the environmental factors that are emblematic to cities (Nowak *et al.*, 2004), and the risk of large-scale catastrophic tree loss from heatwaves and pathogen outbreaks are seen as increasingly likely scenarios (Roloff *et al.*, 2009; Poland & McCullough, 2006), there's an increasing consensus supporting the notion that urban resilience is thoroughly dependent on the resilience of its vegetation-based urban ecosystems to both biotic and abiotic disturbances (Morgenroth *et al.*, 2016; McPhearson *et al.*, 2015). Such resiliency is considered achievable by utilizing plant species that are naturally adapted to warm and dry conditions (Sjöman *et al.*, 2012a), as well as by redundancy through taxonomic diversity, as it reduces the potential impact of any given disastrous pest outbreak (Santamour, 1990). However, the 'diversity approach' may still be vulnerable to infestations of polyphagous pests, which could severely damage large portions of urban forests in spite of managerial measures to improve diversity through expanded taxonomic representation (Sjöman *et al.*, 2014).

1.1.3 Abiotic stress adaptation in trees

As perennial, sessile organisms, trees have been forced by evolutionary selective pressure to develop traits that confers tolerance to a range of environmental circumstances in order to cope with the abiotic stresses of heterogeneous growing locales and shifting seasons, while maintaining a sufficient degree of populationsustaining success in the face of competition (Keddy, 2007). These adaptations are fundamentally physiological processes, controlled by genetic factors, and can be regarded as the basis of a plant's fundamental niche; while its realized niche is determined by external filters such as dispersal history and biotic interactions – dynamics which ultimately shape a species' geographic range and species composition at any particular site (Lambers *et al.*, 2008; Prinzing *et al.*, 2002).

The endogenous and exogenous processes that govern niche occupancy are essentially universal to the degree that clear-cut elementary strategies can be readily distinguished based on the optimal means of improving fitness in relation to each filter. This phenomenon has been concretized by Grime (1977) in the form of his theory of Universal Adaptive Strategies, which describes the relative trade-offs in resource allocation between growth, maintenance and regeneration in relation to external factors; the accompanying C-S-R Triangle model illustrates its implications for plant ecology (Figure 1). The theory posits that the resource trade-off directs adaptation into one of main strategies: competitiveness (C), stress tolerance (S) and ruderal (R). While extreme one-directional strategist species exists, most species are intermediates that partially invest resources towards each strategy, though trees are in a broad sense precluded from strict ruderal adaptations due to trees' innate longevity (Grime, 2006). Within this framework, stress and disturbance are regarded as the main ecological factors that affect habitat characteristics and limits plant growth. The species that are adapted to handle one type of stress or disturbance regime would thus, due to said tradeoff, not be able to efficiently compete, and by extension survive long-term, under contrasting circumstances, with otherwise co-occurring species with more well suited adaptations. Nevertheless, there are strategies that can be rather beneficially congruent for other scenarios; such as the growth and resource acquisition of competitive pioneering species when growing in intermittently disturbed habitats, which makes for an advantageous adaptation compared to stress adaptations and would consequently prevent stress tolerant strategists from flourishing under such disturbance regimes, especially in habitats that are resource-abundant in addition to being frequently disturbed.

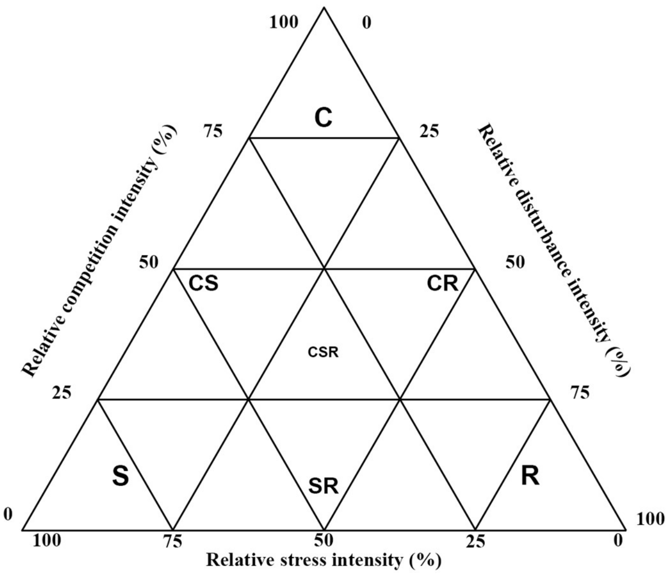

Figure 1. Grime's CSR-Triangle, visualization of his theory of Universal Adaptive Strategies. Adapted from (Grime, 1977).

Stress as induced by water relations, including drought, is to a large degree determinant of species distributions at global scales; the impact of which can be conceptually be quantitatively represented by the atmospheric evaporative demand relating to plant water usage as directed by local thermal energy input (Stephenson, 1998), also known as *potential evapotranspiration* (PET) or by its subcomponents *actual evapotranspiration* (AET) and *deficit/surplus* (D/S), which are mainly regulated by temperature and precipitation and are thus the basis for meteorological drought. This fact is evident when comparing biomes; but the structural makeup and spatial variation becomes more dynamic at smaller scales, in plant communities, where niches are filled according to the relative variation of Grimean strategy combinations, which is illustrated by the spatially and temporally shifting species compositions observed along environmental gradients (clines) that gradually exerts different modes of selective pressure in varying amplitude in accordance with each species' genetic limitations (Schulze *et al.*, 2005b). These gradients and potential distribution overlaps would mean that any given locale could host several species with varying degrees of stress tolerance that might remain relatively cryptic at first glance. Though abiotic disturbances such as drought-induced forest mortality events can serve as empirical evidence for contrasting adaptive aptitudes of co-occurring dominant forest species in relation to geography, climate and plant functional type[1] (e.g. Gitlin *et al.*, 2006; Breshears *et al.*, 2005; Peñuelas *et al.*, 2001).

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[1] Type according to *a priori* classification of a plant species, based on the knowledge of the ascribed group's shared properties (Lavorel *et al.*, 2007).

Adaptive strategies of drought tolerance and drought avoidance

Adaptive strategies are realized as specific adaptive traits that improves a species' performance in a specific environment (Lambers *et al.*, 2008). To withstand environmental water stress from heat and drought, plants have developed various morphological and physiological traits that facilitates growth and survival during intermittent periods of soil water deficits by optimizing 'hydrological economy'.

The strategies for maintaining the hydrological economy and avoiding leaf desiccation from drought can according to Delzon (2015) be divided into three main groups: (1) drought escape, where water stress is averted by the plant's phenology as it times its active phase to periods of ample water availability (e.g. annual plants), (2) drought avoidance, where water potential homeostasis is preserved and stress delayed by minimizing water loss or maximizing water uptake (e.g. stomatal control and extensive rooting systems), (3) drought tolerance, where negative water potentials are tolerated and mitigated by leaf- and vascular physiological traits (e.g. osmotic adjustment and xylem cavitation resistance). There's however no distinct dichotomous divide between *drought avoidance* and *-tolerance*. Instead, tree species can by combination of the two be seen as being part of a drought adaptive spectrum, which is determined most noticeably by how strictly stomatal aperture is regulated to moderate the rate of transpiration over the course of the day, or during drought. The genotypes that tightly regulate stomata and water use fall on the *isohydric* side of the spectrum, while those that allow for certain water loss by a more loose regulation would conversely be more *anisohydric* (Tardieu & Simonneau, 1998). Even though a given tree is well adapted in regards to *avoidance*, it doesn't guarantee success in a multitude of scenarios, as it may risk competitive disadvantages in resource-abundant or moderately stressful sites, since it is a resource-managerially conservative strategy, which would potentially impede photosynthesis and growth during prolonged periods of reduced water potentials (Reich, 2014; Pallardy, 2008).

Since growth is inhibited –either intrinsically or as a temporary stress response– under *avoidant* strategy regimes, it can have impact on which tree species are suitable for use in an urban context. For instance, drought sensitive species may under persistent drought decrease stomatal conductance to *avoid* physiological drought, or even prematurely induce leaf senescence and abscission to conserve water (Bréda *et al.*, 2006; Sperry, 2000; Parker & Pallardy, 1985). There are however drought resilient counterexamples to this. Pines for instance (*Pinus sp.*), are notorious avoidance strategists whom are adept at regulating stomata and develop deep tap roots in response to dry conditions, particularly *hard pines* of the subgenus *Pinus* (Brown & Lacate, 1961). It is by virtue of being evergreen that they can 'afford' avoidance, as the perennial foliage extends the effective vegetation period beyond that of deciduous trees and theoretically grants them the capacity to grow throughout the whole year, allowing spring and autumn photosynthesis to build a carbon buffer, thus compensating to some degree for droughts or relative inactivity in the summer (Michelot *et al.*, 2012; Maseyk *et al.*, 2008). Regardless of specific adaptation, sub-optimally adapted species, with poor site fitness are more likely to be negatively affected by the stress from urban-type droughts, as they may by consequence of recurring or prolonged droughts, experience stunted growth and ultimately risk decline and death, as a net carbon balance won't be maintainable (Scharnweber *et al.*, 2011; Demchik & Sharpe, 2000; Hawkes, 2000); or by the intensity of the drought, suffer acute hydrological failure and desiccation from xylem-cavitation induced embolism or leaf turgor loss (McDowell, 2011; Maherali *et al.*, 2004); depending on modus of adaptation, one would be more likely than the other.

This model for bivariate drought-induced tree mortality has been elaborated on by McDowell *et al.* (2008) and is based on generalized consequences of physiology, anatomy and metabolism on water stress. When the third strategy of drought *tolerance* is taken into consideration, the model can be reworked to illustrate the strategy's situational potential in counteracting intermediate forms of drought (Figure 2). Since tolerance strategies acts to extend the hydrological thresholds of nominal photosynthesis, its associated traits have been suggested as being more accurate and reliable predictor of tree performance under conditions of moderate drought (Mitchell *et al.*, 2013; Bartlett *et al.*, 2012b).

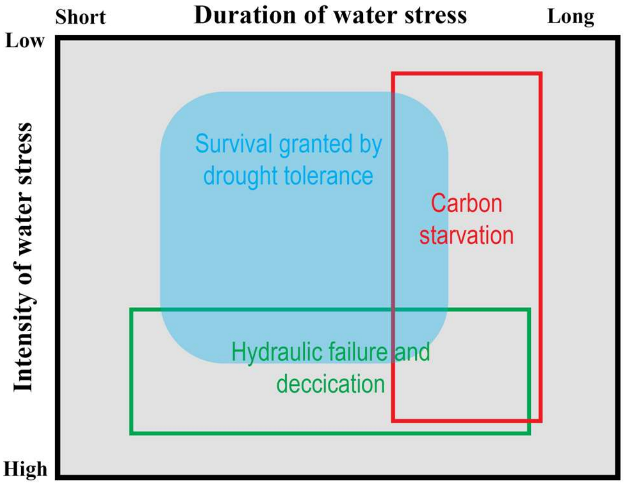

Figure 2. Conceptual model of drought tolerance strategies' role in mitigating fatal drought scenarios. Modified from (McDowell *et al.*, 2008).

Metric of drought tolerance assessment

Seeing as plant survival under drought can be the effect of several contributing strategies and acting mechanisms, which may or may not be interdependent and acting on different time scales, it has historically been a difficult property to measure and develop models from that can accurately account for a potential plethora of traits (Anderegg *et al.*, 2012a; McDowell *et al.*, 2011).

Examples of approaches to assess drought tolerance includes investigations of: proxies for fitness by growth, such as tree ring studies of growth over time in relation to severe drought events (Zang *et al.*, 2014; Adams & Kolb, 2005), plant economic traits such as wood density (Hoffmann *et al.*, 2011), carbon metabolic consequences of prolonged periods of reduced stomatal conductance by carbon isotope discrimination (Levanič *et al.*, 2011), but also in-plant hydrological traits such as leaf osmolality and xylem resistance to embolisms caused by cavitation, which mitigates adverse effects from negative water potentials by preserving symplastic-derived leaf turgor, and vascular integrity under drought conditions (Cochard *et al.*, 2013; Bartlett *et al.*, 2012a). The two latter traits are typically pronounced in genotypes that regularly experiences decreases in internal water potential, which is why anisohydrocity is somewhat analogous to drought tolerance (Hochberg *et al.*, 2017).

In the quest to find accurately representative plant properties linked to drought tolerance, intrinsic traits ought to be preferred over *ex post* mechanistic consequences of drought. This gives prominency to the latter hydrological traits, as both are *de facto* directly linked to a tree's hydrological interactions with its environment by allowing for gas exchange and active photosynthesis to be sustained under more negative soil water potentials through the mechanisms of leaf osmotic adjustment and vascular cavitation resistance (Mitchell *et al.*, 2008; Maherali *et al.*, 2006). The fact that such hydrological traits have been shown to be highly correlated with threes' vulnerability to climate-change-like drought events (Adams *et al.*, 2017), as well as being linked to adaptation to specific climatic biomes (Bartlett *et al.*, 2012b; Bréda *et al.*, 2006), makes them potentially valuable and robust tools for evaluating the drought tolerance of prospective future urban tree genotypes by leveraging the increased sample throughput potential of novel screening techniques, such as vapor-pressure osmometry to establish drought tolerance of leaves by turgor loss point (TLP)[ψ_{P0}] (Sjöman *et al.*, 2015; Bartlett *et al.*, 2012a). Additionally, TLP holds significant advantages as a singular 'higher order' trait due to its association with more fundamental leaf hydraulic traits, while exceeding these in explanatory power of overall drought tolerance, as it's a tangible quantitative measure of a tree's physiological limitations (Bartlett *et al.*, 2012b).

1.1.4 Urban tree selection

The urgency of global warming and rapid urbanization has spurred the academic discourse of urban trees to focus on solving the issue of effectively maintaining an urban forest in spite of increasingly harsh conditions, e.g. by identifying innately drought tolerant species, as well as characterization of the traits that confer said stress tolerance (Calfapietra *et al.*, 2015; Sjöman *et al.*, 2015; Sjöman, 2012). But environmental conditions within the urban landscape aren't homogenous; as parks, urban woodlands, shaded urban canyons and paved plazas can be characterized by contrasting hydrological, solar and thermal properties, which translates into separate environmental stressors that contributes to the site-specific growing conditions (Rotem-Mindali *et al.*, 2015; Coutts *et al.*, 2013; Compagnon, 2004). This adds complexity to the selection process beyond that of mere suitability for dry conditions. Successful tree establishment and long-term survival are thus largely determined at a management level, by the proper matching of tree species and site.

Sustainable tree selection – past and future

"Sustainability" is a term that sees widespread usage, with potentially broad definitions; to understand what encompasses 'sustainable tree selection', one should first define the overarching framework of the sustainable urban forest, to which it carries relevancy. *The Sustainable Urban Forest Guide* defines it as following:

> "**The Sustainable Urban Forest** includes everything needed to assure that the entire forest system achieves and maintains a healthy overall extent and structure sufficient to provide the desired benefits, or ecosystem services, over time" (Leff, 2016).

The tree selection process is therefore a critical aspect of sustainable urban forestry management, as a means to realize sustainable strategies that facilitates for, as well as leverages the inherent longevity of trees; since if young trees are planted and fails to reach maturity within a practical timeframe, or if a maturing tree of dubious site resilience suddenly dies, the investment and effort becomes rather forfeit as the trees won't be able to adequately provide value by living up to set aesthetical or utilitarian expectations, necessary to achieve the strategy goals.

With the accelerated urbanization of the 20th century, conditions and circumstances for tree selection have shifted with the growth of the modern city. For instance, the mature trees of contemporary urban forests are largely a historical legacy from a bygone era, partially attributable to urban development fragmenting previously forested areas and incorporating remnant patches of trees to the growing city (Nielsen *et al.*, 2017); but this historical preference for urban sprawl also meant that trees could, at the time –before urban densification became a factor of relevance, be planted with more confidence as soil- and water conditions would've remained fairly favorable for tree growth due to less frequent points of conflict with existing buildings and infrastructure elements (Gunnarsson, 2015). In Scandinavia this legacy is manifested by the urban forests having a considerably high proportion of native mesophytic species growing in street environments (Sjöman *et al.*, 2012c). However, as these trees can be assumed to have been established under more favorable conditions than a present-day tree would, it remains risky to use these 'snapshots' of mature urban tree assemblages as predictors of the reliability of native species in any modern urban context. To the contrary it has been emphasized how poorly equipped North-European tree species are in dealing with the pending threats to urban trees (Sjöman *et al.*, 2016). The challenge going forward would therefore be the appropriate integration of suitable and drought tolerant ecotypes, of primarily non-native tree species, to adequately improve urban- as well as overall tree resilience.

Tree selection as product development – supplier's perspective

Competition in the nursery sector has elevated the importance of *cash-cow*[2] products to maintain profitability, thus available nursery stock is usually to a significant degree determined by what's in high demand and *in vogue* for clients dealing with large-scale green infrastructure- and urban development projects (Conway & Vander Vecht, 2015). This leaves little headroom for promotion of marginal products and development of prospective new *cash cows*.

The necessity to amend urban tree diversity is however not unheeded from the supply side, as product development is an enduring concept to strengthen competitive edge. Even still, there's a tendency for unsatisfactory nursery offerings as to how it matches urban forestry and –planning demand, since ease of production for certain species segments and the intricacies of forecasting demands contributes to a noticeable market inertia (Sydnor *et al.*, 2010). The matter of product development is, notwithstanding its urgency, subject to a number of bottlenecks that hinders efficient deployment of potentially superior genotypes of amenity trees. Besides aforementioned market inertia, the actual time and resources involved in evaluating the potential of each genotype can be significant hurdles, as factors such as the mere lifespan and drawn-out development phases of trees delays any trial results. The costly approach has acted prohibitively to development and deployment of niche product segments that would cater to small markets, due to their lower profitability (Sundbom, 2013); and the success of future *cash cows* may be elusive

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[2] '*Cash cow' is business [terminology] for a business venture that generates a steady return of profits that far exceed the outlay of cash required to acquire or start it* –Wikipedia

as it’s contingent on proper market penetration in order to give a proportional return on investment.

Sourcing of new genotypes

Working from the assumption that tree nurseries have limited offerings to substantially improve urban tree diversity given currently available nursery stock; where does one go to find novel genotypes or ecotypes?

The necessity of the matter has already incentivized more directed scientific ventures, such as exploratory field studies to gather data –and ultimately plant material– that would aid in species selection of potentially innately resilient tree species and ecotypes, by matching species and functional types to habitat ecology (Sjöman *et al.*, 2012b; Sjöman *et al.*, 2010). Botanical gardens and other arboreta have been suggested as prime examples of third parties to be included in this effort, whose resources could warrant more thorough investigations as sources of new urban trees (Sjöman *et al.*, 2017). This would make for a more regionally-bound approach, supplementary to the aforementioned field studies and subsequent seed collections. As botanical gardens hosts plant material not only wild-collected on their own expeditions, but typically from other expeditions as well (due to seed exchanges with fellow botanical gardens), there’s opportunity for wide taxonomic representation of species, as well as wide geographical and ecotypical representations of conspecific proveniences. Hence, in such extensive collections of woody plants one would be likely to find ample material for evaluation; and due to the diversity of specimens, accurate record-keeping and ostensibly proven local hardiness, these collections offers significant prospects for studies that could efficiently aid in both *vertical-* as well as *horizontal* urban tree selection (i.e. the selection of superior new conspecific genotypes and new species respectively).

Means of investigating the resiliency potential of future urban trees may involve characterization of physiological drought tolerance traits that could serve as a basis for screening protocols for rapid selection of tree individuals with distinguished aptitude for drought tolerance. One such screening method is the measuring of leaf osmotic potential at full turgor in order to infer the plant’s turgor loss point, and while studies of taxonomic variation of TLP have been investigated at an intra-genus level (e.g. Sjöman *et al.*, 2015; Corcuera *et al.*, 2002), little is currently know how this mode of drought tolerance might vary between differentially adapted populations of a given species.

Scientific obscurity may however become an unexpected limitation for such studies if tree species with insignificant bodies of knowledge are investigated primarily, as it could bring difficulties to the appropriate contextualization of the resulting dataset in a broader sense; this would risk becoming the case for exotic tree species. Instead, rather thoroughly familiar species ought to be elected at an initial stage for such pilot studies, as a 'model organism' so to speak –for which common forestry tree species fits the bill.

A suitable, prominent forestry species from a Swedish viewpoint would be silver birch (*Betula pendula* Roth.), which along with downy birch (*Betula pubescens* Ehrh.) make up ca. 66% of Sweden's entire deciduous tree growing stock (Fridman & Wulff, 2018), with the added benefit of a wide, nigh cosmopolitan distribution throughout the temperate and boreal northern hemisphere. It is also an important tree to the urban fabric in the northern countries, accounting for almost 11% of all urban trees in a 2012 survey of 10 major Nordic cities (Sjöman *et al.*, 2012c). Though it has an increasing presence and importance with higher latitudes (Tampere 61°N, 39%), where the climate becomes more boreal in character; as is also the case with the Swedish city of Umeå (63°N), where birches accounts for over 90% of all street trees (Umeå Municipality, personal communication), a historical heritage that has earned the city the reputation as '*The City of Birches*'. The botanical worth of the genus has also been appreciated by scientific institutions, among which Ness Botanic Gardens (NBG) in the UK stands out, having a significant collection of birches, as the genus has been among the preferred areas of study for its prolific acting botanist Hugh McAllister, whom in 2013, along with Kenneth Ashburner authored one of the latest taxonomic treatment of the genus in their first edition of: *The Genus Betula: A Taxonomic Revision of Birches*.

1.2 Aims and objectives

Currently market-available tree species are used preferentially in cities according to how well they are understood to tolerate the urban setting. Within the trade- and academic circles this knowledge has become fairly well-established and is continuously expanded upon through empiric observations of vitality and survival rates. But strategic urban tree selection is still fairly unexplored academically, including evaluation of the innate potential of single species and their ecotypes, which has been neglected and warrants more investigation.

The aim of this this is therefore:

> To examine how knowledge of tree species' various ecotypes could contribute to the selection of new genotypes suitable for use in the urban landscape, by investigating:

- How does the estimated drought tolerance by *turgor loss point* (TLP) vary in *Betula pendula s.l.* specimens of different geographical origins?
- How does the observed drought tolerances relate to the local climate and seasonal water balance from where the birches were collected?

1.2.1 Implementation and delimitations

The practical part of this thesis centers on the investigation of drought tolerance as plant trait, within the experimental confines of what's effectively a *common garden experiment*[3]. Silver birch was elected as model species of investigation due to its numerousness in NBG's collection, including their wide geographical representation of proveniences. TLP is a leaf trait that's supposedly closely tied to drought tolerance at a physiological level; though drought tolerance can also be inferred from morphological factors such as vitality and growth, but such methodologies were excluded from the study as they rely more on longitudinal approaches to establish a baseline in growth response etc. In fact, screening of TLP was purposefully chosen because of its evident advantages of sample throughput and result robustness as 'snapshots' of plant tolerance to low water potentials, which also offers extended flexibility since one is not overly reliant on elaborate trial setups to generate useful data.

While there are additional abiotic stress factors that affect climate- and habitat suitability in our cites, focus herein is on drought tolerance and drought ecotypes, as it's a generally common factor to the urban landscape globally, regardless of geography. The route of tree selection, from site identification to ultimate plant introduction, can be a long one, with many factors determining the end result. Because of this, the study mainly concerns itself with the physiological, phytogeographical and climatological factors that influences a tree genotype's potential for future use in our urban landscapes. Additional factors, such as the biomolecular basis for drought tolerance traits, as well as influencing market aspects such as economic viability and market demand, are thus outside the scope of this study. The main purpose is instead to add to the scientific understanding relevant to the directed effort of procurement of valuable tree genotypes. The intended target group for its content however, are people with backgrounds in either *natural sciences* or *landscape architecture* with interest and curiosity of the topic, or dendrology in general.

It should also be added that the subject matter in this thesis is mainly discussed in a North-European climatic and urban context, which is mainly temperate and boreal. Which is why I, for comparative parity's sake, have mainly referenced studies pertaining to this region and adjacent biome types.

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[3] Common, as in 'mutual', not 'ordinary'.

2 Materials and methods

2.1 Birches

Birches are deciduous shrubs and trees of the genus *Betula* native to the northern hemisphere and a common element in temperate and boreal forests (Ashburner & McAllister, 2016). It forms, along with the genera *Alnus*, *Corylus*, *Carpinus*, *Ostrya* and *Ostryopsis* the plant family *Betulaceae*, which is part of the order *Fagales*, making them close relatives of other plant families native to temperate regions, such as *Fagaceae* and *Juglandaceae* (Soltis *et al.*, 2011).

Most birches are short-lived and fast-growing pioneer species, with exception for the clade of dark-barked birches such as *B. alleghaniensis* and *B. lenta*, which are more shade tolerant and typical of secondary stages of forest succession (Ashburner & McAllister, 2016).

2.1.1 Betula pendula

The silver birch (*Betula pendula* Roth.) is a deciduous tree species native to temperate and boreal forests throughout Eurasia, as well as western North America. It is capable of reaching heights upward to 30 meters and can be recognized by its smooth white bark and upright habit with pendulous branches (Ashburner & McAllister, 2016).

Silver birch share overlapping distribution with the similar species downy birch (*Betula pubescens* Erhr.) throughout most of Europe, and they can be difficult to tell apart by morphology for the untrained eye. Although the latter is more typical for cool and wet locales, while *B. pendula* has preference for slightly drier habitats with ‘light’ soils, such as sandy and stony soil types that are fairly well-drained. (Beck *et al.*, 2016; Atkinson, 1992).

Throughout its range, *B. pendula* is regarded as one of the definitive pioneer species (Ashburner & McAllister, 2016). It is quick to colonize primary- and secondary successions, as seedling recruitment is favored by the newly disturbed soil and ample sunlight, which incidents such as forest fires, landslides or logging would bring (Perala & Alm, 1990). This characteristic is facilitated by the birch's ability to produce large quantities of wind-dispersed seeds, as well as its opportunistic utilization of available resources when compared to late successional vegetation (Davies & Pigott, 1984; Fries, 1984).

2.1.2 Fossil history and genus origin

The progenitor of what we today recognize as the plant family *Betulaceae* is believed to have originated near the end of the Cretaceous period. Going into early Paleocene *Betulaceae* diversified rapidly, giving rise to the ancestral lines of its current constituting genera, including *Betula* which diverged from the common lineage around 50-70 million years ago (Chen *et al.*, 1999). Fossil records indicate Beringia as a plausible center of origin; from there *Betula* quickly became a circumboreal genus as it spread latitudinally throughout the Eurasian and North American continuous temperate forests of the late Tertiary (Ashburner & McAllister, 2016; Crane & Stockey, 1987).

The early birches shared characteristics with today's subgenus of dark-barked birches *Aspera*, indicating the subgenus as being phylogenetically more basal when compared to the subgenus of white-barked birches *Betula*, as these don't share as many of the typical ancestral characteristics, having more derived traits (Ashburner & McAllister, 2016). The white bark birches are thus more recent and are believed to have evolved 7-10 million years ago (Denk *et al.*, 2005), while the earliest fossil record of the progenitor of the European silver birch is from the late Pliocene/early Pleistocene, ca. 2 million years ago (Bennike & Böcher, 1990).

With the onset of the Pleistocene glaciations, the continuous temperate forests that up until that point had dominated the Eurasian continent diminished, becoming fragmented as a consequence of the cooler and drier climate (Ashburner & McAllister, 2016). This effect is today most noticeably exemplified by the arid regions of Central Asia and North-western China. While northern latitudes saw reduced diversity, the climate change also promoted species vicariance as plant populations became divided and gradually withdrew to various refugia, where differentiation in isolation has contributed to the modern diversity of temperate tree species by the process of allopatric speciation (Qian & Ricklefs, 2000).

During the last glacial period, birches could be found near the glacial front, growing in the boreal woodland of the steppes and forests of central Europe (Willis *et al.*, 2000). With the end of the ice age, as the glacial front retreated, *B. pendula* became one of the first tree species to colonize the new land (Ashburner & McAllister, 2016). Molecular evidence indicate that ice-front adjacent populations were the primary colonizers, spreading north as the climate improved, eventually converging with other colonization fronts and relict populations (Palmé *et al.*, 2003).

2.1.3 Taxonomy of Betula

A clear taxonomy of birches has historically been difficult to articulate, though modern taxonomic and phylogenetic overviews have aided in elucidating the matter by investigating the genus' infragenetics and genealogy (Wang *et al.*, 2016; Järvinen *et al.*, 2004; Skvortsov, 2002). However, Ashburner & McAllister's monograph *The Genus Betula* (2016) details one of the most recent taxonomic studies and subsequent revision on the subject.

They suspected that due to fragmentary collections and herbarium specimens, which failed to properly represent the spectra of transitional phenotypes along the geographical cline, that there had been a general overestimation within the taxonomist community of total number of birch taxa, particularly in regards to the circumpolar white-barked birches. One of the goals of the monograph was therefore to illuminate taxonomic uncertainties by identifying synonyms, resolving these and classify them by living material and cytological analysis, instead of by primarily herbarium specimens. The revision resulted in a reclassification of previously over 60 species into 46, as well as alterations to Skvortsov's (2002) previous subdivision of the genus (Table 1). The new subdivision split the genus into four separate subgenera and eight sections.

Table 1. *Subdivision of the genus Betula*

Subgenus	Section	Species
Nipponobetula	*Nipponobetula*	*corylifolia*
Aspera	*Asperae*	*schmidtii, potaninii, caricola, chichibuensis, bomiensis, delavayi, skvortsovii, chinensis, globispica, fargesii*
	Lentae	*lenta, alleghaniensis, grossa, insignis, murrayana, medwediewii, megrelica*
Acuminata	*Acuminatae*	*luminifera, cylindrostachya, alnoides, maximowicziana*
Betula	*Dahuricae*	*nigra, dahurica, raddeana*
	Costatae	*costata, ermanii, utilis, ashburneri*
	Betula	*pendula, populifolia, fontinalis, celtiberica, cordifolia, papyrifera, pubescens*
	Apterocaryon	*nana, michauxii, glandulosa, pumila, humilis, fruticosa, gmelinii*

Taxonomy of Betula pendula s.l.

The complex of Eurasian silver birches have confounded taxonomists for some time; while distinctive features and intermediate forms have been observed, they were rarely recognized as clinal forms and part of a large-scale continuum of the same species (Hultén, 1971; Jansson, 1962). Silver birches were thus frequently independently classified instead of being ascribed to any established taxa, but through comprehensive review of herbarium specimens Ashburner & McAllister (2016) identified a total of 32 taxa that they concluded were synonymous within the *Betula pendula* aggregate.

To resolve that the birches throughout the species' geographical range are distinguishably different in appearance while preserving useful terminology, Ashburner & McAllister proposed three subspecies of *B. pendula* sensu lato: *ssp. betula*, *ssp. mandshurica* and *ssp. szechuanica*, representing the extremities of the contiguous populations of Europe, East-Asia and South-west China respectively (Figure 3).

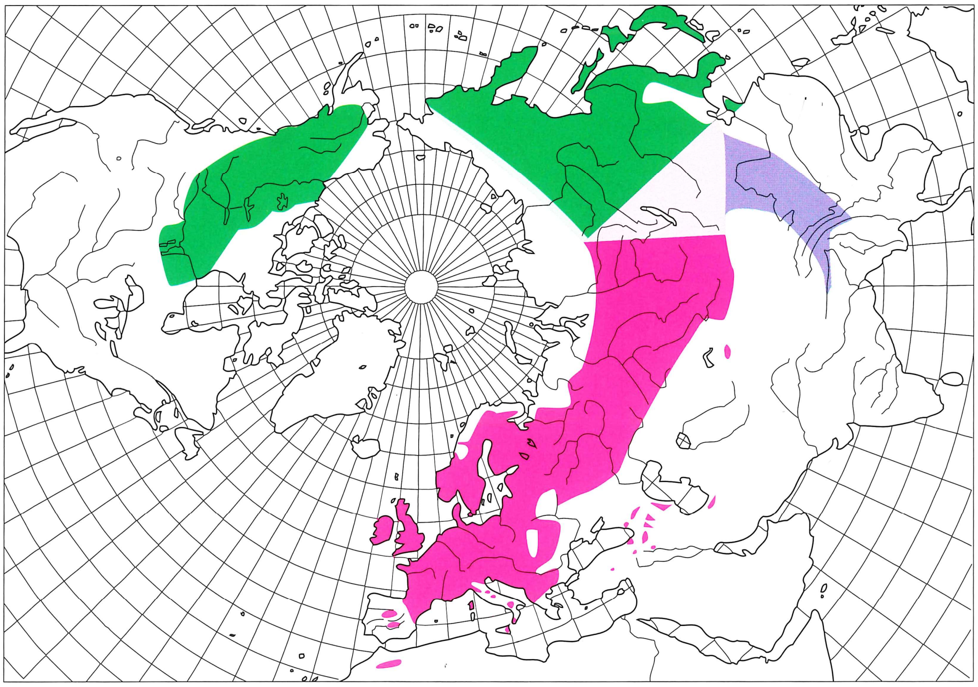

Figure 3. Geographical distribution of *Betula pendula* s.l. 🟪: *Betula pendula ssp. pendula* 🟦: *Betula pendula ssp. szechuanica* 🟩: *Betula pendula ssp. mandshurica.* The area where the subspecies interface hosts intermediary forms of the species. (Ashburner & McAllister 2016). Used with permission: © RBG Kew.

2.2 Plant material for investigation

Plant specimens were procured on the 9th of August 2016, at Ness Botanic Gardens UK (NBG), located near Liverpool in north-western England. NBG hosts a large collection of birches with documented origins, sourced from their own botanical expeditions as well as seed exchange programs with other botanic gardens and collectors. Silver birch (*B. pendula s.l.*) was selected as species of investigation due to its relative habitat ubiquity and large geographical range of distribution. The chosen specimens represented the width of the species' distribution across the northern hemisphere (Figure 4), which included six *ssp. betula*, five *ssp. mandshurica* and two *ssp. szechuanica*, for a total of 13 different proveniences of silver birch (Table 2).

The birches were situated in a park landscape as well-established trees in various group constellations where birches of the same origin were clustered together, the understory of which consisted of grass and/or bramble. The below-ground conditions were deemed typical for a park, with fertile soil and without any apparent restrictive elements in the root zone in regards to root growth and the access to water and nutrients.

Table 2. *Origin and assigned taxa of investigated birch specimens*

Provenience	Country	Subspecies	Approx. geo coordinates		*n*	Ness ID
Listvyanka	Russia	ssp. mandshurica	51.86°N	104.87°E	3	6808
Kuril Islands	Russia	ssp. mandshurica	45.10°N	147.88°E	5	2409
Furano	Japan	ssp. mandshurica	43.33°N	142.35°E	5	3915
Alberta	Canada	ssp. mandshurica	52.68°N	113.49°W	3	3965
Gonggashan Xiang	China	ssp. mandshurica	29.47°N	101.54°E	3	386
Basongtso	China	ssp. szechuanica	29.99°N	94.01°E	3	6293
Paoma Shan	China	ssp. szechuanica	30.04°N	101.97°E	5	5689
Novosibirsk	Russia	ssp. pendula	54.82°N	83.11°E	2	3935
Valais	Switzerland	ssp. pendula	46.19°N	7.31°E	2	3933
Carmolangan	Italy	ssp. pendula	43.96°N	7.74°E	2	3931
Horní Bečva	Czech Republic	ssp. pendula	49.44°N	18.30°E	3	6805
Hauho	Finland	ssp. pendula	61.15°N	24.59°E	2	3930
Mt. Etna	Italy	ssp. pendula	37.77°N	15.05°E	5	3926

Figure 4. Growing locales of the investigated birch proveniences.

2.3 Turgor loss point

Sun-exposed branches without apparent abnormities or signs of abiotic or biotic damages were collected from the birches. The branches were cut again, under water, in order to remove any stem embolism caused by the introduction of air due to the equalization of pressure, as well as to prevent formation of air bubbles that could obstruct the vascular flow of the branch. This was performed at least two nodes- or 20 cm distal to the initial cut. While still submerged the twigs were placed in water-filled vials and placed in a cooler and left overnight to allow for full rehydration.

Work resumed the following day after the twigs had rehydrated to full turgor. The method of investigating leaf osmotic potential was adapted from the protocol of Sjöman *et al.* (2015). Leaf discs were excised with a 7 mm cork-borer. This incision was performed in the mid-lamina area, between the mid-vein and leaf margin, avoiding any second- or third degree veins to minimize possible sources of error. The discs were then swiftly wrapped in aluminium foil and submerged into liquid nitrogen, where they were left for at least 2 minutes, allowing for fracturing of the cellular structure. A total of 8 replicates for each birch provenience were processed in this manner, across 2-5 tree individuals per provenience.

When removed from the nitrogen, the aluminium foil envelope was unwrapped, and to increase evaporation and thus improving equilibration time, the leaf cuticle was wounded through puncturing the leaf disc 10-15 times with the end of a sharp-tipped forceps before inserting the disc into the sample well of a vapor pressure osmometer (Vapro 5600, Wescor, Logan, UT, USA) and sealed. The first reading of solute concentration (cs (mmol kg^{-1})) was taken after 10 minutes of equilibration time, followed by repeated readings every 2 minutes until cs was <5 mmol kg^{-1}, at which point the concentration was recorded (Appendix 1).

The concentration was converted to osmotic pressure ($\psi_{\pi 100}$) using Van't Hoff's equation (Eq. (1)), wherein R represents the ideal gas constant, T the temperature in Kelvin, and c_s the solute concentration.

$$\psi_{\mathrm{P}} = -\mathrm{RTc_s} \qquad (1.)$$

This osmotic pressure was used as input to estimate the turgor loss point (ψ_{P0}) through the equation developed by Sjöman *et al.* (2015) for temperate tree species (Eq. (2)), which was based on the original regression by Bartlett *et al.* (2012b).

$$\psi_{P0} = -0.2554 + 1.1243 \times \psi_{\pi 100} \qquad (2.)$$

2.4 Climate

Climate data was collected from weather stations that were located in the geographical vicinity of the collection sites, in addition to being deemed to be representative of the general provenience and macro climate. Approximate collection site couldn't be ascertained for two sites: Kuril Islands and Valais. Weather stations were in those instances selected on the basis by which one was most likely to be climatically representative, from geographical proximity and forest species inventory data respectively (Zimmermann *et al.*, 2009).

All the data, except for the Italian, were sourced from weather stations associated with the World Meteorological Organization's (WMO) global network of weather stations (Table 3). The WMO database couldn't provide complete statistics for all relevant stations, therefore the dataset was completed with data from tertiary sources, in the form of aggregation websites for WMO climate statistics. The Italian statistics of Liguria and Sicily were collected from the regional agencies: *Agenzia Regionale per la Protezione dell'Ambiente Ligure* and *Dipartimento Regionale dell'Acqua e dei Rifuti* whom are charged with the regional environmental protection and hydrology respectively.

The periods of data collection weren't homogenous for all weather stations. In order to adhere to the WMO's system of periods of climate normal, the divergent datasets were truncated so to match the latest period of 1961-1990. If the collection period didn't match, it was instead truncated to include the closest ≤30-year period to the WMO normal (Appendix 2).

In the case of Italy and China there were substantial differences in elevation between the locations of the chosen weather stations and the habitats where the birches were collected, which would give misleading temperatures due to adiabatic cooling with increasing altitude (MacArthur, 1972). To improve the representativeness of the data, the temperature of these locations were therefore adjusted according to the thermal lapse rates for China produced by Li *et al.* (2013) as well as lapse rates derived from linear regressions of data from Liguria and Sicily respectively (Appendix 3).

Table 3. *Summary of proveniences and corresponding weather station from which climate data was sourced. Weather station serial number corresponds to those assigned by WMO for their network, superscript letter corresponds with source reference.*

Provenience	Coordinates	Elevation (m.a.s.l.)	Weather station	Coordinates	Elevation (m.a.s.l.)
Listvyanka	51.86°N 104.87°E	550	Irkutsk,30710 [a]	52.27°N 104.31°E	469
Kuril Islands	45.10°N 147.88°E	n.a.	Yuzhno-Kurilsk,32165 [a]	44.02°N 145.86°E	49
Furano	43.33°N 142.35°E	300	Asahikawa,47407 [c]	43.76°N 142.37°E	140
Alberta	52.68°N 113.49°W	800	Red Deer,71878 [a]	52.18°N 113.89°W	905
Gonggashan Xiang	29.47°N 101.54°E	3500	Jiulong,56462 [b]	29.00°N 101.50°E	2931
Basongtso	29.99°N 94.01°E	3900	Nyingchi,56312 [b]	29.57°N 94.47°E	3001
Paoma Shan	30.04°N 101.97°E	2910	Kanding,56374 [b]	30.05°N 101.96°E	2617
Novosibirsk	54.82°N 83.11°E	150	Novosibirsk,29638 [e]	54.91°N 82.96°E	131
Valais	46.19°N 7.31°E	n.a.	Montana,67240 [d]	46.11°N 7,51°E	1427
Carmolangan	43.96°N 7.74°E	1130	Colle Belenda [g]	43.98°N 7.70°E	1357
Horní Bečva	49.44°N 18.30°E	600	Ostrava,11782 [a]	49.69°N 18.11°E	256
Hauho	61.15°N 24.59°E	100	Lahti,02965 [f]	60.96°N 25.63°E	84
Mt. Etna	37.77°N 15.05°E	2000	Linguaglossa [h]	37.83°N 15.15°E	530

[a](WMO, 2010), [b](TN, 2017a), [c](JMA, 2017), [d](MeteoSwiss, 2016), [e](Pogodaiklimat, 2017), [f](FMI, 2012), [g](RL, 2017), [h](RSODA, 2017)

2.4.1 Variables and indices

Precipitation and temperature

Monthly precipitation and temperature were extracted from the data to allow for further analysis, including potential evaporation and water balance. Total annual precipitation has also been indicated to drive adaptive differentiation in mesic deciduous tree species (Pluess *et al.*, 2016; Marchin *et al.*, 2008). Annual average temperature was also included as an additional descriptive variable.

Potential evapotranspiration

The birch genotypes represents proveniences scattered widely across Eurasia as well as North America, with different climate characteristics. As precipitation- and evaporation drives patterns of global vegetation types (Stephenson, 1998), potential evapotranspiration (PET) was determined in order to compare the atmospheric water demand, i.e. the amount of water that would be evaporated and transpired by plants, given sufficient water availability, which in turn would impact the local water balance, i.e. the balance when PET is subtracted from the precipitation. To compensate for potentially disparate provenience climates, a basic aridity index was calculated as the ratio of precipitation to PET, which previously have seen use when comparing global variation of plant-adaptive traits (Bartlett *et al.*, 2014). PET was calculated according to the empirically derived formula (Eq. (3)) developed by Thornthwaite (1948), using monthly averages in temperature as well as daylight hours, based on latitude. Accurate length of daylight was calculated using the method established by Meeus (1991), facilitated by spreadsheet provided by *The National Oceanic and Atmospheric Administration* (2010).

$$PET = 16\left(\frac{L}{12}\right)\left(\frac{N}{30}\right)\left(\frac{10T_a}{I}\right)^{\alpha} \tag{3.}$$

$$I = \sum_{i=1}^{12}\left(\frac{T_{ai}}{5}\right)^{1{,}514}$$

$$\alpha = (6{,}75\ \times 10^{-7})I^3 - (7{,}71\ \times 10^{-5})I^2 + (1{,}792\ \times\ 10^{-2})I + 0{,}49239$$

PET = Potential evapotranspiration (mm month^{-1})
L = Average daylength
N = Number of days of the given month
T_a = Average temperature of the given month
I = Heat index, derived from average temperature
α = Empiric variable, derived from I

Growing degree days

Using heat sums to describe the parameters of the growing sesason is a common method in the field of horticulture of characterizing the vegetation period in length and amplitude. Though it has also been used in plant geography to compare vegetation patterns and climate (Yim & Kira, 1975). By adding the daily average temperatures that exceeds a set reference temperature, as well as counting the number of days for which the value is >0, one can determine the accumulated ‘growing degree days’ and length of the vegetation period, which influences plant phenology and development (Tuhkanen, 1980). For this analysis it was performed with the commonly used reference temperature of 5 °C. But since the climate data provided was at a monthly-average resolution, it had to be processed to produce estimates of daily averages. This was achieved by employing a Fourier-based interpolation method by Epstein (1991), which uses harmonic analysis to preserve daily interpolations within the bounds of the monthly averages. Seeing as the length and amplitude of the vegetation period detailed by these variables might independently converge amongst the provenieces, the ratio of GDD to length of growing season was calculated as a *heat intensity index*, to more fully characterize the climate by average daily ‘heat’ throughout the growing season.

2.5 Statistical analysis

The statistical analyses were performed using Minitab v18 (Minitab Ltd., Coventry, UK). One-way analysis of variance (ANOVA) was used to determine difference of TLP in the sample population of birch provenieces, followed by Tukey’s HSD post hoc analysis to identify groupings of homogeneity. Climatic variables and index values were used in a multivariate cluster analysis (complete linkage, Euclidean distance) to identify similarities of the climates within the dataset, and a correlation matrix principal component analysis (PCA) was employed to further elucidate which variables were important to describe the climatic differences. The relationship between climate and drought tolerance was investigated by linear regression analysis with TLP as dependent variable and yearly climate variables as explanatory variables, this was performed for the climate variables independently rather than as a combined regression model. To illustrate regional water balance and how it might be affected runoff caused by soil conditions and topographical factors, incremental ‘runoff percentages’ and monthly water balance was visualized in a contour plot. Diagrams were plotted using Minitab v18 (Minitab Ltd., Coventry, UK), as well as Sigmaplot v14 (Systat Software Inc., San José, CA, USA).

3 Results

3.1 Turgor loss point

Leaf turgor loss point was found to vary significantly, between -2,07 and -2,94 MPa across the examined *B. pendula* proveniencal ecotypes; in *ssp. betula* it varied between -2,32 and -2,94 MPa, in *ssp. mandshurica* -2,07 and -2,46 MPa, and in *ssp. szechuanica* -2,18 and -2,34 MPa (Figure 5), with ANOVA yielding $F_{12,91} = 10,33$, $p < 0.001$. Tukey's test determined significant different subsets within the data, which indicated discrimination in drought tolerance, preferential to increased tolerance in the specimens of *ssp. pendula*. Analysis was performed on the subspecifically pooled data to confirm that there was indeed a statistically significant difference at the subspecific taxonomic level (Figure 6). *B. pendula ssp. pendula var. aetnensis* was treated independently in this analysis since it was significantly separated from the other proveniences of the same subspecies. The result confirmed that the 'core' European subspecies (-2,75 MPa) was more drought tolerant than both the Chinese and East-Asian ones (both -2,28 MPa), as well as the Sicilian variety –which was statistically on par with both Asian subspecies (-2,18 MPa), $F_{3,100} = 26,06$, $p < 0.001$.

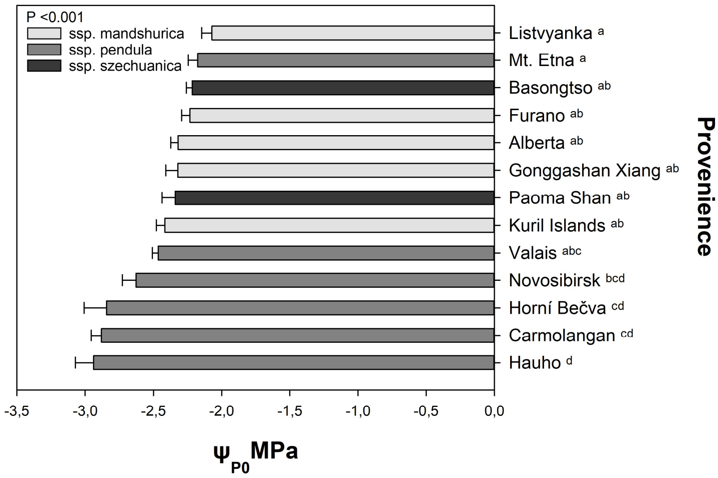

Figure 5. Turgor loss point as predicted by osmometry of fully turgid birch leafs of 13 proveniences. Bars show SE, $F_{12,91}$ = 10,33, p <0.001 across the total dataset according to One-Way ANOVA. Superscript lettering indicate significance at a 95% confidence level as indicated by Tukey's Test.

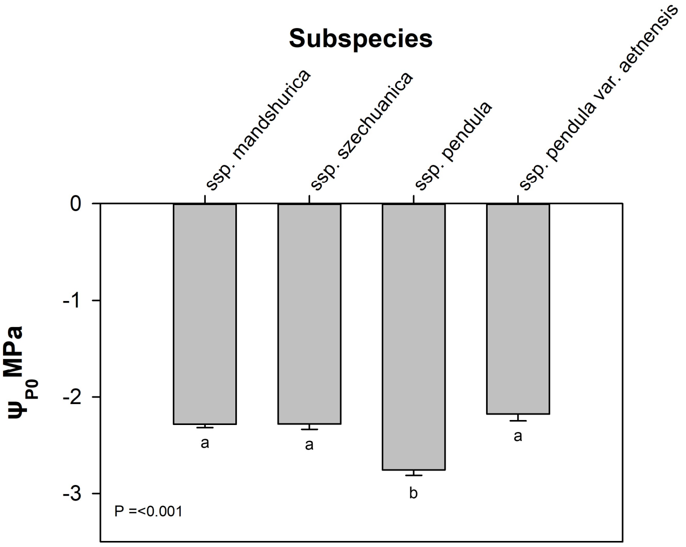

Figure 6. Predicted turgor loss of *B. pendula* subspecies, using data pooled from the 13 proveniences. Bars show SE, $F_{3,100}$ = 26,06, p < 0.001. Letters indicate significance at a 95% confidence level as indicated by Tukey's Test.

3.2 Climate

Yearly accumulated and averaged climate data and -indices showed great variation among the proveniences, with no apparent geography-related patterns (Table 4). Precipitation, yearly average temperature and PET varied between 460-1286 mm year^{-1}, 0-9 °C and 477-612 mm year^{-1} respectively. Growing season and associated growing degree days varied between 154-244 days and 841-1960 GDD, while monthly aridity and heat intensity for the corresponding period between 0,51-2,39 and 4,4-9,8.

Table 4. *Yearly accumulated and averaged climate data.*

Provenience	PET (mm year^{-1})	Precipitation (mm year^{-1})	Average temperature (°C)	Growing degree days[a]	Growing season[a]	Aridity index[b]	Heat intensity index[c]
Listvyanka	497	467	0,0	1245	154	0,72	8,1
Kuril Islands	481	1245	4,7	1130	182	1,96	6,2
Furano	582	1091	6,4	1960	200	1,49	9,8
Alberta	526	470	2,3	1251	179	0,74	7,0
Gonggashan Xiang	528	1010	7,0	1229	231	1,94	5,3
Basongtso	477	748	5,1	841	189	1,56	4,4
Paoma Shan	508	958	6,2	1216	210	1,81	5,8
Novosibirsk	561	460	1,7	1555	170	0,51	9,1
Valais	499	680	5,4	1066	185	0,76	5,8
Carmolangan	609	1286	9,0	1785	244	2,39	7,3
Horní Bečva	612	702	8,2	1851	225	0,95	8,2
Hauho	577	653	4,4	1277	173	0,66	7,4
Mt. Etna	515	1154	6,5	1172	189	0,90	6,2

[a] 5 °C threshold temperature

[b] [Precipitation/PET], averaged for the months exceeding 5 °C

[c] [GDD/Growing season]

In order to further investigate the interrelations of climate characteristics, monthly average temperatures, -precipitation, -PET and water balance, as well as yearly precipitation, PET and water balance was used as variables in a multivariate cluster analysis. The resulting dendrogram quantified similarities in the climatic variables, and a rather conspicuous cutoff point for four separate clusters could be established visually, at a similarity around 66,67 (Figure 7). The West-European, including Russian and Canadian climate made one cluster, the Chinese another, the East-Asian a third and the Italian a fourth. Principal component analysis (PCA) detailed a similar grouping as the cluster analysis (Figure 8) Though its loading plot and adjoining scores allowed for analysis of the impact of each variable on the principle components (Figure 9). The distribution of eigenvectors allowed for a rough estimation of the dominant climate characteristics governing the distribution seen in the scatter plot. But as the number of variables included made the plot rather too cluttered to permit a straight-forward comparison and analysis, the variables were classified according to how and when the influenced the water balance, in order to ease the interpretation (Figure 10). It demonstrated that variables impacting wintertime water balance were dominant for the first quadrant and variables impacting summertime water balance were dominant for the second and fourth quadrant. It thus follows that the common factor for the West-European cluster would be negative water balance during the summer months, a characteristic it shares with the Italian cluster. They are however diametrically opposed along the first component (x-axis), which can be explained by the mild and wet Mediterranean winters disproportionally affecting PC1 and its scoring. The Chinese cluster most prominent characteristic is high water balance during the summer, while the East-Asian cluster remains intermediate in regards to the rest of the dataset. As with the Italian cluster, generalizations can be extracted from the diagram regarding the general climate for the other clusters, where monsoon-affected climates sees heavy summer rains, but sparse precipitation in the winter, and where temperate continental climates are relatively precipitation deficient in the summer and have cold winters.

Plotting of regional water balance for the thirteen proveniences showed the diverse large-scale hydrological conditions under which silver birches grow; where prevalence for water stress is rather high in temperate continental climates, as well as the Mediterranean (Figure 11). The onset of negative water balance under zero surface runoff happens in late spring in most instances, such as: Listvyanka, Alberta, Novosibirsk, Valais, Hauho, Furano and Mt. Etna, while precipitation patterns delays this drought in Horní Bečva and Carmolangan. This contrasts with the Asiatic weather patterns of Basongtso and Gonggashan Xian, Paoma Shan, and to a certain degree The Kuril Islands, where seasonal rain seemingly prevents negative water balance from being caused by evapotranspirational factors alone. The role of surface runoff can be clued from the same plots, as a large runoff coefficient is necessary to cause drought conditions for the Asian proveniences (excluding Furano), while the same conditions would cause water stress earlier in the vegetation period for the already precipitation-deficient proveniences in Europe and Russia; this suggests that water balance in the latter case is strongly dependent on soil conditions and topography in the way it affects distribution of local plant life. Furthermore, the water relations shown in (Figure 11) supports the conclusions drawn from the interpretation of (Figure 10).

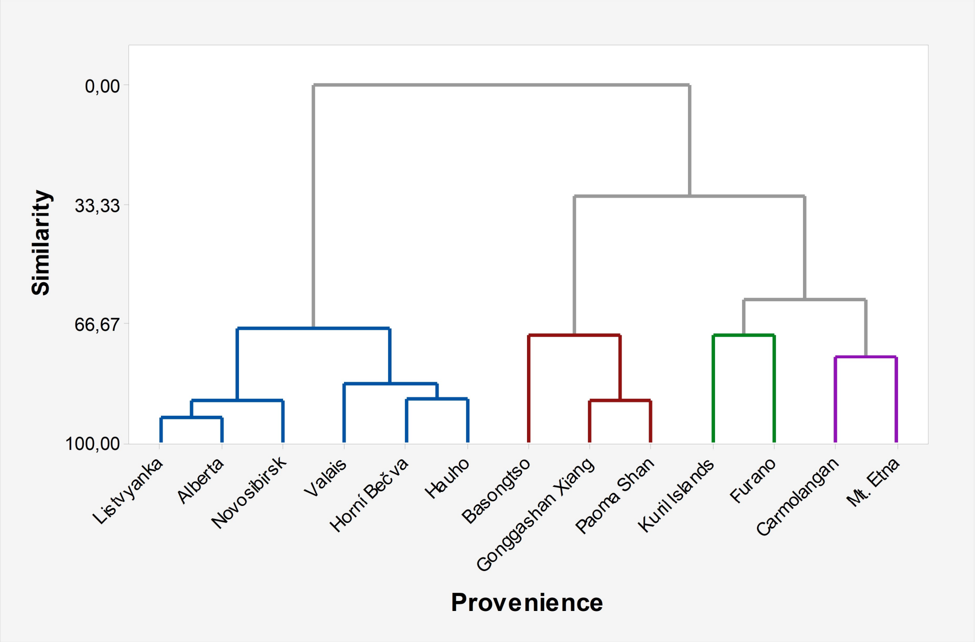

Figure 7. Dendrogram illustrating grouping of birch proveniences according to cluster analysis of climatic variables.

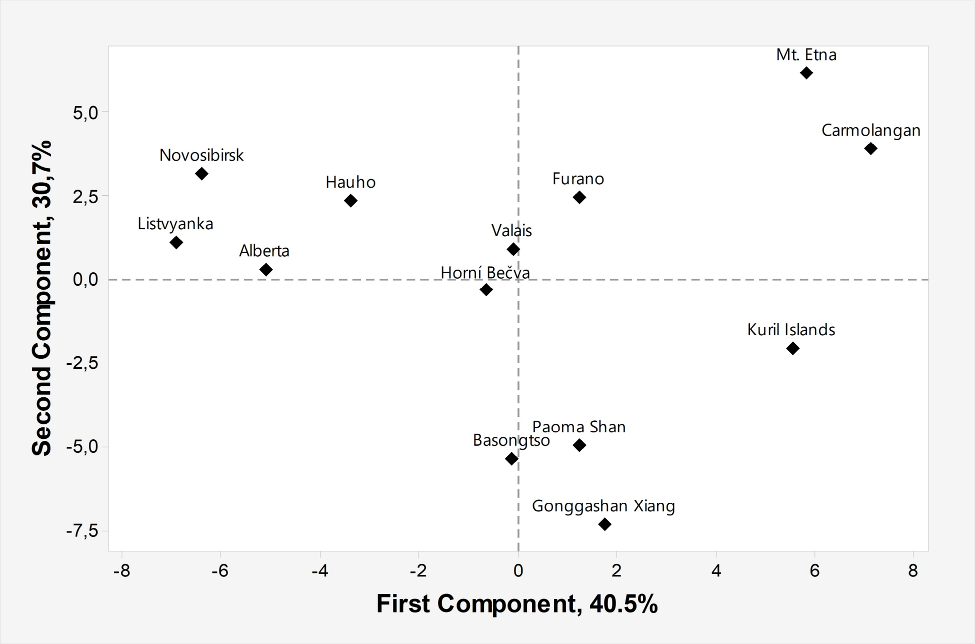

Figure 8. Scatter plot from PCA for the birch proveniences, utilizing the same climatic variables as the cluster analysis (Figure 7).

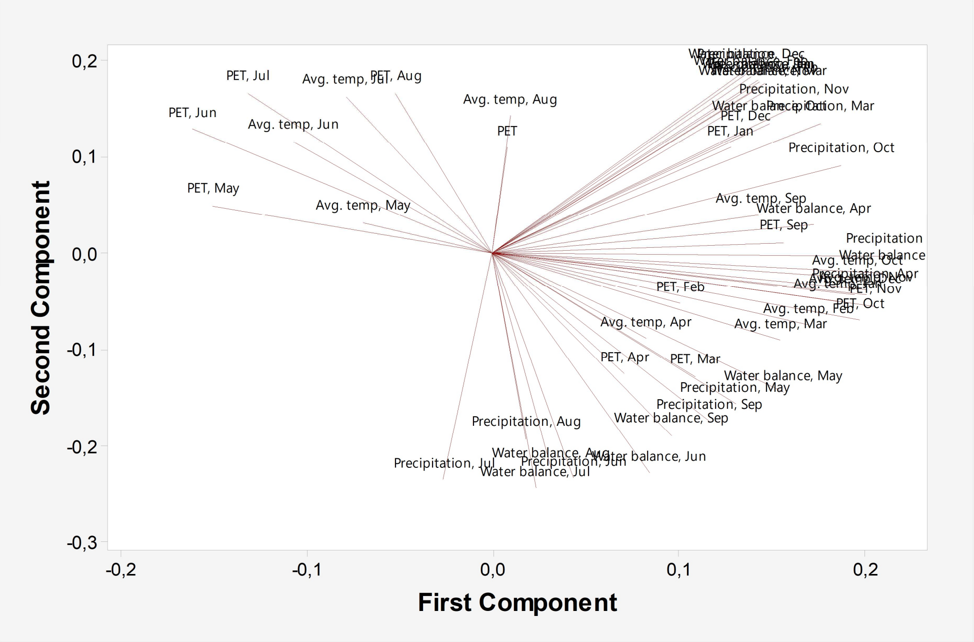

Figure 9. Loading plot of eigenvectors for PCA (Figure 8), showing the vectorial weight of each climatic variable.

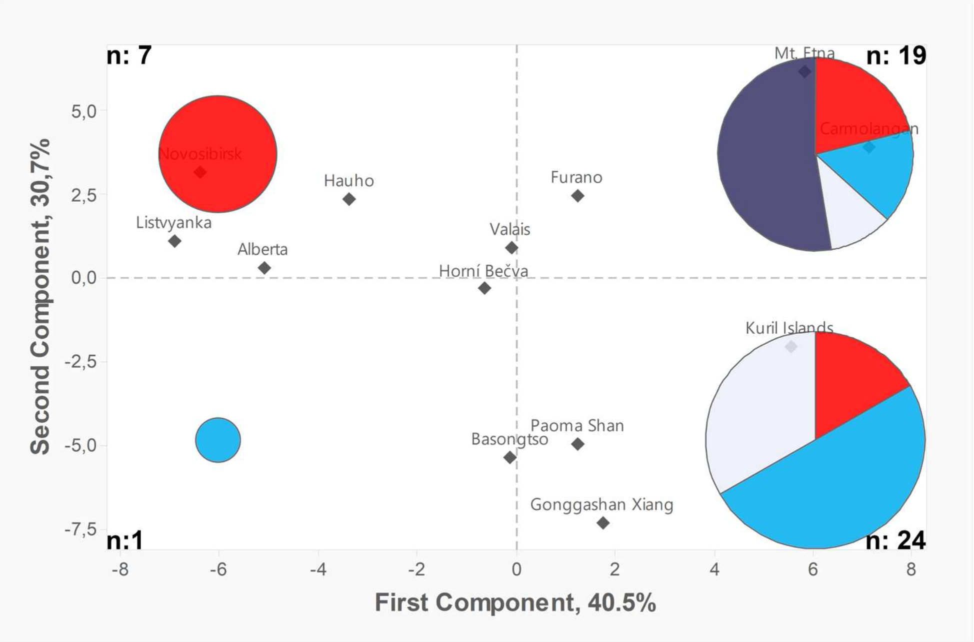

Figure 10. Climatic classification of loading plot, utilizing PC1- and PC2-scores for each quadrant (Figure 9). 🟥: -WB, summer 🟦: +WB, summer ⬜: -WB, winter 🟪: +WB, winter. Pie chart area is proportional to number of variables of that quadrant.

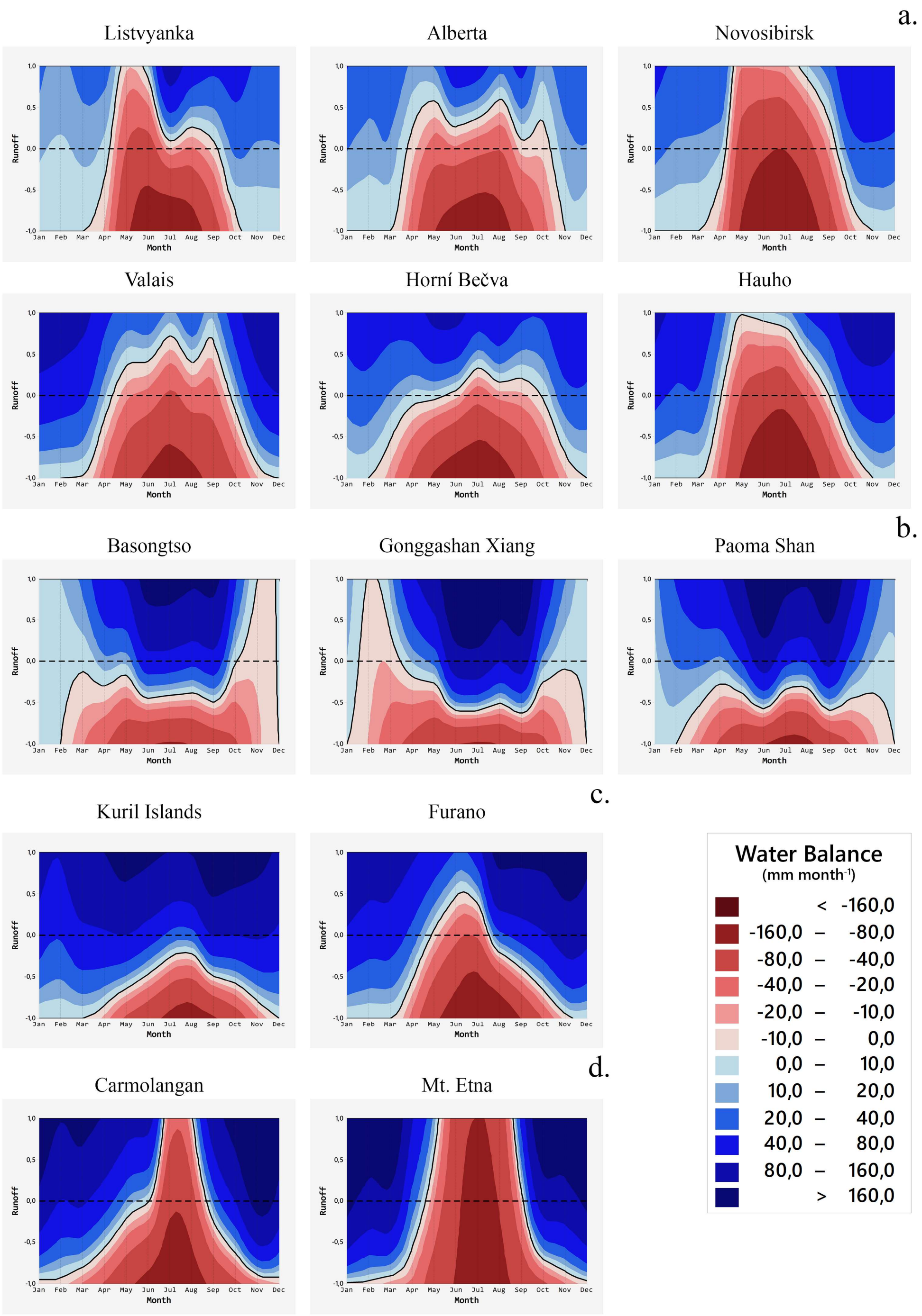

Figure 11. Contour plot of the monthly water balance (mm month^{-1}) for each birch provenience. Y-axis denotes hypothetical positive and negative watershed runoff. Dashed line represents zero runoff, and solid line indicate water balance equilibrium. Plots are grouped according to previously established clustering (Figure 7) a: Western-Europe/North America, b: China, c: East Asia, d: Italy.

3.3 Drought tolerance correlations

Linear regression analysis of TLP as a response of PET showed an inverse correlation, where observed leaf drought tolerance would increase with increased proveniencal annual PET (Figure 12). The inverse relationship was statistically significant at $p = 0.005$ and R^2 of 0.53, which indicates that the model is fairly accurate. No other significant drought tolerance/climate interactions could be established (Table 5). Even though a PET-correlation was observed for the *B. pendula s.l.* proveniences as a whole, the correlation could not be substantiated when the regression analysis was iterated for each subspecies independently (Table 6).

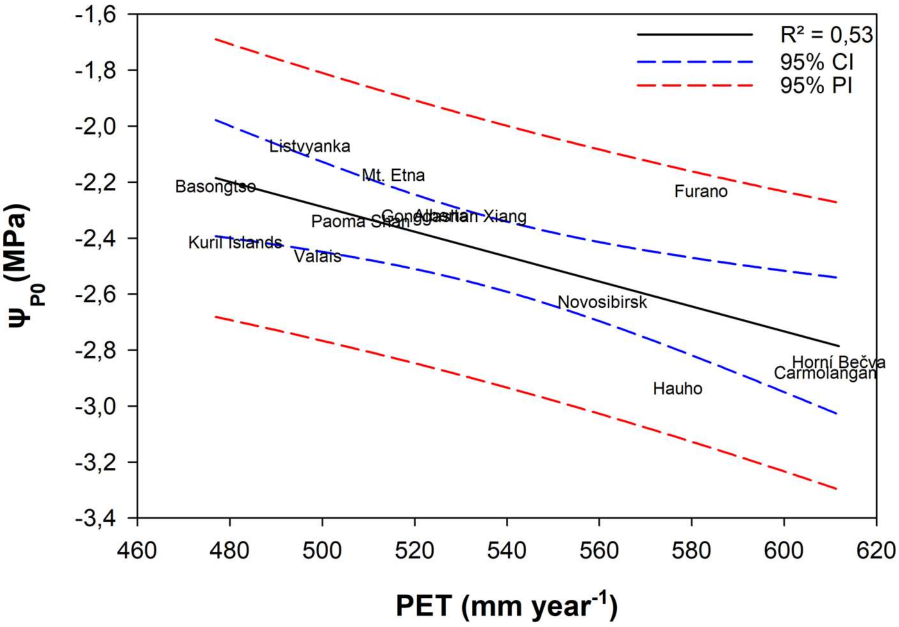

Figure 12. Relationship between drought tolerance (Ψ_{P0}) and potential evapotranspiration (PET). Solid line represents a significant ($R^2 = 0.53$, $F_{1,11} = 12.38$, $p = 0.005$) linear correlation. Blue and red dashed lines represents a 95% confidence- and prediction interval respectively.

Table 5. *Linear regression analysis of TLP-climate interactions.*

	PET	Precipitation	Average temperature	Growing degree days	Growing season	Aridity index	Heat intensity index
R^2	0,530	0,000	0,135	0,197	0,122	0,000	0,063
p	0,005**	0,996	0,217	0,128	0,242	0,987	0,409

Table 6. *Linear regression analysis of TLP-PET interactions for B. pendula subspecies.*

	R^2	p	df_{res}	F
ssp. mandshurica	0,02	0,82	3	0,06
ssp. pendula	0,60	0,069	4	6,07
ssp. szechuanica	n.a.	n.a.	n.a.	n.a

4 Discussion

4.1 Birch drought adaptations

The primary purpose of this thesis was to study the large-scale variation of osmotic adjustment as a drought tolerance strategy in *B. pendula s.l.* In this trait, a separation could be confirmed at the subspecies level, where the European subspecies *pendula* was indicated to have a lower turgor loss point on average than the two Asiatic subspecies *szechuanica* and *mandshurica*.

The reason for this observed difference and its causal genesis may have various modes of likely explanations as to why and when this divergence of adaptive aptitude arose. It may be a ‘remembered’ trait from the recent evolutionary history of *ssp. pendula*, in how it was affected by the Pleistocene glaciations and the ecological implications of growing near the glacial front in the steppe/tundra woodlands that dominated Central Europe at the time (Willis *et al.*, 2000). The dry conditions, as well as poor soils left by retreating glaciers, could very well have exerted significant selective pressure for drought tolerance as well as promoting successive founder events that would favor drought tolerant genotypes as the birches re-colonized the area. Or it may be a trait still under continuous selection and thus an adaptation maintained in response to local conditions. This explanation is supported by the inverse correlation of TLP and PET observed (Figure 12), where climatic evapotranspirational demand is shown to be a possible driving factor for drought tolerance.

Artifacts are however present in the dataset that precludes one from making a definitive call as to which explanation is the most likely. The Mt. Etna provenience is for instance significantly less drought tolerant than majority of the rest of the European subspecies. It is however regarded as a distinct variety: *ssp. pendula var. aetnensis*, which previously was thought of as its own species: *B. aetnensis* Raf. endemic to Sicily, but has as of late become recognized as synonym to *ssp. pendula*

(Ashburner & McAllister, 2016). This relict population have had very limited post-glacial genetic influence on the rest of the European populations, and is effectively isolated to the northern slopes of Mt. Etna at elevations of 850-2100 m.a.s.l. (Bagnato *et al.*, 2014; Palmé *et al.*, 2003). Water relations for these birches may still be excellent, such that adaptations for drought tolerance would be relatively superfluous, in spite of the Mediterranean climate. This would be due to local factors of having Mt. Etna as habitat, as the mountain's geology of porous volcanic rock has been attributed to minimize surface runoff and effectively act as a 'sponge' that efficiently retains the annual water recharge from winter rains and snowmelt, providing ample groundwater to the benefit of plant growth on its slopes (Chester *et al.*, 1985). Furthermore, forest vegetation may see shifts in altitudinal range fairly quickly in response to climate change (Savage & Vellend, 2015). Therefore the Sicilian birches probably wouldn't have been as exposed to persistent selective pressure for drought tolerance, at an evolutionary time scale, as the rest of *ssp. pendula*; as it could've been free to migrate in altitude to adiabatically permitting locales in response to changing climates, thus avoiding the necessity of having to fixate drought tolerance at a population level as a trait.

Another aberration can be found in the data of the TLP-PET regression, where lack of climatic representation for all three subspecies proveniences obscures any possible true correlation at all subspecies levels; i.e. the dataset isn't comprehensive enough to resolve whether it's a true adaptive property or a statistical effect of available samples and their climatic conditions, since no significant correlation could be substantiated for all three subspecies independently. Although this strengthens the conjecture of how the European subspecies would be affected by its ecological history in being conducive for its observed drought tolerance; but a more comprehensive set of sampling materials, representing similar climate gradients at varying –hierarchical– spatial scales for all three subspecies, as well as a complementary genetic analysis, would be necessary in order to fully elucidate the matter.

According to the reproductive tradeoffs in offspring quantity vs. -quality described by the r/K selection theory (Pianka, 1970), most birches would due to their pioneering habitat and fecundity be considered to be strongly r-selected tree species as they are quick to colonize and grow in disturbed habitats and fill empty niches; and by their rapid development can they gain a foothold at the site and produce large quantities of seed before more efficiently competing or more stress tolerant species supplant the birch and its initial dominance (Ashburner & McAllister, 2016; Atkinson, 1992). *B. pendula* has because of these characteristic life history traits been ordinated within Grime's CSR-framework as a primarily ruderate strategist when compared to 36 other European tree species (Brzeziecki & Kienast, 1994). These 'Grimean' qualities of swift resource- (C-strategist) and reproductive turnover (R-strategist) stands ostensibly in direct opposition with what in a broad sense constitutes stress-tolerant plant traits, according to Reich (2014)'s framework of 'fast-slow' plant economics spectrum. E.g. high rate of water use by efficient hydraulic conductivity is a characteristic of mesophytic pioneer species (Aasamaa *et al.*, 2002), and is dictated by vessel size which is correlated with xylem cavitation vulnerability, as well as wood density (Hoffmann *et al.*, 2011; Markesteijn *et al.*, 2011). The drought tolerance of birches therefore seem to be an adaptation to cope with the stress from exposure and radiative heat prevalent to the stages of early forest succession, rather than being a 'permanent' way of upholding growth in drought-prone habitats.

Nevertheless, *Betula sp.* genotypes have in previous studies demonstrated varying degrees of adaptation to drought in their extent of leaf drought tolerance (Ranney *et al.*, 1991), including *B. pendula*, which has also shown support for an increased affinity for tolerance by osmotic adjustment and corresponding growth under drought for North-European *ssp. pendula* clonal genotypes, akin to this study (Aspelmeier & Leuschner, 2004); though the primary plastic response to drought was reduction of stomatal conductance, to conserve hydrological economy, rather than any relating to the leaf osmotic potential. Indeed, *B. pendula* has consistently been observed to respond strongly to reduced water availability by adjusting traits that minimizes water loss, such as stomatal conductance and reduced leaf area (and consequently higher SLA), which both consequently may act significantly restrictive to carbon assimilation and growth potential (e.g. Possen *et al.*, 2011; Aspelmeier & Leuschner, 2006). The species' reliance on morphological adjustments to regulate its hydraulic economy has further been corroborated by a study of genotypic variation in co-occurring trees in a stand, and it was shown to be predominately governed by morphological- rather than physiological leaf traits in how well they grew in response to inter-annual growth conditions (Possen *et al.*, 2014). Even though morphological-physiological interactions were assumed to account for part of the similarities in performance between different genotypes, studies like these highlights the lack of dependence of *Betula sp.* on dynamic drought tolerance traits such as anisohydrocity and osmotic adjustment. Even though species in the genus have displayed differing aptitudes and physiological responses to drought depending on preferred niche habitat (Koike *et al.*, 2003), the genus has generally been noted to lack tolerance for low soil water potentials, while opting for avoidance strategies such as the previously mentioned stomatal regulation, but also premature leaf senescence and abscission as responses to prolonged droughts (Gu *et al.*, 2007; Ranney *et al.*, 1990); even *B. pendula*, which has been described to be typically preferring of well-drained soils, employs such avoidance strategies (Wendler & Millard, 1996). Avoidance strategies can be effective in their own right, as abscission effective prevents fatal water-loss by reducing total leaf area, but ecotypic adaptation towards drought tolerance strategies would allow for maintained physiological integrity and metabolic functioning over a wider span of soil- and plant water potentials (Marchin *et al.*, 2010).

4.2 Environmental gradients and drought adaptations

The importance of adaptive traits to the preservation of tree species populations throughout native distribution ranges under heterogeneous environmental conditions is well-recognized, particularly in light of projected adverse effects of the ongoing climate change (Bussotti *et al.*, 2015). Drought adaptive traits in tree species such as *Acer grandidentatum* Nutt., *Acer rubrum* L., *Fagus sylvatica* L. *Fraxinus americana* L. and *Quercus rubra* L., have been shown to differ between conspecific ecotypes in relation to contrasting positioning along environmental gradients such as habitat type and precipitation (Schuldt *et al.*, 2016; Marchin *et al.*, 2008; Bauerle *et al.*, 2003; Alder *et al.*, 1996; Kubiske & Abrams, 1992).

A particularly nuance picture of clinal plant-environment associations has been provided by a recent influx of published studies of the drought vulnerability of the European beech (*Fagus sylvatica*) and its ecotypic variation across its distribution range, which has provided important data on how drought adaptive traits vary between populations at a global-distribution scale in a species that's akin to *B. pendula*, mesophytic. *F. sylvatica* ecotypes have in these studies been shown to be more drought tolerant by and large from static traits, such as vulnerability to xylem cavitation in response to local climate of precipitation (Bolte *et al.*, 2016; Schuldt *et al.*, 2016), while having a low degree of phenotypic variation of typically plastic traits in response to drought treatments (Knutzen *et al.*, 2015). Strong evidence has also been found for a spatial gradient of ecotypes, from drought sensitive in north-central Europe, to drought tolerance in the southward marginal populations (Cavin & Jump, 2017; Stojnić *et al.*, 2017), where growth proliferation is significantly associated with PET, levels of precipitation and aridity (Hacket-Pain *et al.*, 2016). Even though they're not a part of the more warm-climate South-European marginal populations, eastern marginal populations are too indicated to be more drought tolerant than the nearest latitudinal central counterparts, a property assumed to be linked with the drier summers of the eastern continental climate (Thiel *et al.*, 2014; Rose *et al.*, 2009).

The results of the studies for this thesis are thus in concordance with this wider scope of ecotypic variation, and in addition supports claims of differential physiological adaptation in drought tolerance at an inter-population level, which similarly can be traced to factors of climate and/or geographical history and distribution.

4.3 On refining urban tree selection

The matter of choosing which tree species and cultivars to integrate and fit to the urban landscape is a multifaceted issue, as one has to integrate several domains of tree qualities to the process. These range from *soft qualities*, such as aesthetics and social values, to *utilitarian qualities*, such as habit, shape and size, maintenance requirements and climate-ameliorating potential, to more *immediate qualities* determining survival and establishment potential, such as cold hardiness and drought resiliency (Sjöman *et al.*, 2017). Though, even if there's a tendency of preference for diversity of shape and aesthetics near the 'front-end' of the urban tree sector, the latter qualities should hold primacy overall since they are in essence basal requisites for even coming into eventual consideration for the other 'non-crucial' qualities. The directed selection of new urban trees for market introduction should therefore mainly be focused on finding genotypes of both horticulturally novel- and known three species, with appropriate adaptations considering the increased importance of maintaining ecosystem services in our inner cities. These need to be able to fulfill these said qualities while persevering and thriving in the drought conditions brought on by to the climate- and water balance altering features that are emblematic to these spaces.

Given the potential multitude of options as the where to gather novel and exotic plant material from, a procedure for habitat-based selection was proposed by Sjöman *et al.* (2012a) to rationalize this process and anchor the search of well-adapted urban tree genotypes to a scientific framework. It laid out a 4-step process which combines preparatory desk research and field studies to examine habitat appropriateness that would be conducive for locally drought tolerant dendroflora. More explicitly it consists of: (1) identifying regions with rich dendroflora of similar climate to the area of planned introduction, (2) search for habitats similar in water relations to an urban environment, (3) dendroecological studies to ascertain habitat fitness and development of relevant tree species, (4) collect propagation material for further study of development in a horticultural context.

With this study I'd like to propose a method that potentially could improve the efficacy of this selection procedure. By the association of physiological drought tolerance with climatic atmospheric evaporative water demand by PET, generalized conclusions complementary to steps (2) and (3) can be deduced remotely in advance, during the desk research phase. Using this approach would allow a researcher to cast a wider net when considering prospective habitats of interest, and the numerical nature of the method lends itself to GIS-aided spatial analysis by employing widely available datasets of global climate normal such as WorldClim (Fick & Hijmans, 2017), which along with an appropriate digital elevation model (DEM) allows for fine-scale estimates of PET that takes topography and aspect into account, e.g. (Dyer, 2009). The resulting data of inferred water relations could then be statistically cross-referenced with that of city-centers in the preferred region to yield a wider set if potential habitats to examine further (Figure 13a).

In using species distribution modeling (SDM) software or algorithms, similar datasets and approaches could conversely be applied with forest tree inventory data to predict the potential geoclimatic niche range of species of interest (Figure 13b). These modeling tools have seen extensive use in ecological studies, including predicting present-, forecasting future- and inferring past species distributions and range shifts (Dyderski *et al.*, 2018; Zimmermann *et al.*, 2009; Svenning *et al.*, 2008). Most modeling is done using a standard set of 19 bioclimatic variables that are derived from monthly precipitation and temperatures (WorldClim, 2017); the method is however open to any other predictor variables the user considers viable, including PET (Guisan *et al.*, 2006). Thus SDM may have application in predicting tree survival potential in respect to the urban hydro-climatic landscape. Fine-scale microclimatic data would however be necessary for such modeling to be useful for site-specific recommendations considering the structural heterogeneity of modern cities; such data could however be generated using simulation models (Figure 13d).

The particulars of this study details the atmospheric influence on water relations and the utility of being informed of its characteristics in the methodology of habitat analysis and subsequent tree selection. Though the topographic and edaphic influence on water balance is the remaining puzzle piece to the general availability of water within the habitat as it, post-precipitation, enters the soil and moves through the watershed. Vegetation gradients are usually seen to coincide with shifting topography, and studies have confirmed the differential positioning of drought tolerance functional types in relation to resulting evapotranspiration and soil moisture gradients caused by topographic morphology (Bolstad *et al.*, 1998; Day & Monk, 1974). The local slope and position in relation to the rain catchment area are significant contributing factors to drought-susceptible soil moisture gradients, which re exacerbated by thin soil layers and sharp topographical gradients where lateral water movement outweigh its reloading potential (Yeakley *et al.*, 1998). Ridge-side sites are generally poorer for tree growth as erosion and gravity preferentially causes soil redistribution to lower elevations. Topography has therefore been associated with several aspects of soil quality such as depth of soil profile and availability of nutrients; this consequently has effects on species composition along the resulting topographical gradients, including adaptive traits for water acquisition in relation to site-specific susceptibility to drought (Seibert *et al.*, 2007; Bridge & Johnson, 2000; Yanagisawa & Fujita, 1999).

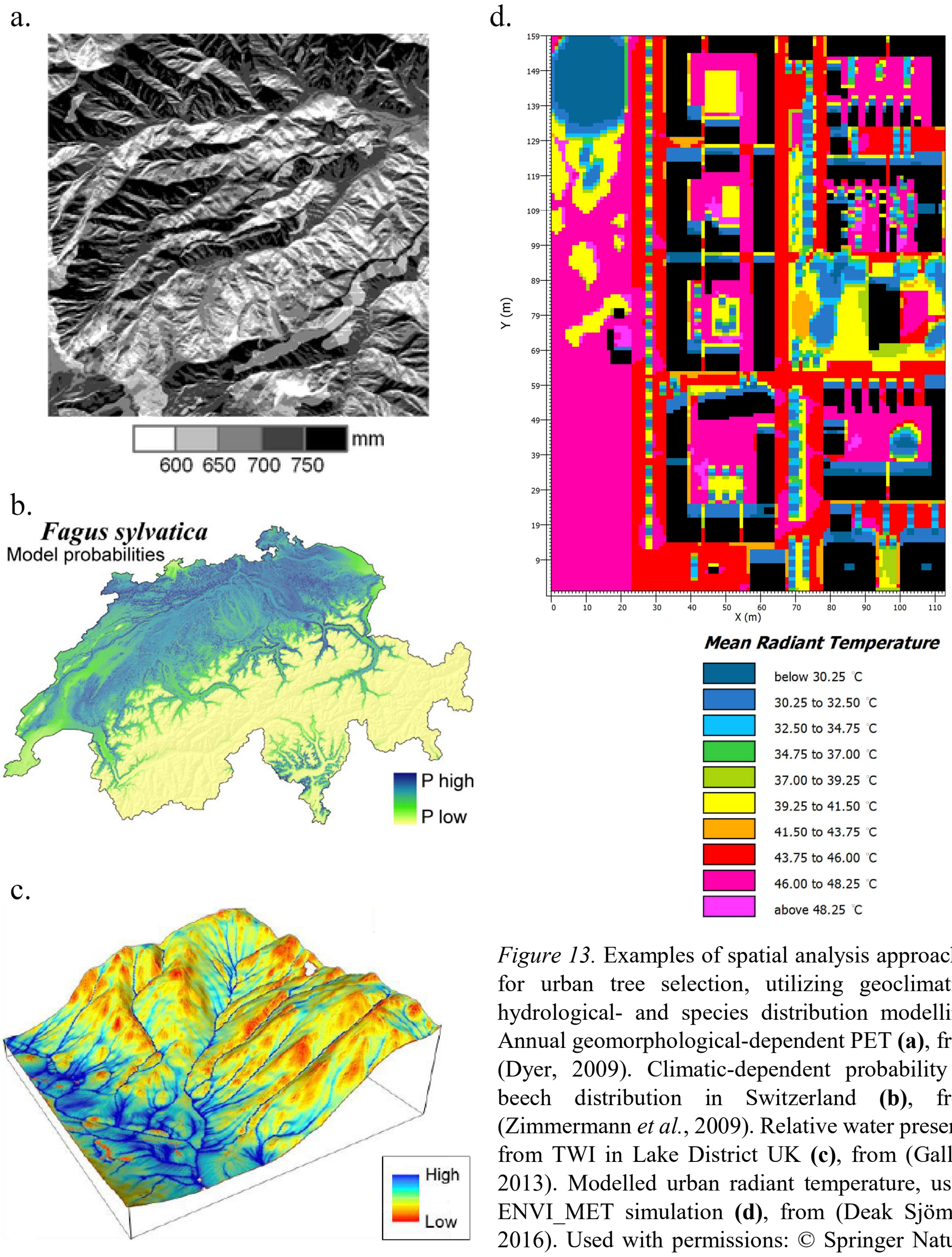

Figure 13. Examples of spatial analysis approaches for urban tree selection, utilizing geoclimatic-, hydrological- and species distribution modelling: Annual geomorphological-dependent PET **(a)**, from (Dyer, 2009). Climatic-dependent probability of beech distribution in Switzerland **(b)**, from (Zimmermann *et al.*, 2009). Relative water presence from TWI in Lake District UK **(c)**, from (Gallay, 2013). Modelled urban radiant temperature, using ENVI_MET simulation **(d)**, from (Deak Sjöman, 2016). Used with permissions: © Springer Nature, © National Academy of Sciences, CC BY 4.0.

Considering these dynamics, it becomes evident that terrain characteristics are determining of local water balance. So in order to gain a more complete picture of how water demand relates to its availability and any causative water stress, one would need quantitative runoff data to amend the model, or at the very least soil type data for a qualitative assessment. Another viable approach to infer topographical effects on hydrology is by using DEM and GIS-assisted modeling of topographical wetness indices (TWI) (Figure 13c), which describes (in relative metrics) the hypothetical lateral water movement as influenced by local terrain (Petroselli *et al.*, 2013; Qin *et al.*, 2011). For this study, in lieu of such data, water balance against a linear runoff gradient was simulated (Figure 11), in order to shed light on the individual provenience's hypothetical water availability and how it may shift depending on soil or terrain. This method could thus in principle be used as heuristic compliment to other qualitative approaches and TWI in the tree selection process when assessing any given habitat and the potential fitness for drought tolerance in its present genotypes.

4.4 The effects of complexity and variability

4.4.1 Climate

A spatio-climatic analysis method is presumably only as good as the representativeness of the data to the actual geographical area that's being investigated. Expected patterns of climatic gradients are known to falter at smaller spatiotemporal scales with increased topographical complexity as altitude increases, due to the effects of orographic precipitation and associated rain shadow (Brunsdon *et al.*, 2001; Whiteman, 2000; Prudhomme & Reed, 1999). Such perturbations of microclimatic factors are thus a relevant concern for this study; due to the coarseness of data used, its validity consequently depends on a relative smoothness in climate homogeneity near the weather stations being used and negligible regression errors. A recent effort by Fick and Hijmans (2017) to generate global climate surfaces by multi-model interpolation further supports this relationship, as statistical cross-validation errors in model estimations were higher in mountainous areas and near coastlines where station density was low. While these estimated errors were highest for precipitation and wind speed, the model had excellent prediction capacity for temperature and thus evapotranspiration (when using a temperature-based equation). This in turn alleviates concern as to the potential magnitude of error in this study caused by suboptimal climate data in relation to intermediate spatial disparities.

Atmospheric evaporative potential by PET served as a backbone for the climate analysis; it's a climate index derived from the physical process of evaporation, which's energy-dependent, hence the inclusion of the temperature variable in Thornthwaite's equation. But it's also a process subject to other forms of energy fluxes than just air temperature, such as local heat fluctuations by radiative sources and air turbulence affecting the vapor pressure gradient near the boundary layer of evaporation. This is why equations based on these physical interactions are generally favored when accuracy is paramount, such as the Penman–Monteith equation, which accounts for wind speed and insolation (Allen *et al.*, 1998; Monteith, 1965), something that's often lacking in equations that are regression-optimized, as is the case with Thornthwaite's. As such detailed data wasn't available in this case the analysis had to settle for the latter, which instead uses average temperature and latitude in a fitted regression function as a shorthand for these interactions, an approach that has been deemed quite satisfactory at larger spatiotemporal scales due to the thermally equalizing effects of weather fluctuations on their corresponding long-term climatic averages (Shaw & Riha, 2011). It does however not detract from the potential risk of generating misgiving PET estimates in cases where the queried regions are particularly prone to extremely clear or cloudy weather, or high wind speeds.

4.4.2 Genetics

Geospatial factors also influence genetic diversity in a tree species at different scales, including the extent of adaptive traits necessary for continued proliferation of populations within its distribution range, as a result of historical migrations and ongoing gene flow (Freeland *et al.*, 2011; Savolainen *et al.*, 2007). Though gene flow has been assumed to act disruptively to the local preservation of adaptive trait alleles, and only as of late has explanatory models for its permissive mechanisms seen improvement by support from empirical genomic evidence (Tigano & Friesen, 2016). In the case of *B. pendula s.l.*, the taxa ha apt capability for extensive geographical coverage in gene flow due to its modus of wind-mediated generative dispersal, which is further compounded by its more or less continuous distribution throughout the Holarctic region. Indeed, birches display a generally lower degree of genetic population differentiation in comparison to other temperate tree species that are more explicitly habitat-associated, or with dispersal strategies not as far-reaching (Maliouchenko *et al.*, 2007; Petit *et al.*, 2003). In spite of such relative 'population homogeneity' among temperate tree species, there are mounting evidence for local genetic differentiation in relation to environmental gradients of precipitation and temperature at micro- as well as macro spatial scales, where active gene flow is assumed, yet adaptive alleles are successfully maintained (Pluess *et al.*, 2016; Roschanski *et al.*, 2016; Eckert *et al.*, 2015; De Kort *et al.*, 2014; Scalfi *et al.*, 2014). The corroboration of fine-scale genetic adaptation in turn validates the genotypic potential of isolated ecotypes as prospective stress tolerant specimens.

However, gene flow may impact phenotypic demography, as is the case where admixture occurs between divergently adapted lineages, resulting in increased variance of clinal adaptations at the interface (De Carvalho *et al.*, 2010). The implications for any urban tree selection scenario is that the resulting area of converging gene flows would host a ‘mixed bag’ of genotypes that would require a more extensive sampling volume (i.e. collection) in order to produce an optimally adapted genotype while fulfilling additional criteria of form and function. This phenomenon further supports the increased utility of searching for well-adapted urban tree genotypes near a species’ ecological limits in marginal populations, as the degree of adaptation increases and any possible deleterious gene flow from core populations are minimized; but it may come with unacceptable tradeoffs in phenotype availability as a consequence of reduction in genetic diversity and competition-associated fitness traits such as growth potential, which instead would motivate selection from intermediately located populations (Price & Kirkpatrick, 2009; Bridle & Vines, 2007; Loehle, 1998). When viewed in this light, there’s reason to question and re-evaluate the potential of botanical collections as contributors of new tree genotypes that would be particularly fitting for urban environments and its limitations. This is because botanical gardens are presumably motivated to collect from areas of high species richness in order to a high taxonomic return, and not necessarily on phytogeographical grounds to gather explicitly stress tolerant specimens. That being said, botanical gardens remain important as promising sources of new genotypes that could make significant contributions to diversity-derived urban forest resilience.

4.4.3 Trait plasticity

Leaf osmotic potential is controlled by ABA-signaling to adjust osmolarity by increasing cellular solute concentrations in response to drought, thus making it an environmentally regulated adaptive trait with a degree of phenotypic plasticity (Schulze *et al.*, 2005a). The plasticity consequently introduces some uncertainties as to the accuracy of the physiological data of this study. Preceding studies have demonstrated how this trait increase with drought and time over the growing season, to culminate in late summer when potential evapotranspiration and atmospheric drought would reach its peak (Sjöman *et al.*, 2015; Bartlett *et al.*, 2014), which is why sampling at NBG took place in August. Errors due to plasticity was however estimated to be negligible due to the rather established overall drought sensitivity of *Betula sp.* coupled with a climatically consistent drought propensity for the region in August, which also was the case during the period of sampling (Appendix 4). Even if drought tolerance from TLP as inferred from osmotic adjustment has an evidently robust connection to taxonomic functional type delineations (Sjöman *et al.*, 2015; Corcuera *et al.*, 2002), and to water use strategy (Nolan *et al.*, 2017), confounding results can still be generated in common garden trials when weather severely mismatches a presumed anisohydric drought tolerant species’ native climate, which risks yielding significantly lower TLP-values than would be expected under ‘native-adjacent’ conditions or drought treatments (Sjöman & Hannus, yet to be published data). The conundrum thusly lies in managing to accurately pin down the extent of phenotypic plasticity in order to fully evaluate drought tolerance potential. Historically, phenotypic plasticity has been investigated through provenance trials e.g. by reciprocal transplantations to compare adaptive response and niche fitness in contrasting environments (Davy & Gill, 1984; Eriksson *et al.*, 1980). For this trait however, the contrasting environments are for all intents and purposes provided along a temporal axis, where readings from newly flushed leaves (Ψ_{Spring}) would represent drought susceptibility early in the season and late readings, from mature leaves (Ψ_{Summer}), represents peak drought tolerance. The net difference ($\Delta\Psi$) would consequently be indicative of the tree’s ability to raise leaf osmotic potential to continuously maintain physiological integrity and fitness in habitats with recurrently dry soils. A recent study by Nolan *et al.* (2017) indicated a greater interconnectedness of leaf osmotic adjustments to the overall hydrological economy in two tree species with contrasting water use strategies; underscoring the importance of experimental design in order to successfully produce satisfactory datasets, with sufficient fidelity to resolve the various traits governing tree’s resilience to drought and their potential interrelations with ecological strategies of resource turnover (e.g. Grime’s CSR). Thus more sophisticated and extensive trial setups may be an inescapable necessity –where the exertion of environmental stressors aren’t left to the behest of luck in weather– to adequately elucidate how such adaptive traits vary and manifests as survival and/or growth, as well as compares between and within different taxa, depending on provenience geoclimate and genetics.

4.5 Urban resilience and drought tolerance

Cities throughout the world are increasingly being confronted with the environmental challenges inherent to the modern urban fabric and densification-type urban development, as the consequences of the shifting climate and extreme weather becomes more noticeable –as well as more exacerbated– by the city’s very makeup and physical structure. Utilization of green infrastructure as a nature-based solution is heralded as a prevailing sustainable strategy to efficiently deal with this problem; in implementation the city is however dependent on a continually healthy and well-integrated urban forest in order for the trees to optimally provide the expected ecosystem services. It is thus highly desirable that all relevant stakeholders build, plan and manage for urban trees in a conscientious, sustainable manner, so that the trees are able to maintain sufficient vitality and growth to fully deliver on their potential values.

TLP therefore has potential as a highly important trait to consider in the decision process of which genotypes to incorporate in the urban landscape, as the trait is typically pronounced in species that are adapted to grow and compete in habitats that experience periodic droughts and thus can tolerate periodically low leaf- and soil water potentials (Nolan *et al.*, 2017; Sjöman *et al.*, 2015; Corcuera *et al.*, 2002). The rationale for this, is the increased proficiency of genotypes with low TLP in *tolerating* drought while maintaining stomatal conductance, meaning that leaf physiological functions are maintained to a significant degree during periods of scarce water availability. The consequences of this property is the potential for a more reliable output of ecosystem services, as gaseous air pollutant removal and evaporative cooling are both reliant on open stomata and ongoing gas exchange (Nowak & Dwyer, 2007). And as carbon depletion is mitigated by the strategy, it also improves the long term prospects of an urban tree's vitality and development into mature size, thus maximizing its beneficial contributions. Increased vitality is not only desirable from an aesthetic standpoint in promoting cultural ecosystem services, but also as a receipt of a tree's health and developmental prospects, as the weakened state caused by low vitality makes the tree susceptible to diseases and pests, thus decreasing urban forest resilience (Raupp & Gonthier, 2017).

With this study we can testify to the phenomenon of differential drought tolerance in contrasting ecotypes of *B. pendula s.l.*, which also has been noted in other taxa common to the urban landscape, such as *Acer rubrum*, *A. saccharum*, *A. grandidentatum*, *Fagus sylvatica*, and *Quercus rubra* (Schuldt *et al.*, 2016; Aspelmeier & Leuschner, 2004; Bauerle *et al.*, 2003; Alder *et al.*, 1996; Kubiske & Abrams, 1992). There's consequently a mounting body of evidence of diversity in conspecific drought tolerance aptitude, which has increasingly made it clear that all trees aren't created equal within their species delineations, and that an individual tree's performance under urban droughts can't be generally presumed as established knowledge nor optimal to all contexts or climates. For instance, market-available 'generic' tree species genotypes may have undocumented and assorted origins with dissimilar degrees of tolerance, thus risking unpredictable establishment- and design results. Similarly, available tree cultivars may not represent optimally adapted phenotypes, since they are typically selected for their morphological properties, such as aesthetics, form and architectural homogeneity. By directing efforts to identify and characterize increasingly drought tolerant genotypes, one can diversify the palette of trees that could confidently be integrated by urban tree planners and landscape architects into the urban fabric to improve urban resilience. Considering the ubiquitous effect of heat waves, there's reason to pursue drought tolerance and raise the bar for species across the board to increase tree resilience, which would primarily concern species frequently used in conjunction with water-restrictive landscape elements, such as impervious surfaces that causes prolonged issues with water infiltration, or concrete slab supported roof gardens, whose thin soils and sparse rooting volume provides poor water retention and is quick to drain; but also species that are more typically park-associated, that too may suffer increased mortality rates from hydrological failure due to the sheer intensity of heat-induced droughts.

The road to resiliency also spells 'diversity' in an additional sense, as it mitigates risk by distributing it amongst more taxa, which acts as a buffer to the urban forest in case any pest, disease or weather event would cause disproportional taxon-specific tree mortality. The increased palette would allow for more viable genotypes to contribute to increased diversity. In the past however, there's been a tendency for complacent restraint in the approach for how urban tree planners have afforested the urban landscape. Tree inventories for Nordic cities have indeed exposed an excessive reliance on just a handful of species, primarily to the detriment of diversity in street environments, which arguably could see the most benefit from increased resilience (Thomsen *et al.*, 2016; Sjöman *et al.*, 2012c). The basis for this seem to be the habitual preference for familiar taxa with proven track records, a bias that lends itself to positive feedback loops unless disrupted for the explicit sake of variation; extreme cases of 'selection by popularity' exists, such as the clone cultivar *Tilia x europaea* 'Pallida' in Oslo, which at one point accounted for 70% of all their newly planted street trees (Pauleit *et al.*, 2002). Skewed selection such as this is common to cities and seem to happen regardless of otherwise excellent total taxonomic diversity, to which trees in park environments generally are the bulk contributors (Sjöman *et al.*, 2012c). Ignorance may be a contributing factor to a perceived street/park dichotomy that restricts diversifying urban tree selection, as park trees might, by lack of proper knowledge and experience, be regarded as exotic botanical curiosities whose potential remain continually unexplored due to risk-aversiveness. It therefore highlights the importance of screening obscure or novel genotypes for drought tolerance, in order to generate communicable data that would prompt and motivate increased cultivation or fast-tracked product development, as well as data that would give urban tree planners the assured confidence to fully and efficiently utilize the complete palette that they have at their disposal to build a more resilient urban forest and city.

5 Conclusions

In this thesis I've examined the drought tolerance of *Betula pendula* Roth. and how it relates to local climate, with the purpose of characterizing its intraspecific variation and substantiate possible links to local conditions that could contribute to improved approaches to the urban tree selection process.

TLP was estimated through vapor pressure osmometry, and significant differences could be demonstrated at an ecotypic and subspecies level. These differences could've arisen from local adaptations or recent evolutionary events. Though regression analysis could show a significant correlation of TLP to annual PET, which suggests it as a driving factor for drought tolerance in *B. pendula*.

This study gives further evidence of local adaptations by drought tolerance in deciduous angiosperms, and could thus provide direction for future studies to advance ecotype-driven tree selection. There are however a couple of limitations to the study that could've influenced the results: e.g. the limited number of sampled individuals which could've skewed the population estimate, as well as the representativeness of the climate data used, which would have implications to the drought selective pressure present in the provenience populations. The number of investigated proveniences could also benefit from being higher, in order to more robustly substantiate the link between drought tolerance and climate. Indeed, additional proveniences representing comparable environmental gradients at different spatial scales (i.e. country, continent, global) would be expedient to a more comprehensive study to more thoroughly examine the possible causal source of the variation in drought tolerance between the European and Americo-Asiatic subspecies witnessed in this particular study.

In order to further investigate and expand on the potential of tree selection process detailed by Sjöman *et al.* (2012a) which ties drought adaptation to habitat fitness, I'd suggest GIS-mediated methods as means of extending the habitat assessment capacity during the desk research phase. Controlled growing trials with drought treatments could also be motivated in order to establish the full extent of a genotype's drought tolerance and how it relates to factors important to trees in the urban landscape, such as growth etc. Moreover, the study illustrates how the *species concept* can be problematic from a tree planner's perspective, as there evidently can be significant differences between conspecific genotypes, which could have negative ramifications to the usage of trees in the urban landscape, as one can't be 100% certain of a tree's limitations and performance over time in a highly urbanized environment, and how it will fare with rising temperatures from a changing climate. Therefore '*genotype*' (or a term which's descriptively equivalent) should enter the terminology and see wider use among tree planners and the nursery sector, to more accurately represent potential trait differences and promote a more context-appropriate usage of available tree genotypes.

References

Aasamaa, K., Sõber, A., Hartung, W. & Niinemets, Ü. (2002). Rate of stomatal opening, shoot hydraulic conductance and photosynthetic characteristics in relation to leaf abscisic acid concentration in six temperate deciduous trees. *Tree physiology,* 22(4), pp. 267-276.

Adams, H.D. & Kolb, T.E. (2005). Tree growth response to drought and temperature in a mountain landscape in northern Arizona, USA. *Journal of Biogeography,* 32(9), pp. 1629-1640.

Adams, H.D., Zeppel, M.J., Anderegg, W.R., Hartmann, H., Landhäusser, S.M., Tissue, D.T., Huxman, T.E., Hudson, P.J., Franz, T.E. & Allen, C.D. (2017). A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nature ecology & evolution,* 1(9), p. 1285.

Akbari, H., Pomerantz, M. & Taha, H. (2001). Cool surfaces and shade trees to reduce energy use and improve air quality in urban areas. *Solar energy,* 70(3), pp. 295-310.

Alder, N., Sperry, J. & Pockman, W. (1996). Root and stem xylem embolism, stomatal conductance, and leaf turgor in Acer grandidentatum populations along a soil moisture gradient. *Oecologia,* 105(3), pp. 293-301.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D. & Hogg, E.T. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management,* 259(4), pp. 660-684.

Allen, R.G., Pereira, L.S., Raes, D., & Smith, M. (1998). Crop evapotranspiration-Guidelines for computing crop water requirements-FAO Irrigation and drainage paper 56. *Fao, Rome, 300(9)*

Anagnostakis, S.L. (1987). Chestnut blight: the classical problem of an introduced pathogen. *Mycologia,* 79(1), pp. 23-37.

Anderegg, W.R., Berry, J.A. & Field, C.B. (2012a). Linking definitions, mechanisms, and modeling of drought-induced tree death. *Trends in plant science,* 17(12), pp. 693-700.

Anderegg, W.R., Berry, J.A., Smith, D.D., Sperry, J.S., Anderegg, L.D. & Field, C.B. (2012b). The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *Proceedings of the National Academy of Sciences,* 109(1), pp. 233-237.

Anderegg, W.R., Kane, J.M. & Anderegg, L.D. (2013). Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change,* 3(1), pp. 30-36.

Ashburner, K. & McAllister, H.A. (2016). *The genus Betula: a taxonomic revision of birches.* Botanical Magazine Monographs. Richmond: Kew publishing.

Aspelmeier, S. & Leuschner, C. (2004). Genotypic variation in drought response of silver birch (Betula pendula): leaf water status and carbon gain. *Tree physiology,* 24(5), pp. 517-528.

Aspelmeier, S. & Leuschner, C. (2006). Genotypic variation in drought response of silver birch (Betula pendula Roth): leaf and root morphology and carbon partitioning. *Trees,* 20(1), pp. 42-52.

Atkinson, M. (1992). Betula pendula Roth (B. verrucosa Ehrh.) and B. pubescens Ehrh. *Journal of Ecology,* 80(4), pp. 837-870.

Bagnato, S., La Piana, V., Mercurio, R., Merlino, A., Scarfò, F., Sciascia, N., Solano, F. & Spampinato, G. (2014). Evolutionary dynamics of birch (Betula aetnensis Rafin) coppices on the Mount Etna (Sicily). *Forest@,* 11(1), pp. 52-65.

Bartlett, M.K., Scoffoni, C., Ardy, R., Zhang, Y., Sun, S., Cao, K. & Sack, L. (2012a). Rapid determination of comparative drought tolerance traits: using an osmometer to predict turgor loss point. *Methods in Ecology and Evolution,* 3(5), pp. 880-888.

Bartlett, M.K., Scoffoni, C. & Sack, L. (2012b). The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecology Letters,* 15(5), pp. 393-405.

Bartlett, M.K., Zhang, Y., Kreidler, N., Sun, S., Ardy, R., Cao, K. & Sack, L. (2014). Global analysis of plasticity in turgor loss point, a key drought tolerance trait. *Ecology Letters,* 17(12), pp. 1580-1590.

Bauerle, W.L., Whitlow, T., Setter, T., Bauerle, T. & Vermeylen, F. (2003). Ecophysiology of Acer rubrum seedlings from contrasting hydrologic habitats: growth, gas exchange, tissue water relations, abscisic acid and carbon isotope discrimination. *Tree physiology,* 23(12), pp. 841-850.

Beck, P., Caudullo, G., de Rigo, D. & Tinner, W. (2016). Betula pendula, Betula pubescens and other birches in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T. & Mauri, A. (eds) *European Atlas of Forest Tree Species*. Luxembourg: Publication Office of the European Union.

Bennike, O. & Böcher, J. (1990). Forest-tundra neighbouring the North Pole: plant and insect remains from the Plio-Pleistocene Kap København formation, North Greenland. *Arctic*, pp. 331-338.

Bolstad, P.V., Swank, W. & Vose, J. (1998). Predicting Southern Appalachian overstory vegetation with digital terrain data. *Landscape Ecology,* 13(5), pp. 271-283.

Bolte, A., Czajkowski, T., Cocozza, C., Tognetti, R., De Miguel, M., Pšidová, E., Ditmarová, Ĺ., Dinca, L., Delzon, S. & Cochard, H. (2016). Desiccation and mortality dynamics in seedlings of different European beech (Fagus sylvatica L.) populations under extreme drought conditions. *Frontiers in plant science,* 7, p. 751.

Bréda, N., Huc, R., Granier, A. & Dreyer, E. (2006). Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science,* 63(6), pp. 625-644.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L. & Belnap, J. (2005). Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America,* 102(42), pp. 15144-15148.

Bridge, S. & Johnson, E. (2000). Geomorphic principles of terrain organization and vegetation gradients. *Journal of Vegetation Science,* 11(1), pp. 57-70.

Bridle, J.R. & Vines, T.H. (2007). Limits to evolution at range margins: when and why does adaptation fail? *Trends in ecology & evolution,* 22(3), pp. 140-147.

Brown, W. & Lacate, D. (1961). *Rooting habits of white and Red Pine*. (Forest Research Branch - Technical Note, #108). CA, Ottawa: Department of Forestry, Canada.

Brunsdon, C., McClatchey, J. & Unwin, D. (2001). Spatial variations in the average rainfall–altitude relationship in Great Britain: an approach using geographically weighted regression. *International Journal of Climatology,* 21(4), pp. 455-466.

Brzeziecki, B. & Kienast, F. (1994). Classifying the life-history strategies of trees on the basis of the Grimian model. *Forest Ecology and Management,* 69(1-3), pp. 167-187.

Bussotti, F., Pollastrini, M., Holland, V. & Brüggemann, W. (2015). Functional traits and adaptive capacity of European forests to climate change. *Environmental and Experimental Botany,* 111, pp. 91-113.

Bühler, O., Kristoffersen, P. & Larsen, S.U. (2007). Growth of street trees in Copenhagen with emphasis on the effect of different establishment concepts. *Arboriculture and Urban Forestry,* 33(5), p. 330.

Calfapietra, C., Peñuelas, J. & Niinemets, Ü. (2015). Urban plant physiology: adaptation-mitigation strategies under permanent stress. *Trends in plant science,* 20(2), pp. 72-75.

Cavin, L. & Jump, A.S. (2017). Highest drought sensitivity and lowest resistance to growth suppression are found in the range core of the tree Fagus sylvatica L. not the equatorial range edge. *Global change biology,* 23(1), pp. 362-379.

Cavin, L., Mountford, E.P., Peterken, G.F. & Jump, A.S. (2013). Extreme drought alters competitive dominance within and between tree species in a mixed forest stand. *Functional Ecology,* 27(6), pp. 1424-1435.

Chen, Z.-D., Manchester, S.R. & Sun, H.-Y. (1999). Phylogeny and evolution of the Betulaceae as inferred from DNA sequences, morphology, and paleobotany. *American Journal of Botany,* 86(8), pp. 1168-1181.

Chester, D.K., Duncan, A.M., Guest, J. & Kilburn, C. (1985). Etna and the Etna region. In: *Mount Etna: The anatomy of a volcano*. London: Chapman and Hall Ltd., pp. 37-64.

Clark, J.R. & Kjelgren, R. (1990). Water as a limiting factor in the development of urban trees. *Journal of Arboriculture,* 16(8), pp. 203-208.

Cochard, H., Badel, E., Herbette, S., Delzon, S., Choat, B. & Jansen, S. (2013). Methods for measuring plant vulnerability to cavitation: a critical review. *Journal of Experimental Botany,* 64(15), pp. 4779-4791.

Compagnon, R. (2004). Solar and daylight availability in the urban fabric. *Energy and buildings,* 36(4), pp. 321-328.

Conway, T.M. & Vander Vecht, J. (2015). Growing a diverse urban forest: Species selection decisions by practitioners planting and supplying trees. *Landscape and Urban Planning,* 138, pp. 1-10.

Corcuera, L., Camarero, J. & Gil-Pelegrín, E. (2002). Functional groups in Quercus species derived from the analysis of pressure–volume curves. *Trees,* 16(7), pp. 465-472.

Coutts, A.M., Tapper, N.J., Beringer, J., Loughnan, M. & Demuzere, M. (2013). Watering our cities: the capacity for water sensitive urban design to support urban cooling and improve human thermal comfort in the Australian context. *Progress in Physical Geography,* 37(1), pp. 2-28.

Crane, P.R. & Stockey, R.A. (1987). Betula leaves and reproductive structures from the Middle Eocene of British Columbia, Canada. *Canadian Journal of Botany,* 65(12), pp. 2490-2500.

Dale, A.G., Youngsteadt, E. & Frank, S.D. (2016). Forecasting the Effects of Heat and Pests on Urban Trees: Impervious Surface Thresholds and the 'Pace-to-Plant'Technique. *Arboriculture & Urban Forestry,* 42(3).

Davies, W. & Pigott, C. (1984). Shade tolerance of forest trees. *NERC News Journal,* 3(1), pp. 17-18.

Davy, A. & Gill, J. (1984). Variation due to environment and heredity in birch transplanted between heath and bog. *New Phytologist,* 97(3), pp. 489-505.

Day, F.P. & Monk, C.D. (1974). Vegetation patterns on a southern Appalachian watershed. *Ecology,* 55(5), pp. 1064-1074.

De Carvalho, D., Ingvarsson, P.K., Joseph, J., Suter, L., Sedivy, C., Macaya-Sanz, D., Cottrell, J., Heinze, B., Schanzer, I. & Lexer, C. (2010). Admixture facilitates adaptation from standing variation in the European aspen (Populus tremula L.), a widespread forest tree. *Molecular ecology,* 19(8), pp. 1638-1650.

De Groot, R.S., Wilson, M.A. & Boumans, R.M. (2002). A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecological economics,* 41(3), pp. 393-408.

De Kort, H., Vandepitte, K., Bruun, H.H., Closset-Kopp, D., Honnay, O. & Mergeay, J. (2014). Landscape genomics and a common garden trial reveal adaptive differentiation to temperature across Europe in the tree species Alnus glutinosa. *Molecular ecology,* 23(19), pp. 4709-4721.

Deak Sjöman, J. (2016). *The hidden landscape.* Diss. Alnarp: Swedish University of Agricultural Sciences.

Deak Sjöman, J., Sjöman, H. & Johansson, E. (2015). Staden som växtplats. In: Sjöman, H. & Slagstedt, J. (eds) *Träd i urbana landskap*. Lund: Studentlitteratur, pp. 231-329.

Delzon, S. (2015). New insight into leaf drought tolerance. *Functional Ecology,* 29(10), pp. 1247-1249.

Demchik, M.C. & Sharpe, W.E. (2000). The effect of soil nutrition, soil acidity and drought on northern red oak (Quercus rubra L.) growth and nutrition on Pennsylvania sites with high and low red oak mortality. *Forest Ecology and Management,* 136(1), pp. 199-207.

Denk, T., Grímsson, F. & Kvaček, Z. (2005). The Miocene floras of Iceland and their significance for late Cainozoic North Atlantic biogeography. *Botanical Journal of the Linnean Society,* 149(4), pp. 369-417.

Donat, M., Alexander, L., Yang, H., Durre, I., Vose, R., Dunn, R., Willett, K., Aguilar, E., Brunet, M. & Caesar, J. (2013). Updated analyses of temperature and precipitation extreme indices since the beginning of the twentieth century: the HadEX2 dataset. *Journal of Geophysical Research: Atmospheres,* 118(5), pp. 2098-2118.

Dyderski, M.K., Paź, S., Frelich, L.E. & Jagodziński, A.M. (2018). How much does climate change threaten European forest tree species distributions? *Global change biology,* 24(3), pp. 1150-1163.

Dyer, J.M. (2009). Assessing topographic patterns in moisture use and stress using a water balance approach. *Landscape Ecology,* 24(3), pp. 391-403.

Eckert, A.J., Maloney, P.E., Vogler, D.R., Jensen, C.E., Mix, A.D. & Neale, D.B. (2015). Local adaptation at fine spatial scales: an example from sugar pine (Pinus lambertiana, Pinaceae). *Tree Genetics & Genomes,* 11(3), p. 42.

Epstein, E.S. (1991). On obtaining daily climatological values from monthly means. *Journal of Climate,* 4(3), pp. 365-368.

Eriksson, G., Andersson, S., Eiche, V., Ifver, J. & Persson, A. (1980). *Severity index and transfer effects on survival and volume production of Pinus sylvestris in northern Sweden*. (Studia Forestalia Suecica, 156). Uppsala: Swedish University of Agricultural Sciences.

Fick, S.E. & Hijmans, R.J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology,* 37(12), pp. 4302-4315.

Fischer, E.M. & Knutti, R. (2015). Anthropogenic contribution to global occurrence of heavy-precipitation and high-temperature extremes. *Nature Climate Change,* 5(6), pp. 560-564.

Flexas, J., Bota, J., Loreto, F., Cornic, G. & Sharkey, T. (2004). Diffusive and metabolic limitations to photosynthesis under drought and salinity in C3 plants. *Plant Biology,* 6(03), pp. 269-279.

FMI (2012). *Tilastoja Suomen ilmastosta 1981–2010*. Available at: https://helda.helsinki.fi/bitstream/handle/10138/35880/Tilastoja_Suomen_ilmastosta_1981_2010.pdf [2017-11-22].

Freeland, J., Petersen, S. & Kirk, H. (2011). *Molecular ecology*. 2nd. ed. Chichester, UK: John Wiley & Sons, Ltd.

Fridman, J. & Wulff, S. (2018). Skogsdata 2018. In: Nilsson, P. & Cory, N. (eds). Umeå: SLU, Department of Forest Resource Management.

Fries, C. (1984). Den frösådda björkens invandring på hygget. *Sveriges Skogsvårdförbunds Tidskrift,* 3(4), pp. 35-49.

Gallay, M. (2013). Direct Acquisition of Data: Airborne laser scanning. In: Clarke, L.E. & Nield, J.M. (eds) *Geomorphological Techniques*. London, UK: British Society for Geomorphology, pp. 90-106.

Gitlin, A.R., Sthultz, C.M., Bowker, M.A., Stumpf, S., Paxton, K.L., Kennedy, K., Muñoz, A., Bailey, J.K. & Whitham, T.G. (2006). Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. *Conservation Biology,* 20(5), pp. 1477-1486.

Gomez-Muñoz, V.M., Porta-Gándara, M. & Fernández, J. (2010). Effect of tree shades in urban planning in hot-arid climatic regions. *Landscape and Urban Planning,* 94(3), pp. 149-157.

Grime, J.P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist,* 111(982), pp. 1169-1194.

Grime, J.P. (2006). *Plant strategies, vegetation processes, and ecosystem properties*: John Wiley & Sons.

Gu, M., Rom, C.R., Robbins, J.A. & Oosterhuis, D.M. (2007). Effect of water deficit on gas exchange, osmotic solutes, leaf abscission, and growth of four birch genotypes (Betula L.) under a controlled environment. *HortScience,* 42(6), pp. 1383-1391.

Guisan, A., Broennimann, O., Engler, R., Vust, M., Yoccoz, N.G., Lehmann, A. & Zimmermann, N.E. (2006). Using niche-based models to improve the sampling of rare species. *Conservation Biology,* 20(2), pp. 501-511.

Gunnarsson, A. (2015). Träden och människan In: Sjöman, H. & Slagstedt, J. (eds) *Träd i urbana landskap*. Lund: Studentlitteratur, pp. 19-54.

Haaland, C. & Konijnendijk van den Bosch, C. (2015). Challenges and strategies for urban green-space planning in cities undergoing densification: A review. *Urban Forestry & Urban Greening,* 14(4), pp. 760-771.

Hacket-Pain, A.J., Cavin, L., Friend, A.D. & Jump, A. (2016). Consistent limitation of growth by high temperature and low precipitation from range core to southern edge of European beech indicates widespread vulnerability to changing climate. *European Journal of Forest Research,* 135(5), pp. 897-909.

Hawkes, C. (2000). Woody plant mortality algorithms: description, problems and progress. *Ecological Modelling,* 126(2), pp. 225-248.

Herms, D.A. & McCullough, D.G. (2014). Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. *Annual review of entomology,* 59, pp. 13-30.

Hochberg, U., Rockwell, F.E., Holbrook, N.M. & Cochard, H. (2017). Iso/Anisohydry: A Plant–Environment Interaction Rather Than a Simple Hydraulic Trait. *Trends in plant science*.

Hoffmann, W.A., Marchin, R.M., Abit, P. & Lau, O.L. (2011). Hydraulic failure and tree dieback are associated with high wood density in a temperate forest under extreme drought. *Global change biology,* 17(8), pp. 2731-2742.

Hultén, E. (1971). *The circumpolar plants. 2. Dicotyledons*: Almqvist & Wiksell. Available from: https://books.google.se/books?id=1OpPNAEACAAJ.

IPCC (2014). *Climate change 2013: the physical science basis: Working Group I contribution to the Fifth assessment report of the Intergovernmental Panel on Climate Change*: Cambridge University Press.

Jansson, C.-A. (1962). Some species and varieties of Betula ser. Verrucosae Suk. *East Asia and NW America. Acta Horti Gotob,* 25, pp. 103-156.

Jansson, M., Persson, A. & Östman, L. (2013). *Hela staden –argument för en grönblå stadsbyggnad.* (Stad & Land, 183). Alnarp: Movium.

Jim, C.Y. (2017). Constraints to urban trees and their remedies in the built environment. In: Ferrini, F., van den Bosch, C.C.K. & Fini, A. (eds) *Routledge Handbook of Urban Forestry*. New York: Routledge, pp. 273-290.

JMA (2017). *Tables of Monthly Climate Statistics*. Available at: http://www.data.jma.go.jp/obd/stats/data/en/smp/index.html [2017-11-22].

Johnson, M.P. (2001). Environmental impacts of urban sprawl: a survey of the literature and proposed research agenda. *Environment and planning A,* 33(4), pp. 717-735.

Järvinen, P., Palmé, A., Morales, L.O., Lännenpää, M., Keinänen, M., Sopanen, T. & Lascoux, M. (2004). Phylogenetic relationships of Betula species (Betulaceae) based on nuclear ADH and chloroplast matK sequences. *American Journal of Botany,* 91(11), pp. 1834-1845.

Kabisch, N., Frantzeskaki, N., Pauleit, S., Naumann, S., Davis, M., Artmann, M., Haase, D., Knapp, S., Korn, H. & Stadler, J. (2016). Nature-based solutions to climate change mitigation and adaptation in urban areas: perspectives on indicators, knowledge gaps, barriers, and opportunities for action. *Ecology and Society,* 21(2).

Keddy, P. (2007). *Plants and vegetation: origins, processes, consequences*: Cambridge University Press.

Knutzen, F., Meier, I.C. & Leuschner, C. (2015). Does reduced precipitation trigger physiological and morphological drought adaptations in European beech (Fagus sylvatica L.)? Comparing provenances across a precipitation gradient. *Tree physiology,* 35(9), pp. 949-963.

Koike, T., Kitao, M., Quoreshi, A. & Matsuura, Y. (2003). Growth characteristics of root-shoot relations of three birch seedlings raised under different water regimes. In: *Roots: The Dynamic Interface between Plants and the Earth* Springer, pp. 303-310.

Konijnendijk, C.C. (2008). *The forest and the city: the cultural landscape of urban woodland*: Springer Science & Business Media.

Kubiske, M.E. & Abrams, M.D. (1992). Photosynthesis, water relations, and leaf morphology of xeric versus mesic Quercus rubra ecotypes in central Pennsylvania in relation to moisture stress. *Canadian Journal of Forest Research,* 22(9), pp. 1402-1407.

Lambers, H., Chapin, F.S. & Pons, T.L. (2008). *Plant Physiological Ecology*. 2nd. ed. (Plant physiological ecology. New York: Springer Science+Business Media, LLC.

Lavorel, S., Díaz, S., Cornelissen, J.H.C., Garnier, E., Harrison, S.P., McIntyre, S., Pausas, J.G., Pérez-Harguindeguy, N., Roumet, C. & Urcelay, C. (2007). Plant functional types: are we getting any closer to the Holy Grail? In: *Terrestrial ecosystems in a changing world* Springer, pp. 149-164.

Leff, M. (2016). *The Sustainable Urban Forest - A Step-by-Step Approach*. Davey Institute/USDA Forest Service.

Levanič, T., Čater, M. & McDowell, N.G. (2011). Associations between growth, wood anatomy, carbon isotope discrimination and mortality in a Quercus robur forest. *Tree physiology,* 31(3), pp. 298-308.

Li, X., Wang, L., Chen, D., Yang, K., Xue, B. & Sun, L. (2013). Near-surface air temperature lapse rates in the mainland China during 1962–2011. *Journal of Geophysical Research: Atmospheres,* 118(14), pp. 7505-7515.

Loehle, C. (1998). Height growth rate tradeoffs determine northern and southern range limits for trees. *Journal of Biogeography,* 25(4), pp. 735-742.

MacArthur, R.H. (1972). *Geographical ecology: patterns in the distribution of species*. New Jersey: Princeton University Press.

Maherali, H., Moura, C.F., Caldeira, M.C., Willson, C.J. & Jackson, R.B. (2006). Functional coordination between leaf gas exchange and vulnerability to xylem cavitation in temperate forest trees. *Plant, Cell & Environment,* 29(4), pp. 571-583.

Maherali, H., Pockman, W.T. & Jackson, R.B. (2004). Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology,* 85(8), pp. 2184-2199.

Maliouchenko, O., Palmé, A.E., Buonamici, A., Vendramin, G. & Lascoux, M. (2007). Comparative phylogeography and population structure of European Betula species, with particular focus on B. pendula and B. pubescens. *Journal of Biogeography,* 34(9), pp. 1601-1610.

Marchin, R., Zeng, H. & Hoffmann, W. (2010). Drought-deciduous behavior reduces nutrient losses from temperate deciduous trees under severe drought. *Oecologia,* 163(4), pp. 845-854.

Marchin, R.M., Sage, E.L. & Ward, J.K. (2008). Population-level variation of Fraxinus americana (white ash) is influenced by precipitation differences across the native range. *Tree physiology,* 28(1), pp. 151-159.

Markesteijn, L., Poorter, L., Paz, H., Sack, L. & Bongers, F. (2011). Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. *Plant, Cell & Environment,* 34(1), pp. 137-148.

Maseyk, K.S., Lin, T., Rotenberg, E., Grünzweig, J.M., Schwartz, A. & Yakir, D. (2008). Physiology–phenology interactions in a productive semi-arid pine forest. *New Phytologist,* 178(3), pp. 603-616.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A. & Williams, D.G. (2008). Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist,* 178(4), pp. 719-739.

McDowell, N.G. (2011). Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant physiology,* 155(3), pp. 1051-1059.

McDowell, N.G., Beerling, D.J., Breshears, D.D., Fisher, R.A., Raffa, K.F. & Stitt, M. (2011). The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in ecology & evolution,* 26(10), pp. 523-532.

McPhearson, T., Andersson, E., Elmqvist, T. & Frantzeskaki, N. (2015). Resilience of and through urban ecosystem services. *Ecosystem Services,* 12, pp. 152-156.

Meeus, J.H. (1991). *Astronomical algorithms*. 1st. ed. Richmond, Virgina: Willmann-Bell, Incorporated.

Mell, I.C. Green infrastructure: concepts and planning. In: *Proceedings of FORUM ejournal*2008, pp. 69-80.

MeteoSwiss (2016). *Climate normals Montana*. Available at: http://www.meteoswiss.admin.ch/product/output/climate-data/climate-diagrams-normal-values-station-processing/MVE/climsheet_MVE_np6190_e.pdf [2017-11-22].

Michelot, A., Simard, S., Rathgeber, C., Dufrêne, E. & Damesin, C. (2012). Comparing the intra-annual wood formation of three European species (Fagus sylvatica, Quercus petraea and Pinus sylvestris) as related to leaf phenology and non-structural carbohydrate dynamics. *Tree physiology,* 32(8), pp. 1033-1045.

Millennium Ecosystem Assessment. (2005). *Ecosystems and Human Well-Being: Biodiversity Synthesis. Published by World Resources Institute, Washington, DC.*

Mitchell, P.J., O'Grady, A.P., Tissue, D.T., White, D.A., Ottenschlaeger, M.L. & Pinkard, E.A. (2013). Drought response strategies define the relative contributions of hydraulic dysfunction and carbohydrate depletion during tree mortality. *New Phytologist,* 197(3), pp. 862-872.

Mitchell, P.J., Veneklaas, E.J., Lambers, H. & Burgess, S.S. (2008). Leaf water relations during summer water deficit: differential responses in turgor maintenance and variation in leaf structure among different plant communities in south-western Australia. *Plant, Cell & Environment,* 31(12), pp. 1791-1802.

Monteith, J.L. (1965) Evaporation and environment. In: *Proceedings of Symp. Soc. Exp. Biol.* (Vol. 19, No. 205-23, p. 4).

Morgenroth, J., Östberg, J., van den Bosch, C.K., Nielsen, A.B., Hauer, R., Sjöman, H., Chen, W. & Jansson, M. (2016). Urban tree diversity—Taking stock and looking ahead. *Urban Forestry & Urban Greening,* 15, pp. 1-5.

Mueller, R.C., Scudder, C.M., Porter, M.E., Talbot Trotter, R., Gehring, C.A. & Whitham, T.G. (2005). Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. *Journal of Ecology,* 93(6), pp. 1085-1093.

NCAS (2016). *Ness Botanic Gardens, The Wirral, United Kingdom* Available at: https://sci.ncas.ac.uk/ness/NOAA/NOAA-2016.txt [2018-03-24].

Nielsen, A.B., Hedblom, M., Olafsson, A.S. & Wiström, B. (2017). Spatial configurations of urban forest in different landscape and socio-political contexts: identifying patterns for green infrastructure planning. *Urban ecosystems,* 20(2), pp. 379-392.

Nielsen, C.N., Bühler, O. & Kristoffersen, P. (2007). Soil water dynamics and growth of street and park trees. *Arboriculture & Urban Forestry,* 33(4), pp. 231-245.

NOAA *Solar Calculations-year*. Available at: https://www.esrl.noaa.gov/gmd/grad/solcalc/calcdetails.html [2017-11-23].

Nolan, R.H., Tarin, T., Santini, N.S., McAdam, S.A., Ruman, R. & Eamus, D. (2017). Differences in osmotic adjustment, foliar abscisic acid dynamics, and stomatal regulation between an isohydric and anisohydric woody angiosperm during drought. *Plant, Cell & Environment,* 40(12), pp. 3122-3134.

Nowak, D.J. & Dwyer, J.F. (2007). Understanding the benefits and costs of urban forest ecosystems. In: *Urban and community forestry in the northeast* Springer, pp. 25-46.

Nowak, D.J., Kuroda, M. & Crane, D.E. (2004). Tree mortality rates and tree population projections in Baltimore, Maryland, USA. *Urban Forestry & Urban Greening,* 2(3), pp. 139-147.

Nowak, D.J., Pasek, J.E., Sequeira, R.A., Crane, D.E. & Mastro, V.C. (2001). Potential effect of Anoplophora glabripennis (Coleoptera: Cerambycidae) on urban trees in the United States. *Journal of Economic Entomology,* 94(1), pp. 116-122.

Oke, T.R. (1973). City size and the urban heat island. *Atmospheric Environment (1967),* 7(8), pp. 769-779.

Orlandini, S., Vanos, J.K., Matzarakis, A., Massetti, L. & Petralli, M. (2017). Urban forestry and microclimate. In: Ferrini, F., van den Bosch, C.C.K. & Fini, A. (eds) *Routledge Handbook of Urban Forestry*. New York: Routledge, pp. 96-111.

Pallardy, S.G. (2008). *Physiology of Woody Plants*. 3rd. ed. San Diego: Academic Press.

Palmé, A., Su, Q., Rautenberg, A., Manni, F. & Lascoux, M. (2003). Postglacial recolonization and cpDNA variation of silver birch, Betula pendula. *Molecular ecology,* 12(1), pp. 201-212.

Parker, W.C. & Pallardy, S.G. (1985). Drought-induced leaf abscission and whole-plant drought tolerance of seedlings of seven black walnut families. *Canadian Journal of Forest Research,* 15(5), pp. 818-821.

Pauleit, S., Jones, N., Garcia-Martin, G., Garcia-Valdecantos, J.L., Rivière, L.M., Vidal-Beaudet, L., Bodson, M. & Randrup, T.B. (2002). Tree establishment practice in towns and cities–Results from a European survey. *Urban Forestry & Urban Greening,* 1(2), pp. 83-96.

Peñuelas, J., Lloret, F. & Montoya, R. (2001). Severe drought effects on Mediterranean woody flora in Spain. *Forest Science,* 47(2), pp. 214-218.

Perala, D.A. & Alm, A.A. (1990). Reproductive ecology of birch: a review. *Forest Ecology and Management,* 32(1), pp. 1-38.

Perkins, S., Alexander, L. & Nairn, J. (2012). Increasing frequency, intensity and duration of observed global heatwaves and warm spells. *Geophysical Research Letters,* 39(20).

Petit, R.J., Aguinagalde, I., de Beaulieu, J.-L., Bittkau, C., Brewer, S., Cheddadi, R., Ennos, R., Fineschi, S., Grivet, D. & Lascoux, M. (2003). Glacial refugia: hotspots but not melting pots of genetic diversity. *Science,* 300(5625), pp. 1563-1565.

Petroselli, A., Vessella, F., Cavagnuolo, L., Piovesan, G. & Schirone, B. (2013). Ecological behavior of Quercus suber and Quercus ilex inferred by topographic wetness index (TWI). *Trees,* 27(5), pp. 1201-1215.

Pianka, E.R. (1970). On r-and K-selection. *The American Naturalist,* 104(940), pp. 592-597.

Pluess, A.R., Frank, A., Heiri, C., Lalagüe, H., Vendramin, G.G. & Oddou-Muratorio, S. (2016). Genome–environment association study suggests local adaptation to climate at the regional scale in Fagus sylvatica. *New Phytologist,* 210(2), pp. 589-601.

Pogodaiklimat (2017). *Климатгорода*. Available at: http://www.pogodaiklimat.ru/climate/29638.htm [2017-03-21].

Poland, T.M. & McCullough, D.G. (2006). Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. *Journal of Forestry,* 104(3), pp. 118-124.

Possen, B.J., Anttonen, M.J., Oksanen, E., Rousi, M., Heinonen, J., Kostiainen, K., Kontunen-Soppela, S., Heiskanen, J. & Vapaavuori, E.M. (2014). Variation in 13 leaf morphological and physiological traits within a silver birch (Betula pendula) stand and their relation to growth. *Canadian Journal of Forest Research,* 44(6), pp. 657-665.

Possen, B.J., Oksanen, E., Rousi, M., Ruhanen, H., Ahonen, V., Tervahauta, A., Heinonen, J., Heiskanen, J., Kärenlampi, S. & Vapaavuori, E. (2011). Adaptability of birch (Betula pendula Roth) and aspen (Populus tremula L.) genotypes to different soil moisture conditions. *Forest Ecology and Management,* 262(8), pp. 1387-1399.

Price, T.D. & Kirkpatrick, M. (2009). Evolutionarily stable range limits set by interspecific competition. *Proceedings of the Royal Society of London B: Biological Sciences*, 276(1661), pp. 1429-1434.

Prinzing, A., Durka, W., Klotz, S. & Brandl, R. (2002). Geographic variability of ecological niches of plant species: are competition and stress relevant? *Ecography,* 25(6), pp. 721-729.

Prudhomme, C. & Reed, D.W. (1999). Mapping extreme rainfall in a mountainous region using geostatistical techniques: a case study in Scotland. *International Journal of Climatology,* 19(12), pp. 1337-1356.

Qian, H. & Ricklefs, R.E. (2000). Large-scale processes and the Asian bias in species diversity of temperate plants. *Nature,* 407(6801), pp. 180-182.

Qin, C.-Z., Zhu, A.-X., Pei, T., Li, B.-L., Scholten, T., Behrens, T. & Zhou, C.-H. (2011). An approach to computing topographic wetness index based on maximum downslope gradient. *Precision Agriculture,* 12(1), pp. 32-43.

Ranney, T., Bir, R. & Skroch, W. (1991). Comparative drought resistance among six species of birch (Betula): Influence of mild water stress on water relations and leaf gas exchange. *Tree physiology,* 8(4), pp. 351-360.

Ranney, T., Whitlow, T. & Bassuk, N. (1990). Response of five temperate deciduous tree species to water stress. *Tree physiology,* 6(4), pp. 439-448.

Raupp, M.J. & Gonthier, P. (2017). Biotic factors: pests and diseases. In: Ferrini, F., Van Den Bosch, C.C.K. & Fini, A. (eds) *Routledge Handbook of Urban Forestry*. New York: Routledge, pp. 251-272.

Raupp, M.J., Shrewsbury, P.M. & Herms, D.A. (2010). Ecology of herbivorous arthropods in urban landscapes. *Annual review of entomology,* 55, pp. 19-38.

Reich, P.B. (2014). The world-wide 'fast–slow'plant economics spectrum: a traits manifesto. *Journal of Ecology,* 102(2), pp. 275-301.

Rennenberg, H., Loreto, F., Polle, A., Brilli, F., Fares, S., Beniwal, R. & Gessler, A. (2006). Physiological responses of forest trees to heat and drought. *Plant Biology,* 8(05), pp. 556-571.

RL (2017). *Temperatura Media Dell'Aria - Colle Belenda*. Available at: http://www.cartografiarl.regione.liguria.it/SiraQualMeteo/script/PubAccessoDatiMeteo.asp [2017-11-22].

Roloff, A., Korn, S. & Gillner, S. (2009). The climate-species-matrix to select tree species for urban habitats considering climate change. *Urban Forestry & Urban Greening,* 8(4), pp. 295-308.

Roschanski, A.M., Csilléry, K., Liepelt, S., Oddou-Muratorio, S., Ziegenhagen, B., Huard, F., Ullrich, K.K., Postolache, D., Vendramin, G.G. & Fady, B. (2016). Evidence of divergent selection for drought and cold tolerance at landscape and local scales in *Abies alba* Mill. in the French Mediterranean Alps. *Molecular ecology,* 25(3), pp. 776-794.

Rose, L., Leuschner, C., Köckemann, B. & Buschmann, H. (2009). Are marginal beech (Fagus sylvatica L.) provenances a source for drought tolerant ecotypes? *European Journal of Forest Research,* 128(4), pp. 335-343.

Rotem-Mindali, O., Michael, Y., Helman, D. & Lensky, I.M. (2015). The role of local land-use on the urban heat island effect of Tel Aviv as assessed from satellite remote sensing. *Applied Geography,* 56, pp. 145-153.

Roy, S., Davison, A. & Östberg, J. (2017). Pragmatic factors outweigh ecosystem service goals in street tree selection and planting in South-East Queensland cities. *Urban Forestry & Urban Greening,* 21, pp. 166-174.

RSODA (2017). *Annali idrologici*. Available at: http://www.osservatorioacque.it/?cmd=page&id=dati_annali_cons&tpl=default [2017-11-22].

Sanders, J.R. & Grabosky, J.C. (2014). 20 years later: Does reduced soil area change overall tree growth? *Urban Forestry & Urban Greening,* 13(2), pp. 295-303.

Santamour, F.S. (1990). Trees for urban planting: diversity uniformity, and common sense. In: *Proceedings of 7th Conference of the Metropolitan Tree Improvement Alliance*, Illinois, pp. 57-65.

Savage, J. & Vellend, M. (2015). Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming. *Ecography,* 38(6), pp. 546-555.

Savi, T., Bertuzzi, S., Branca, S., Tretiach, M. & Nardini, A. (2015). Drought-induced xylem cavitation and hydraulic deterioration: risk factors for urban trees under climate change? *New Phytologist,* 205(3), pp. 1106-1116.

Savolainen, O., Pyhäjärvi, T. & Knürr, T. (2007). Gene flow and local adaptation in trees. *Annu. Rev. Ecol. Evol. Syst.,* 38, pp. 595-619.

Scalfi, M., Mosca, E., Di Pierro, E.A., Troggio, M., Vendramin, G.G., Sperisen, C., La Porta, N. & Neale, D.B. (2014). Micro-and macro-geographic scale effect on the molecular imprint of selection and adaptation in Norway spruce. *PloS one,* 9(12), p. e115499.

Scharnweber, T., Manthey, M., Criegee, C., Bauwe, A., Schröder, C. & Wilmking, M. (2011). Drought matters–declining precipitation influences growth of Fagus sylvatica L. and Quercus robur L. in north-eastern Germany. *Forest Ecology and Management,* 262(6), pp. 947-961.

Schuldt, B., Knutzen, F., Delzon, S., Jansen, S., Müller-Haubold, H., Burlett, R., Clough, Y. & Leuschner, C. (2016). How adaptable is the hydraulic system of European beech in the face of climate change-related precipitation reduction? *New Phytologist,* 210(2), pp. 443-458.

Schulze, E.D., Beck, E. & Müller-Hohenstein, K. (2005a). Stress physiology. In: *Plant Ecology*. Berlin: Springer, pp. 5-252.

Schulze, E.D., Beck, E. & Müller-Hohenstein, K. (2005b). Syndynamics, Synchorology, Synecology. In: *Plant Ecology*. Berlin: Springer, pp. 465-639.

Seibert, J., Stendahl, J. & Sørensen, R. (2007). Topographical influences on soil properties in boreal forests. *Geoderma,* 141(1-2), pp. 139-148.

Shaw, S.B. & Riha, S.J. (2011). Assessing temperature-based PET equations under a changing climate in temperate, deciduous forests. *Hydrological Processes,* 25(9), pp. 1466-1478.

Sieghardt, M., Mursch-Radlgruber, E., Paoletti, E., Couenberg, E., Dimitrakopoulus, A., Rego, F., Hatzistathis, A. & Randrup, T.B. (2005). The abiotic urban environment: impact of urban growing conditions on urban vegetation. *Urban forests and trees. Springer, Berlin*, pp. 281-323.

Sjöman, H. (2012). *Trees for tough urban sites.* Diss. Alnarp: Swedish University of Agricultural Sciences.

Sjöman, H., Busse Nielsen, A., Pauleit, S. & Olsson, M. (2010). Habitat studies identifying potential trees for urban paved environments: A case study from Qinling Mt., China. *Journal of Arboriculture,* 36(6), p. 261.

Sjöman, H., Gunnarsson, A., Pauleit, S. & Bothmer, R. (2012a). Selection Approach of Urban Trees for Inner City Environments: Larning from Nature. *Arboriculture and Urban Forestry,* 38(5), p. 194.

Sjöman, H., Hirons, A. & Deak-Sjöman, J. (2017). Criteria in the selection of urban trees for temperate urban environments. In: Ferrini, F., Van Den Bosch, C.C.K. & Fini, A. (eds) *Routledge Handbook of Urban Forestry*. New York: Routledge, pp. 339-362.

Sjöman, H., Hirons, A.D. & Bassuk, N.L. (2015). Urban forest resilience through tree selection—Variation in drought tolerance in Acer. *Urban Forestry & Urban Greening,* 14(4), pp. 858-865.

Sjöman, H., Morgenroth, J., Sjöman, J.D., Sæbø, A. & Kowarik, I. (2016). Diversification of the urban forest—Can we afford to exclude exotic tree species? *Urban Forestry & Urban Greening,* 18, pp. 237-241.

Sjöman, H., Nielsen, A.B. & Oprea, A. (2012b). Trees for urban environments in northern parts of Central Europe–a dendroecological study in north-east Romania and Republic of Moldavia. *Urban ecosystems,* 15(1), pp. 267-281.

Sjöman, H., Östberg, J. & Bühler, O. (2012c). Diversity and distribution of the urban tree population in ten major Nordic cities. *Urban Forestry & Urban Greening,* 11(1), pp. 31-39.

Sjöman, H., Östberg, J. & Nilsson, J. (2014). Review of host trees for the wood-boring pests Anoplophora glabripennis and Anoplophora chinensis: An urban forest perspective. *Arboricul. Urban For.,* 40, pp. 143-164.

Skvortsov, A. (2002). A new system of the genus Betula L.–the birch. *Bulletin of Moscow Society of Naturalist,* 107, pp. 73-76.

Soltis, D.E., Smith, S.A., Cellinese, N., Wurdack, K.J., Tank, D.C., Brockington, S.F., Refulio-Rodriguez, N.F., Walker, J.B., Moore, M.J. & Carlsward, B.S. (2011). Angiosperm phylogeny: 17 genes, 640 taxa. *American Journal of Botany,* 98(4), pp. 704-730.

Sperry, J.S. (2000). Hydraulic constraints on plant gas exchange. *Agricultural and forest meteorology,* 104(1), pp. 13-23.

Stephenson, N. (1998). Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *Journal of Biogeography,* 25(5), pp. 855-870.

Stojnić, S., Suchocka, M., Benito-Garzón, M., Torres-Ruiz, J., Cochard, H., Bolte, A., Cocozza, C., Cvjetković, B., De Luis, M. & Martinez-Vilalta, J. (2017). Variation in xylem vulnerability to embolism in European beech from geographically marginal populations. *Tree physiology*, pp. 1-13.

Sundbom, J. (2013). *Går det att ha en bred artrikedom i den Norrländska staden?*. Swedish University of Agricultural Sciences. (BSc. thesis, Trädgårdsingenjörsprogrammet).

Svenning, J.C., Normand, S. & Kageyama, M. (2008). Glacial refugia of temperate trees in Europe: insights from species distribution modelling. *Journal of Ecology,* 96(6), pp. 1117-1127.

Sydnor, T.D., Subburayalu, S. & Bumgardner, M. (2010). Contrasting Ohio nursery stock availability with community planting needs. *Journal of Arboriculture,* 36(1), p. 47.

Taha, H. (1997). Urban climates and heat islands: albedo, evapotranspiration, and anthropogenic heat. *Energy and buildings,* 25(2), pp. 99-103.

Taiz, L. & Zeiger, E. (2010). Responses and adaptations to abiotic stress. *Plant Physiology, Fifth Edition. Sunderland, MA: Sinauer Associates, Inc*, pp. 755-778.

Tardieu, F. & Simonneau, T. (1998). Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. *Journal of Experimental Botany*, pp. 419-432.

Tello, M.-L., Tomalak, M., Siwecki, R., Gáper, J., Motta, E. & Mateo-Sagasta, E. (2005). Biotic urban growing conditions—threats, pests and diseases. In: *Urban forests and trees* Springer, pp. 325-365.

Thiel, D., Kreyling, J., Backhaus, S., Beierkuhnlein, C., Buhk, C., Egen, K., Huber, G., Konnert, M., Nagy, L. & Jentsch, A. (2014). Different reactions of central and marginal provenances of Fagus sylvatica to experimental drought. *European Journal of Forest Research,* 133(2), pp. 247-260.

Thomsen, P., Bühler, O. & Kristoffersen, P. (2016). Diversity of street tree populations in larger Danish municipalities. *Urban Forestry & Urban Greening,* 15, pp. 200-210.

Thornthwaite, C.W. (1948). An approach toward a rational classification of climate. *Geographical review,* 38(1), pp. 55-94.

Tigano, A. & Friesen, V.L. (2016). Genomics of local adaptation with gene flow. *Molecular ecology,* 25(10), pp. 2144-2164.

TN (2017). *Climate Jiulong*. Available at: https://en.tutiempo.net/climate/ws-564620.html [2017-11-22].

TN (2017). *Climate Kanding*. Available at: http://en.tutiempo.net/climate/ws-563740.html [2017-11-22].

TN (2017). *Climate Nyingchi*. Available at: https://en.tutiempo.net/climate/ws-563120.html [2017-11-22].

Tubby, K. & Webber, J. (2010). Pests and diseases threatening urban trees under a changing climate. *Forestry,* 83(4), pp. 451-459.

Tuhkanen, S. (1980). *Climatic parameters and indices in plant geography*. (Acta Phytogeographica Suecia, 67). Uppsala: Svenska Växtgeografiska Sällskapet.

Wang, N., McAllister, H.A., Bartlett, P.R. & Buggs, R.J. (2016). Molecular phylogeny and genome size evolution of the genus Betula (Betulaceae). *Annals of botany,* 117(6), pp. 1023-1035.

Wendler, R. & Millard, P. (1996). Impacts of water and nitrogen supplies on the physiology, leaf demography and nitrogen dynamics of Betula pendula. *Tree physiology,* 16(1-2), pp. 153-159.

Whiteman, C.D. (2000). *Mountain meteorology: fundamentals and applications*: Oxford University Press.

Willis, K.J., Rudner, E. & Sümegi, P. (2000). The full-glacial forests of central and southeastern Europe. *Quaternary Research,* 53(2), pp. 203-213.

WMO (2010). *Standard Normals - Dry Bulb Temperature*. Available at: http://www.wmo.int/datastat/wmodata_en.html [2017-11-22].

WorldClim (2017). *Bioclimatic variables*. Available at: http://www.worldclim.org/bioclim [2018-02-13].

Yanagisawa, N. & Fujita, N. (1999). Different distribution patterns of woody species on a slope in relation to vertical root distribution and dynamics of soil moisture profiles. *Ecological Research,* 14(2), pp. 165-177.

Yeakley, J.A., Swank, W., Swift, L., Hornberger, G. & Shugart, H. (1998). Soil moisture gradients and controls on a southern Appalachian hillslope from drought through recharge. *Hydrology and Earth System Sciences Discussions,* 2(1), pp. 41-49.

Yim, Y.-J. & Kira, T. (1975). Distribution of forest vegetation and climate in the Korean peninsula: I. Distribution of some indices of thermal climate. *Japanese Journal of Ecology,* 25(2), pp. 77-88.

Zang, C., Hartl-Meier, C., Dittmar, C., Rothe, A. & Menzel, A. (2014). Patterns of drought tolerance in major European temperate forest trees: climatic drivers and levels of variability. *Global change biology,* 20(12), pp. 3767-3779.

Zimmermann, N.E., Yoccoz, N.G., Edwards, T.C., Meier, E.S., Thuiller, W., Guisan, A., Schmatz, D.R. & Pearman, P.B. (2009). Climatic extremes improve predictions of spatial patterns of tree species. *Proceedings of the National Academy of Sciences,* 106(Supplement 2), pp. 19723-19728.

Östergren, S. (2017). *Utbredning av kastanjeblödarsjuka träd orsakad av Pseudomonas syringae pv. aesculi i centrala Malmö.* Swedish University of Agricultural Sciences. (BSc. thesis, Landskapsingenjörsprogrammet).

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Appendix 1 – Osmometry readings

Table 7. *Osmometry readings (mmol* kg^{-1}*) from B. pendula s.l. Specimens were collected at Ness Botanic Gardens, UK.*

Listvyanka	Basongtso	Kuril Islands	Furano	Valais
769	675	760	781	728
658	697	900	679	820
569	668	791	727	805
635	713	810	640	776
676	750	776	610	811
566	645	712	739	703
612	749	724	720	809
	636	681	615	785
		709	768	

Carmolangan	Horní Bečva	Hauho	Novosibirsk	Gonggashan Xiang
933	895	857	922	744
998	864	1090	749	642
834	822	1128	783	687
875	728	1016	927	729
993	750	897	803	691
838	1049	963	950	628
919	978	713	727	839
1023	1221	909		873

Alberta	Paoma Shan	Mt. Etna
676	770	805
745	809	688
721	913	665
746	636	613
721	704	610
698	753	678
701	675	684
682	624	
865		

Appendix 2 – Climate data

Temperature

Listvyanka (Irkutsk, 30710)

Table 8. *Normal temperatures for Irkutsk[1] (°C)*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1961-1990	-18,80	-16,70	-7,40	1,40	9,30	15,00	17,50	15,10	8,70	0,90	-8,40	-16,00

1. WMO (2010). *Standard Normals - Dry Bulb Temperature.* http://www.wmo.int/datastat/wmodata_en.html. [2017-11-22].

Basongtso (Nyingchi, 56312)

Table 9. *Average temperatures for Nyingchi (1978-2007)[1] (°C)*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1978	-0,5	2,1	4,2	8	12,1	14,6	15,5	15,3	12,8	10	5,2	1,6
1979	0,9	1,9	4,1	9,7	13,4	15,3	15,3	15,6	12,6	8,8	7,4	1,7
1980	0,3	2,1	5,2	9	11,4	15	15,6	15	13,7	8,8	5,3	2,9
1981	0,5	4,3	4,9	8,2	11,9	15,6	16,4	16,3	13,5	11,5	5	1
1982	2	1,2	4,4	8,7	11,8	14,6	15,8	16,2	13,7	9,4	4,2	1,4
1983	-1,5	0,6	4,9	6,9	11,7	14,9	16,8	15,8	14	10,2	5,1	0,8
1984	-0,1	2,9	6,4	8,8	11,1	15,1	15,5	15,3	13,5	12,1	4,6	2,4
1985	0,7	2,3	7,3	9,3	12,1	14,6	14,5	16,5	13,5	9,6	5	2,3
1986	1,3	2,3	4,7	7,7	11,7	15,3	16,2	15,7	12,6	8,2	5,4	1,4
1987	1,1	3,6	5,6	8,5	11,7	15,9	15,1	14,2	13,5	9,4	5,9	1,9
1988	1,4	3,6	6,1	8,9	12,6	15	15,9	15,3	13,4	10,4	4,7	2,8
1989	0,1	1	5,8	7,3	12,1	15,2	16	15,5	14,2	10,6	4,9	0,6
1990	3,2	2,4	4,3	6,8	11,5	14,6	15,5	15,3	13,1	9,8	6,3	2,5
1991	0,1	3,8	6,2	7,9	11,7	14,5	16,1	15,1	13,8	10,5	5,2	0,9
1992	0,5	0,3	6,1	9,5	11,2	15	14,8	15,2	14,3	9,4	4,7	0
1993	1,1	3,4	5,3	9	12	14,2	16,4	15,1	13,2	10,4	5,6	2,5
1994	2,4	2,4	5,6	8,5	12,6	14,9	17,2	15,9	15	10,2	4,7	1,1
1995	0,8	2,7	6,8	9	13,4	16,1	15,7	15,5	13,9	10,8	6,7	3,3
1996	1,4	3,4	6,9	9,5	11,9	14,3	16	16	13,8	10,6	7,2	2,6
1997	0,8	0,8	6	8,1	12,5	14,2	16,1	15,6	13,2	9,1	5,8	2
1998	1	3,3	4,9	9,7	13,7	15,6	16,4	15,3	14,2	12,1	7,6	1,8
1999	1,1	5,8	6,9	11,3	12,8	15,9	16	15,1	14,5	11,3	6,3	1,8
2000	1,2	1,3	5,5	9,3	12,8	15,8	16	15	13,8	10,7	6,3	1,3
2001	1,7	4,3	5,4	8,8	12,6	14,7	17	15,5	14,3	10,4	6,5	2,1
2002	1	4,7	6,3	9,7	11,5	15,6	15,9	15,5	14,2	9,6	6	2,7
2003	1,4	3,4	5,8	10	11,7	14,9	15,7	17	13,9	11,4	6,8	2,6
2004	1,2	2,8	8,7	10	12,9	14,9	15,4	16,3	14,2	10	4,7	1,9
2005	2	4,5	7,3	9,4	11,5	16	17,4	16,6	15,1	10,6	7,1	2,7
2006	3,2	6	6,5	9,3	12,7	15,9	17,5	17	14,7	9,8	6	2,5
2007	1,3	3	7,3	9,6	14	14,7	16,5	16,9	14,2	12	6,7	2,4

1. Tutiempo Network, S.L. (2017). *Climate Nyingchi.* https://en.tutiempo.net/climate/ws-563120.html. [2017-11-22].

Kuril Islands (Juzhno-Kurilsk, 32165)

Table 10. *Normal temperatures for Juzhno-Kurilsk*[1] *(°C)*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1961-1990	-4,90	-6,10	-3,10	1,50	5,30	8,30	12,10	15,60	14,50	10,40	4,10	-1,00

1. WMO (2010). *Standard Normals - Dry Bulb Temperature.* http://www.wmo.int/datastat/wmodata_en.html. [2017-11-22].

Furano (Asahikawa, 47407)

Table 11. *Average temperatures for Asahikawa (1961-1990)*[1] *(°C)*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1961	-9,8	-7,6	-2,4	6,4	11,7	17,8	22	21,2	17,9	8,9	2,2	-4,5
1962	-7,8	-8,1	-3,1	7	12,8	15,6	20,6	19,5	16,2	7,5	0,9	-4,2
1963	-10	-6	-0,8	5,6	12,4	16	21	20,9	14,2	8,7	2,5	-2,6
1964	-8,3	-10,7	-2	4,8	12,3	15,8	18,5	20,3	13,6	7,7	1,8	-4,4
1965	-6	-7,5	-3,6	2,8	10,9	16,4	18,4	21	15,3	8,6	1,4	-4,2
1966	-8	-6,2	-1	3,3	11,2	15,4	18,7	21,4	14,1	10,4	3,1	-6,4
1967	-9,5	-7,5	-1,4	4,9	14,1	15,5	21	21	14,7	8,4	-0,1	-5
1968	-7,3	-10,3	0,5	6,3	11,5	17,5	20,2	19,9	15,4	6,5	3,8	-1,7
1969	-8,7	-8,5	-3,9	4,6	10	15,5	21	18,5	14,1	7,4	1,4	-6
1970	-10,6	-6	-5,1	4,2	13,8	16,2	21,2	20,8	15,5	9,1	2,8	-4,6
1971	-9,2	-7,6	-1,8	5	11,1	15,9	19,4	19,9	14	8,7	2,5	-2,8
1972	-7,6	-7,2	-1,4	6,9	12	16,6	20,9	21	15	9,6	0,7	-3
1973	-6,5	-5,7	-4,7	5,4	11,4	16,6	20,4	22,2	15,1	8	1,8	-3,7
1974	-7,8	-6,9	-3,5	4,8	11,3	15,8	20,5	20,5	15,6	8,1	0,6	-7,1
1975	-7,7	-8,5	-3,4	5,7	11,2	16,4	19,6	21,3	16,6	8,3	1,9	-6,7
1976	-7,4	-5,7	-2,7	4,1	12,4	15,8	20,4	18	14,4	8,4	0,6	-5
1977	-12,2	-10,3	-2,6	3,2	10,7	16,3	21,8	19,2	15,6	8,7	2,8	-4,4
1978	-8,8	-11,8	-4,2	4,6	11,4	18,3	23,9	22	14,7	7,5	1,4	-4,2
1979	-7,8	-5,6	-3,7	2,8	10,4	17,3	19	21,3	14,6	10,5	1,6	-1,7
1980	-7,2	-9,4	-2,9	2,4	11,9	18,2	19,1	18,2	15,1	8,3	2,6	-4,1
1981	-10,2	-7,5	-3,4	5	9,8	15,7	21,2	19,8	14,5	8,7	-0,4	-2,7
1982	-8,1	-9	-1,4	4,8	12,4	15,6	20,3	22,5	15,8	9,9	3	-2,3
1983	-6,8	-8,4	-3,1	8,6	11,7	12,8	18,2	21,5	15,5	6,7	2,4	-5,5
1984	-9	-10,4	-4,5	3,5	11,9	18,8	22,7	22,4	15,5	7,3	1	-4,8
1985	-12,3	-4,8	-2,1	6,8	11,9	15,3	20,3	23,6	14,8	8,5	2,1	-6,7
1986	-9,9	-9,3	-3,2	5,6	10,6	16,3	18,6	22	15,8	6,6	1,2	-5,3
1987	-8,3	-7,5	-2,2	4,2	11,9	16,9	20,1	19,6	16,5	9,6	1,1	-4,8
1988	-5,8	-9,3	-2,5	5,2	10,8	17,6	18,8	22,6	15,7	8,2	-0,6	-3
1989	-5,6	-4,7	0,6	5,8	11,1	15,1	21,9	22	16,4	9,4	4	-4,3
1990	-8,5	-3,6	0,2	6,6	12,7	17,7	21,5	21,8	16,3	9,9	4,6	-0,4

1. JMA (2017). *Tables of Monthly Climate Statistics.* http://www.data.jma.go.jp/obd/stats/data/en/smp/index.html. [2017-11-22].

Valais (Montana, 67240)

Table 12. *Normal temperatures for Montana*[1] *(°C)*

Year	Jan	Feb	Mar	Apr	Maj	Jun	Jul	Aug	Sep	Okt	Nov	Dec
1961-1990	-2,3	-1,9	0,1	3,4	7,9	11,4	14	13,3	11	7,1	1,7	-1,1

1. MeteoSwiss (2016). *Climate normals Montana.* http://www.meteoswiss.admin.ch/product/output/climate-data/climate-diagrams-normal-values-station-processing/MVE/climsheet_MVE_np6190_e.pdf. [2017-11-22].

Carmolangan (Colle Belenda)

Table 13. *Average temperatures for Colle Belenda (2004-2016)[1] (°C)*

Year	Jan	Feb	Mar	Apr	Maj	Jun	Jul	Aug	Sep	Okt	Nov	Dec
2004										9,3	4,8	2,7
2005	0,4	-2,1	2,6	5,1	11	14,3	15,8	14,7	11,9	8,6	3,5	-0,1
2006	-0,6	0,1	2,2	6,7	10,4	14,8	18,2	13,8	13,9	10,9	6,2	3,9
2007	3,5	3,5	4,2	9,3	10,9	13,3	16,6	15,2	12	8,6	4,6	1,8
2008	2,7	2	3,2	5,3	10	13,6		16	11	9,3	3,5	0,4
2009	-0,1	-0,1	3,4	6,2	12,9	14,3	16,6	17,6	13,2	8,9	5,8	1,2
2010	-1,5	-0,3	1,9	6,4	8,5	13,3	17,4	15,1	11,7	8	3,2	-0,2
2011	0,7	2,4	2,9	9,3	11,6	13,6	14,2	17,6	15,1	9,6	6	3,1
2012	2,2	-0,7	6,8	5,4	9,5	15,2	17,5	18,3	12,9	9,1	5,6	1,6
2013	1,8	-1,6	1,6	6,5	7,5	12,9	16,5	16,4	12,7	9,8	4,7	3,4
2014	2	1,3	5	7,3	8,9	13,8	14,4	14,5	13	10,1	6,2	3
2015	2,6	0,7	4,3	7,5	11,5	15	19,8	16,8	11,8	8,5	7,1	4,1
2016	1,4	2,7	2,8	7,2	9,2	13,2	17,6	16,7	13,9	8,7	4,6	4,3

1. Regione Liguria (2017). *Temperatura Media Dell'Aria - Colle Belenda.*

http://www.cartografiarl.regione.liguria.it/SiraQualMeteo/script/PubAccessoDatiMeteo.asp. [2017-11-22].

Horní Bečva (Ostrava, 11782)

Table 14. *Normal temperatures for Ostrava[1] (°C)*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1961-1990	-2,4	-0,7	3,2	8,2	13,2	16,4	17,8	17,2	13,6	8,9	3,7	-0,4

1. WMO (2010). *Standard Normals - Dry Bulb Temperature.* http://www.wmo.int/datastat/wmodata_en.html. [2017-11-22].

Hauho (Lahti, 02965)

Table 15. *Average temperatures for Lahti (1981-2010)[1] (°C)*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1981	-5	-7,3	-7,3	1	10,9	13	16,5	13,6	9,5	5,4	-0,7	-7,5
1982	-12,8	-7,3	-0,9	2,4	9,1	10,9	16,6	14,9	9	3,5	2,5	-1,7
1983	-2,8	-9,7	-3,7	4,7	11,5	13,4	17,3	14,7	10,9	4,7	-3	-4,1
1984	-5,8	-7,1	-5,3	4,3	12,9	13,3	15,2	14,1	9,2	6,2	0,5	-3,1
1985	-17,4	-16,8	-2,8	0,6	8,9	13,2	15,5	15,5	8,5	5,8	-2,3	-8,3
1986	-9,7	-13,6	-1,2	2,1	10,8	16,7	16,8	13,1	6,2	4,6	2,7	-9,3
1987	-19,4	-8,1	-6,7	2,1	8,1	13	14,9	12	8,5	5,7	-2,1	-6
1988	-4,4	-5,3	-3,6	1,2	11,8	17	19,7	14,2	10,7	3,8	-4,5	-7,5
1989	-1,1	-0,6	0,9	5,2	10,7	16,4	17,3	14,2	11	4,3	-0,2	-6,4
1990	-5,9	0,5	0,3	5,6	9,2	13,7	15,5	15,3	8	4,5	-2,2	-2
1991	-5	-7,6	-1,7	3,1	7,4	12,8	17,2	16,1	9,2	5,2	2,2	-2,6
1992	-2,9	-2,9	0,2	1,2	11,1	15,7	16,2	14,4	11,3	-0,8	-2,8	-0,4
1993	-2,9	-3,8	-1	2,7	12,8	11,6	15,7	13,1	5,6	2,4	-4,7	-4,1
1994	-5,4	-14,5	-3,5	4,8	7,9	12,8	19	15,1	10,1	3,8	-1,8	-1,8
1995	-4,2	-1,4	-0,5	2,5	9	17,5	15,6	15,6	10	7,2	-3,4	-10,9
1996	-7,2	-12,2	-4,1	2,7	9	13,5	14,3	16,6	8,1	6	2,4	-6,6
1997	-6	-4,9	-1,6	1,3	7,8	16,4	18,1	17,5	9,6	2,3	-0,8	-4,6
1998	-2,7	-6,6	-5,9	2,4	9,5	14,4	15,9	13,1	10,4	4,3	-4,5	-3,8
1999	-7,5	-9	-2,6	5	7,3	18,1	17,8	14,1	10,8	5,8	0,9	-3,6
2000	-4,3	-3,7	-2,2	5,1	10,1	14	16,3	14,3	7,9	7,4	3,1	0
2001	-3,2	-8,5	-4,9	5,5	8,9	13,9	19,3	15,3	10,9	6,9	-1,4	-8,9
2002	-5,1	-2,1	-0,8	4,8	11,3	15,5	18,4	17,5	9,4	-0,5	-4	-9,6
2003	-11,6	-6,4	-1,5	2,1	10,2	12,7	20	15,2	10,4	2,9	1,7	-2,2

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2004	-8,6	-5,8	-1,8	3,8	9,3	12,6	16,3	15,6	11,6	4,3	-1,3	-2
2005	-2,2	-6,7	-6,8	3,6	9,4	13,9	18,4	15,5	10,9	6	3,2	-4,8
2006	-5,9	-10,3	-7,4	3,4	10,1	15,6	18,1	17,7	12,5	6,4	0,1	2
2007	-3,6	-12,1	1,9	4,7	10,4	14,8	16,7	16,4	9,5	5,5	-0,8	0,7
2008	-1,5	-1	-2	5,4	9,9	13,7	16	14	8,8	6,7	1	-0,9
2009	-5,7	-6,2	-2,5	3,7	11,1	13,5	16,6	15,1	11,4	2,1	1,1	-7,6
2010	-14,2	-10,2	-3,3	4,2	11,2	14,4	21,9	16,8	10,6	3,4	-2,8	-11

1. FMI (2012). *Tilastoja Suomen ilmastosta 1981–2010.* https://helda.helsinki.fi/bitstream/handle/10138/35880/Tilastoja_Suomen_ilmastosta_1981_2010.pdf. [2017-11-22].

Novosibirsk (Novosibirsk, 29638)

Table 16. *Normal temperatures for Novosibirsk*[1] *(°C)*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1961-1990	-16,5	-14,8	-7,6	2,3	11,8	17,1	19,4	16,6	10,2	3,1	-6,9	-14

1. Pogodaiklimat. (2017). *Климатгорода.* http://www.pogodaiklimat.ru/climate/29638.htm. [2017-03-21].

Gonggashan Xian (Jiulong, 56462)

Table 17. *Average temperatures for Jiulong (1978-2007)*[1] *(°C)*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1978	-0,6	3,1	5,9	9,4	11,9	13,5	14,9	14,9	12,2	10	4,7	0,7
1979	0,6	3,1	6	11,1	14,5	13,7	16	15,3	12,9	7,5	5,4	1,2
1980	0,3	3,4	6,9	9,6	12,5	15,2	15,7	14,4	13	9	5,4	2,7
1981	1,1	5,2	5,8	9,9	11,7	14,8	15,7	16,3	13,7	10,5	5,2	1,2
1982	2,2	2,2	7,4	8,5	13,5	13,9	15,6	15,9	13,1	9,8	3,9	0,2
1983	-1,1	0,7	4,6	8,4	13,3	15,7	16,5	14,3	14,1	11,8	5	0
1984	0,8	6,1	7,5	9,9	11,8	15	15,7	14,2	13,4	10,2	4,3	2,4
1985	2	3,6	7,7	9,8	14,3	14,4	15,4	15,6	13,5	9,8	3,9	1,8
1986	1,1	3,6	5,8	9,7	13,3	16,5	14,8	13,7	11,8	7,9	5,4	2,3
1987	1,5	4,4	7,1	10,3	14,4	16,6	15	13,9	12	10	5,7	0,6
1988	2,4	5,1	7,6	8,8	13,6	15,8	15,2	14,9	13	11,6	5,5	2,5
1989	1	3,3	7,6	9,3	12,6	15,3	15	14,8	14,1	9,5	4,5	0,2
1990	1,8	3,4	5,3	9	11,5	13,8	15,7	14,9	12	9,5	5,5	1,8
1991	1,2	4,9	7,7	10,9	13	15,2	15,5	14,6	13	11	4,6	1,5
1992	-0,3	1,4	6,4	9,8	12,4	15,2	14,4	14,5	14,2	8,9	3,4	0
1993	1,4	3,6	7,2	10,1	13,9	14,6	15,8	14,6	12,7	9,8	5,5	2,3
1994	3,4	3,9	5,8	11,2	14,3	15,2	14,6	15,7	14,7	9,4	5,4	1
1995	2,1	2,9	7,6	10,6	13,5	15	15,6	16	13,4	11,5	7,2	2,5
1996	1,8	3,8	8	11,5	13,4	14,8	15,4	15,7	13,2	11,2	6,3	2,3
1997	1	2,2	7,2	8,8	12,9	13,8	14,7	15,9	11,7	9,8	5,4	2
1998	1,7	4,1	7,2	10,3	15,1	15,2	16,2	14,8	13,6	11,1	6,1	2
1999	1,9	6,6	8,8	12,5	11,9	16,2	15	14,5	13,8	11,7	5,6	1,2
2000	1,2	3,8	6,7	9,7	12,8	14,2	15,7	14,7	13	10,7	4,7	1,4
2001	1,9	5	7,1	10,3	11,5	13,8	15,8	14,5	14,2	10,7	5,2	1,8
2002	1,4	5,3	6,6	11,2	11,7	15,4	15,3	13,8	12,4	8,9	5,7	2
2003	1,8	3,6	7,5	11,3	13,5	13,1	16	16,4	13,7	10,9	5,5	2,7
2004	1,6	3,2	8,6	9	12,5	13,8	14,4	15,4	13,3	9,6	4,2	1,9
2005	2,9	4,7	6,5	9,9	14	16,1	15,8	15,3	14,5	10,7	6,8	1,9
2006	3,5	5,5	7,3	10,1	12,5	15,2	16,8	16,3	14	10,2	5	1,6
2007	1,6	3,1	8,7	9,5	13,1	14,6	15,6	15,6	12,9	11,2	5,4	2,3

1. Tutiempo Network, S.L. (2017). *Climate Jiulong.* https://en.tutiempo.net/climate/ws-564620.html. [2017-11-22].

Alberta (Red Deer, 71878)

Table 18. *Normal temperatures for Red Deer[1] (°C)*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1938-1990	-13,5	-10	-4,7	3,7	9,9	14	15,8	15	9,9	4,6	-5,3	-11,9

1. WMO (2010). *Standard Normals - Dry Bulb Temperature.* http://www.wmo.int/datastat/wmodata_en.html. [2017-11-22].

Paoma Shan (Kanding, 56374)

Table 19. *Average temperatures for Kanding (1978-2007)[1] (°C)*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1978	-2,5	-0,2	3,5	8,3	11,1	13,5	15,9	16,6	11,9	8,1	2	2
1979	-1	1,6	3,9	9,9	10,5	12,9	16,3	16,1	11,1	7,8	2,7	0,7
1980	-2	-2,6	4,9	9,6	11,8	13,8	15,4	13,9	10,9	8,3	5,5	-0,4
1981	-0,7	1,4	4,7	8,6	10,3	13,7	16,4	16,4	12,1	6,2	2,5	-2,2
1982	0,5	-1,2	5,1	5,1	11,9	11,4	14,7	16,1	10,9	8,9	2,8	-2,1
1983	-3,5	-2	1,1	7,8	12,4	13,2	15,8	15	13,2	9,1	4,1	-1,4
1984	-4,8	-1,7	3,7	8,4	11	14,7	15,8	15,4	11,9	6,9	4,4	-2,2
1985	-2,6	-0,3	0,5	8	12,3	12,6	15	16,3	11	8,6	3	-0,1
1986	-1,5	-0,7	3,2	6,8	11,6	14,1	15,6	14,7	10,3	7,3	2,9	0,8
1987	0	2,2	6,4	8,2	12	14,5	14,7	14,2	10,9	8,7	4,5	0,3
1988	-0,6	-0,6	2	7,3	12,1	14,8	16,4	15,2	10,7	7,8	3,7	1,4
1989	-2,9	-2,1	2	6	10,2	13,3	15,3	15,5	12,4	7,7	2,6	0,1
1990	-0,5	0,5	4,3	7,3	10,5	13,4	16,1	16,2	11,6	7,3	5,6	1,2
1991	-1,9	0,4	5,8	7,4	10,9	14,6	15,8	15,1	11,9	6,9	2,7	0,2
1992	-1,7	-2,1	2	8,9	10,7	13,9	14,8	15,2	13	6,7	2,9	1,1
1993	-3,7	2,2	4,7	8,2	11,1	13,3	15,6	14,1	11,9	6,5	4,8	-0,1
1994	-1,5	0,8	2,4	9,2	11,7	13,9	16,3	17,3	11,8	7	5,5	-0,1
1995	-3,2	-2,1	2,1	6,7	11,1	13,7	15,9	15,7	12,4	8,4	3,1	-1,2
1996	-2,1	-0,9	4,4	7,3	9,5	13,6	15,4	16,3	12,1	8,5	3,5	-0,2
1997	-0,9	-1,8	4,1	7,5	11,4	12,6	15,8	16,7	11,1	7,5	4,5	-0,1
1998	-2,1	0,7	3,8	11,1	13,5	14	16,5	15	12,7	9,2	5,6	1,2
1999	-1	2,5	5	9,2	9,3	14,1	15,4	15,1	14	8,1	4,4	-0,8
2000	-1,5	-1,9	3	7,2	11,6	13,6	16,5	14,6	11,8	9,5	3	0
2001	-1,1	0,5	4,3	8	10,8	13,5	17,3	14,9	13	9,6	4,1	-0,4
2002	-1,2	1,9	4,9	10	11,2	14,7	15,6	15,1	12	8,9	4,4	0,5
2003	-0,7	3	4,5	9,8	11,2	12,8	16,2	16,3	13,2	7,8	4,4	-0,7
2004	-2,5	0,5	5	9,1	10,3	12	14,9	15,4	11,9	6,7	3,4	0,3
2005	-1,7	0,4	3,8	7,9	11,9	14,1	16,4	14,8	13,8	7,5	6,7	-1,2
2006	-0,3	1,3	4,1	9	11,8	13,7	17,7	17,6	12,9	9,6	4,4	-0,6
2007	-2,7	2,8	8,5	7,7	12,6	13,9	15,7	16,6	12,3	8,4	4,1	0,2

1. Tutiempo Network, S.L. (2017). *Climate Kanding* .http://en.tutiempo.net/climate/ws-563740.html. [2017-11-22].

Mt. Etna (Linguaglossa)

Table 20. *Average temperatures for Linguaglossa (1968-1997)[1] (°C)*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1968	6,6	9,7	9,9	15	17,9	20	24	22,7	20,7	16,9	12,7	9,4
1969	7,6	8,2	9,6	11,9	18,6	19,4	22,2	23,5	20,6	15,5	13,9	8
1970	9,5	9,4	10,5	13,9	14,9	21,7	24	25,3	22	15,7	13,4	10
1971	8,4	7,4	7,2	12,1	16,7	20,4	22,4	25,4	18,2	14,5	11,1	9,4
1972	8,1	8,6	10,4	12,5	15,7	21	22,3	21,9	18,3	13,5	12,9	9,5
1973	7,8	7,3	7,6	10,4	18,3	20,6	24,6	22,6	20,8	17,2	11,7	8,9
1974	8,6	8,7	9,1	10,4	15,9	20,4	23,2	23,9	20,4	14,5	11,3	9,2
1975	8,4	6,4	9	11,5	15,9	19,1	23,5	22	21,3	16,4	11,5	9,7

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1976	8,2	7,7	8,6	11	15,3	19,5	22	20,5	18,4	16	10,9	9
1977	8,7	10,8	11,4	11,9	16,4	19,8	23,7	22,4	19,3	15,8	13,6	9,2
1978	7,7	9	9,7	10,6	14,9	20,2	22,5	22,5	19,6	14,8	10,4	11,1
1979	7,2	9,2	10,7	9,9	16,5	21,7	23,1	23,2	19,7	17,4	11,9	10
1980	7,3	9,7	9,2	9,7	13,6	20,1	22,9	24,4	20,3	16,5	13,7	7,4
1981	5,1	7,1	11,6	12,8	16,1	22,1	22,4	23,5	21	18,6	10,8	10,2
1982	9,8	7,8	8,6	12,2	17	24,4	25,7	24,6	22	16,7	11,1	9
1983	8,7	7	10	14	18,1	20,2	26,2	22,9	20,4	15,8	11,3	9,3
1984	8,3	7,2	8,3	10,5	15,6	20	24,5	22,4	19,8	16,2	13,1	9
1985	7,4	9	9,2	14	16,9	21,6	24,8	24,6	20,9	16,4	13,5	10,6
1986	7,8	8,1	9,9	12,8	19	20,8	23,5	26	21	16,8	11,9	8,9
1987	8,7	8	7,3	13,4	15	21	26,3	25,2	24,1	18,2	12,7	11,5
1988	10,6	8,7	10,1	13,5	17,6	21,3	27,7	25,5	20,6	17,5	10,9	8,6
1989	8,3	9,5	12,3	13,7	15,6	19,7	23,8	24,3	20	15,6	12,7	11,3
1990	8,7	12	12,8	12,8	17	21,8	24,5	23,5	22,2	18,2	13,6	8,7
1991	8,4	8	11,8	11,7	14,2	21,8	24,9	24,8	21,2	16,8	12,4	6,6
1992	8,1	8,1	9,7	13,3	17	19,9	23,1	25,9	21,2	18,3	14,2	9,3
1993	8,6	6,6	9,7	13,3	18,3	23,4	26,2	28,6	23	19	13,8	12,1
1994	10,5	9,8	14,1	13,8	20,4	22,8	27,1	29,6	24,5	18,7	15,6	12,4
1995	9,9	13,1	11,5	13,9	19,9	23,6	27,9	25,7	22,6	18,4	13,4	13,1
1996	11,2	10		13,5	18,4	22,6	25,7	26	20,7	16,9	15	11,9
1997	11,2	11	12,4	11,9	20,3	24,8	26,4	25,1	21,9	17,9	14,3	11,1

1. Regione Siciliana Osservatorio Delle Acque. (2017). *Annali idrologici.* http://www.osservatorioacque.it/?cmd=page&id=dati_annali_cons&tpl=default. [2017-11-22].

Precipitation

Listvyanka (Irkutsk, 30710)

Table 21. *Normal precipitation for Irkutsk*[1] *(mm month^{-1})*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1961-1990	12,00	8,50	12,80	18,90	32,90	61,90	120,10	82,60	50,20	29,90	18,30	19,10

1. WMO (2010). *Standard Normals - Precipitation.* http://www.wmo.int/datastat/wmodata_en.html. [2017-11-22].

Basongtso (Nyingchi, 56312)

Table 22. *Average precipitation for Nyingch (1978-2007)*[1] *(mm month^{-1})*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1978	3,05	3,05	10,18	50,31	102,62	187,72	99,82	46	230,13	32,76	10,42	0
1979	3,05	6,11	49,3	33,78	24,9	175,51	195,85	93,99	126,5	70,86	54,11	8,65
1980	2,54	3,56	15,52	78,99	81,8	144,27	179,34	224,53	201,42	41,42	8,89	0
1981	2,29	2,29	23,63	112,54	83,34	172,21	165,62	85,36	368,06	19,3	2,04	8,12
1982	2,04	3,55	19,55	46,25	39,13	163,84	99,58	24,64	100,6	26,17	10,66	3,05
1983	0,76	8,13	7,13	50,81	31,5	73,41	88,43	83,84	90,16	59,19	6,34	1,27
1984	0,51	1,53	19,06	44,44	54,37	139,7	149,33	160,77	84,07	17,53	0,25	0
1985	0,76	6,36	14,48	43,96	40,13	126,51	191,75	30,23	157,98	20,31	4,32	15,49
1986	0,51	5,34	11,68	142,22	38,35	135,12	153,16	118,37	111	57,4	6,35	0,51
1987	0	3,82	16,52	37,6	33,55	82,04	182,9	187,18	179,33	87,37	6,1	0
1988	92,7	3,04	9,67	42,43	91,2	60,19	90,67	134,11	90,18	50,8	1,27	0
1989	0,25	3,56	3,05	65,03	70,86	109,47	58,94	84,59	90,67	29,48	9,9	0,25
1990	0,51	4,83	6,34	144,02	93,97	148,33	143,77	61,72	172,45	50,05	1,02	0,25
1991	0	2,8	21,58	33,79	87,63	122,44	232,66	123,44	69,86	46,23	1,53	1,01

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1992	1,27	3,3	20,34	19,8	49,01	81,54	89,92	255,28	69,84	73,42	4,57	0,25
1993	0,51	5,84	4,57	22,36	78,25	107,96	105,91	193,8	194,04	50,8	3,55	0,25
1994	0,25	1,78	34,82	53,34	93,48	132,84	91,7	269,48	57,65	50,04	1,27	0
1995	2,8	2,02	7,1	23,89	143,49	162,06	205,23	81,55	101,86	27,68	3,57	0,25
1996	3,31	3,56	31,5	44,72	145,29	244,37	171,17	104,89	78,23	42,44	0,51	0
1997	0,75	6,6	25,15	26,67	25,39	220,48	115,82	54,12	171,98	14,97	5,33	1,53
1998	2,54	3,29	13,98	21,6	96	243,56	152,68	337,09	106,93	29,71	9,9	1,52
1999									36,32	31,98	18,28	3,81
2000	11,41	11,14	75,92	63,25	136,87	128,76	165,62	211,33	91,69	23,84	7,36	2,28
2001	4,56	13,43	23,59	49,78	65,25	146,05	96	190,22	115,02	82,81	7,63	2,02
2002	8,37	7,09	24,35	60,68	55,11	101,59	237,49	118,07	65,52	23,61	8,63	1,27
2003	0	3,55	8,38	63,48	40,36	129,8	241,55	122,43	183,11	36,07	2,54	0,51
2004	2,28	2,28	28,18	30,21	68,08	185,69	191,52	105,94	102,85	80,26	3,05	0
2005	0,25	6,09	51,8	58,42	73,14	101,85	64,5	96,01	62,49	53,6	0	0
2006	0	13,21	29,46	27,16	129,54	79,5	87,86	24,38	106,93	70,87	10,42	0,51
2007	0,25	3,81	19,04	65,79	77,98	141,2	126,49	58,67	131,06	17,26	2,29	0

1. Tutiempo Network, S.L. (2017). *Climate Nyingchi.* https://en.tutiempo.net/climate/ws-563120.html. [2017-11-22].

Kuril Islands (Juzhno–Kurilsk, 32165)

Table 23. *Normal precipitation for Juzhno-Kurilsk[1] (mm month^{-1})*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1961-1990	57,70	42,80	69,30	87,20	123,90	123,10	123,90	134,10	167,20	138,00	107,50	69,90

1. WMO (2010). *Standard Normals - Precipitation.* http://www.wmo.int/datastat/wmodata_en.html. [2017-11-22].

Furano (Asahikawa, 47407)

Table 24. *Average precipitation for Asahikawa (1961-1990)[1] (mm month^{-1})*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1961	101,9	78,9	45,2	42,1	133,7	53,4	212,5	94,3	117,6	83,2	89,1	58,5
1962	51,1	57,3	98	64,8	63,7	83,3	149,3	292,8	134,7	56,8	94,5	73
1963	21,2	19,4	45,3	84,2	71,1	100,2	79,6	266,5	121,7	72,3	87,2	113,3
1964	50,6	37,3	25,2	105,4	72,6	101,1	120,4	298,2	90	54,9	119	92,2
1965	56,1	78,4	64,7	66,1	55,2	110,7	85,4	73,3	242,5	59,2	225,7	109,9
1966	114,3	95,5	113,1	44,4	43,9	111	95,2	228,5	185,2	104,8	114	113,4
1967	117,6	46,7	77,1	66	75,6	122	144,7	22,3	177,7	138,6	118,9	63,1
1968	86	40,5	73	27	92,5	36,5	75	89	108	63	85	88
1969	105,5	95,5	46	18	123	81	77	209	144	96,5	125,5	135,5
1970	57,5	99	78,5	54	35,5	80	125,5	233	151,5	177	116	117,5
1971	63,5	52,5	52,5	36,5	81,5	51,5	145,5	98	175,5	149,5	84,5	120
1972	68,5	43,5	21,5	53,5	62	77	46,5	104,5	99,5	134,5	129	161,5
1973	85	114,5	32	68,5	69,5	18	87,5	251	105,5	156	165	91
1974	33	39,5	41	118,5	70	96	22	158,5	133	119	157,5	136,5
1975	95,5	39,5	34	53	82	59	142	286,5	266,5	142	101,5	47
1976	75,5	51	59,5	47	46	58,5	95	99	60	131	130	115,5
1977	77,5	71,5	69,5	72,5	67	28,5	117	122,5	145	39,5	117,5	79,5
1978	45,5	60	34,5	86,5	106,5	77	85,5	125,5	66,5	108	70,5	94
1979	91,5	61	76,5	30,5	41	104,5	97,5	44,5	135,5	212,5	132	53,5
1980	75,5	66,5	105	86,5	45,5	85	108	106	72,5	129	88	98
1981	57,5	80	61,5	45,5	78,5	81,5	70,5	478	91,5	154	144	74
1982	85,5	22,5	69	32	55,5	44,5	76	70,5	72	61	139,5	85,5
1983	97,5	37	23	19,5	60	91	69,5	87	77,5	203,5	69,5	93,5
1984	85,5	44,5	21	11	29,5	46	77	35	60,5	125	127,5	65,5
1985	49	53,5	34	57	56	29,5	101,5	86	142	132,5	97	96,5
1986	49	30	55,5	63	84,5	10,5	56,5	91,5	177	76	121	71

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1987	104	53,5	92	56,5	79,5	37,5	190,5	145,5	55	89,5	135	97,5
1988	77,5	77	48,5	53,5	28	96,5	49,5	215,5	74,5	126	105	126,5
1989	67	19,5	68	54,5	59,5	67	23,5	216,5	167	110,5	103	96,5
1990	46,5	36	18,5	83	40,5	77,5	53,5	137	298	65	115,5	83

1. JMA (2017). *Tables of Monthly Climate Statistics.* http://www.data.jma.go.jp/obd/stats/data/en/smp/index.html. [2017-11-22].

Valais (Montana, 67240)

Table 25. *Normal precipitation for Montana*[1] *(mm month^{-1})*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1981-2010	63	56	48	39	47	62	61	66	41	52	66	79

1. MeteoSwiss (2016). *Climate normals Montana.* http://www.meteoswiss.admin.ch/product/output/climate-data/climate-diagrams-normal-values-station-processing/MVE/climsheet_MVE_np6190_e.pdf. [2017-11-22].

Carmolangan (Colle Belenda)

Table 26. *Average precipitation for Colle Belenda (2004-2016)*[1] *(mm month^{-1})*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2004										212	57,2	60
2005	19,4	18	30,8	78,6	84,6	134	70,2	41,2	167	108,4	67,2	133,8
2006	156,4	60	52,8	32,4	32,6	13,6	67,8	134	180,4	88,8	57,4	197,6
2007	35,2	22,6	30,8	40,2	100	93,8	2	17,2	27,2	64,2	100,8	71,6
2008	255	29,8	70,4	132,4	81,4	161,2		17,6	49,6	122,4	215,4	186,8
2009	111,6	125	106	326,4	22,4	139,8	55,4	81	141,8	106,4	174,2	269,8
2010	95,8	148	61,8	32,2	129,4	164,6	44	55,8	28,6	207,8	237	223,6
2011	103,6	68,4	245,6	37	29	116,8	62,6	6,8	50,2	140,6	250,2	18,6
2012	60,6	1	12,2	181,8	130,8	38,8	6,8	50	109,2	109,4	340,4	90,8
2013	155,8	41,8	337,8	153,6	185	51,2	66,6	32,4	56,2	60,6	76,6	349
2014	575,6	244	143,2	46	87,4	84,8	66,8	48,2	81,8	63,2	745,4	57,8
2015	84,4	91,8	66,2	52,8	34,6	83,4	14,6	35,6	146	231,6	16,4	23
2016	61	171,2	137,2	52	144,4	79,6	28,8	71,8	96,8	157,4	491	50,4

1. Regione Liguria (2017). *Precipitazione Cumulata - Colle Belenda.* http://www.cartografiarl.regione.liguria.it/SiraQualMeteo/script/PubAccessoDatiMeteo.asp. [2017-11-22].

Horní Bečva (Ostrava, 11782)

Table 27. *Normal precipitation for Ostrava*[1] *(mm month^{-1})*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1961-1990	26,7	30,2	34	52,4	91,2	104,4	91,1	91,8	58,8	42,3	44,6	34,3

1. WMO (2010). *Standard Normals - Precipitation.* http://www.wmo.int/datastat/wmodata_en.html. [2017-11-22].

Hauho (Lahti, 02965)

Table 28. *Average precipitation for Lahti (1981-2010)*[1] *(mm month^{-1})*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1981	63,2	14,1	47,2	17,7	13	130,1	115,2	101,8	42,3	127,8	77,2	81,9
1982	32,9	9,7	20,1	91,7	23,3	72,4	37,3	81,6	36,5	38,3	76,2	71,6
1983	73,9	7,6	35,1	26,6	61	55,4	50,9	46,8	92,2	71,3	44,5	84,7
1984	87,4	38,4	35,8	10,6	48,8	77,5	109,7	93,3	121,6	100,3	39,8	43
1985	31,3	26,1	39,6	31,5	53,6	74,4	91	113,5	56,9	46,3	65,6	58,4
1986	55,2	9,1	29	43,8	47,8	36,2	87,6	114,7	69,6	76,6	78,1	57,8
1987	21,9	34,7	16,7	7,5	44,3	117,7	61,2	89,5	107,3	20,7	50,5	41,7
1988	46,8	54,4	64,5	38,9	42,7	24,6	63,4	86,7	134,2	76,8	15,3	67,8
1989	48,2	58,4	56,5	34,6	30,8	33,4	93,3	115,1	41,9	64,5	37,3	40,7
1990	83	80,7	47,6	24,4	40,6	53,4	73,9	59,3	60,5	35,8	72,6	42,1
1991	62,1	21,9	36,3	19,7	38,4	80,4	45,8	55,6	67,7	46,4	94,4	49,7
1992	39,2	35,1	59	51	10,9	26,5	58,8	105,5	72	87	78	20,9
1993	51,9	23,8	27,9	27,7	27	61,1	96,3	109,5	21,1	53,7	5,5	59,8
1994	51,9	2,5	49,8	53,3	37,7	63,7	29,9	100,5	88,9	76,4	41,8	52,5
1995	52,6	69	45,1	25,5	85,4	16,1	44,6	49,3	56	57,6	74,9	26,6
1996	11	33,8	25,2	27,7	69	70,3	114,5	7,7	28	50,4	136,9	41,5
1997	55,3	42,3	23,8	30,8	15,1	57,2	90,3	48,4	74,7	59	34,9	35,3
1998	55,5	49,6	34,2	13	56,1	108	118,1	95,4	54,5	94,9	26,1	55,3
1999	52,5	68,4	29,2	37,6	10,6	26	37,3	61,2	39	96,6	34,4	87
2000	46,9	40,9	47,4	31	27,8	60,9	174,7	89	29,4	81,6	104,3	65,2
2001	35	43,7	42,9	21,9	33,7	94,3	67,8	24,5	85,7	60,7	37,4	25,9
2002	60,3	58,9	35,4	6,2	53,7	104,8	80,5	48,6	23	15,7	84,6	12,4
2003	40,2	9,1	6,6	23,7	81,6	58,5	72,3	63,7	29	114,7	41,9	74,3
2004	38	42,7	34,8	4,3	64,5	113,5	164	100,8	76,4	46,1	49,9	69,2
2005	89,1	14	5,1	13,9	57,5	82,4	57,1	128,3	29,2	31,7	81,7	47,8
2006	14,2	19	32,1	41,7	36,1	39,5	23,9	43,9	63	141,5	58,6	52,2
2007	52	19,4	26	27,7	47,5	51,7	129	84,3	82,1	47,3	34,4	50,6
2008	73,4	57,2	56,3	39,1	19,4	103,1	53,5	103,9	26,4	113,3	79,4	53,9
2009	37,6	23,6	27	16,5	52,5	46,9	117,7	49,1	30,2	48,2	58,9	40,9
2010	21,4	46,7	49,9	34,2	61,4	32,3	16	45	53,5	32,5	66,4	34,2

1. FMI (2012). *Tilastoja Suomen ilmastosta 1981–2010.*

https://helda.helsinki.fi/bitstream/handle/10138/35880/Tilastoja_Suomen_ilmastosta_1981_2010.pdf. [2017-11-22].

Novosibirsk (Novosibirsk, 29638)

Table 29. *Normal precipitation for Novosibirsk*[1] *(mm month^{-1})*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1961-1990	25	18	17	27	34	55	66	60	43	45	37	33

1. Pogodaiklimat. (2017). *Климатгорода.* http://www.pogodaiklimat.ru/climate/29638.htm. [2017-03-21].

Gonggashan Xian (Jiulong, 56462)

Table 30. *Average precipitation for Jiulong (1978-2007)*[1] *(mm month^{-1})*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1978	1,02	10,16	1,27	25,15	230,63	286,76	210,07	123,2	190,49	119,12	19,56	0
1979	8,13	4,08	13,46	161,29	79,77	230,39	355,34	108,74	197,35	90,96	26,42	11,68
1980	17,02	4,32	30,22	132,36	113,81	133,61	175,26	274,84	160,28	119,14	28,45	4,06
1981	71,12	2,03	23,38	106,69	176,28	189,23	199,38	166,64	182,37	9,65	85,08	2,29
1982	1,02	5,84	4,06	144,28	25,66	170,19	437,14	59,71	360,45	96,25	12,44	5,59
1983	3,05	5,33	16,5	50,54	87,64	144,02	199,64	147,58	165,88	22,62	8,89	3,56

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1984	3,05	0	12,95	48,25	136,67	132,32	185,95	141,98	102,84	37,85	1,27	2,03
1985	0,25	1,02	24,12	45,74	60,18	149,11	119,88	107,18	141,21	26,18	10,16	0
1986	0,25	5,59	18,54	29,72	77,46	191,01	264,66	230,89	197,62	60,96	6,11	0
1987	1,27	12,96	5,07	23,88	114,57	123,96	227,58	172,96	259,61	89,91	6,61	9,14
1988	0,25	2,29	8,63	89,67	53,08	124,96	238,72	161,31	271,01	49,02	11,69	0
1989	100,08	4,32	3,56	36,07	83,02	228,83	190,51	146,55	163,83	78,97	28,96	1,26
1990	7,36	0,51	126,75	17,04	103,9	260,6	146,3	170,93	194,57	87,13	27,68	1,78
1991	4,06	1,01	18,04	32,01	48,78	194,56	248,43	193,03	229,11	22,88	24,13	1,01
1992	16,77	9,13	46,48	64,76	41,4	201,42	239,51	272,81	133,34	36,83	9,64	2,54
1993	13,97	14,98	0,76	20,32	95,51	130,54	190,24	277,37	169,43	26,17	13,72	1,02
1994	1,02	7,11	63,75	21,57	63,25	176,02	164,84	85,6	101,6	67,57	4,58	0
1995	2,55	6,09	28,95	23,36	108,18	246,87	172,96	85,87	122,93	20,32	6,86	2,03
1996	0	1,52	38,85	32,76	79,74	160,01	221,48	83,04	167,64	9,4	1,02	0,25
1997	2,03	3,81	9,91	36,33	84,07	207,76	220,22	59,17	161,27	23,87	35,57	5,59
1998	2,28	0,51	12,96	141,5	46,75	258,31	286,52	236,24	93,98	55,11	19,56	0
1999									51,56	37,08	19,81	4,3
2000	9,65	5,07	9,88	41,13	94,48	248,37	134,36	234,72	98,55	37,31	18,79	3,04
2001	3,8	4,57	13,45	47,97	145,55	238,52	116,32	281,18	199,63	81,79	30,97	3,3
2002	8,37	1,52	27,41	47,73	89,91	206,74	202,67	129,05	130,8	66,03	9,15	0,76
2003	3,04	1,02	4,33	59,69	86,36	335,26	213,11	102,1	183,64	99,06	2,28	7,36
2004	0,25	11,68	21,85	73,91	123,69	190,01	245,37	206,24	220,22	91,95	16,27	2,03
2005	0	12,44	31,25	46,48	39,13	137,9	179,82	252,24	109,73	115,06	0	0
2006	0	11,93	34,79	48,02	99,31	218,17	94,98	37,09	146,81	75,92	41,41	10,67
2007	3,05	0,75	17,27	58,92	164,34	165,09	214,37	95,76	180,36	51,3	38,87	9,91

1. Tutiempo Network, S.L. (2017). *Climate Jiulong.* https://en.tutiempo.net/climate/ws-564620.html. [2017-11-22].

Alberta (Red Deer, 71878)

Table 31. *Normal precipitation for Red Deer*[1] *(mm month^{-1})*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1938-1990	20,7	14,7	16,5	22,9	49,2	85,5	87,9	64,8	54,2	20,2	14,8	18,8

1. WMO (2010). *Standard Normals - Precipitation.* http://www.wmo.int/datastat/wmodata_en.html. [2017-11-22].

Paoma Shan (Kanding, 56374)

Table 32. *Average precipitation for Kanding (1978-2007)*[1] *(mm month^{-1})*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1978	11,18	55,37	21,33	69,59	309,62	219,96	162,83	60,45	151,91	53,34	120,38	0,51
1979	14,99	12,2	55,39	14,49	88,15	172,46	104,67	131,58	185,16	93,47	83,32	10,66
1980	0	4,32	85,35	53,6	138,94	107,71	320,81	174,77	196,34	100,33	1,78	59,19
1981	0,25	5,6	43,45	50,56	142,22	182,91	115,83	187,48	494,31	22,88	54,61	3,05
1982	0,51	11,94	0,25	101,1	133,09	381	163,56	50,32	186,19	43,69	30,22	14,47
1983	12,94	122,17	56,15	66,79	80,26	165,63	117,36	71,39	104,64	43,94	16,75	6,1
1984	6,09	4,56	34,8	81,05	119,91	103,38	115,83	116,59	67,3	85,09	4,32	2,28
1985	12,96	19,56	130,03	62,23	88,14	144,77	94,75	104,64	177,81	45,48	9,4	2,8
1986	13,71	12,96	21,33	45,72	41,68	191,24	88,66	143,26	211,09	60,46	13,71	0,25
1987	5,09	9,15	18,03	34,29	58,93	125,47	233,16	157,49	253	44,97	18,29	14,74
1988	6,6	1,02	19,81	64,53	90,68	127	142,98	134,62	204,71	9,67	13,97	6,6
1989	4,82	17,53	36,57	86,1	88,39	173,73	105,43	92,96	121,14	275,09	24,14	6,61
1990	10,92	3,55	30,22	36,07	52,58	188,19	115,57	100,84	135,65	117,61	59,18	10,16
1991	6,35	80,77	25,15	74,93	86,88	158,01	143,01	130,82	187,45	112	45,44	9,39
1992	7,11	18,03	70,35	31,72	47,75	128,29	229,87	235,96	141,75	72,13	18,28	0,76
1993	5,6	14,22	16,51	85,85	53,09	184,15	158,23	276,88	189,99	107,45	8,64	4,07
1994	0	5,34	44,95	14,74	111,99	195,32	61,96	47,25	104,14	74,17	1,27	6,09
1995	4,31	16,5	46,22	52,82	134,64	248,66	246,62	164,09	130,05	32,77	17,53	7,11

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1996	3,55	13,72	61,47	55,4	170,2	158,25	168,67	60,96	136,63	42,67	34,29	2,04
1997	5,59	17,01	25,38	52,34	106,68	262,91	135,14	42,65	157,74	41,43	8,64	4,06
1998	7,87	26,41	22,61	32,26	71,88	136,88	171,71	196,58	134,09	62,74	19,05	3,56
1999									22,61	71,61	54,09	13,45
2000	10,39	23,1	33,77	89,9	123,93	216,4	116,83	174,98	135,64	25,4	20,32	7,35
2001	11,16	17,49	51,05	90,42	119,11	213,32	50,03	199,38	133,83	37,57	11,41	10,13
2002	15,48	6,84	41,89	79,74	91,17	183,14	107,94	86,61	82,81	70,13	24,38	1,52
2003	4,57	7,36	21,57	52,32	97,79	236,47	209,31	163,08	99,81	67,31	8,11	15,74
2004	12,19	19,81	81,27	26,92	180,83	255,28	146,55	120,65	121,65	85,61	18,03	1,27
2005	5,58	21,08	31,22	80,24	104,64	167,64	66,03	266,95	87,11	117,34	0	0
2006	0,51	53,58	74,93	69,33	125,96	215,39	111,76	32	114,28	62,98	8,37	6,34
2007	5,82	1,77	8,62	104,13	95	183,87	121,93	68,31	127,75	76,46	17,77	3,04

1. Tutiempo Network, S.L. (2017). *Climate Kanding.* http://en.tutiempo.net/climate/ws-563740.html. [2017-11-22].

Mt. Etna (Lingualossa)

Table 33. *Average precipitation for Lingualossa (1968-1997)*[1] *(mm month*$^{-1}$*)*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1968	116,6	109,2	108	8,4	17	68,8	0,2	17,6	26,2	18,4	82	274,2
1969	56	58,6	207,8	55	49,2	4	3,2	13	197,6	270,8	25,2	132,4
1970	81,6	44,8	47,4	12,6	50,8	4	1,6	1,2	83,6	113	30,4	191,4
1971	119,6	127,4	113,6	83,8	13,8	11,8	16,6	0,2	164,2	180,2	189,4	102,8
1972	135,8	194	111,2	65,4	22,2	1,8	14	29,2	45,2	148	1,4	913,8
1973	417,2	91	120,2	35,4	40,4	15,6	69,4	19	29,6	76,2	33,6	302,4
1974	13,4	186,6	252	112,4	10	0,4	2,6	9	24,2	103,2	126,2	37,4
1975	27,2	292,8	77,4	23,2	37,2	17,6	0	58,6	9,6	56,2	179,6	50,6
1976	59,2	208,2	182	27,2	111,8	16	14	20,6	18,4	488	339	486,2
1977	237	17,4	17,8	71	7,4	13,2	1	0,4	48,4	43	21,6	42,8
1978	314,2	69,6	68,8	149,6	24,2	3,8	0	11	23,6	347,4	67,6	52,6
1979	179,8	167,8	89	104,6	10,8	0,2	0,4	7,6	39,2	337,2	118,6	100
1980	353,4	98	201,8	57,2	123,2	1,8	0	48,6	43,2	86,6	19,4	240
1981	161,8	177	6	23,2	17,8	10,2	4,4	25,6	22	3,8	48,6	61,6
1982	209	276,4	89	127,4	6,4	4,8	17,8	11,8	105	265,4	160,6	48,2
1983	59,8	54,6	64	12,2	17,4	4,6	29,4	8	108,8	89,6	319,6	220
1984	54,6	126	330,4	61	11,8	0	1,2	20	18,6	105,8	245,4	264
1985	356,8	79,8	201,4	80,8	52,8	0	1,6	0	112,8	272,4	30,4	85,4
1986	77	83	481,4	9,6	24,8	14,6	9,2	3,8	74	95,8	355	77
1987	91,2	161,6	114,4	16,4	64,8	15	16	7	19,2	82,6	89,8	87,6
1988	260	70,6	178	46,8	16,6	8,2	0	36,8	167,4	33	156,4	95,4
1989	177	25	43,8	32,8	26,6	23,2	18	10,6	35,2	64,2	178,4	248,2
1990	352,8	23,4	27,6	50,4	37,6	4	18	19	8,2	46	134,4	186,8
1991	184,2	149,4	126,2	66,4	6,6	9,8	0	7	36	164,8	48,6	301
1992	720,8	57	112,6	48,2	146,4	26	8,8	1,4	6,8	61,2	19,4	354
1993	143,8	148,4	141,8	14,6	56,6	4,4	0	1,8	14,8	161,2	544,6	47,2
1994	194,6	276,8	3,4	79	11,2	28	57,4	0,2	22,8	343,4	103	27,4
1995	108,5	35	301,6	36,4	17	38,6	1,6	59,8	57,6	45,2	354,6	212,8
1996	683,8	451,2	581,4	23,6	48,2	14	4,6	15,4	54,6	226	11	338
1997	115,2	26,2	54,2	77,2	3,4	0,8	0,2	64,8	154,2	287,8	187	126,6

1. Regione Siciliana Osservatorio DelleAcque. (2017). *Annali idrologici.*

http://www.osservatorioacque.it/?cmd=page&id=dati_annali_cons&tpl=default. [2017-11-22].

Appendix 3 – Thermal Lapse Rates

Mt. Etna

Annual average temperatures

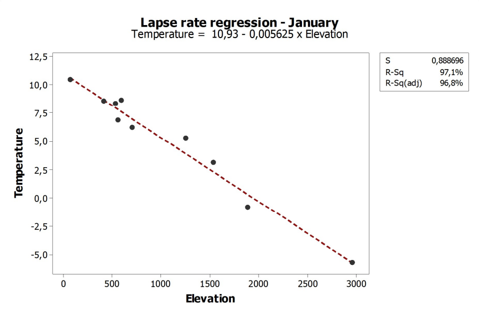
Table 34. *Seasonal temperatures of Sicily (°C)*

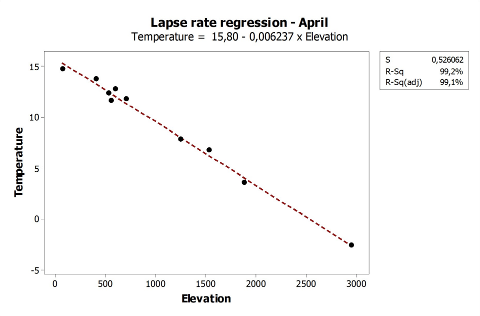
Weather station	Elevation	Jan	Apr	Jul	Oct
Catania[1]	65	10,4	14,8	25,8	19,9
Viagrande[1]	405	8,5	13,8	22,5	18,1
Nicolosi[1]	698	6,2	11,8	23,8	15,6
Catoniera[1]	1882	-0,8	3,6	13,2	8,8
GF observatorie[1]	2950	-5,7	-2,6	8,3	2,8
St. Alfio[1]	550	6,8	11,7	22,9	15,9
Zafferana[1]	590	8,6	12,8	24,1	16,7
Linguaglossa[2]	530	8,3	12,4	24,4	16,8
Pizzo FAO[2]	1525	3,1	6,8	15,1	7,7
Piano Formaggio[2]	1242	5,2	7,8	19,8	10,9

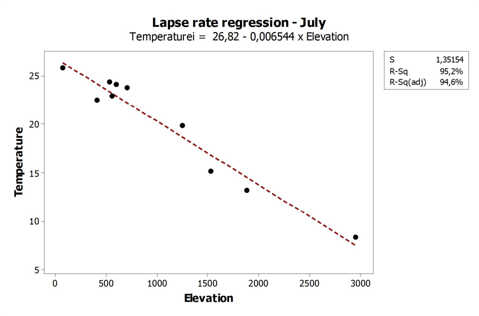
1. Chester, D. K., Duncan, A. M., Guest, J. E., & Kilburn, C. R. J. (1985). *Etna and the Etna region. In Mount Etna* (pp. 37-64). Springer Netherlands.

2. Regione Siciliana Osservatorio DelleAcque. (2017). *Annali idrologici*. http://www.osservatorioacque.it/?cmd=page&id=dati_annali_cons&tpl=default. [2017-11-22].

Regression analysis







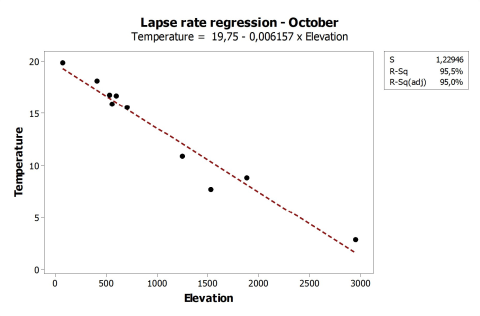


Table 35. *Lapse rates of Mt. Etna (°C km^{-1})*

	Jan	Feb	Mar	Apr	Maj	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Lapse rate	5,6	5,6	5,6	6,3	6,3	6,3	6,5	6,5	6,5	6,1	6,1	6,1

Carmolangan

Annual average temperatures

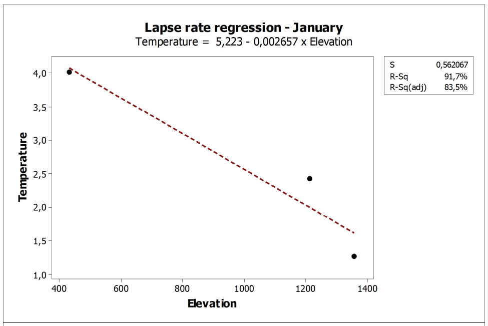
Table 36. *Seasonal temperatures of Carmolangan*[1] *(°C)*

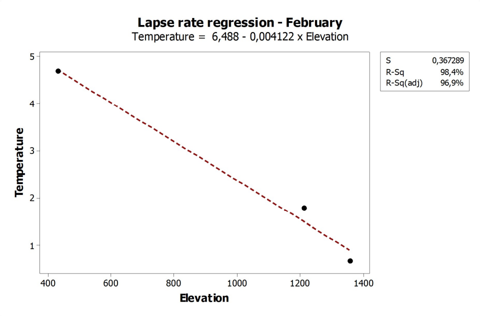
Weather station	Elevation	Jan	Feb	Mar	Apr	Maj	Jun	Jul	Aug	Sep	Okt	Nov	Dec
Buggio	430	4,01	4,67	7,14	10,74	14,21	17,72	20,20	19,92	16,80	13,20	8,50	4,94
ColleBelenda	1357	1,26	0,66	3,41	6,85	10,16	13,94	16,78	16,06	12,76	9,18	5,06	2,25
Sella di gouta	1212	2,43	1,77	4,52	8,05	11,08	14,82	17,53	17,39	13,80	10,05	5,96	2,80

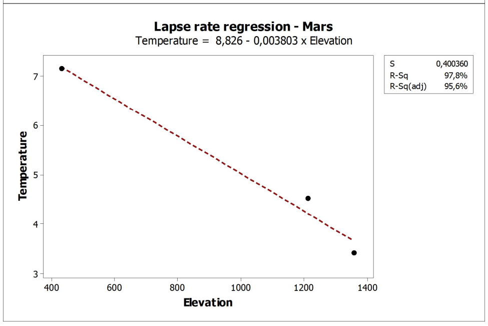
1. Regione Liguria (2017). *Temperatura Media Dell'Aria.*

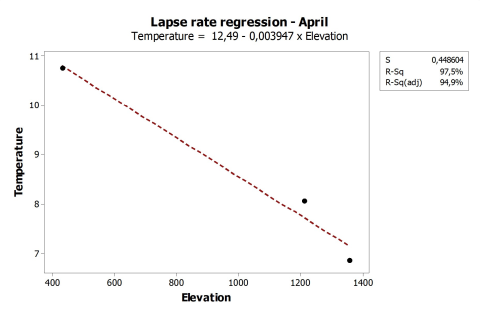
http://www.cartografiarl.regione.liguria.it/SiraQualMeteo/script/PubAccessoDatiMeteo.asp. [2017-11-22].

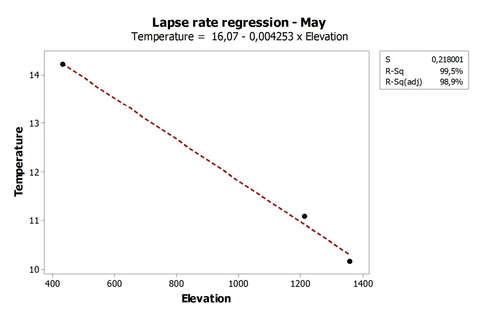
Regression analysis

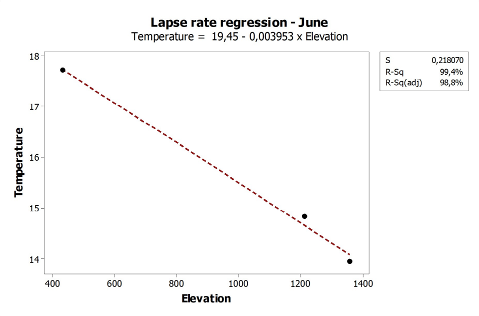


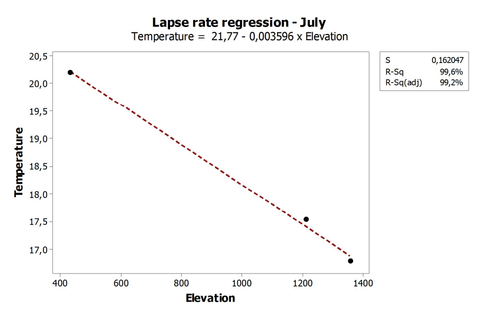


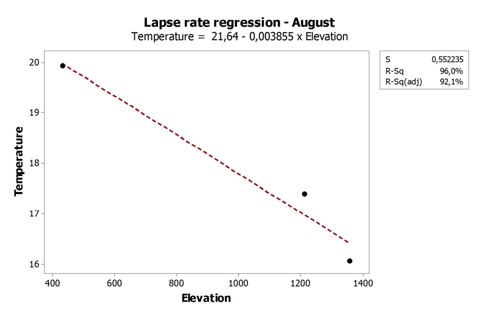


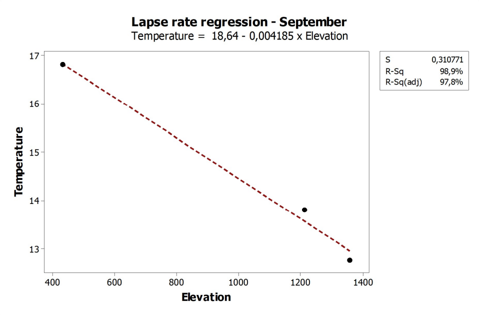


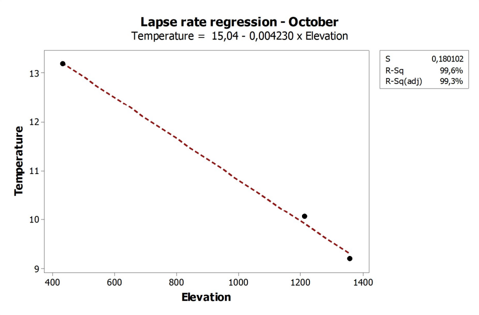


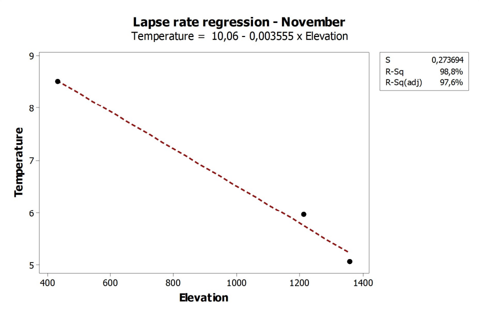












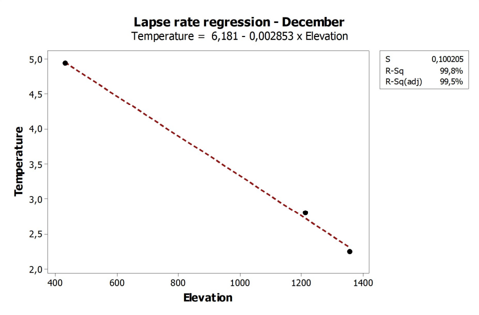


Table 37. *Lapse rates for Carmolangan (°C km^{-1})*

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Carmolangan	2,57	4,12	3,80	3,95	4,25	3,95	3,60	3,86	4,19	4,23	3,56	2,85

China

Table 38. *Lapse rates for China*[1] *(°C km^{-1})*

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Okt	Nov	Dec
Gonggashan Xian	4	4	4,2	4,6	4,8	5	5	5	4,6	4,5	4,5	4
Paoma Shan	4	4	4,2	4,6	4,8	5	5	5	4,6	4,5	4,5	4
Basongtso	4	4	4,2	4,6	4,8	5	5	5	4,6	4,5	4,5	4

1. Li, X., Wang, L., Chen, D., Yang, K., Xue, B., & Sun, L. (2013). Near-surface air temperature lapse rates in the mainland China during 1962–2011. Journal of Geophysical Research: Atmospheres, 118(14), 7505-7515.

Appendix 4 – Ness climate

Table 39. *Monthly average climate for Ness Botanic Gardens (2016)*[1]

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Okt	Nov	Dec
Temperature *(°C)*	6,3	5,5	6,4	7,8	12,7	15,2	16,2	16,6	15,7	11,0	10,2	7,3
Precipitation *(mm month^{-1})*	95,8	46,4	50,0	70,0	41,2	45,6	28,2	44,2	49,8	28,0	101,0	22,4
PET *(mm month^{-1})*	18,3	17,1	27,1	38,8	79,6	100,7	108,6	100,3	78,4	44,9	32,7	20,2

1. (NCAS, 2016)

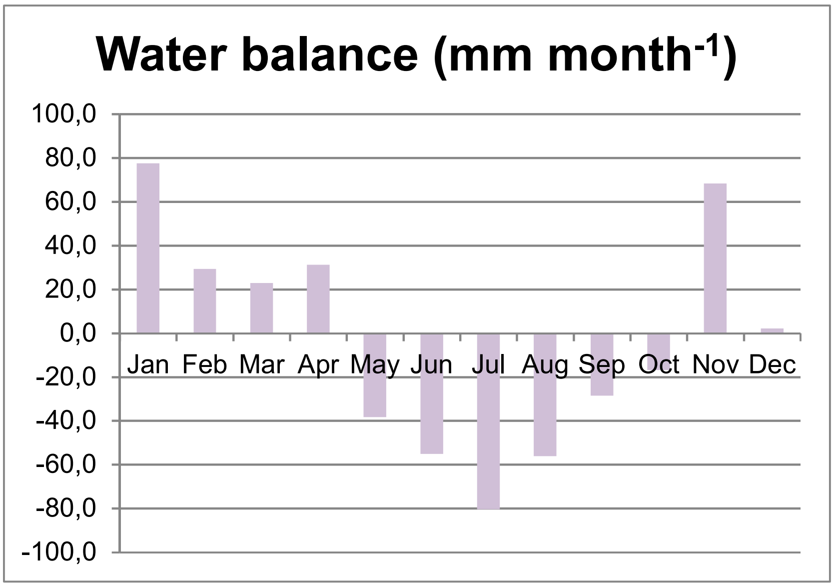


Figure 14. Water balance for Ness Botanic Gardens (2016)