

The physiological basis of plant responses to climate change

Plants are fundamental to life, utilising the sun's radiant energy to combine carbon dioxide and water to produce sugars and oxygen by the process of photosynthesis. The sugars are combined with nutrients from the soil to produce proteins and other complex compounds which enable the plant to grow and to function. The pattern of growth and development from seed to flowering plant producing more seeds is governed by many factors such as carbon dioxide concentration, the quantity, quality and duration of light and availability of water and nutrients. Each species of plant has evolved to suit a particular ecological niche, using signals from the environment - especially temperature and day length - to synchronise their growth with seasonal changes. This chapter provides a basic outline of how plants function and explores how changes in climate might affect their growth.

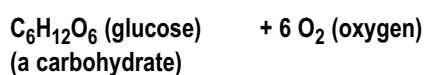
3.1 Plant growth and development

Plants *grow*, by accumulating material to become larger, and they *develop*, in response to internal and external stimuli, from juvenile to mature state, from vegetative to flowering, and from active to dormant for example.

The fundamental process driving plant growth is photosynthesis, by which the green tissues of the plant, especially its leaves, combine carbon dioxide from the air with water taken up from the soil by roots to produce carbohydrates (sugars, starch and cellulose), the basic building materials of the plant. Oxygen is also produced in the process. The photosynthesis process may be summarised as;



→ with energy from sunlight →



The carbon dioxide needed for photosynthesis diffuses into the leaves through small pores (stomata) mainly in the undersides of the leaf. In order to survive the plant has to balance its need to take in carbon dioxide with the need to reduce loss of water vapour through the stomata. It does this by opening and closing the stomata through very sensitive feedback mechanisms which respond to carbon dioxide and water availability. The energy required for photosynthesis comes from sunlight.

The plant then combines the products of photosynthesis with nitrogen (usually as nitrate), phosphorus, potassium and other nutrients taken up from the soil in solution, to produce proteins and other complex materials. The factors which most affect the growth of a plant are those required for photosynthesis (light, water and carbon dioxide) and the levels of available nutrients (nitrogen, phosphorus, potassium and minor nutrients).

Water plays a key role in plant growth by making nutrients in the soil available to the plant, but it is also vital in keeping the plant turgid. If water supplies in the soil are inadequate, or if evaporation from the plant's leaves exceeds the ability of the plant roots to replenish this loss, the plant will suffer water stress.

The immediate response to water stress is closure of the stomata, thereby preventing further water loss but at the cost of cutting off the carbon dioxide supply needed for growth. If water stress continues the plant will usually react by wilting, then shedding leaves to reduce its evaporative surface. Continued water stress will lead to damage to cell tissues and ultimately to the death of the plant.

Plants not only grow, by accumulating carbohydrates and proteins, but they develop by germinating from seed, producing new shoots and leaves, by flowering, and setting seed. In a temperate climate such as that experienced in the UK, perennial

plants (those which live for several, often many, years) have yearly cycles in which they produce leaves, flowers and seed then prepare for winter, for example by developing underground resting organs (bulbs, tubers) or by losing their leaves and producing resting buds tolerant of low temperatures. This winter resting state often develops into true dormancy which can only be broken by a period of low temperatures or short day lengths or both. When dormancy is broken the plant is ready to begin growth again as soon as the temperature increases sufficiently.

The growth of a plant is controlled mainly by light levels, the availability of carbon dioxide, water and nutrients, and temperature. Its development, from vegetative to flowering to resting for example, is often controlled by more complex mechanisms such as changes in day length or changes in temperature. The onset of dormancy and release from it are particularly complex processes. In some plants temperature change is the main stimulus. In others the process is entirely or predominantly controlled by day length while in other plants day length and low temperature will substitute for each other in varying degrees.

From this brief and very much simplified description of plant growth and development it is clear that some aspects of growth and development will be significantly affected by climate change (when carbon dioxide concentration, temperature or water availability are important for example) while other aspects, especially those controlled by day length, will be largely unaffected.

Plants grow and develop in response to a range of stimuli but especially to the availability of carbon dioxide, water and mineral nutrients and to the quality and quantity of light. Most of these stimuli will be affected directly or indirectly by climate change, except that light quality and the natural rhythm of variation in day length will remain unaltered.

3.2 Plant responses to carbon dioxide

In most climate change impact studies carbon dioxide concentration is important only insofar as it is the principal driver of climate change. In studying the impact of climate change on gardens, as with agriculture, forestry and nature conservation, carbon dioxide itself has a significant impact by its involvement in photosynthesis.

3.2.1 CARBON DIOXIDE AND GROWTH

If other factors remain favourable, increased carbon dioxide concentrations will lead to greater rates of photosynthesis in plants. Current carbon dioxide concentrations limit plant photosynthesis. Growers of protected horticultural crops have known for some many years that artificially raising the concentration of carbon dioxide in greenhouses can substantially increase crop growth and yield. It is generally accepted (Kimball *et al.*, 1983; Poorter, 1993) that a doubling of carbon dioxide concentrations will lead to approximately a 40-50% increase in the growth of plants. However, there are strong interactions between increased temperature and carbon dioxide such that increases in carbon dioxide concentration will not always lead to increases in the yield of food crops for example (see Section 3.3.6).

Response to elevated carbon dioxide concentrations varies between different species. A review by Poorter (1993) indicates that herbaceous crop plants responded more than herbaceous wild species (58% vs 35%), and potentially fast growing wild species increased more than slow growing species (54% vs 23%). Leguminous species capable of symbiosis with nitrogen fixing organisms had larger responses to carbon dioxide compared to other species. There is also a tendency for herbaceous dicotyledons (broadleaved plants) to show a larger response than monocotyledons like grasses. Poorter (1993) suggests that the more responsive plants are those with a greater sink strength, that is in those plants with active regions such as developing fruits or rapidly expanding shoots capable of utilising the products of photosynthesis.

There have also been comprehensive reviews of the effects of elevated carbon dioxide levels on woody

plants, notably Curtis and Wang (1998). The rate of growth accumulation in trees will be significantly higher as a result of elevated carbon dioxide concentrations (Jach and Ceulemans, 1999). Recent findings have shown that forests are currently growing at an accelerated rate, particularly in the northern hemisphere. Annual increase of wood volume in coniferous and hardwood forests in Sweden, Germany, France and other European countries has increased by up to 50% as a result of rising carbon dioxide levels, a longer growing season and increasing nitrogen deposition (Spiecker *et al.*, 1996; Scarascia-Mugnozza *et al.*, 2001). Broadmeadow (2002b) suggests that timber yields in the UK may be 20-40% higher over the course of the 21st century as a result of higher carbon dioxide levels.

The benefits of elevated carbon dioxide levels may, however, be relatively short term. A process of acclimation (becoming adapted to) is often seen in plant responses to carbon dioxide. Here, the short term photosynthetic response to instantaneous changes in carbon dioxide is much larger than the long term response. Long term exposure to elevated carbon dioxide leads to the accumulation of carbohydrates in the photosynthetic tissues of the plant and this accumulation leads to a reduction in photosynthetic rates (Clough *et al.*, 1981). Medlyn *et al.* (2000) noted an initial 20% increase in net primary productivity of coniferous forests in response to a doubling of carbon dioxide concentration but the increase was not persistent, whereas a 2°C increase in temperature caused a 10-15% increase in long term productivity in both cool (Swedish) and warm (Australian) climates. (Medlyn attributed this temperature effect to increased soil nitrogen availability at the higher temperatures.)

In the long term, leaves developing under elevated carbon dioxide concentrations appear, in many species, to have fewer stomata than under lower carbon dioxide levels (Woodward, 1993). In fact, studies of herbarium specimens indicate that stomatal numbers in leaves collected from tree species at early stages of the industrial revolution were higher than present day numbers (Woodward, 1987, Penuelas and Matmala, 1990). Since the late 18th century the mean atmospheric carbon dioxide concentration has increased from about 277 parts

per million by volume (ppmv) to current levels of over 350 ppmv and thus there appears to be a close relationship between the historical trends in stomatal number and carbon dioxide concentration.

Nevertheless, although photosynthetic responses to carbon dioxide are less marked in the long term than those anticipated from short term measurements, these responses are significant and contribute substantially to the increase in growth and dry matter accumulation under climate change conditions. The increase in carbohydrate concentration of tissues leads to higher dry matter content (cellulose, starch etc) of plant tissues which could have implications for the quality of some horticultural products. This may have less importance in gardens than in commercial horticulture but it could, for example, affect the storage life of allotment and kitchen garden produce. It might also affect pest and disease incidence (Ciesla, 1995) (see section 3.5).

3.2.2 PARTITIONING OF ASSIMILATES

About half of all assimilates (carbohydrates and proteins) are exported from the shoot to below ground parts of the plant where they are used for root respiration, nutrient uptake and transport processes in the roots, and as an energy source for nitrogen fixing bacteria and mycorrhizal fungi associated with the plant (Lambers, 1987). Under optimal levels of water and nutrient supply, this partitioning of assimilates to the roots does not appear to be changed by elevated carbon dioxide concentrations (Stulen and Hertog, 1993). When nutrients are in limited supply, varying responses have been noted but some experiments (eg Oberhauer *et al.*, 1986) have demonstrated a higher allocation to roots in elevated carbon dioxide conditions where naturally occurring species are growing under nutrient limited conditions. This suggests that, in soils with low nutrient status, the higher carbon dioxide concentrations associated with climate change may enable plants to forage more effectively for their nutrients.

Experiments in which the effects of elevated carbon dioxide on the responses of plants to water stress have been examined show a variable

response. In some species, partitioning to the root is not influenced by elevated carbon dioxide concentration whereas in other species there is an increased proportion of photosynthetic products moving to the root system implying a greater investment in roots to increase their access to available soil moisture (Tolley and Strain, 1985). In these species, higher carbon dioxide concentrations in the air will enable the plant to tap limited soil water resources more effectively.

3.2.3 CARBON DIOXIDE AND DEVELOPMENT

In addition to their impact on photosynthesis and therefore plant size, carbon dioxide levels can also affect other aspects of plant development. Cannell (1990) noted an effect on timing of bud burst and the cessation of growth: altered concentrations of carbohydrates and plant hormones in turn altered the dormancy status of trees thereby changing the timing of bud burst and the length of the active growing period. Jach *et al.* (2001) compared thirteen different studies of the effects of doubling of carbon dioxide concentrations on bud burst in nine different tree species. They showed that, whilst time of bud burst of five species was unaffected by elevated carbon dioxide concentrations, one species (Scots Pine [*Pinus sylvestris*]) was advanced and three were delayed (Sitka spruce (*Picea sitchensis*), Sweet chestnut (*Castanea sativa*) and the hybrid poplar (*Populus trichocarpa x Populus deltoides*). There did not appear to be any differences in the responses between coniferous and broad leaved species. In addition, elevated carbon dioxide resulted in a shortening of the growing season in three species (*Castanea sativa*, *Picea sitchensis* and *Populus sp.*). In one of the reported studies on *Pinus sylvestris* (Jach and Ceulemans, 1999), elevated carbon dioxide also stimulated the buds to develop more rapidly than under ambient conditions. However, there appears to be strong interaction between these responses and nutrient availability. Increased nutrient availability increases the growing season in many tree species (Bigras *et al.*, 1996) and may mask the effects of elevated carbon dioxide concentration.

Flowering and fruiting of trees are likely to be hastened under conditions of elevated carbon dioxide.

For example, flowering of roses is hastened and the number of flower buds is increased (Andersson, 1991). The yields of Valencia orange (*Citrus sinensis*) (Downton *et al.*, 1987) and orange trees (*Citrus aurantium*) (Idso and Kimball, 1997) were increased when they were grown in elevated carbon dioxide levels. These increases in yield resulted from increases in both fruit numbers and fruit size.

The evidence for an effect of carbon dioxide concentration on leaf senescence and leaf fall is rather contradictory and may be species dependant. Some studies (eg, McConnaughay *et al.*, 1996) suggest that leaf fall could be accelerated by elevated carbon dioxide. However, others (eg, Gunderson *et al.*, 1993) suggest that leaf fall in some species is unaffected whilst yet other studies suggest that leaf fall can be delayed (Norby *et al.*, 1986, McConnaughay *et al.*, 1996). Clearly, the effect of carbon dioxide concentration on leaf senescence is still poorly understood and requires further study.

Most predictions of the direct effects of carbon dioxide suggest that average yields will increase by about 40-50% with a doubling of carbon dioxide concentrations. However, this does not address how plant growth responses to carbon dioxide are affected by changes in other climatic variables such as water and soil nutrient availability or temperature conditions. Interactions of carbon dioxide and temperature are particularly important and are described in section 3.3.6 below.

3.2.4 INTERACTION OF RESPONSES TO CARBON DIOXIDE AND WATER

The plant manages its intake of carbon dioxide and its control of water loss by the same mechanism, the opening and closing of its stomata. As mentioned briefly in section 3.1 and discussed more fully in section 3.4 the plant responds to water stress by closing its stomata. Conversely, if the supply of carbon dioxide is greater than the plant can utilise, it will react by closing its stomata and it will, in so doing, reduce its water use.

Leaves are able to detect and respond rapidly to carbon dioxide concentration. Stomatal opening decreases in response to increased carbon dioxide

concentrations (Woodward *et al.*, 1991). Decreased stomatal aperture under conditions of elevated carbon dioxide also leads to an increased resistance to water loss from leaves. Thus, as carbon dioxide concentration increases, the water use efficiency (carbon dioxide gained in relation to water lost) also increases. This suggests that the rate of evapotranspiration decreases under conditions of elevated carbon dioxide. Crop simulations used to predict the irrigation requirements of potatoes under climate change conditions suggest that there will be very little change in irrigation requirements under most climate change scenarios, as reduced precipitation is balanced by increased water use efficiency (Wolf, 2000). Indeed, use of an earlier crop variety and an earlier planting date, made possible by increased temperatures, could considerably reduce irrigation requirements.

Taking into account long term reductions in stomatal numbers and short term closure of stomata in response to increased carbon dioxide concentration, Woodward (1993) estimates that leaf water use efficiency has increased by about 28% over the last century. Kimball *et al.* (1983,1984) measured seasonal water use (essentially evapo-transpiration) for well watered, field grown cotton in open top carbon dioxide chambers. Although not very consistent the data overall showed a slight decrease in water use at elevated carbon dioxide concentrations. This, coupled with the large increase of yields, suggest that these beneficial effects of elevated carbon dioxide may, in some instances at least, compensate for increased evaporation from plants in the drier conditions anticipated by climate change scenarios.

Response to elevated carbon dioxide may be influenced by water stress. Kimball *et al.* (1993) again showed that seed cotton yields were increased more by a doubling of carbon dioxide concentrations under drier than under wetter conditions (74% compared to 54%).

It is important to remember, though, that while the impact of the environment (in terms of higher carbon dioxide levels) on the plant may be to increase the efficiency of water use, the impact of the plant on the environment will be to reduce humidity

(Ciesla, 1995) and, by not using energy for evaporation, to increase the temperature of both the plant and its surroundings. The valuable air-conditioning effect of plants will be reduced during periods of water stress.

3.2.5 INTERACTION OF RESPONSES TO CARBON DIOXIDE AND NITROGEN

The increase in carbohydrate content of tissues under elevated carbon dioxide is not necessarily accompanied by increases in nitrogen uptake and so a likely response to climate change is a decrease in the nitrogen concentration in plant tissue and an increase in the nitrogen efficiency of plants. Overall, therefore, nitrogen use by plants may stay essentially the same and fertiliser requirements will be unaltered by increasing carbon dioxide levels.

One of the many uncertainties surrounding climate change impacts on gardens is whether nitrogen availability in the soil will increase (as a result of higher nitrous oxide levels in the atmosphere and higher rates of mineralisation in soils) (Medlyn *et al.*, 2000) or will decrease as a result of increased leaching (Jeffery, 2001). This would be a fruitful area for research.

The response to carbon dioxide may also change under conditions of low soil fertility. Data from Kimball *et al.* (1993) show that, even under nitrogen limited conditions, the response to a near doubling of carbon dioxide concentration led to a 53% increase in seed cotton yields under both irrigated and dry conditions.

Carbon dioxide is important because carbon atoms form the structural skeleton of the plant. A doubling of carbon dioxide levels may increase plant growth by 40-50% though continuous high levels saturate the plant's ability to use carbon dioxide and the benefits decrease with time. Higher carbon dioxide levels also allow the plant to use water more efficiently and may make the plant sturdier, more fruitful and more resistant (or less appetising) to pests.

3.3 Plant responses to temperature

There are two main categories of temperature effects on plant growth and development. The first is the effect of temperature and temperature fluctuations on general growth and development; the second is the effect of temperature extremes on survival.

3.3.1 TEMPERATURE AND GROWTH

Each plant species has its own characteristic response to temperature. Most biological activity slows almost to zero below 5°C. At still lower temperatures cell functions may be impaired and the plant damaged. At some point below 0°C ice may form between and within plant cells, causing damage or death of the plant, although many plants have strategies for surviving temperatures far below 0°C.

Above 5°C growth increases exponentially towards an optimum which varies widely from plant to plant, usually reflecting the natural climate within which a particular species has evolved.

Higher summer temperatures, like higher carbon dioxide concentrations, will favour plant growth if other factors are not limiting. As temperatures exceed the optimum for any particular plant its growth rate then falls, often sharply, to the point at which damage to tissues leads to complete cessation of growth and ultimately to the death of the plant. Temperatures in the UK are unlikely to reach levels in the next 50-100 years at which they cause direct damage to plants (essentially 'cooking' the plant) rather than causing indirect damage by increasing water stress, although the possibility can not be ruled out on very hot days, especially in greenhouses.

3.3.2 TEMPERATURE AND DEVELOPMENT

Plant developmental responses are somewhat different to the growth response to temperature, in that developmental rates increase approximately linearly with temperature above a threshold temperature which is often referred to as the 'base temperature' for plant development (Ellis *et al.*, 1990). As for growth (see section 3.3.1 above) this base temperature is about 4.5-5°C for many species but can be lower for some species such as some

Brassicacae (Hadley and Pearson, 1999) and higher for species from a tropical or subtropical origin (Hadley *et al.*, 1984). This linear increase in the rate of plant development reaches an optimum typically at between 20°C and 25°C but again this varies between species, varieties and even different developmental processes in the same plant. Above this optimum temperature, developmental rates often decline at approximately the same rates at which they increase at sub-optimal temperatures.

Because rates of plant development increase linearly with temperatures above a threshold, events such as germination, leaf appearance and flowering of day length insensitive species and varieties often occur after a fixed accumulation of heat above this base temperature, often called 'thermal time' and measured in day degrees (number of days multiplied by degrees above the base temperature). This can be very useful in predicting the effects of climate change. For example, if time from germination to flowering for a particular species occurs after the accumulation of 900 day degrees above 5°C, then flowering time will be 90 days at 15°C (90 days x 10 degrees above 5°C). The effects of an average increase in season temperature of 2°C above 15°C over the period of flower development would then lead to a date of flowering 15 days earlier (75 days at 12 degrees above 5°C). Thus, providing that the thermal time requirements for particular events are known, the effects of increased temperature on these events can be estimated relatively easily. However, the resources needed to determine thermal time requirements are such that the information is likely to be available only for important crop plants. This may yield useful information for the management of kitchen gardens and allotments but for most ornamental plants, phenological studies of flowering dates and other developmental responses to temperature change are likely to be more informative.

As already stated, higher temperature generally increases the rate of growth and of development of plants, particularly at the lower end of the range of temperatures suitable for growth. One effect of an extended growth period which has thus far been little studied is that plants will be growing at substantially lower light levels and in shorter days at any given temperature than at present (van de Geijn

et al., 1998). The effect of this on quality of growth and, for example, on susceptibility to pest attack, needs further investigation.

One of the most important effects of climate warming is likely to be changes to the onset and cessation of growth (i.e. the beginning and the end of the growing season). Current estimates suggest that spring is advancing by 2-6 days per decade and autumn is delayed by about two days per decade (see section 2.1.1), and it is anticipated that a year round thermal growing season may be experienced in the south of England before the 2080s in the high emissions scenario (Hulme *et al.*, 2002). This will affect the rate of development (the ‘phenology’) of the plant.

Temperature has very complicated effects on plant growth. Higher temperatures increase growth and speed up the rate of plant development so plants will flower earlier, though the scale of the response is different in different plants. In recent decades spring has been advancing by 2-6 days per decade and autumn has been delayed by two days per decade. With temperature increases anticipated in the high emissions scenario, a year round growing season in the south of England will be likely in some years before the 2080s.

3.3.3 PLANT PHENOLOGY

As mentioned in section 2.1.1, examples of long delayed autumn leaf fall, flowering extending into

the winter months, ‘unseasonal’ flowering of spring bulbs, and other indicators of climatic change are widespread in the horticultural and national press (see, eg, Anderton, 2000; Fletcher, 1999; Greenwood, 2000) to the extent that it is becoming necessary to redefine what is meant by ‘unseasonal’. Observations show already that in years with mild winter temperatures and warmer springs, bud burst is advanced and the onset of growth occurs earlier (Last, 2001).

The most conspicuous manifestation of climate warming in a garden situation will be earlier flowering times of many plants. Historical data on flowering times of many of our garden species provide a useful guide to how our gardens may change under conditions of climate change. Many long term records exist and already show substantial changes in flowering time as a result of recent changes in our climate. Analysis of long term records of flowering of a number of garden plants (eg Last, 2001) suggests that some species, including Mexican orange (*Choisya ternata*) and *Rhododendron* ‘Praecox’ will be very responsive to climate change, whilst others, such as Honesty (*Lunaria annua*) and bleeding heart (*Dicentra formosa*) will flower at approximately the same time as they do now.

Table 2 shows trends in flowering times of some common garden plants recorded by Mary Manning in her garden since the mid 1960s (Sparks and Manning, 2000) with flowering times for many species advancing by one to two weeks per decade over the last twenty years.

Table 2: Flowering time of some common garden plants recorded in East Anglia over the last forty years expressed as a mean date of flowering averaged over the periods 1965-1980, 1981-1990 and 1991-2000

Source: Sparks and Manning (2000)

	1965-1980	1981-1990	1991-2000	Days earlier per decade
Primrose (<i>Primula vulgaris</i>)	Feb 8	Jan 6	Nov 23	23.1
Aconite (<i>Eranthis hyemalis</i>)	Jan 11	Jan 12	Dec 14	10.7
Hazel (<i>Corylus avellana</i>)	Feb 3	Jan 14	Dec 14	10.7
Daffodil (<i>Narcissus cv.</i>)	Mar 10	Mar 7	Feb 25	7.9
Crocus (<i>Crocus sp.</i>)	Feb 8	Jan 22	Jan 24	7.1
Snowdrop (<i>Galanthus nivalis</i>)	Jan 19	Jan 10	Jan 6	5.5
Willow (<i>Salix sp.</i>)	Feb 16	Feb 19	Feb 8	–

A more detailed analysis of 23 British native and garden species is given by Sparks *et al.* (2000). This shows that 22 out of 23 species showed a significant advancement in flowering time with a 1°C increase in temperature (Table 3).

The results suggest a 2-10 day earlier flowering for each degree Centigrade of temperature rise. Interestingly, autumn crocus produced the only positive response, an indication that in plants responding to declining temperatures as a stimulus for autumn flowering, flowering may be delayed as mean temperatures increase.

Butterfield *et al.* (2000) simulated the effect of climate change on grape vine production in the UK and showed that under climate change conditions predicted by the HadCM2 climate model, date of bud burst occurs 10 to 25 days earlier, while date of maturity occurs 20-50 days earlier. Currently the area suitable for grape production (where grapes are able to reach maturity by 15 November) covers the southern and central counties of England, with Lancashire in the west and

Humberside in the east marking the northern limits. Maturity in the UK varies from late September to mid November with maximum achievable yields varying from 175-200 grams per square metre (gm⁻²). Although temperature has a negative effect on grape yields this is more than offset by the substantial positive effect of increased carbon dioxide. The net effect will be increases in yield ranging from 10-25% by 2050. It is estimated that mean yield, quality and quantity of grapes used for wine making in the UK will increase under conditions of climate change (Bindi and Fibbi, 2000). Grape production, at present on the northern limit for economic production in the UK, could extend into Scotland as the Iberian peninsula becomes less and less suitable (Schulz, 2000). In gardens, the grape might eventually replace such fruits as raspberry and blackcurrant which will not respond well to increasing temperatures.

One result of warming at the lower end of the temperature range is already, and will increasingly be, the near continuous growth of lawns through the winter months. In recent research at the Cambridge

Table 3: Results from stepwise regression of flowering time on Central England monthly temperatures (from the preceding October through to the month of mean flowering of that species). Source: Sparks *et al.*, 2000

The value in the second column gives the pooled effect of a 1°C rise across all months on the date of flowering (expressed in days). A negative sign indicates an advancement in flowering time, a positive sign indicates a delay in flowering time. Six species for which 58 years of data exist are given first followed by species with 20 years of data.			
Species	Net effect (days)	Species	Net effect (days)
Greater bindweed (<i>Calystegia silvatica</i>)	-9.9	Ox-eye daisy (<i>Leucanthemum vulgare</i>)	-4.9
Bird cherry (<i>Prunus padus</i>)	-9.1	Redcurrant (<i>Ribes rubrum</i>)	-4.9
Almond (<i>Prunus dulcis</i>)	-8.9	Horse-chestnut (<i>Aesculus hippocastanum</i>) – leafing	-4.9
Purple lilac (<i>Syringa vulgaris</i>)	-8.8	Winter aconite (<i>Eranthis hyemalis</i>)	-4.7
Hawthorn (<i>Crataegus monogyna</i>)	-8.6	Coltsfoot (<i>Tusilago farfara</i>)	-4.2
Dog rose (<i>Rosa canina</i>)	-8.2	Hazel (<i>Corylus avellana</i>)	-4.1
Laburnum (<i>Laburnum anagyroides</i>)	-7.9	Garlic mustard (<i>Alliaria petiolata</i>)	-4.1
Horse Chestnut (<i>Aesculus hippocastanum</i>) – flowering	-7.7	Wood anemone (<i>Anemone nemorosa</i>)	-3.6
Ivy (<i>Hedera helix</i>)	-7.3	Snowdrop (<i>Galanthus nivalis</i>)	-3.4
Lesser celandine (<i>Ranunculus ficaria</i>)	-6.7	Harebell (<i>Campanula rotundifolia</i>)	-2.6
Elder (<i>Sambucus nigra</i>)	-6.5	Christmas rose (<i>Helleborus niger</i>)	-1.9
Madonna lily (<i>Lilium candidum</i>)	-6.4	Autumn crocus (<i>Colchicum speciosum</i>)	+3.8
Yellow crocus (<i>Crocus aureus</i>)	-5.8		

Botanic Garden, Jeffery (2001) found that lawn growth in plots heated to 3°C above ambient was higher in March (a small but significant increase) and 18% higher in April.

Another effect of a general increase in temperature, especially if combined with wetter winters, might be the increased incidence of mosses and algae, many of which have lower threshold temperatures for growth than those of most flowering plants. Hotter and drier summers may limit or counter this increase, or at least result in the mosses and algae adopting their dry resting state for a larger proportion of the summer. However, difficulties could well arise as more gardens open earlier in the year in response to progressively earlier flowering seasons: algae and mosses will exacerbate the slipperiness of wet paths.

3.3.4 DORMANCY

Much of the UK garden flora consists of species that have a perennial habit, for example, trees, shrubs and herbaceous perennials. These have distinct annual growth cycles which can be divided into three phases; a rest period, a period of quiescence and an active growth period (Leinonen, 1996; Battey, 2000). The rest period and the quiescent period together constitute the dormant period. The rest and quiescent period are often described as periods of innate and induced dormancy respectively and have evolved to ensure that plants have no soft, young growing tissues that could be damaged by the unfavourable conditions that prevail during the winter period.

During the autumn and winter, active growth ceases and plants then have very limited ability to grow even if placed in conditions that allow active growth. Although the plant appears to be inactive during dormancy, this is often a period of high internal activity, with the plant producing leaf and flower initials in readiness for rapid spring growth. Exposure to a period of low ‘chilling’ temperatures is required before a plant can resume active growth. This chilling requirement is often measured as the accumulation of temperature below a particular threshold temperature. For example, sweet cherry requires the accumulation of 1000

chill units at 3.8°C in order to complete or ‘break’ dormancy (Mahmood *et al.*, 2000). If chilling is inadequate, the development and/or the later expansion of leaf and flower buds may be impaired. Problems have already been experienced with poor cropping of blackcurrant after mild winters (Carew, *pers. comm.*) and the same might happen with raspberry, apple and other fruits as winter temperatures continue to increase.

After the completion of the rest period, plants enter a quiescent period in which they have the potential to grow but are limited by the prevailing conditions in late winter and early spring. Once temperatures attain a certain threshold, plants then begin their active growth period. During this growth phase, providing the temperature is warm enough, the amount of growth is a function of the amount of light intercepted by the plant canopy and the efficiency of photosynthesis. Finally, growth is brought to a halt again by a combination of shortening day lengths, lower light levels and cooler temperatures during the autumn.

Cannell (1989) assumes a continuously changing response to temperature for woody perennials from autumn through to spring flowering, so that the need for chilling temperatures is related to the thermal time requirement for flowering. Thus, as autumn progresses and the tree accumulates exposure to chilling temperatures, the thermal time required for flowering decreases progressively. Using Cannell’s approach, Battey (2000) points out that beech (*Fagus sylvatica*), which has a large chilling requirement and thermal time for bud burst (beech is one of the last trees to leaf out in the spring), will accumulate less chilling under conditions of climate change. This will increase the thermal time for bud burst and make bud burst even later. However, species such as hawthorn (*Crataegus monogyna*) have a small chilling requirement which is easily met by the British climate. Here climate warming would cause earlier bud burst.

Although dormancy has been studied widely in woody plants, it has received less attention in herbaceous perennials. However, commonly the underground resting organs of species from temperate regions require a period of chilling before

growth can recommence (Heide, 2001). Many herbaceous perennials possess prominent winter buds, whilst the shoot dies down in the autumn. Studies by Heide (2001) on *Sedum telephium*, and preliminary studies on three other herbaceous perennials with prominent winter buds, *Rhodiola rosea*, *Epilobium adencaulum* and *Oxyria digyna*, suggest that dormancy was controlled by day length rather than by temperature, with the plants becoming dormant under short days and being released from dormancy under long days. Clearly, this suggests that, for those herbaceous perennials which are under strict photoperiodic control for dormancy release, this mechanism will prevent early growth initiation in mild winters and suggests a much greater stability of emergence under conditions of climate change.

Many perennials found in cool temperate climates adapt to low winter temperatures by becoming dormant, in which state they are resistant to low temperature damage. Many trees and shrubs in particular have periods of dormancy which can only be broken by more or less prolonged periods of chilling, which is most effective at 0-5°C. Although externally dormant, many plants undergo active internal development, producing leaves and flowers which will emerge in the following spring.

Higher mean winter temperatures will have a variety of effects. Some plants, such as hawthorn, have a small chilling requirement so higher temperatures will accelerate growth. Others, notably beech, have a longer chilling requirement. If this is not met, growth in spring will be delayed, so increasing winter temperatures will result in later leafing. In blackcurrant, raspberry, apple and other fruits the plant needs a cold period to form flower buds. Insufficient chilling will result in delay, abnormality or failure of flowers.

3.3.5 FROST SUSCEPTIBILITY

A widely expressed concern among horticulturists and gardeners is that climate change will lead to earlier growth and therefore to greater susceptibility to, and damage from, late spring frosts. Increases

in winter temperatures, anticipated in all scenarios, will result in a very substantial increase in the number of days with temperatures above freezing, and above 5°C, thus extending and advancing the growing season. The concern expressed is that such early onset of growth as a result of climate change may increase the risk of frost damage to plants (Hanninen, 1991).

However, the earlier onset of spring growth in perennial species has to be seen in the context of a decline in the number of damaging spring frosts. For tree species, modelling exercises suggest a probable decline of spring frost damage in trees with climate warming, at least in the Netherlands and Germany (Kramer, 1994). Other predictions (eg, Hanninen, 1997) range from no change to a moderate increase in the incidence of frost damage.

Although this aspect of climate change merits further study, it is logical that damage to precocious young growth from late frosts is unlikely to increase in response to an increase in average temperature. At worst, damage may occur earlier in the year but at the same erratic frequency and with the same unpredictability as at present. What is more likely is that the reduced frequency and severity of frosts as average temperatures increase will result in less frost damage, including less damage to precocious growth. This is not to say that growers and gardeners can ignore the possibility of a severe frost. In terms of mathematical probability it is unlikely that another winter of 1962/3 severity will occur but, taking an indefinitely long term view, another winter of 1962/3 severity is almost inevitable at some time in the future.

Although the incidence of spring frost damage to precocious growth is not expected to increase with climate change, there is some indication that autumn frosts may become more damaging. Reduced or delayed hardening of plants in the autumn combined with reduced cloud cover and an increased diurnal temperature range could lead to increased damage (Broadmeadow, 2002a).

Frost damage can also occur during the dormant period, so the ability of plants to withstand winter frosts may also be affected by climatic warming.

Higher rates of tree activity under elevated carbon dioxide concentrations may result in increased metabolic activity during the dormant period, particularly at elevated temperatures. Plants may become less deeply dormant, leading to an increased probability of frost damage (Repo *et al.*, 1996; Ogren *et al.*, 1997). However, equally, increased soluble carbohydrate concentrations under future elevated carbon dioxide conditions (effectively increasing the concentration of antifreeze in dormant plants) may improve frost hardiness in some species (Ogren *et al.*, 1997). In a UK context, Murray *et al.* (1994) concluded that elevated carbon dioxide concentrations and climatic warming would reduce the risk of frost damage to Sitka spruce (*Picea sitchensis*) in Scotland. Nevertheless, mild winters could also lead to higher rates of respiratory activity, resulting in a decrease in soluble sugars and thus a loss of cold tolerance (Ogren, *et al.*, 1997). Certainly, the range of possible outcomes to the effects of climate change on the internal tissue conditions during the dormant phase reflects the spectrum of responses that have been recorded on frost hardiness in dormant tree species (Jach *et al.*, 2001) which range from increased frost hardiness in Scots pine (*Pinus sylvestris*) to increased frost injury in Black spruce (*Picea mariana*).

In colder climates than that of the UK, snow can play an important role in gardens in protecting plants against winter injury, by providing a protective blanket against freezing in very low winter temperatures and desiccation in cold winter winds. However, the climate of the UK is not usually such that the protection from snow cover is vital. In most of the UK, lack of snow will signify more genial growing conditions and reduced winter injury rather than an increased risk of low temperature damage.

An important aspect of temperature on plant growth is the effect of very low temperatures which may freeze plant tissues and kill the plant. Plants vary enormously in their tolerance of low temperatures. Some people fear that climate change will encourage earlier growth of soft new shoots

and that this will increase risk of frost damage. It is more likely in most cases that precocious growth will be paralleled by reduced incidence of frost. The timing of frost damage to precocious growth may change but its frequency will not increase. As frost becomes increasingly rare, especially in the south, then frost damage will also be reduced.

There is some risk that clearer skies in autumn and delayed dormancy in plants may lead to increased frost damage in autumn, and possibly in winter.

Reduced snow cover will not usually result in increased winter damage to plants.

3.3.6 INTERACTIONS OF RESPONSES TO TEMPERATURE AND CARBON DIOXIDE

There is widespread evidence of a positive interaction between carbon dioxide concentration and temperature. Response to higher carbon dioxide concentrations is greater at higher temperatures (Idso *et al.*, 1987) and the optimum temperature for photosynthesis increases with increasing carbon dioxide concentration (Allen *et al.*, 1990). The combination of increased temperature and increased carbon dioxide predicted in all climate change scenarios suggests that for some species the growth stimulation may be greater than the 40-50% suggested above (section 3.2.1). Kimball (1993) predicts from an extensive data set, that a doubling of carbon dioxide concentration combined with a 3°C increase in temperature could lead to a 56% stimulation in growth. This is similar to values obtained for carrots under increased temperature and carbon dioxide concentrations presented below (Wheeler *et al.*, 1994). Conversely Kimball *et al.* (1993) suggest that the response to carbon dioxide may be very variable or even negative at cool temperatures, suggesting that photosynthesis may be stimulated less, or even be reduced, at cool temperatures by increasing carbon dioxide concentration. This implies that an increase in temperature should be even more effective in stimulating the benefits of increased carbon dioxide levels at the low end of the temperature range than at the higher end.

Although very little information exists for ornamental garden plants, studies of the effects of climate change, including the interaction of carbon dioxide and temperature, on growth, development and yield of several important crop plants have been conducted over the last decade. Most of these are also widely grown in gardens.

In general, all crops show a positive effect of carbon dioxide on yield. However, it appears that only crops that are harvested at an early stage of their physiological development (eg, carrot) show a positive effect of increased temperature. Crops that are harvested later in their physiological development (eg, onion and cauliflower) show a negative effect of increasing temperature. The net effect of increased carbon dioxide levels and increased temperatures therefore varies from plant to plant.

Carrot yields are likely to increase substantially with predicted changes in climate in the UK. Studies by Wheeler *et al.* (1994) showed that carrot growth is stimulated by increases in temperature, although temperatures greater than 18°C lead to progressively more foliage growth than root growth. A 1°C increase in soil temperature increased yield by 34%. Responses to increased carbon dioxide are also large: an increase in carbon dioxide concentration from 325 to 530 ppm also increased yield by 34%. This reflects the responses to climate change of most root crops which are considered to be larger and more positive than most other crops (Kimball, 1983).

In onion, warmer temperatures shorten the duration of growth whilst elevated carbon dioxide stimulates growth with no overall effect on crop duration (Daymond *et al.*, 1997). However, the negative effect of temperature on crop duration appears to predominate, so that the overall effect of climate change is likely to reduce yield, because the stimulation in growth brought about by carbon dioxide is more than offset by a shorter period of bulb growth brought about by elevated temperatures. In general, it appears that a 1°C increase in average temperature decreases bulb yield by 3.5-15% whereas an increase in carbon dioxide levels, from current ambient levels to 530 ppm, lead to an increase in bulb onion yield of 30-50%.

It has long been known that reproductive growth in cauliflower and broccoli (the initiation and growth of the cauliflower curd or broccoli spears) is very sensitive to temperature (Salter, 1969). Thus, the date of curd or spear initiation is advanced by increased temperature but unaffected by light and carbon dioxide (Wheeler *et al.*, 1995). Curd or spear growth for both species is increased by temperature up to a maximum of 14-15°C, but temperatures above this lead to a decrease in growth (Hadley and Pearson, 1999). Although mean curd dry matter yield is increased by 34% when carbon dioxide concentrations are increased from ambient levels to 530 ppm, a 1°C rise in temperature reduces yield by approximately 6% (Wheeler *et al.*, 1995).

The optimum temperature conditions for production of potato, the main tuber crop grown in the UK and an important plant in many gardens, are typically those that are currently experienced (Wolf, 2000). Increases in temperature alone, as a result of climate change, will accelerate the senescence and death of foliage and therefore precipitate the end of growth. There are also more days with reduced growth as a result of higher temperatures, resulting in lower tuber production. However, this is compensated for by a positive response to increased carbon dioxide concentrations so that, for most climate change scenarios, small yield increases are expected. Warmer seasons offer the possibility of earlier planting dates than are presently possible, although the risk of frost during the early spring will limit the earliest date of planting. Earlier planting dates will give higher potato yields and this yield increase will become larger if carbon dioxide levels continue to increase.

There are varietal effects on potato yield. In general, early maturing varieties have a lower optimal temperature range than late maturing varieties, suggesting that earlier varieties may be more negatively affected by increases in temperature. The variation will inevitably be exploited to produce new potato varieties suited to changing climatic conditions, so potato yields are not likely to change significantly in response to climate change.

Temperature and carbon dioxide concentrations interact. Higher temperatures and higher carbon dioxide levels combine to stimulate more rapid growth and development but the end result is not always a higher yield. Increased speed of development may mean that the plant is unable to use the full length of the growing season before it dies. Plants like carrot, which are harvested early in their development, will increase in yield.

Plants harvested at the end of their natural growing season, like broccoli, cauliflower and onion, may produce lower yields as the accelerating effect of temperature exceeds the increase in growth caused by carbon dioxide.

There has been little work on ornamental plants but it is likely that they will respond in the same way. Hardy annuals, in particular, may go to seed earlier so their flowering season will be curtailed.

3.3.7 PLANT ADAPTABILITY AND PLANT BREEDING

The facts, cited above, that the optimum temperatures for tuber production in potato are typically those currently experienced, and that early varieties have a lower optimum temperature range than later maturing varieties, indicate a very important aspect of the responses and adaptations of cultivated plants to climate change. There is variability within the population of any one species and this will lead to some adaptation to climate change by natural selection. The pace of change anticipated by climate change scenarios is such that plants in the natural environment may be unable to adapt sufficiently quickly and may face elimination, but in a horticultural context the plant breeder will have a marked influence in accelerating the selection process and in shaping plant responses to the environment. This will be the case especially in annual plants, where the life-cycle is very short, and in plants of widespread use and value, such as turf grasses. For trees and for plants which have very limited commercial importance, intervention by plant breeders is unlikely.

As an example of past success, old varieties of beetroot were subject to bolting (accelerated flowering instead of root formation) in cold springs and

this restricted sowing dates. ‘Boltardy’ beet was selected for reduced susceptibility to bolting in response to low spring temperatures, allowing earlier production. Similarly the production of sweet corn varieties able to mature in shorter and cooler seasons has greatly extended the range of UK gardens in which sweet corn can be cultivated. These selection and breeding practices will undoubtedly make a significant contribution in the adaptation of annual garden plants, especially, to climate change.

3.4 Plant responses to water

Water plays a vital role in plant growth and survival in three ways: as one of the ‘raw materials’ of photosynthesis, in transport of dissolved nutrients from the soil into and through the plant, and in maintaining plant turgor. Before one can consider the impacts of climate change resulting from plant responses to water, it is necessary to have a basic understanding of the distinction between water supply and water availability.

3.4.1 WATER SUPPLY

Water supply to the plant is derived from precipitation and in some situations from the net result of inflow to and outflow from the catchment area in streams or rivers. In all the UKCIP02 scenarios, water supply to the plant is expected to decrease in spring, summer and autumn. Although precipitation is expected to increase throughout the UK in the winter, evaporation will also increase in the south, so winter water supply will be increased in the north but reduced in the south. The wider environmental implications of water supply in affecting run-off, erosion and flooding, for example, are considered in section 6.2.

3.4.2 WATER AVAILABILITY

Water availability to the plant depends in part on the presence of an adequate water supply, but it is also affected by evaporation from the plant which, in turn, depends on solar radiation. Water evaporates from the cells inside the leaf and is lost to the atmosphere through the stomata. This process of transpiration uses energy supplied by solar radiation and depends on the humidity of the air and on windspeed.

As the temperature increases, the capacity of the air to carry water vapour increases very steeply. The humidity of the air decreases or, put another way, its drying capacity (and therefore its capacity to 'pull' water from a plant) increases. If water is available it will evaporate and, by absorbing very large amounts of energy in so doing, will cool the plant and its surroundings (or prevent them heating up). If the water supply is limited, evaporation is necessarily reduced and more energy will be used in heating the plant and its surroundings. The valuable air-conditioning role of plants will decrease when they are subjected to water stress.

The plant is not a passive tube conducting water from the soil to the air. Water movement through the plant results partly from active uptake by the roots (requiring food reserves and oxygen) and partly from evaporation by the leaves. If root uptake cannot keep pace with evaporative loss, as is often the case in hot, dry and windy weather, the plant will close its stomata. This prevents further water loss, but also prevents carbon dioxide uptake for photosynthesis.

The impacts of climate change on water availability and the resulting impacts on plant growth will arise in part from changes in the water supply itself, but also from increased temperatures and decrease in atmospheric humidity. Changes in supply to the plant will result from increased precipitation in the winter (when water is least useful for growth) and decreased precipitation in the summer and autumn, when high light levels and increasingly high temperatures combine to maximise potential evapo-transpiration. The change in temperature is expected to be upwards in all seasons in all scenarios, leading to increased evaporation of water.

3.4.3 IMPACTS OF WATER DEFICITS

As discussed briefly in section 3.1, water deficits in the plant will lead in the short term (seconds, minutes, hours), to closure of stomata, loss of ability to take up carbon dioxide for photosynthesis and wilting of soft plant tissues. Even short periods of wilting can cause substantial reductions in plant growth.

In the longer term (days, weeks, months), the plant will respond to water stress by shedding its older

leaves and by becoming more compact with smaller, thicker leaves. It may also divert more resources to root development in order to exploit water resources in a greater soil volume. Annual plants, especially, will often flower more rapidly in conditions of water stress in order to set seed before they die, so the flowering season will be curtailed.

In the very long term (centuries, millennia), plants subject to the continuous selective pressure of water stress evolve adaptive mechanisms such as hairiness (to reflect light and thus reduce evaporation) or waxiness (to reflect light and reduce water loss through the surface), resulting in grey or silver foliage. In continuously dry environments, evolution results in very compact habits, succulent water storage tissues (as in cacti and succulents), and specialised metabolism to allow photosynthesis to take place while stomata are closed. These long term adaptations, which often have an ornamental value in themselves, are also subject to short term variation. In low light conditions or with plentiful water supplies, leaf hairiness will be reduced and normally grey or silver leaved plants will become more green. Plants grown in gardens for their grey leaves usually look less attractive in the winter months but in the wetter and duller winters anticipated in climate change scenarios they will look worse.

The impact of decreased precipitation in other seasons will depend on the interaction of many factors, especially on regional variation and on soil type. In the north and west, reduced summer precipitation and higher light levels (from reduced cloudiness) may result in a more favourable climate for plant growth. Those plants attuned to a cool, moist climate, such as *Meconopsis*, primulas and ferns, may suffer. In the south and east, already the driest parts of the UK, temperature increases and precipitation decreases are anticipated to be greater than elsewhere. Water deficits and their impacts on plant survival and growth may be severe, especially for long established plants attuned to a softer climate. Particular concern has been expressed for the future of beech trees (Harrison *et al.*, 2001; Wade *et al.*, 1999), an important and characteristic component of the landscape in the south east of England and an important feature of many larger gardens (see section 6.3.1).

Paradoxically, though, adaptation to increasing water deficits may be easier in some respects in the south east than in other regions. There are many highly attractive plants which will tolerate very dry conditions, but they will only flourish if they can escape winter wet. Although winter precipitation is anticipated to become higher in all parts of the UK, higher temperatures in winter are expected to result in reductions of soil moisture content in the south east, rather than increases. In areas in which the summer becomes drier but the winters distinctly wetter the potential of adapting by using 'xeriscape' planting schemes (i.e. using xerophytic, or drought tolerant, plants) will be severely limited.

Soil type will also have a major influence. The drying of heavy and poorly drained soils in reduced precipitation scenarios will increase the range of plants which can be grown, and will reduce the risk of waterlogging, though it will, of course, reduce the opportunity to grow plants specifically adapted to wet conditions (and may have serious implications for factors other than plant growth, such as the oxidation of soils, as discussed in section 6.1).

3.4.4 IMPACTS OF WATER SURFEITS

Increase in winter precipitation is a feature of all UKCIP02 scenarios, but more rain does not necessarily mean more waterlogging. On light soils, increasing winter precipitation will be a great benefit in improving the health of trees and in recharging the water table, thus extending the period for which water will be available for growth in spring and summer.

Water surplus will only be damaging to the plant if it causes waterlogging of the soil. The impact of waterlogging is to deprive the plant roots of oxygen so that they cease to function. In the short term, the symptoms of waterlogging of leafy plants are similar to those of drought: roots are unable to pump water into the plant, so the upper part of the plant wilts. More seriously, in the anaerobic conditions of waterlogged soils, plant metabolism is altered and toxic compounds accumulate. If conditions do not improve, the roots and then the whole plant will die.

Some plants are highly adapted to waterlogged conditions in the soil, with air channels in the leaves, stems and roots - or the pneumatophores ('knees') of swamp cypress (*Taxodium distichum*) - conducting atmospheric oxygen down to the roots. Many other plants will tolerate short periods (hours, days, even weeks) of waterlogging especially if the plant is inactive in winter so that oxygen demand is minimal. Others are very intolerant of waterlogging, or even of wet soils, and will quickly be killed either as a direct result of reduced oxygen supply or indirectly as a result of succumbing to root pathogens. In general, those plants which are most highly adapted to dry conditions (xerophytes) are the least tolerant of wet and especially waterlogged soils.

One important implication of climate change is that increasing winter temperatures will increase the activity (and therefore the oxygen demand) of plants in the winter, so roots may become less tolerant of waterlogging. This will especially be so in the south west, where both temperature increases and winter precipitation increases are expected to be high.

Water is vital to plant growth and to all life. Water availability to the plant depends on the relative rates at which water is taken up from the soil by the roots and lost from the leaves. If water is in short supply in the soil, or water loss from the leaves is too high because of increasing temperatures and increasing light levels, the plant will suffer water stress. It will react by closing its stomata (leaf pores) to conserve water and will therefore shut off its carbon dioxide supply. Growth will suffer. Prolonged stress will cause loss of leaves and hardening of the plant. Extreme stress will kill it.

Adaptability to water stress varies greatly. Plants adapted to growing in cool, shady positions, ferns for example, will wilt after a few minutes in full sun even if the roots are freely supplied with water. Succulents, on the other hand, have reduced or fleshy leaves and very thick, waxy or hairy light-reflecting leaf surfaces, so can tolerate very severe drought for months or years.

With too much water, plant roots will be deprived of oxygen and will die. Again, plants differ widely in their tolerance of waterlogging, but those most adapted to very dry conditions will be least tolerant of wet soils and vice versa. Where drier summers are combined with wetter winters, plant choice will present considerable challenges, but it will often be possible to circumvent the worst effects of waterlogging by improving drainage.

3.5 Plant responses to changes in pest, disease and weed incidence

The general increase in summer and winter temperatures, combined with wetter winters and drier summers, are likely to have considerable impact on the severity of pest and disease attack on horticultural plants. These effects are among the most difficult to extrapolate from climate change scenarios because of the complexity of interactions, particularly in relation to specialised feeding relationships of pests. For example Visser and Holleman (2001) found that increasing spring temperatures advanced the hatching of oak moth (*Operophtera brumata*) more than they accelerated the unfolding of the oak leaves on which it feeds. Such disruption of the synchrony could have disastrous consequences for the moth but would result in reduced pest damage to oaks unless and until the moth, is able to evolve sufficiently rapidly to adapt to the changing situation. Where the interactions extend to the synchronous development of the host plant, an insect pest and a disease transmitted by the insect, each with its own particular responses to climate change, attempts to extrapolate from climate change scenarios to disease incidence become increasingly difficult.

This is clearly an area in which further research is needed in relation to garden plants.

3.5.1 CLIMATE CHANGE AND PESTS

The focus in this section is on those insects and other arthropods which cause damage to plants but consideration is also given to other species associated with gardens, such as butterflies and bees.

For example, an increase in the mean annual temperature of 2°C (as anticipated for south east England by the 2050s under the medium high emissions scenario), will mean that butterflies will appear 2-3 weeks earlier (Sparks and Yates, 1997) and the range and distribution of butterflies will shift dramatically (Fox *et al.*, 2001). Many native butterflies will extend their territories northwards while new species, or those with only a localised existence in southern England, will migrate from the European mainland. The same will be true for pest species of insects. On the other hand, warmer winter temperatures are already leading to greater winter activity in bee populations and are resulting in poorer winter survival (Fletcher, 2000).

Many insect pests cause damage by eating leaves and other plant parts, so the nutrient status of the plant has a very significant effect on its susceptibility to attack. Increasing carbon dioxide levels will result in 'harder', less succulent plants which should be more resistant to attack (Ciesla, 1995). A well documented effect of increased carbon dioxide is a decrease in the nitrogen concentration of plant tissues, leading to a reduced nutritive value to insects (Nicolas and Sillans, 1989). Leaf nitrogen is a limiting nutrient in many herbivorous insect diets (Lincoln *et al.*, 1986). When feeding on leaves of low protein content, insects respond in a number of ways including increasing consumption, choosing more nutritious leaves or species, reduced fecundity (production of young) and/or survival, reduced population density or more efficient food use (Scriber and Slansky, 1981). Such responses have also been observed when insects feed on plants that have been grown in elevated carbon dioxide concentrations. Consumption can be increased by 20-40%, compared to feeding on plants grown under ambient carbon dioxide conditions (Lincoln *et al.*, 1986). This has been attributed directly to the reduction of nitrogen concentration in the leaf (Lincoln, 1993).

On the other hand, reduced water supplies will lead to increases in cell sap concentration. Sucking insects and mites will have a more concentrated food supply and may increase more rapidly. It is well known that low humidity in greenhouses encourages the build up of red spider mite. In the

very dry summer of 1995, red spider mite and aphids were major problems on outdoor crops, such as lettuce, apple and raspberry (Orson, 1999). In experiments with sap feeding insects on plants grown in elevated carbon dioxide concentrations, responses varied from no significant effect (Docherty *et al.*, 1997; Salt *et al.*, 1996; Butler *et al.*, 1996) to increased settling times (Smith, 1996) and increased fecundities (Awmack *et al.*, 1996).

There is little direct evidence that chemical deterrents in the leaf, which many plants have evolved to resist pest or grazing attack, will be altered in plants growing under elevated carbon dioxide concentration.

Arthropod species that are likely to be most responsive to the effects of climate change are those that produce many generations in a single season ('multivoltine' arthropods). These include, for example, thrips, aphids and spider mites and represent the opportunistic insects and mites which, given a suitable food supply, will multiply rapidly on plants. Many of these cannot survive cold winters as adults and so the first insects to appear in the spring hatch from overwintered eggs. However, the speed of development and thus the number of generations that will be produced, is a direct function of temperature. Two components of climate change will have a direct impact on this type of pest.

First, milder winters will enable some species to overwinter as adults rather than as eggs as at present. This will allow the pest to have a significant head start given the appropriate food supply, since they will not need to go through an initial generation prior to reproducing. Zhou *et al.* (1995) showed that warmer winter and spring temperatures will increase the overwintering survival of aphid species in the UK and, in some cases, advance the appearance of winged adults by as much as a month. An increase in spring temperatures of 2°C will mean that cabbage root fly will also become active a month earlier than at present (Collier *et al.*, 1991). Mild winters will also favour such insects as green spruce aphid (*Elatobium abietinum*) which can feed and multiply throughout the year (AAIS, 1999).

Second, higher average temperatures will mean shorter intervals between generations.

Both factors will increase the potential for earlier pest attacks than at present, and for more serious attack as a result of rapid population growth. This effect will be exacerbated in the case of many sucking pests, as higher temperatures will be accompanied by increased water stress, leading to increased uptake of increasingly concentrated plant sap, as referred to above (Orson, 1999) in relation to red spider mite.

Insect population growth increases by 10-14 fold between generations, so that just one more generation over a growing season can have a profound effect on population numbers. A good example of an insect pest in this group is the cabbage aphid (*Brevicoryne brassicae*) which in a mild winter will overwinter in rural areas on oil seed rape. This pest can then attack a wide range of garden brassicas (cabbage, cauliflower, Brussels sprout) in the spring and, since the population is initiated by adults, generations of invasive winged aphids occur much earlier than after a cold winter, when populations are initiated from eggs. Work at the Institute of Arable Research, Rothamsted has shown that typically, aphid attacks occur approximately two weeks earlier for every 1°C increase in average temperature. This has been confirmed by observations made over the last twenty years, during which spring temperatures have increased.

Many aphid species in particular are of concern to gardeners, not only as plant pests but as vectors (transmitters) for a number of serious virus diseases. Many of the impacts of climate change on population dynamics of aphids will, therefore, have consequential effects on virus disease attack. Zhou *et al.* (1996) conclude that the severity of aphid outbreaks in the UK will be increased under climate change conditions and will lead to an increase in the period of virus infestation further into the growing season (see section 3.5.2 below)

Warmer autumns may lead also to greater numbers of aphid vectors later in the season and may give greater problems to overwintering plants. Climate change, whilst increasing the opportunities for over

wintering of vegetables and bedding plants, for example, may also be responsible for direct effects of later surviving insect pests and their indirect effect through the spread of virus diseases.

Water stress in plants results in greater nutrient concentration in the sap, and thus in greater growth rates and fecundity in aphids feeding on the plants. However, predator levels would also be expected to build up in response to increased food supply. One of the most important natural controls of aphid populations is rainfall, as the impact of raindrops dislodges the aphids or damages their feeding parts (Doggett, 1863; van Emden, *pers. comm.*). Whether lower summer rainfall will reduce the operation of this control mechanism, or less frequent but heavier rainfalls will increase it, is uncertain.

Higher temperatures may allow some pests that are largely confined to the sheltered environment of the glasshouse to move out into the open. This is already happening with red spider mite (*Tetranychus urticae*). However, while extending the period of pest activity, warmer conditions may also extend the period during which biological control agents can operate. Currently the nematode used for biological control of vine weevil is not as effective outside as it is under glass, because soil temperatures are too low. Consistently higher outdoor temperatures may result in better control, and perhaps even control by naturally accumulating nematode populations.

There is considerable evidence of changes in the natural distribution of birds and butterflies with a general northward movement of species as temperatures rise (Fox *et al.*, 2001). This leads to loss of species favoured by low temperatures, but inward migration of species from mainland Europe. This same phenomenon can be expected for insect and other pests, especially if the spread of exotic species is exacerbated by international transport of crops or individual plants.

Termites have already been found in Cornwall. Japanese beetle, spruce moth, and stem-borers of birch, *Sorbus* and other woody species make the cultivation of many garden plants difficult in the USA where summer temperatures are substantially higher than in Britain. *Cameraria ohridella*, the

moth which has devastated horse chestnuts in Spain (Bedoya, *pers. comm.*) and has recently spread into northern Italy (Garibaldi, *pers. comm.*), is now to be found in Belgium and, as of July 2002, in Wimbledon (Prior, *pers. comm.*). A small colony of the voracious Asian gipsy moth already present in Epping Forest could spread if a series of dry springs allows it to gain a firm foothold (Gruner, 2000). A comprehensive review of the effects of climate change on insect pests is given by Canon (1998).

Among larger organisms, roe deer and grey squirrel are both favoured by warm winters, and are both likely to survive in increasing numbers as a result of climate change. The grey squirrel has a particular predilection for the bark of beech trees. The combined effects of increasing squirrel damage and direct impacts of climate change on attempts to retain or regenerate plantings of beech in gardens, parks and woodlands will pose major challenges in the future. Attempts to regenerate beech woodland on Box Hill, Surrey in the past fifty years have failed because of the total destruction of the young trees by bark stripping (Piggott, 1988). Grey squirrels have also caused widespread damage to sycamore and Japanese maples in National Trust and other gardens, including the University campus at Reading.

3.5.2 CLIMATE CHANGE AND DISEASES

As with pests, with diseases it is very difficult to determine the exact impact of climate change on the development of a particular disease because of the complexity of the relationship between pest, host plant and environment. It is also very difficult to differentiate between the effects of climate change and the effects of increased international travel as causes of increased attack. The general impact of climate change on diseases, however, can be summarised as follows:

- wetter, warmer winters will favour diseases such as *phytophthora* that need water to spread;
- drier, warmer summers will favour disease such as powdery mildew that can spread in dry conditions;

- warmer conditions will allow diseases that cannot establish under current climatic conditions in the UK to survive and establish, but will cause the decline of existing diseases unable to adapt to higher temperatures.

For most diseases, the important epidemiological implications of climate change stem from warmer winters, which will result in greater availability of surviving host material, greater survival of overwintering inoculum (spores or growing fungi), and thus a more rapid onset and spread of disease as the growing season proper begins. However, this could be offset by greater dryness in the summer. Perennial plants growing on the margins of their climatic tolerance are likely to be subjected to long term, chronic stresses, resulting in a decline in plant health and increased susceptibility to diseases.

Faster rates of reproductive development under higher temperature conditions may well also increase the rate of disease spread, as will the more rapid increase of insect vectors of disease. For example, higher aphid vector populations generally mean that virus diseases will increase (Zhou *et al.*, 1995). Moreover, earlier attacks by aphid vectors will lead to virus disease infection occurring earlier in the development of plants. Generally, virus diseases are always more serious when plants are infected at an early stage of development. As a plant becomes older it has a greater inherent tolerance of attack by virus diseases. Thus, the effects of climate change on virus diseases may well be more serious plant infection.

This may have implications for the Scottish seed potato industry. Some of the important potato viruses are aphid vectored. By raising the seed in Scotland, growers are currently able to produce virus free stock because the low temperatures inhibit the development sufficiently to allow the potatoes to produce tubers before the virus gets into them. Warmer, earlier seasons in Scotland could eliminate that advantage. The same problems arise with raspberry and strawberry, threatening the supply of virus free plants for gardens as well as for commercial growers.

Milder winters will also favour winter activity of a wide range of bark and wood invading fungi which

are able to overcome the defences of trees during dormancy, and are likely to result in increasing severity of fungi which are currently limited by low temperatures (such as *Phytophthora cinnamomi*), while summer drought will favour diseases such as sooty bark disease of sycamore (*Cryptostroma corticale*) which attack drought stressed trees (AAIS, 1999). In a survey of horticultural crop responses to the hot, dry summer of 1995, Orson (1999) found reduced disease levels overall, but higher incidence of powdery mildews, rusts and *Fusarium* diseases.

The establishment of exotic diseases in the UK under conditions of climate change will provide great challenges for quarantine research in the UK. A number of diseases which have a wide host range and which are currently ubiquitous in the tropics and subtropics could prove major threats. For example, *Athelia (Corticium) rofsii* is a wide spread disease in warmer climates where it infects a number of species including cotton, tomatoes and groundnuts. It is a soil borne disease, which is equivalent to *Sclerotinia sclerotiorum* and, given the opportunity, will attack a wide range of garden plants. *A. rofsii* is known to have been accidentally introduced into the UK once (where it was a problem during the season of its introduction), but died out. Under climate change conditions, the likelihood is that, if reintroduced, it would be able to survive the winter. Quite clearly, there is a threat waiting to happen.

Climate change conditions will offer an opportunity to introduce new plants into the UK, but each will have its own suite of pathogens. This will put great pressure on plant health authorities to ensure that future quarantine measures are effective. There are already instances where lack of plant quarantine measures have led to the introduction of diseases, because quarantine is usually imposed only when plants are of economic importance. For this reason, no quarantine measures were approved when mature olive trees were imported into the UK, with the result that olive scab (*Spillocaea oleagina*), a major disease of olive in Mediterranean areas, was introduced. The problem is already here, therefore, if olives become a more common feature in the UK in the future.

Other problems are likely to occur if plant health authorities concentrate their quarantine efforts only on plants of economic importance and not on plants of garden interest. Camellia petal blight (*Ciborinia camelliae*), a disease of the petals at flowering time, originated in Japan but has spread around the world. It poses a threat to UK gardens as it is spreading up through Europe. The plant health authorities did not think it necessary to impose strict quarantine measures on imported Camellias but posters were distributed alerting the nursery industry to the chances of this disease. Within months of the issue of the posters, the disease was found in Cornwall and Devon, where it had probably already been present for several years. Under current conditions the disease is not devastating, presumably because the fungus is at its northern limit. However, under conditions of climate change its effects could be more severe and the potential for its spread to the rest of the UK much greater. In 2002 there has in fact been a significant spread eastwards to the south and east of England.

Many diseases are spread by insect vectors and the effect of climate change on the biology of vectors may also effect the spread of disease. For example, Oak Wilt (*Ceratocystis fagacearum*) is a North American disease spread by insect vectors which are not found in Britain. Their distribution and activity and the number of generations each year are limited by climate in North America. Under conditions of climate change, the environment of the UK could become more favourable for these insects, increasing the potential threat from the disease.

Aphids and thrips are vectors for a number of diseases. The potential impact of climate change on virus transmission in Scottish seed potatoes, for example, has already been discussed. Western flower thrips, a pest that was introduced a few years ago from Holland, is a major vector for tomato spotted wilt virus and impatiens necrotic spot virus. Currently this insect is mainly a problem under greenhouse conditions, but it could move outside under climate change conditions and could then attack a range of vegetables. This could be accompanied by a large increase in other viruses spread by thrips.

Popular garden species such as yew (*Taxus baccata*) and box (*Buxus sempervirens*) have recently been affected by serious diseases. Box, a major feature of many formal gardens and shrubberies, is under increasing threat by box blight (*Cylindrocladium buxicola*) (Henricot *et al.*, 2000). This is a disease which is dependent on water splash for its spread and will therefore be favoured by wetter, warmer conditions. *Phytophthora* root rot of Yew is a very destructive disease of hedges caused by *Phytophthora cinnamomi*. This is also likely to be more severe under wetter warmer winters. Brasier and Scott (1994) suggest that, under climate change conditions, the fungus will cause more severe damage in the regions where it is currently present and will tend to spread northwards and eastwards. They also predict that the host range of the fungus will increase if it spreads into areas where it is not currently present. *Phytophthora* is an important disease associated with poor drainage, as its spores are spread by water movement through the soil and host plant resistance is decreased in anaerobic conditions. Increased rainfall and higher winter temperatures, allowing the fungus to develop during periods of waterlogging, are likely to lead to increased incidence of the disease and symptoms will be exacerbated when plants suffering root loss caused by *Phytophthora* are further stressed by summer drought.

Holly is affected by holly leaf blight caused by *Phytophthora ilicis*, a disease that was first described in the USA but came to Britain in the 1980s. Recently, in the late 1990s, there have been upsurges of the disease for reasons that are unclear, but may be associated with wetter, warmer winters. It has caused serious damage to hollies at the National Trust's garden at Nymans, Sussex, in 2001/02.

Lawsons Cypress is attacked by *Phytophthora lateralis*, a disease which is native to the northern United States but has spread to other countries, and, for example, is present in France. It is not thought to exist in Britain but, as with all *Phytophthoras*, it is favoured by warmer wetter winters, so that the threat from other disease will be greater under conditions of climate change and exacerbated by the free movement of plants throughout the European nursery industry. As with

yew, a combination of warmer and wetter winters, predisposing to infection, and of hotter, drier summers increasing root stress will greatly increase potential damage from these root pathogens.

Brasier (2000) has studied a new *Phytophthora* disease affecting alder. This is an interesting potential effect of climate change since it is believed that this new disease has arisen as a result of the hybridisation between two *Phytophthora* species which may have come into contact as a result of flooding. Although the individual parent species do not attack alder, the hybrid does. This clearly introduces new possibilities for the threat by *Phytophthora* diseases.

On lawns one might expect an increase in red thread (*Laetisaria* (formerly *Corticium*) *fuciformis*) which has a high optimum temperature and perhaps a reduction in the incidence of snow mould (*Monographella nivalis*), which thrives at lower temperatures (Dawson, 1977). However, if climate change results in longer periods when the temperature is at 5°C rather than zero, for example, snow mould could increase rather than decrease in severity.

Reasons for a widespread decline in tree health in Britain are not well understood, but stress caused by water shortage in the summer (as a result of decreasing precipitation, increased evaporation and higher rates of extraction), or flooding in the winter, is probably already contributing to accelerated losses of trees and shrubs to *Armillaria*, *Phytophthora* and other pathogens.

Plants will be affected by climate changes indirectly, by the effects of these changes on the virulence of pest and disease attack, as well as directly. Pests and diseases are likely to be more troublesome as a result of climate change, because higher temperatures will allow increased survival and activity in winter and more rapid increase in spring. Some pests (mites, aphids) and diseases (powdery mildews, rusts) will be favoured by hot, dry summers. Leaf eating pests may be slightly disadvantaged by the higher

carbohydrate status (and therefore reduced protein content) of host plants growing in the higher concentrations of carbon dioxide, and higher light levels associated with climate change. Warmer but wetter winters will favour root rots of various kinds, especially phytophthora.

Hotter summers will encourage the spread of new pests from warmer parts of Europe as well as the northward migration of pests found commonly only in the south of England. With increasing human mobility from other parts of the world, more care will be needed to monitor pests and to develop quarantine procedures to prevent the import of new pests and diseases.

3.5.3 CLIMATE CHANGE AND WEEDS

As weeds are simply plants in the wrong place, the effect of climate change on weeds will be as for plants in general. Higher carbon dioxide levels, higher winter temperatures and perhaps greater water availability in early spring will favour earlier germination and growth of weeds. This will especially be the case for highly competitive annual weeds which demonstrate the high sink strength identified by Poorter (1993) (see section 3.2.1). Many annuals will be able to germinate and grow through the winter and to set seed before the onset of summer drought. The result will be a need for increased garden maintenance.

Drier summer conditions may reduce weed growth, but will also reduce the effectiveness of glyphosate and hormone weedkillers such as 2-4D and MCPA which work best when the treated plants are in active growth. It will be more necessary to ensure that herbicide spraying is carried out earlier in the year, with a narrower window between the weed achieving sufficient leaf cover for chemical uptake and the onset of dry conditions, and the prospect of having to spray at a time when maintenance demands are at a peak.

Bracken (*Pteridium aquilinum*) is expected to benefit significantly from climate change (Farrar and Vaze, 2000; Pakeman and Marrs, 1996). Intolerant of exposure or shade, it will be able to

colonise at higher altitudes as the temperature increases and to penetrate further into thin woodland as light levels increase.

Garden escapes which come from warmer and/or drier climates will also be favoured by climate change. The classic example is Oxford Ragwort (*Senecio squalidus*), a native of Sicily and southern Italy which is thought to have escaped from the Oxford Botanic Garden (Clapham *et al.*, 1962). It was first noticed on walls in Oxford and subsequently spread through much of lowland Britain, its spread accelerated in the 19th century by the development of the railway system. The ballast on which the rails were laid provided the very dry conditions needed by the plant and the air currents caused by the trains helped to distribute the wind borne seeds along the track. In the late 20th and early 21st centuries the road system has had the same effect: dry embankments and expanses of gravel or coarse stone along hard shoulders and on traffic islands - and the wind currents created by speeding juggernauts - have created enormously expanded areas suited to the weed. Hotter and drier summers have also undoubtedly assisted in the Ragwort's success.

Rhododendron ponticum, Himalayan balsam (or 'policeman's helmet', *Impatiens glandulifera*) and Japanese knotweed (*Fallopia japonica*) have also invaded large areas of the UK, the north and west in the first two cases (Farrar and Vaze, 2000), the south in the case of Japanese knotweed. In this last case, human activity in spreading the plant, initially deliberately as a garden ornamental and more recently accidentally in transporting knotweed-contaminated soil, has been a major factor in its invasion, but all three have been, and will increasingly be, favoured by climate change. The spread of these plants erodes the biodiversity of habitats and the quality of parks and gardens.

Vines (2002), refers to the "tender" and very ornamental perennial *Hedychium gardnerianum*, as now growing out of doors in Durham in a sheltered garden. *Hedychium* is becoming a major pest in New Zealand in a climate not dissimilar to that of southern England.

There are very well documented cases of damaging spread of introduced plants in the hotter parts of the world: water hyacinth blocking African rivers, prickly pear in the Australian desert and Kudzu vine engulfing areas of the southern United States for example. *Phormium tenax* has naturalised on St Helena to the exclusion of large areas of natural vegetation (though mainly because of its tolerance of the heavy grazing pressures imposed by feral goats), and *Gunnera manicata* is becoming naturalised in southern Ireland. As the UK climate continues to heat up, it will be necessary to monitor carefully the potential and observed threats of invading exotic plants.

It is important, though, to maintain a sense of proportion when dealing with this potential problem. To speak in terms of 'alien invasions' raises the spectre of a triffid conquest. The first 150 years of increasing temperatures in the UK have not resulted in a dramatic change in its vegetation cover, other than that attributable directly to habitat destruction due to urbanisation and changes in farming practice (Bailey, 2000; Milne and Hartley, 2001). *Rhododendron ponticum* (introduced in 1763), Oxford ragwort (1794) and Japanese knotweed (1886) have become serious weeds in some locations, but only in recent years (in part, at least, because of changes in land use and management) and have not yet colonised to the exclusion of other species.

Clearly, the rate of temperature change, in particular, is accelerating and it will be necessary to monitor carefully the distribution and activity of any potentially invasive species. Hossell *et al.* (2001) suggest that attention should be given to updating the list of invasive species in Schedule 9 of the Wildlife and Countryside Act to include species with the potential to become invasive. However, given a history of exotic plant introductions to Britain extending over at least a thousand years and an immensely rich and widely distributed garden flora, there is as yet a conspicuous absence of invasive species.

A review of the characteristics of potentially invasive plants and the potential causes and impacts in a UK context would be very helpful, not only in iden-

tifying the nature of any potential risk but equally in reducing the likelihood of any panic reaction which might pose an even greater risk to UK gardens, by limiting the movement and use of exotic plants.

The impacts of climate change on weeds will be the same as for plants in general. Increased carbon dioxide levels will favour growth of competitive annual weeds more than it will favour plants in general. Higher winter temperatures and increased water availability, where the latter does not result in waterlogging, will allow overwinter growth of many annuals, more rapid growth in spring and earlier seeding as summers become hotter and drier. Perennial weeds will grow more quickly and most will flower earlier, if not controlled. Chemical weed control, with glyphosate in particular, will be less effective in hot, dry conditions.

A small number of introduced plants have become serious nuisances in recent decades. The reasons for the recent territorial expansion of plants present in the UK for a century or more are not clear, but a combination of climate change and changes in land management are probable contributors to the spread. Other garden species have the potential to become weeds if climate change accelerates, so careful monitoring will be needed.

carbon dioxide enriched plants so that more carbon is available for mycorrhizal associations (Norby *et al.*, 1986, 1987). Similarly, the greater allocation of carbon to the roots of carbon enriched legumes leads to increased nitrogen fixation as a result of greater nodule mass, although there is little evidence for any effect on specific nodule activity. This ability of mycorrhizae to extend their exploitation of soil nutrients and to supply their host plant with additional nitrates could help to offset some of the disadvantages associated with reduced summer precipitation and drier soils.

More research is needed to investigate the impacts of increasing temperatures and increasing water stress on the mycorrhizae themselves and on the potential uses of mycorrhizae to aid tree establishment and growth.

3.6 Climate change and symbiotic organisms

Many plants have symbiotic (mutually beneficial) relationships with other organisms. This is most commonly seen in the relationships between leguminous plants (peas and beans for example) and nitrogen fixing bacteria, and between many coniferous trees and mycorrhizal fungi. The microorganisms benefit from the photosynthates produced in the leaves of the trees and provide in return soil mineral nutrients which the tree roots are themselves unable to acquire.

Although there has been limited research in the area of climate change impacts on these symbiotic relationships, it appears that the exudation of soluble compounds from roots tends to be greater in