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POPLARS AND WILLOWS IN THE WORLD

CHAPTER 7 ABIOTIC STRESSES



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CHAPTER 7

ABIOTIC STRESSES

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7.1 Introduction

[Abiotic stresses](#) are usually defined as nonliving environmental factors that have harmful effects on organisms. They are generally classified in two categories according to their origin: [edaphic stresses](#), such as water deficit, salinity, lack of nutrients or soil pollution, and atmospheric stresses, such as ozone, elevated carbon dioxide (CO₂), increased temperature, frost or high irradiance. Abiotic stress conditions cause extensive losses to agricultural production worldwide. Individually, stress conditions such as drought, salinity or heat have been the subject of intense research. However, in the field, trees as well as other plants are routinely subjected to a combination of different [abiotic stresses](#). In drought-stricken areas, for example, many trees encounter a combination of drought and other stresses, such as heat or salinity. Recent studies have revealed that the molecular and metabolic response of trees to drought and heat is unique and cannot be directly extrapolated from the response to each of these different stresses applied individually (Mittler 2006).

Members of the Salicaceae family are known to be particularly sensitive to environmentally-induced stresses, the cumulative effects of which determine their distribution, reproductive success, and productivity (Neuman *et al.* 1996). However, within this overall sensitivity, the range of variation in terms of tolerance (i.e. severity of the impact on biomass production) is generally very wide in the family. At this time, the selection efforts for the creation of new varieties are essentially focused on traits such as resistance to diseases, in particular foliar rust, productivity and wood quality. Tolerance to environmental constraints is not yet taken into account as a selection criterion for new [genotypes](#) in breeding programmes. However, such criteria have to be considered with much more attention because of two current tendencies: climate changes and the present extension of willow and poplar cultivation for bioenergy production purposes towards non-alluvial zones more frequently subjected to drought and less fertile than riverside zones in such a way as to avoid competition for land use with food agriculture (Dreyer *et al.* 2004).

This chapter will focus on the responses and resistance mechanisms used by poplars and willows to survive a variety of environmental stresses. The chapter is notably composed of two bibliographical tables compiling scientific studies carried out on drought and elevated carbon dioxide responses ([Tables 7.1](#) and [7.5](#), respectively) of poplars and willows between the beginning of the nineties and 2006. These two tables present the objectives, the growth conditions, the measured traits, and the main conclusions of hundreds of studies carried out worldwide during the last decades and dealing with drought and elevated CO₂ conditions.

7.2 Edaphic stresses

7.2.1 Water deficit

7.2.1.1 Context – Fresh water is one of the most unequally distributed resources around the world and this disparity is likely to be aggravated by the current climate changes. At continental and regional scales, more intense and longer droughts have indeed been observed over wide areas since the 1970s. Increased drying linked with higher temperatures and decreased precipitation has contributed to changes in drought and it is very likely that extreme events will become frequent in the future (IPCC 2007). Even if poplars are considered as the most sensitive trees to water deficit, the wide diversity of the 29 species of the *Populus* genus in terms of resistance strategies has made possible the colonization of many types of ecosystems, including very dry areas and deserts. Furthermore, from a farming point of view, poplars are among the fastest growing trees in temperate latitudes but their high productivity is associated with high water requirements. As a consequence, their productivity may be strongly limited by water availability (Tschaplinski, Tuskan and Gunderson 1994, Zsuffa *et al.* 1996). To sustain the extension of poplar cultivation from flood plains and bottomlands to uplands where soil water availability is subject to seasonal changes, more water-use-efficient hybrids are required. At whole plant level, [water-use efficiency \(WUE\)](#) is defined as the ratio between biomass production and water consumption. The identification of poplars combining satisfactorily high productivity and high [water-use efficiency](#) would be a considerable advantage in moderately drought-constrained areas (Braatne, Hinckley and Stettler 1992, Marron *et al.* 2005, Monclus *et al.* 2005, Monclus *et al.* 2006).

The study of drought resistance is an ambitious objective because it depends on numerous, complex and often interdependent traits. The identification of these traits is not complete yet and the approach used by scientists is often empirical. It consists in subjecting homogenous plant material to water withholding and to record the subsequent molecular (transcriptomics and proteomics analysis), cellular (growth reduction, changes in metabolic activities) and whole-plant modifications (water flows, photosynthesis, organ growth, etc.). However, these modifications are more an adjustment of the plant functioning in response to constraining conditions than a real adaptive response associated to a given level of resistance. Poplar is one of the model plants for which catalogues of complete genes are available (with *Arabidopsis* and rice, for instance) and for which it is possible to lead integrative biology studies, combining ecophysiology and genomics. It has, for instance, already been shown that, for clone ‘Beaupré’ (*P. ×canadensis*) at an early stage after the beginning of the constraining episode, and before any effect on growth, photosynthesis and [water potential](#), a very neat response in terms of DNA transcription was observed (Dreyer *et al.* 2004).

7.2.1.2 Strategies of drought resistance – A crucial step in the colonisation of terrestrial environments by plants has been the evolution of mechanisms that enable plants to control their water loss while continuing to fix carbon dioxide in photosynthesis. This step has been so important because the availability of water is probably the key factor determining plant distribution and survival in natural ecosystems, and it is also the most important limiting factor in agricultural production. All mechanisms that tend to maintain plant survival or productivity under conditions of limited soil water supply can be described as drought resistance mechanisms (Passioura 2002). Ecophysiologicalists have shown that different strategies can contribute to explaining drought resistance (Jones 1993). *The first strategy* consists in avoiding water deficit. Drought avoidance involves completion of the life/reproductive cycle during favourable conditions, limitation of transpiration and maximisation of root uptake, and would include (1) perennial/deciduous plants that remain [dormant](#) during drought and (2) species of arid environments with a permanent access to the water table ([phreatophyte species](#) such as *Populus euphratica*). These mechanisms allow plant survival at the expense of biomass production. *The second strategy* consists in tolerating water deficit. Drought tolerance is prevalent under temperate climates, in plants for which drought occurs at random, and encompasses mechanisms allowing the maintenance of water flow, [gas exchange](#) and cell [turgor](#) under drought conditions. Consequently, these mechanisms allow the preservation of biomass production and not only plant survival during drought. The concept of [tolerance to water deficit](#), when applied to cultivated tree species such as poplars, has been defined as the ability to limit the decrease in biomass production in response to a moderate water deficit (Passioura 2002). Additionally, some authors consider that diversity in [WUE](#) could be associated with diversity in drought resistance and they classify the ability to show high [WUE](#) in an independent third category of drought resistance strategy (i.e. efficiency mechanisms). The aim of *this third strategy* is to optimize the utilization of resources under drought conditions, and especially water (Jones 1992, 2004). At the whole plant level, [WUE](#) is defined as the ratio between biomass production and water consumption. At the leaf level, intrinsic [WUE](#) is defined as the ratio between assimilation and [stomatal conductance](#). Although the relationship between [WUE](#) and drought resistance is known to be variable among species, identification of poplars combining a satisfactorily high productivity and a high [WUE](#) would be a considerable advantage in moderately dry areas (Braatne, Hinckley and Stettler 1992, Marron *et al.* 2005, Monclus *et al.* 2005, 2006). In spite of an overall sensitivity to drought in all the species belonging to the *Populus* genus, a very wide diversity in their drought tolerance levels, in their response patterns to water deficit as well as in their [water-use efficiency](#), has been reported (Pallardy and Kozlowski 1981, Gebre and Kuhns 1991, Liu and Dickmann 1992b, Brignolas *et al.* 2000, Marron *et al.* 2003, Zhang, Zang and Li 2004, Marron *et al.* 2005, Monclus *et al.* 2005, Monclus *et al.* 2006).

7.2.1.3 Chronology of the response to drought – Globally, poplar response to drought involves different mechanisms that can be ranked into short, medium and long-term processes. The earliest plant response to drought is the reduction of cell growth and the decrease in [stomatal conductance](#) (Blake, Sperry and Tschaplinski 1996) ([Figure 7.1](#), [Table 7.1A](#)). Cell water uptake, responsible for growth, is linked to the difference in [water potential](#) between the [xylem](#) and the tissues in elongation, and to the water conductance of the tissues. Cell expansion occurs when water penetrates into the cell and allows expansion while maintaining cell [turgor](#) above a threshold (Lockhart 1965). So, during drought, cell growth reduction can be due (1) to decreased [turgor](#), (2) to a reduction in [cell wall](#) extensibility, or (3) to an increase in the [cell wall](#) deformation threshold (Passioura and Fry 1992). The relative importance of these three parameters is very variable, but it seems that [cell wall](#) extensibility is the most important in many situations (Cosgrove 1993). [Stomatal](#) closure is a very quick and flexible process limiting the risk of [xylem cavitation](#) (i.e. loss of [xylem](#) conductivity) under low [water potential](#) due to reduced soil water availability (Harvey and Van den Driessche 1997, Sperry *et al.* 2002) ([Table 7.1B](#)). When the soil water content decreases, the tension responsible for water rising in the plant increases and can cause a disruption of the water columns which can lead to the phenomenon of [cavitation](#) and to irreversible [embolism](#) ([Table 7.1C](#)). Among woody species of the temperate zone, poplars display the highest vulnerability to [cavitation](#), which tends to confirm their strong susceptibility to drought ([Figure 7.2](#)). [Stomatal](#) closure can be induced by an increase in the content of [abscisic acid](#) (ABA) in the vicinity of the [guard cells](#) of the [stomata](#). This [phytohormone](#) is released by the roots and transported by the rising sap flow (Davies and Zhang 1991). However, an important variability of [stomatal](#) sensitivity has been observed among poplars. For example, some *P. trichocarpa* [ecotypes](#) and *P. koreana* × *trichocarpa* ‘Peace’ are known to present [stomata](#) that are insensitive to exogenous ABA applications (Hinckley and Braatne 1994, Ridolfi *et al.* 1996).

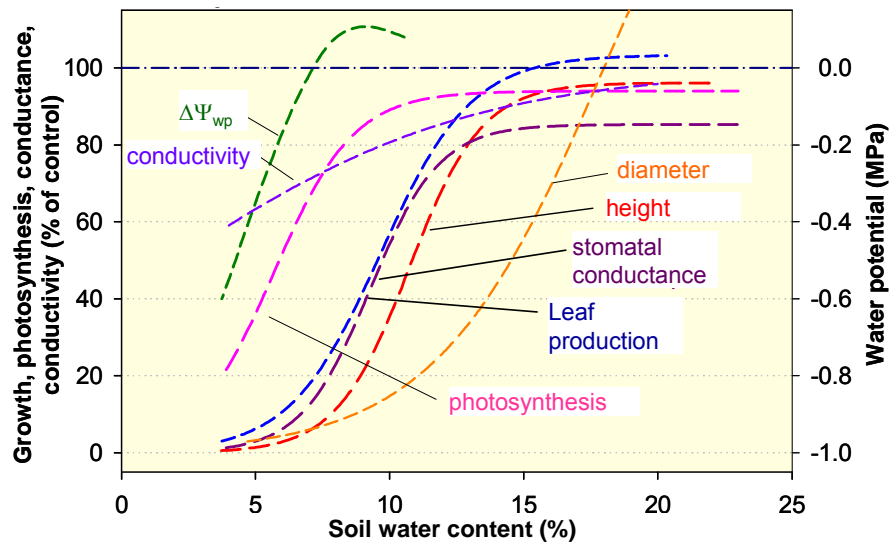


Figure 7.1. Response of different processes to the decrease of soil water availability in young plants of *Populus euphratica*: growth in diameter and height, stomatal conductance, leaf production, photosynthesis, stem hydraulic conductivity and leaf water predawn potential (Ψ_{wp}) (Dreyer *et al.* 2004).

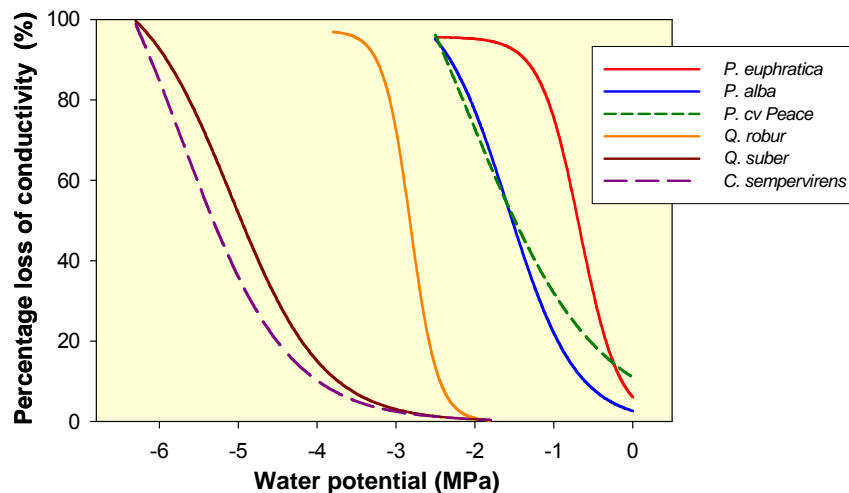


Figure 7.2. Vulnerability to cavitation according to water potential for *Populus euphratica*, *P. alba*, *P. koreana* × *P. trichocarpa* ‘Peace’, *Quercus robur*, *Q. suber* and *Cupressus sempervirens* (Hukin *et al.* 2005).

At medium term, an [osmotic adjustment](#) can occur, i.e. an increase in the [osmotic potential](#) due to an accumulation of solutes or to a reduction in cell volume (Morgan 1984) ([Table 7.1D](#)). Cell growth is mainly dependent on cell [turgor](#), the two major components of which are water and [osmotic potentials](#). Under drought conditions, transpiration results in a (passive) decrease of water and [osmotic potentials](#) caused by water loss. To counterbalance this, an accumulation of solutes

can occur, resulting in an (active) reduction of the [osmotic potential](#) and so, in an increase in cell [turgor](#) due to water penetration into the cell. The accumulated solutes are various and belong to diverse biochemical families. However, [proline](#) and sugars are known to be the main contributors to [osmotic adjustment](#) (Costa *et al.* 1998). For various poplar species, it has been shown that [sucrose](#) is the main contributor to [osmotic adjustment](#) during drought, followed by [glucose](#), [fructose](#) and [myo-inositol](#) (Gebre, Kuhns and Brandle 1994, Pelah *et al.* 1997, Sibout and Guerrier 1998). However, it has also been shown that the contribution of the sugar accumulation under drought conditions is often small and that other drought resistance mechanisms contributed to the genotypic differences in the field (Gebre *et al.* 1998).

At longer term, drought is responsible for morphological and anatomical changes resulting from the reduction in cell expansion and from modifications of carbon allocation to the different organs of the plant ([Table 7.1F](#)). Roots are favoured at the expense of stems and leaves. Consequently, the ratios roots/stem and roots/foilage increase and the leaf area is reduced, due to a decrease in both individual size and number of the leaves (Braatne, Hinckley and Stettler 1992, Liu and Dickmann 1993, Van Splunder *et al.* 1996, Ibrahim, Proe and Cameron 1997, Tschaplinski *et al.* 1998, Marron *et al.* 2003). These modifications have the dual advantage of improving root water uptake and reducing transpiration and subsequent risks of [cavitation](#) (Braatne, Hinckley and Stettler 1992, Tschaplinski *et al.* 1998). Three phenomena aiming to reduce leaf area coexist in poplar: (1) loss of leaves, (2) reduction in the individual size of leaves, and (3) decrease in the number of simultaneously expanding leaves. Leaf loss is commonly observed under natural conditions notably for *P. trichocarpa* and *P. deltoides* (Cooper and Van Haverbeke 1990, DeBell 1990). However, leaf loss is a drastic strategy and the first response to water deficit is often a reduction in leaf growth. A reduction in the number of leaves dominates the adaptive response of the leaf area to drought, but a reduction in the individual leaf size and a coexistence of both strategies have also been observed in poplar (Liu and Dickmann 1993, Ibrahim, Proe and Cameron 1997, Marron *et al.* 2003). A combined reduction in cell growth and cell division is responsible for the decrease in leaf size (Dale 1988). Leaf structural modifications are also commonly observed under drought conditions. Indeed, drought frequently causes a reduction in the [specific leaf area](#) ([SLA](#), defined as the ratio between leaf area and leaf dry weight) due to an increase of leaf density (Niinemets 2001, Marron *et al.* 2003). This density increase is linked to thicker [cell walls](#) and to smaller and more packed cells in the leaves expanded under drought conditions (Niinemets 1999). An improved water status has been shown to occur for species with low [SLA](#) (i.e. high leaf density), but the physiological basis of the relationships is still unknown (Nautiyal, Rachaputi and Joshi 2002).

All the previously listed mechanisms aim to limit water losses and to improve water uptake, but some of them provoke damaging consequences which the plant has to confront ([Table 7.1E](#)).

Due to [stomatal](#) closure, a slight water deficit decreases CO₂ absorption necessary for photosynthesis. If drought conditions persist, a direct inhibition of photosynthesis occurs. In both cases, the result is an exposure of the [chloroplast](#) to an excess of [excitation energy](#). Several protection processes exist such as leaf movements, aiming to reduce light absorption, and increase overall heat dissipation in the [light harvesting antenna](#) (Chaves and Oliveira 2004). In addition, limitation of CO₂ fixation provides an insufficient [sink](#) for electrons generated in the [electron-transport chains](#) (ETC). In this case, alternative outlets for electrons gain in importance and lead to over-production of [reactive oxygen species](#) (ROS) and to potential oxidative damage (Edreva 2005). Under such conditions, oxygen acts as an alternative electron acceptor resulting first in the production of the superoxide radical (O₂^{•-}), and then in the formation of various [ROS](#) such as the hydroxyl free radical (OH[•]) and hydrogen peroxide (H₂O₂) (Edreva 2005). [ROS](#) are highly toxic and can cause [lipid peroxidation](#) and consequently membrane injury, protein degradation, enzyme inactivation, pigment bleaching and disruption of DNA strands (Smirnoff 1993). Allen (1995) reported that much of the injury to plants caused by exposure to various constraints is associated with oxidative damage at the cellular level. Plant cells are normally protected against the detrimental effects of reactive oxygen by a complex antioxidant system; active [oxy-free radicals](#) can be scavenged by both enzymatic and non-enzymatic detoxification mechanisms (Smirnoff 1993, Edreva 2005). Oxidative stress can occur when the scavenging of [ROS](#) is overwhelmed by the production. In poplar, it has been shown that protection against oxidative stress generated by elevated CO₂, [paraquat](#) and ozone mainly involved [superoxide dismutase](#) (SOD), [catalase](#) and [peroxidase](#) (Arisi *et al.* 1998, Strohm *et al.* 1999, Schwanz and Polle 2001, Strohm *et al.* 2002). During drought, an enhancement of the activity of most of the antioxidant enzymes has been observed in poplar, but no clear link with the level of drought tolerance of the tested clones has been established (Courtois, Boudouresque and Guerrier 1999, Guerrier *et al.* 2000, Marron *et al.* 2006). On the other hand, the non-enzymatic pathway seems to have a limited influence under drought conditions in poplar (Marron *et al.* 2002).

7.2.1.4 Relationships between water-use efficiency and drought resistance – Some authors consider the ability to present and to maintain a high [WUE](#) under drought conditions as an important mechanism for plant resistance to water deficit, entirely independent from the widely described tolerance and avoidance strategies (Jones 1992, 2004) ([Table 7.1G](#)). However, the links between [WUE](#) and drought resistance are still unclear and only a few studies have tried to clarify the links between these two properties along with the physiological determinism of [WUE](#).

In *P. ×canadensis* hybrids, a negative correlation has been observed between [WUE](#) determined from gas exchange rates (intrinsic [WUE](#)) and carbon isotope discrimination (Δ), while a positive correlation has been demonstrated between Δ and [stomatal conductance](#) under moderate drought. This suggests that the diversity for Δ was mainly driven by [stomatal conductance](#) (Monclus *et al.* 2006). On the other hand, no relationship between Δ and biomass production could be established among different kinds of poplar hybrids, providing opportunities for selecting poplar clones combining high productivity and high [WUE](#) (Rae *et al.* 2004, Marron *et al.* 2005, Monclus *et al.* 2005). Likewise, no direct relationship was found between [WUE](#) and drought resistance in *P. ×canadensis* hybrids (Monclus *et al.* 2006). But it is noteworthy that, in this latter study, none of the poplar genotypes for which Δ tended to increase in response to drought was a drought-resistant [genotype](#). This result suggested that the genotypic ability to increase [WUE](#) is necessary to produce a high level of drought resistance. However, the whole range of drought resistance levels was observed among the [genotypes](#) for which Δ decreased or tended to decrease, suggesting that the ability to increase [WUE](#) is necessary, but not sufficient, to explain genotypic diversity of drought resistance among *P. ×canadensis* hybrids. It is also clear that drought resistance is not only governed by [WUE](#), but probably includes a lot of other traits that also contribute to the overall drought resistance capacity of a particular genotype (Liu and Dickmann 1992b, Gebre, Kuhns and Brandle 1994, Chen *et al.* 1997, Ibrahim, Proe and Cameron 1997, Tschaplinski *et al.* 1998, Marron *et al.* 2002, 2003).

7.2.1.5 Conclusions and perspectives – From many studies, it has become clear that the members of the Salicaceae family are useful and elegant model trees for drought studies. All aspects of the response of poplars and willows to drought have been extensively studied during the last decade, from the biochemical response to whole population and ecosystem behaviour ([Table 7.1H](#)). There is, however, an imbalance between drought studies conducted on poplars and drought studies on willows during the period 1998-2006 (about 85% of the total number of studies on poplars vs. 15% on willows; [Figure 7.3](#)). Within the *Populus* genus, the disequilibrium between species is also striking: 24% of the drought studies concern cottonwoods (*P. deltoides*), because of the many studies carried out on riverside forests in the USA. This phenomenon also explains the equal proportions of experiments with pure *Populus* species in controlled versus natural conditions, with plantation studies being minor in all cases. With regard to *Populus* hybrids, almost 43% of all studies concern *P. ×canadensis* hybrids, primarily under controlled conditions, versus of the predominance of pure species in natural stands. Drought studies conducted with *P. nigra* and *P. alba* remain anecdotic in comparison with more exotic species, such as *P. euphratica*. For a more comprehensive insight into the response of poplar and willow to drought, efforts have to be made to

relate controlled environment studies to the field, and to encompass a larger range of species within the *Populus* and *Salix* genera.

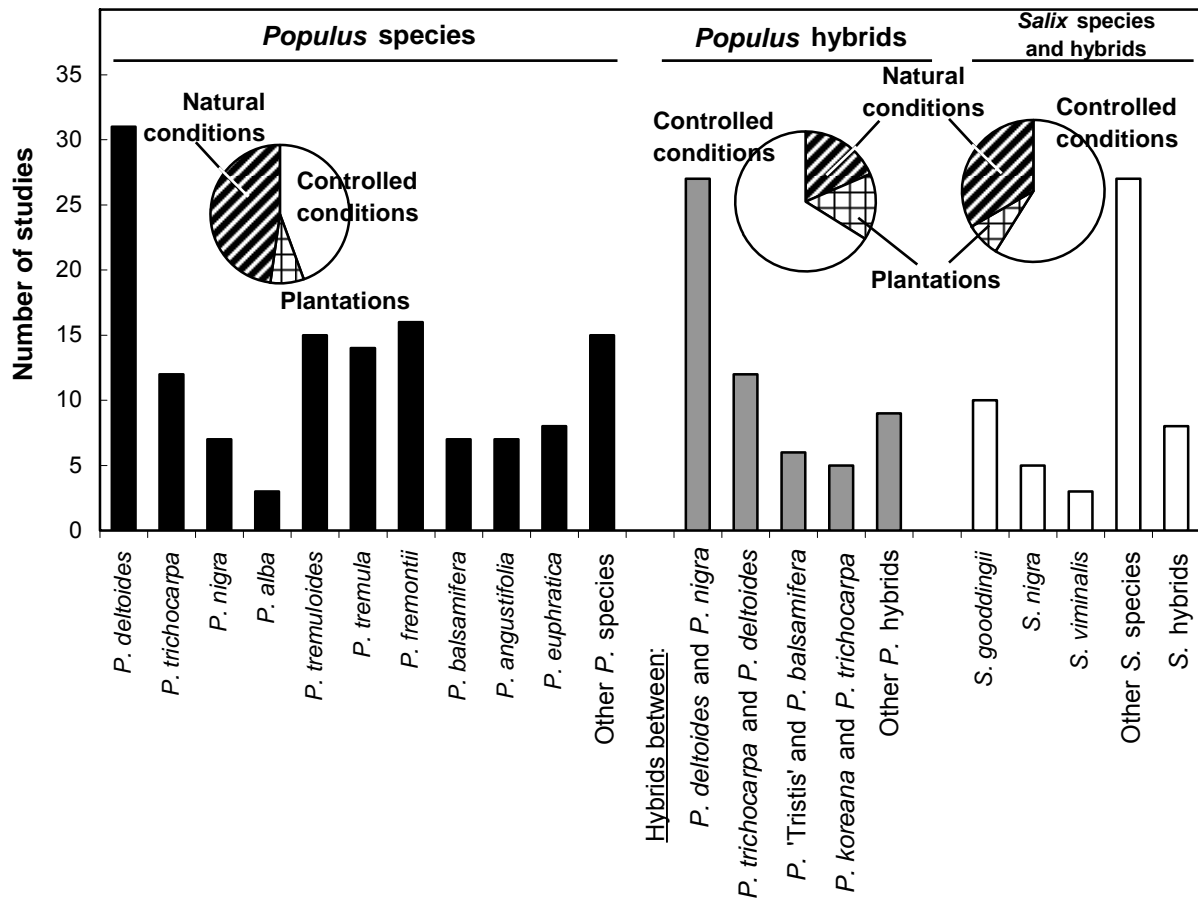


Figure 7.3. Absolute number of studies performed on different *Populus* and *Salix* species and interspecific hybrids (histograms) and under different conditions (controlled conditions, plantations, natural conditions; sectors) during the period 1998-2006 to investigate responses to drought.

Poplar cultivation may lead to high biomass production under adequate conditions. The *Populus* genus remains an interesting model for the study of the mechanisms of response to drought and an invaluable pool of diversity in drought resistance levels and [WUE](#). However, drought resistance appears to be a very complex and multigenic property, resulting from the combination of various mechanisms. From a practical view-point, the overall sensitivity of poplar to drought represents a severe limit to the future development of its cultivation. Within the light of the present climatic and economic contexts, selection criteria of commercial poplar [genotypes](#) need to be re-oriented in order to take into account resistance to abiotic constraints in general, and to drought in particular. In the near future, selection will have to focus on [genotypes](#) combining an optimal water-use with a maximum biomass production.

(NM / FB)

7.2.2 Desertification

Desertification is a global environmental problem. It is defined in the United Nations Convention to Combat Desertification (UNCCD) as land degradation in dry lands resulting from various factors, including climate variations and human activities (UNCCD 2004). According to UNCCD, over 250 million people are directly affected by desertification. In addition, some one billion people in over one hundred countries are at risk. There are a number of examples of how desertification is being addressed in various world situations. China has been recognized for implementation of tree planting programs, based to a significant degree on the genus *Populus*, as a means of addressing desertification, therefore a discussion of the role of poplar in China's desertification control program is worth while.

Deserts cover an area of over 1.5 million km² in China. It is estimated that mean annual rate of desertification in China is approximately 2100 km² (Zhu and Chen 1994). Desertification has led to a significant decline in agricultural productivity in northern China and as a result the national and local governments have implemented a number of practices to restore vegetation on affected lands and reduce the rapid expansion of deserts (Xang *et al.* 2005) To address the issue of desertification, as well as other environmental issues, in 1978 the Chinese government implemented the Three North Shelterbelt Development program (FAO 2002). The overall objective of the program is to improve environmental conditions, control dust storms and soil and water erosion, and fundamentally improve the local livelihood and economy, through the formation what is popularly referred to as the "Green Great Wall" (Lu *et al.* 2000).

The Three North Shelterbelt Programme in China is the largest multi-purpose protection forestry project in the world with plans to plant more than 35 million hectares of trees from 1978 to 2050 (FAO 2002). The Program covers a total area of 4 million km², accounting for over 40% of the total land surface of China, including 551 counties of 13 provinces, autonomous regions and municipalities in the Three North Region (Anonymous 2000). By the end of 2003, a cumulative area of 22 million hectares had been added to the forested land in north China since 1978, leading to an increase in forest cover in the area from 5% to 10% (Yin and Lu 2005). The *Populus* genus has a significant role in the Three North Shelterbelt Development program. From 1990 to 2000, the area covered by poplar (natural and planted) in the Three North Region has increased from 4.8 million hectares to 6.0 million hectares (Lu *et al.* 2000).

Planting poplars has been a common practice used in China to reclaim sandy lands and prevent desertification (Zhu and Chen 1994). The rapid growth and protective role of *Populus* in reducing wind speed and controlling wind erosion have made it the genus of choice in the majority of tree planting programs to control desertification in northern China (Lu and Zhang 2000). The poplars used in the Three North Region are mainly clones and hybrids of *P. simonii*, *P.*

szechuanica, *P. ×tomentosa* and the exotic *P. alba* var. *pyramidalis* ‘Bolleana’ (Lu and Zhang 2000). There are two common approaches in which poplars are used to combat desertification (Anonymous 1977).

1. Arable land protection involves the protection of farmland from desert encroachment through the establishment of poplar forest belts on their periphery, together with establishment of shelterbelt networks within the farming area. Poplar shelterbelts are first established on the fringe of the farmland and then on low-lying land between the major dunes encroaching the arable land. The goal is to surround the dunes with vegetation and reduce their encroachment on arable land by reducing wind velocity. Within the arable farmland shelterbelt systems are established. The system is made up of main tree belts 10 to 12 m wide consisting of five to six rows of poplar and other species, and secondary tree belts 6 to 8 m wide with three to four rows of poplar. The main belts follow main irrigation canals and roads whereas the secondary belts are located on the periphery of individual fields.
2. To stabilize moving sands poplars are planted on low-lying land among sand dunes. Once dunes have been fixed using stabilizing plant species (grasses and shrubs), poplars are planted in these areas. In some cases, irrigation may be used to assist with establishment of the poplars.

The project “Afforestation, Research, Planning and Development in the Three North Region of China”, jointly financed by the Belgian and Chinese governments and FAO, is an example of a successful poplar-based project to address the problems of ever-increasing soil erosion, decreasing soil fertility and lack of wood products needed by local inhabitants with emphasis on the genetic development and utilization of poplar to accomplish afforestation objectives (Anonymous 2000). In this project a major goal was to expand the genetic base of poplar clones used in desertification planting projects in order to increase productivity, resistance to frost and drought and overall resistance to insects and disease. The project followed three strategies to accomplish these goals: 1) the development of a long-term poplar breeding and selection program; 2) *ex situ* conservation of remaining natural populations (Wang *et al.* 2000b); and 3) a short term poplar evaluation and selection program to identify adapted poplar clones with superior vigour, form, and resistance to frost and pests (Lu *et al.* 2001). The project also developed mechanized afforestation techniques suitable for large-scale poplar planting in desertification projects. The technique developed involves mechanical planting of 80 cm long cuttings 70 cm into the sand. This technique proved to be more efficient and cost effective than traditional methods of hand planting rooted poplars.

Northern China has a number of native poplar species that are rarely found elsewhere in the world. For many years, desertification, drought, excessive firewood collection, and water diversion projects have caused serious decline of the natural poplar resource in China. For example in the Tarim Basin of Xinjiang Autonomous region, *P. euphratica* forests that once covered 5200 km² are now reduced to an area of only 3500 km² (Lu, Zhang and Bao 2000). The disappearance of these natural poplar resources is serious, and proper measures are required to protect them. It is important that concerted efforts are made to establish poplar gene banks and poplar clone arboretums in order to preserve these valuable poplar germplasm resources.

Given the massive planting efforts of poplar in northern China over the past 20 years in what previously was a treeless landscape, it is not surprising that significant pest problems have developed. Large monocultures of any plant are inevitably linked to pest outbreaks especially in environments less than optimal for tree growth. The most serious pest that has been encountered to date is the [Asian longhorn beetle](#) (*Anoplophora glabripennis*) which is seriously hindering the development of poplar resources in north China (Lu *et al.* 2004). Since 1998, the damage to poplar tree plantations and shelterbelts caused by the [Asian longhorn beetle](#) has become critical. This insect pest is now distributed in 240 counties of 13 provinces in northern China (Pan 2005). According to Yin and Lu (2005), [Asian longhorn beetle](#) infestation has significantly reduced the life span of poplar shelterbelts from 20 years to 10 years or less. The overall impact of the infestation has been devastating resulting in the demise of thousands of hectares of poplars. The reasons for the epidemic have been attributed to a number of factors including the limited number of poplar varieties used in China and that the clones used are highly susceptible or have limited resistance to [Asian longhorn beetle](#); secondly, most affected areas are not source areas of longhorn beetles, thus in these areas the beetles have few natural enemies; and finally, poor tree growth due to environmental stresses (i.e. drought and extreme temperatures) predisposes poplars to pest infestation (Lu *et al.* 2004).

The choice of poplar clones used in planting programs and their spatial deployment are crucial considerations when combating pest problems such as [Asian longhorn beetles](#). It makes sense to select the most resistant lines for planting; however, these resistant lines should not be planted in monocultures. The use of clonal mixes, where several clones varying in their resistance to [Asian longhorn beetles](#) are used in construction of shelterbelts, is recommended. The use of three to four clones should be considered the minimum. Using clonal mixtures is desirable because of the increased heterogeneity within the shelterbelt system. The goal of clonal mixes is to prevent pests from responding uniformly to the resistant traits of the most resistant clones and in so doing developing counter measures through mutation or other adaptation responses. In addition, by retaining some clones with limited or little resistance, there will likely be enough beetles around to

sustain any populations of natural enemies. These more susceptible trees also provide a focal point for control measures. For example, the *P. szechuanica* clones ‘Opera’ and ‘Popularis’ have been widely used for tree planting in northern China (Lu *et al.* 2004). These varieties are highly susceptible to the [Asian longhorn beetle](#) and were replaced by varieties of the Leuce section that had always proved resistant to the longhorn beetle. However, with the reduction in tree species diversity due to high mortality resulting from longhorn beetle infestations poplar clones such as ‘Bolleana’ poplar (*P. alba* var. *pyramidalis*) and ‘Hebei’ poplar (*P. ×hopeiensis*), which had originally been considered resistant to the longhorn beetle are now being infested. (Yin and Lu 2005). Yin and Lu (2005) reported that in farmland shelterbelts in the Ningxia irrigation area, when *P. szechuanica* ‘Opera’ is planted as bait species along with Bolleana poplar, which is the primary shelterbelt species in this region, longhorn beetle infestation of Bolleana poplar is reduced from 60-70% to less than 15%.

Poplars have an important role in China’s efforts to combat desertification. Massive tree plantings have been completed over the past 60 years, but overall success has been impacted by pest infestations and poor growing conditions characteristics of landscapes prone to desertification. Recently poplar breeding strategies for shelterbelts have been implemented that focus on improving adaptation to regional environmental conditions with greater emphasis on native Chinese species. The main criteria for consideration in these programs are cold and drought hardiness, pest resistance and adaptation to poor growing conditions. Genetic gains in these traits will increase survival of trees and reduce the risk of future catastrophic pest infestation. In addition, research and development of new transgenic poplar varieties is being actively carried out in China.

(WRS)

7.2.3 Salinity

7.2.3.1 Background: changing environmental conditions, risks and countermeasures – Worldwide, almost 1 billion ha of land are affected by soil salinity (Szabolcs 1994). Today, soil [salinization](#) is still increasing mainly because of unsuitable irrigation practices causing secondary [salinization](#) (Williams 1999, Munns 2005). Salinity has a major impact on plant growth and productivity. It was estimated that the world is losing at least three hectares of arable land every minute because of soil salinity (<http://www.fao.org/ag/AGL/agll/spush/>). If re-cultivation measures are lacking, the land is prone to soil erosion and desertification. To cope with this enormous problem, efforts are undertaken to increase the salt tolerance of economically important plants, including tree species, with the goal of obtaining [genotypes](#) able to cope with excess salinity. Currently different strategies are employed, e.g. exploring the natural diversity, traditional breeding, and genetic engineering for higher salt tolerance.

The genus *Populus* is of interest in this respect because it contains a wide variety of species (~30) from different areas around the world displaying a range of different growth characteristics and tolerance towards various stress conditions (Gielen and Ceulemans 2001, Taylor 2002). This includes significant variability in salt tolerance between poplar species and within species (Fung *et al.* 1998, Singh, Jain and Pant 1999, Chen *et al.* 2002b, Sixto *et al.* 2005). Apparently, this genus is an interesting resource of traits relevant for salinity tolerance. Furthermore, *Populus* is amenable to [transgenesis](#) and, thus, improving salt tolerance by biotechnological approaches is a feasible option.

7.2.3.2 Identification and occurrence of salt-tolerant poplar species – Recently, Sixto *et al.* 2005 tested physiological responses and survival of 13 poplar [genotypes](#) under salinity stress. *P. ×canadensis* (= *P. ×euramericana*) was the most sensitive species; intermediate sensitivity was found in *P. alba* and in hybrids of *P. deltoides* × *P. alba*; highest tolerance was present in *P. euphratica* ([Table 7.2](#)). Among these species, *P. ×canadensis* is currently of the highest and *P. euphratica* of the lowest commercial interest. *P. alba*, which is widespread in the Mediterranean Basin, Central Europe and Middle East, is gaining commercial importance. In optimal conditions, it can grow in dense plantations that give high biomass volumes in short rotations. *P. alba* is a typical riparian tree species; still some provenances are adapted to drought, saline soil conditions and high temperatures such as those occurring in south Mediterranean areas close to the sea (Sekawin 1975, Gellini 1980, Piazzai *et al.* 2003, Beritognolo *et al.* 2003, Paolucci *et al.* 2003). In Italy, the native populations of *P. alba* are shrinking. Nevertheless, the contrasting ecological conditions to which this species is adapted have favoured the maintenance of intraspecific genetic variability, as assessed by phenological traits and [DNA polymorphism](#) (Paolucci *et al.* 2003). Recently, in *P. alba* neutral [molecular markers](#) able to distinguish between a salt-tolerant (14P11) and a salt-susceptible (6K3) *P. alba* [ecotype](#) were identified (Beritognolo *et al.* 2003). The tolerant [ecotype](#) was from the south of Italy close to the sea (14P11) and the sensitive one from the inland north of Italy (6K3). It is possible that exposure to sea sprays resulted in adaption of *P. alba*-14P11 to elevated salinity. This shows that even within one poplar species, [ecotypes](#) for salt tolerance can be identified.

Table 7.2. Mean survival rate and confidence interval ($P = 0.95$) of poplar clones exposed for two months to 138 mM NaCl. Table adapted from Sixto *et al.* 2005.

Species	Survival (% of control)	Confidence interval	No. of genotypes tested
<i>P. ×canadensis</i>	2.5	0 – 13	4
<i>P. deltoides</i> × <i>P. alba</i>	45	22- 67	2
<i>P. alba</i>	50	37- 63	6
<i>P. euphratica</i>	100	70 – 100	1

P. euphratica is another example of a highly stress resistant species. Its native distribution ranges from the semiarid areas of northwest China to Western Morocco and from south to north from Kazakhstan to Kenya (Browicz 1977, Xu 1988). It grows under unfavourable conditions such as in saline and alkaline soils (Kang *et al.* 1996, Watanabe *et al.* 2000, Chen *et al.* 2001). The total salt content in the soil, where the forests of *P. euphratica* occur, is about 1%, but can reach 2-3% or more (Ma *et al.* 1997). *P. euphratica* can also be found growing around the Mediterranean Sea at sites with salty water. In *in vitro* tests *P. euphratica* can tolerate up to 450 mM NaCl (Gu *et al.* 2004). Existing *P. euphratica* forests survive very cold winters (down to -40 °C) and hot summers (up to 43 °C) and exist in areas with low rainfall and high evaporation rates. At the first glance, it appears paradoxical that *P. euphratica* is very drought-sensitive since its water transport system is damaged by [cavitation](#) even at mild water deficits (Hukin *et al.* 2005). However, there is evidence that natural *P. euphratica* stands in desert sites, which can occur at large distances from the nearest river, still have access to the ground water (Gries *et al.* 2003). *P. euphratica* develops an extremely deep root system connecting the tree to the water table, thereby avoiding drought stress. In the Taklemakan desert (Xinjiang Uygur Autonomous Region, northwest China) natural populations of *P. euphratica* are endangered (Anonymous 2005) because a growing population with increased water consumption leads to a decreasing water table and in consequence causes a decline in *P. euphratica* stands whose survival depends on access to ground water ([Figure 7.4](#)).



Figure 7.4. Native vital stands of *Populus euphratica* close to the Tarim river in Xinjiang Uygur Autonomous Region (Northwest China) and a declining stand at a distance of ca. 20 km from the river bed. Photocredit: A. Polle and X. Jiang.

P. euphratica is not abundant in Europe though some populations are found (e.g. in Bulgaria and Spain) and also in Morocco. However, the European populations are probably not native but have been introduced into Spain and multiplied by clonal propagation (Fay *et al.* 1999). Due to early bud flush, *P. euphratica* is sensitive to late frost events in spring, which have prevented its cultivation in middle and northern Europe.

P. euphratica has been used successfully for large-scale afforestation projects on saline desert sites in China (Wei 1993), where these trees play very important roles in stabilizing fragile environments such as the riparian ecosystems and protecting oases from invading wandering dunes. Maintenance and restoration of the ecological balance is, therefore, an important environmental issue. The capacity of *P. euphratica* to regenerate through root suckers makes it an excellent species for shelterbelts and for sand dune stabilization, particularly since *P. euphratica* also tolerates strong winds (Ball, Russo and Thomson 1996). However, for large scale multiplication it is disadvantageous that cuttings are difficult to root and that seeds lose viability extremely rapidly. These problems can be circumvented by establishment of *P. euphratica* tissue cultures and [micropropagation](#) systems, for which reliable protocols have been established (Huang, Yuan and Dong 1992, Phan *et al.* 2004). A drawback of these methods is that they require expert know-how and advanced laboratory facilities, which makes them expensive on the one hand and more difficult to implement in underdeveloped areas on the other hand.

In conclusion, *P. alba* and *P. euphratica* are promising species for breeding programmes aimed at increasing salt tolerance and as pioneering species for tree plantations on salty soils. An acute concern is that native populations of these two species are quickly shrinking because of strong competition from agriculture and other land uses (Ball, Russo and Thomson 1996, Sabatti, Scarascia-Mugnozza and Anselmi 1998). The conservation of these genetic resources is an important priority that requires fast and reproducible experimental protocols for vegetative propagation. Since *P. euphratica* grows relatively slowly, a further goal is to combine traits of fast growth and salt tolerance in hybrids for stabilization and reclamation of saline areas.

7.2.3.3 Mechanisms of salt tolerance in Populus – Salt imposes several kinds of stresses upon plants. Increases in sodium chloride in the soil solution cause [hypo-osmotic stress](#) by decreasing the [water potential](#). Colloquially speaking, this makes water uptake more difficult causing symptoms similar to drought stress in salt-exposed plants (Polle, Altman and Jiang 2006). At the whole-plant level, [non-halophytes](#), to which the Salicaceae belong, try to exclude salt to avoid over accumulation of sodium and disturbances in the cellular ion balance (Munns 2005). If salt uptake cannot be avoided, excess salt leads to membrane disorganization and ion toxicity at the cellular level (Hasegawa *et al.* 2000, Zhu 2001). Both mechanisms, drought and ion imbalances may cause the production of [reactive oxygen species](#) as a secondary stress (Gueta-Dahan *et al.* 1997, Savouré *et al.* 1999, Borsani, Valpuesta and Botella 2001). The consequences of the oxidative stress are: damage to important macromolecules such proteins, lipids and DNA, subsequently reduced or complete loss of growth, and eventually cell death. This typical response pattern to excess salinity occurred e.g. in the salt-sensitive poplar hybrid *P. ×canescens* (Bolu and Polle 2004).

To cope with salinity, defense responses are activated at different levels. Common metabolic answers to salt stress are the synthesis of stress-related enzymes like antioxidant systems, [chaperones](#) (e.g. salt-shock proteins) and compatible solutes (Hasegawa *et al.* 2000, Wang, Vinocur and Altman 2003). While these reactions are important to protect metabolic functions under increasing salt concentrations, a primary defense is the avoidance of excessive Na^+ accumulation in the [cytosol](#) (Blumwald, Aharon and Apse 2000). In this context, so-called [sodium/proton antiporters](#) play crucial roles. Once sodium reaches the [plasma membrane](#), it will be taken up readily by unspecific ion transporters leading to increases in [cytosolic](#) Na^+ ([Figure 7.5](#)). This activates Na^+/H^+ [antiporters](#), which are localized in the [plasma membrane](#) and in the [tonoplast](#). These transporters remove Na^+ from the [cytosol](#), either exporting it into the [vacuole](#) or into the [apoplastic space](#) of the [cell wall](#) ([Figure 7.5](#)). The counterion for Na^+ export is a proton (H^+). Therefore, the function of Na^+/H^+ [antiporters](#) requires the maintenance of a pH-gradient across the membrane ([Figure 7.5](#)). The pH gradient is generated by [ATPases](#) under consumption of energy provided by the hydrolysis

of ATP ([Figure 7.5](#)). The key role of Na^+/H^+ [antiporters](#) in salt protection was shown by constructing transgenic plants. Overexpression of *SOS1* (a so-called NHX-type Na^+/H^+ [antiporter](#)) resulted in increased salt tolerance in various species underlining the importance of sodium export for [cytosolic ion homeostasis](#) (Apse *et al.* 1999, Hamada *et al.* 2001, Shi *et al.* 2000, Shi *et al.* 2003). Such functional approaches are still lacking in trees but in *P. euphratica* a new NhaD-type Na^+/H^+ [antiporter](#) (PeNhaD1) was detected (Ottow *et al.* 2005a). The transcription of this [antiporter](#) was, in contrast to a salt-sensitive poplar, maintained during salt stress (Ottow *et al.* 2005a) and it was possible to complement a salt-sensitive bacterial [mutant](#) (*Escherichia coli* [mutants](#)) with PeNhaD1 and to restore the salt tolerance of these bacteria (Ottow *et al.* 2005a). The function of these Na^+/H^+ [antiporters](#) is keeping salt out of the cell. This example shows that genes regulated in *P. euphratica* in response to excess salinity can be used to find traits that are important for salt tolerance.

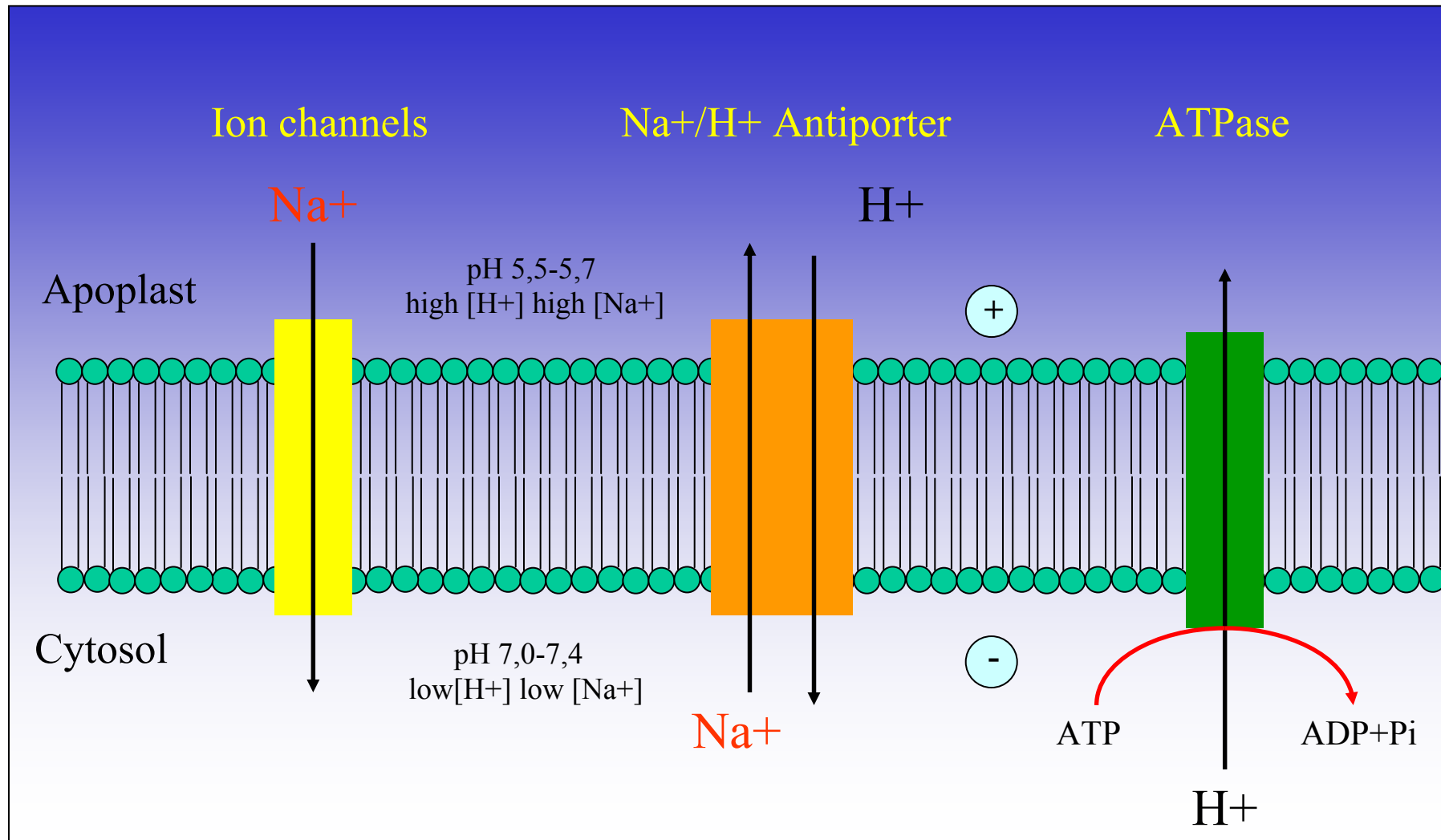


Figure 7.5. Scheme of Na⁺ transport across the plasma membrane (after Ottow 2005). See text for details (Section 7.2.3.3).

It is remarkable that at the whole plant level Na⁺-uptake into roots of *P. euphratica* is similar to that observed in salt-sensitive poplar species (Chen *et al.* 2001). However, [xylem](#) loading and translocation to leaves was more restricted than in salt-sensitive poplar species (Chen *et al.* 2003b). Under field conditions salt exudation was also found. These exudates form a crust of salt on bark cracks of *P. euphratica*. Salt exudation may also be an important factor contributing to the salt tolerance of this species.

A key issue in salt adaptation is [osmotic adjustment](#). Salinity decreases soil [water potential](#) and thus acts like drought stress leading to [turgor](#) loss in non-acclimated plants. To maintain water uptake, adjustment of the [osmotic potential](#) of the cells is required by compensatory changes in bulk solutes. Typically involved in these responses are sugars, sugar alcohols, amino acids, organic acids or inorganic ions (Munns 2005). Plants with increased concentrations of [proline](#), [mannitol](#) or other products of sugar metabolism displayed increased salt tolerance (Kishor *et al.* 1995, Karakas *et al.* 1997, Garg *et al.* 2002, Taji *et al.* 2002). However, the significance of these [osmolytes](#) in conferring increased salt tolerance by [osmotic adjustment](#) has been questioned (Blum *et al.* 1996). Sodium itself may act as an [osmoticum](#) (Munns 2005) but it displaces other cations such as Ca²⁺ and K⁺, which are important for membrane integrity, ion selectivity, and which also function as plant [osmolytes](#) (Epstein 1998, Tester and Davenport 2003).

In leaves of *P. euphratica*, high sodium concentrations are tolerated because the salt accumulates in the [apoplastic space](#) of the [cell wall](#) and not in the [cytosol](#) (Ottow *et al.* 2005b). [Osmotic adjustment](#) was attained by uptake of sodium, moderate increases in amino compounds, and decreases in calcium, [glucose](#), and [fructose](#) (Ottow *et al.* 2005b). Apparently, *P. euphratica* employs the strategy of using mainly sodium ions for [osmotic adjustment](#). This is energetically favorable since the synthesis of compatible solutes is metabolically expensive, whereas Na is a cheap and abundant [osmoticum](#). To unravel the regulatory steps which enable *P. euphratica* to cope with excess salt, molecular techniques such as differential display, [EST \(Expressed Sequence Tag\)](#) sequencing and [microarray](#) analysis have been employed (Gu *et al.* 2004, Brosché *et al.* 2005). The identification of genes involved in acclimatory responses and their functional analysis is a promising way to increase the understanding of the complex molecular mechanisms involved in mediating salt tolerance. Furthermore these strategies are likely to unravel [candidate genes](#) for improving salt tolerance by [transgenesis](#).

7.2.3.4 Biotic interactions with [mycorrhizal](#) fungi affect salt resistance of trees - [Mycorrhizae](#) are [mutualistic fungal symbionts](#). Associations of fungi with plant roots are found in up to 80% of plant species worldwide. Seven types of [mycorrhizae](#) exist with differences in structure and function depending on the plant and fungus involved (Smith and Read 1997). In

woody species, only two groups are commonly found, the ecto[mycorrhizae](#) and the arbuscular [mycorrhizae](#). Ecto[mycorrhizal](#) fungi form [extramatrical hyphae](#) and [rhizomorphs](#), up to 200 µm wide that extend well into the surrounding soil (Marschner 1995). The main function of these symbiotic interactions is improved nutrient supply to the host, especially that of phosphorus and nitrogen (Smith and Read 1997). But [mycorrhizae](#) can also protect plants from soil-born stresses, e.g. heavy metals, drought, etc. The protective effect of [mycorrhizae](#) against environmental constraints has recently been reviewed (Hall 2002, Schützendübel and Polle 2002, Polle and Schützendübel 2003).

Populus is one of the genera known to form both arbuscular and ecto[mycorrhizal](#) associations (Lodge 1989, Vozzo and Hackaylo 1974). In natural environments, arbuscular colonisation is often variable and depends on soil moisture (Lodge 1989, Al-Agely and Reeves 1995), soil nutrient status (Silva *et al.* 1993), season (Khan 1974) and fungal species (Abbot and Robson 1991). Khasa *et al.* (2002) reported arbuscular [mycorrhizal](#) colonisation in different poplar clones to be between 20 and 50%.

Only a few studies on trees have addressed the role of [mycorrhizae](#) during salt stress. In crops such as maize, arbuscular [mycorrhizae](#) improved resistance against salt, probably through increased concentrations of osmotically active sugars in the roots (Feng *et al.* 2002). Similar results have been reported for lettuce and tomato inoculated with arbuscular [mycorrhizae](#) (Al-Karki 2000, Ruiz-Lozano and Azcon 2000). Musin and Zwiazek (2002) showed that ecto[mycorrhizae](#) of *Hebeloma crustuliniforme*-*Picea glauca* significantly inhibited sodium uptake and improved nutrition and transpiration compared with non-inoculated salt-exposed seedlings. For poplar, very little information is available. In a survey of the [mycorrhization](#) of *P. euphratica* under field conditions (Ein Avdat canyon, Israel), only vesicular arbuscular [mycorrhizae](#) were found (Godbold, unpublished results). The degree of colonisation varied between 14% and 28 % of the roots and was generally lower in roots exposed to higher salinity than in those exposed to lower salinity (Godbold, unpublished results). However, controlled experiments addressing the role of these [mycorrhizae](#) in salt tolerance of *P. euphratica* have not been conducted. Ecto[mycorrhizae](#) of *Paxillus involutus* stimulated growth of the poplar hybrid *P. ×canescens* (Figure 7.6) and partially protected its biomass formation against the negative influence of excess salinity and improved nutrition of poplar (Langenfeld-Heyser *et al.* 2007). Although the current data are very fragmentary, they suggest that inclusion of [mycorrhizal](#) management in reclamation strategies of salinity affected land may increase the success of such measures. It is obvious that more information is needed on the interaction and possible ameliorative influence of [mycorrhizae](#) for poplar under salt stress.

(GJ / AP)

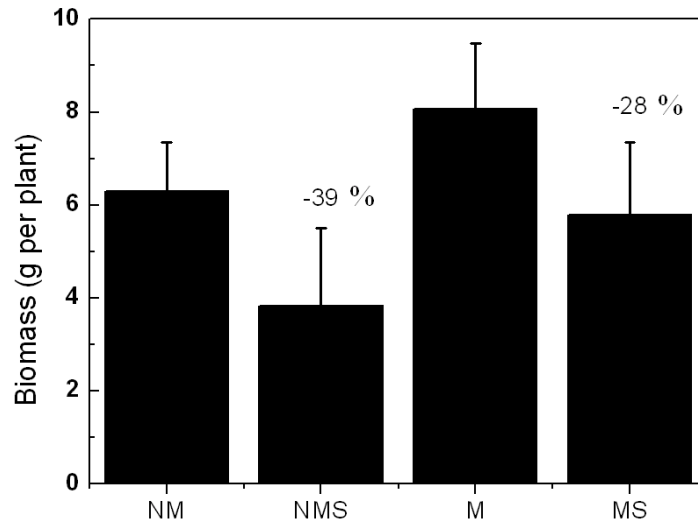


Figure 7.6. Biomass of young poplar plantlets in the presence (M) and absence of mycorrhiza (NM) exposed to salt (MS and NMS). Poplar plantlets were multiplied by micropropagation and grown either without or with *Paxillus involutus*, strain MAJ (as described by Gafur *et al.* 2004). After establishment of mycorrhiza, the plants were exposed to 100 mM NaCl for 6 weeks. Subsequently, fresh biomass was recorded ($n = 5 \pm SD$).

7.2.4 Soil nutrient status

7.2.4.1 Introduction – Poplars and willows evolved in soils affected by water, known as riparian areas. Fertility of riparian soils ranges from highest in alluvial [floodplains](#) to lowest in newly scoured gravel bars within stream channels. Alluvial [floodplains](#) derive their fertility from periodic flooding that deposits nutrient-laden sediments on these sites. Some of the most productive agriculture as well as poplar and willow plantations occur in these soils. At the other extreme in fertility are the gravel bars that consist of large soil particles with little or no organic material present ([Figure 7.7a](#)). Nearly all of the fertility in such situations is supplied by dissolved nutrients in the stream waters, which are usually quite low. As a result of evolving in the variable soil fertility found in riparian areas, poplars and willows are able to grow in a wide range of soil fertility. In high fertility soils, both poplars and willows show some of the fastest growth of all tree species, whereas in the nearly nutrient-devoid gravel bars, the trees survive, but grow very slowly. Their survival in these gravel bars, usually at very high stem densities, has the effect over many years of slowing stream flow, which increases the deposition of nutrient-containing sediments. This is the first step in the process of developing rich alluvial soils ([Figures 7.7b](#) and [c](#)). As the site fertility slowly increases, poplars and willows possess the ability to respond to this increasing fertility by increasing their growth.

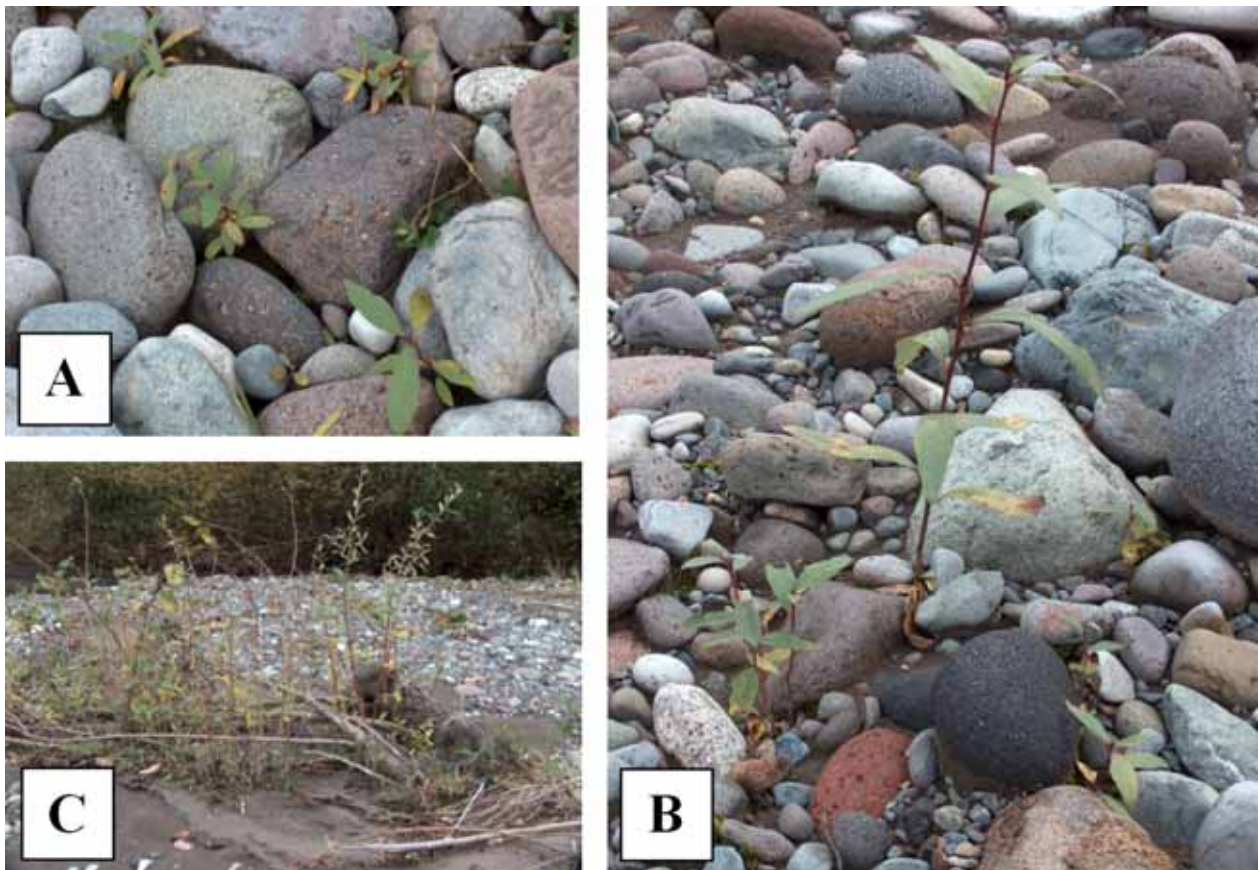


Figure 7.7. Succession of black cottonwood (*Populus trichocarpa*) and willow (*Salix spp.*) on a gravel bar in the Carbon River, Pierce County, Washington, USA. A. Cottonwood seedlings after first year of growth; B. One- and two-year old cottonwood seedlings; C. Sediment accumulation around a clump of willow sprouts and cottonwood seedlings in the early development of an alluvial floodplain. Photocredit: Jon D. Johnson.

Within riparian zones, poplars and willows occupy distinct, but overlapping, niches. For example, willows can withstand growing season floods for up to 110 days compared to less than 50 days for poplars (FAO 1980). Hence, willows are usually found in wetter areas closer to streams and lakes than poplars. Conversely, poplars are able to grow in drier, more upland soils than willows. Dickmann and Stuart (1983) reported that poplars - and the statement is undoubtedly true also for willows - can be planted on almost any site and with proper care will survive and can actually grow better than other tree species.

7.2.4.2 Characteristics of good poplar and willow sites – In the 1980 FAO book on Poplars and Willows, the discussion on site selection concentrated primarily on root access to groundwater, stating “...euramerican poplars can be planted wherever the roots have access to underground water, no matter the [soil texture](#)...” and “willows can be planted on bottom lands, with accessible underground water, unsuitable for euramerican poplars...” (FAO 1980). [Soil texture](#) was mentioned as reducing growth on heavy soils with groundwater deeper than 2 m, and on light soils (sands and gravels) that are saline. Schreiner (1959) and Heilman *et al.* (1995) identified five important characteristics when selecting a site to support good tree growth: soil depth, soil fertility,

soil pH, and soil moisture and aeration. Along with deep soils (> 1m) and a water table between 1 to 2 m deep (0.5 to 1.5 m for willow), soil fertility traits should include an undisturbed site or one with <5 years of cultivation, organic matter >3% in the [A-horizon](#) (that is >15 cm), a source of calcareous (basic) parent material in the rooting zone, and pH ranging between 5.5 and 7.5. In contrast, any soil trait not meeting these criteria can cause low site fertility, leading to reduced tree growth.

7.2.4.3 Poor fertility and nutrient deficiencies – In most soils, it is not uncommon to have nutrient levels that limit tree growth potential, and in many of these situations, classic deficiency symptoms such as leaf [chlorosis](#) may not be evident. It has been shown that trees cope with limiting soil nutrients by reducing overall tree growth rate and thereby reducing the quantity of nutrients required by the trees ([Figure 7.8](#)); the lower the nutrient availability, the slower the trees grow. As they grow more slowly, it has been found that trees also reallocate carbon from aboveground organs such as leaves, branches and stem to the root system to enable greater soil exploration for the limiting nutrient.



Figure 7.8. Growth response to different levels of nitrogen nutrition. The hybrid poplar cutting on the right was grown at a nitrogen addition rate (NAR) of 8% per day whereas the cutting on the left was grown at an NAR of 1.5%. The photo was taken after 42 days of growth. Note the differences in overall tree size as well as individual leaf size, leaf number, the lack of branches in the low N treatment and lack of any nitrogen deficiency symptoms. Photocredit: Jon D. Johnson.

Severe nutrient deficiencies can be encountered in highly altered or disturbed soils such as mine spoils, or over-irrigated soils leached of soluble nutrients like Mg and K, but this topic is outside of the scope of this section. Erickson, Rytter and Linder (1992) provided a comprehensive review of nutritional requirements of short rotation forests. The nutrients that appear to be most limiting in natural soils are nitrogen and phosphorus, though sulphur has received some attention in the literature recently (Brown and van den Driessche 2002, Liang and Chang 2004, van den Driessche 2000).

7.2.4.4 Tree response to poor fertility – When growing in poor soils, poplars and willows reduce their growth, especially diameter growth, by decreasing their leaf area. This is accomplished in several ways. First, there is a general reduction in individual leaf area resulting from changes in [cell wall](#) properties during leaf development caused by the nutrient limitation (Taylor *et al.* 1993). Two hybrid poplar clones grown for 42 days at two nitrogen addition rates, 1.5 and 8%, showed increases in mean individual leaf area of 50 and 82% respectively, whereas whole plant leaf area increased between 854 and 1098% depending on the hybrid ([Table 7.3](#), [Figures 7.8](#) and [7.9](#)).

Table 7.3. Total leaf area and mean individual leaf area of two hybrid poplar clones in response to two nitrogen addition rates (NAR). Clone 1 was a *P. deltoides* × *P. trichocarpa* cross whereas clone 2 was a reciprocal cross between a *P. trichocarpa* female and a *P. deltoides* male.

	1.5% NAR		8% NAR	
	Total Leaf Area	Mean leaf area	Total Leaf Area	Mean leaf area
Clone 1 (DxT)	628 cm ²	34.4 cm ²	7525 cm ²	62.7 cm ²
Clone 2 (TxD)	620 cm ²	33.2 cm ²	5915 cm ²	49.6 cm ²

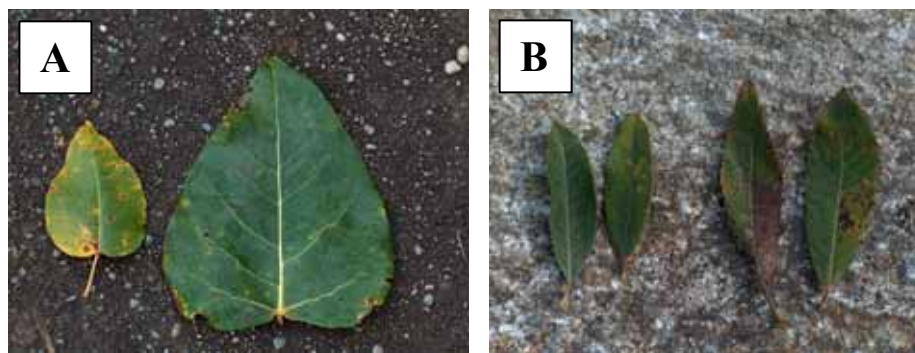


Figure 7.9. Black cottonwood (*Populus trichocarpa*: A) and willow (*Salix* spp.: B) leaves showing smaller individual leaves on the left in each photograph resulting from poor fertility. Photocredit: Jon D. Johnson.

Under low fertility, tree canopy leaf area is reduced by the presence of fewer, smaller leaves, which reduce light interception and photosynthesis. In addition, trees grown under low fertility have fewer branches and those branches are thinner, having less biomass ([Table 7.4](#)). Bowman and Conant (1994) reported similar responses in *Salix glauca* growing along a soil fertility and moisture gradient. During early stand development, height growth has been found to be less affected by site fertility than diameter growth. Maximum height, however, is ultimately controlled by site fertility and is the basis for [Site Index](#) curves.

Table 7.4. Percent change in branch number, total and mean branch biomass after the first and second years of a field nitrogen study using six-hybrid poplar clones. The percent increases represent the increase from the lowest N to highest N treatment.

Response Variable	Year 1	Year 2
No. of branches	+28%	+16%
Branch Biomass	+82%	+36%
Mean Branch biomass	+47%	+27%
Leaf biomass	+31%	+32%

Associated with the reduction in aboveground biomass, there is a re-allocation of carbon to the root system that enables the tree to explore the soil for additional nutrients (Ibrahim, Proe and Cameron 1998). In the same study in [Table 7.4](#), the percent biomass in roots increased from 25% in the high N treatment to over 30% in the low N treatment. Woolfolk and Friend (2003) found that the form of nitrogen, nitrate or ammonium, affected the development of *P. deltoides* roots. The ratio of 20:80 (NH₄:NO₃) resulted in the greatest root length, specific root length and root N concentration. In a study comparing the sprouting of *Salix viminalis* grown under two nitrogen levels, von Fircks and Sennerby-Forsse (1998) reported higher starch levels in the roots of the low-N trees, which they found to support greater sprouting the following spring.

7.2.4.5 Other consequences of reduced growth from poor fertility – In addition to the direct effects of low fertility discussed above, there have been reports of other secondary responses. Because of the slower growth, the density of the wood produced under limiting nutrition is higher and has been shown to be a result of the production of vessels with smaller diameters (Harvey and van den Driessche 1997, 1999). A physiological consequence of smaller vessel diameter was an increased resistance to [cavitation](#) during drought. The slowest-growing native willows were found to be less sensitive to both nutrient and water stress (Weih 2001). Glynn *et al.* (2003) found altered insect resistance in poplar resulting from nutrient availability. Under low fertility, constitutive resistance to [gypsy moth](#) increased as well as the rapid induced resistance to [whitemarked tussock moth](#).

(JDJ)

7.3 Atmospheric stresses

Most of the observed increase in global average temperatures since the mid-20th century is very likely due to the increase in anthropogenic greenhouse gas concentrations. Global atmospheric concentrations of carbon dioxide, methane, ozone and nitrous oxide have indeed increased markedly as a result of human activities since 1750 and now far exceed pre-industrial values

determined from ice cores spanning many thousands of years (IPCC 2007). If the future evolution is difficult to predict, this phenomenon is likely to continue to increase during the next decades and is not without consequences for plant growth and physiology.

7.3.1 Tropospheric ozone levels

Concurrently with increasing CO₂ concentration in the earth's atmosphere, tropospheric ozone (O₃) has risen sharply in the post-industrialization period and is expected to be at toxic levels for sensitive vegetation (where peak concentrations exceeding 60 ppb) for some 50% of the world's forests by 2100 (Fowler *et al.* 1999). It is well-known that poplars are generally sensitive to O₃ (Karnosky *et al.* 1996, Dickson *et al.* 1998, Isebrands *et al.* 2001). Although there is a large amount of genetic variation in poplar responses to O₃ (Karnosky 1977, Berrang *et al.* 1986, Karnosky *et al.* 2005), overall the poplars are among the most sensitive tree species to elevated O₃. Adverse effects of O₃ on poplar foliage include visible foliar symptoms (Karnosky 1976, Karnosky *et al.* 1996), decreased chlorophyll content (Gagnon *et al.* 1992), decreased leaf size (Oksanen, Sober and Karnosky 2001), increased [peroxisome](#) accumulation (Oksanen *et al.* 2003), and premature leaf abscission (Karnosky *et al.* 1996). Physiologically, O₃ decreases maximal photosynthetic levels in both sun and shade leaves (Coleman *et al.* 1995), alters [stomatal conductance](#) and respiration (Noormets *et al.* 2001), decreases height and diameter growth (Karnosky *et al.* 1996, Isebrands *et al.* 2001), changes crown architecture (Dickson *et al.* 2001), affects competitive ability (McDonald *et al.* 2002), and decreases fitness (Karnosky *et al.* 2003a).

In addition, and importantly for risk analysis for global change, elevated O₃ can modify poplar responses to important insect and disease pests. For example, with the important cyclic pest, the [forest tent caterpillar](#), developing larval growth rates were increased and the fecundity of the adult female moths was increased under elevated O₃ (Kopper and Lindroth 2003, Holton, Lindroth and Nordheim 2003). Also, aphid populations were significantly larger on aspen trees under elevated O₃ (Percy *et al.* 2002, Awmack, Harrington and Lindroth 2004, Mondor *et al.* 2004).

For diseases, Karnosky *et al.* (2002) have reported a 3- to 5-fold increase in *Melampsora* leaf rust under elevated O₃ at the AspenFACE experiment over several growing seasons. Ozone-induced changes in the leaf surface waxes are likely predisposing aspen to the important leaf rust (Karnosky *et al.* 2002, Percy *et al.* 2002).

(DFK)

7.3.2 Effects of elevated CO₂ and combinations with ozone

During the last centuries we have increasingly been using natural non-renewable resources to satisfy our needs; fossil fuel is one of those resources. Among others, emission from fossil fuel

burning is causing a steady increase of CO₂ concentration in the earth's atmosphere, which may reach 550 μmol mol⁻¹ by the middle of the 21st century (Schimel *et al.* 1996). This rising CO₂ is the main driver of ongoing climatic changes (IPCC 1995). [Table 7.5](#) gives an overview of the available literature on elevated CO₂ effects on poplar investigated using field experiments (Gielen and Ceulemans 2001). In contrast to other greenhouse gases, CO₂ is a plant fertilizer rather than a pollutant. Elevated atmospheric CO₂ initially causes a photosynthetic stimulation resulting in faster growth and higher production (Long and Drake 1992). As a consequence, the capacity of ecosystems to store part of the excess carbon is of main interest as a possible feedback mechanism to global climate change.

Populus is characterized by a high growth rate, high plasticity, and unusually high [sink strength](#) (Scarascia-Mugnozza *et al.* 1997) related to an indeterminate growth pattern and the continuous production of [sylleptic branches](#) (not all species) during periods of active growth. Therefore a sustained photosynthetic enhancement under elevated CO₂ may be expected for poplar, which could make short-rotation forestry interesting as a mitigation strategy for the increase of atmospheric CO₂ concentration. Indeed, light-saturated net photosynthesis at the leaf level was consistently enhanced by elevated CO₂ among different *Populus* species, clones, and experiments (Gielen and Ceulemans 2001). After long-term exposure to elevated CO₂, a reduced stimulation of photosynthesis may occur due to [acclimation](#) processes, considered to improve plant performance through increased resource use efficiency, or due to accumulation of excess [carbohydrates](#) (Sage 1994). [Acclimation](#) of C₃ photosynthesis has been frequently observed (Ainsworth and Long 2005), and it may cause a reduction of growth stimulation under elevated CO₂. Two [free-air CO₂ enrichment](#) (FACE) experiments have been set-up to increase our understanding of the effects of elevated atmospheric CO₂ on poplar trees, POP-EUROFACE (<http://www.unitus.it/euroface>, [Figures 7.10a](#) and [b](#)) and AspenFACE (<http://aspenface.mtu.edu>, [Figures 7.11](#) and [7.12](#)). In POP-EUROFACE, photosynthesis per unit land surface, i.e. [gross primary production](#) (GPP) was stimulated by elevated CO₂ in all three years of the first rotation cycle, with the largest stimulation during the first year (Wittig *et al.* 2005). In the second and third years, there was a decline in stimulation due to canopy closure rather than to photosynthetic [acclimation](#) (Wittig *et al.* 2005). Similarly, results from AspenFACE showed a sustained stimulation of photosynthesis in the upper, but not in the lower canopy (Takeuchi *et al.* 2001).



Figure 7.10a. Aerial view of the POPFACE site. Photocredit: S. Bunn, University of Southampton.

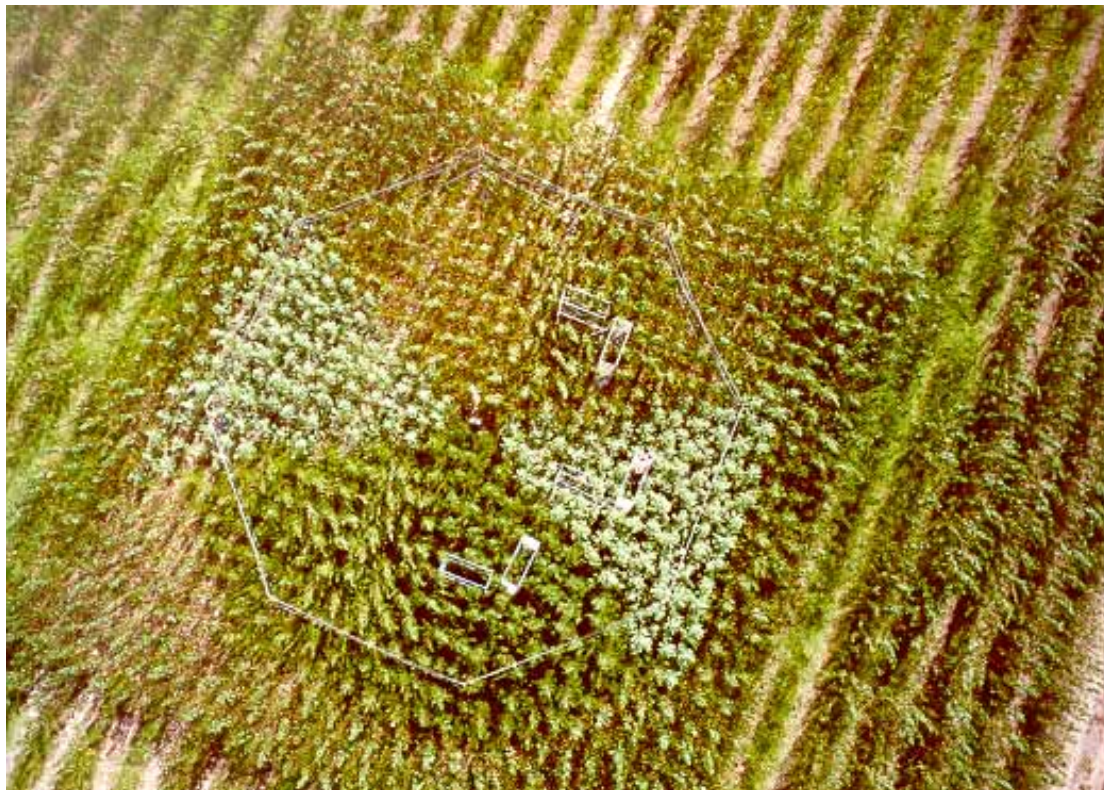


Figure 7.10b. Aerial view of one plot at the POPFACE site with three different *Populus* clones. Photocredit: S. Bunn, University of Southampton.



Figure 7.11. The twelve treatment rings of the aspen FACE experiment are shown here. This experiment recently completed its eighth treatment season with three replicate rings each for control, elevated CO₂, elevated O₃, and elevated CO₂+O₃. Photo credit: R. Anderson.



Figure 7.12. A typical 30-m wide FACE treatment ring with 5 aspen clones (left ½) and mixed aspen/maple (lower right) and mixed aspen/birch (above right). Photo credit: D.F. Karnosky.

In view of the effects of rising atmospheric CO₂ on productivity and carbon balance, respiratory carbon losses need to be accounted for. At present, no clear consensus has emerged concerning respiration of poplar trees under elevated CO₂ concentrations but in general, respiration is expected to increase because of the increase in biomass. Soil respiration will likely increase as has been observed in large-scale field experiments (King *et al.* 2004) and at the [Biosphere 2 Laboratory](#) (Barron-Gafford *et al.* 2005).

The most striking and important effect of elevated CO₂ concentrations is the stimulating effect on above- and below-ground growth (Gielen and Ceulemans 2001, Calfapietra *et al.* 2003a, Karnosky *et al.* 2003b). Gielen and Ceulemans (2001) reported a mean biomass stimulation of 33% in elevated CO₂ conditions across poplar studies published between 1990 and 2000. Recent results from the two field [FACE](#) experiments showed a consistent increase in biomass production in elevated CO₂ (Calfapietra *et al.* 2003b, Karnosky *et al.* 2003b, Liberloo *et al.* 2005).

Plant productivity is determined by photosynthetic efficiency in combination with light interception, which in turn depends on tree architecture and leaf area (Monteith 1977). Particularly in high-density poplar plantations, leaf area development is considered to be extremely important for productivity (Stettler *et al.* 1993); thus responses of leaf area to elevated CO₂ will definitely influence wood productivity. Overall, an increase of total leaf area under elevated CO₂ concentration has been reported in poplar, though this is dependent on nitrogen availability and the developmental stage of the canopy (Curtis *et al.* 2000, Gielen *et al.* 2001, Gielen *et al.* 2003, Karnosky *et al.* 2003b, Liberloo *et al.* 2005). Not only total leaf area and leaf area distribution, but also the length of the growing season determines productivity, and may be influenced by rising CO₂. Previously, advanced budset of poplar has been observed in open-top-chamber studies indicating a shorter growing season (Ceulemans, Jiang and Shao 1995a, Sigurdsson 2001). This was not confirmed in the two [FACE](#) studies as budset was not significantly affected in POP-EUROFACE, and was delayed in AspenFACE (Calfapietra *et al.* 2003b, Karnosky *et al.* 2003b). Alternatively, the leaf area duration can be compared between treatments; Curtis *et al.* (1995) reported a stimulation of 39% indicating a prolongation of the growing season under elevated CO₂. Research in this field is still ongoing at both [FACE](#) sites.

Further, an increase in belowground biomass in response to elevated CO₂ was observed (Zak *et al.* 1993, Dickson *et al.* 1998, Mikan *et al.* 2000, Pregitzer *et al.* 2000, King *et al.* 2001a, Calfapietra *et al.* 2003b, Lukac, Calfapietra and Godbold 2003). Although the relative stimulation of fine root production is often larger than aboveground biomass stimulation, recent field studies provide evidence for unchanged partitioning between above- and belowground biomass (Calfapietra *et al.* 2003b). Despite a stimulation of above- and belowground biomass production, the net carbon

storage capacity of a short-rotation forest plantation in the first rotation cycle was not enhanced by elevated CO₂ due to increased losses of soil carbon (Gielen *et al.* 2005).

Predicting terrestrial [carbon sequestration](#) and understanding ecosystem functioning under rising atmospheric CO₂ concentrations ultimately requires an integrated understanding of carbon and nitrogen cycling. Changes in root turnover, root nitrogen concentrations, and leaf litter chemistry could alter microbial substrate availability and consequently microbial communities, decomposition, and carbon - nitrogen cycles. Zak *et al.* (2000b) did not support the hypothesis of increased nitrogen cycling in future terrestrial ecosystems because neither the amount of biomass and community composition of soil micro-organisms, nor nitrogen mineralization were affected by elevated CO₂ in [open-top chambers](#). Unchanged gross rates of [nitrification](#) and nitrate immobilisation were also confirmed in the AspenFACE field experiment (Holmes *et al.* 2003). At the [Biosphere 2 Laboratory](#), elevated CO₂ accelerated depletion of soil nutrients, but not of nitrogen (Barron-Gafford *et al.* 2005). At the POP-EUROFACE site, a decrease of soil nitrogen was observed under elevated CO₂ at the end of the first rotation cycle probably due to a decreased input from leaf litter and decreased decomposition rate (Calfapietra *et al.*, submitted). Further, FACE treatment significantly increased [nitrogen-use efficiency \(NUE\)](#), i.e. the woody biomass produced per unit of nitrogen, decreased nitrogen concentration in all plant tissues as a result, and did not change total nitrogen uptake of poplar trees (Calfapietra *et al.*, submitted). For a discussion of poplar litter decomposition under elevated CO₂ concentration, we refer to Cotrufo, De Angelis and Polle (2005).

Typically, global change studies are performed in a controlled environment, without constraints on water and nutrient availability. It has been emphasized, however, that ecosystem responses to elevated CO₂ will be influenced by variable climate and environmental conditions (Luo, Canadell and Mooney 1999, Scholes *et al.* 1999). Thus local climate or site conditions complicate predictions about production and yield responses of natural and managed poplar stands to rising atmospheric CO₂. Therefore, efforts have been and are being made to study tree responses to CO₂ in interaction with ozone (O₃), nutrient availability, drought, temperature, or radiation.

When investigating poplar trees under concurrent exposure to CO₂ and O₃, the gases tend to counteract one another. Damages caused by O₃ are generally offset under elevated CO₂ (Volin and Reich 1996, Dickson *et al.* 1998, Noormets *et al.* 2001, Taylor *et al.* 2001) but sometimes elevated CO₂ can exacerbate the O₃ effects (Kull *et al.* 1996, Wustman *et al.* 2001). For the longest running experiment (8 years of AspenFACE) examining the combined effects of elevated CO₂ and O₃, the effects on trembling aspen growth (Isebrands *et al.* 2001, Percy *et al.* 2002, Karnosky *et al.* 2003b, Karnosky *et al.* 2005) and productivity (King *et al.* 2005) have largely cancelled one another so that the combined treatments are not significantly different from the controls.

Besides various abiotic factors, a number of biotic factors also directly or indirectly interact with the effect of increased atmospheric CO₂ on poplar growth, productivity and physiology. A brief literature review on biotic interactions through insect and [mycorrhizal](#) activities on the CO₂ responses of poplar can be found in Gielen and Ceulemans (2001). In summary, soil conditions and especially sensitivity of certain poplar clones to insects, fungi and air pollutants (e.g. O₃) will influence growth and functioning of natural and managed plantations, and interact with CO₂. Nonetheless, only a minority of studies supported strong interactive effects of biotic variables with atmospheric CO₂.

From a forestry viewpoint, possible alterations in wood quality under elevated CO₂ conditions have to be accounted for, but research is still ongoing. Responses of poplar to elevated CO₂ can also have practical implications. For example, Tupker, Thomas and Macdonald (2003) suggested the application of elevated CO₂ concentrations in the greenhouse in order to facilitate early selection of fast-growing clones under future atmospheric conditions.

In brief, ample evidence has been found to suggest that poplar will profit considerably from CO₂ enrichment at least in the short-term, but it is uncertain whether this will improve the long-term C storage capacity of poplar in natural stands or plantations. Soil conditions and especially sensitivity of certain poplar clones to insects, fungi and air pollutants (e.g. O₃) will influence growth and functioning of natural and managed poplar stands, and interact with CO₂.

(BG / DFK / GSM / RC)

7.3.3 Increased temperature

7.3.3.1 Context – Although trees have responded to global warming in the past, the rate of change currently observed and predicted for the next decades is likely to be unprecedented. Continued greenhouse gas emissions at or above current rates would cause further warming and induce many changes in the global climate system during the 21st century that would very likely be larger than those observed during the 20th century. For the next two decades, a warming of about 0.2°C per decade is projected for a range of IPCC scenarios (IPCC 2007). The photosynthetic optimum of plants is generally between 20 and 30°C, but the range can be enlarged from 15 to 45°C according to the temperature experienced during growth or the biological type to which the plants belong. However, 50°C is generally considered as the limiting temperature for photosynthetic activity of vascular plants (Berry and Björkman 1980, Saugier 1983). Trees belonging to the *Populus* genus are known to be particularly sensitive to temperature rise.

7.3.3.2 Physiological basis – Tolerance of the photosynthetic apparatus to high temperature is thought to be mainly related to the thermostability of [photosystem II \(PSII\)](#) [photochemistry](#), which

seems to be one of the most sensitive components of the [electron-transport chain](#) of the [thylakoids](#) to most of the major environmental constraints, such as ultra-violet radiation or heat (Trabaud and Méthy 1992, Schumaker *et al.* 1997). [PSII](#) deactivation induced by heat leads to damages such as protein denaturation and dissociation of pigments. These alterations result in changes in the interactions between lipids and proteins associated with an increase in membrane fluidity (Sundby *et al.* 1986, Thompson *et al.* 1989). The critical temperature (T_C) depends on both species and [genotypes](#) (Epron 1997, Knight and Ackerly 2002), but is also modulated to a large extent by climate. It increases after short periods of exposure to higher temperatures and in response to drought stress, [abscisic acid](#) application, or growth in high CO₂ concentration (Ivanov *et al.* 1992, Havaux 1993, Ladjal, Epron and Ducrey 2000, Taub, Seemann and Coleman 2000).

7.3.3.3 Experimental assessment – Three different kinds of experiments have been conducted in order to estimate the impact of high temperature on poplar plants: (1) plant growth under heated soil conditions, (2) plant growth in heated growth chambers, or (3) direct heating of the leaves.

- (1) A minimum soil temperature of 14°C during several days is needed to sustain rooting in poplar (Zalesny *et al.* 2005). As compared with several conifer species, trembling aspen (*P. tremuloides*) has been shown to be particularly sensitive to soil temperature. Its optimal soil temperature for total biomass was 19.4°C, leaves showing a higher optimum temperature than roots (Tryon and Chapin 1983, Peng and Dang 2003). [Specific leaf area](#) showed a large decrease with the rise of soil temperature. Physiologically, photosynthesis was progressively less limited by [stomatal conductance](#) (relative to [mesophyll](#) limitation) as soil temperature increased (Dang and Cheng 2004). Both the maximal rate of [carboxylation](#) (V_{cmax}) and the maximum rate of [electron transport](#) (J_{max}) increased with soil temperature, up to an optimum (generally around 25°C), and then decreased with further increases in soil temperature (Cai and Dang 2002).
- (2) [Acclimation](#) is commonly observed for poplar plants grown under high temperature. Notably, respiration of roots and shoots has been observed to be largely inferior for plants grown under elevated temperature (Tjoelker, Oleskyn and Reich 1999). This [acclimation](#) of respiration could play an important role in determining the relationships between respiration and photosynthesis (Loveys *et al.* 2003).
- (3) With regard to the last type of procedure, the critical temperature (T_C) for the stability of [photosystem II](#) can be estimated (i) as the point at which [basal chlorophyll a fluorescence](#) (F_0) begins to increase under gradually increasing temperatures (generally between 42 and 50°C) or (ii) as the temperature for which the [photosystem II quantum yield](#), monitored in

darkness, is decreased by 15% in response to a gradual increase in temperature (generally between 35 and 40°C) (Bilger *et al.* 1987, Froux *et al.* 2004). For quaking aspen (*P. tremuloides*), the critical temperature for the stability of [photosystem II](#), estimated by monitoring initial [fluorescence](#), has been shown to be around 49°C (Logan and Monson 1999). On the other hand, for several clones of *P. ×canadensis*, it has been shown that T_C could vary from 43 to 47°C among leaves of a given plant differing in age or in stage of development (Marron 2003). Structural changes in leaves during growth and aging have been evidenced as a possible cause for this wide variation in terms of T_C .

As for many of the abiotic stresses described in this chapter, poplar and willow show, on the one hand, a very large range of diversity in their response to warming depending on growth conditions and used plant material and, on the other hand, they are apparently able to acclimate to quite extreme conditions. With regard to the current and future changes in climate, the diversity in the heat responses observed within the Salicaceae family is encouraging for the selection of varieties adapted to upcoming climate conditions.

(NM)

7.3.4 High irradiances ([photoinhibition](#))

The photosynthetic system of tree leaves can be damaged by very high irradiances. In fact, [photoinhibition](#), which includes photodamage and protective down-regulation of photosynthesis, is characteristic for the photosynthetic process (Long, Humphries and Falkowski 1994, Osmond 1994, Niinemets and Kull 2001). [Photoinhibition](#) occurs at all light intensities, but increases with increasing irradiance (Tyystjärvi and Aro 1996). In the field, the largest part of the decline in photosynthetic efficiency during the day, for example at midday when light intensity is high, results from down-regulation without irreversible damage to the photosynthetic system (Demmig-Adams and Adams III 1996, Demmig-Adams *et al.* 1996). Ögren and Sjöström (1990) estimated that upper canopy leaves of *Salix* lost about 6.3 – 12.6% of potential C gain because of [photoinhibition](#), while Niinemets and Kull (2001) pointed out that this is an overestimation because [stomatal](#) closure was not taken into account. They found that [photoinhibition](#) is indeed common in upper canopies of *Populus tremula*, whereas the influence on daily photosynthesis is moderate (Niinemets and Kull 2001). Differences in resistance to light stress among poplar or willow clones have not often been investigated (e.g. Zhang and Gao 2000). The sensitivity of trees to high irradiance primarily depends on the degree of shade-adaptation, and on other stresses. Therefore, [photoinhibition](#) is important when poplar or willow trees are subjected to drought or extreme temperatures.

(BG)

7.4 Conclusion

Worldwide, poplars and willows have colonized numerous kinds of environments and can subsequently be subjected to conditions faraway from their growth optima. These conditions are likely to be aggravated in response to the current global changes affecting atmospheric as well as soil compartments. However, a very wide range of diversity exists within the *Salix* and *Populus* genres both in terms of level of resistance (defined as the ability to survive and/or to sustain a production of biomass under constraining conditions) and in terms of mechanisms used to face these constraints occurring both at edaphic and atmospheric levels. Moreover, members of the Salicaceae family show an impressive acclimation ability in response to most stresses.

References

- Aasamaa, K. & Söber, A.** 2001. Hydraulic conductance and stomatal sensitivity to changes of leaf water status in six deciduous tree species. *Biol. Plantarum*, 44(1): 65-73.
- Aasamaa, K., Söber, 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 Physiol.*, 22(4): 267-276.
- Aasamaa, K., Söber, A., Hartung, W. & Niinemets, Ü.** 2004. Drought acclimation of two deciduous tree species of different layers in a temperate forest canopy. *Trees – Struct. Funct.*, 18(1): 93-101.
- Abbot, L.K. & Robson, A.D.** 1991. Factors influencing the occurrence of vesicular arbuscular mycorrhizae. *Agr. Ecosyst. Environ.*, 35: 121-150.
- Abrams, M.D. & Mostoller, S.A.** 1995. Gas exchange, leaf structure and nitrogen in contrasting successional tree species growing in open and understory sites during a drought. *Tree Physiol.*, 15(6): 361-370.
- Acosta-Avalos, D., Alvarado-Gil, J. & Vargas, H.** 2005. Monitoring ethylene and oxygen emission during water stress of *Populus alba* leaves. *J. Phys. IV*, 125: 817-819.
- Ainsworth, E.A. & Long, S.P.** 2005. What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. *New Phytol.*, 165: 351-372.
- Al-Agely, A.K. & Reeves, F.B.** 1995. Inland sand dune mycorrhizae: Effects of soil depth and pH on colonisation of *Oryzopsis hymenoides*. *Mycologia*, 87: 54-60.
- Al-Karki, G.N.** 2000. Growth of mycorrhizal tomato and mineral acquisition under salt stress. *Mycorrhiza*, 10: 51-54.
- Allen, R.D.** 1995. Dissection of oxidative stress tolerance using transgenic plants. *Plant Physiol.*, 107(4): 1049-1054.
- Allen, S.J., Hall, R.L. & Rosier, P.T.W.** 1999. Transpiration by two poplar varieties grown as coppice for biomass production. *Tree Physiol.*, 19(8): 493-501.
- Ambus, P. & Robertson, G.P.** 1999. Fluxes of CH₄ and N₂O in aspen stands grown under ambient and twice-ambient CO₂. *Plant Soil*, 209: 1-8.
- Amlin, N.M. & Rood, S.B.** 2002. Comparative tolerances of riparian willows and cottonwoods to water-table decline. *Wetlands*, 22(2): 338-346.
- Ananyev, G., Kolber, Z.S., Klimov, D., Falkowski, P.G., Berry, J.A., Rascher, U., Martin, R. & Osmond, B.** 2005. Remote sensing of heterogeneity in photosynthetic efficiency, electron transport and dissipation of excess light in *Populus deltoides* stands under ambient and elevated CO₂ concentrations, and in a tropical forest canopy, using a new laser-induced fluorescence transient device. *Global Change Biol.*, 11: 1195-1206.
- Andersen, D.C. & Nelson, S.M.** 2003. Effects of river flow regime on cottonwood leaf litter dynamics in semi-arid northwestern Colorado. *Southwest. Nat.*, 48(2): 188-201.
- Anonymous** 1977. *Combating desertification*. Institute of glaciology, cryopedology, and desert, Chinese Academy of Forestry, Lanzhou.
- Anonymous** 2000. Tackling desertification in the Korqin Sandy lands through integrated afforestation. *In* Research, planning and development in the Three North region of China. Yachen Printing Ltd., Tongliao, Inner Mongolia.
- Anonymous** 2005. Remote sensing of land-cover change: Investigations and design of a dynamic monitoring system in northwest China: Case study in the Tarim Basin, Xinjiang (available at www.geo.ucl.ac.be/Recherche/Teledetection/Projects/China_Tarim.html).
- Apse, M.A., Aharon, G.S., Snedden, W.A. & Blumwald, E.** 1999. Salt tolerance conferred by overexpression of a vacuolar Na⁺/H⁺ antiport in *Arabidopsis*. *Science*, 285: 1256-1258.

- Arisi, A.-C., Cornic, G., Jouanin, L. & Foyer, C.H.** 1998. Overexpression of FeSOD in transformed poplar modifies the regulation of photosynthesis at low CO₂ partial pressures or following exposure to the prooxidant herbicide methyl viologen. *Plant Physiol.*, 117(2): 565-574.
- Arndt, S.K., Arampatsis, C., Foetzki, A., Li, X.Y., Zeng, F.J. & Zhang, X.M.** 2004. Contrasting patterns of leaf solute accumulation and salt adaptation in four phreatophytic desert plants in a hyperarid desert with saline groundwater. *J. Arid Environ.*, 59(2): 259-270.
- Awmack, C.S., Harrington, R. & Lindroth, R.L.** 2004. Individual performance does not predict aphid population responses to elevated atmospheric CO₂ or O₃. *Global Change Biol.*, 10: 1414-1423.
- Ball, J., Russo, L. & Thomson, L.** 1996. Status of *Populus euphratica* and proposal for its conservation. Working Party on Breeding and selection, XX Session, International Poplar Commission FAO, Budapest, Hungary. 1-12 October, 1996.
- Barron-Gafford, G., Martens, D., Grieve, K., Biel, K., Kuderyarov, V., McClain, J.E.T., Lipson, D. & Murthy, R.** 2005. Growth of Eastern Cottonwoods (*Populus deltoides*) in elevated [CO₂] stimulates stand-level respiration and rhizodeposition of carbohydrates, accelerates soil nutrient depletion, yet stimulates above- and belowground biomass production. *Global Change Biol.*, 11: 1220-1233.
- Bassman, J.H. & Zwier, J.C.** 1991. Gas exchange characteristics of *Populus trichocarpa*, *Populus deltoides* and *Populus trichocarpa* x *P. deltoides* clones. *Tree Physiol.*, 8(2): 145-159.
- Beritognolo I., Piazzai, M., Muleo, R., Paolucci, I., Kuzminsky, E., Sabatti, M. & Scarascia-Mugnozza, G.** 2003. Molecular response to salt stress of three Italian *Populus* genotypes from different latitudes. Proceeding of the XLVII Italian Society of Agricultural Genetics - SIGA Annual Congress, Poster Abstract - 5.18, Verona, Italy, 24-27 September 2003.
- Bernacchi, C.J., Calfapietra, C., Davey, P.A., Wittig, V.E., Scarascia-Mugnozza, G.E., Raines, C.A. & Long, S.P.** 2003. Photosynthesis and stomatal conductance responses of poplars to free-air CO₂ enrichment (PopFACE) during the first growth cycle and immediately following coppice. *New Phytol.*, 159: 609-621.
- Berrang, P.C., Karnosky, D.F., Mickler, R.A. & Bennett, J.P.** 1986. Natural selection for ozone tolerance in *Populus tremuloides*. *Can. J. Forest Res.*, 16: 1214-1216.
- Berry, J. & Björkman, O.** 1980. Photosynthetic response and adaptation to temperature in higher plants. *Annu. Rev. Plant Physiol.*, 31: 491-543.
- Bigler, C., Kulakowski, D. & Veblen, T.T.** 2005. Multiple disturbance interactions and drought influence fire severity in Rocky Mountain subalpine forests. *Ecology*, 86(11): 3018-3029.
- Bilger, W., Schreiber, U. & Lange, O.L.** 1987. Chlorophyll fluorescence as an indicator of heat induced limitation of photosynthesis in *Arbutus unedo* L. *Plant Resp. Stress*, 15: 391-399.
- Blake, T.J., Sperry, J.S. & Tschaplinski, T.J.** 1996. Water relations. In R.F. Stettler, H.D.J. Bradshaw, P.E. Heilman and T.M. Hinckley, eds. *Biology of Populus and its implications for management and conservation*, pp. 401-422. Ottawa, ON, NRC Research Press, National Research Council of Canada. 539 p.
- Blum, A., Munns, R., Passioura, J.B. & Turner, N.C.** 1996. Genetically engineered plants resistant to soil drying and salt stress: how to interpret osmotic relations? *Plant Physiol.*, 110: 1051-1053.
- Blumwald, E., Aharon, G.S. & Apse, M.P.** 2000. Sodium transport in plant cells. *Biochim. Biophys. Acta*, 1465: 140-151.
- Bolu, W.H. & Polle, A.** 2004. Growth and stress reactions in roots and shoots of a salt-sensitive poplar species (*Populus xcanescens*). *Trop. Ecol.*, 45: 161-171.
- Borsani, O., Valpuesta, V. & Botella, M.** 2001. Evidence for a role of salicylic acid in the oxidative damage generated by NaCl and osmotic stress in *Arabidopsis* seedlings. *Plant Physiol.*, 126: 1024-1030.
- Bovard, B.D., Curtis, P.S., Vogel, C.S., Su, H.B. & Schmid, H.P.** 2005. Environmental controls on sap flow in a northern hardwood forest. *Tree Physiol.*, 25(1): 31-38.

- Bowman, W.D. & Conant, R.T.** 1994. Shoot growth dynamics and photosynthetic response to increased nitrogen availability in the alpine willow *Salix glauca*. *Oecologia*, 97: 93-99.
- Braatne, I.H., Hinckley, T.M. & Stettler, R.F.** 1992. Influence of soil water on the physiological and morphological components of plant water balance in *Populus trichocarpa*, *Populus deltoides* and their F1 hybrids. *Tree Physiol.*, 11(4): 325-339.
- Brignolas, F., Thierry, C., Guerrier, G. & Boudouresque, E.** 2000. Compared water deficit response of two *Populus x euramericana* clones, Luisa Avanzo and Dorskamp. *Ann. Forest Sci.*, 57(3): 261-266.
- Brosché, M., Vinocur, B., Alatalo, E.R., Lamminmäki, A., Teichmann, T., Ottow, E.A., Djilianov, D., Afif, D., Triboulot-Bogeat, M.B., Altman, A., Polle, A., Dreyer, E., Rudd, S., Paulin, L., Auvinen, P. & Kangasjärvi, J.** 2005. Gene expression and metabolite profiling of *Populus euphratica* growing in the Negev desert. *Genome Biol.*, 6: R101.
- Browicz, K.** 1977. Chorology of *Populus euphratica* Olivier. *Arboretum Kórnickie*, 22: 5-27.
- Brown, K.R. & van den Driessche, R.** 2002. Growth and nutrition of hybrid poplars over 3 years after fertilization at planting. *Can. J. Forest Res.*, 32: 226-232.
- Cai, T. & Dang, Q.L.** 2002. Effects of soil temperature on parameters of a coupled photosynthesis-stomatal conductance model. *Tree Physiol.*, 22: 819-827.
- Calfapietra, C., Gielen, B., Sabatti, M., De Angelis, P., Scarascia-Mugnozza, G. & Ceulemans, R.** 2001. Growth performance of *Populus* exposed to "Free Air Carbon dioxide Enrichment" during the first growing season in the POPFACE experiment. *Ann. Forest Sci.*, 58: 819-828.
- Calfapietra, C., Gielen, B., Sabatti, M., De Angelis, P., Miglietta, F., Scarascia-Mugnozza, G. & Ceulemans, R.** 2003a. Do above-ground growth dynamics of poplar change with time under CO₂ enrichment? *New Phytol.*, 160: 305-318.
- Calfapietra, C., Gielen, B., Galema, A.N.J., Lukac, M., De Angelis, P., Moscatelli, M.C., Ceulemans, R. & Scarascia-Mugnozza, G.** 2003b. Free-air CO₂ enrichment (FACE) enhances biomass production in a short-rotation poplar plantation (POPFACE). *Tree Physiol.*, 23: 805-814.
- Calfapietra, C., Tulva, I., Eensalu, E., Perez, M., De Angelis, P., Scarascia-Mugnozza, G. & Kull, O.** 2005. Canopy profiles of photosynthetic parameters under elevated CO₂ and N fertilization in a poplar plantation. *Environ. Pollut.*, 137: 525-535.
- Caruso, A., Morabito, D., Delmotte, F., Kahlem, G. & Carpin, S.** 2002. Dehydrin induction during drought and osmotic stress in *Populus*. *Plant Physiol. Biochem.*, 40(12): 1033-1042.
- Ceulemans, R., Van Praet, L. & Jiang, X.N.** 1995. Effects of CO₂ enrichment, leaf position and clone on stomatal index and epidermal cell density in poplar (*Populus*). *New Phytol.*, 131: 99-107.
- Ceulemans, R., Jiang, X.N. & Shao, B.Y.** 1995a. Effects of elevated atmospheric CO₂ on growth, biomass production and nitrogen allocation of two *Populus* clones. *J. Biogeogr.*, 22: 261-268.
- Ceulemans, R., Jiang, X.N. & Shao, B.Y.** 1995b. Growth and physiology of one-year old poplar (*Populus*) under elevated atmospheric CO₂ levels. *Ann. Bot.*, 75: 609-617.
- Ceulemans, R., Shao, B.Y., Jiang, X.N. & Kalina, J.** 1996. First- and second-year aboveground growth and productivity of two *Populus* hybrids grown at ambient and elevated CO₂. *Tree Physiol.*, 16: 61-68.
- Ceulemans, R., Taylor, G., Bosac, C., Wilkins, D. & Besford, R.T.** 1997. Photosynthetic acclimation to elevated CO₂ in poplar grown in glasshouse cabinets or in open top chambers depends on duration of exposure. *J. Exp. Bot.*, 48: 1681-1689.
- Chaves, M.M. & Oliveira, M.M.** 2004. Mechanisms underlying plant resilience to water deficits: prospects for water-saving agriculture. *J. Exp. Bot.*, 55(407): 2365-2384.

- Chen, S., Wang, S., Altman, A. & Hüttermann, A.** 1997. Genotypic variation in drought tolerance of poplar in relation to abscisic acid. *Tree Physiol.*, 17(12): 797-803.
- Chen, S., Li, J., Wang, S., Hüttermann, A. & Altman, A.** 2001. Salt, nutrient uptake and transport, and ABA of *Populus euphratica*; a hybrid in response to increasing soil NaCl. *Trees – Struct. Funct.*, 15: 186-194.
- Chen, S.L., Wang, S.S., Hüttermann, A. & Altman, A.** 2002a. Xylem abscisic acid accelerates leaf abscission by modulating polyamine and ethylene synthesis in water-stressed intact poplar. *Trees – Struct. Funct.*, 16(1): 16-22.
- Chen, S., Li, J., Fritz, E., Wang, S. & Hüttermann, A.** 2002b. Sodium and chloride distribution in roots and transport in three poplar genotypes under increasing NaCl stress. *Forest Ecol. Manag.*, 168: 217-230.
- Chen, Y.N., Chen, Y.P., Li, W.H. & Zhang, H.F.** 2003a. Response of the accumulation of proline in the bodies of *Populus euphratica* to the change of groundwater level at the lower reaches of Tarim River. *Chinese Sci. Bull.*, 48(18): 1995-1999.
- Chen, S., Li, J., Wang, S., Fritz, E., Hüttermann, A. & Altman, A.** 2003b. Effects of NaCl on shoot growth, transpiration, ion compartmentation, and transport in regenerated plants of *Populus euphratica* and *Populus tomentosa*. *Can. J. Forest Res.*, 33: 967–975.
- Chen, Y.N., Li, W.H., Chen, Y.P., Zhang, H.F. & Zhuang, L.** 2004. Physiological response of natural plants to the change of groundwater level in the lower reaches of Tarim River, Xinjiang. *Prog. Nat. Sci.*, 14(11): 975-983.
- Clary, W.P.** 1999. Stream channel and vegetation responses to late spring cattle grazing. *J. Range Manage.*, 52: 218-227.
- Cochard, H., Ridolfi, M. & Dreyer, E.** 1996. Responses to water stress in an ABA-unresponsive hybrid poplar (*Populus koreana* x *trichocarpa* cv. Peace). II. Hydraulic properties and xylem embolism. *New Phytol.*, 134: 455-461.
- Coleman, M.D., Dickson, R.E., Isebrands, J.G. & Karnosky, D.F.** 1995. Photosynthetic productivity of aspen clones varying in sensitivity to tropospheric ozone. *Tree Physiol.*, 15: 585-592.
- Cooper, D.T. & Van Haverbeke, D.F.** 1990. *Populus deltoides* Bartr. ex Marsh.: eastern cottonwood. In USDA Forest Service, ed. *Silvics of North America: Volume 2, Hardwoods*, pp. 530-543. Washington, D.C., Agric. Handbook. 877 pp.
- Cooper, D.J., Andersen, D.C. & Chimner, R.A.** 2003. Multiple pathways for woody plant establishment on floodplains at local to regional scales. *J. Ecol.*, 91(2): 182-196.
- Cooper, D.J., D'Amico, D.R. & Scott, M.L.** 2003. Physiological and morphological response patterns of *Populus deltoides* to alluvial groundwater pumping. *Environ. Manage.*, 31(2) 215-226.
- Cosgrove, D.J.** 1993. How do plant cell walls extend? *Plant Physiol.*, 102(1): 1-6.
- Costa, P., Bahrman, N., Frigerio, J.M., Kremer, A. & Plomion, C.** 1998. Water-deficit-responsive proteins in maritime pine. *Plant Mol. Biol.*, 38(4): 587-596.
- Cotrufo, M.F., De Angelis, P. & Polle, A.** 2005. Leaf litter production and decomposition in a poplar short rotation coppice exposed to free air CO₂ enrichment (POPFACE). *Global Change Biol.*, 11: 971-982.
- Courtois, M., Boudouresque, E. & Guerrier, G.** 1999. Comparative anatomical, morphological, and physiological parameters controlling photosynthesis in two *Populus* x *euramericana* clones during short-term osmotic treatment. *Photosynthetica*, 37(1): 87-96.
- Cox, G., Fischer, D., Hart, S.C. & Whitham, T.G.** 2005. Non-response of native cottonwood trees to water additions during summer drought. *West. N. Am. Naturalist*, 65(2): 175-185.
- Curtis, P.S. & Teeri, J.A.** 1992. Seasonal responses of leaf gas exchange to elevated carbon dioxide in *Populus grandidentata*. *Can. J. Forest Res.*, 22: 1320-1325.
- Curtis, P.S., Zak, D.R., Pregitzer, K.S. & Teeri, J.A.** 1994. Above- and belowground response of *Populus grandidentata* to elevated atmospheric CO₂ and soil N availability. *Plant Soil*, 165: 45-51.

- Curtis, P.S., Vogel, C.S., Pregitzer, K.S., Zak, D.R. & Teeri, J.A.** 1995. Interacting effects of soil fertility and atmospheric CO₂ on leaf area-growth and carbon gain physiology in *Populus xeuramericana* (Dode) Guinier. *New Phytol.*, 129: 253-263.
- Curtis, P.S., Vogel, C.S., Wang, X., Pregitzer, K.S., Zak, D.R., Lussenhop, J., Kubiske, M. & Teeri, J.A.** 2000. Gas exchange, leaf nitrogen, and growth efficiency of *Populus tremuloides* in a CO₂-enriched atmosphere. *Ecol. Appl.*, 10: 3-17.
- Dale, J.E.** 1988. The control of leaf expansion. *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 39: 267-295.
- Dang, Q.L. & Cheng, S.** 2004. Effects of soil temperature on ecophysiological traits in seedlings of four boreal tree species. *Forest Ecol. Manag.*, 194: 379-387.
- Davies, W.J. & Zhang, J.** 1991. Root signal and the regulation of growth and development of plant in drying soil. *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 42: 55-76.
- DeBell, D.S.** 1990. *Populus trichocarpa* Torr. and Gray: black cottonwood. In USDA Forest Service, ed. *Silvics of North America: Volume 2, Hardwoods*, pp. 570-576. Washington, D.C., Agric. Handbook. 877 pp.
- Demmig-Adams, B. & Adams III, W.W.** 1996. Xanthophyll cycle and light stress in nature: uniform response to excess direct sun-light among higher plant species. *Planta*, 198: 460-470.
- Demmig-Adams, B., Adams III, W.W., Barker, D.H., Logan, B.A., Bowling, D.R. & Verhoeven, A.S.** 1996. Using chlorophyll fluorescence to assess the fraction of absorbed light allocated to thermal dissipation of excess excitation. *Physiol. Plantarum*, 98: 253-264.
- Dickmann, D. I. & Stuart, K.W.** 1983. *The Culture of Poplars in Eastern North America*. East Lansing, MI, Michigan, State University. 168 pp.
- Dickson, R.E., Coleman, M.D., Riemenschneider, D.E., Isebrands, J.G., Hogan, G.E. & Karnosky, D.F.** 1998. Growth of five hybrid poplar genotypes exposed to interacting elevated CO₂ and O₃. *Can. J. Forest Res.*, 28: 1706-1716.
- Dickson, R.E., Coleman, M.D., Pechter, P. & Karnosky, D. F.** 2001. Growth and crown architecture of two aspen genotypes exposed to interacting ozone and carbon dioxide. *Environ. Pollut.*, 115: 319-334.
- Dong, X. & Zhang, X.** 2001. Some observations of the adaptations of sandy shrubs to the arid environment in the Mu Us Sandland: leaf water relations and anatomic features. *J. Arid Environ.*, 48: 41-48.
- Dreyer, E., Bogeat-Triboulot, M.B., Le Thiec, D., Guehl, J.M., Brignolas, F., Villar, M., Bastien, C., Martin, F. & Kolher, A.** 2004. Tolérance des peupliers à la sécheresse : peut-on espérer l'améliorer ? *Biofutur*, 247: 54-58.
- Dudek, D.M., McClenahan, J.R. & Mitsch, W.J.** 1998. Tree growth responses of *Populus deltoides* and *Juglans nigra* to streamflow and climate in a bottomland hardwood forest in central Ohio. *Am. Midl. Nat.*, 140(2): 233-244.
- Dunlap, J.M. & Stettler, R.F.** 2001. Variation in leaf epidermal and stomatal traits of *Populus trichocarpa* from two transects across the Washington Cascades, *Can. J. Bot.*, 79 (5): 528-536
- Edjolo, A., Laffray, D. & Guerrier, G.** 2001. The ascorbate-glutathione cycle in the cytosolic and chloroplastic fractions of drought-tolerant and drought-sensitive poplars. *J. Plant Physiol.*, 158(12): 1511-1517.
- Edreva, A.** 2005. Generation and scavenging of reactive oxygen species in chloroplasts: a submolecular approach. *Agr. Ecosyst. Environ.*, 106(2-3): 119-133.
- El-Khatib, R.T., Hamerlynck, E.P., Gallardo, F. & Kirby, E.G.** 2004. Transgenic poplar characterized by ectopic expression of a pine cytosolic glutamine synthetase gene exhibits enhanced tolerance to water stress. *Tree Physiol.*, 24(7): 729-736.
- Engel, V.C., Griffin, K.L., Murthy, R., Patterson, L., Klimas, C. & Potosnak, M.** 2004. Growth CO₂ concentration modifies the transpiration response of *Populus deltoides* to drought and vapor pressure deficit. *Tree Physiol.*, 24(10): 1137-1145.
- Epstein, E.** 1998. How calcium enhances plant salt tolerance. *Science*, 280: 1906-1907.

- Erickson, T., Rytter, L. & Linder, S.** 1992. Nutritional dynamics and requirements of short rotation forests. In C.P. Mitchell, J.B. Ford-Robertson, T. Hinckley & L. Sennerby-Forsse, eds. *Ecophysiology of short rotation forest crops*. London, Elsevier Applied Science. 308 pp.
- Epron, D.** 1997. Effects of drought on photosynthesis and on the thermotolerance of photosystem II in seedlings of cedar (*Cedrus atlantica* and *C. libani*). *J. Exp. Bot.*, 48: 1835-1841.
- FAO.** 1980. *Poplar and willows in wood production and land use*. Rome. 328 pp.
- FAO.** 2002. Afforestation, Forestry Research, Planning and Development in the Three North Region of China, Technical Project Review Document (1991-2002). Rome.
<http://www.fao.org/DOCREP/005/AC613E/AC613E00.HTM>
- Fay, M.F., Lledó, M.D., Kornblum, M.M., & Crespo, M.B.** 1999. From the waters of Babylon? *Biodiversity and Conservation*, 8: 769-778.
- Feng, G., Zhang, F.S., Li, X.L., Tian, C.Y., Tang, C. & Rengel, Z.** 2002. Improved tolerance of maize plants to salt stress by arbuscular mycorrhiza is related to higher accumulation of soluble sugars in roots. *Mycorrhiza*, 12: 185-190.
- Ferris, R., Sabatti, M., Miglietta, F., Mills, R. & Taylor, G.** 2001. Leaf area is stimulated in *Populus* by free-air CO₂ enrichment (POPFACE), through increased cell expansion and production. *Plant Cell Environ.*, 24: 305-316.
- Fowler, D., Cape, J.N., Coyle, M., Flechard, C., Kuulenstierna, J., Hicks, K., Derwent, D., Johnson, C. & Stevenson, D.** 1999. The global exposure of forests to air pollutants. *Water Air Soil Pollut.*, 116: 5-32.
- Francis, R.A., Gurnell, A.M., Petts, G.E. & Edwards, P.J.** 2005. Survival and growth responses of *Populus nigra*, *Salix elaeagnos* and *Alnus incana* cuttings to varying levels of hydric stress. *Forest Ecol. Manag.*, 210(1-3): 291-301.
- Frey, B.R., Lieffers, V.J., Hogg, E.H. & Landhausser, S.M.** 2004. Predicting landscape patterns of aspen dieback: mechanisms and knowledge gaps. *Can. J. Forest Res.*, 34(7): 1379-1390.
- Froux, F., Ducrey, M., Epron, D. & Dreyer, E.** 2004. Seasonal variations and acclimation potential of the thermostability in four Mediterranean conifers. *Ann. Forest Sci.*, 61: 235-241.
- Fung, L.E., Wang, S., Altman, A. & Hüttermann, A.** 1998. Effect of NaCl on growth, photosynthesis, ion and water relations of four poplar genotypes. *Forest Ecol. Manag.*, 107: 135-146.
- Funk, J.L., Mak, J.E. & Lerdau, M.T.** 2004. Stress-induced changes in carbon sources for isoprene production in *Populus deltoides*. *Plant Cell Environ.*, 27(6): 747-755.
- Gafur, A., Schützendübel, A., Langenfeld-Heyser, R., Fritz, E. & Polle, A.** 2004. Compatible and incompatible *Paxillus involutus* isolates for ectomycorrhization in vitro with poplar (*Populus x canescens*) differ in H₂O₂ production. *Plant Biol.*, 6: 91-99
- Gagnon, Z.E., Karnosky, D.F., Dickson, R.E. & Isebrands, J.G.** 1992. Effect of ozone on chlorophyll content in *Populus tremuloides*. *Amer. J. Bot.*, 79(6): 107.
- Garg, A.K., Kim, J.K., Owens, T.G., Ranwala, A.P., Choi, Y.D., Kochian, L.V. & Wu, R.J.** 2002. Trehalose accumulation in rice plants confers high tolerance levels to different abiotic stresses. *Proc. Natl Acad. Sci. USA*, 99: 15898-15903.
- Gebre, G.M. & Kuhns, M.R.** 1991. Seasonal and clonal variations in drought tolerance of *Populus deltoides*. *Can. J. Forest Res.*, 21: 910-916.
- Gebre, G.M., Kuhns, M.R. & Brandle, J.R.** 1994. Organic solute accumulation and dehydration tolerance in three water-stressed *Populus deltoides* clones. *Tree Physiol.*, 14(6): 575-587.
- Gebre, G.M., Brandle, J.R. & Kuhns, M.R.** 1997. Influence of rewatering and time of sampling on solute accumulation of two *Populus deltoides* clones. *Tree Physiol.*, 17(5): 341-346.
- Gebre, G.M., Tschaplinski, T.J., Tuskan, G.A. & Todd, D.E.** 1998. Clonal and seasonal differences in leaf osmotic potential and organic solutes of five hybrid poplar clones grown under field conditions. *Tree Physiol.*, 18(10): 645-652.

- Gellini, R.** 1980. *Botanica forestale*. Padova, Italy, CEDAM. 201 pp.
- Gielen, B. & Ceulemans, R.** 2001. The likely impact of rising atmospheric CO₂ on natural and managed *Populus*: a literature review. *Environ. Pollut.*, 115: 335-358.
- Gielen, B., Calfapietra, C., Sabatti, M. & Ceulemans, R.** 2001. Leaf area dynamics in a closed poplar plantation under free-air carbon dioxide enrichment. *Tree Physiol.*, 21: 1245-1255.
- Gielen, B., Calfapietra, C., Claus, A., Sabatti, M. & Ceulemans, R.** 2002. Crown architecture of *Populus* spp. is differentially modified by free-air CO₂ enrichment (POPFACE). *New Phytol.*, 153: 91-100.
- Gielen, B., Liberloo, M., Bogaert, J., Calfapietra, C., De Angelis, P., Miglietta, F., Scarascia-Mugnozza, G. & Ceulemans, R.** 2003. Three years of free-air CO₂ enrichment (POPFACE) only slightly affect profiles of light and leaf characteristics in closed canopies of *Populus*. *Global Change Biol.*, 9: 1022-1037.
- Gielen, B., Scarascia-Mugnozza, G. & Ceulemans, R.** 2003. Stem respiration of *Populus* species in the third year of free-air CO₂ enrichment. *Physiol. Plantarum*, 117: 500-507.
- Gielen, B., Calfapietra, C., Lukac, M., Wittig, V.E., De Angelis, P., Janssens, I.A., Moscatelli, M.C., Grego, S., Cotrufo, M.F., Godbold, D.L., Hoosbeek, M.R., Long, S.P., Miglietta, F., Polle, A., Bernacchi, C.J., Davey, P.A., Ceulemans, R. & Scarascia-Mugnozza, G.** 2005. Net carbon storage in a poplar plantation (POPFACE) after three years of free-air CO₂ enrichment. *Tree Physiol.*, 25: 1399-1408.
- Glenn, E.P. & Nagler, P.L.** 2005. Comparative ecophysiology of *Tamarix ramosissima* and native trees in western US riparian zones. *J. Arid Environ.*, 61(3): 419-446.
- Glynn, C., Herms D.A., Egawa, M., Hansen, R. & Mattson, W.J.** 2003. Effects of nutrient availability on biomass allocation as well as constitutive and rapid induced herbivore resistance in poplar. *Oikos*, 101: 385-397.
- Glynn, C., Rönnerberg-Wästljung, A.C., Julkunen-Tiitto, R. & Weih, M.** 2004. Willow genotype, but not drought treatment, affects foliar phenolic concentrations and leaf-beetle resistance. *Entomol. Exp. Appl.*, 113: 1-14.
- Gries, D., Zeng, F., Foetzki, A., Arndt, S.K., Bruelheide, H., Thomas, F.M., Zhang, X. & Runge, M.** 2003. Growth and water relations of *Tamarix ramosissima* and *Populus euphratica* on Taklamakan desert dunes in relation to depth to a permanent water table. *Plant Cell Environ.*, 26(5): 725-736.
- Griffin, D.H., Schaedle, M., DeVit, M.J. & Manion, P.D.** 1991a. Clonal variation of *Populus tremuloides* responses to diurnal drought stress. *Tree Physiol.*, 8(3): 297-304.
- Griffin, D.H., Schaedle, M., Manion, P.D. & DeVit, M.** 1991b. Clonal variation in amino acid contents of roots, stems, and leaves of aspen (*Populus tremuloides* Michx.) as influenced by diurnal drought stress. *Tree Physiol.*, 8(4): 337-350.
- Gu, R., Fonseca, S., Puskas, L.G., Hackler, L. Jr., Zvara, A., Dudits, D. & Pais, M.S.** 2004. Transcript identification and profiling during salt stress and recovery of *Populus euphratica*. *Tree Physiol.*, 24: 265-276.
- Guerrier, G., Brignolas, F., Thierry, C., Courtois, M. & Kahlem, G.** 2000. Organic solutes protect drought-tolerant *Populus x euramericana* against reactive oxygen species. *J. Plant Physiol.*, 156(1): 93-99.
- Gueta-Dahan, Y., Yaniv, Z., Zilinskas B.A. & Ben-Hayyim, G.** 1997. Salt and oxidative stress: similar and specific responses and their relation to salt tolerance in Citrus. *Planta*, 203: 460-469.
- Guignard, C., Jouve, L., Bogaert-Triboulot, M.B., Dreyer, E., Hausman, J.F. & Hoffmann, L.** 2005. Analysis of carbohydrates in plants by high-performance anion-exchange chromatography coupled with electrospray mass spectrometry. *J. Chromatogr. A*, 1085: 137-142.
- Hacke, U.G., Stiller, V., Sperry, J.S., Pittermann, J. & McCulloh, K.A.** 2001. Cavitation fatigue. Embolism and refilling cycles can weaken the cavitation resistance of xylem. *Plant Physiol.*, 125(2): 779-786.
- Hale, B.K., Herms, D.A., Hansen, R.C., Clausen, T.P. & Arnold, D.** 2005. Effects of drought stress and nutrient availability on dry matter allocation, phenolic glycosides, and rapid induced resistance of poplar to two Lymantriid defoliators. *J. Chem. Ecol.*, 31(11): 2601-2620.

- Hall, R.L., Allen, S.J., Rosier, P.T.W. & Hopkins, R.** 1998. Transpiration from coppiced poplar and willow measured using sap-flow methods. *Agr. Forest Meteorol.*, 90(4): 275-290.
- Hall, J.L.** 2002. Cellular mechanisms for heavy metal detoxification and tolerance. *J. Exp. Bot.*, 366: 1-11.
- Hamada, A., Hibino, T., Nakamura, T. & Takabe, T.** 2001. Na⁺/H⁺ antiporter from *Synechocystis* species PCC 6803, homologous to SOS1, contains an aspartic residue and long C-terminal tail important for the carrier activity. *Plant Physiol.*, 125: 437-446.
- Harvey, H.P. & van den Driessche, R.** 1997. Nutrition, xylem cavitation and drought resistance in hybrid poplar. *Tree Physiol.*, 17(10): 647-654.
- Harvey, H.P. & van den Driessche, R.** 1999. Nitrogen and potassium effects on xylem cavitation and water-use efficiency in poplars. *Tree Physiol.*, 19(14): 943-950.
- Hasegawa, P.M., Bressan, R.A., Zhu, J.K. & Bohnert, H.J.** 2000. Plant cellular and molecular responses to high salinity. *Annu. Rev. Plant Physiol. Mol. Biol.*, 51: 463-499.
- Havaux, M.** 1993. Rapid photosynthetic adaptation to heat stress triggered in potato leaves by moderately elevated temperatures. *Plant Cell Environ.*, 16: 461-467.
- Heilman, P.E., Stettler, R.F., Hanley, D.P. & Carkner, R.W.** 1995. High yield hybrid poplar plantations in the Pacific Northwest. Washington State University Cooperative Extension Bulletin PNW356. 41 pp.
- Hessl, A.E. & Graumlich, L.J.** 2002. Interactive effects of human activities, herbivory and fire on quaking aspen (*Populus tremuloides*) age structures in western Wyoming. *J. Biogeogr.*, 2002, 29(7): 889-902.
- Hinckley, T.M. & Braatne, J.H.** 1994. Stomata. In R.E. Wilkinson, ed. *Plant-environment interactions*, pp. 323-355. New York, USA, Marcel Dekker. 456 pp.
- Hogg, E.H., Saugier, B., Pontailier, J.Y., Black, T.A., Chen, W., Hurdle, P.A. & Wu, A.** 2000. Responses of trembling aspen and hazelnut to vapor pressure deficit in a boreal deciduous forest. *Tree Physiol.*, 20(11): 725-734.
- Hogg, E.H., Brandt, J.P. & Kochtubajda, B.** 2002. Growth and dieback of Aspen forests in northwestern Alberta, Canada, in relation to climate and insects. *Can. J. Forest Res.*, 2002, 32 (5): 823-832
- Hogg, E.H., Brandt, J.P. & Kochtubajda, B.** 2005. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951-2000. *Can. J. Forest Res.*, 35(3): 610-622.
- Hogg, E.H. & Wein, R.W.** 2005. Impacts of drought on forest growth and regeneration following fire in southwestern Yukon, Canada. *Can. J. Forest Res.*, 35: 2141-2150.
- Holmes, W.E., Zak, D.R., Pregitzer, K.S. & King, J.S.** 2003. Soil nitrogen transformations under *Populus tremuloides*, *Betula papyrifera* and *Acer saccharum* following 3 years exposure to elevated CO₂ and O₃. *Global Change Biol.*, 9: 1743-1750.
- Holton, M.K., Lindroth, R.L. & Nordheim, E.V.** 2003. Foliar quality influences tree-herbivore-parasitoid interactions: effects of elevated CO₂, O₃, and genotype. *Oecologia*, 137: 233-244.
- Hoosbeek, M.R., Lukac, M., van Dam, D., Godbold, D.L., Velthorst, E.J., Biondi, F.A., Peressotti, A., Cotrufo, M.F., de Angelis, P. & Scarascia-Mugnozza, G.** 2004. More new carbon in the mineral soil of a poplar plantation under Free Air Carbon Enrichment (POPFACE): Cause of increased priming effect? *Global Biogeochem. Cy.*, 18: GB1040, doi:10.1029/2003GB002127.
- Horton, J.L. & Clark, J.L.** 2001. Water table decline alters growth and survival of *Salix gooddingii* and *Tamarix chinensis* seedlings. *Forest Ecol. Manag.*, 140(2-3): 239-247.
- Horton, J.L., Kolb, T.E. & Hart, S.C.** 2001a. Physiological response to groundwater depth varies among species and with river flow regulation. *Ecol. Appl.*, 11(4): 1046-1059.
- Horton, J.L., Kolb, T. & Hart, S.C.** 2001b. Leaf gas exchange characteristics differ among Sonoran Desert riparian tree species. *Tree Physiol.*, 21(4): 233-241.

- Horton, J.L., Kolb, T.E. & Hart, S.C.** 2001c. Responses of riparian trees to interannual variation in ground water depth in a semi-arid river basin. *Plant Cell Environ.*, 24(3): 293-304.
- Horton, J.L., Hart, S.C. & Kolb, T.E.** 2003. Physiological condition and water source use of Sonoran Desert riparian trees at the Bill Williams River, Arizona, USA. *Isot. Environ. Health. S.*, 39(1): 69-82.
- Huang, Q., Yuan, Q. & Dong, M.** 1992. Tissue culture of *Populus euphratica*. *Forest Res.*, 5:125-130 (in Chinese).
- Hughes, F.M.R., Barsoum, N., Richards, K.S., Winfield, M. & Hayes, A.** 2000. The response of male and female black poplar (*Populus nigra* L. subspecies *betulifolia* (Pursh) W. Wettst.) cuttings to different water table depths and sediment types: implications for flow management and river corridor biodiversity. *Hydrol. Process.*, 14: 3075-3098.
- Hukin, D., Cochard, H., Dreyer, E., Le Thiec, D. & Bogeat-Triboulot, M.B.** 2005. Cavitation vulnerability in roots and shoots: does *Populus euphratica* Oliv., a poplar from arid areas of Central Asia, differ from other poplar species? *J. Exp. Bot.*, 56(418): 2003-2010.
- Ibrahim, L., Proe, M.F. & Cameron, A.D.** 1997. Main effects of nitrogen supply and drought stress upon whole-plant carbon allocation in poplar. *Can. J. Forest Res.*, 27(9): 1412-1419.
- Ibrahim, L., Proe, M.F. & Cameron, A.D.** 1998. Interactive effects of nitrogen and water availabilities on gas exchange and whole-plant carbon allocation in poplar. *Tree Physiol.*, 18(7): 481-487.
- IPCC** 1995. Climate change 1995. In Houghton, J.T., Meira Filho, L.G., Callader, B.A., Harris, N., Kattenberg, A. & Maskell, K., eds. *The Science of Climate Change*. Cambridge New York, Cambridge University Press.
- IPCC** 2007. Summary for Policymakers. In Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor M. & Miller, H.L., eds. *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, New York, Cambridge University Press.
- Isebrands, J.G., McDonald, E.P., Kruger, E., Hendrey, G., Percy, K., Pregitzer, K., Sober, J. & Karnosky, D.F.** 2001. Growth responses of *Populus tremuloides* clones to interacting elevated carbon dioxide and tropospheric ozone. *Environ. Pollut.*, 115: 359-371.
- Ivanov, A.G., Kitcheva, M.I., Christov, A.M. & Popova, L.P.** 1992. Effects of abscisic acid treatment on the thermostability of the photosynthetic apparatus in barleys chloroplasts. *Plant Physiol.*, 98: 1228-1232.
- Johnson, J.D., Tognetti, R. & Paris, P.** 2002. Water relations and gas exchange in poplar and willow under water stress and elevated atmospheric CO₂. *Physiol. Plantarum*, 115(1): 93-100.
- Jones, H.G.** 1992. Drought and drought tolerance. In H.G. Jones, ed. *Plants and Microclimate: A Quantitative Approach to Environmental Plant Physiology*. Cambridge University Press, Cambridge, UK, pp 212-237.
- Jones, H.G.** 1993. Drought tolerance and water-use efficiency. In J.A.C. Smith & H. Griffiths, eds. *Water Deficit: Plant Responses From Cell To Community*, pp. 193-201. Oxford, UK, Bios Scientific Publishers. 345 pp.
- Jones, H.G.** 2004. What is water use efficiency? In M.A. Bacon & J.A. Roberts, eds. *Water Use Efficiency in Plant Biology*. Blackwell Publishing, CRC Press, Oxford, UK, pp 27-41.
- Kalina, J. & Ceulemans, R.** 1997. Clonal differences in the response of dark and light reactions of photosynthesis to elevated atmospheric CO₂ in poplar. *Photosynthetica*, 33: 51-61.
- Kang, J.M., Kojima, K., Ide, Y. & Sasaki, S.** 1996. Growth response to the stress of low osmotic potential, salinity and high pH in cultured shoot of Chinese poplars. *J. Forest Res.*, 1: 27-29.
- Karakas, B., Ozias-Akins, P., Stushnoff, C., Suefferheld, M. & Rieger, M.** 1997. Salinity and drought tolerance in mannitol-accumulating transgenic tobacco. *Plant Cell Environ.*, 20: 609-616.
- Karnosky, D.F.** 1976. Threshold levels for foliar injury to *Populus tremuloides* Michx. by sulfur dioxide and ozone. *Can. J. Forest Res.*, 6: 166-169.

- Karnosky, D.F.** 1977. Evidence of genetic control of response to sulfur dioxide and ozone in *Populus tremuloides* Michx. *Can. J. Forest Res.*, 7: 437-440.
- Karnosky, D.F., Gagnon, Z.E., Dickson, R.E., Coleman, M.D., Lee, E.H. & Isebrands, J.G.** 1996. Changes in growth, leaf abscission, and biomass associated with seasonal tropospheric ozone exposures of *Populus tremuloides* clones and seedlings. *Can. J. Forest Res.*, 26: 23-37.
- Karnosky, D.F., Podila, G.K., Gagnon, Z., Pechter, P., Akkapeddi, A., Sheng, Y., Riemenschneider, D.E., Coleman, M.D., Dickson, R.E. & Isebrands, J.G.** 1998. Genetic control of responses to interacting tropospheric ozone and CO₂ in *Populus tremuloides*. *Chemosphere*, 36: 807-812.
- Karnosky, D.F., Percy, K.E., Xiang, B., Callan, B., Noormets, A., Mankovska, B., Hopkin, A., Sober, S., Jones, W., Dickson, R.E. & Isebrands, J.G.** 2002. Interacting elevated CO₂ and tropospheric O₃ predisposes aspen (*Populus tremuloides* Michx.) to infection by rust (*Melampsora medusae* f. sp. *tremuloidae*). *Global Change Biol.*, 8: 329-338.
- Karnosky, D.F., Percy, K., Mankovska, B., Prichard, T., Noormets, A., Dickson, R.E., Jepsen, E. & Isebrands, J.G.** 2003a. Ozone affects the fitness of trembling aspen. In D.F. Karnosky, K.E. Percy, A.H. Chappelka, C. Simpson, & J.M. Pikkarainen, eds. *Air Pollution, Global Change and Forests in the New Millennium*, pp. 199-209. Amsterdam, Elsevier Press. 469 pp.
- Karnosky, D.F., Zak, D.R., Pregitzer, K.S., Awmack, C.S., Bockheim, J.G., Dickson, R.E., Hendrey, G.R., Host, G.E., King, J.S., Kopper, B.J., Kruger, E.L., Kubiske, M.E., Lindroth, R.L., Mattson, W.J., McDonald, E.P., Noormets, A., Oksanen, E., Parsons, W.F.J., Percy, K.E., Podila, G.K., Riemenschneider, D.E., Sharma, P., Thakur, R., Sober, A., Sober, J., Jones, W.S., Anttonen, S., Vapaavuori, E., Mankovska, B., Heilman, W. & Isebrands, J.G.** 2003b. Tropospheric O₃ moderates responses of temperate hardwood forests to elevated CO₂: a synthesis of molecular to ecosystem results from the Aspen FACE project. *Funct. Ecol.*, 17: 289-304.
- Karnosky, D.F., Pregitzer, K.S., Zak, D.R., Kubiske, M.E., Hendrey, G.R., Weinstein, D., Nosal, M. & Percy, K.E.** 2005. Scaling ozone responses of forest trees to the ecosystem level in a changing climate. *Plant Cell Environ.*, 28: 965-981.
- Khan, D.** 1974. The occurrence of mycorrhizae in halophytes, hydrophytes and xerophytes of endogone spores in adjacent soils. *J. Gen. Microbiol.*, 81: 7-14.
- Khasa, P.D., Chackravarty, P., Robertson, A., Thomos, B.R. & Dancik, B.P.** 2002. The mycorrhizal status of selected poplar clones introduced into Alberta. *Biomass Bioenerg.*, 22: 99-104.
- King, J.S., Pregitzer, K.S., Zak, D.R., Kubiske, M.E., Ashby, J.A. & Holmes, W.E.** 2001a. Chemistry and decomposition of litter from *Populus tremuloides* Michaux grown at elevated atmospheric CO₂ and varying N availability. *Global Change Biol.*, 7: 65-74.
- King, J.S., Pregitzer, K.S., Zak, D.R., Sober, J., Isebrands, J.G., Dickson, R.E., Hendrey, G.R. & Karnosky, D.F.** 2001b. Fine-root biomass and fluxes of soil carbon in young stands of paper birch and trembling aspen as affected by elevated atmospheric CO₂ and tropospheric O₃. *Oecologia*, 128: 237-250.
- King, J.S., Hanson, P.J., Bernhardt, E., De Angelis, P., Norby, R.J. & Pregitzer, K.S.** 2004. A multiyear synthesis of soil respiration responses to elevated atmospheric CO₂ from four forest FACE experiments. *Global Change Biol.*, 10: 1027-1042.
- King, J.S., Kubiske, M.E., Pregitzer, K.S., Hendrey, G.R., McDonald, E.P., Giardina, C.P., Quinn, V.S. & Karnosky, D.F.** 2005. Tropospheric O₃ compromises net primary production in young stands of trembling aspen, paper birch and sugar maple in response to elevated atmospheric CO₂. *New Phytol.*, 168: 623-636.
- Kishor, P.B.K., Hong, Z., Miao, G.H., Hu, C.A.A. & Verma, D.P.S.** 1995. Overexpression of Δ-pyrroline-5-carboxylate synthetase increases proline production and confers osmotolerance in transgenic plants. *Plant Physiol.*, 108: 1387 – 1394.
- Knight, C.A. & Ackerly, D.D.** 2002. An ecological and evolutionary analysis of photosynthetic thermotolerance using the temperature-dependent increase of fluorescence. *Oecologia*, 130: 505-514.
- Kopper, B. J. & Lindroth, R. L.** 2003. Effects of elevated carbon dioxide and ozone on the phytochemistry of aspen and performance of an herbivore. *Oecologia*, 134: 95-103.

- Kranjcec, J., Mahoney, J.M. & Rood, S.B.** 1998. The responses of three riparian cottonwood species to water table decline. *Forest Ecol. Manag.*, 110: 77-87.
- Kubiske, M.E., Pregitzer, K.S., Mikan, C.J., Zak, D.R., Maziasz, J.L. & Teeri, J.A.** 1997. *Populus tremuloides* photosynthesis and crown architecture in response to elevated CO₂ and soil N availability. *Oecologia*, 110: 328-336.
- Kubiske, M.E., Pregitzer, K.S., Zak, D.R. & Mikan, C.J.** 1998. Growth and C allocation of *Populus tremuloides* genotypes in response to atmospheric CO₂ and soil N availability. *New Phytol.*, 140: 251-260.
- Kull, O., Sober, A., Coleman, M.D., Dickson, R.E., Isebrands, J.G., Gagnon, Z. & Karnosky, D.F.** 1996. Photosynthetic responses of aspen clones to simultaneous exposures of ozone and CO₂. *Can. J. Forest Res.*, 26: 639-648.
- Ladjal, M., Epron, D. & Ducrey, M.** 2000. Effects of drought preconditioning on thermotolerance of photosystem II and susceptibility of photosynthesis to heat stress in cedar seedlings. *Tree Physiol.*, 20: 1235-1241.
- Lambs, L. & Muller, E.** 2002. Sap flow and water transfer in the Garonne River riparian woodland, France: first results on poplar and willow. *Ann. Forest Sci.*, 59(3): 301-315.
- Lamers, J.P.A., Khamzina, A. & Worbes, M.** 2006. The analyses of physiological and morphological attributes of 10 tree species for early determination of their suitability to afforest degraded landscapes in the Aral Sea Basin of Uzbekistan. *Forest Ecol. Manage.*, 221: 249-259.
- Landhäusser, S.M., Silins, U., Lieffers, V.J. & Liu, W.** 2003. Response of *Populus tremuloides*, *Populus balsamifera*, *Betula papyrifera* and *Picea glauca* seedlings to low soil temperature and water-logged soil conditions. *Scand. J. Forest Res.*, 18(5): 391-400.
- Langenfeld-Heyser, R., Gao, J., Ducic, T., Tachd, Ph., Lu, C.F., Fritz, E., Gafur, A. & Polle, A.** 2007. *Paxillus involutus* mycorrhiza attenuate NaCl-stress responses in the salt-sensitive hybrid poplar *Populus x canescens*. *Mycorrhiza*, 17:221-231
- Leffler, A.J., England, L.E. & Naito, J.** 2000. Vulnerability of fremont cottonwood (*Populus fremontii* Wats.) individuals to xylem cavitation. *West. N. Am. Naturalist*, 60(2): 204-210.
- Leffler, A.J. & Evans, A.S.** 2001. Physiological variation among *Populus fremontii* populations: short- and long-term relationships between $\delta^{13}\text{C}$ and water availability. *Tree Physiol.*, 21(15): 1149-1155.
- Li, Y.G., Li, L.H., Jiang, G.M., Niu, S.L., Liu, M.Z., Gao, L.M., Peng, Y. & Jiang, C.D.** 2004a. Traits of chlorophyll fluorescence in 99 plant species from the sparse-elm grassland in Hunshandak Sandland. *Photosynthetica*, 42: 243-249.
- Li, S., Pezeshki, S.R., Goodwin, S. & Shields, P.D. Jr.** 2004b. Physiological responses of black willow (*Salix nigra*) to a range of soil moisture regimes. *Photosynthetica*, 42: 585-590.
- Li, C.Y., Yin, C.Y. & Liu, S.R.** 2004. Different responses of two contrasting *Populus davidiana* populations to exogenous abscisic acid application. *Environ. Exp. Bot.*, 51(3): 237-246.
- Liang, H. & Chang, S.X.** 2004. Response of trembling and hybrid aspens to phosphorus and sulfur fertilization in a Gray Luvisol: growth and nutrient uptake. *Can. J. Forest Res.*, 34: 1391-1399.
- Liberloo, M., Gielen, B., Calfapietra, C., Veys, C., Pigliacelli, R., Scarascia-Mugnozza, G. & Ceulemans, R.** 2004. Growth of a poplar short rotation coppice under elevated atmospheric CO₂ concentrations (EUROFACE) depends on fertilization and species. *Ann. Forest Sci.*, 61: 299-307.
- Liberloo, M., Dillen, S., Calfapietra, C., Marinari, S., Luo, Z.B., De Angelis, P. & Ceulemans, R.** 2005. Elevated CO₂ concentration, fertilization and their interaction: growth stimulation in a short-rotation poplar coppice (EUROFACE). *Tree Physiol.*, 25: 179-189.
- Lite, S.J. & Stromberg, J.C.** 2005. Surface water and ground-water thresholds for maintaining *Populus-Salix* forests, San Pedro, Arizona. *Biol. Conserv.*, 125(2): 153-167.
- Liu, Z. & Dickmann, D.I.** 1992a. Abscisic acid accumulation in leaves of two contrasting hybrid polar clones affected by nitrogen fertilization plus cyclic flooding and soil drying. *Tree Physiol.*, 11(2): 109-122.

- Liu, Z. & Dickmann, D.I.** 1992b. Responses of two hybrid *Populus* clones to flooding, drought, and nitrogen availability. I. Growth and morphology. *Can. J. Bot.*, 70: 2265-2270.
- Liu, Z. & Dickmann, D.I.** 1993. Responses of two hybrid *Populus* clones to flooding, drought, and nitrogen availability. II. Gas exchange and water relations. *Can. J. Bot.*, 71: 927-938.
- Liu, Z. & Dickmann, D.I.** 1996. Effects of water and nitrogen interaction on net photosynthesis, stomatal conductance, and water-use efficiency in two hybrid poplar clones. *Physiol. Plantarum*, 97: 507-512.
- Lockhart, J.A.** 1965. Cell extension. In J. Bonner & J.E. Varner, eds. *Plant biochemistry*, pp. 826-849. New York, USA, Academic Press. 1054 pp.
- Lodge, D.J.** 1989. The influence of soil moisture and flooding on formation of VA, endo- and ectomycorrhizae in *Populus* and *Salix*. *Plant Soil*, 117: 243-253.
- Loewenstein, N.J. & Pallardy, S.G.** 1998. Drought tolerance, xylem sap abscisic acid and stomatal conductance during soil drying: a comparison of canopy trees of three temperate deciduous angiosperms. *Tree Physiol.*, 18(7): 431-439.
- Logan, B.A. & Monson, R.K.** 1999. Thermotolerance of leaf disks from four isoprene-emitting species is not enhanced by exposure to exogenous isoprene. *Plant Physiol.*, 120: 821-825.
- Long, S.P. & Drake, B.G.** 1992. Photosynthetic CO₂ assimilation and rising atmospheric CO₂ concentrations. In Baker, N.R. & Thomas, H. eds. *Topics in Photosynthesis*. Elsevier, Amsterdam, The Netherlands, pp. 69-103.
- Long, S.P., Humphries, S. & Falkowski, P.G.** 1994. Photoinhibition of photosynthesis in nature. *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 45: 633-662.
- Loveys, B.R., Atkinson, L.J., Sherlock, D.J., Roberts, R.L., Fitter, A.H. & Atkin O.K.** 2003. Thermal acclimation of leaf and root respiration: an investigation comparing inherently fast- and slow-growing plant species. *Global Change Biol.*, 9: 895-910.
- Lower, S.S. & Orians, C.M.** 2003. Soil nutrient and water availability interact to influence willow growth and chemistry but not leaf beetle performance. *Entomol. Exp. Appl.*, 107: 69-79.
- Lu, W., Zhang, W. & Bao, J.** 2000. Poplar development and the Three North Shelterbelt project. *Prot. Forest Sci. Technol.*, 5(360): 7-9 (in Chinese).
- Lu, W. & Zhang, W.** 2000. The role and position of poplar development in the creation of protective forests in the Three North Region of China. *Prot. Forest Sci. Technol.*, 2(43): 84-86 (in Chinese).
- Lu W., Song, B., Han, Y., Zhang, W. & Feng, Z.** 2001. Preliminary study on evaluation of poplar clones for introduction to the Korgin sandy lands. *Sci. Silvae Sin.*, 37(1): 72-82 (in Chinese).
- Lu, W., Hu, M., Hu, J. & Yao, X.** 2004. Discussion on severity and control of Asian longhorn beetle of poplar trees in the Three North Shelterbelt Program. *Prot. Forest Sci. Technol.*, 1(58): 39-41 (in Chinese).
- Lukac, M., Calfapietra, C. & Godbold, D.L.** 2003. Production, turnover and mycorrhizal colonization of root systems of three *Populus* species grown under elevated CO₂ (POPFACE). *Global Change Biol.*, 9: 838-848.
- Luo, Y., Canadell, J. & Mooney, H.A.** 1999. Interactive effects of carbon dioxide and environmental stress on plants and ecosystems: a synthesis. In Y. Luo & H.A. Mooney, eds. *Carbon Dioxide and Environmental Stress*, pp. 393-408. San Diego, USA, Academic Press.
- Luo, Z.B., Langenfeld-Heyser, R., Calfapietra, C. & Polle, A.** 2005. Influence of free air CO₂ enrichment (EUROFACE) and nitrogen fertilization on the anatomy of juvenile wood of three poplar species after coppicing. *Trees – Struct. Funct.*, 19: 109-118.
- Lussenhop, J., Treonis, A., Curtis, P.S., Teeri, J.A. & Vogel, C.S.** 1998. Response of soil biota to elevated atmospheric CO₂ in poplar model systems. *Oecologia*, 113: 247-251.
- Lytle, D.A. & Merritt, D.M.** 2004. Hydrologic regimes and riparian forests: A structured population model for cottonwood. *Ecology*, 85(9): 2493-2503

- Ma, H.C., Fung, L., Wang, S.S., Altman, A. & Hüttermann, A.** 1997. Photosynthetic response of *Populus euphratica* to salt stress. *Forest Ecol. Manag.*, 93: 55-61.
- Mahoney, J.M. & Rood, S.B.** 1991. A device for studying the influence of declining water table on poplar growth and survival. *Tree Physiol.*, 8(3): 305-314.
- Marron, N., Delay, D., Petit, J.-M., Dreyer, E., Kahlem, G., Delmotte, F.M. & Brignolas F.** 2002. Physiological traits of two *Populus x euramericana* clones, Luisa Avanzo and Dorskamp, during a water stress and re-watering cycle. *Tree Physiol.*, 22(12): 849-858.
- Marron, N.** 2003. Ecophysiologie des peupliers euraméricains en réponse à la sécheresse. Orléans, France : Ph.D. thesis, University of Orléans. 237 pp.
- Marron, N., Dreyer, E., Boudouresque, E., Delay, D., Petit, J.-M., Delmotte, F.M. & Brignolas, F.** 2003. Impact of successive drought and re-watering cycles on growth and specific leaf area of two *Populus x canadensis* (Moench) clones, 'Dorskamp' and 'Luisa_Avanzo'. *Tree Physiol.*, 23(18): 1225-1235.
- Marron, N., Villar, M., Dreyer, E., Delay, D., Boudouresque, E., Petit, J.-M., Delmotte, F.M., Guehl, J.-M. & Brignolas, F.** 2005. Diversity of leaf traits related to productivity in 31 *Populus deltoides x Populus nigra* clones. *Tree Physiol.*, 25(4): 425-435.
- Marron, N., Maury, S., Rinaldi C. & Brignolas, F.** 2006. Impact of drought and leaf development stage on enzymatic antioxidant system of two *Populus deltoides x nigra* clones. *Ann. Forest Sci.*, 63: 323-327.
- Marschner, H.** 1995. *Mineral nutrition of higher plants*. 2nd edition. London, UK, Academic Press.
- Mazzoleni, S. & Dickmann, D.I.** 1988. Differential physiological and morphological responses of two hybrid *Populus* clones to water stress. *Tree Physiol.*, 4(1): 61-70.
- McDonald, E. P., Kruger, E.L., Riemenschneider, D.E. & Isebrands, J.G.** 2002. Competitive status influences tree-growth responses to elevated CO₂ and O₃ in aggrading aspen stands. *Funct. Ecol.*, 16(6): 792-801.
- Merritt, D.M. & Cooper, D.J.** 2000. Riparian vegetation and channel change in response to river regulation: A comparative study of regulated and unregulated streams in the Green River Basin, USA. *Regul. River.*, 16(6): 543-564.
- Michael, D.A., Isebrands, J.G., Dickmann, D.I. & Nelson, N.D.** 1988. Growth and development during the establishment year of two *Populus* clones with contrasting morphology and phenology. *Tree Physiol.*, 4(2): 139-152.
- Miglietta, F., Peressotti, A., Vaccari, F.P., Zaldei, A., De Angelis, P. & Scarascia-Mugnozza, G.** 2001. Free-air CO₂ enrichment (FACE) of a poplar plantation: the POPFACE fumigation system. *New Phytol.*, 150: 465-476.
- Mikan, C.J., Zak, D.R., Kubiske, M.E. & Pregitzer, K.S.** 2000. Combined effects of atmospheric CO₂ and N availability on the belowground carbon and nitrogen dynamics of aspen mesocosms. *Oecologia*, 124: 432-445.
- Mittler, R.** 2006. Abiotic stress, the field environment and stress combination. *Trends Plant Sci.*, 11: 15-19.
- Monclus, R., Dreyer, E., Delmotte, F.M., Villar, M., Delay, D., Boudouresque, E., Petit, J.-M., Marron, N., Bréchet, C. & Brignolas, F.** 2005. Productivity, leaf traits and carbon isotope discrimination in 29 *Populus deltoides x P. nigra* clones. *New Phytol.*, 167(1): 53-62.
- Monclus, R., Dreyer, E., Villar, M., Delmotte, F.M., Delay, D., Petit, J.M., Barbaroux, C., Le Thiec, D., Bréchet, C. & Brignolas, F.** 2006. Impact of drought on productivity and water-use efficiency in 29 genotypes of *Populus deltoides* Bartr. Ex Marsh. x *P. nigra* L.. *New Phytol.*, 169: 765-777.
- Mondor, E.B., Tremblay, M.N., Awmack, C.S. & Lindroth, R.L.** 2004. Divergent pheromone-mediated insect behaviour under global atmospheric change. *Global Change Biol.*, 10: 1820-1824.
- Monteith, J.L.** 1977. Climate and efficiency of crop production in Britain. *Philos. T. Roy. Soc. B*, 281, 277-294.
- Morabito, D. & Guerrier, G.** 2000. The free oxygen radical scavenging enzymes and redox status in roots and leaves of *Populus x euramericana* in response to osmotic stress, dessication and rehydration. *J. Plant Physiol.*, 157: 74-80.
- Morgan, J.M.** 1984. Osmoregulation and water stress in higher plants. *Annu. Rev. Plant Physiol.*, 35: 299-319.

- Moscatelli, M.C., Lagomarsino, A., De Angelis, P. & Grego, S.** 2005a. Seasonality of soil biological properties in a poplar plantation growing under elevated atmospheric CO₂. *Appl. Soil Ecol.*, 30: 162-173.
- Moscatelli, M.C., Lagomarsino, A., Marinari, S., De Angelis, P. & Grego, S.** 2005b. Soil microbial indices as bioindicators of environmental changes in a poplar plantation. *Ecol. Indic.*, 5: 171-179.
- Munns, R.** 2005. Genes and salt tolerance: bringing them together. *New Phytol.*, 167: 645-663.
- Murthy, R., Barron-Gafford, G., Dougherty, P.M., Engel, V.C., Grieve, K., Handley, L., Klimas, C., Potosnak, M.J., Zarnoch, S.J. & Zhang, J.W.** 2005. Increased leaf area dominates carbon flux response to elevated CO₂ in stands of *Populus deltoides* (Bartr.). *Global Change Biol.*, 11(5): 716-731.
- Musin, T.M. & Zwiazek, J.J.** 2002. Colonization with *Hebeloma crustuliniforme* increases water conductance and limits shoot sodium uptake in white spruce (*Picea glauca*) seedlings. *Plant Soil*, 238: 217-225.
- Nagler, P.L., Glenn, E.P. & Thompson, T.L.** 2003. Comparison of transpiration rates among saltcedar, cottonwood and willow trees by sap flow and canopy temperature methods. *Agr. Forest Meteorol.*, 116(1-2): 73-89.
- Naumburg, E., Mata-Gonzalez, R., Hunter, R.G., McLendon, T. & Martin, D.W.** 2005. Phreatophytic vegetation and groundwater fluctuations: A review of current research and application of ecosystem response modeling with an emphasis on Great Basin vegetation. *Environ. Manage.*, 35(6): 726-740.
- Nautiyal, P.C., Rachaputi, N.R. & Joshi, Y.C.** 2002. Moisture-deficit-induced changes in leaf-water content, leaf carbon exchange rate and biomass production in groundnut cultivars differing in specific leaf area. *Field Crop Res.*, 74: 67-79.
- Neuman, D.S., Wagner, M., Braatne, J.H., Howe, J.** 1996. Stress physiology – abiotic. In R.F. Stettler, H.D.J. Bradshaw, P.E. Heilman and T.M. Hinckley, eds. *Biology of Populus and its implications for management and conservation*, pp. 423-458. Ottawa, ON, NRC Research Press, National Research Council of Canada. 539 p.
- Niinemets, Ü.** 1999. Components of leaf dry mass per area - thickness and density - alter leaf photosynthetic capacity in reverse directions in woody plants. *New Phytol.*, 144(1): 35-57.
- Niinemets, Ü.** 2001. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology*, 82: 453-469.
- Niinemets, Ü., Bilger, W., Kull, O. & Tenhunen, J.D.** 1999a. Responses of foliar photosynthetic electron transport, pigment stoichiometry, and stomatal conductance to interacting environmental factors in a mixed species forest canopy. *Tree Physiol.*, 19(13): 839-852.
- Niinemets, Ü., Sober, A., Kull, O., Hartung, W. & Tenhunen, J.D.** 1999b. Apparent controls on leaf conductance by soil water availability and via light-acclimation of foliage structural and physiological properties in a mixed deciduous, temperate forest. *Int. J. Plant Sci.*, 160(4): 707-721.
- Niinemets, Ü., Kull, O. & Tenhunen, J.D.** 1999. Variability in leaf morphology and chemical composition as a function of canopy light environment in coexisting deciduous trees. *Int. J. Plant Sci.*, 160(5): 837-848.
- Niinemets, Ü. & Kull, O.** 2001. Sensitivity of photosynthetic electron transport to photoinhibition in a temperate deciduous forest canopy: Photosystem II center openness, non-radiative energy dissipation and excess irradiance under field conditions. *Tree Physiol.*, 21(12-13): 899-914.
- Niinemets, Ü., Sonninen, E. & Tobias, M.** 2004. Canopy gradients in leaf intercellular CO₂ mole fractions revisited: interactions between leaf irradiance and water stress need consideration. *Plant Cell Environ.*, 27(5): 569-583.
- Nixon, D.J., Stephens, W., Tyrrel, S.F. & Brierley, E.D.R.** 2001. The potential for short rotation energy forestry on restored landfill caps. *Bioresource Technol.*, 77(3): 237-245.
- Noormets, A., Sôber, A., Pell, E.J., Dickson, R.E., Podila, G.K., Sôber, J., Isebrands, J.G. & Karnosky, D.F.** 2001. Stomatal and non-stomatal limitation to photosynthesis in two trembling aspen (*Populus tremuloides* Michx.) clones exposed to elevated CO₂ and/or O₃. *Plant Cell Environ.*, 24: 327-336.
- Ögren, E. & Sjöström, M.** 1990. Estimation of the effect of photoinhibition on the carbon gain in leaves of a willow canopy. *Planta*, 181: 560-567.

- Oksanen, E., Sober, J. & Karnosky, D.F.** 2001. Impacts of elevated CO₂ and/or O₃ on leaf ultrastructure of aspen (*Populus tremuloides*) and birch (*Betula papyrifera*) in the Aspen FACE experiment. *Environ. Pollut.*, 115: 437-446.
- Oksanen, E., Häikiö, E., Sober, J. & Karnosky, D.F.** 2003. Ozone-induced H₂O₂ accumulation in field-grown aspen and birch is linked to foliar ultrastructure and peroxisomal activity. *New Phytol.*, 161: 791-799.
- Orians, C.M., Bolnick, D.I., Roche, B.M., Fritz, R.S. & Floyd, T.** 1999. Water availability alters the relative performance of *Salix sericea*, *Salix eriocephala*, and their F₁ hybrids. *Can. J. Bot.*, 77(4): 514-522.
- Osmond, C.B.** 1994. What is photoinhibition? Some insights from comparison of shade and sun plants. In N.R. Baker & J.R. Bowyer, eds. *Photoinhibition of Photosynthesis: From Molecular Mechanisms to the Field*, pp. 1-24. Oxford, Environmental Plant Biology, Bios Scientific Publishers.
- Ottow, E.A.** 2005. Molecular and ecophysiological responses of *Populus euphratica* (Oliv.) and *Arabidopsis thaliana* (L.) to salt stress. Thesis, Göttingen, Germany, Cuvillier Verlag. 131 pp.
- Ottow, E.A., Polle, A., Brosche, M., Kangasjärvi, J., Dibrov, P., Zörb, C. & Teichmann, T.** 2005a. Molecular characterisation of PeNhaD: the first member of the NhaD type Na⁺/H⁺ antiporter of plant origin. *Plant Mol. Biol.*, 58: 73-86.
- Ottow, E.A., Brinker, M., Teichmann, T., Fritz, E., Kaiser, W., Brosché, M., Kangasjärvi, J., Jiang, X. & Polle, A.** 2005b. *Populus euphratica* displays apoplastic sodium accumulation, osmotic adjustment by decreases in calcium and soluble carbohydrates, and develops leaf succulence under salt stress. *Plant Physiol.*, 139: 1625-1634.
- Ozolincius, R., Miksys, V., Stakenas, V.** 2005. Growth-independent mortality of Lithuanian forest tree species. *Scand. J. Forest Res.*, 20(6): 153-160.
- Ozolincius, R., Stakenas, R. & Serafinaviciute, B.** 2005. Meteorological factors and air pollution in Lithuanian forests: Possible effects on tree condition. *Environ. Pollut.*, 137(3): 587-595.
- Pallardy, S.G. & Kozlowski, T.T.** 1981. Water relations in *Populus* clones. *Ecology*, 62(1): 159-169.
- Pan, H.Y.** 2005. Review of the Asian longhorned beetle - Research, biology, distribution and management in China. In Forest Health & Biosecurity Working Papers, Working Paper FBS/6E, FAO, Rome, Italy.
- Paolucci, I., Pagnotta, M.A., Sabatti, M., Dominaci, L., Tanzarella, O.A. & Scarascia-Mugnozza, G.** 2003. Analisi genetica e della variabilità in Pioppo bianco (*Populus alba* L.) mediante marcatori RFLP e RAPD. *Atti Società Italiana di Selvicoltura ed Ecologia Forestale*, 3: 29-36.
- Passioura, J.B. & Fry, S.C.** 1992. Turgor and cell expansion: Beyond the Lockhart equation. *Aust. J. Plant Physiol.*, 19: 565-576.
- Passioura, J.B.** 2002. Environmental biology and crop improvement. *Funct. Plant Biol.*, 29: 537-546.
- Pataki, D.E., Oren, R. & Smith, W.K.** 2000. Sap flux of co-occurring species in a western subalpine forest during seasonal soil drought. *Ecology*, 81(9): 2557-2566.
- Pavlović, P., Mitrović, M. & Djurdjević, L.** 2004. An ecophysiological study of plants growing on the fly ash deposits from the "Nikola tesla-A" thermal power station in Serbia. *Environ. Manage.*, 33(5): 654-663.
- Pegoraro, E., Rey, A., Bobich, E.G., Barron-Gafford, G., Grieve, K.A., Malhi, Y. & Murthy, R.** 2004. Effect of elevated CO₂ concentration and vapour pressure deficit on isoprene emission from leaves of *Populus deltoides* during drought. *Funct. Plant Biol.*, 31(12): 1137-1147.
- Pegoraro, E., Rey, A., Barron-Gafford, G., Monson, R., Malhi, Y. & Murthy, R.** 2005a. The interacting effects of elevated atmospheric CO₂ concentration, drought and leaf-to-air vapour pressure deficit on ecosystem isoprene fluxes. *Oecologia*, 2: 1-11.
- Pegoraro, E., Abrell, L., Van Haren, J., Barron-Gafford, G., Grieve, K.A., Malhi, Y., Murthy, R. & Lin, G.H.** 2005b. The effect of elevated atmospheric CO₂ and drought on sources and sinks of isoprene in a temperate and tropical rainforest mesocosm. *Global Change Biol.*, 11(8): 1234-1246.

- Pelah, D., Shoseyov, O. & Altman, A.** 1995. Characterization of BspA, a major boiling-stable, water-stress-responsive protein in aspen (*Populus tremula*). *Tree Physiol.*, 15(10): 673-678.
- Pelah, D., Wang, W., Altman, A., Shoseyov, O. & Bartels, D.** 1997. Differential accumulation of water stress-related proteins, sucrose synthase and soluble sugars in *Populus* species that differ in their water stress response. *Physiol. Plantarum*, 99(1): 153-159.
- Peng, Y.Y. & Dang, Q.L.** 2003. Effects of soil temperature on biomass production and allocation in seedlings of four boreal tree species. *Forest Ecol. Manag.*, 180: 1-9.
- Percy, K.E., Awmack, C.S., Lindroth, R.L., Kubiske, M.E., Kopper, B.J., Isebrands, J.G., Pregitzer, K.S., Hendrey, G.R., Dickson, R.E., Zak, D.R., Oksanen, E., Sober, J., Harrington, R. & Karnosky, D.F.** 2002. Altered performance of forest pests under CO₂- and O₃-enriched atmospheres. *Nature*, 420: 403-407.
- Pezeshki, S.R., Anderson, P.H. & Shields, F.D. Jr.** 1998. Effects of soil moisture regimes on growth and survival of black willow (*Salix nigra*) posts (cuttings). *Wetlands*, 18: 460-470.
- Phan, C.T., Jørgensen, J., Jouve, L., Hausman, J.F., Polle, A. & Teichmann, T.** 2004. Micropropagation of *Populus euphratica* Olivier. *Belg. J. Bot.*, 137: 175-180.
- Piazzai, M., Beritognolo, I., Abruzzese, G., Kuzminsky, E., Sabatti, M., Muleo, R. & Scarascia-Mugnozza, G.** 2003. Strategie di risposta allo stress salino in differenti genotipi di *Populus alba*. IV congresso della Società Italiana di Selvicoltura ed Ecologia Forestale. Rifreddo, Italy, 7-10 October 2003 (Poster).
- Pockman, W.T. & Sperry, J.S.** 2000. Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. *Am. J. Bot.*, 87(9): 1287-1299.
- Polle, A. & Schützendübel, A.** 2003. Heavy metal signalling in plants: linking cellular and organismic responses. In H. Hirt & K. Shinozaki, eds. *Plant responses to abiotic stresses, vol. 4, Topics in current genetics*, pp.167-215. Berlin, Germany, Springer Verlag.
- Polle, A., Altman, A. & Jiang, X.** 2006. Towards genetic engineering for drought tolerance in trees. In M. Fladung & D. Ewald, eds. *Recent Developments in Tree Transgenesis*, Heidelberg, Germany, Springer Verlag. In press.
- Ponzio, K.J., Miller, S.J., Underwood, E., Rowe, S.P., Voltolina, D.J. & Miller, T.D.** 2006. Responses of a willow (*Salix caroliniana* Michx.) community to roller-chopping. *Nat. Area. J.*, 26: 53-60.
- Potts, D.L. & Williams, D.G.** 2004. Response of tree ring holocellulose delta $\delta^{13}\text{C}$ to moisture availability in *Populus fremontii* at perennial and intermittent stream reaches. *West. N. Am. Naturalist*, 64(1): 27-37.
- Powell, G.W. & Bork, E.W.** 2004. Competition and facilitation in mixtures of aspen seedlings, alfalfa, and marsh reedgrass. *Can. J. Forest Res.*, 34 (9): 1858-1869
- Pregitzer, K.S., Zak, D.R., Curtis, P.S., Kubiske, M.E., Teeri, J.A. & Vogel, C.S.** 1995. Atmospheric CO₂, soil nitrogen and turnover of fine roots. *New Phytol.*, 129: 579-585.
- Pregitzer, K.S., Zak, D.R., Maziasz, J., DeForest, J., Curtis, P.S. & Lussenhop, J.** 2000. Interactive effects of atmospheric CO₂ and soil-N availability on fine roots of *Populus tremuloides*. *Ecol. Appl.*, 10: 18-33.
- Rae, A.M., Robinson, K.M., Street, N.R. & Taylor, G.** 2004. Morphological and physiological traits influencing biomass productivity in short-rotation coppice poplar. *Can. J. For. Res.*, 34: 1488-1498.
- Randlett, D.L., Zak, D.R., Pregitzer, K.S. & Curtis, P.S.** 1996. Elevated atmospheric carbon dioxide and leaf litter chemistry: influences on microbial respiration and net nitrogen mineralization. *Soil Sci. Soc. Am. J.*, 60: 1571-1577.
- Ridolfi, M., Fauveau, M.L., Label, P., Garrec, J.P. & Dreyer, E.** 1996. Response to water stress in an ABA-unresponsive hybrid poplar (*Populus koreana* x *trichocarpa* cv. Peace). I. Stomatal function. *New Phytol.*, 134: 445-454.
- Ridolfi, M. & Dreyer, E.** 1997. Responses to water stress in an ABA-unresponsive hybrid poplar (*Populus koreana* x *trichocarpa* cv. Peace). III. Consequences for photosynthetic carbon assimilation. *New Phytol.*, 135: 31-40.

- Rier, S.T., Tuchman, N.C., Wetzel, R.G. & Teeri, J.A.** 2002. Elevated-CO₂-induced changes in the chemistry of quaking aspen (*Populus tremuloides* Michaux) leaf litter: subsequent mass loss and microbial response in a stream ecosystem. *J. N. Am. Benthol. Soc.*, 21: 16-27.
- Rhodenbaugh, E.J. & Pallardy, S.G.** 1993. Water stress, photosynthesis and early growth patterns of cuttings of three *Populus* clones. *Tree Physiol.*, 13(3): 213-226.
- Robison, D.J. & Raffa, K.F.** 1998. Productivity, drought tolerance and pest status of hybrid *Populus*: Tree improvement and silvicultural implications. *Biomass Bioenerg.*, 14(1): 1-20.
- Roden, J., Van Volkenburgh, E. & Hinckley, T.M.** 1990. Cellular basis for limitation of poplar leaf growth by water deficit. *Tree Physiol.*, 1990, 6(2): 211-219
- Rönnerberg-Wästljung, A.C., Glynn, C. & Weih, M.** 2005. QTL analyses of drought tolerance and growth for a *Salix dasyclados* x *Salix viminalis* hybrid in contrasting water regimes. *Theor. Appl. Genet.*, 110: 537-549.
- Rood, S.B., Patino, S., Coombs, K. & Tyree, M.T.** 2000a. Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. *Trees – Struct. Funct.*, 14(5): 248-257.
- Rood, S.B., Zanewich, K., Stefura, C. & Mahoney, J.M.** 2000b. Influence of water table decline on growth allocation and endogenous gibberellins in black cottonwood. *Tree Physiol.*, 20(12): 831-836.
- Rood, S.B., Braatne, J.H. & Hughes, F.M.R.** 2003. Ecophysiology of riparian cottonwoods: stream flow dependency, water relations and restoration. *Tree Physiol.*, 23(16): 1113-1124.
- Rowland, D.L., Biagini, B. & Evans, A.S.** 2000. Variability among five riparian cottonwood (*Populus fremontii* Wats.) populations: An examination of size, density and spatial distribution. *West. N. Am. Naturalist*, 60(4): 384-393.
- Rowland, D.L., Beals, L., Chaudhry, A.A., Evans, A.S. & Grodeska, L.S.** 2001. Physiological, morphological, and environmental variation among geographically isolated cottonwood (*Populus deltoides*) populations in New Mexico. *West. N. Am. Naturalist*, 61(4): 452-462
- Ruiz-Lozano, J.M. & Azcon, R.** 2000. Symbiotic efficiency and infectivity of an autochthonous arbuscular mycorrhizal *Glomus* sp. from saline soils and *Glomus deserticola* under salinity. *Mycorrhiza*, 10: 137-143.
- Sabatti, M., Scarascia-Mugnozza, G.E. & Anselmi, N.** 1998. Conservazione e caratterizzazione del germoplasma di popolazioni naturali italiane di *Populus alba* L. In S.I.S.E.F. Atti I, “La Ricerca Italiana per le Foreste e la Selvicoltura”, pp. 165-170. Legnaro (Padova), 4 - 6 Giugno 1997..
- Sage, R.F.** 1994. Acclimation of photosynthesis to increasing atmospheric CO₂ - The gas-exchange perspective. *Photosynth. Res.*, 39: 351-368.
- Saugier, B.** 1983. Plant growth and its limitations in crop and natural communities. In H.A. Mooney & M. Godron, eds. *Disturbance and ecosystems, components of response, ecological studies* 44, pp. 159-174. Berlin, Springer-Verlag.
- Savouré, A., Thorin, D., Davey, M., Hua, X.J., Mauro, S., Van Montagu, M., Inzé, D. & Verbruggen, N.** 1999. NaCl and CuSO₄ treatments trigger distinct oxidative defence mechanisms in *Nicotiana plumbaginifolia* L. *Plant Cell Environ.*, 22: 387-396.
- Scarascia-Mugnozza, G.E., Ceulemans, R., Heilman, P.E., Isebrands, J.G., Stettler, R.F. & Hinckley, T.M.** 1997. Production physiology and morphology of *Populus* species and their hybrids grown under short rotation. II. Biomass components and harvest index of hybrid and parental species clones. *Can. J. Forest Res.*, 27: 285-294.
- Scarascia-Mugnozza, G., De Angelis, P., Sabatti, M., Calfapietra, C., Ceulemans, R., Peressotti, A. & Miglietta, F.** 2000. A FACE experiment on short rotation, intensive poplar plantation: objective and experimental set up of POPFACE. In M.A. Sutton, J.M. Moreno, W.H. van der Putten & S. Struwe, eds. *Terrestrial Ecosystem Research in Europe: successes, challenges and policy*, pp. 136-140. Luxembourg, Office for Official Publications of the European Communities.
- Schaff, S.D., Pezeshki, S.R. & Shields, F.D. Jr.** 2002. Effects of pre-planting soaking on growth and survival of black willow cuttings. *Restor. Ecol.*, 10: 267-274.

- Schimel, D., Alves, D., Enting, D., Heimann, M. & Joos, F.** 1996. Radiative forcing of climate change. In J.T. Houghton, L.G.M. Filho, B.A. Callander, N. Harris, A. Kattenberg & K. Maskell, eds. *Climate Change 1995: The Science of Climate Change*, pp. 65-132. Cambridge, Cambridge University Press.
- Scholes, R.J., Schulze, E.-D., Pitelka, L.F. & Hall, D.O.** 1999. Biogeochemistry of terrestrial ecosystems. In B. Walker, W. Steffen, J. Canadell & J. Ingram, eds. *The Terrestrial Biosphere and Global Change. Implications for Natural and Managed Ecosystems*, pp. 271-303. Cambridge, UK, Cambridge University Press.
- Schreiner, E.J.** 1959. *Production of poplar timber in Europe and its significance and application in the U.S.* USDA Forest Service Ag. Handbook No.150. 124 pp.
- Schulte, P.J. & Hinckley, T.M.** 1987. Abscisic acid relations and the response of *Populus trichocarpa* stomata to leaf water potential. *Tree Physiol.*, 3(2): 103-113.
- Schumaker, M.A., Bassman, J.H., Robberecht, R. & Rademaker, G.K.** 1997. Growth, leaf anatomy, and physiology of *Populus* clones in response to solar ultraviolet-B radiation. *Tree Physiol.*, 17: 617-626.
- Schützendübel, A. & Polle, A.** 2002. Plant responses to abiotic stresses: heavy metal-induced oxidative stress and protection by mycorrhization. *J. Exp. Bot.*, 53: 1351-1365.
- Schwanz, P. & Polle, A.** 2001. Growth under elevated CO₂ ameliorates defences against photo-oxidative stress in poplar (*Populus alba* × *tremula*). *Environ. Exp. Bot.*, 45(1): 43-53.
- Scott, M.L., Shafroth, P.B. & Auble, G.T.** 1999. Responses of riparian cottonwoods to alluvial water table declines. *Environ. Manage.*, 23(3): 347-358.
- Scott, M.L., Lines, G.C. & Auble, G.T.** 2000. Channel incision and patterns of cottonwood stress and mortality along the Mojave River, California. *J. Arid Environ.*, 44: 399-414.
- Sekawin, M.** 1975. La génétique du *Populus alba* L. *Annales Forestales, Zagreb.* 6: 157-189.
- Shafroth, P.B., Auble, G.T. & Scott, M.L.** 1995. Germination and establishment of the native plains cottonwood (*Populus deltoides* Marshall subsp. *monilifera*) and the exotic Russian-olive (*Elaeagnus angustifolia* L.). *Conserv. Biol.*, 9(5): 1169-1175.
- Shafroth, P.B., Stromberg, J.C. & Patten, D.T.** 2000. Woody riparian vegetation response to different alluvial water table regimes. *West. N. Am. Naturalist*, 60(1): 66-76.
- Shi, H., Ishitani, M., Kim, C. & Zhu, J.K.** 2000. The *Arabidopsis thaliana* salt tolerance gene *SOS1* encodes a putative Na⁺/H⁺ antiporter. *P. Natl Acad. Sci. USA*, 97: 6896-6901.
- Shi, H., Lee, B.H., Wu, S.J. & Zhu, J.K.** 2003. Overexpression of a plasma membrane Na⁺/H⁺ antiporter gene improves salt tolerance in *Arabidopsis thaliana*. *Nat. Biotechnol.*, 21: 81-85
- Sibout, R. & Guerrier, G.** 1998. Solute incompatibility with glutamine synthetase in water-stressed *Populus nigra*. *Environ. Exp. Bot.*, 40(2): 173-178.
- Siemens, J.A. & Zwiazek, J.J.** 2003. Effects of water deficit stress and recovery on the root water relations of trembling aspen (*Populus tremuloides*) seedlings. *Plant Sci.*, 165(1): 113-120.
- Siemens, J.A. & Zwiazek, J.J.** 2004. Changes in root water flow properties of solution culture-grown trembling aspen (*Populus tremuloides*) seedlings under different intensities of water-deficit stress. *Physiol. Plantarum*, 121(1): 44-49.
- Sigurdsson, B.D.** 2001. Elevated (CO₂) and nutrient status modified leaf phenology and growth rhythm of young *Populus trichocarpa* trees in a three-year field study. *Trees – Struct. Funct.*, 15: 403-413.
- Silva, D.M., Hammond, L.C., Bennet, J.M., Hass, J.H. & Linda, S.B.** 1993. Field response of maize; *Zea mays* L. to a VAM fungus and water management. *Agron. J.*, 85: 193-198.
- Singh, M., Jain, M. & Pant, R.C.** 1999. Clonal variability in photosynthetic and growth characteristics of *Populus deltoides* under saline irrigation. *Photosynthetica*, 36: 605-609.

- Sixto, H., Grau, J.M., Alba, N. & Alia, R.** 2005. Response to sodium chloride in different species and clones of genus *Populus* L. *Forestry*, 78: 93-1004.
- Smirnoff, N.** 1993. The role of active oxygen in the response of plants to water deficit and desiccation. *New Phytol.*, 125(1): 27-58.
- Smith, S.E. & Read, D.J.** 1997. *Mycorrhizal Synthesis*. 2nd edition. San Diego, CA, USA, Academic Press.
- Smith, S.D., Devitt, D.A., Sala, A., Cleverly, J.R. & Busch, D.E.** 1998. Water relations of riparian plants from warm desert regions. *Wetlands*, 18(4): 687-696.
- Souch, C.A. & Stephens, W.** 1998. Growth, productivity and water use in three hybrid poplar clones. *Tree Physiol.*, 18(12): 829-835.
- Sparks, J.P. & Black, R.A.** 1999. Regulation of water loss in populations of *Populus trichocarpa*: the role of stomatal control in preventing xylem cavitation. *Tree Physiol.*, 19(7): 453-459.
- Sperry, J.S., Hacke, U.G., Oren, R. & Comstock, J.P.** 2002. Water deficits and hydraulic limits to leaf water supply. *Plant Cell Environ.*, 25(2): 251-263.
- Stettler, R.F., Braatne, J., Ceulemans, R., Clum, P., Dunlap, J., Newman, D., Smit, B., Scarascia-Mugnozza, G. & Van Volkenburgh, E.** 1993. Growth dynamics and canopy structure. In C.P. Mitchell, J.B. Ford-Robinson, T.M. Hinkley & L. Sennerby-Forsse, eds. *Ecophysiology of Short-rotation Forest Crops*, pp. 1-34. London, Elsevier.
- Strohm, M., Eiblmeier, M., Langebartels, C., Jouanin, L., Polle, A., Sandermann, H. & Rennenberg, H.** 1999. Responses of transgenic poplar (*Populus tremula* × *P. alba*) overexpressing glutathione synthetase or glutathione reductase to acute ozone stress: visible injury and leaf gas exchange. *J. Exp. Bot.*, 50(332): 365-374.
- Strohm, M., Eiblmeier, M., Langebartels, C., Jouanin, L., Polle, A., Sandermann, H. & Rennenberg, H.** 2002. Responses of antioxidative systems to acute ozone stress in transgenic poplar (*Populus tremula* × *P. alba*) overexpressing glutathione synthetase or glutathione reductase. *Trees – Struct. Funct.*, 16(4-5): 262-273.
- Sundby, C.A., Melis, P., Mäenpää, P. & Andersson, B.** 1986. Temperature-dependent changes in the antenna size of photosystem II. *Biochim. Biophys. Acta*, 851: 475-483.
- Szabolcs, I.** 1994. Soils and Salinization. In M. Pessarakli, eds, *Handbook of Plant and Crop stress*, pp. 3-11. New York, NY, Marcel Dekker.
- Taji, T., Oshumi, C., Luchi, S., Seki, M., Kasuga, M., Kobayashi, M., Yamaguchi-Shinozaki, K. & Shinozaki, K.** 2002. Important roles of drought- and cold inducible genes for galactinol synthase in stress tolerance in *Arabidopsis thaliana*. *Plant J.*, 29: 417-426.
- Takeuchi, Y., Kubiske, M.E., Isebrands, J.G., Pregitzer, K.S., Hendrey, G. & Karnosky, D.F.** 2001. Photosynthesis, light and nitrogen relationships in a young deciduous forest canopy under open-air CO₂ enrichment. *Plant Cell Environ.*, 24: 1257-1268.
- Tang, Y.H. & Liang, N.S.** 2000. Characterization of the photosynthetic induction response in a *Populus* species with stomata barely responding to light changes. *Tree Physiol.*, 20(14): 969-976.
- Tardieu, F. & Simonneau, T.** 1998. Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. *J. Exp. Bot.*, 49: 419-432.
- Taub, D.R., Seemann, J.R. & Coleman, J.S.** 2000. Growth in elevated CO₂ protects photosynthesis against high-temperature damage. *Plant Cell Environ.*, 23: 649-656.
- Taylor, G., McDonald, J., Stadenberg, I. & Freer-Smith, P.H.** 1993. Nitrate supply and the biophysics of leaf growth of *Salix viminalis*. *J. Exp. Bot.*, 44: 155-164.
- Taylor, G., Ceulemans, R., Ferris, R., Gardner, S.D.L. & Shao, B.Y.** 2001. Increased leaf area expansion of hybrid poplar in elevated CO₂. From controlled environments to open-top chambers and to FACE. *Environ. Pollut.*, 115: 463-472.
- Taylor, G.** 2002. *Populus: Arabidopsis* for forestry. Do we need a model tree? *Ann. Bot.*, 90: 681-689.

- Taylor, G., Tricker, P.J., Zhang, F.Z., Alston, V.J., Miglietta, F. & Kuzminsky, E.** 2003. Spatial and temporal effects of free-air CO₂ enrichment (POPFACE) on leaf growth, cell expansion, and cell production in a closed canopy of poplar. *Plant Physiol.*, 131: 177-185.
- Taylor, G., Street, N.R., Tricker, P.J., Sjödin, A., Graham, L., Skogström, O., Calfapietra, C., Scarascia-Mugnozza, G. & Jansson, S.** 2005. The transcriptome of *Populus* in elevated CO₂. *New Phytol.*, 167: 143-154.
- Tester, M. & Davenport, R.** 2003. Na⁺ tolerance and Na⁺ transport in higher plants. *Ann. Bot.*, 91: 503-527.
- Thomas, F.M., Arndt, S.K., Bruelheide, H., Foetzki, A., Gries, D., Huang, J., Popp, M., Wang, G., Zhang, X.M. & Runge, M.** 2000. Ecological basis for a sustainable management of the indigenous vegetation in a Central-Asian desert: Presentation and first results. *J. Appl. Bot.*, 74(5-6): 212-219.
- Thompson, L.K., Blaylock, R., Sturtevant, J.M. & Brudvig, G.W.** 1989. Molecular basis of heat denaturation of photosystem II. *Biochemistry*, 28: 6686-6695.
- Tjoelker, M.G., Oleskyn, J. & Reich, P.B.** 1999. Acclimation of respiration to temperature and CO₂ in seedlings of boreal tree species in relation to plant size and relative growth rate. *Global Change Biol.*, 49: 679-691.
- Tognetti, R., Longobucco, A., Raschi, A., Miglietta, F. & Fumagalli, I.** 1999. Responses of two *Populus* clones to elevated atmospheric CO₂ concentration in the field. *Ann. Forest Sci.*, 56: 493-500.
- Tognetti, R., Longobucco, A. & Raschi, A.** 1999. Seasonal embolism and xylem vulnerability in deciduous and evergreen Mediterranean trees influenced by proximity to a carbon dioxide spring. *Tree Physiol.*, 19(4-5): 271-277.
- Trabaud, L. & Méthy, M.** 1992. Effets de températures sub-latérales sur l'appareil photosynthétique du chêne vert (*Quercus ilex* L.). *Ann. Forest Sci.*, 49: 637-349.
- Tricker, P.J., Calfapietra, C., Kuzminsky, E., Puleggi, R., Ferris, R., Nathoo, M., Pleasants, L.P., Alston, V., De Angelis, P. & Taylor, G.** 2004. Long-term acclimation of leaf production, development, longevity and quality following 3 years exposure to free-air CO₂ enrichment during canopy closure in *Populus*. *New Phytol.*, 162: 413-426.
- Tricker, P.J., Trewin, H., Kull, O., Clarkson, G.J.J., Eensalu, E., Tallis, M.E., Colella, A., Doncaster, C.P., Sabatti, M. & Taylor, G.** 2005. Stomatal conductance and not stomatal density determines the long-term reduction in leaf transpiration of poplar in elevated CO₂. *Oecologia*, 143: 652-660.
- Tryon, P.R. & Chapin III, F.S.** 1983. Temperature control over root growth and root biomass in taiga forest trees. *Can. J. Forest Res.*, 13: 827-833.
- Tschaplinski, T.J., Tuskan, G.A. & Gunderson, C.A.** 1994. Water-stress tolerance of black and eastern cottonwood clones and four hybrid progeny. I. Growth, water relations and gas exchange. *Can. J. Forest Res.*, 24: 364-371.
- Tschaplinski, T.J., Tuskan, G.A., Gebre, G.M. & Todd, D.E.** 1998. Drought resistance of two hybrid *Populus* clones grown in a large-scale plantation. *Tree Physiol.*, 18(10): 653-658.
- Tupker, K.A., Thomas, B.R. & Macdonald, S.E.** 2003. Propagation of trembling aspen and hybrid poplar for agroforestry: potential benefits of elevated CO₂ in the greenhouse. *Agroforest. Syst.*, 59: 61-71.
- Turnbull, M.H., Tissue, D.T., Murthy, R., Wang, X., Sparrow, A.D. & Griffin, K.L.** 2004. Nocturnal warming increases photosynthesis at elevated CO₂ partial pressure in *Populus deltoides*. *New Phytol.*, 161: 819-826.
- Turtola, S., Rousi, M., Pusenius J., Yamaji, K., Heiska, S., Tirkkonen, V., Meier, B. & Julkunen-Tiitto, R.** 2005. Clone-specific responses in leaf phenolics of willows exposed to enhanced UVB radiation and drought stress. *Global Change Biol.*, 11: 1655-1663.
- Turtola, S., Rousi, M., Pusenius, J., Yamaji, K., Heiska, S., Tirkkonen, V., Meier, B. & Julkunen-Tiitto, R.** 2006. Genotypic variation in drought response of willows grown under ambient and enhanced UV-B radiation. *Environ. Exp. Bot.*, 56: 80-86.
- Tyree, M.T., Alexander, J. & Machado, J.L.** 1992. Loss of conductivity due to water stress in intact juveniles of *Quercus rubra* and *Populus deltoides*. *Tree Physiol.*, 10(4): 411-415.

- Tyree, M.T., Kolb, K.J., Rood, S.B. & Patiño, S.** 1994. Vulnerability to drought-induced cavitation of riparian cottonwoods in Alberta: a possible factor in the decline of the ecosystem? *Tree Physiol.*, 14(5): 455-466.
- Tyystjärvi, E. & Aro, E.M.** 1996. The rate constant of photoinhibition, measured in lincomycin-treated leaves, is directly proportional to light intensity. *P. Natl. Acad. Sci. USA*, 93: 2213-2218.
- UNCCD**, 2004. *Preserving our common ground. UNCCD 10 years on.* United Nations Convention to Combat Desertification. Bonn, Germany.
- van den Driessche, R.** 2000. Phosphorus, copper and zinc supply levels influence growth and nutrition of a young *Populus trichocarpa* (Torr. & Gray) x *P. deltoides* (Bartr.ex Marsh) hybrid. *New Forest.*, 19: 143-157.
- Vandersande, M.W., Glenn, E.P. & Walworth, J.L.** 2001. Tolerance of five riparian plants from the lower Colorado River to salinity drought and inundation. *J. Arid Environ.*, 49(1): 147-159.
- Van Splunder, I., Voeselek, L.A.C.J., Coops, H., De Vries, X.J.A. & Blom, C.W.P.M.** 1996. Morphological responses of seedlings of four species of *Salicaceae* to drought. *Can. J. Bot.*, 74: 1988-1995.
- Volin, J.C. & Reich, P.B.** 1996. Interaction of elevated CO₂ and O₃ on growth, photosynthesis and respiration of three perennial species grown in low and high nitrogen. *Physiol. Plantarum*, 97: 674-684.
- von Fircks, Y. & Sennerby-Forsse, L.** 1998. Seasonal fluctuations of starch in root and stem tissues of coppiced *Salix viminalis* plants grown under two nitrogen regimes. *Tree Physiol.*, 50: 1797-1806.
- Vozzo, J.A. & Hackaylo, E.** 1974. Endo- and ectomycorrhizal association in five poplar species. *B. Torrey Bot. Club*, 101: 182-186.
- Wang, X.Z., Curtis, P.S., Pregitzer, K.S. & Zak, D.R.** 2000a. Genotypic variation in physiological and growth responses of *Populus tremuloides* to elevated atmospheric CO₂ concentration. *Tree Physiol.*, 20(15): 1019-1028.
- Wang, Y., Lu, W., Zhang, W., Bao, J., van Slycken, J. & Sigaud, P.** 2000b. Research advances with *Populus simonii* Carr. *Prot. Forest Sci. Technol.*, 3(44): 66-70 (in Chinese).
- Wang, W.X., Pelah, D., Alergand, T., Shoseyov, O. & Altman, A.** 2002. Characterization of SP1, a stress-responsive, boiling-soluble, homo-oligomeric protein from aspen. *Plant Physiol.*, 130(2): 865-875.
- Wang, W., Vinocur, B. & Altman, A.** 2003. Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. *Planta*, 218: 1-14.
- Watanabe, S., Kojima, K., Ide, Y. & Sasaki, S.** 2000. Effects of saline and osmotic stress on proline and sugar accumulation in *Populus euphratica* in vitro. *Plant Cell Tiss. Org.*, 63(3): 199-206.
- Wei, Q.J.** 1993. *Euphratica poplar*. Beijing, China, Chinese Forestry Press, 3 pp. (in Chinese).
- Weih, M.** 2001. Evidence for increased sensitivity to nutrient and water stress in a fast-growing hybrid willow compared with a natural willow clone. *Tree Physiol.*, 21(15): 1141-1148.
- Weih, M., Rönnerberg-Wästljung, A.C. & Glynn, C.** 2006. Genetic basis of phenotypic correlations among growth traits in hybrid willow (*Salix dasyclados* x *S. viminalis*) grown under two water regimes. *New Phytol.*, 170: 467-477.
- Wikberg, J. & Ögren, E.** 2004. Interrelationships between water use and growth traits in biomass-producing willows. *Trees – Struct. Funct.*, 18: 70-76.
- Will, R.E. & Ceulemans, R.** 1997. Effects of elevated CO₂ concentration on photosynthesis, respiration and carbohydrate status of coppice *Populus* hybrids. *Physiol. Plantarum*, 100: 933-939.
- Williams, W.D.** 1999. Salinization: a major threat to water resources in the arid and semi-arid regions of the world. *Lake Reserv. Manage.*, 4: 85-91.
- Williams, C.A. & Cooper, D.J.** 2005. Mechanisms of riparian cottonwood decline along regulated rivers. *Ecosystems*, 8(4): 382-395.

- Wittig, V.E., Bernacchi, C.J., Zhu, X., Ceulemans, R., De Angelis, P., Gielen, B., Miglietta, F., Morgan, P.B. & Long, S.P.** 2005. Gross primary production is stimulated for three *Populus* species grown under free-air CO₂ enrichment from planting through canopy closure. *Global Change Biol.*, 11: 644-656.
- Woolfolk, W.T.M. & Friend, A.L.** 2003. Growth response of cottonwood roots to varied NH₄:NO₃ ratios in enriched patches. *Tree Physiol.*, 23: 427-432.
- Wustman, B.A., Oksanen, E., Karnosky, D.F., Sober, J., Isebrands, J.G., Hendrey, G.R., Pregitzer, K.S. & Podila, G.K.** 2001. Effects of elevated CO₂ and O₃ on aspen clones varying in O₃ sensitivity: Can CO₂ ameliorate the harmful effects of O₃. *Environ. Pollut.*, 115: 473-481.
- Xiao, C.W., Zhou, G.S., Zhang, X.S., Zhao, J.Z. & Wu, G.** 2005. Responses of dominant desert species *Artemisia ordosica* and *Salix psammophila* to water stress. *Photosynthetica*, 43: 467-471.
- Xu, W.H.** 1988. *Poplar*. Harbin, China, Heilongjiang People's Press. 167 pp. (in Chinese).
- Yang, J., Zhao, H. & Zhang, T.** 2004. Heat and drought tolerance of two willow species, *Salix gordejewii* and *Salix babylonica*: A comparative study. *Israel J. Plant Sci.*, 52: 301-306.
- Yin, C.Y., Duan, B.L., Wang, X. & Li, C.Y.** 2004. Morphological and physiological responses of two contrasting Poplar species to drought stress and exogenous abscisic acid application. *Plant Sci.*, 167(5): 1091-1097.
- Yin, W. & Lu, W.** 2005. Review of tree selection and afforestation for control of Asian longhorned beetle in north China. In Forest Health & Biosecurity Working Papers, Working Paper FBS/7E, FAO, Rome, Italy.
- Yin, C.Y., Wang, X., Duan, B.L., Luo, J.X. & Li, C.Y.** 2005a. Early growth, dry matter allocation and water use efficiency of two sympatric *Populus* species as affected by water stress. *Environ. Exp. Bot.*, 53(3): 315-322.
- Yin, C.Y., Peng, Y.H., Zang, R.G., Zhu, Y.P. & Li, C.Y.** 2005b. Adaptive responses of *Populus kangdingensis* to drought stress. *Physiol. Plantarum*, 123(4): 445-451.
- Yin, C.Y., Berninger, F. & Li, C.Y.** 2006. Photosynthetic responses of *Populus przewalski* subjected to drought. *Photosynthetica*, 44: 62-68.
- Yuceer, C., Kubiske, M.E., Harkess, R.L. & Land, S.B.** 2003. Effects of induction treatments on flowering in *Populus deltoides*. *Tree Physiol.*, 23(7): 489-495.
- Xang, X., Zhang, K., Jia, B. And Ci, L.** 2005. Desertification assessment in China: An overview. *J. Arid Environments*, 63: 517-531.
- Zak, D.R., Pregitzer, K.S., Curtis, P.S., Teeri, J.A., Fogel, R. & Randlett, D.L.** 1993. Elevated atmospheric CO₂ and feedback between carbon and nitrogen cycles. *Plant Soil*, 151: 105-117.
- Zak, D.R., Pregitzer, K.S., Curtis, P.S. & Holmes, W.E.** 2000a. Atmospheric CO₂ and the composition and function of soil microbial communities. *Ecol. Appl.*, 10: 47-59.
- Zak, D.R., Pregitzer, K.S., Curtis, P.S., Vogel, C.S., Holmes, W.E. & Lussenhop, J.** 2000b. Atmospheric CO₂, soil-N availability, and allocation of biomass and nitrogen by *Populus tremuloides*. *Ecol. Appl.*, 10: 34-46.
- Zalesny, R.S.Jr, Hall, R.B., Bauer, E.O. & Riemenschneider, D.E.** 2005. Soil temperature and precipitation affect the rooting ability of dormant hardwood cuttings of *Populus*. *Silvae Genet.*, 54(2): 47-58.
- Zhang, H.P., Morison, J.I.L. & Simmonds, L.P.** 1999. Transpiration and water relations of poplar trees growing close to the water table. *Tree Physiol.*, 19(9): 563-573.
- Zhang, S.-R. & Gao, R.-F.** 2000. Effects of light stress on oxygen evolution and photochemical energy storage of hybrid poplar clones determined by photoacoustic technique. *Acta Bot. Sin.*, 42: 818-823.
- Zhang X., Zang, R. & Li, C.** 2004. Population differences in physiological and morphological adaptations of *Populus davidiana* seedlings in response to progressive drought stress. *Plant Sci.*, 166(3): 791-797.
- Zhang, X., Wu, N. & Li, C.** 2005. Physiological and growth responses of *Populus davidiana* ecotypes to different soil water contents. *J. Arid Environ.*, 60(4): 567-579.

Zhu, Z. & Liu, S. 1988. Desertification processes and their control in northern China. *Chinese Journal of Arid Land Research*, 1(1): 27-36 (in Chinese).

Zhu, Z. & Chen, G.T. 1994. *Sandy desertification in China*. Science Press, Beijing (in Chinese).

Zhu, J.K. 2001. Plant salt tolerance. *Trends Plant Sci.*, 6: 66-71.

Zsuffa, L., Giordano, E., Pryor, L.D. & Stettler, R.F. 1996. Trends in poplar culture: some global and regional perspectives. In R.F. Stettler, H.D.Jr Bradshaw, P.E. Heilman & T.M. Hinckley, eds. *Biology of Populus and its implications for management and conservation*, pp. 515-539. Ottawa, ON, Canada, NRC Research Press, National Research Council of Canada. 539 pp.

Glossary

Abiotic stress: Stress caused in living organisms by nonliving environmental factors, such as drought, extreme temperatures, edaphic conditions, and high winds, that substantially limit plant growth and survival.

Abscisic acid (ABA): Plant growth regulator found in plants that acts as a signalling molecule which helps to control overall growth and physiology. It regulates responses to environmental stresses such as drought, cold, salinity and heat, but also leaf abscission, seed [dormancy](#), [stomatal closure](#), shoot growth.

Acclimation: Phenotypic adaptation to environmental fluctuations; the gradual and reversible adjustment of physiology or morphology as a result of changing environmental conditions.

A-horizon: Top layer of the soil, commonly referred to as topsoil.

Antiporter: A transporter that moves two substrates in opposite directions across the membrane.

Apoplast: Region of the plant body outside of the living cell contents; typically limited to the [cell wall](#) and intercellular spaces.

Asian longhorn beetle (*Anoplophora glabripennis*): A beetle from China that has been found in the United States and is a threat to hardwood trees; lives inside the tree; no natural predators in the United States.

ATPase: An enzyme that hydrolyzes ATP into ADP and phosphate.

Basal fluorescence: [Fluorescence](#) emission in the darkness.

Biosphere 2 Laboratory: A dome-shaped laboratory in Arizona which contains 3.15 acres (13 000 m²) of a closed man-made ecosystem.

C₃ plants: C₃ carbon fixation is a pathway for carbon fixation in photosynthesis. This process converts carbon dioxide and ribulose biphosphate (RuBP, a 6-carbon sugar) into phosphoglycerate (a C₃ carbohydrate). This reaction occurs in all plants as the first step of the Calvin cycle. In C₄ plants, carbon dioxide is drawn out of malate and into this reaction rather than directly from the air.

Candidate gene: A gene that has been implicated in causing or contributing to a particular function.

Carbohydrates: Biochemical name for sugar containing molecules including single sugar (monosaccharides) as [glucose](#) and galactose, but also polysaccharides (complex carbohydrates) as starch (poly-[glucose](#)), cellulose (plant fiber material), chitin (hard shells of insects), and more complex carbohydrate component parts of lipids and proteins.

Carbon sequestration: Uptake and storage of carbon. Trees and plants absorb carbon dioxide, release the oxygen and store the carbon. Fossil fuels were at one time biomass and continue to store the carbon until burned.

Carboxylation: Introduction of a carboxyl group (-COOH) or carbon dioxide into a compound.

Catalase: Enzyme catalysing the destruction of oxygen peroxide.

Cavitation: The rupture of a water column in [xylem](#) when tension overcomes the cohesive nature of water; an [embolism](#) forms.

Cell wall: The rigid outermost cell layer observed in plants and certain algae, bacteria, and fungi but characteristically absent from animal cells.

Chaperone (chaperon protein): Proteins that assist the non-covalent folding/unfolding and the assembly/disassembly of other macromolecular structures, but do not occur in these structures when the latter are performing their normal biological functions.

Chloroplast: The organelle that carries out photosynthesis and starch grain formation. A chlorophyll-containing organelle in plants that is the site of photosynthesis.

Chlorosis: Abnormal yellowing or bleaching of the leaves due to lack of chlorophyll.

Cytosol: The fluid portion of the cytoplasm, outside the organelles.

DNA polymorphism: Difference in DNA sequence among individuals or lines that permits genetic linkage analysis or DNA marker-aided selection.

Dormancy: The resting or inactive phase of plants or seeds. Dormancy of shoots is usually in response to unfavorable environmental conditions.

Ecotype: The smallest taxonomic subdivision of an ecospecies, consisting of populations adapted to a particular set of environmental conditions. The populations are infertile with other ecotypes of the same ecospecies.

Edaphic stress: Stress due to soil conditions.

Electron-transport chain: (also called the electron-transfer chain, ETC, e-train, or simply electron transport), is any series of protein complexes and lipid-soluble messengers that convert the reductive potential of energized electrons into a cross-membrane proton gradient.

Embolism: Blocking of vessels by a foreign material, air when it results from [xylem cavitation](#).

***Escherichia coli*:** Common bacterium that has been studied intensively by geneticists because of its small genome size, normal lack of pathogenicity, and ease of growth in the laboratory.

Excitation energy: The minimum energy required to change a system from its ground state to a particular excited state.

Expressed Sequence Tag (EST): Small part of the active part of a gene, made from cDNA, which can be used to fish the rest of the gene out of the chromosome, by matching base pairs with part of the gene. The EST can be radioactively labelled in order to locate it in a larger segment of DNA.

Extramatrix: Outside the body substance in which tissue cells are embedded.

Floodplain: Low area of land surrounding water bodies, which holds the overflow of water during a flood.

Fluorescence: Property of certain molecules that will emit light at another frequency than the frequency they absorb. This property is especially useful in biology due to indicator dyes whose amount of fluorescence change under certain conditions, typically calcium concentration, acidity (pH) or voltage.

Forest tent caterpillar (*Malacosoma disstria*): Native North American insect and pest of hardwoods. The insect is widely distributed from coast to coast and defoliates trembling aspen (*Populus tremuloides*). During outbreaks it will attack other hardwood species.

Free-air CO₂ enrichment (FACE): Technique that is used to deliver CO₂-enriched air to entire ecosystems located under natural field settings. The delivery system is usually constructed out of pipes and tubes that are arranged in a circle. Because these units do not employ walls or enclosures, FACE experiments are considered to be on the cutting edge of CO₂ enrichment technology.

Fructose: A very sweet sugar occurring in many fruits and honey, and used as a preservative for foodstuffs and as an intravenous nutrient. Also called *fruit sugar*, *levulose*.

Gas exchange: The diffusion of gases from an area of higher concentration to an area of lower concentration, especially the exchange of oxygen and carbon dioxide between an organism and its environment. In plants, gas exchange takes place during photosynthesis and respiration.

Genotype: Assembly of all genetic constituents of an individual, whether expressed or not.
A group of genetically identical organisms.

Glucose: A type of sugar; the main source of energy for living organisms.

Gross primary production (GPP): Total amount of solar or geothermal energy converted into chemical energy over a certain time period by organisms in a given region.

Guard cell: Epidermal cells that open and close to let water, oxygen, and carbon dioxide pass through the [stomata](#).

Gypsy moth (*Lymantria dispar*): European race - Defoliating insect introduced into North America in 1869. This alien species has become a serious pest of hardwoods and its range now includes the Maritimes, Quebec, Ontario, and British Columbia.

Halophyte: Plant capable of living under salty conditions.

Homeostasis: The inherent tendency in an organism toward maintenance of physiological and psychological stability.

Hyphae: Filaments that make up the body of a fungus.

Light harvesting antenna: System of proteins that can trap photons over a wide spectral range and transfer them efficiently to the reaction centre.

Lipid peroxidation (= lipoperoxidation): The process whereby free radicals “steal” electrons from the lipids in [cell membranes](#), resulting in cell damage and increased production of free radicals.

Mannitol: A sugar alcohol widely distributed in plants.

Mesophyll: Plant tissue formed by the inner cells of a leaf, i.e. the tissue layer which lies between the upper and lower epidermis. The mesophyll is comprised of palisade cells and spongy cells.

Microarray: A method for profiling gene and protein expression in cells and tissues.

Micropropagation: *In vitro* clonal propagation of plants from shoot tips or nodal explants, usually with an accelerated proliferation of shoots during subcultures.

Molecular marker: Gene or DNA sequence that can be used to identify an organism, species, or strain or phenotypic trait(s) associated with it.

Mutant: A cell microorganism that manifests new characteristics due to a change in its genetic material.

Mutualistic symbiosis: Symbiosis in which all partners obtain an advantage.

Mycorrhizae: A symbiotic relationship between a fungus and the roots of a plant.

Myo-inositol: A form of inositol that is a component of the vitamin B complex and occurs widely in microorganisms, higher plants, and animals.

Nitrification: The process whereby ammonia in wastewater is oxidized to nitrite (NO_2^-) and then to nitrate (NO_3^-) by bacterial or chemical reactions.

Nitrogen-use efficiency (NUE): The ratio between nitrogen consumption and produced biomass.

Open-top-chamber (OTC): Structures within which plants are grown in CO_2 enrichment experiments, generally consisting of transparent side-walls and open tops, through which either ambient or CO_2 -enriched air is continually pumped.

Osmolyte: A neutral solute that reacts minimally with the contents of a cell while protecting it from drying out, or in a cell's response to salinity changes.

Osmotic adjustment: Physiological process of accumulation of solute molecules inside the cells in response to a decline in external [water potential](#). This adjustment may postpone and contribute to lessen tissue death after desiccation by maintaining cell [turgor](#) pressure.

Osmotic potential: Potential brought about by dissolving a substance, especially in water.

Osmotic stress: Osmotic stress occurs when the concentration of molecules in solution outside of the cell is different than that inside the cell. When this happens, water flows either into or out of the cell by osmosis, thereby altering the intracellular environment. Hyper-osmotic stress causes water to diffuse out of the cell while hypo-osmotic stress causes water to diffuse in the cell, resulting in cell shrinkage, which can lead to DNA and protein damage, cell cycle arrest, and ultimately cell death.

Osmoticum: A molecule, such as [mannitol](#), [glucose](#) or [sucrose](#), employed to maintain the [osmotic potential](#).

Oxy-free radical (OFR): A highly reactive chemical that contains oxygen (O^*) and is produced when molecules are split to give products that have unpaired electrons (a process called oxidation). Free radicals can damage important cellular molecules such as DNA or lipids or other parts of the cell such as [thylakoid](#) membranes.

Paraquat: A standard herbicide used to kill various types of crops, including marijuana. Causes lung damage if smoke from the crop is inhaled.

Peroxidase: Any of a group of enzymes that occur especially in plant cells and catalyze the oxidation of a substance by a peroxide.

Peroxisome: Small membrane-bounded organelle that uses molecular oxygen to oxidize organic molecules. Contains some enzymes that produce hydrogen peroxide and others that degrade hydrogen peroxide (H₂O₂).

Photochemistry: Study of the chemical and physical changes occurring when a molecule or atom absorbs light.

Photoinhibition: State of physiological stress that occurs in all oxygen evolving photosynthetic organisms exposed to light.

Photosystem II (PSII): In the process of photosynthesis, light is absorbed by a photosystem (ancient Greek: *phos* = light and *systema* = assembly) to begin an energy-producing reaction. The photosystems are contained within the [chloroplasts](#) in the leaves of plants. Two types of photosystems exist: photosystem I (P700) and photosystem II (P680). Each photosystem is differentiated by the wavelength of light to which it is most reactive (700 and 680 nm, respectively), and the type of terminal electron acceptor.

Phreatophyte species: A plant that obtains its water supply either directly from the zone of saturation or through the capillary fringe.

Phytohormone: Plant hormone, plant growth regulator.

Plasma membrane (cell membrane): The cell's outer membrane made up of a double layer of phospholipids with embedded proteins.

Proline: One of the 20 amino acids directly coded for in proteins.

Quantum yield: The ratio of the amount of light emitted from a sample to the amount of light absorbed by the sample.

Reactive oxygen species (ROS): Damaging molecules, including oxygen radicals (i.e. superoxide radical) and other highly reactive forms of oxygen (i.e. singlet oxygen) that can harm biomolecules and contribute to disease states. Other oxygen-containing radicals, such as the hydroxyl and peroxy radicals, are often classified as ROS too.

Rhizomorph: A root-like aggregation of [hyphae](#), with a well-defined apical meristem and often differentiated into a rind of small, dark cells surrounding a central core of elongated hyaline cells.

Salinization: The condition in which the salt content of soil accumulates over time to above normal levels; occurs in some parts of the world where water containing high salt concentration evaporates from fields irrigated with standing water.

Sink: Place where carbon is stored, mostly used for forests and underground/deep sea reservoirs of CO₂.

Sink strength: Demand for [carbohydrates](#) by a specific plant organ. Strength or magnitude of the carbon [sink](#).

Site Index: A measure of forest site quality (i.e. the actual or potential productivity of a site) based on the height of dominant trees at a specified age.

Soil texture: The relative proportions of clay, silt and sand (less than 2 mm in diameter) within the soil.

Specific leaf area (SLA): The ratio between leaf area and leaf dry weight.

Stoma (plural: **stomata**): One of the minute pores in the epidermis of a leaf or stem through which gases and water vapor pass. Also called *stomate*.

Stomatal conductance: Measure of how easily water molecules can escape from inside of plant leaves through the tiny pores ([stomata](#)) on the leaf surface to the free air. It is highly positively correlated with transpiration rate.

Sucrose: Sugar composed of two molecules, one [glucose](#) molecule and one [fructose](#) molecule.

Superoxide dismutase (SOD): This enzyme catalyzes the dismutation of superoxide into oxygen and hydrogen peroxide. As such it is an important antioxidant defense in nearly all cells exposed to oxygen.

Syllepsis: Development of a lateral branch without a period of [dormancy](#), i.e. simultaneous with its parent axis. Hence sylleptic branch is a branch developed by syllepsis.

Thylakoid: A small closed membranous sac within a [chloroplast](#); thylakoids are often stacked into piles called grana; the molecules that perform the light reactions of photosynthesis are all embedded within the membranes of the thylakoids

Tolerance to water deficit: The ability of the plant to survive and yield under periods of limited moisture.

Tonoplast: The limiting membrane surrounding a [vacuole](#).

Transgenesis: The introduction of foreign genes into an organism to confer new properties on that organism. This method is generally used to study the function of genes in the context of a living organism.

Turgor: The pressure that can build-up in a space that is enclosed by a membrane that is permeable to a solvent of a solution, such as water, but not to the solutes of the solution.

Vacuole: A cavity in a plant cell, bounded by a membrane; in which various plant products and by-products are stored.

Water potential: Difference between the activity of water molecules in pure distilled water at atmospheric pressure and 30°C (standard conditions), and the activity of water molecules in any other system. The activity of these water molecules may be greater (positive) or less (negative) than the activity of the water molecules under standard conditions.

Water-use efficiency (WUE): A measure of the amount of water used by plants per unit of plant material produced. The term can be applied at the leaf, whole-plant, and ecosystem levels. At the leaf level, it is more precisely referred to as the instantaneous transpiration efficiency, the CO₂ assimilation rate (photosynthesis) divided by the transpiration rate (the moles of CO₂ taken up divided by the moles of water lost through transpiration in a unit of time per unit leaf area).

Whitemarked tussock moth (*Orgyia leucostigma*): Widely distributed moth throughout eastern North America, as far west as Texas and Colorado in the United States. The larvae are known to feed on foliage of a wide variety of trees, both conifers and hardwoods. Hardwood hosts include basswood, maple, sycamore, apple, oak, poplar, willow, and elm.

Xylem: The supporting and water-conducting tissue of vascular plants, consisting primarily of tracheids and vessels.

Table 7.1. Overview of recent available literature on drought response of *Populus* and *Salix* experiments in ISI (Thompson Institute) scientific journals (period 1998 – 2006) and of former keystone studies (1987-1997). Studies are ordered according to their main topic, i.e., A: Leaf structure, physiology and growth; Water relations (B: Stomatal behaviour and C: Hydraulic components); Leaf biochemistry (D: Osmotic adjustment, E: Antioxidant ability, or other biochemical aspects); F: Plant growth – Biomass allocation; G: Water-use efficiency; H: Population biology and management. Within each category, studies are ordered according to the age of the plant material, and then chronologically (year of publication). Abbreviations used are listed at end of table.

	Species	Plant material	Experiment location	Growth conditions	Substrate	Water deficit intensity	Objectives of the study	Traits	Main conclusions	Authors	Year
								examined			
A. Leaf structure, physiology and growth											
	<i>P. trichocarpa</i> <i>P. deltoides</i> <i>P. trichocarpa</i> × <i>P. deltoides</i>	Young cuttings	Seattle, Washington, USA	Gh	Pumice / peat / fine bark	0 < Fraction of transpirable soil water < 1	Assessment of the relationships between soil water, leaf growth, transpiration and plant water balance during a complete drought cycle	LA / g _s / T / SD / LA _{nat} / g _n	Maintenance of growth differ between parents and F ₁ in a pattern characteristic of an overdominant mode of inheritance - F ₁ hybrids were more drought resistant than either parental species	Braatne, Hinckley and Stettler	1992
	<i>P. tremula</i>	4 to 5-week-old plantlets	Rehovot, Israel	IvC		20 and 30% plant water loss	Description of the cloning, sequence analysis, isolation and characterization of the SP1 protein and its stress responsiveness, boiling solubility, and oligomeric structure	EG / [SP1]	SP1 proteins are hydrophilic and remain soluble upon boiling - They represent a new class of protein involved in the plant's response to abiotic stress	Wang <i>et al.</i>	2002
	<i>P. koreana</i> × <i>P. trichocarpa</i>	2-month-old plants	Tsukuba, Japan	Pt	Gravel / vermiculite	-0.74 < Ψ _{leaf} < -1.27 MPa	Examination of the induction responses of leaves of well-watered and dehydrated plants grown at high-light or low-light regime	GE / g _s	Mild water stress may have reduced steady-state assimilation and g _s , but it had little impact on the photosynthetic induction response in high-light leaves	Tang and Liang	2000
	<i>P. × canadensis</i>	2-month-old cuttings	Orléans, France	Gh	Sand / peat moss / clay	-3.5 < Ψ _{wp} < -0.4 MPa	Test of the drought behaviour of two contrasting clones in terms of leaf growth and water relations	LA / LN / LG	The growth advantage of clone 'Luisa_Avanzo' under control conditions appeared to be counterbalanced by its higher susceptibility to water stress	Brignolas <i>et al.</i>	2000
	<i>P. × canadensis</i>	2-month-old cuttings	Orléans, France	Gh	blond peat / brown peat / horse manure / compost	-2.20 < Ψ _{wp} < -0.65 MPa	Assessment of the impact of successive drought and re-watering cycles on plant water relations, growth and SLA parameters	g _s / LG / SLA / DLE	Differences in drought impact between clones is mainly attributable to differences in plasticity after re-watering rather than to clonal differences in drought responses	Marron <i>et al.</i>	2003
	<i>P. trichocarpa</i> × <i>P. koreana</i> <i>P. × canadensis</i>	4 to 5-month-old plants	Nancy, France	GC	Sand / blond peat	-1.4 < Ψ _{wp} < -0.2 MPa	Detection of possible stomata-independent limitations of photosynthesis in response to an imposed short-term drought	GE / Y / J / δ ¹³ C	Reduced CO ₂ influx was a major cause of the limitation of net CO ₂ assimilation during drought in 'Robusta' but not in 'Peace', where drought probably reversibly reduced the apparent carboxylation efficiency of Rubisco	Ridolfi and Dreyer	1997
	<i>P. deltoides</i>	6-month-old coppiced shoots	Oracle, Arizona, USA	SRC	Bare soil / Organic matter	0.10 < Soil volumetric water content < 0.27 m ³ m ⁻³	Study of the effects of elevated CO ₂ and VPD on isoprene emission rates during drought stress	GE / [Isop] / CL	Drought and high VPD dramatically increased the proportion of assimilated carbon lost as isoprene	Pegoraro <i>et al.</i>	2004
	<i>P. deltoides</i>	9-month-old trees	Oracle, Arizona, USA	IFB		-1.50 < Ψ _{leaf} < -0.70 MPa	Understanding of leaf-level responses to drought stress and evaporative demand under elevated CO ₂	LMA / LAI / SA / Ht / Cc / T	The transpiration responses at high VPD in the presence of high SWC and throughout the low SWC treatment suggest some hydraulic limitations to water use occurred	Engel <i>et al.</i>	2004
	<i>P. tremula</i> × <i>P. alba</i>	9 to 12-month-old cuttings		GC	Peat-based commercial growth medium	-3 < Ψ _{soil} < 0 MPa	Comparison of the ecophysiological performance of transgenic poplars overexpressing the pine GS1 gene with non-transgenic plants before, during and after the transient imposition of water stress	GE / F / [Chl] / [Gly] / [GS] / [GOGAT] / [Rub]	The overexpression of pine cytosolic GS1 enhanced sustained photosynthetic electron transport capacity during severe stomatal limitation	El-Khatib <i>et al.</i>	2004
	<i>S. psammophila</i>	1-year-old seedlings	Ordos Sandland Ecological Station, China	Gh	Sand	19.7% of SWC decrease	Investigation of how a 50% decrease in precipitation affects growth and physiology and how physiology and structure is adjusted to the low precipitation conditions	Y / Ht / LN / LA / SLA / RSR / BA / WUE / g _s / GE / T	Instantaneous WUE was not affected by the water deficit – SLA and RSR were decreased in response to drought	Xiao <i>et al.</i>	2005
	<i>P. trichocarpa</i>	1-year-old trees	Puyallup / Wenatchee, Washington, USA	P		200 < Average annual precipitation < 2030 mm	Epidermal and stomatal cell traits examination on late leaves of 40 black cottonwood clones originating from a mesic and a xeric river valley	LA _{nat} / SD / LA	Acclimation to the hotter, drier summer climate was evident, as the clones generally had smaller epidermal cell diameter, and higher cell density and abaxial stomatal density	Dunlap and Stettler	2001
	<i>P. deltoides</i>	1-year-old coppiced plants	Oracle, Arizona, USA	IFM	Silt loam	0.31 < Soil volumetric water content < 0.41 m ³ m ⁻³	Understanding of the relationship between CO ₂ , water availability and isoprene emission	[Isop] / GE	Water limitation can override the inhibitory effect of elevated CO ₂	Pegoraro <i>et al.</i>	2005a
	<i>P. deltoides</i>	1-year-old coppiced plants	Oracle, Arizona, USA	IFM	Silt loam	0.13 < Soil volumetric water content < 0.27 m ³ m ⁻³	Exploration of the relationship between isoprene uptake and atmospheric CO ₂ concentration and drought	[Isop] / K	Drought suppressed the sink capacity, but the full sink capacity of dry soil was recovered within a few hours upon rewetting	Pegoraro <i>et al.</i>	2005b

<i>P. deltoides</i>	2-year-old plants	Stony Brook, New York, USA	Gh		$-1.3 < \Psi_{\text{leaf}} < -0.5 \text{ MPa}$	Examination of the role of alternative carbon sources in isoprene production during conditions of water stress and high leaf temperature	GE / $\delta^{13}\text{C}$ / g_s / [Isop]	Across water- and heat-stress experiments, allocation of photosynthate was negatively correlated to the ratio of isoprene emission to photosynthesis	Funk, Mak and Lerdau	2004
<i>P. grandidentata</i>	Adult trees	Pennsylvania, USA	F		$-0.8 < \Psi_{\text{wp}} < -0.2 \text{ MPa}$	Measurements of gas exchange, water potential, leaf structure, leaf nitrogen and the microenvironment during a seasonal drought	GE / N / LA / SLA / LAnat	Significant amount of plasticity for most gas exchange and leaf structural parameters	Abrams and Mostoller	1995
<i>P. tremula</i>	Adult trees	Järvselja, Estonia	F	Loamy soil	$-4 < \Psi_{\text{soil}} < 0 \text{ MPa}$	Study of the limitations caused by variations in leaf temperature and water availability on photosynthetic electron transport rates	J / N / [Pig]	Chlorophyll fluorescence restricts potential carbon gain under conditions of water limitation less than does stomatal conductance	Niinemets <i>et al.</i>	1999a
<i>P. tremula</i>	Adult trees	Järvselja, Estonia	F	Loamy soil	$-4 < \Psi_{\text{soil}} < 0 \text{ MPa}$	Investigation of morphology, chemical composition and photosynthetic capacity of leaf laminae along a canopy light gradient	LG / $\delta^{13}\text{C}$ / SLA / J / N / C / [Lignin]	Leaf water stress is a major factor altering foliage structure and assimilative capacity	Niinemets, Kull and Tenhunen	1999
<i>P. alba</i>	Adult trees	Nikola Tesla-A, Serbia	PTS	Fluvisol	Leaf Water Saturation Deficit = 16.4	Ecophysiological research on the ash deposits covering 10 plant species	Y / [B, Cu, Mn, Zn, Pb, Cd]	High Boron concentrations in <i>P. alba</i> tissues (superior to $100 \mu\text{g g}^{-1}$) - Low photosynthetic efficiency during the period of summer drought (0.43 to 0.62)	Pavlović, Mitrović and Djurdjević	2004
<i>P. tremula</i>	Adult trees	Järvselja, Estonia	F	Loamy soil	$-4 < \Psi_{\text{soil}} < 0 \text{ MPa}$	Test of the hypothesis that water stress effects significantly modify canopy gradients in intercellular CO_2 mole fractions	[Sugar] / g_s / GE	Stress effects influence C_i more strongly than within-canopy light gradients - Leaves acclimated to different water stress conditions may regulate water use largely independent of foliar photosynthetic potentials	Niinemets, Sonninen and Tobias	2004
<i>P. fremontii</i> <i>S. gooddingii</i>	Adult trees	Wickenburg, Arizona, USA	F		$-1.3 < \Psi_{\text{wp}} < -0.3 \text{ MPa}$	Investigation of the physiological and growth responses of riparian trees to ground water availability	GE / SG / BG / $\delta^{13}\text{C}$	<i>S. gooddingii</i> appears to be more sensitive than <i>P. fremontii</i> to declines in water availability and is more responsive to increased water availability	Horton, Kolb and Hart	2001a
<i>P. fremontii</i> <i>S. gooddingii</i>	Adult trees	Maricopa County, Arizona, USA	D		131 < Annual precipitation < 386 mm	Investigation of leaf gas exchange responses to leaf temperature, VPD, and predawn and midday shoot water potential of two native Sonoran Desert riparian tree species	GE / SLA	High VPD had a smaller effect on leaf gas exchange in willow than in cottonwood - Willow had a less negative Ψ_{wp} threshold for stomatal closure than cottonwood	Horton, Kolb and Hart	2001b
<i>P. fremontii</i> <i>S. gooddingii</i>	Adult trees	Bill Williams river and Hassayampa river / Arizona, USA	AV		$-4.0 < \Psi_{\text{wp}} < -0.5 \text{ MPa}$	Investigation of the physiological response to groundwater availability along gradients of depth to groundwater at two rivers	GE / g_s / S	The study provides estimates of the range of depth to groundwater that can maintain healthy, mature trees	Horton, Kolb and Hart	2001c
<i>P. tremula</i>	Adult trees	Järvselja, Estonia	F	Loamy soil		Investigation of the responses of photosystem II quantum yield to light availability in the short- and in the long term	Y / J / q_p / q_{np} / [Ch]	Foliar water stress scales positively with long-term quantum flux density - Inverse patterns of variation in water and light availabilities in the canopy result in a greater decline in assimilation than is predicted by decreases in stomatal conductance alone	Niinemets and Kull	2001
<i>S. gordejvii</i> <i>S. microstachya</i>	Adult trees	Hunshandak Sandand, inner Mongolia, China	D	Sand	Wetland / Lowland / Dunes	Investigation of the maximum quantum efficiency of 99 native plant species distributed in fixed sand dunes, lowland and wetland	Y	Based on maximum quantum yield measurements, <i>Salix gordejvii</i> is among the species recommended as ideal species for ecological restoration in degraded sand-land ecosystems	Li <i>et al.</i>	2004a
<i>S. gordejvii</i> <i>S. babylonica</i>	Adult trees	Horqin Sandy Land, inner Mongolia, China	N	Sand	$-1.25 < \pi_{\text{O}} < 0 \text{ MPa}$	Examination of the heat and drought tolerance of <i>S. gordejvii</i> compared with <i>S. babylonica</i>	Y / EL / F	<i>S. gordejvii</i> has a higher capacity for drought tolerance and a lower capacity for heat tolerance than <i>S. babylonica</i> , indicating that <i>S. gordejvii</i> inhabits desert environments mainly due to its high drought tolerance	Yang, Zhao and Zhang	2004
<i>P. tremuloides</i>	80-year-old trees	Saskatchewan, Canada	F		$-1.75 < \Psi_{\text{leaf}} < -0.20 \text{ MPa}$	Monitoring of photosynthesis and transpiration over a 42-day midsummer period	GE / g_s	Strong reductions in carbon uptake may be expected at the more extreme values of vapour pressure deficit that occur during periods of regional drought, even if soil water is not locally limiting	Hogg <i>et al.</i>	2000

Water relations

B. Stomatal behaviour

<i>P. canadensis</i> <i>P. 'Tristis' × P. balsamifera</i>	Young cuttings	East Lansing, Michigan, USA	Gh	Sandy-loam soil	$-0.5 < \Psi_{\text{soil matrix}} < 0 \text{ MPa}$	1. Comparison of soil drying and flooding in the ability to induce ABA accumulation - 2. Exploration of the role of leaf-N in modifying stomatal response - 3. Examination of the relationship between stomatal conductance and ABA accumulation	[ABA] / GE	Contrasting physiological strategies between clones for survival under prolonged drying conditions	Liu and Dickmann	1992a
<i>P. angustifolia</i> , <i>P. balsamifera</i> , <i>S. drummondiana</i> , <i>S. exigua</i> , <i>S. lutea</i>	Young saplings and seedlings	Lethbridge, Alberta, Canada	Rz / Gh	Coarse gravel / medium sand / fine gravel	0, 1, 2, 3, 4 or 8 cm day^{-1} water-table decline	Investigation of the relative tolerances of saplings and seedlings of different willow and cottonwood species to different rates of water-table decline	Ht / RL / BA / S	Willow and cottonwood saplings similarly affected by abrupt water-table decline, but willow seedlings slightly more vulnerable than cottonwood seedlings	Amlin and Rood	2002

<i>P. trichocarpa</i>	7-week-old cuttings	Toronto, Canada	Gh		$-2.8 < \Psi_{\text{epidermis}} < -0.4 \text{ MPa}$	Examination of the role of ABA in the mediation of stomatal responses to low water potential	$[\text{ABA}] / g_s / g_{\text{leaf}}$	The unresponsiveness of <i>P. trichocarpa</i> stomata to water potentials is not due to the inability of this species to produce an increase concentration of ABA in response to water stress	Schulte and Hinckley	1987
<i>S. nigra</i>	2 to 6-month-old cuttings	Columbia, Missouri, USA	Gh	Sand / peat moss / silt-loam	$-3 < \Psi_{\text{wp}} < 0 \text{ MPa}$	Comparison of the patterns of water relations, xylem sap ABA concentration and stomatal aperture in drought-sensitive black walnut and black willow, less drought-sensitive sugar maple and drought-tolerant white oak	$g_s / [\text{ABA}]$	In the early stages of drought, increased ABA concentration in the xylem sap of black willow was probably of root origin and provided a signal to the shoot of the water status of the roots	Loewenstein and Pallardy	1998
<i>P. trichocarpa</i> × <i>P. koreana</i> <i>P. × canadensis</i>	4 to 5-month-old plants	Nancy, France	GC	Sand / peat	$-0.8 < \Psi_{\text{wp}} < -0.2 \text{ MPa}$	Report of the leaf-age dependency of the lack of sensitivity of the stomata of clone Peace to exogenous abscisic acid	$g_s / T / [\text{Ca}]_{\text{xylem}}$	Drought control of stomatal conductance in clone Peace is ABA-independent and could involve calcium ions	Ridolfi <i>et al.</i>	1996
<i>P. × canadensis</i>	6-month-old plants	Montpellier, France	Gh		$-1.5 < \Psi_{\text{wp}} < -0.1 \text{ MPa}$	Joint analysis of the stomatal control of different species under naturally fluctuating evaporative demand and soil water status	$g_s / [\text{ABA}]_{\text{xylem}}$	ABA content in xylem was related to soil water status with common relationships for different experimental conditions, but with markedly different responses among species	Tardieu and Simonneau	1998
<i>P. trichocarpa</i> × <i>P. deltoides</i> <i>P. deltoides</i> × <i>P. nigra</i>	1-year-old coppiced plants	Swanbourne, UK	SRC	Clay loam	$0.12 < \text{SWC} < 0.40$	Report of field measurements of transpiration during the summer of 1994 for two contrasting clones, Beaupré and Dorskamp	$\text{Cc} / T / g_s$	Leaf conductance declines slightly with increasing atmospheric vapour pressure deficit in both clones, but only in Beaupré did leaf conductance decrease as soil water deficit increase	Allen, Hall and Rosier	1999
<i>P. × canadensis</i> <i>P. 'Popularis'</i>	1-year-old cuttings	Beijing, China	Gh	Loam soil	$-0.6 < \Psi_{\text{wp}} < -0.1 \text{ MPa}$	Investigation of the effects of water stress and external ABA supply on shoot growth, stomatal conductance and water status of a drought-sensitive and a drought-tolerant genotype	$\text{SG} / \text{GE} / g_s$	Sensitivity of poplar roots to variation in soil water content varies by clone - A rapid short-term accumulation of ABA in shoots in response to water stress may contribute to drought tolerance	Chen <i>et al.</i>	1997
<i>P. trichocarpa</i> × <i>P. deltoides</i> <i>S. dasyclados</i>	3-year-old coppiced plants	Hunstrete, UK	P	Clay loam	$450 < \text{Soil water content} < 600 \text{ mm}$	Measurement of the transpiration rates of SRC grown at a site with a more freely-draining soil	$\text{LA} / \text{LAI} / T / g_s / \text{SCA}$	The high stomatal conductances were maintained even when atmospheric humidity deficits and soil water deficits were large	Hall <i>et al.</i>	1998
<i>P. trichocarpa</i> × <i>P. balsamifera</i>	6-year-old trees	Reading, UK	P	Sandy loam	$-1.3 < \Psi_{\text{leaf}} < -0.2 \text{ MPa}$	Description of the diurnal and seasonal patterns of sap flow of isolated poplar trees growing close to the water table in a mild, temperate climate	SF / g_s	Poplar trees took 15 to 60% of water transpired from groundwater, with the proportion increasing as the soil in the unsaturated zone dried out	Zhang, Morison and Simmonds	1999
<i>P. fremontii</i> <i>P. angustifolia</i> <i>P. fremontii</i> × <i>P. angustifolia</i>	10-year-old cuttings	Ogden, Utah, USA	P		$-0.9 < \Psi_{\text{wp}} < -0.4 \text{ MPa}$	How do some riparian poplars respond to pulse increases in water availability in previously dry zones?	$T / g_h / \text{LA} / \text{SA}$	Trees were insensitive to water addition to the surface soil that were twice the magnitude of whole-tree transpiration rates	Cox <i>et al.</i>	2005
<i>P. tremula</i>	Adult trees	Järvselja, Estonia	F	Loamy soil	$-4 < \Psi_{\text{soil}} < 0 \text{ MPa}$	Study of the control of stomatal conductances imposed by soil water availability and foliage acclimation to long-term integrated irradiance	$\pi_o / g_s / \text{SLA} / \text{LWC} / [\text{Osmo}] / [\text{ABA}]_{\text{xylem}}$	No evidence that ABA increased with advancing water stress - Stomatal sensitivity to ABA is not constant along the canopy light gradient	Niinemets <i>et al.</i>	1999b
<i>P. tremula</i>	Adult trees	Tartu, Estonia	F		$-0.7 < \Psi_{\text{xp}} < 0 \text{ MPa}$	Examination of the correlations between leaf ABA content, stomatal conductance, hydraulic conductance and photosynthetic characteristics	$[\text{ABA}] / \text{GE} / g_s / g_h$	ABA correlated with stomatal conductance, stomatal sensitivity to an increase in leaf water potential, shoot hydraulic conductance and photosynthesis	Aasamaa <i>et al.</i>	2002
<i>P. euphratica</i>	Adult trees	Qira oasis, China	O		$-3.0 < \Psi_{\text{leaf}} < -0.2 \text{ MPa}$	Test of the hypothesis that growth of <i>P. euphratica</i> in a Chinese desert depends on vertical distance to a permanent water table	$\text{SG} / g_s / g_h$	Stomatal conductance of <i>P. euphratica</i> was more strongly reduced in response to decreasing leaf water potential than that of <i>Tamarix ramossisima</i>	Gries <i>et al.</i>	2003
<i>P. tremula</i>	Adult trees	Järvselja, Estonia	F	Podzolic soil	$-2.5 < \Psi_{\text{shoot}} < -0.3 \text{ MPa}$	Determination of the characteristics of drought acclimation - Clarification of the role of ABA in these strategies	$[\text{ABA}] / g_s / g_h / [\text{Osmo}]_{\text{leaf}}$	Leaf ABA content not significantly changed - Xylem ABA content increased during the drought period	Aasamaa <i>et al.</i>	2004
<i>P. grandidentata</i>	Adult trees	Pellston, Michigan, USA	F		$5 < \text{Soil water content} < 25\%$	Detailed understanding of how PAR, VPD and soil water interact to control transpiration	T / SF	Moderate increases in stomatal sensitivity to VPD during dry periods	Bovard <i>et al.</i>	2005
<i>P. deltoides</i>	Adult trees	Green river, Utah / Yampa river, Colorado, USA	AV		$-0.5 < \Psi_{\text{wp}} < -0.15 \text{ MPa}$	Understanding of the impacts of reduced peak flow and soil water recharge on the physiological functioning, morphology and future of Fremont cottonwood forest	$D / g_s / \text{RG}$	Water relations at the leaf and stem level are currently similar for the two rivers due to structural adjustments	Williams and Cooper	2005
C. Hydraulic components										
<i>S. viminalis</i> <i>S. viminalis</i> × <i>S. schwererii</i> <i>S. purpurea</i>	Young cuttings	Umeå, Sweden	GC	Fertilized peat / granular soil conditioner	$20 < \text{Soil water content} < 100\%$	Assessment of the range of variation in hydraulic properties and stomatal regulation - Assessment of the resulting variation in drought responses - Investigation of the degree to which drought resistance can be enhanced	$\text{LA} / \text{LW} / g_h / \text{SG} / \text{PLC} / g_s$	Drought resistance was negatively related to maximum growth yields - Because the level of drought resistance was negatively related to maximum stomatal conductance, growth may have been adversely affected as a result of reduced photosynthesis	Wikberg and Ögren	2004
<i>P. deltoides</i>	2-month-old scions	Burlington, Vermont, USA	Gh	Peat / vermiculite mix	$-2.5 < \Psi < -0.5 \text{ MPa}$	Does cutting stems in air introduce unnatural embolism into the xylem at the cut surface?	PLC	Sharp increase of conductivity loss below water potentials of -1 MPa, with 100% loss by -2 MPa	Tyree, Alexander and Machado	1992

<i>P. euphratica</i> <i>P. alba</i> <i>P. trichocarpa</i> × <i>P. koreana</i>	8 to 16-week-old cuttings	Champenoux, France	Gh	Sand / Peat	4, 5, 7.5 and 10% of soil volumetric water content	Test whether the hydraulic architecture of <i>P. euphratica</i> differs from that of other poplars	PLC / g_s	From the point of view of its hydraulic architecture, <i>P. euphratica</i> displays a very poor level of drought tolerance, confirming its phreatophytic habit	Hukin <i>et al.</i>	2005
<i>P. trichocarpa</i>	3-month-old cuttings	Pullman, Washington, USA	Gh	Peat / moss / vermiculite mix	$-2.9 < \Psi < -0.6$ MPa	Determination of variations in drought-induced xylem cavitation, xylem air-entry points, stomatal behaviour and hydraulic conductivity in four populations	PLC / g_s / g_h	Interpopulation differences in resistance to drought-induced xylem cavitation, stomatal behaviour and hydraulic conductivity within <i>P. trichocarpa</i>	Sparks and Black	1999
<i>P. trichocarpa</i> <i>P. deltoides</i> <i>P. trichocarpa</i> × <i>P. deltoides</i>	3-month-old cuttings	Victoria, British Columbia, Canada	Gh	Sand	$-1.91 < \Psi_{xp} < -0.76$ MPa	Examination of N and K nutrition on drought and cavitation resistance	GE / WUE / PLC / LA / SD	Drought-resistant clones exhibited similar WUE to drought-susceptible clones, but had smaller, more numerous stomata and greater leaf retention under drought conditions	Harvey and van den Driessche	1999
<i>P. tremuloides</i>	3.5-month-old seedlings	Edmonton, Alberta, Canada	GC	Nutrient solutions	- Mild drought: $\Psi_{shoot} = -1.1$ MPa - Severe drought: $\Psi_{shoot} = -2.3$ MPa	Test of the hypothesis that mild drought, contrary to severe one, increase root hydraulic conductivity	g_h / g_s / RVFD	Aquaporin-mediated transport is important in the regulation of root water flow under drought / Root water flow properties are strongly affected by the stress level	Siemens and Zwiazek	2004
<i>P. tremuloides</i>	4-month-old seedlings	Edmonton, Alberta, Canada	GC	Washed coarse sand	- Mild drought: $\Psi_{shoot} = -1.3$ MPa - Severe drought: $\Psi_{shoot} = -2.5$ MPa - Stress recovery: $\Psi_{shoot} = -1.8$ MPa	Test of the hypothesis that mild and severe levels of water deficit would have opposite effects on root water flow properties	g_h / g_s / RVFD / R_{root} / AE	Root water flow properties were modified differently depending on the water deficit stress level	Siemens and Zwiazek	2003
<i>P. trichocarpa</i> × <i>P. koreana</i> <i>P. canadensis</i>	4 to 5-month-old plants	Nancy, France	GC	Sand / peat	10% < SWC	Comparison of the xylem hydraulic properties of two clones known to differ in their ability to close their stomata during a period of drought	PLC	Efficient stomatal regulation is essential for maintaining the integrity of xylem sap flow under drought conditions - Peace shows an exception to the general rule of stomatal control of embolism	Cochard, Ridolfi and Dreyer	1996
<i>P. nigra</i> <i>P. × canadensis</i> <i>S. alba</i>	5 to 10-year-old trees	Garonne river, France	AV		0 < Daily rainfall < 18 mm	Test of the active sapwood depth of poplar - Comparison of the sapflow of the three species - Comparison of the sap flows at two distinct ages	SF / D / Ht / Cc / SG	Under the worst conditions, e.g., the especially long drought in the summer 1998, the values of sap flux density dropped to $40 \text{ dm}^3 \text{ day}^{-1}$, and even to $12 \text{ dm}^3 \text{ day}^{-1}$ for a few days	Lams and Muller	2002
<i>P. tremula</i> <i>S. caprea</i>	8 to 10-year-old saplings	Tartu, Estonia	P	Clay loam	Mild water deficit	Study of the relationship between shoot hydraulic conductance and stomatal sensitivity to changes in leaf water status	GE / g_h / g_s	Hydraulic conductance in the tree shoots changed significantly during only a few days of mild water stress or starvation in darkness	Aasamaa and Söber	2001
<i>P. fremontii</i>	23 to 30-year-old trees	Bernardo, New Mexico, USA	F	Sand / gravel	$-2.25 < \Psi_{xp} < 0$ MPa	1- Construction of vulnerability curves, 2- Calculation of native embolism, 3- Calculation and report of Ψ_{cav}	PLC / PNE	This population is very vulnerable to cavitation - Native state embolism is between 19 and 42%	Leffler, England and Naito	2000
<i>P. deltoides</i> <i>P. balsamifera</i> <i>P. angustifolia</i>	Adult trees 1-year-old stems	Lethbridge, Alberta, Canada	AV		Range of xylem water potentials	Examination of vulnerability to cavitation in three riparian cottonwood	PLC	The three species are the most vulnerable tree species reported so far in North America	Tyree <i>et al.</i>	1994
<i>P. tremula</i>	Adult trees	Rapolano Terme, Italy	AV		$-2 < \Psi_{xp} < 0$ MPa	Investigation of how proximity to natural CO ₂ springs affected the seasonal patterns of xylem embolism	PLC / Cc / k	The interaction with seasonal stress events might strongly influence the competitive ability in a global change scenario	Tognetti, Longobucco and Raschi	1999
<i>P. fremontii</i> <i>S. gooddingii</i>	Adult trees	Cienega Creek Natural Preserve, Arizona, USA	D		$-10 < \Psi_{xp} < 0$ MPa	Evaluation of how the limitation of xylem pressure by cavitation corresponded with plant distribution along a moisture gradient	PLC / T / k	Cavitation vulnerability limits plant distribution by defining maximum drought tolerance across habitats and influencing competitive ability of drought tolerant species in mesic habitats	Pockman and Sperry	2000
<i>P. tremuloides</i>	Adult trees	Medicine Bow Mountains, Wyoming, USA	F	Inceptisol	$-1.7 < \Psi_{wp} < -0.2$ MPa	Evaluation of seasonal patterns of water use at the canopy level and mechanisms underlying contrasting responses to seasonal drought	SF / g_h / T / LAI / D / SCA	<i>P. tremuloides</i> showed less sensitivity to soil moisture than the other species, with relatively high sap flux continuing late into the season and intermediate change in the response of sap flux with decreasing soil moisture	Pataki, Oren and Smith	2000
<i>P. deltoides</i> , <i>P. fremontii</i> , <i>P. trichocarpa</i> , <i>P. balsamifera</i> , <i>P. angustifolia</i>	Adult trees	British Columbia / Missouri / Montana / Nevada / California / Utah, Canada / USA	AV		$-1.7 < \Psi_{leaf} < -0.8$ MPa	Investigation of xylem cavitation and precocious senescence and branch die-back in cottonwood	PLC / Cc	'Branch sacrifice' describes the cavitation-associated senescence and branch die-back that may provide a drought adaptation for the prairie and Fremont cottonwoods	Rood <i>et al.</i>	2000a

	<i>S. psammophila</i>	Adult trees	Mu Us Sandland, inner Mongolia, China	D		Water spender vs. water saver species	Use of the leaf water potential components to elucidate the major types of functional adaptations of the dominant shrubs to drought stress	BEM / π_o / LANat	Drought adaptations can to some extent be interpreted within the framework of the water-spending/water-saving paradigm	Dong and Zhang	2001	
	<i>P. angustifolia</i> <i>P. tremuloides</i>	Adult trees	Salt Lake City, Utah, USA	AV		$-4.0 < \Psi_{xp} < 0$ MPa	Determination of the effect of a cavitation and refilling cycle on cavitation resistance	PLC	Considerable reduction in cavitation resistance was observed after cavitation-refilling cycle for <i>P. angustifolia</i> and <i>P. tremuloides</i>	Hacke <i>et al.</i>	2001	
Leaf biochemistry												
D. Osmotic adjustment												
	<i>P. deltoides</i>	Young cuttings	Lincoln, Nebraska, USA	P		Vermiculite / peat / silty clay loam	$-0.7 < \Psi_{wp} < 0$ MPa	Comparison of seasonal and clonal variations in leaf water potential, leaf osmotic potential and dry weight fraction of three <i>P. deltoides</i> clones	π_o / RWC / II	All clones had drought hardened indicating that they have some degree of drought tolerance	Gebre and Kuhns	1991
	<i>P. deltoides</i> <i>P. trichocarpa</i> <i>P. trichocarpa</i> × <i>P. deltoides</i>	Young cuttings	Oak Ridge, Tennessee, USA	Gh		Promix BX	$-2.0 < \Psi_s < -0.03$ MPa	Characterization of the limits of water-stress tolerance	RGR / SV / BA / π_o / RWC / GE / g_s / T	Three of the four hybrids displayed some degree of osmotic adjustment at saturation after bud set - Screening clones of <i>Populus</i> should take into account the segregating tendency of hybrids to allocate carbon to lateral meristems under stress	Tschaplinski, Tuskan and Gunderson	1994
	<i>P. euphratica</i> <i>P. alba</i> × <i>P. × tomentosa</i>	<i>In vitro</i> shoot	Tokyo, Japan	MpS		MS medium (NAA / agar)	0, 200, 300, 400 mM of Mannitol	Evaluation of osmotic and salt tolerance and the effects of salt and mannitol in the medium on proline and sugar accumulation	Biomass / [Pro] / [Sugar]	Accumulated proline and sugars promote osmotic and salt stress	Watanabe <i>et al.</i>	2000
	<i>P. simonii</i>	1-month-old cuttings	Maoxian Field Ecological Station, China	Gh			100, 50, 25% of field capacity	Understanding of the mechanisms responsible for adaptation to drought and growth maintain	BA / GE / OA / LAP / [ABA]	Large set of parallel changes in morphological, physiological and biochemical responses, possibly enhancing capability to survive and to maintain growth	Yin <i>et al.</i>	2005b
	<i>P. tremuloides</i>	3-month-old cuttings	Syracuse, New York, USA	Gh		Hydroponic conditions	$-3.0 < \Psi_{leaf} < -1.0$ MPa	Description of an hydroponic droughting technique and demonstration that it causes responses in leaf water, solute and turgor potentials and growth	SG / [AA] / P_t	The growth inhibitions observed during drought could not have been the consequence of loss of turgor	Griffin <i>et al.</i>	1991a
	<i>P. tremuloides</i>	3-month-old cuttings	Syracuse, New York, USA	Gh		Hydroponic conditions	$-3.0 < \Psi_{leaf} < -1.0$ MPa	Determination of the effects of diurnal drought stress on the free amino acid contents of leaves, stems and roots	[AA]	Drought stress caused both organ-specific and clone-specific changes in amino acid concentrations - The method of inducing drought stress affects the responses observed	Griffin <i>et al.</i>	1991b
	<i>P. deltoides</i>	3-month-old cuttings	Oak Ridge, Tennessee, USA	Gh		Vermiculite / peat / perlite / soil	$-1.02 < \Psi_{leaf} < -0.03$ MPa	Comparison of organic solute accumulation in two poplar clones before and after rewatering	π_o / [Sugar]	There was a significant accumulation of glucose and fructose at predawn and either no accumulation or a significant reduction of these solutes at midday before and after rewatering	Gebre, Brandle and Kuhns	1997
	<i>P. deltoides</i>	4-month-old cuttings	Oak Ridge, Tennessee, USA	Gh		Vermiculite / peat / perlite / soil	$-1.74 < \Psi_{leaf} < -0.08$ MPa	Identification of solutes that contribute to osmotic adjustment in three <i>P. deltoides</i> clones	π_o / [Sugar]	The solutes that contribute at least -0.05 MPa each to leaf osmotic potential in any clone were sucrose, malic acid, glucose, fructose, myo-inositol and salicin	Gebre, Kuhns and Brandle	1994
	<i>P. euphratica</i>	1-year-old seedlings	Champenoux, France	Gh		Peat / sand	5% soil humidity during 10 days	Technical improvements allowing the MS analysis of carbohydrates and presentation of results obtained on drought-stressed poplar	[Salicin], [Gluc], [Suc], [Fruc], [Galac]	Different responses to water deficit and re-hydration were obtained for several carbohydrates, suggesting different roles in osmoprotection processes	Guignard <i>et al.</i>	2005
	<i>P. trichocarpa</i> × <i>P. deltoides</i> <i>P. deltoides</i> × <i>P. nigra</i>	2 to 5-year-old trees	Wallula, Washington / Boardman, Oregon, USA	P		Active dune land / Mixed sand	$-1.20 < \Psi_{wp} < -0.65$ MPa	Characterization of the leaf osmotic potential at full turgor and the major solutes that contribute to osmotic potential	π_o / [Sugar] / [Ion] / [AA]	The extent of osmotic adjustment was small - Other drought resistance mechanisms contributed to the clonal differences in field performance	Gebre <i>et al.</i>	1998
	<i>P. nigra</i>	Adult trees	Orléans, France	N			$0 < [\text{Mannitol}] < 0.5$ M	Comparison of the ability of several solutes accumulated by stressed poplars to affect the GS activity	GS	Proline and putrescine were the most effective in alleviating the inhibitory effect of mannitol	Sibout and Guerrier	1998
	<i>P. euphratica</i>	Adult trees	Tarim River Basin, China	AV		Sandy loam	2.47 < Groundwater level < 10.16 m	Study of the relationship between the proline accumulation in the bodies of <i>P. euphratica</i> and the change of groundwater level	[Pro]	The constraining groundwater depth for the normal growth and the critical one for the survival of <i>P. euphratica</i> are below 4.5 m and 10 m, respectively at the lower reaches of the Tarim River	Chen <i>et al.</i>	2003a
	<i>P. euphratica</i>	Adult trees	Qira oasis, China	O			Seasonal groundwater variation in desert	Investigation of variation of leaf solutes in order to elucidate their adaptation to saline groundwater	[Cation] / [Anion] / [Acid] / [Sugar]	All plants were well adapted to the moderate salinity of the NaCl dominated groundwater and no signs of salt related drought stress were observed	Arndt <i>et al.</i>	2004
E. Antioxidant ability												
	<i>P. × canadensis</i>	1-month-old cuttings	Orléans, France	Gh			$-0.336 < \text{Osmotic potential} < 0$ MPa	Assessment of the relationships between drought response and anatomical/physiological properties	GE / [Rub] / [Chl] / [Car] / [Asc] / [Glu] / AP / GR	The drought-tolerant poplar exhibited higher net photosynthetic rate and contents of antioxidants and antioxidative enzymes following an exposure to 150 mM mannitol than the drought-sensitive one	Courtois, Boudouresque and Guerrier	1999

<i>P. x canadensis</i>	1-month-old cuttings	Orléans, France	Gh		Leaf and root fresh weight loss of 85% of the original fresh weight	Study of the redox status and the activities of antioxidant enzymes in leaves and roots exposed to wilting or to osmotic stress	LAP	Enhanced capability to dismutase superoxide and of ascorbate peroxidase activity in wilted leaves	Morabito and Guerrier	2000
<i>P. x canadensis</i>	1-month-old cuttings	Orléans, France	lVC	Murashige and Skoog (1962) solution	150 mmol L ⁻¹ mannitol (-0.336 MPa)	Appreciation of the mechanisms by which drought-induced oxidative stress is tolerated in poplar	<u>MDH</u> / <u>SOD</u> / <u>Cat</u> / <u>AP</u> / <u>GR</u>	Exposure to osmotic stress resulted in a decrease in Cat and GR activities, in an enhancement of SOD and AP activities, but did not affect the contents of spermine, spermidine and ascorbate	Guerrier <i>et al.</i>	2000
<i>P. x canadensis</i>	1-month-old cuttings	Orléans, France	Gh	Hydroponic conditions	Addition of mannitol	Determination whether a drought tolerant <i>P. x canadensis</i> clone exhibits a more efficient reactive oxygen species scavenging system than a drought-sensitive one	<u>Pod</u> / <u>GR</u>	The efficiency of the ascorbate - glutathione cycle operating in cytosol and chloroplast seemed to be sufficient for avoiding the deleterious effects of ROS on the plastidial GR activity of the tolerant clone	Edjolo, Laffray and Guerrier	2001
<i>P. x canadensis</i>	2-month-old cuttings	Orléans, France	Gh	Sand / clay / brown peat / composted cluster pine bark / wood fiber / blond peat / moss	-1.6 < Ψ_{wp} < -0.8 MPa	Association of variations in leaf polyphenols and antioxidant activity with variations in water relations parameters	LG / SLA / g_s / N / [Chl] / [Sugar] / [Flav] / LAP / [Phe]	Earlier stomatal closure for the drought sensitive clone and better Ψ_{wp} maintain - Antioxidant activity decrease in response to drought for the drought-sensitive clone only	Marron <i>et al.</i>	2002
<i>P. x canadensis</i>	2-month-old cuttings	Orléans, France	Gh	blond peat / brown peat / horse manure / compost	-2.52 < Ψ_{wp} < -0.59 MPa	Investigation of the impact of mild and severe constraints on leaf protein content and activities of SOD, catalase and peroxidase	[Prot] / <u>SOD</u> / <u>Cat</u> / <u>Pod</u>	Activities of the three enzymes were stimulated in response to drought depending on constraint intensity, leaf age and clone	Marron <i>et al.</i>	2006
<i>S. viminalis</i> x <i>S. dasyclados</i>	3-month-old cuttings	Uppsala, Sweden	Gh	Clay / peat	55% irrigation of the well-watered plants	Examination of the effect of willow genotype and irrigation regime on growth parameters, foliar N, phenolic content and on preference and performance of the blue leaf beetle	Biomass / N / SLA / [Phe] / FP	There was significant genotypic variation in each of the phenolic substances – There was no effect of irrigation treatment on larval performance	Glynn <i>et al.</i>	2004
<i>S. myrsinifolia</i> <i>S. myrsinites</i> x <i>S. myrsinifolia</i>	2-month-old plantlets	Punkaharju, Finland	Gh	Peat	20 < SWC < 50%	Study of the effects of enhanced UVB radiation and drought stress on willow secondary phenolics	[Phe]	The response of salicylates, flavonoids and phenolic acids to enhanced UVB and drought stress was clone-specific, which may indicate that climatic changes will alter the genetic composition of northern forests	Turtola <i>et al.</i>	2005
<i>P. euphratica</i>	Adult trees	Tarim River Basin, China	AV		5 < Groundwater level < 12 m	Determination of the optimal depth of groundwater for restoring the local ecosystem and provide a scientific basis for efficient use of limited water resources	[Pro] / [SOD] / [Pod]	The stress groundwater depths for the <i>Phragmites communis</i> , <i>Tamarix</i> spp. and <i>P. euphratica</i> are 3.5, 5 and 4.5 m, respectively	Chen <i>et al.</i>	2004
Other biochemical aspects										
<i>P. 'Popularis'</i> <i>P. x tomentosa</i>	Softwood cuttings	Rehovot, Israel	Gh	Perlite / vermiculite	-3.2 < Ψ_{leaf} < -0.8 MPa	Investigation of the relationship between the presence of proteins and water stress tolerance	EL / [Prot] / [Sugar]	Increased water stress tolerance is positively correlated with accumulation of BspA, dehydrin homologue and sucrose synthase	Pelah <i>et al.</i>	1997
<i>P. x canadensis</i>	Young cuttings	Orléans, France	GC	Peat	-1.5 < Ψ_{wp} < -0.5 MPa	Analysis of dehydrin gene expression under dehydration conditions	LG / g_s / EG	A cDNA encoding a dehydrin was characterized - It was induced by withholding water, salt stress, cold and osmotic stress	Caruso <i>et al.</i>	2002
<i>P. tremula</i>	4 to 5-week-old plantlets	Rehovot, Israel	lVC		20 and 30% plant water loss	Description of the cloning, sequence analysis, isolation and characterization of the SP1 protein and its stress responsiveness, boiling solubility, and oligomeric structure	EG / [SP1]	SP1 proteins are hydrophilic and remain soluble upon boiling - They represent a new class of protein involved in the plant's response to abiotic stress	Wang <i>et al.</i>	2002
<i>P. tremula</i>	2-month-old shoot explants	Rehovot, Israel			Weight loss to 80 or 60% of the shoot original fresh weight	Report of the temporal expression, response to ABA and partial characterization of a boiling-stable protein found in gradually water-stressed shoot cultures	[Prot]	The BspA protein was the only major, water stress-responsive boiling-stable protein detected in aspen	Pelah, Shoseyov and Altman	1995
<i>P. trichocarpa</i>	2-month-old cuttings	Lethbridge, Alberta, Canada	Gh	Natural river valley sand and gravel	Reservoir water decline from 0 to 4 cm day ⁻¹	Investigation of phytohormonal involvement in the growth reallocation that follows changes in water table depth	SG / [Gib] / Ψ_{xp}	Little evidence that endogenous gibberellins play a primary role in the regulation of root elongation in response to water table decline	Rood <i>et al.</i>	2000b
<i>S. sericea</i>	3-month-old cuttings	Waltham, Massachusetts, USA	N	Loam / peat moss / vermiculite	Dry / field capacity / flooded	Investigation of the effects of soil nutrient and water availability on the growth and chemistry of the silky willow, and on the performance of the imported willow leaf beetle	RWC / N / Biomass / LG / [Salicortin]	Nutrient-water interactions influence plant traits that are potentially important for insect performance	Lower and Orians	2003
<i>P. x canadensis</i> <i>P. 'Popularis'</i>	1-year-old cuttings	Beijing, China	N	Loam	70 and 30% of field capacity	Investigation of the effects of endogenous and exogenous ABA on polyamines and ethylene synthesis in a drought-sensitive and a drought-tolerant poplar genotypes	LL / [ABA] _{xylem} / EER / [Polya]	Inhibitory effect of ABA on polyamines synthesis more pronounced in the drought-sensitive genotype - More important production of ethylene in the drought-sensitive genotype	Chen <i>et al.</i>	2002a

	<i>P. alba</i>						Investigation of the temporal changes in the emission of ethylene and oxygen of water stressed leaves of <i>P. alba</i> using photoacoustic techniques	EER	Information obtained could be used to analyze the stomatal closure dynamics and processes related to photosynthesis and cell death	Acosta-Avalos, Alvarado-Gil and Vargas	2005
F. Plant growth - Biomass allocation											
	<i>P. × canadensis</i> <i>P. 'Tristis' × P. balsamifera</i>	Young cuttings	East Lansing, Michigan, USA	Gh	Sandy-loam soil	-0.5 < Ψ_{soil} < 0 MPa	Examination of growth and morphological responses induced by the onset and release of cycles of water stress under two levels of N availability	Biomass / BA / [Chl] / N / LN / LA / SLA / RSR	Soil moisture determined the amount of biomass that accumulated in roots - Leaves became thinner as soil moisture decreased from flooding	Liu and Dickmann	1992b
	<i>P. deltoides</i>	Young seedlings	Fort Collins, Colorado, USA	OC	Coarse sand	20 < Water level < 100 cm	Examination of germination and establishment of Russian-olive and cottonwood under a range of experimental moisture and light conditions	Biomass / BA	Russian-olive succeeds under conditions optimal for cottonwood establishment and under many conditions unfavourable for cottonwood	Shafroth, Auble and Scott	1995
	<i>P. balsamifera</i> × <i>P. trichocarpa</i>	Young cuttings	Craigiebukler, UK	Gh	Sand	Watering every 2 or 10 days	Study of the effects of nitrogen supply and drought stress	BA / Biomass / LA / LN / N / SLA / GE	Whole plant respiration decreased in the water stressed trees due to a reduction in total biomass and lower rates of respiration per unit tissue	Ibrahim, Proe and Cameron	1997
	<i>S. nigra</i>	Young cuttings	Memphis, Tennessee, USA	Gh	Sand / Sharkey Clay Series soil	- 200 < Soil redox potential < 700 mV	Evaluation of the effects of static and dynamic flooding regime and drought on root and shoot development, pattern of root distribution, biomass production and its allocation	GE / g_s / LA / LW / Biomass / Chl / RSR / BA	Maximum photosynthesis and growth in willow cuttings required ample soil moisture and adequate drainage in the top 60 cm of soil	Pezeszki, Anderson and Shields	1998
	<i>P. nigra</i>	Young cuttings	Cambridge-shire, UK	AV	Various sediment types	-1 < Ψ_{soil} < 0 MPa	Investigation of the differences in the responses of male and female black poplars to a variety of soil moisture conditions	LW / RGR / Ht / Biomass	Some limited spatial segregation of the sexes does occur in response to soil moisture availability	Hughes <i>et al.</i>	2000
	<i>P. angustifolia</i> , <i>P. balsamifera</i> , <i>S. drummondiana</i> , <i>S. exigua</i> , <i>S. lutea</i>	Young saplings and seedlings	Lethbridge, Alberta, Canada	Rz / Gh	Coarse gravel / medium sand / fine gravel	0, 1, 2, 3, 4 or 8 cm day ⁻¹ water-table decline	Investigation of the relative tolerances of saplings and seedlings of different willow and cottonwood species to different rates of water-table decline	Ht / RL / BA / S	Willow and cottonwood saplings similarly affected by abrupt water-table decline, but willow seedlings slightly more vulnerable than cottonwood seedlings	Amlin and Rood	2002
	<i>S. nigra</i>	Young cuttings	Loosahatchie River, Tennessee, USA	Gh	Sand / field soil (Sharkey Clay)	6 < soil redox potential < 451 mV	Quantification of the overall effects of soaking across various soil moisture regimes	S / RSR / Biomass	Soaking had significant effects on willow post success when evaluated across all soil moisture regimes	Schaff, Pezeszki and Shields	2002
	<i>P. tremuloides</i>	Young seedlings	Edmonton, Alberta, Canada	P	Slit / clay / loam	6 < Volumetric Soil Moisture < 20%	Isolation and quantification of the relative competitive and facilitative effects present within mixtures of aspen seedlings, alfalfa and marsh reedgrass	SG / LA / LN / BA / RGR / NPP	Evidence of facilitation was found when aspen was grown with alfalfa, including increases of overall available soil N and transient increases in soil moisture with pulsed precipitation during drought	Powell and Bork	2004
	<i>S. nigra</i>	Young cuttings	Memphis, Tennessee, USA	Gh	Sand / soil	-0.6 < Ψ_{soil} < 0 MPa	Quantification of the physiological responses of black willow to four soil moisture regimes	F / g_s / Ht / RSR / RG / SG	Photosynthesis and growth of black willow cuttings in response to both reduced soil conditions and moisture deficits were limited by stomatal closure	Li <i>et al.</i>	2004b
	<i>P. nigra</i> <i>S. elaeagnos</i>	5 to 74-day-old cuttings		Rz / Gh	Sand or gravel	Water table decline from 0 to 3 cm day ⁻¹	Investigation of the influence of different periods of inundation and rates of water table decline on the survival and growth rate	S / LN / LL / BA / RG	Restoration schemes utilizing <i>S. elaeagnos</i> cuttings may experience a greater success than those using <i>P. nigra</i> - <i>P. nigra</i> cuttings may establish more easily if situated where inundation does not occur often or for prolonged periods	Francis <i>et al.</i>	2005
	<i>P. balsamifera</i> × <i>P. deltoides</i> (= <i>P. × acuminata</i>)	2-week-old seedlings	Lethbridge, Alberta, Canada	Rz / Gh	Sand / gravel	0, 1, 2, 4 and 8 cm day ⁻¹ water decline	Investigation the influence of the rate of water table decline on poplar seedling growth and survival	S / LA / LN / RL / RW / Ht	Maximum root mass and length were observed in plants subjected to declines in water table level of 0 and 1 cm day ⁻¹ , respectively	Mahoney and Rood	1991
	<i>P. 'Tristis' × P. balsamifera</i> <i>P. × canadensis</i>	1-month-old cuttings	East Lansing, Michigan, USA	GC	Sandy loam soil	-1 < Ψ_{soil} < -0.007 MPa	Observation of early patterns of growth and water relations in response to changing conditions of water stress	g_s / BA / Ht / LA	The higher root/leaf weight ratio of the <i>P. 'Tristis' × P. balsamifera</i> clone enabled it to maintain a more favourable plant water status	Mazzoleni and Dickmann	1988
	<i>P. 'Tristis' × P. balsamifera</i> <i>P. × canadensis</i>	1-month-old cuttings	Rhineland, Wisconsin, USA	SRC		Seasonal variations of Ψ_{soil}	Monitoring of growth and development of two <i>Populus</i> clones during their establishment year	LA / LN / SLA / Ht	The high shoot/root ratio developed by the <i>P. × canadensis</i> clone limited its development during periods of low soil water potential	Michael <i>et al.</i>	1988
	<i>S. alba</i> , <i>S. triandra</i> , <i>S. viminalis</i> , <i>P. nigra</i>	1-month-old seedlings	River Rhine, the Netherlands	Gh	Clay / sand	0.10 < SWC < 0.30 cm ³ cm ⁻³	Assessment of differences in drought-resistance properties among floodplain species during their seedling stage	LA / SLA / RSR / BA / RL / T	<i>P. nigra</i> is most resistant to drought followed by <i>S. alba</i> and then <i>S. triandra</i> and <i>S. viminalis</i> - These differences are reflected in the distribution patterns of these species observed on the banks of the River Rhine	Van Splunder <i>et al.</i>	1996
	<i>P. deltoides</i> <i>P. balsamifera</i> <i>P. angustifolia</i>	1-month-old cuttings	Lethbridge, Alberta, Canada	Rz / Gh	Commercial potting mixture	0, 4 and 10 cm day ⁻¹ water decline	Study of the influence of the rate of water table decline with three North American cottonwood species	Ht / RL / BA / T / LA / LN	The tolerance to water table decline varies across cottonwood genotypes and <i>P. balsamifera</i> saplings are the most vigorous	Kranjcec, Mahoney and Rood	1998

<i>S. gooddingii</i>	1-month-old seedlings	Flagstaff, Arizona, USA	Gh	Sand / river gravel	0.06 < Volumetric soil water content < 0.30 m ³ m ⁻³	Investigation of the effects of differing rates of ground water decline on growth and survival of <i>S. gooddingii</i>	S / Ht / RL / LA / RSR	Lateral root development may help to protect <i>Salix</i> seedlings from late season flood scour	Horton and Clark	2001
<i>S. dasyclados</i> × <i>S. viminalis</i>	2-month-old cuttings	Uppsala, Sweden	Gh	Clay / peat	55% of the water given to the well-watered plants	Identification and localization of QTL for growth, nutrient and water economy - Quantification of the effect of the QTL and evaluation of common QTL in two contrasting treatment : well watered and drought stressed	RGR / δ ¹³ C / N / Ht / Cc / RW / Biomass	QTL specific for each treatment were found, but QTL common across the treatments were also detected	Rönnerberg-Wästljung, Glynn and Weih	2005
<i>S. myrsinifolia</i> <i>S. myrsinifolia</i> × <i>S. myrsinifolia</i>	2-month-old plantlets	Punkaharju, Finland	Gh	Peat	20 < SWC < 50%	Study of the response of growth of willows to combinations of UVB radiation and drought stress	Ht / Biomass / BA / RSR	Drought stress produced family- and clone-specific reactions, whereas the response of studied willow genotypes to enhanced UVB and UVB x drought was mostly similar	Turtola <i>et al.</i>	2006
<i>P. balsamifera</i> <i>P. trichocarpa</i> <i>P. nigra</i> × <i>P. nigra</i>	6-10-week-old cuttings	Columbia, Missouri, USA	Gh	Peat moss / sand / silt loam	-3.5 < Ψ _{leaf} < -0.5 MPa	Identification of traits associated with superior growth potential on sites where water could be a limiting factor	GE / BA / LA / SLA / LAR	Rapid early leaf and root growth appear to be key attributes associated with productivity regardless of soil water availability	Rhodenbaugh and Pallardy	1993
<i>P. trichocarpa</i> × <i>P. balsamifera</i>	1 to 4-month-old cuttings	Aberdeen, UK	Gh	Coarse, medium and fine sand	-2 < Ψ _{leaf} < -1 MPa	Examination of the interaction of water and nitrogen availabilities on gas exchange and whole-plant carbon allocation	Biomass / BA / N / g _s / GE	Preferential allocation of biomass to roots under drought conditions and reduced rate of net photosynthesis associated with reductions in stomatal conductance and SLA	Ibrahim, Proe and Cameron	1998
<i>P. deltoides</i>	3-month-old cuttings	Mississippi state, Mississippi, USA	Gh	Pro-Mix / sand	-0.5 < Ψ _{wp} < 0 MPa	Evaluation of the influence of various treatments on flowering in rooted cuttings from mature and juvenile trees	SG	The new set of modified treatments failed to induce precocious flowering in rooted cuttings from juvenile trees only	Yuceer <i>et al.</i>	2003
<i>P. nigra</i>	2 to 6-month-old cuttings	Wooster, Ohio, USA	OC	Premier Pro-Mix BX	-3 < PMMT < -25 kPa	Quantification of the effects of water and nutrient availability on carbon assimilation, growth, and total foliar phenolic glycoside concentration and on constitutive and rapid induced resistance to gypsy moth and whitemarked tussock moth	Biomass / BA / LA / SLA / RGR / GE / N / larval growth / [Phenols]	Drought decreased net assimilation rate and growth, while increasing total phenolic glycoside concentrations - Drought decreased the growth of gypsy moth larvae but had no effect on whitemarked tussock moth	Hale <i>et al.</i>	2005
<i>P. fremontii</i> <i>S. gooddingii</i>	4 to 5-month-old cuttings	Tucson, Arizona, USA	OC	Sand / potting mix	Withholding water	Determination if remotely sensed canopy temperatures could be used to estimate transpiration or water stress	Biomass / LA / LAI / LW / SW / SF / g _s	All species depleted soil moisture to the same extent and reached the wilt point at about the same time, saltcedar has adaptations that allow it to recover from drought better than the other species	Nagler, Glenn and Thompson	2003
<i>P. trichocarpa</i> <i>P. deltoides</i> <i>P. trichocarpa</i> × <i>P. deltoides</i>	1-year-old coppiced plants	Seattle, Washington, USA	P		Two consecutive contrasting years in terms of rainfall	Determination of the effects of irrigation on stem volume production and leaf expansion	SG / g _s / π _o	Unlike its effect on leaf area growth, irrigation increased stem volume growth of the hybrid and the parental species by a similar amount	Roden, Van Volkenburgh and Hinckley	1990
<i>S. sericea</i> <i>S. eriocephala</i> <i>S. sericea</i> × <i>S. eriocephala</i>	1-year-old seedlings	Williamstown, Massachusetts, USA	Gh	Soil / peat / vermiculite	-2.5 < Ψ _{stem} < -0.1 MPa	Quantification of the relative performance of <i>S. sericea</i> , <i>S. eriocephala</i> and their F ₁ hybrids to varying levels of water availability	LWC / SG / LN / LL / BA / LG	Temporal and spatial variability in water availability could determine the survivorship of hybrids and the frequency of introgression	Orians <i>et al.</i>	1999
<i>P. nigra</i> , <i>P. euphratica</i> , <i>S. nigra</i>	1 to 2-year-old trees	Khiva, Khorezm, Uzbekistan	P	Sandy site + Loamy site	0 < Monthly precipitations < 27 mm	Study over 24 month of the growth and development of 10 trees differing in their tolerance to drought and salinity	Cc / RGR / SLA / LAI / LAR / RSR / LMR / GE	Ranking of all parameters concurrently showed the high potential of <i>Elaeagnus angustifolia</i> and <i>P. euphratica</i> , which matched previous rankings based on total biomass and financial added value	Lamers, Khamzina and Worbes	2006
<i>Populus</i> spp.	0 to 6-year-old trees	Arlington, Wisconsin, USA	P	Plano silt loam	Natural variations in rainfalls between years	Examination of the survival, productivity, drought tolerance and pest status of 16 hybrid poplars	S / Ht / Cc / Biomass / PI	Differential responses among clones to drought	Robison and Raffa	1998
<i>P. trichocarpa</i> × <i>P. deltoides</i> <i>P. deltoides</i> × <i>P. nigra</i>	2 to 3-year-old trees	Wallula, Washington, USA	D	Active dune land	-1.2 < Ψ _{wp} < -0.4 MPa	Assessment of the role of the osmotic potential in determining drought tolerance	π _o / RGR / SG / RW	The higher drought resistance of clone DN compared with clone TD was the result of the maintenance of a more favourable water balance by stomatal regulation and greater carbon allocation to roots during the early stages of drought	Tschaplinski <i>et al.</i>	1998
<i>P. fremontii</i> <i>S. gooddingii</i>	2 to 4-year-old seedlings and saplings	Central Arizona, USA	AV		-3 < Water table depth < 0 m	Quantification of the response of three riparian species to different water table dynamics	RL / SCA	Plant response is likely mediated by factors such as soil texture and stratigraphy, availability of precipitation-derived soil moisture, physiological and morphological adaptations to water stress, and tree age	Shafroth, Stromberg and Patten	2000
<i>P. deltoides</i>	Adult trees	Oientangy river, Ohio, USA	AV	Silt loam	Palmer Drought Severity Index	Investigation of the influence of climate and streamflow data on productivity	D / SG / SCA	Growth of eastern cottonwood was not related to streamflow, but was reduced by excess summer precipitation	Dudek, McClenahan and Mitsch	1998
<i>P. deltoides</i>	Adult trees	Denver, Colorado, USA	AV	Gravel or loam / gravel	-0.8 < Ψ _{wp} < -0.2 MPa	Examination of the physiological and morphological response patterns of plains cottonwood to acute water stress imposed by groundwater pumping	LL / g _s	<i>P. deltoides</i> responded to abrupt alluvial water table decline with decreased shoot water potential followed by leaf mortality	Cooper, D'Amico and Scott	2003

<i>P. tremuloides</i>	41 to 81-year-old trees	British Columbia to Manitoba, Canada	F	Sand / silt / clay	-30 < Climate moisture index < +20 cm year ⁻¹	Examination of the cause and magnitude of interannual variation in aspen growth	Ht / Cc / SG / PI / Biomass	A major collapse in aspen productivity likely occurred during the severe drought that affected much of the region during 2001-2003	Hogg, Brandt and Kochtubajda	2005
<i>P. deltooides</i>	80 to 200-year-old trees	Deerlodge Park, Colorado, USA	AV	Sands / silts / clays	0 < Mean daily river discharge < 275 m ³ s ⁻¹	Comparison of production and breakdown of leaf litter at matched floodplain sites on a regulated and an unregulated rivers	N / OM / MiC / SC	Factors reducing flood flow frequency and magnitude will reduce overall breakdown rates on the floodplain towards those found in drier upland environments	Andersen and Nelson	2003

G. Water-use efficiency

<i>P. x canadensis</i> <i>P. 'Tristis' x P. balsamifera</i>	Young cuttings	East Lansing, Michigan, USA	Gh	Sandy-loam soil	-0.5 < $\Psi_{soil\ matrix}$ < 0 MPa	Investigation of how plants with low- or high-N status physiologically respond to drought and flooding	GE / g _s / WUE	Drought-stressed plants gained full and quick recovery of photosynthesis upon relief from stress	Liu and Dickmann	1993
<i>P. x canadensis</i> <i>P. 'Tristis' x P. balsamifera</i>	Young cuttings	East Lansing, Michigan, USA	Gh	Sandy-loam soil	0, -0.02, -0.05, -0.1 and -0.5 MPa of soil matric potential	Examination of the interactions of water and nitrogen availability	GE / WUE	The highest water-use efficiency was found on the high-N/severe drought zone for clone 'Eugenei' whereas it was found on the high-N/mild drought zone for 'Tristis'	Liu and Dickmann	1996
<i>P. fremontii</i> <i>S. gooddingii</i>	Young cuttings	Tucson, Arizona, USA	Gh	Washed river and potting medium	Treatment with NaCl solutions	Determination of the interaction of salt and water stress on survival, salt tolerance, WUE and growth	RGR / WUE / τ_0	At the control salinity level, the two species were able to extract water from a drying soil equal to that of <i>Tamarix</i> species	Vandersande, Glenn and Walworth	2001
<i>S. viminalis</i> <i>S. schwerinii x S. viminalis</i>	Young cuttings	Uppsala, Sweden	OC	Pure sand	Low and high irrigation	Test of the hypothesis that fast-growing breeds of willow are more sensitive to nutrient and water stress and less efficient in nutrient- and water-use than slower-growing clones	BA / N / $\delta^{13}C$ / SLA / LA / LAR / RGR	Fast-growing hybrids are more sensitive to nutrient and water stress - Natural clones have higher water-use efficiency than fast-growing hybrids	Weih	2001
<i>P. balsamifera</i> <i>P. tremuloides</i>	Young cuttings or seedlings	Edmonton, Alberta, Canada	Gh	Coarse sand / peat	Water table at 15 or 30 cm below the soil surface	Monitoring of the water use under different water-table conditions and soil temperatures	ODR / GE / WUE / LW / LA / LMR / BA	<i>P. balsamifera</i> is likely to be a good hydrological nurse crop to lower the water table when soil are warm	Landhäusser <i>et al.</i>	2003
<i>P. cathayana</i> <i>P. simonii</i>	Young cuttings	Maoxian Field Ecological Station, China	Gh		100, 25% of field capacity	Determination of drought effects on two sympatric species	BA / WUE	Existence of interspecific genetic differences as affected by drought, useful as criteria for selection and tree improvement	Yin <i>et al.</i>	2005a
<i>P. simonii</i> <i>P. cathayana</i>	Young cuttings	Maoxian Field Ecological Station, China	Gh		100, 25% of field capacity	Investigation of the physiological basis involved in drought tolerance and the interrelationships between ABA and WUE	BA / GE / [ABA] / WUE	Evidence for adaptive differentiation between the two contrasting species	Yin <i>et al.</i>	2004
<i>P. przewalski</i>	Young cuttings	Maoxian Field Ecological Station, China	Gh		100, 25% of field capacity	Investigation of the photosynthetic responses of <i>P. przewalski</i> subjected to drought stress	gs / WUE / Y / q _{np} / T / GE	Drought stress decreased plant assimilation and increased dissimilation through affected gas exchange, the diurnal pattern of gas exchange, and photosynthesis-PAR response curve, thereby reducing plant growth and productivity	Yin, Berninger and Li	2006
<i>P. trichocarpa</i> <i>P. deltooides</i> <i>P. trichocarpa x P. deltooides</i>	3-week-old cuttings	Pullman, Washington, USA	Gh	Sand	-2.40 < Ψ_{sp} < -0.75 MPa	Evaluation of some physiological characteristics that may be related to productivity on dry continental sites	GE / LA / WUE	Introduction of clones of eastern cottonwood into breeding programs is likely to yield lines with favourable growth characteristics combined with enhanced WUE and adaptation to soil water deficits	Bassman and Zwier	1991
<i>P. tremula</i>	1-month-old seedlings	Helsinki, Finland	Gh	Sand	100, 50% of field capacity	Investigation of the physiological basis of climatic adaptation involved in drought tolerance and the interrelationship between endogenous ABA concentration and water-use efficiency	Ht / LA / BA / GE / [ABA] / WUE	Compared with the wet climate population, the dry climate population was more responsive to exogenous ABA application	Li, Yin and Liu	2004
<i>P. davidiana</i>	1-month-old seedlings	Helsinki, Finland	Gh	Peat	100, 80, 60, 40, 20% of field capacity	Underlining of differences between three contrasting ecotypes	BA / GE / [ABA] / WUE	Prodigal WUE and quick growth of the wet climate ecotype - Conservative WUE and slow growth of the dry climate ecotype	Zhang, Zang and Li Zhang, Wu and Li	2004 2005
<i>S. dasyclados x S. viminalis</i>	5 to 9-week-old cuttings	Uppsala, Sweden	Gh	Clay / peat	55% of the water given to the well-watered plants	Analysis of phenotypic correlations and QTL for important growth traits and a surrogate of WUE in a willow pedigree	RGR / LAR / SLA / N / Biomass / $\delta^{13}C$	The results demonstrate a genetic basis for phenotypic correlations among growth traits, and provide evidence for the existence of 'master switches' regulating some of the traits	Weih, Rönning-Wästljung and Glyn	2006
<i>P. trichocarpa x P. deltooides</i> <i>Salix sp.</i>	2-month-old cuttings	Gainesville, Florida, USA	Gh	Sand / peat moss	-1.2 < Ψ_{wp} < -0.4 MPa	Characterization of the responses to elevated CO ₂ and water stress and determination if elevated CO ₂ mitigated drought stress effects	GE / WUE / Ht / Cc	Elevated CO ₂ did mitigate the effects of water stress in willow, but not in poplar	Johnson, Tognetti and Paris	2002
<i>P. trichocarpa</i> <i>P. deltooides</i> <i>P. trichocarpa x P. deltooides</i>	3-month-old cuttings	Victoria, British Columbia, Canada	Gh	Sand	-1.91 < Ψ_{sp} < -0.76 MPa	Examination of N and K nutrition on drought and cavitation resistance	GE / WUE / PLC / LA / SD	Drought-resistant clones exhibited similar WUE to drought-susceptible clones, but had smaller, more numerous stomata and greater leaf retention under drought conditions	Harvey and van den Driessche	1999

<i>P. x canadensis</i>	3-month-old coppiced plants	Orléans, France	P	Loamy sand	-0.6 < Ψ_{xp} < 0 MPa	Study of the relationships between productivity, WUE and drought tolerance and test whether some leaf traits could be used predictors for productivity, WUE and drought tolerance	SLA / N / C / LA / $\delta^{13}C$ / SG / Cc / Biomass / GE / g_s / SD	Most of the productive genotypes displayed a low level of drought tolerance, and conversely - The ability to increase WUE in response to water deficit was necessary but not sufficient to explain the genotypic diversity of drought tolerance	Monclus <i>et al.</i>	2006
<i>P. trichocarpa</i> × <i>P. deltoides</i> <i>P. deltoides</i> × <i>P. nigra</i> <i>P. trichocarpa</i> × <i>P. trichocarpa</i>	1 and 2-year-old trees	Bedford-shire, UK	Gh	Sandy loam / pit mix	- Medium drought: Ψ_{soil} ~ -0.1 MPa - Severe drought: Ψ_{soil} ~ -1MPa	Determination of clonal differences in drought response and quantification of relationships between WUE and biomass production	BA / LA / WUE	Highest reduction in biomass accumulation for clone Trichobel - Relationships between WUE and biomass production constant over both years	Souch and Stephens	1998
<i>P. deltoides</i>	3-year-old coppiced plants	Oracle, Arizona, USA	P		25 < Volumetric soil water content < 39%	Examination of the effects of atmospheric vapour pressure deficit and soil moisture stress on leaf- and stand-level CO ₂ exchange	GE / WUE	The limitation of assimilation because of canopy light environment switched to a predominantly individual leaf limitation in response to water stress	Murthy <i>et al.</i>	2005
<i>P. fremontii</i>	Adult trees	New Mexico to Northern California, USA	F	Sand / gravel	0.2 < Precipitation < 299.5 mm	Examination of $\delta^{13}C$ variation among populations from central New Mexico to Northern California	$\delta^{13}C$	Water availability can account for some of the $\delta^{13}C$ variation among populations but, given the large residual variance, other factors are important	Leffler and Evans	2001
<i>P. fremontii</i> <i>S. gooddingii</i>	Adult trees	Bill Williams river / Arizona, USA	AV		-1.5 < Ψ_{wp} < -0.3 MPa	Investigation of the environmental water sources used in mid-summer at sites that differed in water table depth	$\delta^{13}C$	This study highlights the difficulty in sampling all water sources in large scale studies of riparian ecosystems with complex subsurface hydrogeology	Horton, Hart and Kolb	2003
<i>P. fremontii</i>	15 to 50-year-old trees	San Pedro river, Arizona, USA	AV	Coarse, alluvial soil	40 < August precipitations < 150 mm	Assessment of intra- and interannual variation in integrated leaf gas exchange responses to monsoonal moisture inputs	$\delta^{13}C$	Intra- and interannual variation in integrated photosynthetic response exists at the population-scale - Changes in monsoonal precipitation and stream flow may differentially alter photosynthetic gas exchange	Potts and Williams	2004
<i>P. deltoides</i>	30 to 40-year-old trees	Rio Grande basin, New Mexico, USA	AV	Sand / clay / silt	0.5 < Depth of the groundwater < 2 m	Quantification of variability among four study sites in both soil and groundwater conditions - Examination of physiological and morphological characters on trees at these sites	GE / g_s / T / WUE / Ψ_{xp} / LA / [Chl] / SLA / SD	Physiological and morphological trait variability among populations is ecologically important and may be of use in present reclamation and conservation efforts in these areas	Rowland <i>et al.</i>	2001
<i>Populus</i> spp. <i>Salix</i> spp.			Review		-2.53 < Ψ_{wp} < -1.15 MPa	Review of the water relations of riparian plants from desert regions of North America	GE / N / $\delta^{13}C$ / WUE / SF / SG / g_s	Management efforts aimed at maintaining native forests must include at least partial reintroduction of historical flow regimes, which favour the recruitment of native riparian species and reverse long-term desiccation of desert floodplain environments	Smith <i>et al.</i>	1998

H. Population biology and management

<i>P. deltoides</i>	2 to 10-year-old trees	Western USA	F			Modeling to aid in planning prescribed floods by projecting how altered flow regimes might affect populations	S / D	Mature cottonwood forest should be most abundant near the observed natural flow regime - High flood frequencies result in stable population sizes, while stable flows result in highly variable population sizes	Lytle and Merritt	2004
<i>P. deltoides</i>	Adult trees	South Platte river, Colorado, USA	AV		-1.5 < Relative water table elevation < 1 m	Quantification of the changes in morphology, growth and mortality in response to measured declines in alluvial water table	S / D / Ht	Gradual water table declines had no measurable effect on mortality, stem growth or live crown volume, and produced significant declines only in annual branch growth increment	Scott, Shafroth and Auble	1999
<i>Salix</i> spp.	Adult trees	Stanley Creek, Idaho, USA	AV	Silty clay loam / sandy clay loam	Years of moderate drought	Examination of the response of a cold mountain meadow riparian system to 3 intensities of controlled late June cattle grazing	D / stream characteristics	A decrease in wet-site rhizomatous graminoids during drought suggests a depletion of meadow conditions	Clary	1999
<i>P. deltoides</i> <i>S. exigua</i>	Adult trees	Green river, Utah / Yampa river, Colorado, USA	AV		50 < Instantaneous peak discharge < 1100 m ³ s ⁻¹	Evaluation of the effects of river damming on geomorphic processes and riparian vegetation	D	The probable long-term effects of channel and hydrologic changes include the eventual replacement of <i>Populus</i> -dominated riparian forest by drought tolerant desert shrublands	Merritt and Cooper	2000
<i>P. fremontii</i>	Adult trees	Rio Grande basin, New Mexico, USA	AV		0 < Distance from river < 450 m	Estimation of the variability among five riparian cottonwood populations in terms of size, density and spatial distribution	D / Ht	Tree size of the five populations appeared to be affected by environmental factors	Rowland, Biagini and Evans	2000
<i>P. fremontii</i> <i>S. gooddingii</i>	Adult trees	Mojave river, California, USA	AV	Gravel / sand / silt	-2 < Relative water-table depth < 0 m	Test of a set predictions based on the inference that cottonwood decline was an indirect result of lowered water-table levels following flood-related channel incision	S / SCA	The integrity of riparian forests along arid region rivers with coarse alluvial flood-plain soils can be threatened by physical processes and human activities that result in sustained ground-water declines as small as 1 m	Scott, Lines and Auble	2000
<i>P. euphratica</i>	Adult trees	Qira oasis, China	O		0 < Soil water content < 100%	To provide an ecological basis for the regeneration and the sustainable use of the vegetation at the transition between oases and sandy desert	SCA / SW	Presentation and objectives of the joint European-Chinese project "Ecological basis for a sustainable management of the indigenous vegetation in a Central-Asian desert"	Thomas <i>et al.</i>	2000

<i>P. tremuloides</i>	Adult trees	Jackson Hole, Wyoming, USA	F		-5 < Palmer drought severity index < 5	Analysis of the relationship between the rates of aspen regeneration, biophysical factors and human land use since 1830	Ht / D	No apparent relationship between periods of aspen regeneration and drought conditions was found	Hessl and Graumlich	2002
<i>P. tremuloides</i>	Adult trees	Northwestern Alberta, Canada	F		-20 < Climate moisture index < 30 cm	Tree-ring analyses and forest health assessments in healthy and stressed aspen forests as a means of determining the onset, magnitude and causes of reduced stem growth, mortality and crown dieback	SG / PI	Under global change, the severity of the stressors may increase, which would pose a serious concern for the future health, productivity and carbon sequestration of aspen forests in the region	Hogg, Brandt and Kochtubajda	2002
<i>P. deltoides</i>	Adult trees	Northwestern Colorado / Eastern Utah, USA	AV		River flow variations	Study of the recruitment along broad, alluvial valley segments and canyon segments	Ht	The current regime mimics drought in a canyon setting, accelerating <i>Tamarix</i> invasion whereas in valleys the ongoing geomorphic adjustment of the channel, combined with reduced flow variability has nearly eliminated <i>Populus</i> establishment	Cooper, Andersen and Chimner	2003
<i>P. fremontii</i> <i>S. gooddingii</i>	Adult trees	San Pedro river, Arizona, USA	AV		Depth to ground water: 3.8 / 4.2 m	Quantification of changes in population stand structure traits across gradients of ground-water depth and fluctuation and surface flow permanence	D / Ht / SCA	The altered vegetation structure along dewatered rivers may lower wildlife habitat quality	Lite and Stromberg	2005
<i>P. tremula</i>	Adult trees	Lithuania	F			Investigation of growth-independent tree mortality in central Europe	S	More than 60% of dead trees had symptoms of wind damage - Significant fluctuations in tree mortality rate over time were caused by extreme meteorological conditions (wind, drought)	Ozolincius, Miksys and Stakenas	2005
<i>P. tremula</i>	Adult trees	Lithuania	F		142 < Annual precipitations < 393 mm	Presentation of the changes in the health of the dominant tree species in Lithuania between 1991 and 2001	LL	Average temperature, amount of precipitation and background air pollution during the active growing season can be regarded as a complex of factors influencing crown condition	Ozolincius, Stakenas and Serafinaviciute	2005
<i>P. tremuloides</i>	Adult trees	Rocky Mountains, Colorado, USA	F		2002 drought	Investigation of the combined effects of past disturbances, current vegetation and topography on spatial variability of the severity of a fire during the extreme drought of 2002	Fire severity	Pre-burn stand conditions are important influences on burn severity even for fires burning during extreme drought	Bigler, Kulakowski and Veblen	2005
<i>P. tremuloides</i>	Adult trees	Southwestern Yukon, Canada	F	Sand to clay loam and silty clay	Annual precipitations < 300 mm	Determination of the most important climatic factors governing growth and regeneration of trembling aspen and white spruce in Yukon	Ht / SG	Growth of both species was most strongly related to variation in precipitations - The regenerating aspen had a wide age-class distribution (1959-2000) and their growth was also positively related to precipitation	Hogg and Wein	2005
<i>S. caroliniana</i>	Adult trees	St. John River, Florida, USA	AV	Peat soils	-0.5 < Water depth < 0 m	Evaluation of the use of roller-chopping as a management technique to reduce willow cover and restore herbaceous marsh in an area where fire was no longer a viable option	D	Under dry conditions followed by flooding, roller-chopping can be an effective method of willow control	Ponzio <i>et al.</i>	2006
<i>Populus</i> spp. <i>Salix</i> spp.			Review			Examination of the potential for producing biomass on restored landfills using willow and poplar species in short rotation energy forestry		The responses of poplars and willows to drought may be the key constraint to productivity since their natural distribution and productivity are closely related to the seasonal availability of soil water	Nixon <i>et al.</i>	2001
<i>Populus</i> spp.			Review			Review of studies conducted after 1990 on cottonwood water relations, impacts of damming, and life history and conservation		The conservation and restoration of cottonwoods will rely on the provision of river flow regimes that satisfy the ecophysiological requirements for survival, growth and reproduction	Rood, Braatne and Hughes	2003
<i>P. tremuloides</i>			Review			Identification of potential processes that contribute reduced vigour and dieback of aspen stands		Among inciting factors, severe episodes of drought have been implicated in the decline and death of aspen trees in western Canada	Frey <i>et al.</i>	2004
<i>Populus</i> spp. <i>Salix</i> spp.			Review			Comparison of the ecophysiology of <i>Tamarix ramosissima</i> and native trees in western US riparian zones		An effective management strategy for saltcedar must include the return of a more dynamic hydrological regime to regulated rivers, allowing saltcedar and native trees to coexist	Glenn and Nagler	2005
<i>P. deltoides</i>			Review			Development of two conceptual models synthesizing processes affecting vegetation under fluctuating groundwater and identification of information gaps	Biomass	Such models provide a valuable tool for managing vegetation and groundwater use in areas where groundwater is important to both plants and humans, particularly in the context of climate change	Naumburg <i>et al.</i>	2005

Abbreviations:

Growth conditions: AV, alluvial valley; D, desert; F, forest; GC, growth chamber; Gh, greenhouse; IFB, intensive forestry biome; IFM, intensive forest mesocosm; IvC, *in vitro* culture; MpS, micropropagation system; N, nursery; O, oasis; OC, outdoor containers; P, plantation; Pt, phytotron; PTS, power thermal station; Rz, rhizopods; SRC, short rotation culture

Traits examined: **AA**, amino acids; **ABA**, abscisic acid; **AE**, activation energy; **AP**, ascorbate peroxidase; **Asc**, ascorbate; **BA**, biomass allocation; **BEM**, bulk elastic modulus; **BG**, branch growth; **C**, carbon; **Car**, carotenoids; **Cat**, catalase; **Cc**, stem circumference / diameter; **Chl**, chlorophylls; **CL**, carbon loss; **D**, population density; $\delta^{13}\text{C}$, carbon isotope discrimination; **EG**, expression of genes; **DLE**, duration of leaf expansion; **EER**, ethylene emission rate; **EL**, electrolyte leakage; **F**, fluorescence; **Flav**, flavanols; **FP**, feeding preference; **Fruc**, fructose; **g**, conductance; **GE**, gas exchange; **g_h**, hydraulic conductance; **Galac**, galactose; **Gib**, gibberelins; **Glu**, glutathione; **Gluc**, glucose; **Gly**, glycine; **GR**, glutathione reductase; **g_s**, stomatal conductance; **GS**, glutamine synthase; **Ht**, stem height; **II**, injury index; **Isop**, isoprene; **J**, rate of photosynthetic electron transport; **k**, specific conductivity; **K**, soil activity factor; **LA**, leaf area; **LAI**, leaf area index; **LAnat**, leaf anatomy; **LAP**, leaf antioxidant properties; **LAR**, leaf area ratio; **LG**, leaf growth; **LL**, leaf loss; **LMA**, leaf mass area; **LMR**, leaf mass ratio; **LN**, number of leaves; **LW**, leaf dry weight; **LWC**, leaf water content; **MDH**, malate dehydrogenase; **MiC**, macroinvertebrate collection; **N**, nitrogen content; **NA**, nutrient allocation; **NPP**, net primary production; **OA**, osmotic adjustment; **ODR**, oxygen diffusion rate; **OM**, organic matter; **Osmo**, osmoticum; **Phe**, phenolic compounds; **PI**, pathogen incidence; **Pig**, pigments; **PLC**, percentage loss of conductivity; **PMMT**, potting medium moisture tension; **PNE**, percentage native embolism; π_0 , osmotic potential; **Pod**, peroxidase; **Polya**, polyamines; **Pro**, proline; **Prot**, protein; **P_t**, turgor pressure; **q_p**, photochemical quenching; **q_{np}**, non-photochemical quenching; **RG**, root growth; **RGR**, relative growth rate; **RL**, root length; **RSR**, root to shoot ratio; **Rub**, rubisco; **RVFD**, root volume flow density; **RW**, root dry weight; **RWC**, relative water content; **S**, survival; **SA**, sapwood area; **SC**, standing crop; **SCA**, stem cross-sectional area; **SD**, stomatal density / dimension; **SF**, sap flux; **SG**, stem growth; **SLA**, specific leaf area; **SOD**, superoxide dismutase; **Suc**, sucrose; **SV**, stem volume; **SW**, stem dry weight; **SWC**, soil water content; **T**, transpiration; **WUE**, water-use efficiency; **Y**, quantum yield; Ψ_{xp} , xylem water potential; [], content / concentration; **_**, enzyme activity

Table 7.5. Overview of available literature on elevated CO₂ responses of *Populus* in field experiments (period 1990 - present). Table adapted from Gielen and Ceulemans (2001).

Species	Clone	Location	Facility	Age at start	Duration of enrichment	Interaction	Reference
<i>P. tremuloides</i>		Siena, IT	natural CO ₂ spring			/	(Tognetti, Longobucco and Raschi 1999)
<i>P. grandidentata</i>		Pellston, MI, USA	OTC (pots)	seedlings (60 days)	10 weeks	/	(Curtis and Teeri 1992)
<i>P. grandidentata</i>		Pellston, MI, USA	OTC (OBRB)	rooted cuttings	1 growing season	N	(Zak <i>et al.</i> 1993, Curtis <i>et al.</i> 1994)
<i>P. tremuloides</i>		Pellston, MI, USA	OTC (OBRB)	rooted cuttings	2 growing seasons	N	(Kubiske <i>et al.</i> 1997, Kubiske <i>et al.</i> 1998, Mikan <i>et al.</i> 2000)
<i>P. tremuloides</i>	early/late leaf drop	Pellston, MI, USA	OTC (OBRB)	rooted cuttings	2.5 growing season	N	(Curtis <i>et al.</i> 2000, Pregitzer <i>et al.</i> 2000, Wang <i>et al.</i> 2000a, Zak <i>et al.</i> 2000a, Zak <i>et al.</i> 2000b, King <i>et al.</i> 2001a)
<i>P. tremuloides</i>		Pellston, MI, USA	OTC (OBRB)	4-year old	1 growing season	/	(Rier <i>et al.</i> 2002)
<i>P. tremuloides</i>	O ₃ tolerant O ₃ sensitive	Alberta, MI, USA	OTC	young trees (8 months)	3 growing seasons	O ₃	(Kull <i>et al.</i> 1996, Karnosky <i>et al.</i> 1998, Ambus and Robertson 1999)
<i>P. ×canadensis</i>	‘Eugenei’	Pellston, MI, USA	OTC (OBRB)	cuttings	1 growing season	N	(Curtis <i>et al.</i> 1995, Pregitzer <i>et al.</i> 1995, Randlett <i>et al.</i> 1996, Lussenhop <i>et al.</i> 1998)
<i>P. ×canadensis</i> <i>P. nigra</i> × <i>P. maximowiczii</i>	‘DN-33’, ‘DN-44’, ‘DN-70’, ‘DN-74’, ‘NM-6’	Alberta, MI, USA	OTC (pots)	cuttings	1 growing season	O ₃	(Dickson <i>et al.</i> 1998)
<i>P. ×canadensis</i> <i>P. trichocarpa</i> × <i>P. deltoides</i>	‘Robusta’ ‘Beaupré’	Antwerp, BE	OTC	cuttings	2 growing seasons + 1 growing season after coppice	/	(Ceulemans, Jiang and Shao 1995a, Ceulemans, Jiang and Shao 1995b, Ceulemans, Van Praet and Jiang 1995, Ceulemans <i>et al.</i> 1996, Ceulemans <i>et al.</i> 1997, Kalina and Ceulemans 1997, Will and Ceulemans 1997)
<i>P. trichocarpa</i> × <i>P. deltoides</i>	‘Boelare’	Hampshire, UK	OTC (pots)	cuttings	2 growing seasons (coppice after first)	O ₃	(Taylor <i>et al.</i> 2001)

<i>P. ×canadensis</i> <i>P. deltooides</i>	I-214 'Lux'	Siena, IT	FACE- system rings	cutting	1 growing season		(Tognetti <i>et al.</i> 1999)
<i>P. alba</i> <i>P. nigra</i> <i>P. ×canadensis</i>	'2AS-11' 'Jean_Pourtet' 'I-214'	Viterbo, IT	FACE	cuttings	3 growing seasons + 3 growing seasons after coppice	N (second rotation)	http://www.unitus.it/euroface (Scarascia-Mugnozza <i>et al.</i> 2000, Calfapietra <i>et al.</i> 2001, Ferris <i>et al.</i> 2001, Gielen <i>et al.</i> 2001, Miglietta <i>et al.</i> 2001, Taylor <i>et al.</i> 2001, Gielen <i>et al.</i> 2002, Bernacchi <i>et al.</i> 2003, Calfapietra <i>et al.</i> 2003a, Calfapietra <i>et al.</i> 2003b, Gielen <i>et al.</i> 2003, Gielen, Scarascia-Mugnozza and Ceulemans 2003, Lukac, Calfapietra and Godbold 2003, Taylor <i>et al.</i> 2003, Hoosbeek <i>et al.</i> 2004, King <i>et al.</i> 2004, Liberloo <i>et al.</i> 2004, Tricker <i>et al.</i> 2004, Calfapietra <i>et al.</i> 2005, Cotrufo, De Angelis and Polle 2005, Liberloo <i>et al.</i> 2005, Luo <i>et al.</i> 2005, Moscatelli <i>et al.</i> 2005a, Moscatelli <i>et al.</i> 2005b, Taylor <i>et al.</i> 2005, Tricker <i>et al.</i> 2005, Wittig <i>et al.</i> 2005)
<i>P. tremuloides</i>	6 different clones	Rhineland, WI, USA	FACE	< 1 year	start: 1998	O ₃	http://aspensface.mtu.edu (Isebrands <i>et al.</i> 2001, King <i>et al.</i> 2001b, Noormets <i>et al.</i> 2001, Oksanen, Sober and Karnosky 2001, Takeuchi <i>et al.</i> 2001, Karnosky <i>et al.</i> 2002, Holmes <i>et al.</i> 2003, Karnosky <i>et al.</i> 2003b, Karnosky <i>et al.</i> 2005)
<i>P. deltooides</i>	Bartr.	Biosphere 2 Laboratory, Oracle, AZ, USA	Bays at 430, 800 and 1200 μmol mol ⁻¹ CO ₂	cuttings	start: 1998 (coppiced yearly)	drought	(Pegoraro <i>et al.</i> 2004, Turnbull <i>et al.</i> 2004, Ananyev <i>et al.</i> 2005, Barron-Gafford <i>et al.</i> 2005, Murthy <i>et al.</i> 2005, Pegoraro <i>et al.</i> 2005a, Pegoraro <i>et al.</i> 2005b)

Abbreviations: FACE = free-air CO₂ enrichment, N = nitrogen, OBRB = open bottom root boxes, OTC = open-top-chamber