Flooding following Drought: a Swift and Subtle Killer of Stressed Trees

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Introduction

After the prolonged dry period experienced in south-eastern Australia from 1998-2010, large numbers of trees suffered significant stress in both urban and their natural environments. Many older and stressed exotic and native trees, including large numbers of river red gums, plane trees and conifers, such as pines and cypresses, died.

The last two years, 2010-11 and 2011-12, have seen La Nina climatic events with their associated higher than average rainfall affecting the previously dry part of the nation. In many places floods have replaced drought as a major concern. Many trees have recovered brilliantly from the stress caused by the long dry period – many eucalypts and elms have been spectacular in their re-foliation and growth.

However, it has become evident that some trees and some species have continued to decline, and in some cases trees that had survived the long dry period succumbed in the wetter months. The question has been raised as to why these trees have died during the "good times' when they had coped with such a long period of stress. Perhaps the answer lies in an understanding of the subtle and lethal effects on trees of flooding, waterlogging and low levels of soil oxygen, especially after a long dry period. It is not uncommon for a second dose of stress to kill trees that have survived a previous bout of stress.

Some Relevant Basic Root Anatomy

In most urban trees, the root system consists of a root plate consisting of structural and absorbing roots which are often only 200-300mm deep (Figure 1), from which descending roots (also called vertical or sinker roots) emerge and go to deeper soil depths of 500-1000mm or, in some soils, deeper (Moore, 2008). The fine absorbing roots, usually predominantly in the root plate, produce very delicate root hairs that extend from epidermal cells and non-suberised feeder roots at the zone of elongation, just behind the root cap and tip. The root hairs are very fine and increase the absorbing surface area of the root system enormously. They are responsible for most of the nutrient and water uptake. Being in the upper 200-300mm of the soil profile, they are prone to changes in the edaphic environment, such as water deficits, waterlogging and soil oxygen levels.

The root hairs persist for a very short period of time, frequently a matter of a few days before they are damaged or die off. Without them the surface area of the tree's root system would be insufficient to sustain its supply of water and nutrients for the basic metabolic processes such as photosynthesis and respiration (Kujawski, 2011). However, in all tree species studied mycorrhizal fungi form symbiotic relationships with the roots. These fungi may grow around the roots and root cells (ectomycorrhizae) or in between and into the root cells (endomycorrhizae). The association between tree roots and mycorrhizal fungi is an intimate mutualistic symbiosis which persists for the life of the tree. The benefits for the tree are that the fungal hyphae increase the absorbing surface area for the uptake of water and nutrients, while the fungus shares some of the carbohydrate that is directed to the root system from photosynthesis in the canopy.

The production, growth and development of fine roots, root hairs and mycorrhizae are influenced by the edaphic environment (May *et al*, 2012). They both grow well in moist, nutrient-rich, well-aerated soils with a low bulk density, but both can be damaged or killed by dry soil conditions and by flooding, waterlogging or compaction which can lead to hypoxia and anoxia. Hypoxia occurs as soon as the level of oxygen limits mitochondrial (aerobic) respiration, while anoxia occurs when such respiration is halted (Parent *et al,* 2008).The loss of root hairs or mycorrhizal fungi leads to a reduced root absorbing surface area, which often gives symptoms of wilting and nutrient deficiency, regardless of the cause.

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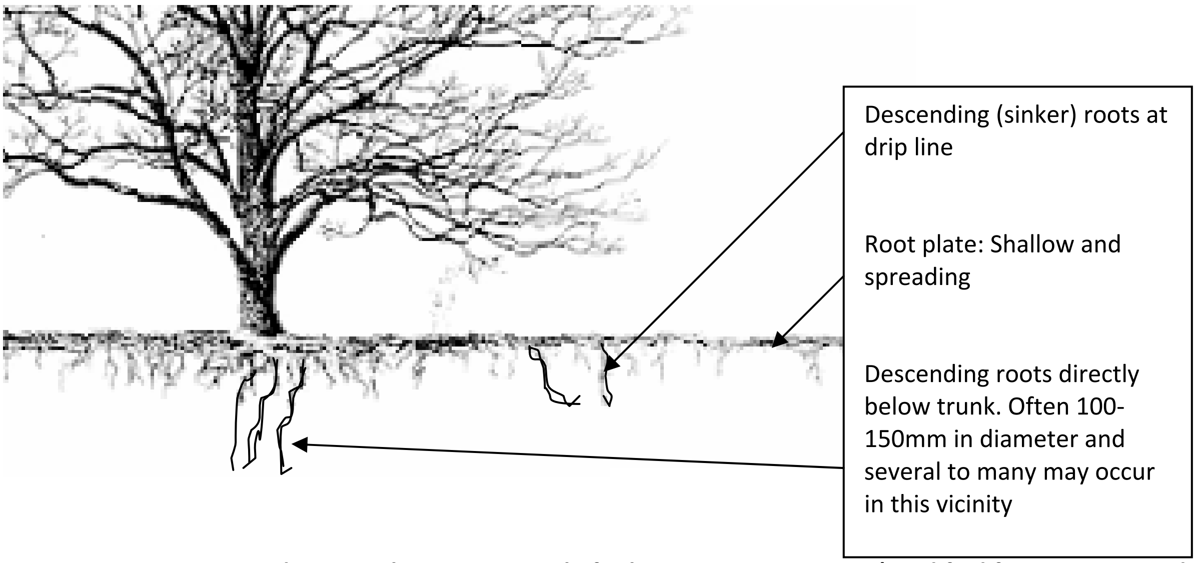

Figure 1. Descending or sinker roots typical of urban tree root systems (Modified from Watson and Neely, 1994)

The mycorrhizal relationship with the host tree is very complex, and there may be a number of different fungal species that can form the relationship with the host, but not all are of equal benefit to the tree. In many cases there will be more than one species of fungi in association with the host roots. Furthermore, the benefit of the fungi to the host is not confined to the increased absorbing surface. The suite of mycorrhizal fungi in association with the host often confers a degree of protection on the host from attack by pathogenic fungi. This protection may come from the mycorrhizal fungi outcompeting potential pathogens and making the root surface unavailable for colonisation, but they may also be actively antagonistic to the pathogens.

If edaphic conditions change through drought, flooding or waterlogging and the mycorrhizal fungi cease growing or are reduced, the protection that they afforded the host may also be diminished. This may be part of the explanation as to why a number of trees succumbed to fungal diseases during and immediately after the long dry period.

Trees and water

Water plays a vital role in the life of all terrestrial organisms including plants (Taiz and Zeiger, 2010). Typically the non-woody biomass of plants is composed of between 70 and 80% water (Lambers, Chapin and Pons, 2008) and, in trees, if the water content of cell walls falls below about 78% its effect on tree physiology is such that the tree will be stressed and may die.

Water uptake in trees is predominantly through the intimate contact of root hairs and mycorrhizal hyphae with the rhizosphere where they have direct contact with the soil water over the very large surface area needed for effective uptake. Mature roots are less permeable or impermeable to water because of the development of an outer layer of protective tissue, called exodermis or hypodermis (Taiz and Zeiger, 2010). Woody roots that have undergone secondary growth are incapable of absorption.

Water is taken up by the root system of the tree, which can be seen as the supply system and passes through the living (symplast) and inert (apoplast) anatomical components of the tree where it can be utilised by cells for metabolism as it passes or is transported through the xylem tissues or as part of the phloem transport to the foliage. Once in the leaves, the water evaporates from the surface of the leaf cells into the surrounding atmosphere mainly through stomatal apertures. The combined evaporation of water and its metabolic use constitute the demand side of the tree's water balance equation.

While the role of water in transpiration is often well understood by those managing trees, its roles in osmoregulation and metabolism are often forgotten. The availability of water can significantly impact on the uptake of nutrients, the transportation of metabolites and the efficiency and effectiveness of basic physiological processes, such as photosynthesis and respiration. Tees cannot survive and grow without assimilating carbon dioxide, which makes them vulnerable to drought because it is inevitably accompanied by loss of water through transpiration (Pate and McComb, 1981).

Water stress can occur through either too little or too much soil water, both of which can reduce the rates of physiological processes, such as photosynthesis, respiration and protein synthesis (Lambers *et al*, 2008). Drought, flooding and waterlogged soil can have profound effects on energy (ATP, the energy rich molecule of cellular metabolism) production, the availability of oxygen and carbon dioxide and the efficiency of plant metabolism, all of which impact on plant growth, development and survival.

Effects of Prolonged Dry Periods (Drought)

For the purposes of this paper, the term drought refers to a period of time over which the water content of the soil is reduced by inadequate precipitation to an extent where plants suffer from a lack of water sufficient to disrupt normal life processes (Larcher, 1995; Coder, 1999). Drought is a common environmental stress that may damage trees directly by severe seasonal drought, or damage may be cumulative over several consecutive years (Schoeneweiss, 1986). Droughts may occur over one or a couple of years and may be described as acute, but those where rainfall is below average over longer periods of time, such as those which affected South Australia and Victoria at the turn of the nineteenth and Twentieth centuries (sometimes referred to as the Federation drought) and that besetting south-eastern Australia from 1997-2010 are chronic droughts with below average rainfall year after year (Moore, 2009).

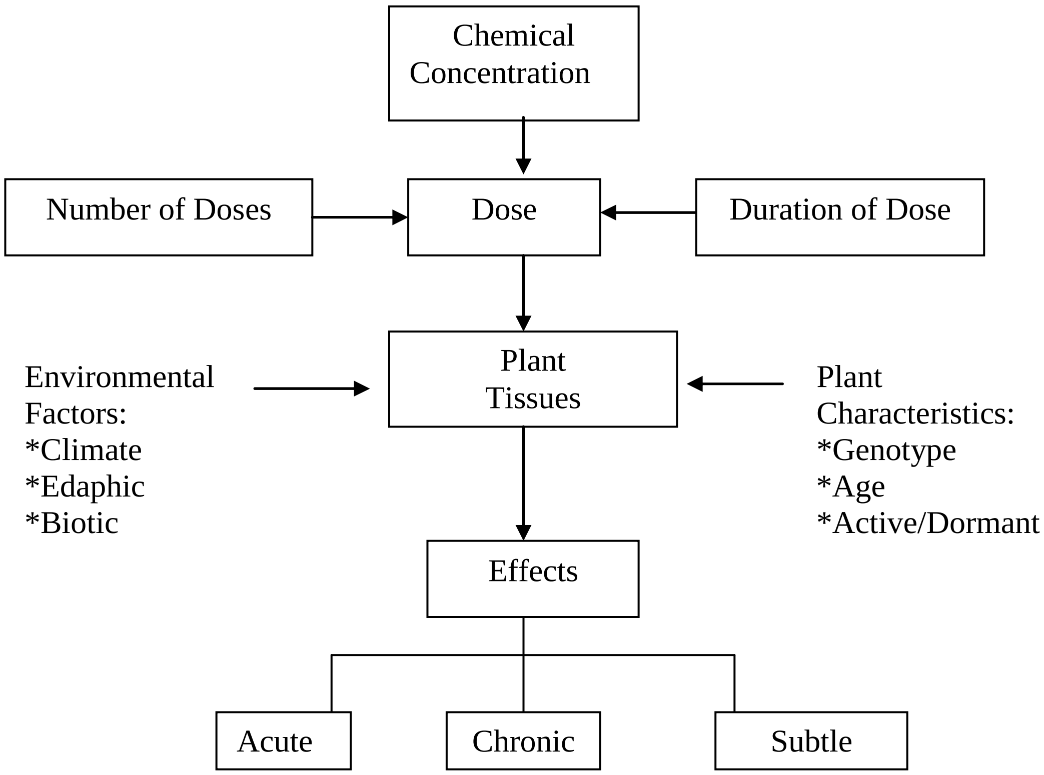

Figure 2. The dose model that can be applied to multiple stress scenarios, including period of water deficit followed by flooding, waterlogging and hypoxia and anoxia.

In the current era of climate change and uncertainty, it is not known whether the prolonged dry period is a drought and part of a regular natural pattern that occurs over a longer period of time. It might be the one in five hundred year or perhaps the once in a millennium drought for example, but current meteorological data are too recent to reveal such patterns. However, it could be a dry period that introduces a more permanent climate change with lower rainfall. It can only be decided when data are analysed in future and it may take 15-20 years before the answer is known.

During a long period of below average rainfall, trees are subjected to a chronic rather than acute period of water stress (Figure 2). There are a number of ways in which trees can respond to such conditions (Coder, 1999):

- close their stomata, which conserves water but impacts on transpiration and aspects of
- plant metabolism such as photosynthesis and respiration
- production of the stress hormone Abscisic Acid (ABA)
- show signs of wilting

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- increase their root to shoot ratio by extending their roots system
- exploiting a greater soil volume and providing a greater opportunity for water uptake
- shed foliage, and even limbs, as a way of adjusting foliage surface area to the reduced
- water availability
- altering their osmoregulatory environment by adjusting internal solute concentrations
- modifying turgor pressure (Figure 3)

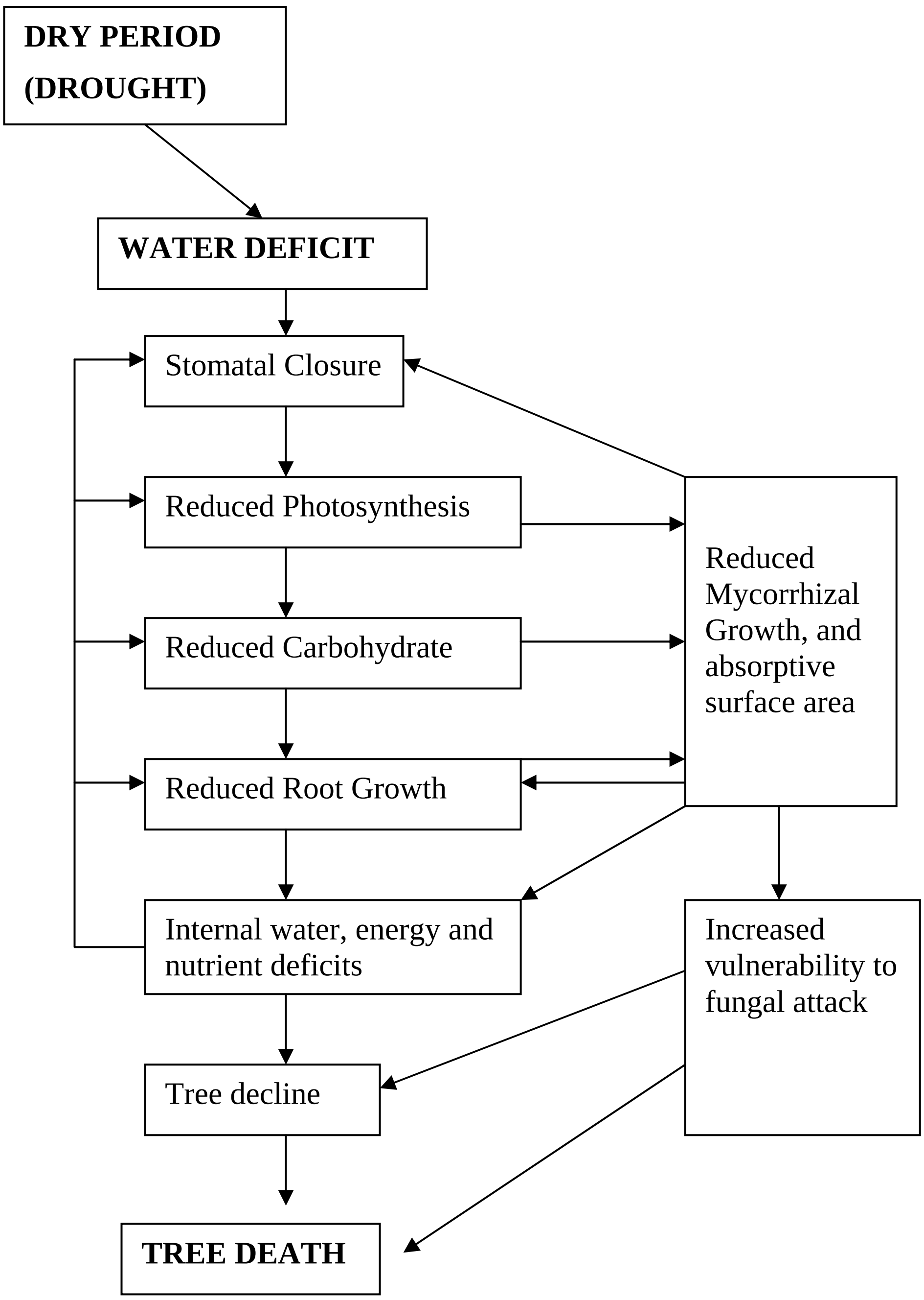

Figure 3. **Some of the major effects of water deficit (drought) on trees.**

Perhaps the best known response of trees, and plants in general, to low water availability and drought is complete or partial stomatal closure, which often occurs in the early stages of water deficit (Kujawski, 2011; Coder, 1999). This closure can be precipitated by the direct hydraulic effects of water scarcity, but often long before leaves wilt, the stress stimulates the production of ABA (Lambers et al, 2008). ABA is often described as the stress hormone and its synthesis from carotenoids can be triggered in the roots (Moore, 1998; Lambers et al, 2008). The hormone stimulates responses in other parts of the trees, one of which is stomatal closure in leaves (Larcher, 1995; Kujawski, 2011).

ABA is a significant hormone produced by roots in contact with drying soils. Soil drying increases the concentration of ABA in the xylem sap as well as in the leaves (Lambers *et al*, 2008) and as a consequence there can be a rapid stomatal closure which minimises water loss (Taiz and Zeiger 2010). It has been postulated that roots might sense drying soils because of ABA release into the soil (Lambers *et al*, 2008). Abscission of leaves is a significant long term adjustment that improves the trees chances of survival and results from enhanced synthesis of ethylene (Taiz and Zeiger, 2002). Leaf shedding in eucalypts is often observed (Pook, 1984) and reduces both transpirational surface area and photosynthetic activity. However, when water becomes available many eucalypt species re-foliate rapidly and photosynthetic activity is restored.

With a focus on water conservation, stomatal closure by plants is usually seen as an efficient and effective response to water scarcity. However, it can come at a significant cost as the closure impacts on photosynthetic activity as carbon dioxide uptake is reduced, which then affects other metabolic processes (Kozlowski, Kramer and Pallardy, 1991). In some situations and for some species not all stomata will close. Trees that reduce stomatal conductance in the middle of the day may only close some of their stomata, whilst others remain open allowing uptake of carbon dioxide for photosynthesis (Lambers *et al*, 2008). Stomatal responses corresponding to pre-drought conditions may not occur for a long period after rehydration (Coder, 1999).

As soils dry the tree may make osmotic adjustments either by taking more nutrients from the soil or by releasing more sugars (Lambers *et al*, 2008). Taking up more nutrients is difficult as the soils are dry and so the uptake of ions in solution is low and to increase the uptake would require extra energy. This is also difficult as photosynthetic activity has diminished due to complete or partial stomatal closure. However, most trees if they have not been stressed for too long have significant starch reserves stored in root cells, and also in the trunks and leaves.

If a tree has closed its stomata as a response to drought it can use carbohydrate stored as starch as a substrate for the maintenance of normal respiratory metabolism and function, provided there is sufficient gaseous exchange. Starch is readily broken down by amylase enzymes into its constituent glucose molecules. These not only provide a substrate for respiratory metabolism, but also a solute that helps maintain osmotic and water potential and osmoregulation within the tree and are part of the tree's response to drought stress. In making these osmotic adjustments, the tree can maintain cell turgor as the water potential of the soils decrease as they dry, which may allow the tree to take up more water in drying soil.

Drought also has a significant effect on turgor pressure which is not only affected by osmoregulatory components such as water potential but also by the level of cell wall elasticity. The more elastic the cell walls, the more water cells can hold and the longer the tissues can maintain turgor under water deficit. The loss of turgor can affect plant transport, but effects on osmoregulatory processes impact on cellular metabolism such as photosynthesis (Lambers *et al*, 2008). Turgor is lost when the hydrostatic pressure in the cell sap falls below atmospheric pressure and the cell walls collapse (Taiz and Zeiger, 2010).

Whether a tree reaches the turgor loss point can depend on the cell wall elasticity. Cell walls can be made more elastic by the actions of hormones such as auxins and ethylene (Taiz and Zeiger, 2010). The production of ethylene can be stimulated by the increased level of ABA. Trees may make the cell wall softer over a period of weeks. The adjusted elasticity allows transpiration to continue for longer before there is a loss of turgor, which permits metabolic processes such as photosynthesis to continue. While each cell may only hold a small amount of extra water, trees contain a great many cells and so the little bit of extra water in each cell might be the difference between the loss of turgor and survival.

Fine root growth occurs in spring and is dependent on soil moisture content. Water deficit in spring means that trees may not have been able to produce new fine roots for several years, which leads to a decline in root system health (May *et al*, 2012). Furthermore, under severe water deficit, the water tends to pull away from the surface of the fine absorbing roots (Kujawski, 2011) creating a gap which interferes in the continuum between the soil, plant and atmosphere. If the plant continues to lose water in transpiration then the water is drawn from root cells causing shrinkage in the membranes and exacerbating the gap.

The overall effect of drought on a tree can be profound. Leaves tend to be smaller and thicker, xylem vessels are smaller, and the root:shoot ratio increases (Harris, Clark and Matheny, 2004). Drought can affect photosynthesis for weeks or months depending on the extent of the drought (Kozlowski *et al*, 1997). Foliage symptoms of water stress include, bending, rolling, mottling, scorching, chlorosis, and shedding of leaves as well as early autumn coloration. It may also cause dieback of twigs and branches in the extremities of the tree crowns (Coder, 1999). The width of growth rings for drought years will be narrower, because cambial growth slows or accelerates with rainfall. Furthermore, last season's supply of growth material and resources limits the current year's growth, so this year's drought will effect next year's cambial growth (Coder, 1999). So when water becomes limiting, tree growth is stunted.

Trees take time to recover photosynthetic activity and from permanent damage to stomata and root tips (Coder, 1999; Parent *et al,* 2008) and so become more prone to insect and disease attacks (Stolzy and Sojka, 1984). Drought stress can decrease resistance to trunk-invading organisms such as wood borers, bark beetles, fungi, and vascular diseases (Schoeneweiss, 1986). This is typically described as secondary attack, where opportunistic fungi and insects, among them boring insects and bark beetles, attack trees weakened by water stress (Schoeneweiss, 1986; Iles & Gleason, 2008). Drought also limits nutrient availability by preventing the absorption of essential nutrients. The tree may actually succumb 2 or 3 years later to what may have been considered an innocuous secondary infection or stress.

Effects of Flooding and Waterlogging

Tree roots require aerated soil so the effects of flooding, even what might be considered short term inundation, can be injurious to trees (Schoeneweiss, 1986). Soil oxygen is displaced by water and the diffusion coefficient of oxygen in water is approximately 10,000 times lower than in the air, giving rise to hypoxia and anoxia (Niki, Takahashi and Gladish, 2011). If the water is not moving, the rate of diffusion can be even slower and the amount of dissolved oxygen in still water may fall to as little as 3% of that of a similar volume of air. This oxygen is rapidly used by respiring roots and aerobic microorganisms (Martens-Mullaly, 2012). The impact of anoxia can be quite rapid, with the roots of some tree species starting to die within a few hours of being exposed to anaerobic conditions (Pallardy, 2008).

As in waterlogging, flooding leads to a reduced soil aeration which can result in tree roots respiring anaerobically (Figure 4). Not only is anaerobic respiration much less efficient than aerobic respiration in terms of ATP and energy production (approximately 5% as efficient), but it also produces lactic acid or ethanol, both of which are phytotoxic (Coder, 2011; Pallardy, 2008). These can kill delicate root cells containing root hairs and also reduce the growth of mycorrhizal fungi that are associated with all tree root systems.

The reduced energy output from anaerobic respiration may sustain a tree for short periods of time, but it consumes the carbohydrate reserves of the root tissues. If the period of waterlogging, flooding or anoxia extends over a long period of time, it can deplete these reserves completely (Figure 5). This effectively starves the root system and there is a cessation of root tip growth as root tip elongation requires oxygen (Pezeshki, 1991). Many tree species that are tolerant of flooding continue to undertake glycolysis for the production of energy, but they must have substantial carbohydrate reserves to survive. Furthermore, many plants switch metabolism to the production of about 20 anaerobic stress proteins (ANPs) that enable energy generation independent of oxygen availability when oxygen is limiting.

The loss of fine roots, root hairs and perhaps more importantly mycorrhizal fungi can have a profound impact on the trees capacity for absorbing water and nutrients. This can manifest itself in the tree displaying symptoms that are very similar to those of drought – wilting, leaf chlorosis and leaf shedding. The reason for these symptoms is the loss of absorbing surface area. This scenario often leads home gardeners, and even professionals who have failed to check soil moisture conditions, to apply water to already stressed trees in the mistaken belief that they are suffering from a lack of water.

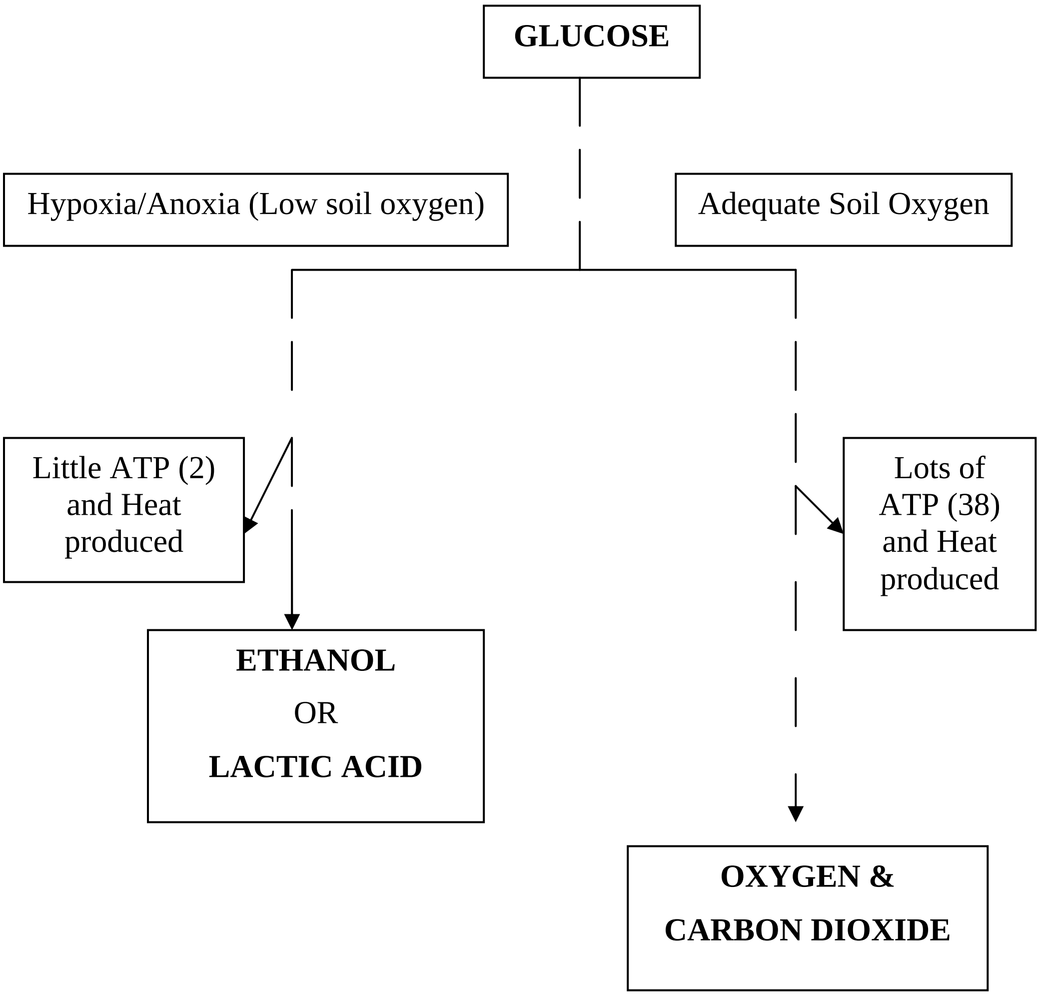

Figure 4. **Aerobic and anaerobic respiratory metabolism. Under hypoxic and anoxic soil conditions, ethanol and lactic acid are produced both of which are phytotoxic.**

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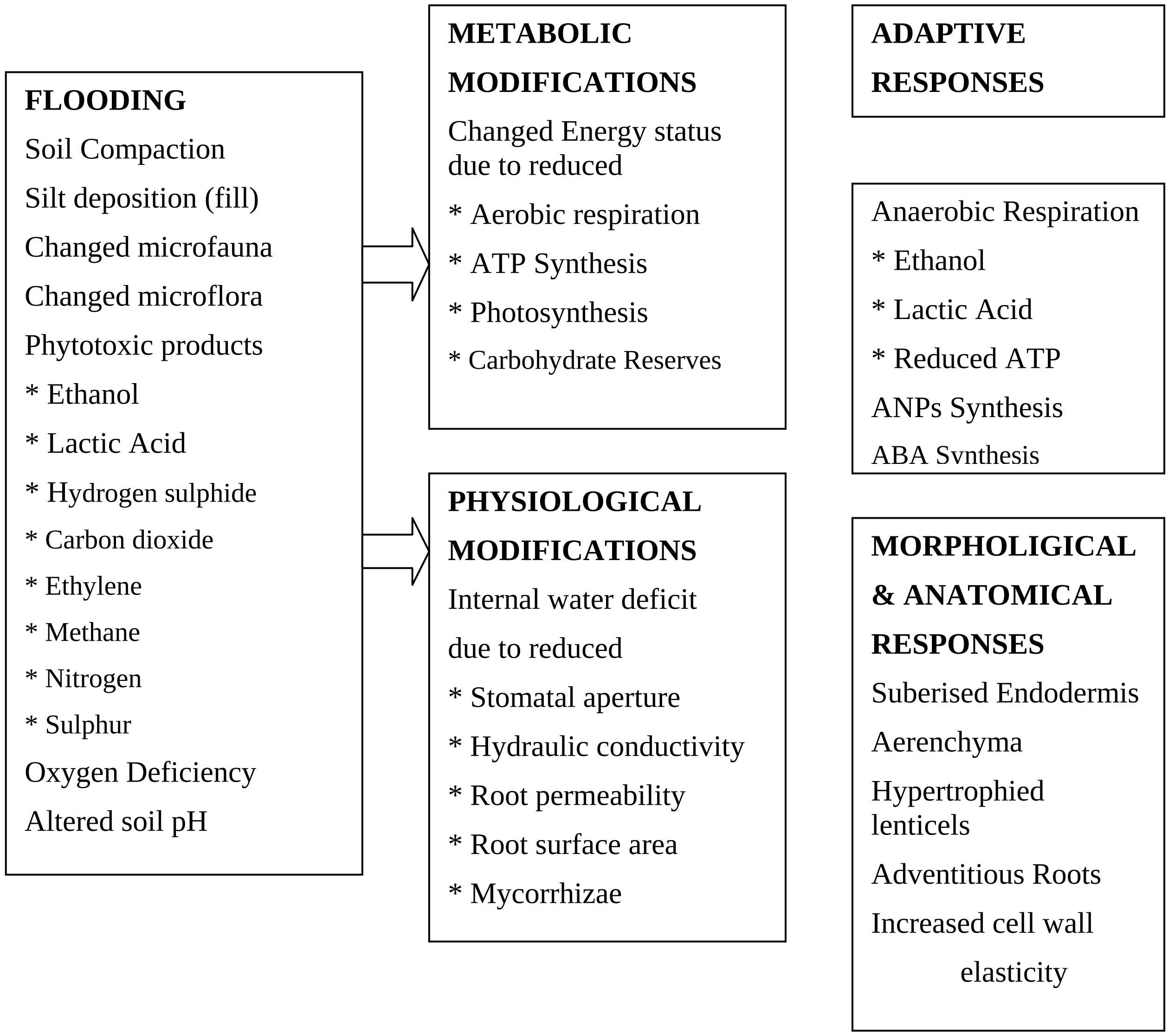

Figure 5. **The effects of flooding on soil and some of the metabolic, physiological, morphological and anatomical modification and responses of trees (modified and extended from Parent *et a*l, 2008).**

However, it should not be forgotten that flooding, water-logging and anoxia can also lead to high levels of ethanol, lactic acid, hydrogen sulphide, carbon dioxide, ethylene, methane, nitrogen, sulphur and cyanogenic compounds in soils, some of which are toxic to trees or influence plant growth and function (Martens-Mullaly, 2012; Iles and Gleason, 2008). The longer the period of inundation persists, the poorer the soil conditions and the more rapidly and significantly the health of the tree deteriorates.

Trees that have been flooded may be more prone to windthrow and total tree failure because of the loss of root mass. Furthermore, if the soils remain wet, soil strength is diminished and combined with a loss of root mass, tree failure in strong winds is more likely. This situation can be made worse by the deposition of a layer of fine silt and mud by flood waters (Iles and Gleason, 2008), which like any fill placed over the root system can stress a tree due to changes in the edaphic environment. The strong currents and soil particles suspended in flood waters can erode soil from the base of trees, exposing tree roots, which are then more vulnerable to drying, mechanical injury and windthrow (Iles and Gleason, 2008).

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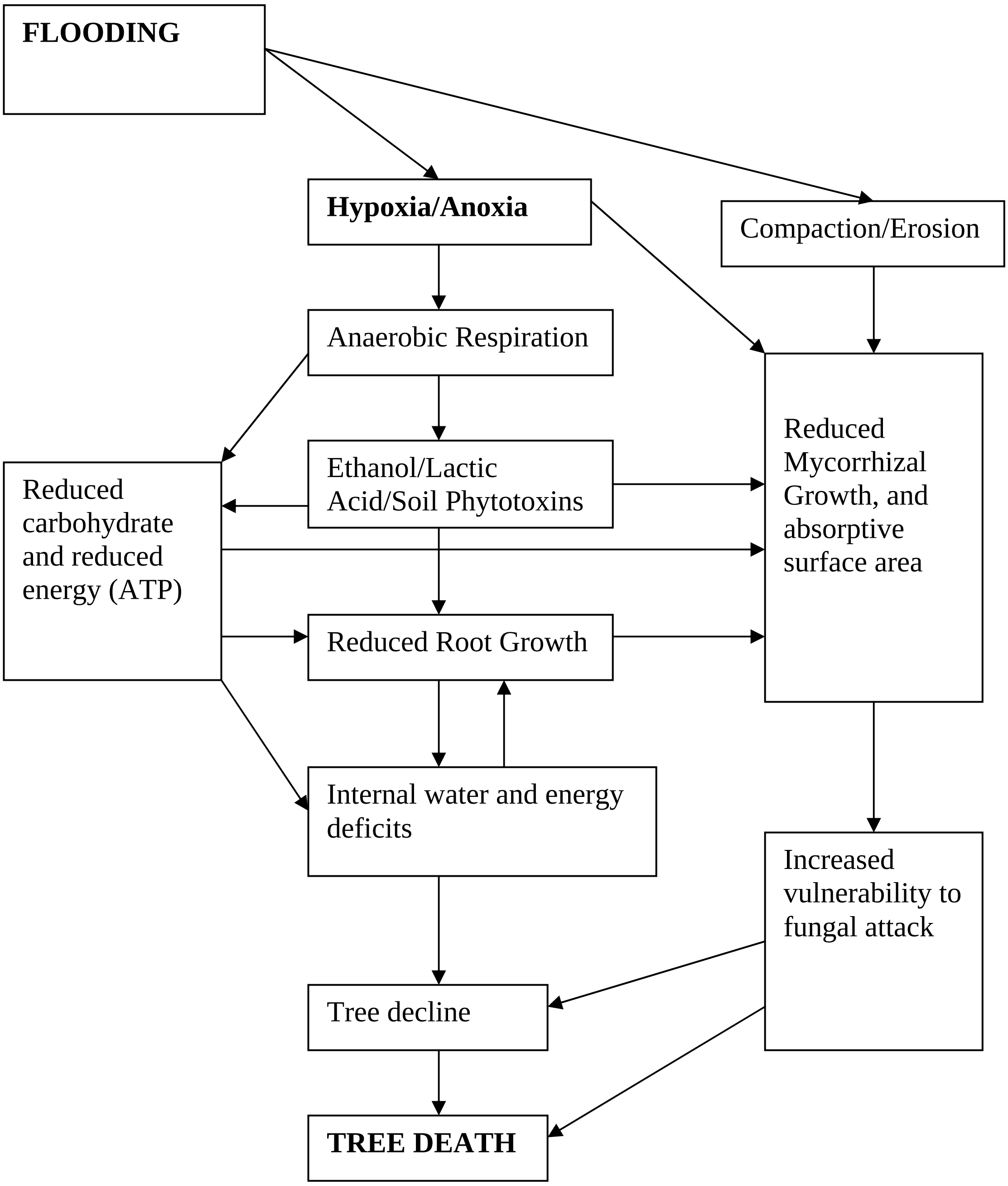

Figure 6. Some of the major effects of flooding and waterlogging that lead to hypoxia and anoxia of trees.

Flooding that leads to soil anoxia and anaerobiosis adversely affects the shoot growth of trees by inhibiting internode elongation and the formation and expansion of leaves. Flood induced chlorosis can lead to premature senescence and abscission (Kozlowski, Kramer and Pallardy, 1991). Experiments with potted plants showed reduced height and growth in many flooded conifers and broad leaved trees (Kozlowski, Kramer and Pallardy, 1991). The effects of flooding on growth are not just due to the effects of oxygen. Mineral uptake can be reduced (Kozlowski, 1984) as a consequence of the decline in active transport due to the reduced rate of respiration and roots may lose minerals by leaching (Pallardy 2008).

As for most environmental stresses, flooding during the growing season when there is active tree growth is more harmful to trees than flooding during dormant periods (Figure 6). During the growing season and over summer, higher soil temperatures can also result in more rapid changes in soils that also impact upon root and tree growth. Trees weakened by flooding stress are also prone to secondary infections by fungi, such as cankers and insects (Iles and Gleason, 2008).

Flooding following Drought

The compounding effects of different stresses on tree health are well documented (Moore, 1999). Trees may survive one environmental stress, but often succumb to a second dose of stress that might be applied simultaneously or sequentially. The dose model that considers the level of a particular stress, its duration and the number of doses in relation to the plant and its environment (Figure 2) is useful in considering this phenomenon (Moore, 1999). In southeastern Australia, the long period of below average rainfall was followed by a period of higher than average rainfall that exposed many trees to waterlogging, flooding or anoxia. Thus there is double dose of stress, and the following scenario may have unfolded (Figure 7):

Long Dry Period (drought):

- Over the long dry period (13 years) many trees were significantly impacted by water stress. As a consequence root growth was reduced and in many instances fine absorbing roots and absorbing surfaces were reduced
- The period of water stress also led to the depletion of root carbohydrate reserves as stomata were closed or other tree responses to dry soil conditions reduced or modified photosynthetic and respiratory metabolism
- Mycorrhizal growth also diminished due to the combined effects of the low soil water and a lack of carbohydrate supply from the stressed tree symbiotic partner
- The loss of fine absorbing roots and mycorrhizal associates rendered the trees prone to greater stress as the dry period extended and some of the plants died
- The loss of root carbohydrate reserves also delayed new root production when water became available as root growth was dependent on renewed photosynthetic activity
- Furthermore, the diminished mycorrhizal fungal populations associated with the trees rendered them susceptible to pathogen and other fungal attack as the defensive role played by the mycorrhizal partners was reduced
- Trees were then dying from fungal diseases, some of them rare and previously undescribed, after several years of below average rainfall

Coincident with the occurrence of the two La Nina years was an above average rainfall. This brought relief for many stressed trees and they recovered rapidly with restored canopies and leaf area indices. However, to the surprise of many people, some trees that had survived the dry period for over a decade died in the wetter and apparently better conditions. Perhaps the following scenario may explain these observations:

Flooding, waterlogging or hypoxia and anoxia:

- Stressed trees begin to regrow fine absorbing roots and mycorrhizal partners resume growth when soil moisture increases after the dry period
- The loss of root carbohydrate reserves delayed new root production when waterbecame available as root growth was dependent on renewed photosynthetic activity
- However, some trees with insufficient time to recover fine absorbing roots or the normal mycorrhizal density, experience waterlogged soils, flooding or periods of soil hypoxia and anoxia. They experience a second dose of stress
- These already stressed trees further deplete their carbohydrate reserves and so root growth ceases, water uptake even when water is abundant is reduced and metabolic processes such as photosynthesis and respiration are adversely affected
- The diminished mycorrhizal fungal populations associated with the trees again rendered them susceptible to pathogen and other fungal attack due to the reduced defensive role played by the mycorrhizal partners
- Trees then die from fungal diseases, and other pest attack

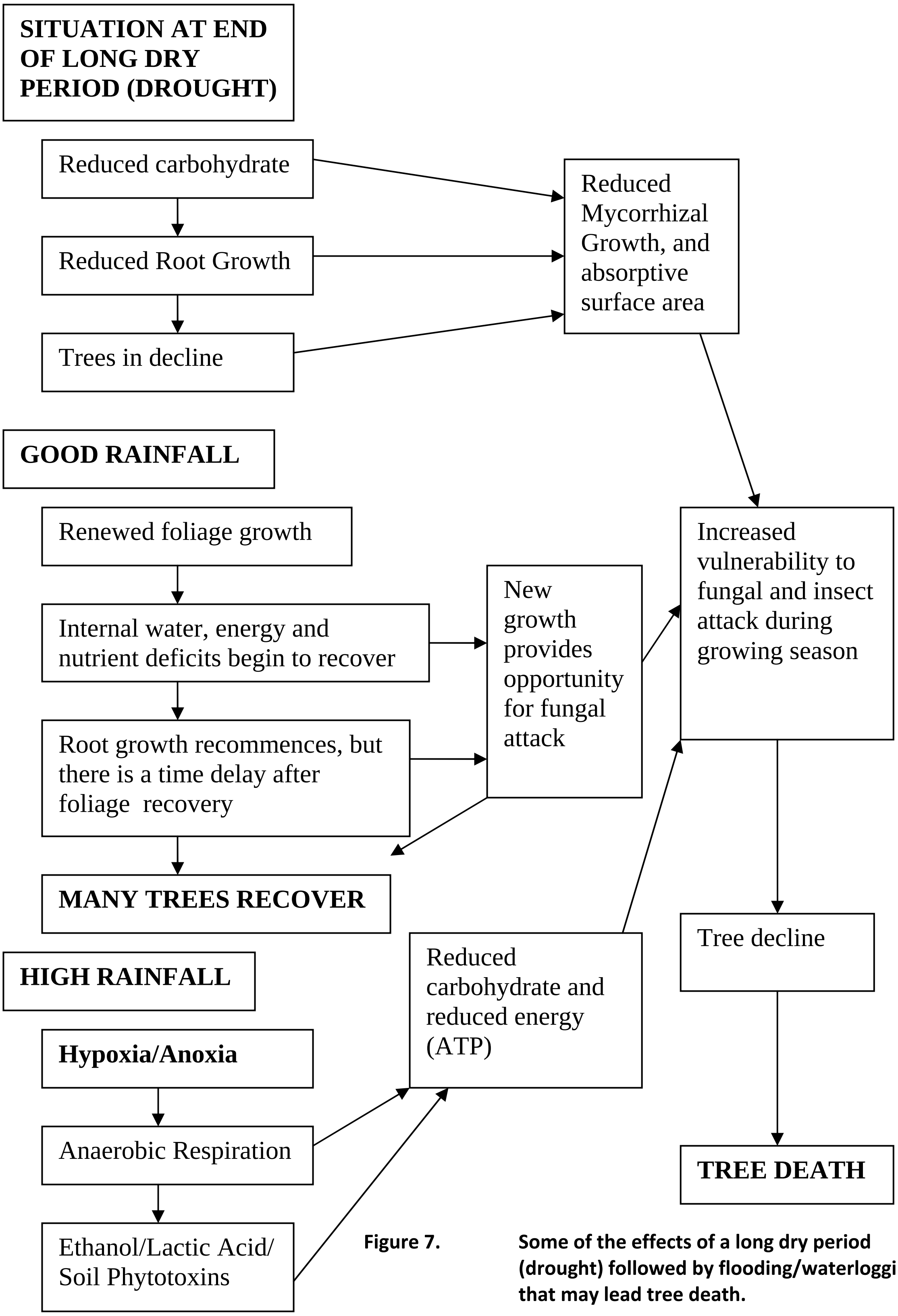

Figure 7. **Some of the effects of a long dry period (drought) followed by flooding/waterlogging that may lead tree death.**

Discussion

Under the climate change predictions for south eastern Australia, there is likely to be a general decline in rainfall (usually estimated at 10-15%), but the rainfall is more likely to be over late Spring and Summer. This means that the effective precipitation is likely to be less then the raw rainfall figure might suggest due to the higher rates of evaporation. While La Nina events will still occur, it is also likely that southeastern Australia will experience more droughts and prolonged dry periods.

In cities, the higher summer rainfall is likely to lead to local flooding which could affect urban trees through waterlogging and soil hypoxia and anoxia. Furthermore, a compounding factor could be that much of the open space in cities was once swampy or prone to flooding. Such land will be at risk as sea levels rise and with the tidal push back of rivers and streams, this land will be vital in local flood mitigation and stream flow retardation. Thus many local parks and open spaces will be prone to more regular flooding and waterlogging than in the past century, which in turn could impact on tree root systems. Many trees are also going to experience longer, warmer, dry periods followed by periods of high rainfall leading to flooding, water logging and soil anoxia.

Urban tree managers may wish to consider planning for an increased frequency of prolonged dry periods followed by bouts of high rainfall, waterlogging and flooding. Such a scenario could pose a significant threat to the health and viability of trees in those urban landscapes that form part of catchments and flood mitigation basins. Tree selection criteria that include endurance of waterlogging and hypoxic and anoxic soil conditions, particularly over summer would seem prudent. Proper forward planning could minimise the threats to trees in such situations and enhance their prospects of full life spans.

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