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Water Stress and Afforestation: A Contribution to Ameliorate Forest Seedling Performance During the Establishment

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1. Introduction

For hundreds of years, forest ecosystems have been supplying human needs with timber and non-timber products such as oils, resins, tannins and other goods like wood or medicine. Beyond material goods, forests also provide a range of other relevant environmental benefits. The accelerating loss of forests represents one of the major environmental challenges. Intensive commercial logging focused mainly on timber products cause unfortunately degradation of extensive areas and, at the same time, the conversion of forest land for commercial agriculture, subsistence farming and logging for fuel wood are considered the main factors of deforestation. Both degradation and deforestation lead to a considerable reduction in the world forest resources. In the last decades worldwide concern about the necessity to protect native forests emerged and a shift in silviculture occurred, changing into a broader concern where environmental values and diversified interests are becoming more important (Food and Agriculture Organization of the United Nations [FAO], 2009, 2010).

Historically, an increase in economic growth and population has been the main force fuelling global wood consumption. The expected increase in world population in the next years and the rise in the standards of living will increase wood demand. As this additional wood demand cannot come from further increases in the harvest of natural forests, it must come from planted forests. Reforestation and afforestation seem to be effective alternatives to increase forest production land, thus covering those timber needs and at the same time contributing to reduce timber extraction in many natural forests (FAO, 2009, 2010; Paquette & Messier, 2010; United Nations Framework Convention on Climate Change [UNCCC]).

Commercial plantations can provide large quantities of timber to keep up with the increasing demand of forest products (sawmills, pulp and particle board industries mainly), and can also be used to provide environmental benefits. It is important to consider that the potential supply of wood arising from forest plantations will depend on the capacity to

maintain the rate of new planting and forest productivity. Forest plantations have greater structural diversity than agricultural crops (Lindenmayer et al., 2003; Viglizzo et al., 2011); they can reduce wind and soil erosion (Kort et al., 1998) and are particularly important for carbon sequestration, contributing to climate change mitigation (Laclau, 2005; Vitousek, 1991). Apart from these plantations benefits and according to environmental conditions of the site, some trade-offs need to be considered (Jackson et al., 2005; Jobbágy & Jackson, 2004).

Forest productivity is determined by genetic potential and is closely linked with environmental resources. Both genetic and environmental factors control plant physiological processes regulating the biomass production of forest stands. The growth depends on solar energy captured by the canopy and water and nutrients provided by the soil for converting CO₂ to photoassimilates (Kozłowski & Pallardy, 1997). Unfortunately, the environment imposes many resource limitations to growth; therefore, forest stands can rarely achieve their potential productivity for extended periods. Indeed, over a wide range of climatic and soil conditions there is a large variation in forest net primary productivity around the world (Gowers et al., 1992; Kozłowski, 2002; Perry et al., 2008; Waring & Schlesinger, 1985).

Plantation performance is commonly hindered by both biotic and abiotic factors. The rapid growth rates of the species used in commercial plantations (like *Pinus*, *Eucalyptus*, *Populus*) are based on their high water demands (Braatne et al., 1992; Florence, 1996; Monclus et al., 2006; Whitehead & Beadle, 2004). But the availability of water, one of the main factors related to plant growth, varies both seasonally and from year to year, regulating forest productivity. During the rotation cycle trees are often subjected to periods of soil and atmospheric water deficit but the effects on plant performance are more serious during the establishment period because they may not only reduce seedlings growth but also compromise their survival. Besides climatic factors, soil water availability is determined by soil factors, stand density and levels of understory competition.

It is crucial to understand the physiological processes that determine growth and survival during the establishment and the response of tree seedling to environmental stimuli because they deeply influence future productivity. Nowadays, all of these issues face new challenges which are expected to come out in the actual context of climate change. In the future an increase in the frequency of drought events is predicted even outside semi-arid and arid areas (Intergovernmental Panel on Climate Change [IPCC], 2007). Under stressful and/or unexpected weather conditions a careful silvicultural planning is essential to ensure success. Silvicultural decisions including the selection of high quality plant material and practices applied during the establishment are tightly connected with plantation performance (Smith et al., 1997).

In this chapter, among the multiple factors that influence growth during the forest establishment, we chiefly discuss the importance of water supply on tree growth and how water stress compromises plant performance. We take into account the interactions between water deficiencies and other abiotic and biotic factors that in fact modulate survival and plant growth. We analyze the potential mechanisms that tree seedlings exhibit to overcome serious stressful conditions during the establishment phase and the effects of nursery techniques applied to produce good quality stock, particularly those imposed to acclimate seedlings to water stress before outplanting. We include results of several studies in species of great importance in afforestation programs.

2. Water stress on tree function and growth

Water is an essential resource for plant function and growth. Most of physiological processes are directly or indirectly regulated by tissue water content. Water is solvent of gases, salts and solutes within and among cells and from organ to organ; it is required to provide a substrate and a medium for biochemical reactions and for the transport of mineral ions, as well as to maintain cell turgor for cell enlargement, stomatal opening and the maintenance of the form of young leaves and slightly lignified structures. Only a small fraction of water that passes through the plant and is lost by transpiration during its whole life remains in plant tissue. When leaving the plant through transpiration, chiefly from the leaves, water has an additional cooling effect that allows a plant to maintain a temperature suitable for metabolic reactions and life (Kozloswki & Pallardy, 1997). Zhaner (1968) reviewed the importance of an adequate water supply for woody plants. There is a very high correlation between the amount of wood production and the available soil moisture. As a matter of fact, a large proportion of the variation in diameter growth can be attributed to variation in the availability of water. Although it is one of the most abundant substances in the environment, there is a great temporal and spatial variation in water supply for plants. Water deficit is mainly caused by droughts that refer to periods in which rainfall fails to keep up with potential evaporation, generating the exhaustion of soil water content. Insufficient water supply to plant leaves can also arise in response to other circumstances, either abiotic or biotic. For instance when, despite the existence of adequate water in the soil, there is large air humidity deficit (Hirasawa & Hsiao, 1999; Levin et al., 2009). Regardless of the amount of precipitation, water may not be available because it is frozen. Several soil properties, like soil texture, salinity and/or hydraulic conductivity reduce water supply. Plants can have difficulties in obtaining water from the soil if salts are present in the root zone (osmotic effect). Generally, the need of energy to allow water uptake is greater when the soil solution is saline than when it is not. Competition of neighboring vegetation is also another cause of water depletion to the tree crop (Nielsen & Orcutt, 1996; Passioura, 1996). When soil water availability is scarce, the magnitude of plant transpiration losses is usually greater than root absorption and therefore plants are prone to experience water stress, which is mainly evidenced through a lowering in the plant relative water content and/or in the water potential, decreasing tissue turgor and compromising cellular expansion. Stomatal closure has been identified also as an early response to water deficit that limits the photosynthesis rate leading to a limitation in plant carbon fixation. It is still under debate whether stomatal closure is triggered by chemical signals synthesized in dehydrating roots or by changes in plant hydraulic conductivity (Brodribb, 2009; Brodribb & McAdam, 2011; Cochard et al., 2002; Davies et al., 1986). The depression in gas exchange also reduces water loss leading generally to higher water use efficiency, but the lowering in the photosynthesis rate as well as the decrease in plant leaf area due to leaf desiccation and shedding causes a reduction in plant growth (Chaves et al., 2003; Hsiao, 1973; Kozlowski, 1982; Kramer & Boyer, 1995). Excess of radiation constitutes another concomitant type of stress under water limited conditions. As water stress reduces the rate of photosynthesis, the absorption of light exceeds its utilization. If plants lack the ability to dissipate that excess of energy through external and internal mechanisms of protection, they undergo photoinhibition, i.e. the oxidative damage in the photosynthetic apparatus (Adir et al., 2003; Chaves et al., 2003; Powles, 1984).

As well as affecting plant growth, water scarcity modifies the pattern of carbon allocation (Cannell & Dewar, 1994; Turner, 1986a). More photoassimilates are transferred to belowground components, especially to the fine roots and higher root-shoot ratios can be found in plants experiencing water stress in comparison to plants under high water availability (Guarnaschelli, 2009; Guarnaschelli et al., 2006; Li et al., 2009). In addition, droughts may change diverse morphological and anatomical characteristics. For example, leaves are usually smaller, thicker, more cutinized and their vessels diameter, whereas cell walls are thicker and more lignified. Plant chemical composition may be altered, which means that it can influence the way plants protect themselves against other stressful factors. Plant vigor and overall resistance to stress from insects and/or diseases are influenced by water status (Kozłowski, 1982; Kozłowski & Pallardy, 1997).

Tree species differ in their optimal water requirements and in their susceptibility to water stress. Certain stages of plant growth are more sensitive to water stress than others. While some species are well-adapted to short period of water deficit, they become vulnerable to prolonged water deficit decreasing stomatal conductance and leaf area, changing the pattern of biomass allocation and reducing stemwood production. Water stress compromises cambial growth in different ways. It slows or stops the production of xylem cells and influences the seasonal duration of xylem production and the time of initiation and duration of the latewood production (Kozłowski & Pallardy, 1997). Besides differences among species, the effects and the magnitude of loss caused by droughts vary among provenances or clones (Arend et al., 2011; Guarnaschelli, 2009; Guarnaschelli et al., 2010b) and depend on the season in which the water deficiency occurs (Guarnaschelli, 2009), as well as the intensity and duration of drought (Guarnaschelli et al., 2003c; Guo et al., 2010; Osório et al., 1998). Damage is also linked to the health and vigour of the plants previous to the drought. Plants with healthy root systems and adequate carbohydrate reserves will behave much better during and after a drought period (Kozłowski, 1992; Marshall, 2006).

3. Problems during the forest establishment

Planting has become the main method of reforestation in many parts of the world. It is more predictable and reliable than natural regeneration and allows a more effective control of stand density. When planting nursery grown seedlings or cuttings, the most critical processes of natural regeneration, from seed production to the early seedling developmental phase, are skipped (Stoneman, 1994; Tappeiner & Helms, 1973). Forest plantation area has increased considerably in the last years and today includes different species selected due to the good availability of planting material, clear silvicultural management techniques and high productivity. In South America, for instance, forest plantations consist of different introduced species like *Eucalyptus* (*Eucalyptus grandis*, *Eucalyptus globulus*, *Eucalyptus camaldulesis*, *Eucalyptus urophylla* as well as interspecific hybrids), *Pinus* (*Pinus taeda*, *Pinus elliottii*, *Pinus caribaea*, *Pinus ponderosa*), *Populus* (*Populus deltoides*, *Populus xcanadensis*), *Salix*, *Gmelina*, *Toona* among others. The development of forest nurseries, which can produce large quantities of tree seedlings annually, allowed the possibility of establishing large areas of forest plantations.

Planted material is generally exposed to, and has to overcome stressful conditions after planting. Several factors are found to affect the early establishment of forest plantations. However, among abiotic ones, water deficiency is the most common limitation for seedlings from outplanting and all over the establishment (Burdett, 1990; Close et al.,

2005; Margolis & Brand, 1900). Water limitations, derived from periods of soil and/or atmospheric water deficiencies, affect plantations both directly by reduced growth and increased mortality, and indirectly by increased susceptibility to, or damaged by, other abiotic and/or biotic stress factors.

Immediately after being planted, seedlings are subjected to transplant shock, a phenomenon characterized by a depression in the physiological status mainly associated with moisture stress. The alteration in plant water status, caused by limited contact between roots' seedlings and soil, impairment of seedling root function, high evaporative demand, low hydraulic conductance of suberized roots and/or root confinement, constitutes the main constraint for plant survival and growth after planting (Burdett, 1990; Grossnickle, 2005; Kozłowski & Davies, 1975; Rietveld, 1989; Sands, 1984). Low root-soil contact can occur even if soil water potential is near to zero. Therefore transplant shock is not necessarily associated with the soil water status, but low water availability or post-planting droughts intensifies that condition and aggravates it.

The first physiological symptom of transplanting shock is the lowering in predawn water potential. As water potential becomes more negative, other physiological symptoms appear like reduced stomatal conductance, photosynthesis, transpiration and growth (Grossnickle, 1988; Guehl et al., 1989; Jacobs et al., 2009; Sands, 1984). These symptoms were observed by Mena-Petite et al. (2005) after transplanting seedlings of *Pinus radiata* both under drought and under well-watered conditions. Reduced leaf area, leaf shedding, shoot growth and needle length area are the principal morphological symptoms (Haase & Rose, 1993; Struve & Joly, 1992).

The improvement in root-soil contact is mediated by the extension of new root growth. The ability to regenerate new roots after planting is a key process to reduce the effects of transplanting shock and assure plant survival after planting (Rietveld, 1989; Sands, 1987). It has been observed in some Conifer species that new root growth is largely dependent on current photosynthesis (Maillard, 2004; Phillipson, 1998; van den Driessche, 1987), also in some Hardwoods species (Sloan & Jacobs, 2008). Seedlings that develop their root systems after planting reestablish a proper water balance. With a favorable water status they can have a cycle of root growth supported by photosynthesis and photosynthesis supported by root growth. Therefore, high seedling water potential during the outplanting is a favorable condition to initiate new root growth. All plant attributes that ensure a better water balance will benefit the process of transplanting by granting more resistance to water stress (Burdett, 1990).

Bare root plantings are specially accompanied by specific transplanting stress. When plants are lifted for transplanting, a large percentage of the absorbing roots are severed and/or damaged, therefore, the newly transplanted tree suffers from water stress. Even trees that have been grown in containers and could retain their whole root system suffer from some degree of transplant shock. However, container seedlings have proved to have better performance than bare root plants, especially when conditions are more stressful (Barnett & McGilvray, 1993).

When transplanting shock has been overcome, additional drought events that may occur several times along the rest of the establishment period may cause depression in plant function and growth. Forest sites are frequently subjected to periodic droughts. On drought-prone sites a successful regeneration will depend mainly on the ability of plants to tolerate moisture stress.

As mentioned above, other abiotic factors can affect independently or interact with the water availability and cause serious damage in recently planted tree seedlings. Usually several stress act simultaneously with droughts such as heat and high irradiance intensifying moisture deficiencies. By contrast low temperatures may arise. Freezing temperatures induce cell dehydration, which is the most common damage. In specific tissue and organs damage can occur for other reasons, like cell death, separation of cell layers, creation of cavities and frost cracks, xylem embolism among other (Pearce, 2001). Drought as well as low temperature and water-logging reduce water uptake and hence the rate of photosynthesis. An increase in irradiance may cause photoinhibition. Nevertheless, photoinhibition may arise indirectly from the action of all stress factors that cause a reduction in photosynthesis and induce excess light absorption. The effects of competing vegetation, restricting resource availability and herbivory damaging leaf tissues on seedlings performances are discussed later (Burdett, 1990; Close et al., 2005).

4. Strategies to cope with water deficiencies during the establishment

As the establishment of forest plantations requires long-term investments, it is crucial to select the best management options in order to improve forest productivity in site-specific conditions and to make cost-effective decisions. Moreover, when stressful and/or unexpected weather conditions are predicted, careful silvicultural planning is essential to ensure success. Silvicultural decisions including the selection of high quality plant material and the application of adequate site preparation techniques, proper planting and plantation maintenance practices are the key to a successful establishment and are tightly connected with plantation performance (Blum, 2003; Smith et al., 1997; Tappeiner et al., 2007). In fact, they may be adjusted to withstand water stressful conditions since transplanting generates a severe physiological shock and moisture conditions exclude the establishment of trees. There are many textbooks on Silviculture and availability of information that discuss thoroughly the effects of alternative cultural practices before and after plantation. Our analysis will focus mainly on the strategies to improve seedling quality.

The use of high quality seedlings as well as the application of several cultural practices before and after planting can help to overcome stressful conditions and enhance plantation performance. Regarding particularly outplanting stress, although some level of transplant shock is unavoidable, stock with high performance will minimize the event (Burdett, 1990; Close et al., 2005; Grossnickle, 2005; Rietveld, 1989).

The quality of seedlings is the result of its genotype, growing conditions and cultural practices applied in nurseries. In the context of transplanting process, the utilization of provenances or clones that have been tested as drought tolerant and that have been subjected to appropriate nursery management will show a better performance.

4.1 Mechanisms associated with drought tolerance

Chaves et al. (2003) suggested that it is essential to have a holistic understanding of plant resistance to water stress to improve crop management and breeding techniques. As originally defined by Ludlow (1989), under drought conditions there are physiological processes and morphological attributes that could extend the period of active growth by controlling water uptake, water loss and hence cell turgor. Water loss can be effectively controlled by stomatal closure and, ultimately, by leaf shedding. To maintain to some extent

cell turgor and stomatal conductance and a sizeable photosynthesis rate under drought conditions, plants have developed particular physiological processes. Species possessing these attributes are very sensitive to dehydration and avoid water deficits when soil moisture limitation occurs. Conversely, other species tolerate dehydration mainly through osmotic adjustment or changes in tissue elasticity.

Drought avoidance, a strategy held by many tree species, is characterized by relatively high lethal water potential or high relative water content with relatively little osmotic adjustment, while drought tolerance species have lower lethal water status values and relative water content and display much more active changes in osmotic potential when subjected to drought conditions. Not all plants fit closely in one category or another but the division in plant responses helps to understand consequences for the species like survival, potential for carbon fixation, maintenance of growth under drought, and metabolic costs of drought resistance mechanisms (Ludlow, 1989).

Schulte & Hinckley (1987) observed that the ability of stomatal closure varied among *Populus* species and their interspecific hybrids, and some of them required a large change in tissue water content for stomatal closure. For example, *P. deltoides* and its hybrids display a large number of strategies avoiding water deficiencies. Among them a reduction in stomatal conductance and transpiration (Marron et al., 2002; Silim et al., 2009), leaf abscission, and decreases in shoot:root ratio (Liu & Dickman, 1992).

For some species, greater biomass allocation to roots relative to shoots, that increase root growth and reduced leaf area, as well as stomatal regulation seem to be effective mechanisms to resist moisture stress (Jacobs et al., 2009). As it has been suggested, plants respond to shifts in resource supply by allocating carbon to the organ involved in capturing the limited resource. Root development is fundamental under water and nutrient deficiency, resulting in plants that have lower shoot:root ratios and greater capacity to absorb water and minerals relating to the shoots that must be supported. The possession of a deep and thick root is considered highly important because it allows access to water deep in the soil profile. The investment of carbon in a deep root system may have, however, a yield implication due to lost carbon allocation to the shoot.

Under water stress, plants of *Alnus rubra* may show leaf senescence and shedding. These processes lead to a favorable decrease in shoot:root ratio and high survival, whereas the reduction in the photosynthetic area resulted in a reduced shoot growth (Pezeshki & Hinkley, 1988).

Thus, mechanisms that allow plants to avoid water deficiencies present some disadvantages because they imply a reduction in leaf area and gas exchange, then the photosynthetic capacity is reduced and at the same time the change in the pattern of carbon allocation favoring root growth reduces shoot growth.

Among the drought tolerance mechanisms, osmotic adjustment implies the accumulation of organic and inorganic solutes in the cell that reduces water potential and allows plants to obtain water from a lower water potential medium and sustain the physiological processes. The capability of osmotic adjustment appears to be controlled by only one or two genes and is simply inherited (Morgan & Condon, 1986). This mechanism may be an advantageous strategy to maintain cell water status (Ashraf et al., 2011; Morgan, 1984). The maintenance of cellular turgor by lowering the osmotic potential in plants exposed to low water conditions is considered to be one of the most important mechanisms of plant adaptation to environmental stresses (Turner, 1986a, 1986b; Turner & Jones, 1980).

The drought induced lowering in osmotic potential has been observed in many coniferous tree species (Edwards & Dixon, 1995; Nguyen-Queyrens & Bouchet Lannat, 2003) as well as in hardwood species (Abrams, 1990; Arndt et al., 2000; Marron et al., 2002; Tschaplinski et al., 1998). In some cases the magnitude of adjustment was related to the maintenance of plant growth rate (Johnsen & Major, 1999; Meier et al., 1992; Pita & Pardos, 2001; Tan et al., 1992).

Considerable variation in the osmotic adjustment capacity has been observed. Among *Eucalyptus* species Lemcoff et al. (1994, 2009) detected different magnitude of osmotic adjustment among seedlings of *E. grandis*, *Eucalyptus tereticornis*, *Eucalyptus viminalis* and *E. camaldulensis*. Other studies that considered different species of *Eucalyptus* reached similar results confirming genetic variability for this mechanism (Merchant et al., 2006; Merchant et al., 2007; White et al., 2000). Variability is also present among provenances of a single species (Guarnaschelli et al., 2001; Guarnaschelli et al., 2006; Tuomela, 1997) or among clones (Pita & Pardos, 2001). Guarnaschelli (2009) compared the response to drought conditions in 13 provenances of *E. globulus* and found differences both among subspecies and also among provenances within some of the subspecies.

As originally stated by Turner (1986a), osmotic adjustment would only represent a useful strategy to tolerate drought if it also develops in the root system (Merchant et al., 2006; Nguyen & Lamant, 1989; Parker & Pallardy, 1988). Guarnaschelli & Lemcoff (2001) detected osmotic adjustment in both shoot and roots of *E. globulus* subsp. *maidenii* provenances and difference in the capacity to adjust cell-wall elasticity.

Gebré & Tschaplinski (2000) indicated that drought tolerance in *Populus* is not only related to the capacity of solute accumulation, but also to low values of osmotic potential itself. Consistent with this statement, Guarnaschelli et al. (2010b), evaluating the drought tolerance of several *P. deltoides* clones, recently showed that they have low osmotic adjustment capacity but in contrast there were consistent differences in osmotic potential among them.

Osmotic adjustment has been recognized as an important cellular drought-responsive trait and, despite past speculations, there is no definitive proof that the osmotic adjustment capacity entails a compromise to potential crop yield (Blum, 2005). Moreover, after stress relief it has been observed greater capacity of stem diameter and height growth in seedlings of *E. globulus* subsp. *globulus* that had shown higher osmotic adjustment capacity (Guarnaschelli, 2009), results that present similarities with those of Osorio et al. (1998).

Although the maintenance of leaf turgor is often linked to osmotic adjustment, changes in tissue elasticity may also contribute to turgor maintenance in plants with (Guarnaschelli, 2009; Lemcoff et al., 2002; Pita & Pardos, 2001) and without osmotic adjustment. The regulation of cell-wall elasticity, generally called elastic adjustment and measured as the change in maximum bulk modulus of elasticity, also aids some species to maintain tissue hydration (Pita & Pardos, 2001; Prior & Eamus, 1999; Stoneman et al., 1994)

Under moderate water stress an increase in tissue elasticity would allow the maintenance of tissue turgor and physiological functions and growth (Fan et al., 1994; White et al., 1996). But also a decrease could represent a useful strategy to overcome low water availability (Nielsen & Orcutt, 1996) while conditioning a decrease in plant water potential, increasing the water potential gradient between plant and soil allowing water uptake. An additional consequence of this kind of cell-wall adjustment, and the concomitant rapid lowering in the water potential, is the closure of stomata that prevents severe water deficit conditions (Dumbroff, 1999; Lemcoff et al., 2002). It has been observed that under moisture stress some

species increase cell-wall elasticity while others decrease it (White et al., 1996; White et al., 2000); this behavior was also detected among provenances of a single species (Guarnaschelli, 2009). A decrease in cell-wall elasticity has been associated with tissue maturation (Bowman & Roberts, 1985; Parker et al., 1982), which commonly occurs during fall and winter. Water stress conditions of similar intensity and duration may exert different responses in cell-wall elasticity, like was observed in subspecies and provenances of *E. globulus* (Guarnaschelli et al., 2001; Guarnaschelli, 2009).

It is important to highlight that the expression of drought tolerance mechanisms may vary if multiple stress factors are simultaneously affecting plants, phenomenon which in fact occurs quite often in nature. Some studies under controlled conditions assessed the responses of several *Eucalyptus* provenances and *Salix* clones submitted to different water and light availability regimes, analyzing the genetic contribution as well as the level of restriction and the interaction effects. In saplings of *Salix* submitted to drought conditions, a decrease in osmotic potential at full turgor and at the turgor loss point occurred in plants growing under full sunlight but also in those that were growing under moderate shade conditions (Guarnaschelli et al., 2010b). These results contrast with those that argue that only dryness and high sunlight trigger a lowering in osmotic potential, stating that under high irradiance conditions there is a higher capacity to accumulate solutes and where osmotic adjustment can take place (Aranda et al., 2005; Uemura et al., 2000). Thus, osmotic adjustment contributed to turgor maintenance processes, allowing an increase in the drought tolerance under full sunlight and moderate shade conditions, without a compromise between the plants adjustments to cope with those two kinds of stress factors (Smith & Huston, 1989). These responses indicate that shade could alleviate the effects of drought (Guarnaschelli et al., 2007; Guarnaschelli et al., 2008), although this is not always the case. Recently lower water potential values were observed in droughted seedlings of *E. grandis* and *E. grandis* x *E. camaldulensis* clones that were growing under shade conditions in contrast to those that were under full sunlight. All shaded plants displayed high plasticity increasing their leaf area as an strategy to increase the uptake of light, but the decrease in shoot:root ratio observed in water stressed plants was not as effective as the change that occurred in water stress plants growing under full sunlight, which allowed better water acquisition under moisture deficit conditions (Guarnaschelli et al., unpublished data).

Breeding for drought tolerance

Tree selection can be a relevant component when dealing with moisture stress. In fact, species, provenances and/or clones genetically adapted to certain levels of water deficiencies can overcome soil and atmospheric water deficits. Plants originating from drier sites are more likely to survive drought than those from mesic sites because they have different mechanisms that help them to tolerate low water availability.

As discussed previously, trees possess a varied number of mechanisms to compensate for water limitation that allow the acquisition of water resources or limit water loss, and indeed represent useful tools in the context of the establishment. Genetic variability in the responses to water stress has been tested in different tree species, among populations or even clones of a single species. It is accepted that high levels of genetic variation within any species improve the potential to withstand abiotic stress, such as droughts and biotic stress as well. However, the ability of plants to sense stressful conditions and environmental change through plastic responses is part of this genetic variation. Trees may also exhibit certain level of physiological and/or morphological change, which is defined as the capacity of

organisms to produce different phenotypes according to environmental changes (Schlichting, 1986; Valladares, 2006). Phenotypic plasticity has been recognized now as a heritable characteristic and can be genetically controlled (Bradshaw, 2006; Lande, 2009). It has a great potential importance in plant evolution (Nicotra et al., 2010).

Mechanisms or traits that avoid or tolerate the dry conditions include a variety of morphological, physiological and biochemical attributes at biochemical, cellular, tissue and whole-organism levels, as discussed previously. Most of them are dependent on other mechanisms; in fact, a sequence of adjustments occurs simultaneously in plants.

Breeding for drought stress tolerance in forest trees should be given high research priority in plant biotechnology programs. Plant response to abiotic stress like water deficiency involves many genes and biochemical-molecular mechanisms. Plant modification to enhanced stress tolerance is based on manipulation of genes that protect and maintain the function and the structure of the cellular components. Due to the complex responses to stress it is more difficult to control and engineer in contrast to traits of engineered resistance to pests or herbicides. Although the improvement of stress tolerance by gene transformation has resulted in important achievements, the complexity of the mechanisms involved makes this task very difficult.

Despite the existence of multiple traits related to drought resistance, the selection of improved growth in water limited environments may not be generalized because it may lead to a trade-off between traits related to both drought resistance and growth. The selection of drought-resistant and productive material may not be simple to achieve, as we mentioned previously. Some species exhibit numerous drought resistance strategies that may impact on productivity differently, like lower leaf area, leaf abscission, enhanced root growth, stomatal closure among others as has been noted before.

But although drought tolerance may be considered as a penalty towards potential productivity, it is not necessarily the case (Blum, 2005). To maintain growth and productivity under water limited conditions, plants have to exercise specific tolerance mechanisms. Plant breeders have improved the performance of crops by breeding for improved yield or quality under conditions of water shortage; however the selection of this kind of plant material is nowadays becoming more important. The development of new tools for monitoring and understanding plant responses to water deficit, ranging from molecular, plant and ecosystem, will allow a better understanding of plant performance under stress, which will be very useful to breeding programs (Chaves et al., 2003).

Pita et al. (2005) discussed the use of particular physiological traits in breeding programs for improved yield under drought conditions focusing mainly in *E. globulus* experience in southern Spain. They explained that *E. globulus* must be considered a species with avoidance capacity because high survival and growth were observed through lower water use efficiency and embolism tolerance. They highlighted the relevance of several hydraulic characteristics, like maximum permeability, maximum leaf conductivity and vulnerability to cavitation and its relationship to stomatal conductance. Osmotic adjustment capacity, a drought tolerance strategy, has also been observed in this species (Guarnaschelli, 2009; Guarnaschelli et al., 2003; Guarnaschelli et al., 2006; Pita & Pardos, 2001; White et al., 1996).

4.2 Nursery conditions and culture

Nursery conditions and culture affect the structural and functional characteristics of tree seedlings. They can produce planting stock of different size and physiological state;

however, each ecological condition needs a different type of plant according to it. If field site conditions where seedlings are going to be transplanted differ from those at nurseries, they may be severely stressed because the process of acclimation in the field occurs over several days, or even weeks. Therefore, it is necessary to use plants suited to the environmental restrictions in which they will be planted (Burdett, 1990).

Nurseries adapt their environmental conditions and cultural practices to produce target seedlings that will assure survival and growth according to the species and site conditions. The alternative methods of seedling production are outlined in several manuals, which cover all phases of production from seed collection to seedling storage and provide detailed information about nursery practices, allowing to secure high quality material (Duryea & Landis, 1984; Landis et al., 1989, 1990, 1992).

Characteristics of target seedlings include height, stem diameter, root volume, root growth potential, plant water status, drought resistance and frost hardiness among others (Rose et al., 1990). Seedlings' height and stem diameter, the most common traits used to assess seedling quality are not always accurate predictors of performance after outplanting. As stated by Burdett (1990), it appears that the central processes in plantation establishment are root growth and photosynthesis in mutual dependence. All attributes that assure a better seedling water balance favor the maintenance of photosynthesis and root growth and benefit the process of transplanting shock in coping with water stress.

In the context of establishment commonly hindered by water stress, plants with root systems of high morphological and physiological standards enable them to establish rapidly and succeed upon outplanting. Large root volume, high root fibrosity and an increased number of first-order lateral roots have shown some correlation with improved field performance (Landis, 2010). Leaf area, shoot:root ratio, the capacity to regulate stomatal conductance as well as the development of osmotic and elastic adjustment will help seedlings performance. Water and nutrient regimes are of particular importance during seedlings production because they control both the rate and type of growth and hence have relevant impact on morphological and physiological attributes mentioned above (Duryea & Landis, 1984; Landis et al., 1989).

Drought acclimation

Plant drought acclimation is a process that results after the exposure to stress conditions that induce structural and functional adjustments, allowing the acquisition of tolerance to drought. Acclimation is a process that occurs spontaneously in nature, helping plants to survive and grow under stress. For example, many plants increase their freezing tolerance at the end of summer and fall upon exposure to low non-freezing temperatures and short days, a phenomenon known as cold acclimation that increases their cold tolerance. At the beginning of spring, when temperatures are rising, this process is reversed. Other plants experience drought acclimation when exposed to moisture stress (Kozłowski & Pallardy 2002; Yordanov et al., 2000).

Drought preconditioning or drought hardening is a common practice applied in nurseries, which entails exposure to sublethal stress and allows seedlings to trigger plastic responses associated with drought acclimation, finally resulting in protection against lethal stress. Submitting tree seedlings to nursery stress conditions may render them more protected from injuries or reduced growth when environmental stresses are abruptly imposed than plants not previously stressed. It is accepted that drought preconditioning helps seedlings to improve their performance, competitiveness and productivity under field conditions. The

process of acclimation occurs over days or weeks. In contrast, poor drought acclimated seedlings will exacerbate transplanting shock.

Drought preconditioning consists in withholding irrigation or restricting the amount of water supplied for short periods. It is generally applied during the last weeks of seedlings production (Landis et al., 1989; Vilagrosa et al., 2006). An irrigation regime that restricts the water availability will induce adjustments in several morphological attributes such as aerial growth and the pattern of dry matter partitioning, reducing leaf area and shoot:root ratio (Lamhamedi et al., 2001; Stewart & Lieffers, 1993). Stock types with low leaf area and shoot:root ratio perform better under drought conditions, since a more favorable balance between water uptake and loss is reached (Cregg, 1994). In addition, physiological adjustments like stomatal regulation, osmotic adjustment and/or elastic adjustment may also contribute to better performance after planting. Several Conifer species deliberately exposed to water deficit displayed drought hardiness and were able to maintain more favorable water status and gas exchange (Edward & Dixon, 1995; van den Driessche, 1991; Zine El Abidine et al., 1994; Zwiazek & Blake, 1989), and greater survival after plantation compared to non-conditioned plants (van den Driessche, 1992).

Among hardwood species, in several *Salix* cultivars drought acclimation was manifested in decreased stomatal conductance, osmotic potential and leaf area to vessel internal cross-sectional area ratio, and increased shoot hydraulic conductance. An increase resistance to stem xylem cavitation was observed in only one clone (Wikberg & Ogren, 2007). Seedlings of three provenances of *E. globulus* that were submitted during one month to drought cycles of 6 and 9 days, considered as moderate and severe stress, displayed plastic changes: osmotic adjustment and reduced leaf area. The extent of osmotic adjustment was influenced by the degree of drought preconditioning; osmotic potential at full turgor in severe stressed plants was significantly lower than in moderate stressed plants. Thus, the magnitude of the adjustment increased with the intensity of water stress, suggesting an additive effect in this drought tolerance mechanism. When non conditioned plants (daily irrigated) and drought conditioned were all evaluated under a new drought cycle, the last showed higher water status and stomatal conductance (Guarnaschelli et al., 2003c). Similar results were observed with three representative Mediterranean species (Vilagrosa et al., 2003; Villar-Salvador et al., 2004).

Plants may display different phenotypic plasticity in their attributes according to the intensity of the drought preconditioning (Guarnaschelli et al., 2003c). Medium and moderate levels of water stress induced a higher level of hardiness in comparison with severe water stress conditioning (Villar Salvador et al., 2004). It is important to highlight that severe water stress preconditioning is likely to induce some level of tissue damage and a higher decrease in growth due to the high dehydration experienced or low growth rate after transplanting.

As for bareroot seedlings, the control of water irrigation may be more difficult to achieve, preconditioning includes root pruning. After being root-pruned, seedling of *Quercus rubra* and *Juglans nigra* experienced water stress, which triggered many changes in growth as well as morphological and physiological attributes. Undercutting reduced seedling growth and shoot:root ratio and increased the number of first order lateral roots, which increased field survival (Schultz & Thompson, 1997). These results show that drought preconditioning triggers morphological and physiological adjustments associated with an increase in drought tolerance.

Several studies have also tested the effects of preconditioning on growth and survival after planting. Some of them indicate that there is a positive effect on survival (Guarnaschelli et

al., 2003a; Guarnaschelli et al., 2006; van den Driessche, 1992), whereas only a few show a positive effect on growth (Arnott et al., 1993).

Guarnaschelli et al. (2006) evaluated the effect of drought preconditioning after transplanting. Three provenances of *E. globulus* subsp. *bicostata* were subjected to moderate water deficit conditions. They evidenced drought acclimation capacity showing osmotic adjustment, a reduction in seedlings size, leaf area, shoot:root ratio and stomatal conductance. After being transplanted under moisture stress conditions, drought preconditioned plants showed better water status, gas exchange capacity and higher levels of survival than well irrigated plants. It was observed that midday relative water content (RWC) was closely correlated with survival as also found by Mena-Petite et al. (2005), while survival was inversely correlated with shoot:root biomass ratio. Both RWC and shoot:root ratio could be considered reliable indicators of potential initial survival and are closely associated with establishment success (Grossnickle & Folk, 1993).

Several processes involved in drought tolerance confer also an increase in cold tolerance (Bigras & Dumais, 2005; Moraga et al., 2006). It has been observed that drought resistant genotypes of *E. globulus* showed greater cold tolerance than drought susceptible ones (Costa e Silva et al., 2009). The application of drought hardening treatments may also increase cold tolerance. The accumulation of solutes that commonly occurs under water stress decreases the osmotic potential and may cryoprotect freezing labile cell structures. Coopman et al. (2010) applied two drought hardening treatments to different genotypes of *E. globulus* subsp. *globulus* under nursery conditions that resulted in an increase in the seedlings drought tolerance but also in their freezing tolerance. They observed that the freezing tolerance varied with the genotypes and the level of water stress preconditioning.

The interactive effects of water and other factors during seedlings production

When dealing with a process of drought acclimation, many other factors can influence plant responses to drought preconditioning, as is the case of nutrition, age and/or growing media conditions. In fact the nutrient regime as well as the growing media used to produce forest containerized seedlings can strongly affect plant during the drought preconditioning period and their performance after outplanting.

The growing media usually consists of a mix of organic materials, like sphagnum peat moss, composted pine bark, coco fiber or other local organic products with inorganic components as perlite, vermiculite or sand. The mix is selected in order to obtain a growing media of slightly acid pH, high cation exchange capacity, low inherent fertility, adequate porosity, and freedom of pests, all characteristics that allow the production of healthy seedlings. Both the water-holding and nutrient supplying properties are functions of the different growing medium components; therefore the irrigation and fertilization have to be adjusted according to their characteristics (Landis et al., 1990). Artificial mixes dry out much more rapidly than surrounding soil, so watering is very important. Verdaguer et al. (2011) observed that when seedlings of *Quercus coccifera* were grown in natural soil compared to standard nursery growing medium growth rates were higher. Results suggest that the former were acclimated to the soil and higher photosynthetic rate, transpiration and stomatal conductance were observed in those seedlings.

Besides irrigation regime, fertilization can have important effects on plant quality modifying their performance under drought during the establishment. Harvey & van den Driessche (1999) observed that increasing nitrogen (N) supply under dry conditions increase leaf loss

and decrease water potential in *Populus trichocarpa*, making them more vulnerable to cavitation. The effects of N fertilization on drought and cold acclimation were assessed on several forest Mediterranean species. High N level decreased frost hardiness in *Pinus* species. In all species high N increased shoot:root ratio and in some of them stomatal conductance, which might impair seedlings water balance if soil water content is low after planting (Villar Salvador et al., 2005).

van Den Driessche (1992) analyzed the responses of *Pseudotsuga menziesii*, *Pinus contorta* and *Picea glauca* seedlings that were grown in containers in a greenhouse and submitted to two N treatments and three potassium (K) treatments with three drought treatments. A positive relation between shoot:root ratio and survival in *P. contorta* and *P. glauca* indicated that increase in N increased both shoot growth and drought resistance over the N range investigated, while *P. menziesii* showed an interaction between drought and N treatment and a small response in both survival and dry weight to potassium (K) application.

K plays important physiological functions in plants. It regulates cell membrane activity, it is an enzyme cofactor and one of the main ions that contribute to plants osmoregulation, improving the tissue water content and regulating stomatal closure among others (Morgan, 1984; Taiz & Zeiger, 2002). While high N fertilization stimulates rapid soft growth, adequate K promotes firmer tissue. K addition increases water uptake, decreases transpiration losses, leaf area ratio and desiccation damage. It has been shown that K, with calcium and magnesium, increases leaf waxes, protecting plants during the hardening process. Thicker cuticles also protect to insect feedings and penetration fungi (Cakman, 2005; Landis, 2005). Nurseries have traditionally applied extra K as part of the hardening process.

Several studies showed that K fertilized seedlings had better performance under water stress conditions (Garau et al., 2004a; Garau et al. 2004b). The responses of *E. camaldulensis* and *E. globulus* seedlings submitted to different treatments of fertilization and water availability were analyzed at the nursery stage and after plantation. Nursery treatments involved two levels of K and two levels of water availability. Results indicated that drought conditioning and K fertilization in nursery improve seedlings growth after plantation (Garau et al., 2005).

Guarnaschelli et al. (2010b) observed a decrease in the osmotic potential in water stressed and K fertilized plants of *E. globulus*, which would imply an increase in the water potential gradient between the plant and the soil, facilitating water uptake. In addition, treated plants showed higher relative water content and stomatal conductance.

Recently, Oddo et al. (2011) analyzed the effects of short-term K fertilization on plants of *Laurus nobilis*. They observed an enhancement in hydraulic conductance following short-term K fertilization; phenomenon that can be quite advantageous for maintaining cell turgor, stomatal aperture and gas exchange rates under moderate drought stress.

Apart from previous results, Römheld & Kyrkby (2010) argued that it is still necessary to explore the influence of K on plants under stressful conditions. In fact, there is no clear evidence that K addition may increase cold tolerance as well.

5. Effects of vegetation competition and herbivory during the tree establishment

5.1 Weed competition: The main biotic cause of water and resource deficiencies

During plantation establishment conditions of high levels of light and, sometimes, increased availability of water and nutrients favor the development of opportunistic, fast-growing

herbaceous and/or woody species that invade the disturbed site from wind-blow seeds, seeds stored in the seed soil-bank or by sprouting. Although the surrounding vegetation may play important functions in the forest system (reduce soil erosion, retain and recycle nutrients, add organic matter to the soil) and in certain environments can facilitate the growth of tree seedlings, it commonly interferes and captures resources at the expense of trees seedling performance (Cannell & Grace, 1993; Nambiar & Sands, 1993). Only shade tolerant tree species can become established beneath such vegetation. Herbaceous and/or woody vegetation which limits resource availability, hindering seedlings' expected growth and survival has been cited as one of the main causes of low plantation success (Smith et al., 1997; Close et al., 2005; Tappeiner et al., 2007).

Weed vegetation reduces the levels of water availability in the soil and affects negatively seedling water status (Dinger & Rose, 2009, 2010; Löf & Welander, 2004; Picon-Cochard et al., 2006), representing the main biotic cause of water stress (Lamhamedi et al., 1998; Picon-Cochard et al., 2001). Differences in weed density (Florentine & Fox, 2003; Garau et al., 2008b) and growth forms (Balandier et al., 2006; Coll et al., 2004; Provendier & Balandier, 2008) may cause variations in water restriction. Nevertheless, weeds will significantly interfere with forest seedlings only during "the critical period" (Adams et al., 2003).

Plant responses to competition are similar to those that allow coping with abiotic resource deficiencies and involve several physiological and/or morphological adjustments. Seedlings of shade intolerant trees, commonly used in many commercial plantations, are generally characterized by a great physiological plasticity that enables them to better utilize the higher light levels of open environments, and to withstand better the associated environmental stresses (Peltzer & Köchy, 2001; Picon-Cochard et al., 2006). Some responses are rapid and potentially lead to greater survival (i.e. stomatal closure), whereas others are delayed for hours or days, representing new capabilities and allocation patterns, providing some degree of resistance to the stress.

Numerous studies demonstrated that tree seedlings responded to weed imposed water deficit by anticipating stomatal closure and showing a reduction in leaf water potential (Coll et al., 2004; Dinger & Rose, 2009, 2010; Garau et al., 2008b; Picon-Cochard et al., 2001, 2006; Provendier & Balandier, 2008; Rey Benayas et al., 2003; Watt et al., 2003). Even with high soil water availability, the presence of weeds produced a significant decrease in leaf stomatal conductance (Garau et al., 2008b; Watt et al., 2003). Reductions between 30 and 80% in seedlings stomatal conductance reflect a useful response to limit water loss under soil water deficit (Garau et al., 2008b; Picon-Cochard et al., 2001).

Changes in tissue water relation parameters can help to withstand water stress induced by weed competition. A higher bulk modulus of cell wall elasticity and a lower osmotic potential or both were found in tree seedlings in response to neighboring competition (Rey Benayas et al., 2003). Garau et al. (2008b) observed that the restriction of soil water by weeds induced an osmotic adjustment of 0.38 MPa in seedlings of *E. globulus* subsp. *maidenii* and of 0.65 MPa when, additionally, a water restriction condition was imposed. Similarly, a cell wall stiffening of 8.0 MPa was induced independently of the level of water availability. Together, both strategies ensure water uptake while maintaining both cell turgor and volume. These features also allowed the maintenance of higher rates of gas exchange at low soil water content, being crucial for the establishment of tree seedlings (Lopez et al., 2009; Rodriguez-Calcerrada et al., 2010; Serrano & Peñuelas, 2005).

Some studies showed an increase in the intrinsic tree seedlings water-use efficiency (WUE) in response to soil dehydration caused by weed competition. Stomatal closure enabled seedlings to limit water stress, and since the decrease in stomatal conductance was faster than the decrease in CO₂ assimilation rate, an increase in the intrinsic WUE occurred (Garau et al., 2008b; Picon-Cochard et al., 2001; Picon-Cochard et al., 2006).

Other morphological adjustments that imply the postponement of dehydration by lessening the loss and increasing the uptake of water allow withstanding the low water availability. The presence of neighbouring vegetation may reduce seedlings above and below ground biomass to values 60- 80% lower than those obtained without competition (Garau et al., 2008b; Picon-Cochard et al., 2006; Watt et al., 2003). Under such conditions tree seedlings show lower leaf area and shoot:root ratio (Coll et al., 2004; Garau et al., 2008b; Picon-Cochard et al., 2006; Shipley & Meziane, 2002; Watt et al., 2003).

It is not possible to have water stress through competition without having some degree of nutrient stress, and although water stress has been implicated as the main regulator of seedlings performance, it is likely that competition for light also occurs. In fact, weeds are considered "multiple stressors" that compete not only for water but also for nutrients and light (Adams et al., 2003; Caldwell et al., 1995; Nambiar & Sands, 1993). Significant reductions in nutrients (mainly N) and light availability were observed in several studies attributed to competing vegetation (Cogliastro et al., 2006; Davis et al., 1999; Powell & Bork, 2004). Garau et al. (2008b) found a 50-75% reduction in photosynthetically active radiation when eucalypt seedlings were growing under a 100% of weed cover, condition that triggered the greatest leaf osmotic adjustment capacity. Significant increases in free amino acids that contribute to osmoregulation were observed in response to water stress and shade conditions (Showler, 2002; Valladares & Percy, 2002). Their synthesis may be associated with increasing weed competition.

Implication for plantation establishment

It is possible to mitigate the effects of competition effectively by selecting plant material and applying cultural practices during the establishment (Adams et al., 2003; Jacobs et al., 2004). There are species or genotypes that during the critical initial stage of plantation establishment can demonstrate a "strong tolerance ability" (Goldberg, 1996) because they can maintain a high water status, particularly in the presence of weed competition. Physiological and morphological differences within species can thus form a basis for matching plant material to site, although survival and growth will ultimately depend on the levels of water stress experienced.

As discussed above, differences in the response of water-relations parameters to water stress induced by weeds can potentially be used to match genetic material to specific sites. Net solute accumulation could hence favor drought-tolerance beyond the seedling stage and be used as preliminary prediction for genetic screening studies and of field performance studies (Lemcoff et al., 1994; López et al., 2009). As observed by Garau et al. (2008b) seedlings with greater capacity for osmotic adjustment and cell wall stiffening were able to maintain a higher water status under severe weed cover. Garau (2003) found that although two provenances *E. globulus* subsp. *maidenii* presented similar drought-tolerance mechanisms, they have different capacity of acclimation. Murrabrine seedlings showed a higher water-stress threshold (a better combination of processes for "reduced water loss" and "maintenance of water uptake") than Tantawanglo, which allowed Murrabrine seedlings to maintain higher rates of growth under weed competition.

In addition to genetic characteristics, nursery practices and silvicultural techniques can have an important effect on the seedling's growth and competition effects. Planting large seedlings allows withstanding competition from herbaceous or shrubby vegetation and minimizes the period of susceptibility to competition and also to animal damage (Noland et al., 2001; South et al., 2005). Cuesta et al. (2010) observed that large, nitrogen enriched seedlings of *Pinus halepensis* in the presence of weeds had higher water potential, gas exchange, and root growth and had finally a better transplanting performance.

Several measures are used also to regulate competition: weeding, plowing and application of herbicides (Smith et al., 1997; Tappeiner et al., 2007). Alternative methods of weed control are very effective because a greater number of seedlings can be established on treated sites. Different herbicides have been used to keep plantations weed-free. However, restrictions on the use of herbicides and worries about their environmental effects are generating some changes in silvicultural decisions. It has been agreed that it is necessary to adopt a new approach to weed control towards and "integrated vegetation management". For example, reducing the area of weed control according to the tree crop and weed growth habit characteristics seems to be an appropriate and effective option which causes less environmental impact and at the same time is less expensive (Garau et al., 2008a).

5.2 Herbivory and its interaction with water deficiencies

Trees are subjected to the negative impact of herbivory that removes biomass that might be allocated to grow and increases mortality. Different insect, rodent and mammalian species affect seedlings establishment both in natural forests and in commercial plantations (Becerra & Bustamante, 2008; Dulamsuren et al., 2008; Meiners et al., 2000). They are known to affect tree seedlings, especially during their first year of growth, but the intensity of damage is related to the population density of herbivores and to habitats' food offer. Plantation productivity is reduced due to the decrease in seedling growth, seedling survival and the development of multiple leaders. In Central and South America leaf-cutting ants are one of the main plagues that threaten seedlings growth and survival during the establishment (Della Lucia, 1993; Forti & Castelli Boaretto, 1997; Vasconcelos & Cherrett, 1997).

Plants have developed different kinds of defences, which allow their successful survival against herbivores. Some species have physical barriers (such as thorns and trichomes) or biomechanical properties in their leaves (such as strength and toughness) as anti-herbivore defences. Other plants produce chemical defences; mostly secondary metabolites like alkaloids, glucosinolates, terpenes, phenols, hydroxamic acids, tiophenes, and cyanogenic glycosides, among others. Secondary metabolites represent adaptive characters that have been subjected to natural selection during evolution and are thus important for plant survival and reproductive fitness (Benett & Walsgrove, 1994; Thies & Lerda, 2003; Wink, 2003). For instance, *Eucalyptus* species contain high concentrations of monoterpenic and sesquiterpenic compounds in their foliage, which have proved to be responsible for their ability towards different herbivores (Marsaro et al., 2004; Moore et al., 2004).

Genetic and environmental factors contribute to modulate the level at which different types of defence responses occur in plant species. Guarnaschelli et al. (2000) observed significant differences in leaf thickness and toughness among seedlings of provenances of *E. globulus* subsp. *maidenii*. Leaf-cutting ants caused higher damage in the provenance with lower toughness. Although nutritional quality of plant tissue can influence herbivore host choice, the structural and chemical defences are the major determinants of leaf and twigs

palatability. Most of those attributes are under genetic control (Raymond, 1995) and inter- and intra-provenance variation in resistance to insect damage has been reported in *Eucalyptus* sp. (Floyd et al., 1995).

Abiotic stresses such as drought can have important effects on plant-herbivore interactions, modifying herbivore population dynamics and anti-herbivore defences. Different hypotheses predict how plants under stress should respond to herbivory. However, it is difficult to generalize the effects of abiotic stress on host quality and herbivore damage (Wise & Abrahamson, 2007) since, although some herbivores are favored by unstressed plants, others are favored by moderately stressed plants or by severely stressed plants. Caffarini et al. (2006) observed in seven provenances of three subspecies of *E. globulus* that droughted plants or leaves (field and lab tests, respectively) were preferred by the leaf cutting ant *Acromyrmex lundii* to unstressed ones, overriding subspecies or provenance.

The decreased performance of herbivores on water stressed plants may be caused by several non-exclusive reasons: an increase in plant defense levels, a decrease of carbohydrate levels and/or a decrease in foliar water content (Scheirs & De Bruyn, 2006). But drought may increase or decrease secondary metabolism, increasing or decreasing host quality of trees for insect herbivores. For example, in several *Eucalyptus* species Muller da Silva et al. (2006) observed that water restriction decreased essential oil production while Stone & Bacon (1994) reported no modifications in total terpenoids yield.

The concentration of total phenolic glycosides increased in leaves of poplars that were growing under water stress conditions, however the growth of only one species of herbivore was negatively affected (Hale et al., 2005).

Sometimes the impact of herbivory is often greater if other original stress damage and lead to important tree losses. In young plantations of *E. camaldulensis* stressed by moisture deficit and in two young plantations of *E. dunnii* stressed by flooding and weed competition, Stone (2001) observed that the stress-inducing agents reduced canopy growth rates and architecture so that the proportion of leaf tissue damage by insects increased and the tree's ability to tolerate that damage decreases in all three cases.

Herbivory is thought to increase on water stress plants due to induced changes in plant physiology, specifically N availability. Water stress mediates N availability and then modifies the quality of the leaves and the population dynamics of insect herbivores (Huberty & Denno, 2004). Self-pruning of old leaves in combination with a reduction in leaf area of new leaves may allow the reallocation of foliar proteins to young leaves, explaining the enhanced foliar protein concentration in water stressed plants (Scheirs & De Bruyn, 2005). It was found that a greater availability of nutrients increased total essential oil and cineole levels in eucalypt leaves (Close et al., 2003; O'Reilly-Wapstra, 2005), however complex the effects of nutrients and secondary compounds on herbivores responses may be esteemed.

The susceptibility of pinyon pine (*Pinus edulis*) to the stem-and cone-borer increased in sites with intense water and nutrient deficiencies and the release from stress led to increased resistance to insect attack (Coob et al., 1997). *Eucalyptus* plants with high levels of fertilization showed higher levels of herbivory (Paine & Hanlon, 2010). Similarly, *Eucalyptus* seedlings, which had higher foliage N, lower tanin and higher essential oil levels were more browsed (Close et al., 2004).

Other abiotic stresses such as shade can affect the levels of damage by herbivores. A number of studies have reported lower tolerance of herbivory under shade conditions (Baraza et al.,

2004; McGraw et al., 1990; Norghaver et al., 2008; Salgado-Luarte & Gianoli, 2011). Differential herbivory in contrasting light environments may reflect light-induced differences in plant defensive traits such as leaf toughness and carbon-based secondary compounds. Plants' resistance may be greater in the sun probably due to their lower specific leaf area (SLA) (Salgado-Luarte & Gianoli, 2011). While comparing several characteristics in *Eucalyptus* seedlings growing under different levels of light, Guarnaschelli et al. (2003a, 2003b) found higher levels of herbivory damage in shaded plants, which had lower leaf thickness and toughness associated with higher SLA. Although Nichols-Orians (1991) detected much higher foliar concentrations of condensed tannins in plants growing in full sunlight compared to those growing in the understory, leaf-cutting ants found these leaves more acceptable because of the higher concentrations of foliar nutrients that override the benefits of increased concentrations of tannins. In other studies shade affected the chemical defences of *Acer*, *Quercus* and *Pinus* seedlings lowering the levels of total phenols and condensed tannins and increasing the levels of N (Baraza et al., 2004; Baraza et al., 2010). Moreover, plant resistance to herbivory can be influenced not only by the independent effects of plant genotype and environmental variation, but also by interactions between the two. A significant genotype x fertilizer interaction was found in the defensive compounds of *E. globulus* and their resistance to mammalian herbivores (O'Reilly-Wapstra et al., 2005). Some differences were recently found in the levels of leaf damage caused by *Leptocybe invasa* in seedlings of several clones of *E. grandis* and *E. grandis* x *E. camaldulensis* that were growing under alternative water and light availability regimes. Attacks were concentrated only in plants of *E. grandis* x *E. camaldulensis* clones, particularly in plants under drought, shade and drought plus shade conditions (Guarnaschelli et al., unpublished data).

Management options

Interestingly enough, induction of intra-specific herbivore resistance is possible through manipulation of light, nutrients and water in the nursery environment or water and nutrient availability during the establishment. In fact, the potential of nursery preconditioning to enhance survival chances of future trees by reducing palatability or attracting beneficial insects as a result of changes in physical and/or chemical defences seems to be promising. Water availability manipulation during the nursery period of *E. camaldulensis* seedlings modified leaves essential oil composition, and drought triggered a significant increase in several oxygenated terpenes production (particularly linalool and 1,8-cineole) known to repel different defoliator species (Leicah et al., 2010).

Seedlings of *E. globulus* and *E. nitens* with high-fertilizer nursery treatment were browsed more than the low-fertilizer nursery treatment, the results being consistent with their differences in foliar N and tannins (Close et al., 2004). Similarly, the young foliage of *E. nitens* seedlings that receive medium and high levels of nutrient regime was intensively consumed. High levels of N in young leaves outweighed the presence of sideroxylonals and essential oils that generally act as deterrents to herbivores (Loney et al., 2006).

In contrast, low nutritional quality seems to be a plant defence against herbivores. Haukioja et al. (1991) demonstrated that the low nutritional quality is a potential active defence against herbivory in the mountain birch (*Betula pubescens* subsp. *tortuosa*), especially when it is correlated with repellent allelochemicals. In field trials Paine & Hanlon (2010) found that *Eucalyptus* trees treated with higher levels of irrigation and no fertilization demonstrated lower levels of damage by a psyllid.

Therefore, manipulation of seedlings or saplings chemistry through the application of particular fertilizer regimes as well as the regulation of water availability are useful tools for managers wishing to decrease damage by herbivory during the establishment. Alleviating tree stress through improved silvicultural practices or improved site selection techniques may indirectly reduce the impact of insect herbivory. In resource-limiting environments, an alternative approach may be planting species of slower growth that are predicted to have better defended foliage. Manipulation of these natural antiherbivore plant strategies is not exclusive of other management approaches, such as the genetic selection of natural insect resistance and selective chemical control techniques (Stone, 2001).

6. Conclusions

Water stress is the main cause of alteration of plant physiological processes and reduction of plant growth, which affects considerably tree seedlings performance immediately after plantation and during the whole establishment stage, causing serious losses and affecting tree regeneration and, consequently, future stand productivity. Water stress, itself and together with other abiotic and biotic factors, affects the dynamics of forest establishment, having an enormous impact on seedling performance. Multifactor stress conditions or sometimes the impact of secondary factors are often greater than the original drought effects, leading to greater tree losses. The enhancement of forest regeneration is a key process to ensure high forest productivity to supply timber needs in the present scenario of increasing demand of forest products. As discussed above, successful establishment depends on several management aspects. Breeding for drought tolerance should be given high priority in all research programs, considering genetic variation and phenotypic variation. In order to mitigate the transplanted shock, we also highlighted the importance of regulating water and nutrient regimes in nursery as useful tools not only to modify drought tolerance but also to reduce seedling's palatability, and hence herbivory damage in plantation forestry. Previous exposure to stress conditions, or a natural hardening period, can markedly influence future plant responses. Drought resistant seedling, nursery hardened, suited to the particular environmental condition, will have better field performance.

Some of the factors associated with successful forest establishment which have not been reviewed here, such as cultural practices applied before and over the establishment, have been widely studied; however, it is still necessary to foster new research in other areas. More information concerning seedling physiology is required, especially in relation of how seedlings adapt to particular plantation environments. The effects of water deficit and freezing temperatures, as well as the mechanisms that govern plant drought and frost tolerance, closely related to plant survival and growth during the establishment, have been analyzed in depth due to their great economic impact and relevance to stand productivity. Nowadays, climate change is altering environmental conditions. It is expected that drought conditions will become more frequent in extended areas. Changes in water availability and temperature will probably interact with other abiotic and biotic factors that may have a high effect during the forest establishment and the whole rotation. Under this environmental challenge it will be necessary for any species, provenances and clones, to understand the physiological basis of plant responses to water stress and together with interacting stressful factors that will be crucial also for predicting forest productivity. At the same time, nurseries' managers will be requested to adapt their cultural techniques in order to produce

high quality stock seedlings according to good field performance. Irrigation and nutritional protocols at nurseries should also be adjusted not only taking into account their influence on abiotic stress tolerance but also considering their impact on plant nutritional status and the host quality of trees for insect herbivores. It is necessary to establish relationships between field performance and physiological and morphological properties of nursery stock for each species, which will allow the implementation of the most adequate practices to produce stock of high quality. Finally, foresters will be requested to adapt the silvicultural planning to the present environmental concerns applying low impact practices and implementing integrative vegetation and pests control programs according to the principles of sustainable management.

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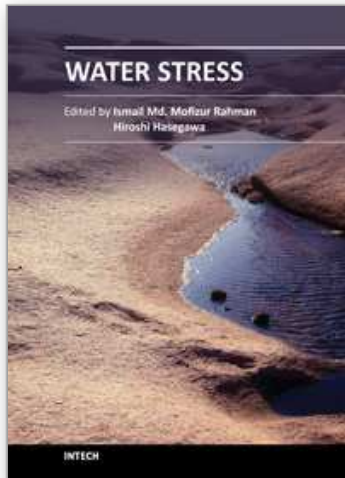
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Plants experience water stress either when the water supply to their roots becomes limiting, or when the transpiration rate becomes intense. Water stress is primarily caused by a water deficit, such as a drought or high soil salinity. Each year, water stress on arable plants in different parts of the world disrupts agriculture and food supply with the final consequence: famine. Hence, the ability to withstand such stress is of immense economic importance. Plants try to adapt to the stress conditions with an array of biochemical and physiological interventions. This multi-authored edited compilation puts forth an all-inclusive picture on the mechanism and adaptation aspects of water stress. The prime objective of the book is to deliver a thoughtful mixture of viewpoints which will be useful to workers in all areas of plant sciences. We trust that the material covered in this book will be valuable in building strategies to counter water stress in plants.

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