Physiological Factors - trees and environment

INTRODUCTION: Physiological factors

The basic physiological principles of photosynthesis, respiration, growth and development are similar in all plants but the details of how individual plants react can be vastly different. In this article we focus on the way in which trees respond to the major environmental variables of light, water and nutrients. This type of analysis is sometimes called environmental ecology and is the way in which plant physiology and ecology are linked.

Trees, as distinct from herbaceous plants, (e.g. cabbages and pansies) behave in a particular way to their environment. This is most obvious during establishment, and these differences are emphasised here as establishment is the most critical phase of tree growth.

The environmental factors of temperature, light, water and nutrients are the major influences on plants in the field and are interconnected, seldom acting alone. Light and temperature are closely linked, as are water and nutrients. In order to understand how these factors work on tree growth and distribution the following account is in three parts:

- Firstly a brief look at the important plant structures that are involved in the reactions;
- Secondly we look at the major environmental factors; and
- Thirdly some real life examples of how multiple factors control important aspects of plant establishment.

A reader may note in passing the distinction between the observed responses to environment (empirical) and the underlying principles (fundamental) that control that response.

Critical Plant Structures

Apart from reproductive structures, plants can be reduced to three critical structures that connect physically and functionally to each other in significant ways.

Leaves

For most plants, leaves are thin, flat, contain chlorophyll, are normally oriented at right angles to the light and are held above the ground. They function as light collecting organs and are oriented to intercept maximum light. Very importantly they are covered by a waterproof layer (cuticle), which has many thousands of controlled pores, called stomata, opening into the interior of the leaf.

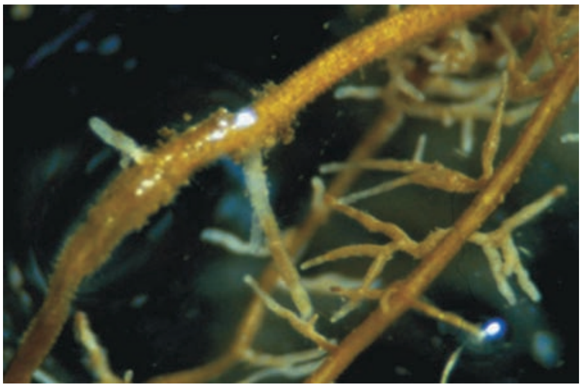
Stems

Stems are vertical pipes constituting the wood and bark of trees and serve both to display the leaves and to act as the pipelines or conduits connecting the leaves to the roots. Water and soil nutrients pass up from the roots to the leaves and sugars, produced by the leaves, pass down and along the stem to the roots and other organs.

Roots

Roots are often forgotten but are equally important, and in the establishment of new plants they are critical. They

distribute horizontally and vertically providing support for the plant and most importantly provide for the uptake and transport of both water and nutrients (see the Short Digressions on Fine and Coarse Roots and on R/S to see other aspects of roots that are important for plant establishment).



Mycorrhiza are fungi that most plants have on their roots where they increase the surface area of roots aiding absorption of nutrients. These ectomycorrhiza on the root system of a beech tree can be seen as Y-shaped white tips attached to the roots.

A Short Digression on Fine and Coarse Roots

We distinguish between coarse roots being those thicker than about 1 mm and fine roots, being 1 mm or less. This structural difference has important functional significance because of the large surface area that fine roots display.

The ability to absorb water is a function of the surface area of a structure and this is true whether the structure is alive or dead. A root of say 20 mm diameter has a low surface area to volume ratio of 0.2 while a root of 2 mm diameter has a surface area to volume ratio of 2. A 0.2 mm diameter root, which is about as fine as they get, has a ratio of 20 which is 100 times as much surface for the same volume or weight as a 20 mm diameter root. This is what separates coarse from fine roots. Fine roots are the organs that are critical in the uptake of water and nutrients, and it is only the finest terminal roots that can effectively function in this way. In addition to this most plants have associated fungal symbionts called mycorrhizas that extend the effective fine root area way beyond the root

A Short Digression on Root Shoot Ratio (R/S)

Another feature of roots is the balance between roots and shoot (shoot = stems + leaf). Plants in general have a similar mass (weight) of roots as shoots. This root/shoot ratio is a function of normal plant growth and is the expression of the way in which plants allocate growth to either root or shoot. Under low nutrition, especially nitrogen and phosphorus deficiency, shoot growth may be reduced at the expense of root growth and R/S may go to two (i.e. twice as much root as shoot). You can think of this as a mechanism by which the plant allocates more growth to roots so that more soil is explored to obtain more nutrients. Conversely under low light R/S may be as low as 0.5 i.e. twice as much shoot as root.

The plant has a large element of control over the allocation of resources, and will allocate disproportionately to that organ that is most limited, i.e. to shoots under low light and to roots under low nutrition and low water. This has quite far reaching implications for seedling establishment, as we shall see later.

In summary the root system and the shoot system are complementary systems that often mirror each other in uptake function and in mass; they both display high surface area and are strongly responsive to nutrients and water (roots) and to light (shoots).

THE MAJOR ENVIRONMENTAL FACTORS

Light, leaves and photosynthesis

Leaves are oriented to the sun, they intercept the visible light and a small proportion of that energy, no more than 5%, is converted by photosynthesis into chemical energy in the form of carbohydrate, which then becomes plant structure. The leaf is enclosed in a waterproof cuticle, which prevents too much water loss, but has thousands of small pores (stomata) that open in the light and close at night (Figure 1). The number of stomata varies widely, but for New Zealand conifers varies from 22 per mm^2 in a mature rimu *(Dacrydium cupressinum)* leaf to over 120 per mm^2 in tanekaha, which is illustrated in Figure 2 (Page 4). (For those who know tanekaha *(Phyllocladus trichomanoides)*, you will know that it does not have leaves but the organs we see looking like leaves are actually flattened petioles). These pores allow entry of carbon dioxide (CO_2) which provides the basis of photosynthesis and allows oxygen (O_2) to diffuse out. Water vapour also passes out of the stomata and this is equally important in understanding the functioning of leaves. The leaf is therefore a gas exchange organ and it is the stomata that control the influx and efflux of these gases.

Stomata open and close under the joint control of light and water availability. A simple model of the daily activity of a leaf will help to illustrate this. As the sun rises in the morning stomata open, CO2 enters the leaf and photosynthesis commences. The top line of Figure 3, (Page 4) shows a normal rise and fall of photosynthesis during a day in which no significant water stress occurs. The rate of photosynthesis follows the increase in light, peaks at midday and then falls away again. Most herbaceous plants follow this trend in which stomata remain open all day and photosynthesis is light dependent. However many woody plants, especially trees, respond as in line B in Figure 3 . At some time in the morning photosynthesis suddenly declines, not through lack of light but because stomata close in response to water stress. The open stomata lose too much water and this signals a partial closure of stomata, which constrains CO_2 uptake, giving rise to what is called the midday slump of photosynthesis. Later in the day water stress is relieved and photosynthesis increases as stomata reopen.

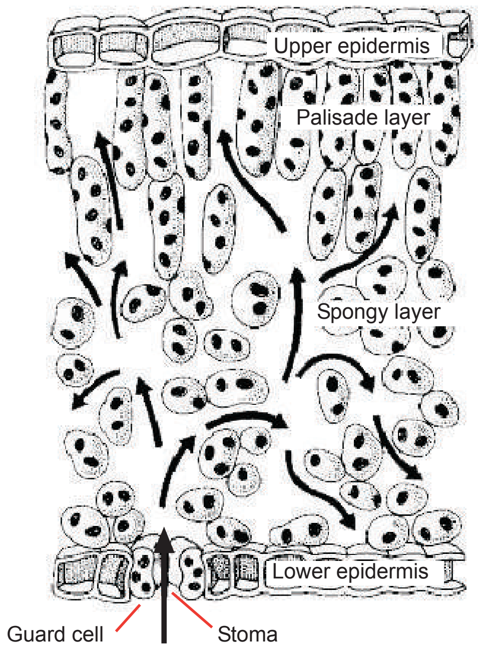


Figure 1: A cross-section of a leaf showing a pore or stoma which allows the controlled flow of the gases CO_2 into the leaf (arrows) and O_2 to diffuse out. Water vapour also passes out of the stomata.

Some plants are able to grow and perform best in full sun, while others are restricted to shady environments. The former are called sun plants and the latter are shade plants. Sun plants respond to light as shown in Figure 4, increasing their photosynthetic rate with increasing light right up to 100% sunlight. Shade plants show a photosynthetic saturation at low light levels often as low as 20% of full sun. Further light gives no further increase, in fact will simply cause more water loss with no growth benefit.

Under heavy water stress the lower line in Figure 3 holds and stomata remain partially closed all day, reducing critical water loss but also reducing photosynthesis. Options B and C are exacerbated under very dry soil conditions. When the loss of water cannot be contained the leaf loses most of its water and wilts. For many plants, wilting and recovery overnight can occur many times but if a critical amount of water is lost the plant will die. These examples illustrate the close coupling of light, water and photosynthesis in the SPAC (see panel next page).

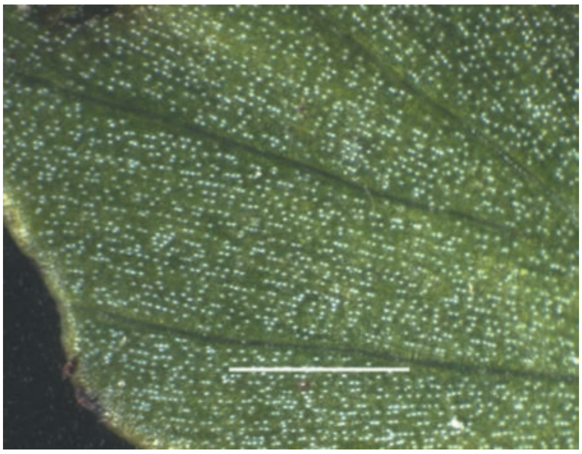


Figure 2: Surface view of underside of leaf, (technically a phyllode) of tanekaha showing stomata as white dots. Bar is 3 mm.

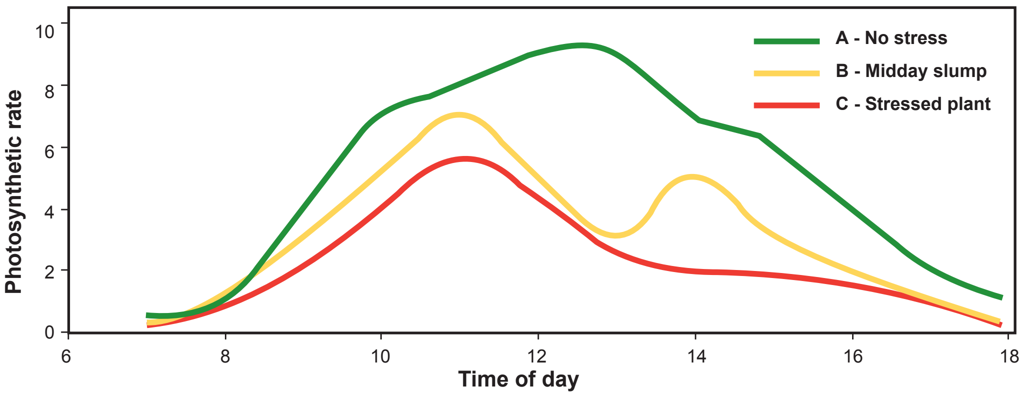


Figure 3: Photosynthetic response of plants under varying water stress.

Temperature

Temperature has profound effects on how plants grow and is one of the main ecological factors controlling plant distribution. Temperature effects are of two types; growth optima (or maxima) and cold temperature lethal effects. Like light it cannot be considered on its own as temperature has important effects on water, especially atmospheric water (humidity). The so-called temperature optima for growth show marked differences across many plants and these optima can often be traced to the climate under which that plant evolved. One of the best and most dramatic effects can be seen every spring in ryegrass pastures across New Zealand. Rye grass is a plant from the temperate climate of Europe it has a maximum growth temperature of 17°C and every year the enormous spring flush of growth completely dominates our pastures and certainly overwhelms such grasses as paspalum which has a temperature optimum of 27°C.

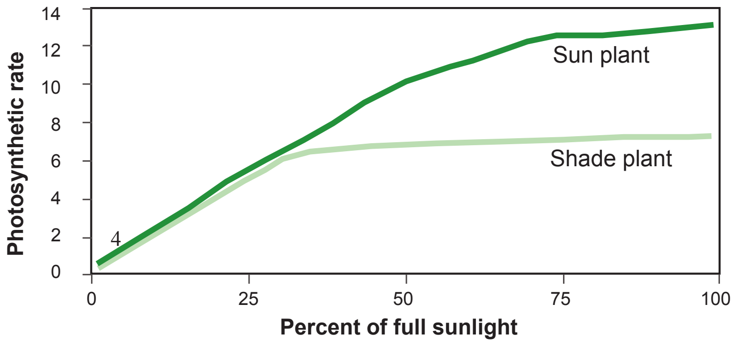


Figure 4: Photosynthetic response of sun and shade plants.

Amongst our native trees we can contrast kauri *(Agathis australis)*, with an optimum of c. 24°C, due to its tropical origins and affinities, with that of New Zealand beech *(Nothofagus* spp.*)*, having a temperature optimum of less than 20°C due to its southern origins. These two species are distributed in New Zealand areas that largely reflect that temperature difference. However, in many cases it is not the optimum that determines the range of a species but the minimum it can withstand, in other words - its frost tolerance. The best example of this is the 38°S line in New Zealand which is the natural distribution limit of many species, e.g. kauri, puriri *(Vitex lucens)*, mangrove (*Avicennia marina* subsp. *resinifera*) and pohutukawa *(Metrosideros excelsa)*. This has little to do with optimum growth temperatures, which for these species is bound to be on the high side, but has more to do with frost tolerance. We know for example that all these species can grow well outside that latitudinal range but are killed by a ground temperature of -2°C. Establishment is thus highly constrained by the frost level that a seedling can withstand.

SPAC

The three structural elements (leaves, stems, roots) are interconnected and form what is called the SPAC: **S**oil – **P**lant – **A**tmosphere – **C**ontinuum. This linkage is critical to understanding almost all of the ways in which plants interact with their environment. For example, there is a physical continuity of water from the soil through the plant to water vapour in the atmosphere. The atmospheric water deficit (drying power) draws water out of leaves and draws water through the plant and thence from the roots and the soil water. This is called the transpiration stream. Understanding the controls on this are fundamental to understanding how plants work. Under dry conditions the flow of water may be restricted, and the plant is put under stress, which may cause it to wilt.

Water and wind

Water and wind are so closely linked in controlling plant growth they can be treated together. Water that controls plant growth is of two types, soil water and atmospheric water. **Soil water** is provided by rainfall and soil moisture availability is a function of both rainfall and soil type. Light soils store very little water and, for a given rainfall, light sandy soils will be able to provide very much less water than heavy clay or organic soils. Thus again we see the interaction of two factors, rainfall and soil, determining the single factor soil water. In New Zealand we are fortunate in having reasonable rainfall frequency, with all months of the year receiving some rain in most areas, but periodicity is a significant variable in many parts of the world.

Atmospheric water, also termed humidity, is critical to water loss by plants. At 100% humidity the atmosphere is saturated with water vapour and wet surfaces cannot lose water to the air. Hence, you can't dry clothes in a saturated atmosphere. A dry atmosphere, e.g., 70% humidity, has enormous capacity to dry things and it is this 30% water deficit at say 70% humidity that causes plants to lose water from their stomata. The drier the air, the faster is the rate of water loss. Harking back to Figure 3, the midday slump in photosynthesis can be reduced by increasing humidity and thus decreasing water loss. This is what the moist tropics are like.

So as humidity decreases, water loss by plants increases and plants become stressed, not solely by soil water but also by water demand from the atmosphere. It is this characteristic that separates trees from herbaceous species more than anything else. Trees 'anticipate' water deficits by closing stomata during the morning as humidity decreases, probably because the water conduction pathways are so much longer. For this reason, an internal water deficit can build up much more severely in a tall tree than in a small cabbage plant.

Now this is where **wind** becomes important and interacts with humidity. As water evaporates from the leaf, the surface layers of the leaf, called the barrier layer, accumulate high humidity and this slows down evaporation.

Wind removes this barrier layer and stimulates more evaporation and so wind accelerates water loss. This is exactly the same phenomenon that we see with washing on the line – it dries twice as fast on a windy day for exactly this reason. **This factor is critical to the establishment of native tree seedlings.**

Nutrients and soil

A large number of interrelated factors are controlled by soils and nutrients. An initial one of importance for seedling establishment is compaction. While mature plants can force through compacted soils, seedlings are less able and soil may need ripping or otherwise treating. Plants obviously require a suite of mineral elements of which nitrogen (N), phosphorous (P) and potassium (K) are normally most critical. Almost all plants have fungi on their roots called mycorrhiza that effectively increase the surface area of roots and enable them to obtain nutrients that are in low supply. This is particularly important for P, which is often in limiting amounts, particularly in old soils.

THREE PRACTICAL EXAMPLES OF HOW PHYSIOLOGICAL PRINCIPLES WORK AND CAN BE MANAGED

The natural establishment of native tree seedlings can be observed in the field, and, using the empirical approach, experiments can be conducted to confirm these observations. We can also attempt to understand from first principles why such things should happen. Presented here are three examples of observations, along with the practices and the principles that underlie the observations.

1. MULCHING

Mulching of seedlings is seen as useful and important in seedling establishment. Certainly the natural regeneration of seedlings is often successful in an understorey with heavy ground litter. The natural litter is usually leaf and twig material decomposing on the forest floor. When we dig through this we find the fine feeding roots of the tree immediately below the decaying litter horizon spreading out into the litter above and into the soil below.

Why is this important? There are two reasons relating firstly to water and secondly to nutrition. The litter layer reduces direct evaporation of water and traps the moisture rising from the soil below, thus conserving and concentrating moisture in this zone. This provides an additional benefit, as it is this soil zone where most of the nutrients are concentrated. Keeping this area moist allows the roots to proliferate there and encourages nutrient turnover, providing a double benefit for plant establishment. Such a scenario is even more beneficial to seedlings planted out in the open where surfaces can dry very rapidly and destroy those superficial fine roots which are the water and nutrient uptake organs of the plant. An added benefit is the elimination of weeds that compete for water and nutrients. Thus, a mulch of leaf litter, chips, compost or even old carpet has significant benefit to establishment.

Mulching with material such as bark or wood chips is only likely to be practical on a small scale. However, for larger-scale planting, the cover of dead grass from spot spraying planting spots is likely to assist conserving moisture in the short term as newly planted seedlings become established.

Where practical, a mulch of leaf litter, bark, compost or even old carpet helps trap moisture in the upper part of the soil, encouraging root growth within this nutrient-rich zone. For larger-scale planting, retaining the dead grass cover from pre-plant spot-spraying of herbicide may assist in conserving moisture in the short-term.

2. SHADING

Shading seems to be the norm for tree establishment. The majority of native tree seedlings only thrive in various degrees of shade. Few are relatively shade intolerant, such as totara which bucks that trend. Many (e.g., tawa *(Beilschmiedia tawa)*, matai *(Primnopitys taxifolia)*, miro *(Primnopitys ferruginea)*, taraire *(Beilschmiedia tarairi)*) will only establish in sheltered environments, and others like kauri, beech and maybe kahikatea may grow in the open but certainly perform better in shelter. The reasons behind these observations relate again to the light/moisture/wind combination. A young seedling, especially a recently planted one, is subject to enormous water stress. It may have reduced root mass and it may take up to three years for the root/shoot balance to be regained.

So while many plants can use up to full sun, the reasons for shading and hence shelter are three-fold:

- It reduces light therefore reduces stomatal opening and thus, reduces water loss.
- It reduces wind and therefore has a marked effect on water loss.
- It provides a wind-still environment where humidity can build up.

The combination of these three effects results in the ideal environment, mirroring the natural shrub nursery that supports seedling establishment. However, too much shade will affect a tree's ability to photosynthesise, so a compromise approach is to provide partial shade or side shade with a light-well.

Left: This small group of puriri planted within a natural gap in a manuka (Leptospermum scoparium) and kanuka (Kunzea ericoides) dominated shrub cover are benefiting from the side shelter provided by the surrounding vegetation but still have overhead light to encourage good growth.

Below: Different species tolerate different levels of light such as shade tolerant ferns found within the understorey of dense forest and emergent canopy trees in full sun.

Kauri seedlings planted within artificial enclosures mimic the shelter provided if they were regenerating within the shelter of natural shrub vegetation.

Inset: A newly planted seedling is subject to enormous water stress. The side shelter reduces the wind and therefore has a marked effect on reducing water loss at the same time as increasing humidity.

3. ROOT PRUNING AND WRENCHING

A good understanding of the principles of SPAC and R/S applies to raising seedlings as open-ground transplants as well as to the common practice of transferring plants from the wild to new sites. Plants require conditioning involving root pruning and wrenching otherwise their R/S can be markedly compromised.

Bare-root seedling production

Seedlings grown in a seedbed which are to be planted as bare rooted or open-ground transplants are conditioned before out-planting. This conditioning aims to develop a compact fibrous root system up to 3 months before lifting of the seedlings. It involves:

1. Passing a sharp bar beneath the seedlings to cut off the taproot after which they are left to recover, which simply means they must grow new roots to compensate for the lost ones;
2. Then several side cuts are made to sever side roots and left to grow more roots. By this time, each plant has a bunch of new roots that can provide the plant with enough water in the new environment; and
3. Finally, immediately before lifting, a wrenching bar is used to jostle the seedlings to help further loosen the soil to allow seedlings to be lifted easily by hand ready for planting.

Mechanised root pruning and wrenching works extremely well for radiata pine (*Pinus radiata*) where tens of millions of pines are produced as one-year-old bare-root seedlings every year for commercial forestry in New Zealand. Production of bare-root seedlings has been developed for many native tree and shrub species and is being refined with ongoing nursery and planting trials (refer to Section 5 on Seed and Propagation in this Handbook).

Transplanting wildings

To improve chances of survival, transferring a native tree seedling from the bush to a new site also requires conditioning involving root pruning and wrenching. Starting in late summer this firstly involves cutting the tap root using a spade inserted on an angle beneath the plant. Then the lateral roots are cut on the south, east, west, and north sides sequentially over a period of three months. In this way roots are encouraged to regenerate prior to removal. Toward the end of the conditioning period the plant should be relatively loose in the soil.

When the plant is moved, up to half of the foliage should then be cut off to ensure the R/S ratio is re-established. This is especially necessary for larger seedlings.

A dense fibrous root system has developed on this manuka seedling by a series of root pruning and wrenching operations performed by tractor machinery over a 3 month period before the seedling is lifted for planting out.

CONCLUSION

All plants have a common physiology. However trees are particularly sensitive to atmospheric water stress and spend a lot of time during the day with stomata partially, sometimes completely, closed. Kauri is a good example of this – in open environments stomata partially close by morning teatime, only to open fully again in the mid-afternoon when the temperature drops and the humidity rises. Knowledge of principles that control a plant's growth and survival help us to design planting and establishment regimes in which trees may thrive under cultivation.

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