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INVESTIGATIONS ON FACTORS AFFECTING NET PHOTOSYNTHESIS IN TREES: GAS EXCHANGE IN CLONES OF *PICEA ABIES* (L.) KARST.

Olavi Luukkanen

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OLAVI LUUKKANEN

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PREFACE

This study consists of experiments carried out at the Department of Silviculture and the Forestry Field Station of the University of Helsinki during the years 1972 and 1973. However, it also summarises much of the recent work conducted within the research group formed at the time when the present experiments were started.

I am indebted to a great number of persons for providing the spiritual and material support which has been necessary for this work and its present continuation. Most of all I am grateful to Professor Paavo Yli-Vakkuri, former Head of the Department of Silviculture, for suggesting the photosynthesis work and providing the means for its continuation up to the present date.

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Within the present research group on forest ecophysiology at the Department of Silviculture and the Forestry Field Station of the University of Helsinki, close contacts with Dr. Pertti Hari have been of decisive importance not only for this work but also for the development which has led to the activity of the research group today.

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Helsinki, 1 December 1977

OLAVI LUUKKANEN

1 INTRODUCTION

11 CO_2 exchange as a genetically controlled process in trees

Several reviews of photosynthesis and respiration in forest trees have been published. KOZLOWSKI and KELLER (1966) summarised the major factors controlling gas exchange. LARCHER (1969 b) compiled data from many sources for the rates of both photosynthesis and respiration and emphasised that environmental factors render genetic comparisons of gas exchange difficult. He also discussed (LARCHER 1969 a) techniques of measuring CO_2 exchange in trees, particularly those in which infrared gas analysers (IRGA) were used. Edaphic factors affecting photosynthesis and respiration were reviewed by KELLER (1972). Genetic parameters, including estimates of heritability for CO_2 exchange rates in trees, have also been measured (CAMPBELL and REDISKE 1966; LEDIG and PERRY 1967, 1969). The thorough methodological review, edited by ŠESTÁK *et al.* (1971 a), discusses the different aspects of gas exchange measurement techniques applied to laboratory as well as to field conditions.

The status of research on physiological genetics of forest trees has been rather recently summarised (CANNELL and LAST 1976), and reviews of different aspects of the genetic variation in CO_2 exchange in trees are available (FERRELL 1970, LUUKKANEN 1972 a, b; GORDON and PROMNITZ 1976, HELMS 1976, LEDIG 1976, ZELAWSKI 1976). A short general review of variation in Γ[1]) and photorespiration has also been presented earlier (LUUKKANEN 1976).

One of the earliest investigations with a genetic point of view was the work of HUBER and POLSTER (1955) on gas exchange in *Populus*. Their field studies dealt with a large number of clones belonging to the *Aigeiros* and *Tacamahaca* sections (black and balsam poplars respectively) and to intersectional hybrids. Differences among clones in net CO_2 uptake were positively correlated with growth rates. Variation in dark respiration and the total amount of foliage were also found to reflect clonal differences.

GATHERUM *et al.* (1967) demonstrated differences in the photosynthesis of clones of aspen-poplar hybrids. Variations in net and »total» photosynthesis were attributed to differences in photosynthetic efficiency, *i.e.* rate per unit of foliage, and, to a lesser degree, in plant size. However, no significant variation in dark respiration was found among clones. BOURDEAU (1958) indicated that differences between female and male clones of the same species might be important enough to be considered as a form of intraspecific variation. However, MUHLE LARSEN (1970) emphasised that sexually determined differences in growth rates of *Populus* clones still need further study to be firmly established.

In another study on *Populus* (LUUKKANEN 1971, LUUKKANEN and KOZLOWSKI 1972), differences in net photosynthetic rate per unit of foliage (as well as in the photorespiration rate and Γ) were found among six clones representing different species of the *Aigeiros* and *Tacamahaca* sections and one intersectional hybrid. These differences reflected the distribution of clones between the two sections (the hybrid representing an intermediary rate). Dark respiration rates also varied among the clones, but this variation did not follow the distribution of clones between the sections.

Among conifers, clones of *Larix decidua* have also been found to possess significant variation as far as photosynthetic rates per unit of foliage are concerned. This result was obtained by POLSTER and WEISE (1962), who also found similar differences between the two species *L. decidua* and *L. leptolepis*.

Population analyses within a species have also demonstrated intraspecific variation in the photosynthetic performance of trees. In *Pseudotsuga menziesii*, for instance, geographical origin and ecological adaptation

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[1]) Γ — CO_2 compensation point

is reflected in net photosynthetic rates, although within a geographical variety the differences may equal those found between varieties on an average (KRUEGER and FERRELL 1965, ZAVITKOVSKI and FERRELL 1970, SORENSEN and FERRELL 1973). Preconditioning of the experimental material was also found to affect the photosynthetic rate and the observed differences between ecotypes or varieties in these studies.

In general, short-term measurements have shown that within a species originating from the northern boreal or temperate regions, trees from higher latitudes often photosynthesise at a faster rate per unit of foliage than trees of more southern origin. This relationship has been found in Finnish populations of *Pinus sylvestris* (TIGERSTEDT 1965, GORDON and GATHERUM 1968), *Picea abies* (PELKONEN 1973, PELKONEN and LUUKKANEN 1974; cf. NEUWIRTH 1969, SCHMIDT—VOGT 1977, p. 392), and *Betula pubescens* (VAARAMA 1970). In other regions distinct differences in photosynthetic rate also occur, as shown for the tropical species *Pinus merkusii* (LUUKKANEN *et al.* 1976 a). In *Pinus sylvestris* the geographically determined differences in CO_2 exchange have been found to vary according to the time of year when the measurements are made (ZELAWSKI and GÓRAL 1966, ZELAWSKI and KINELSKA 1967) or to the age of the material being assessed (GORDON and GATHERUM 1969). The difficulties brought about by the techniques of CO_2 measurement used in such studies have also been discussed earlier (LUUKKANEN 1973).

The progeny test carried out by CAMPBELL and REDISKE (1966) with 100 full-sib families of *Pseudotsuga* indicated that only a relatively small proportion of the genetic variation in net photosynthetic rate per unit of foliage was additive. When the total variation caused by the controlled environmental conditions was taken into account the »narrow sense» heritability (h^2) was 0.21. However, it reached a value of 0.53 when only the environmental variance within families was used as a basis. It was also concluded in this study that the net photosynthetic rate per unit of foliage can be used as a criterion in selection for rapid growth, if seedling characteristics and those of mature trees have a high mutual correlation.

The relationship between several structural characteristics and CO_2 exchange in trees has been studied, and in particular, the effects of the amount of foliage, leaf anatomy (including stomatal distribution and function), and chlorophyll content have been discussed (KOZLOWSKI and KELLER 1966, KRAMER and KOZLOWSKI 1960, POLSTER 1967; KOZLOWSKI 1971a, b). If the rate of photosynthesis per unit of foliage is assumed to be constant, then an increase in the amount of photosynthesising tissue will also increase the photosynthetic rate per individual tree. This relationship is supported by evidence from studies carried out on forest stands in which the total amount of foliage and growth were found to be intercorrelated (BURGER 1937). Experiments on the variation in total foliage and chlorophyll content after silvicultural practices, including fertilisation (VIRO 1965), are in accord with this point of view. Consequently it has been suggested that selection for rapid growth be based on crown size and foliage volume (WAREING 1964).

The structural differences between sun and shade needles and the correlation between these morphological characteristics and CO_2 exchange have earlier been discussed in the literature (cf. STÅLFELT 1921, 1924). Sun needles of *Picea abies* are known to be larger, to have thicker walls and cuticles, and to contain less chlorophyll per unit of needle weight than shade needles of the same species. Shade needles are also dorsiventrally flattened compared with sun needles, the cross section of which is more or less square. Shade needles of *Picea abies* also have a low light compensation point in CO_2 exchange but a lower net photosynthetic rate at saturating light intensities. This variation is considered to be environmentally controlled.

As with different parts of an individual tree, different species may have become adapted in different ways to the light climate; in this case the variation is obviously also genetically controlled. As shown by STÅLFELT (1924), Scots pine *(Pinus sylvestris)* has a higher rate of photosynthesis per unit of foliage at high light intensities than Norway spruce *(Picea abies)*; however, at low light intensities spruce photosynthesises more efficiently. The variation in adaptation

to light regime in *Pinus sylvestris* has also been studied by ZELAWSKI and his coworkers. They explained part of the variation in net photosynthetic efficiency among Polish pine populations (which were described as ecotypes) by differences in genetically controlled needle morphology and subsequent light adaptation (ZELAWSKI *et al.* 1968, 1969).

The size, number, and distribution of the stomata in leaves or needles are morphological characteristics which undoubtedly affect CO_2 exchange (cf. BERTSCH and DOMES 1969, DOMES and BERTSCH 1969). Among trees, such characteristics have been especially studied in broadleaved species. In poplars, environmental and ontogenic factors seem to determine the stomatal pattern (CRITCHFIELD 1960). Among different *Populus* clones the distribution of stomata between the lower and upper epidermis, as well as the number of stomata per unit of leaf area and stomatal size, varied distinctly (SIWECKI and KOZLOWSKI 1973). However, only stomatal size was found to correlate (positively) with photosynthetic rates per unit of foliage in the clones in which these stomatal analyses were made (LUUKKANEN 1971, LUUKKANEN and KOZLOWSKI 1972).

Leaf age has a profound effect on CO_2 exchange in trees (cf. KOZLOWSKI 1971 a, p. 231). This variation should be borne in mind when relationships between other factors and CO_2 exchange are discussed. For instance, very young leaves of *Populus deltoides* have a negative rate of net photosynthesis; successively older leaves possess a higher net photosynthesis/respiration ratio (LARSON and GORDON 1969). KOCH and KELLER (1961) also demonstrated increasing ratios of photosynthesis to respiration in young leaves and a declining ratio in senescing leaves of *Populus*. In perennial leaves and needles the photosynthetic rate per unit of foliage reaches its maximum during the first season, when the leaves have reached maximum size (FREELAND 1952, NIXON and WEDDING 1956, RICHARDSON 1957). The variation in CO_2 exchange with leaf age, during the season follows the changes in activity of several enzymes involved in CO_2 metabolism, according to the studies on *Perilla frutescens* carried out by HARDWICK *et al.* (1968). Apart from leaf age, leaf dimorphism, which may be observed in different parts of a shoot, also seems to affect CO_2 exchange (cf. CRITCHFIELD 1960; KOZLOWSKI 1971 a, pp. 191, 219; ZIMMERMANN and BRAUN 1971, p. 47).

Much attention has sometimes been paid to chlorophyll content when the effects of genetic or environmental factors (including those observed in connection with light adaptation) on CO_2 exchange are discussed. Clear positive relationships between the chlorophyll content of leaves or needles and tree growth have been demonstrated (BOURDEAU 1959, MCGREGOR and KRAMER 1963, KELLER 1972). This has also been observed in experiments in which mineral nutrients are added; changes in chlorophyll content have been assessed in these studies (which have included such species as *Picea abies* and *Pinus sylvestris)* either from needle extracts (VIRO 1959; LUUKKANEN 1969) or using ocular methods based on standard colour charts (LUUKKANEN *et al.* 1971, 1972).

In broadleaved species the relationships between chlorophyll content and CO_2 exchange have been especially studied in *Populus* species. Positive correlations between growth and photosynthetic rate on the one hand and chlorophyll content of leaves on the other have been established (KELLER 1972).

In early works, chlorophyll content was considered to be a genetically determined factor which directly limited photosynthesis (WILLSTÄTTER and STOLL 1918). However, at the present time the chlorophyll content is assumed to limit photosynthesis only in extreme cases, for instance in mutants with a genetic chlorophyll deficiency (cf. GABRIELSEN 1948, 1960; ANDERSON 1967; HEATH 1969, p. 210).

Extreme nutrient deficiency (leading to chlorotic leaves) or other environmentally imposed disturbances in chlorophyll synthesis may also be reflected in low photosynthetic rates under normal conditions. Since the supply of available nutrients strongly affects cholorophyll content (cf. VIRO 1965; LUUKKANEN *et al.* 1971, 1972), the observed increases in growth and photosynthesis per individual tree may be a result of the increased supply of nutrients without there being any causal relationship between increased chlorophyll content and growth.

For instance, there is convincing evidence that despite a positive correlation between nutrient supply and chlorophyll content, photosynthesis need not necessarily be proportional to chlorophyll content (KELLER and KOCH 1962 a, b, 1964; KELLER 1972). Nevertheless, other factors, such as changes in plant hormone levels, which accompany variations in chlorophyll content, may affect photosynthesis (KOZLOWSKI 1961).

FERRELL (1970) discussed investigations into the two photosystems involved in photosynthesis, and concluded that genetic (ecotypic) adaptations concerning resistance against damage by high light intensity (cf. BJÖRKMAN 1968) may also occur in forest trees. Genetic variation in the net photosynthesis of trees may be directly associated with intraspecific variation in the activity of carboxylation or respiratory enzymes, as has already been demonstrated in herbaceous plants (EAGLES and TREHARNE 1969, TREHARNE and EAGLES 1970, TREHARNE and NELSON 1975). As shown by TREHARNE and STODDART (1968) variations in ribulose diphosphate (RuDP) carboxylase activity also depend on changes in plant hormone levels (in their studies gibberellin and auxin levels were investigated).

Genetically controlled variation in the dark respiration rates of trees has been frequently demonstrated using different materials. In poplar clones (HUBER and POLSTER 1955, LUUKKANEN 1971, LUUKKANEN and KOZLOWSKI 1972), however, the variation in dark respiration rates seems to be smaller than that in net photosynthetic rates. SCHMIDT (1961) found that *Picea abies* provenances from a northern region had higher dark respiration rates than those from the south and assumed this to be the cause of the lower net photosynthetic rates observed in the former group. Also PISEK and WINKLER (1959) observed that northern spruce populations had higher dark respiration rates than southern ones. In Finland similar variation has also been reported in a study (PELKONEN 1973, PELKONEN and LUUKKANEN 1974) which demonstrated significantly higher dark respiration rates in two spruce stands from northern Finland as compared to one stand from southern Finland. In one of the northern and in the southern stand, distinct variation was also found among half-sib families originating from the same stand. Dark respiration rates of Finnish *Betula pubescens* populations reported by VAARAMA (1970) may also be interpreted as indicating high rates in northern and low rates in southern individuals of this species. The studies on the tropical species *Pinus merkusii* demonstrated the importance of distinguishing between the concepts of respiration rate per unit of foliage and respiration rate per individual; as in the case with net photosynthesis, distinct differences may be found, but the ranking of populations may be completely reversed depending on the measuring unit employed (LUUKKANEN *et al.* 1976 a).

12 Photorespiration and photosynthesis

Photorespiration is generally defined as the total CO_2 output from photosynthesising tissues in light; this output differs from that of dark respiration since in most plants a biochemical pathway differing from normal mitochondrial respiration seems to be responsible for a considerable part of CO_2 output in light. The review by JACKSON and VOLK (1970) summarises much of the work carried out on this process, the adaptive significance of which is not yet understood. However, the biochemical pathways associated with photorespiration and their relationships with other processes involved in CO_2 metabolism have already been clarified in great detail (cf. BURRIS and BLACK 1976). In particular, the action of the common enzyme for both photosynthetic carboxylation and photorespiration, ribulose diphosphate (RuDP) carboxylase-oxygenase has been studied (JENSEN and BAHR 1976, 1977). New aspects of photorespiration have also been discussed by ZELITCH (1971), BJÖRKMAN (1973), and recently by LAISK (1970, 1977; LAÏSK 1977).

The CO_2 compensation point, Γ, is one of the most distinct indicators of apparent photorespiration and it is also commonly used in measurements of photorespiration by the so-called extrapolation method (cf. FORRESTER *et al.* 1966, LUUKKANEN and KOZLOWSKI 1972).

Photosynthesising plants have been clas-

sified into those with high compensation points or those with low ones (Moss *et al.* 1969). Plants of the former group, which is by far the larger one, are characterised 1) by the lack of the alternative CO_2 fixing pathway which operates through phosphoenol pyruvate (PEP) carboxylase (the Hatch-Slack or C_4 dicarboxylic acid cycle); 2) by a finite minimum concentration of CO_2 in the external atmosphere (caused by the large apparent output of CO_2); 3) by an increase in photosynthesis with decreasing concentrations of O_2; and 4) by generally low net photosynthesis rates (Jackson and Volk 1970).

The CO_2 output resulting from photorespiration is associated with microbodies or peroxisomes (cf. Tolbert 1971, Luukkanen 1972 a), which utilise glycolate produced by photosynthesis in light. According to a commonly accepted hypothesis, the glycolate pathway culminates in production of serine and the release (in the mitochondria) of one mole of CO_2 per mole of serine synthesised.

Photorespiration has been demonstrated and measured by the CO_2 outburst in the dark following illumination, by release of CO_2 into a CO_2-free air stream, by radiotracer investigations, or by examining the relationship between net photosynthesis and external concentrations of CO_2 or O_2 (Jackson and Volk 1970). The extrapolation method, in which the net photosynthetic rate at a known CO_2 concentration and the CO_2 compensation point are determined, is widely applied, although it apparently underestimates photorespiration; further complications are caused by observed variations in photorespiration with changes in the external CO_2 concentration (cf. Laïsk 1977, p. 44).

Genetic variation in apparent photorespiration (as determined, for instance, by the extrapolation method) seems to be expressed in several different ways. One of the most important of these is due to differences in leaf anatomy (cf. Frederick and Newcomb 1971). These differences become evident when the anatomy of high and low compensation point species of grasses are compared, the former group not having distinct vascular bundle sheaths or any large variation in chloroplast structure. In these plants CO_2 is also fixed uniformly throughout the photosynthesising leaf tissues.

Low compensation point species, on the other hand, have a well developed vascular bundle sheath which often contains cells with large but weakly differentiated chloroplasts. These chloroplasts are the main sites of CO_2 incorporation; the alternative Hatch-Slack cycle in these species, however, is not located in these exceptional chloroplasts but in cells outside the bundle sheath. Recyling of CO_2 (instead of a total lack of CO_2 release) seems to be responsible for the apparent low photorespiration rate (Hatch and Slack 1970).

The existence of quantitative differences in enzyme activity which cause variation in photorespiration was demonstrated by Zelitch and Day (1968), who found differences in photorespiration between varieties of tobacco plant. These were also inversely correlated with net photosynthesis.

Tolbert (1971) concluded that synthesis of glycolate from carbohydrate reserves and subsequent photorespiration are unavoidable (but, at least in part, probably adaptive in genetic implications) at high O_2 or low CO_2 concentrations and at high light intensity. Algae, which excrete large amounts of glycolate in the absence of CO_2, are examples of this response. Similarly, higher plants oxidise reserve foods to glycolate and further to CO_2 in the absence of CO_2. When plants having high compensation points are enclosed in an environment with a low CO_2 concentration, they lose CO_2 continuously and eventually die. Possible genotypes with lower than average compensation points (and a lower rate of photorespiration) could consequently be detected on the basis of survival at low CO_2 concentrations (Mentz *et al.* 1969). In field crops, screening for »photorespiration-defective» mutants has not given any confirmed positive results (Curtis *et al.* 1969, Ogren and Widholm 1970; Moss 1970, 1976; Ogren 1976). Intraspecific variation in photorespiration may, however, differ in groups of plants having different genetic constitutions; according to Stebbins (1967, p. 99), mutation rates become smaller with increasing genetic stability through inbreeding. The latter phenomen is common in field crops but not in forest trees (Sarvas 1967,

Stern and Tigerstedt 1974, p. 184).

Photorespiration has been demonstrated in forest trees, for instance in *Pinus sylvestris* (Zelawski 1967), *Pseudotsuga* (Brix 1968), *Picea glauca* (Poskuta 1968), *Populus* clones (Luukkanen 1971, Luukkanen and Kozlowski 1972), and *Picea abies* (Pelkonen 1973, Pelkonen and Luukkanen 1974). Photorespiration (as reflected in Γ) has been suggested by Decker and his coworkers (Decker and Tió 1959, Decker 1970) as a criterion in selection for rapid growth. Decker also suggested that the photosynthetic and photorespiratory pathways might, at least in part, be under different types of genetic control and thus separable in tree breeding. He argued that the CO_2 compensation point is a good indicator of photosynthetic capacity, in contrast to photosynthetic efficiency (or photosynthesis rate per unit of plant tissue) which is not necessarily correlated with plant growth (cf. Ferrell 1970). In closely related species, of course, photosynthetic efficiency comparisons are more justified.

In the earlier study on *Populus* (Luukkanen 1971, Luukkanen and Kozlowski 1972), six contrasting clones were used to investigate variation in net photosynthetic rate, Γ, and rates of photorespiration and dark respiration. Particular attention was focused on relationships between Γ and net photosynthetic efficiency, and the possibility that photosynthesis and photorespiration were under separate genetic control. However, as the plant material did not include families, genetic parameters such as heritability could not be determined.

The black poplar clones (within the species *Populus nigra* and *P. deltoides)* had higher CO_2 compensation points than three balsam poplar clones (representing two species, *P. trichocarpa* and *P. maximowiczii).* High photosynthetic rates were associated with low Γ and rapid photorespiration. However, when photorespiration rates were adjusted to average photosynthetic rates, using covariance analysis, these *relative* photorespiration rates seemed to be correlated positively with Γ and inversely with photosynthesis. That is, clones with the lowest measured rates of photorespiration had the fastest photorespiration rates in proportion to their rates of photosynthesis. High photosynthetic rates were observed in an interspecific cross, *P. maximowiczii* x *P. nigra*, which had the fastest rates of relative photorespiration over most of the temperature range (15 – 30° C) and also large Γ values at higher temperatures. This hybrid seemed to combine the properties of both parental species. A *P. nigra* clone included in the material had high Γ and high rates of relative photorespiration, but low photosynthetic rates. Two *P. maximowiczii* clones, on the other hand, had low Γ and low rates of relative photorespiration, but high photosynthetic rates.

Overall, a significant inverse relationship was found between estimates of Γ and net photosynthetic rates per unit of foliage, although it was strongly affected by temperature. Thus Γ alone may provide a criterion for photosynthetic efficiency, although further work is needed concerning the nature of the observed differences in relative photorespiration, albeit that they are in accordance with Decker's proposed model.

Two northern Finnish populations of *Picea abies* were found to have larger Γ values and higher rates of net photosynthesis and photorespiration per unit of foliage than a southern Finnish population (Pelkonen 1973, Pelkonen and Luukkanen 1974). Values of Γ and net photosynthetic rates were not significantly related, taking the material as a whole, but seemed to be inversely related within each population (cf. Pelkonen 1973). Thus it is possible that if Γ is used to predict net photosynthetic efficiency, better correlations may be found within genetically homogeneous groups of trees than, for instance, among a range of provenances or ecotypes.

In the tropical species *Pinus merkusii*, the variation in Γ was not statistically confirmed among the three provenances studied, but photorespiration rate per unit of foliage was clearly the highest in the provenance with the highest values of Γ (Luukkanen *et al.* 1976 a). This provenance also possessed the highest photorespiration/net photosynthesis ratio, but since photorespiration was measured at one temperature only, it was not possible to analyse whether the relationship between this ratio and other CO_2 exchange characteristics clearly

differed from the situation found in the poplar clones discussed above.

It may thus be concluded that in some instances, the CO_2 compensation point, Γ, seems to be an inherent characteristic of forest trees, which is inversely related to their carbon fixation efficiency, although the relationship may be obscured by environmental factors.

It is well recognised that photosynthetic rates, when expressed per unit of foliage, are at best unreliable indicators of photosynthetic performance over long periods of time (Decker 1955, Ferrell 1970). Estimates of Γ may give more useful information about the plant's complex gas exchange processes and inherent differences in its responses to the environment. For instance, Γ values may reflect genetic variation in resistance to water stress, although stomatal movements alone cannot affect Γ (cf. Luukkanen and Kozlowski 1972).

Recent studies have to some extent clarified the still disputed mechanisms of photorespiration and given new background for discussion of the result of studies on photorespiration in trees referred to in the foregoing review. It is now generally accepted that photorespiration is the unavoidable result of the dual action of the CO_2-fixing enzyme found in C_3 plants, RuDP carboxylase-oxygenase or ribulose 1,5-bisphosphate (RuBP) carboxylase-oxygenase (cf. Jensen and Bahr 1976, 1977). The enzyme-RuDP complex produces C_3 sugars in the Calvin cycle using CO_2 as the substrate, whereas O_2 attached to the same enzyme-RuDP complex produces glycolate. The kinetics of photorespiration — as an integral part of the entire light-dependent CO_2 metabolism — has also been given a mathematical formulation (Laïsk 1977).

The ratio of CO_2 fixed in the Calvin cycle to CO_2 released through glycolate metabolism is supposed to be stoichiometric at given CO_2 and O_2 concentrations and at a given temperature (Lorimer *et al.* 1977). Consequently the genetic variation of this ratio among different species or genotypes within a species would also be difficult to explain. According to this model, Γ would also be constant over a wide range of environmental conditions and internal plant factors. For instance, light intensity would not affect Γ, except at very low intensities (cf. Laïsk 1977, p. 81). On the other hand, increasing temperature and especially increasing O_2 concentrations would shift both Γ and the photorespiration rate towards higher values.

Thus it would seem that the model of »light-dependent gas exchange» *(fotogazoobmen)* summarised by Laisk does not allow one to explain the genetic variation in net photosynthesis by changes, for instance, in photorespiration. If the postulated stoichiometric relationship between photosynthesis and photorespiration is valid, such environmental effects as water stress should not affect the photorespiration/photosynthesis ratio.

The seemingly contradictory conclusions made in earlier studies on the variation in photorespiration in trees (*e.g.* Luukkanen and Kozlowski 1972, Pelkonen and Luukkanen 1974) on the one hand and in the review by Laisk on the other, may, however, be explained by the use of different methods and different definitions of such terms as CO_2 compensation point and photorespiration.

Earlier studies on forest trees dealt with characteristics at the leaf level, whereas Laisk, excluding the effect of dark respiration, emphasises the CO_2 »photocompensation point» and refers to gas exchange processes on the cellular level, *i.e.* at the surface of the liquid phase of the mesophyll cells. Thus any change in dark respiration would be reflected in the conventionally measured CO_2 compensation point and photorespiration values obtained through the ordinary extrapolation method (*e.g.* Forrester *et al.* 1966, Luukkanen and Kozlowski 1972) but not in those values referred to by Laisk. The latter author also emphasises that the commonly applied extrapolation method does not take into account the recycling of respiratory CO_2 within the leaf, which results in underestimation of photorespiration rates (Laïsk 1977, p. 43). Any change in the recycling process, brought about, for instance, by changes in stomatal resistance, would be reflected in the photorespiration rate determined at the leaf level but not necessarily in that at the cellular level.

The approach by LAISK discussed above also excludes other effects of stomatal regulation. Obviously this is an important point of view to be considered when the effects of water stress on CO_2 exchange are discussed. Apart from all the different regulating mechanisms which operate through stomatal action, a few other processes allow the environmentally or genetically determined variation to be reflected in photorespiration (or photorespiration/photosynthesis ratios) without conflicting with the model for CO_2 exchange presented by LAISK. The variation in dark respiration remains as one of the most important of these factors, mainly because the conventional methods of measuring photorespiration do not separate dark respiration and »true» photorespiration. The commonly approved result of dark respiration being suppressed in light (cf. JACKSON and VOLK 1970) does not render this factor less important.

The present knowledge concerning the Calvin cycle does not exclude the possibility of such changes in the activity of RuDP carboxylase-oxygenase which could be brought about by water stress. It is already known, for instance, that the ratio of carboxylase to oxygenase activities is strongly affected by pH in the stroma (JENSEN and BAHR 1976, p. 9). Variation in O_2 and CO_2 concentrations in the mesophyll are factors which also could mediate such an environmentally imposed effect and cause an increase in photorespiration rate in relation to photosynthetic rate with a subsequent increase in Γ.

It may thus be concluded the genetically controlled variation in Γ and photorespiration observed in trees in earlier studies offer an interesting starting point for further work in which the mechanisms of CO_2 exchange processes will be analysed in more detail.

13 Water balance and CO_2 exchange

As frequently discussed in the literature (*e.g.* SLATYER 1967, p. 295; KRAMER 1969, p. 356), water deficit affects virtually every aspect of plant metabolism. Correlation was found between the variation in net photosynthetic rate and water relations in early investigations on CO_2 exchange in trees. For instance, STÅLFELT (1921) found that a decrease in net photosynthetic rates of *Pinus sylvestris* and *Picea abies* were associated with a decrease in soil moisture.

During water deficit, net photosynthesis may be limited by a decrease in the carboxylation process (including changes in the »light» as well as »dark» reactions of photosynthesis), by an increase in respiration, and by stomatal regulation of CO_2 diffusion (cf. LAÏSK 1977, p. 9). According to the gas exchange model presented by GAASTRA (1959), a change in carboxylation or respiration is reflected in the mesophyll component of CO_2 diffusion resistance (and is largely independent of variation in transpiration rate), whereas stomatal regulation implies a positive relationship between net photosynthetic rate and transpiration.

Population analyses have indicated that the variation in CO_2 exchange within a species is, at least in some cases, parallel to differences in the transpiration pattern observed in the same varieties or ecotypes; thus the variation in net photosynthetic rates among such populations would largely depend on stomatal regulating mechanisms. In *Pseudotsuga*, rates of transpiration and net photosynthesis both decrease more rapidly in populations adapted to dry sites as compared to those originating from a moist environment, when studied simultaneously during decreasing soil moisture (ZAVITKOVSKI and FERRELL 1968, 1970; UNTERSCHEUTZ *et al.* 1974). Such a variation may also be associated with differences in endogenous abscisic acid (ABA) levels, as shown in recent investigations (BLAKE and FERRELL 1977).

The adaptive significance of such regulating and water-conserving mechanisms is obvious, and it is also clear that the total amount of CO_2 fixed over a longer period of time is not determined by the photosynthetic rates under favourable conditions alone, but also by these rates during water deficit. This was shown clearly in comparisons between both CO_2 exchange and water balance in *Populus tremula* and *P. nigra* (NEUWIRTH and POLSTER 1960). In the study in question, rapid stomatal closure (and subsequent decrease in the transpiration

and photosynthetic rates) was observed during water deficit in *P. tremula*, whereas very little change in gas exchange was found in *P. nigra* under similar conditions. Prolonged water deficit caused, however, leaf damage and leaf abscission in the latter species. During conditions of sufficient water supply, *P. tremula* nevertheless had a higher transpiration rate and it utilised more water per unit of new biomass produced. The difference in water balance between these two species also explained the fact that *P. tremula* was better adapted to habitats with intermittent water deficits, despite the temporary high transpiration rate in this species.

In *Pinus sylvestris* the variations in CO_2 exchange and water relations have been studied among Polish populations of this species. However, no clear causal relationships between these processes have yet been established (Zelawski *et al.* 1969). On the other hand, water relations (as indicated by transpiration rates or the water potential) are known to differ among genotypes of *Pinus sylvestris* (Hellkvist 1970, 1973; Hellkvist and Parsby 1976, 1977) and subsequent investigations will possibly demonstrate a genetically fixed correlation between water relations and photosynthesis also in this species.

The daily variation in the net photosynthetic rate, commonly known as the »midday depression», generally seems to be accompanied by variations in the water deficit of the plant tissue, although several other processes also show similar daily fluctuations, as discussed, for instance, by Kramer and Kozlowski (1960, p. 71) and Molchanov (1977).

Direct stomatal control of CO_2 exchange, caused by a decrease in the turgor pressure of the guard cells after an increase in the transpiration rate, seems to be an important mechanism underlying this variation, as frequently discussed in the literature (Pisek and Winkler 1956, Stålfelt 1956, Barrs 1968, Hsiao 1973, Moldau 1973, Kozlowski 1976). Other processes may, however, be also involved, as emphasised by Stocker (1960, p. 467) who reported that a decrease in the photosynthetic rate may occur before the stomata begin to close and that an increase in the cytoplasmic resistance to CO_2 diffusion may instead be the primary cause. Similarly Slatyer (1967, p. 293) pointed out that CO_2 diffusion, as compared to transpiration, is controlled by several additional components of diffusion resistance (in the liquid phase and within the chloroplast, cf. Gaastra 1959), and that net photosynthetic rates may in effect be controlled by this mesophyll part of resistance under conditions where the stomata regulate H_2O diffusion. The same author thus concluded that even parallel variations found in photosynthesis and transpiration during water stress may in fact be brought about by two different mechanisms: the variation in photosynthesis by the effect of turgor on biochemical processes and the variation in transpiration by the effect of turgor on the stomata. An increase in mesophyll resistance to CO_2 diffusion may be, however, visible within a few minutes after water stress imposition, but the degree of the increase is proportional to the duration of water deficit (Laïsk and Oya 1971).

Measurements made on tobacco leaves by Redshaw and Meidner (1972) indicated that only about 50 % of the reduction in the net photosynthetic rate during a rapidly imposed water deficit was due to an increase in stomatal resistance and that the rest was probably caused by an increase in the carboxylation part of mesophyll resistance or in respiration. However, as emphasised by Björkman (1973, p. 36), the mesophyll resistance cannot be measured directly and the rôles of the different processes involved in it (carboxylation and liquid phase diffusion) during changing environmental conditions remain unclear.

Stomatal movements are controlled by a number of factors other than variations in turgor pressure, as also discussed by Hsiao (1973) and Raschke (1975). Under natural conditions, the build-up of CO_2 in the intercellular space of the mesophyll seems to induce stomatal closure; thus a possible increase in Γ accompanying water deficit would more likely be the cause than the result of stomatal closure which is observed during the midday depression of photosyntesis (Heath and Meidner 1961, Meidner 1967; Meidner and Mansfield 1968, p. 94). Actual field measurements have

also supported this hypothesis and indicated that stomatal movements may in some cases be of secondary importance in controlling net photosynthetic rates even under severe water deficit (SCHULZE 1972).

Variations in net photosynthetic rates, observed during varying degrees of water deficit, may also be brought about by changes in respiration rates, as discussed by SLATYER (1967, p. 294) and KRAMER (1969, p. 367). Both authors summarise the results obtained by several investigators and conclude that a rapidly imposed water deficit may cause an increase in dark respiration rate as reported by BRIX (1962) in *Pinus taeda* seedlings, but that water deficits generally result in a gradual decline in respiration rates. Furthermore, SLATYER also suggests that different responses of the respiration rate in different species to water deficit may be caused by different rates of water deficit imposition.

Modelling of the relationship between water deficit and CO_2 exchange in trees has been given a conceptual framework in recent Finnish studies summarised by HARI (1976). These studies are based on a model in which the net photosynthetic rate is assumed to be controlled by light intensity and temperature in trees not exposed to water deficit. During water deficit such a model does not explain the variation in net photosynthesis, as demonstrated in *Alnus incana* seedlings under laboratory conditions (HARI and LUUKKANEN 1973) and in a young stand of *Betula* in the field (HARI and LUUKKANEN 1974). Instead, a new variable, called physiological water stress (w) in these studies, has to be added to the model in this situation. This variable cannot be measured directly, but it can be calculated from temperature, light intensity, and CO_2 exchange data by minimising a residual sum of squares. The model including w explains the variation in CO_2 exchange during water deficit, and the value of w increases and the net photosynthetic rate decreases successively with increasing water deficit. This is observed particularly well at high temperatures, which indicates that an interaction between w and temperature is a peculiar feature of this model.

The concept in physiological water stress has recently also proved to be useful in explaining the decrease in net photosynthetic rate observed during the beginning and end of the growing season in connection with the build-up and discharge of the processes known collectively as hardening (PELKONEN 1977, PELKONEN *et al.* 1973, 1977). It seems conceivable to broaden this concept to a more general term, *physiological stress*.

The effect of water deficit on CO_2 exchange has also been further analysed by comparing observed rates of net photosynthesis and transpiration with theoretical estimated values (HARI *et al.* 1975 a). Theoretical values may be obtained by assessing comparable plant material which is maintained at a favourable water balance, or from a model based on light and temperature data (as in the case of CO_2 measurements), or from a model of potential evapotranspiration (when analysing the variation in transpiration), as shown by HARI *et al.* (1975 b) and SMOLANDER *et al.* (1975).

The ratio of observed to calculated values, *i.e.* the degree of photosynthetic control *(CP)* and the degree of transpirational control *(CT)* in photosynthesis and transpiration studies respectively, is less than unity when gaseous diffusion is impaired. The ratios *CP* and *CT* thus also quantify the effect of water deficit, and an estimate of the mesophyll component of diffusion resistance is obtained by comparing *CP* and *CT* to each other. They may also be followed as functions of time during varying moisture conditions. Genetically determined variation in CO_2 exchange, effected, for instance, through stomatal action, would consequently also be detected by such comparisons. The results obtained in studies in which these models were applied, indicated that in some cases net photosynthetic rates may remain at a low level after the water balance has been restored to the level which prevailed before the onset of water deficit (HARI *et al.* 1975 a). This is in accordance with earlier results reported in the literature which show that a decrease in net photosynthesis during a slight water deficit is completely and rapidly reversible as soon as the water balance has been restored, whereas a prolonged deficit results in a slow increase in net photosynthetic rates to the initial level even if water deficit is no

longer detectable. Several possible mechanims for such an »after-effect» have been discussed in the literature (KOZLOWSKI 1949, BRIX 1962, MEIDNER and MANSFIELD 1968, ORTON and MANSFIELD 1974).

A comparison between the calculated variables *CP* and *CT* indicated that processes other than stomatal mechanisms in the control of net photosynthesis during water deficit cannot be excluded in *Betula* (HARI *et al.* 1975 a). On the other hand, in clones of *Picea abies*, the pattern of variation in *CT* with soil moisture seemed to differ among ten clones (HALLMAN 1976), but this variation was not unlike the variation in *CP* in the two clones of this material in which both net photosynthesis and transpiration were measured (LUUKKANEN *et al.* 1975, 1976 b; HALLMAN 1976).

14 The aim of the study

The aim of the present study was to investigate the variation in net photosynthetic rate per unit of foliage in contrasting genotypes of *Picea abies* and to study the correlation between the photosynthetic performance and dark respiration or photorespiration. For further evaluation of different CO_2 exchange processes from the point of view of net CO_2 fixation, these processes were studied under different environmental conditions, including varying temperature and soil moisture. An attempt was also made to investigate transpiration and other characteristics of the water balance in the experimental material in connection with the study on CO_2 exchange.

2 MATERIAL AND METHODS

21 Material

The material consisted of two-year old, greenhouse-grown cuttings of Norway spruce, *Picea abies* (L.) Karst. The cuttings were rooted at the Haapastensyrjä Breeding Center of the Foundation for Forest Tree Breeding in spring, 1971. They were also transplanted into peat beds in a greenhouse at the same nursery during the first growing season.

The four experimental clones were chosen among clones originating from phenotypically selected plus trees considered to be of potential value for commercial mass propagation in Finland. A considerable part of the large number of spruce clones collected for this purpose are of foreign origin; therefore only one clone in the experimental material represented an autochtonous Finnish clone. The origin of the experimental material, as well as the clonal identification numbers used in this study, are shown in Table 1.

Table 1. Identification numbers used in the present study, register labels, and origins of the experimental clones, with register labels of the female parent or (in the case of controlled crosses) both parents of the ortet.

No.	Register	Origin
1	V-374	Pieksämäki, Finland (K-1399 x K-1398)
2	V-376	Czechoslovakia (Pc-Cs-545)
3	V-380	Lohja, Finland x Germany, Springelau, through Punkaharju, Finland (E-268 x E-1485)
4	V-393	Czechoslovakia (Pc-Cs-547)

In spring 1972, the cuttings were lifted and shipped to the Hyytiälä nursery at the Univeristy of Helsinki Forestry Field Station. The cuttings were then transplanted at the nursery into clay pots, each containing about 1.3 liters of horticultural fertilised *Sphagnum* peat, and grown in a plastic greenhouse in randomised blocks, each including one cutting from each clone. In the greenhouse, temperatures of 30 to 35° C were reached during clear days, whereas the lowest temperatures at night varied between 5 and 10° C. The cuttings were watered frequently and given a modified Hoagland nutrient solution twice during the summer. At the end of the growing season the cuttings were transferred to a heated greenhouse at the Department of Silviculture in Helsinki, where they were kept until the gas exchange measurements were started. In the greenhouse, the day temperature generally varied between 10 and 20° C, and the night temperature between 8 and 15° C. Artificial fluorescent light was given to the plants, so as to maintain the daylength at 12 h.

Prior to the gas exchange measurements all cuttings were watered frequently (until 14 December 1972). Thereafter only five blocks of the experimental material, each containing one cutting from each clone, were watered daily, whereas an equal number of pots was allowed to dry out slowly. Thus the experimental material consisted of ten blocks with four cuttings (representing different clones) in each, or a total of 40 cuttings.

The amount of water available to the stressed plants was assessed indirectly, using oat seedlings (c. v. 'Sol') as indicators. The oat seedlings were transplanted, when about 10 cm long, into the pots of the stressed group before the stress treatment was initiated. As soon as the permanent wilting point of the oat seedling was reached, the stressed spruce cuttings were given small amounts of water, roughly equalling the daily water loss from the pot and the cutting. However, no water was given during the two days prior to the gas exchange measurement of any stressed cutting.

Gas exchange measurement were conducted using four cuttings, each representing a different clone, from a control block and a stressed block alternately. After the CO_2 measurements had been carried out with a stressed plant (this was completed within

one day), the pot in question was watered in the evening with 100 ml of water. Gas exchange measurements were repeated with the same cutting the following day. Immediately after the second series of measurements and, in the case of unstressed plants, after the first series of CO_2 measurements, fresh and oven-dry weights of the peat substrate in the pot were determined. These determinations allowed calculations to be made of the soil water content (expressed as % of dry weight of the peat) during each series of gas exchange measurements.

22 Equipment and methods for CO_2 measurements in the laboratory

The equipment used for CO_2 exchange measurements consisted of a closed IRGA system with a Hartmann-Braun URAS 1 analyser as the central unit. The setup was basically the same as that described earlier (LUUKKANEN *et al.* 1976 a). The total air volume of the system was 2 790 ml. The water-jacketed plexiglass gas exchange chamber had a volume of 560 ml. The air flow was maintained during the measurements at 60 l min^{-1}, and air humidity stabilised by cooling the circulating air in an ice bath which was placed between the chamber and the URAS. The air entering the chamber was rehumidified to about 80 % relative humidity in a flask containing distilled water and some H_2SO_4 to prevent CO_2 absorption.

The output from the URAS was monitored by a MINIGOR chart recorder. Before starting each series of CO_2 measurements, daily calibrations of the URAS were made using N_2 and a mixture containing 283 ± 6 ppm CO_2 in N_2 as reference gases. The output from the URAS was transformed to final CO_2 concentration values using the calibration curve provided by the manufacturer of the URAS. During CO_2 measurements and the calibration procedure, special attention was paid to air pressure in the URAS. The air pressure was read using a water manometer connected to the system near the URAS.

A growth chamber was used to stabilise the environment of the gas exchange chamber and the experimental plant during CO_2 exchange measurements. The experimental plant was illuminated inside the growth chamber by two 500 W incandescent/mercury vapour mixed light bulbs, placed on both sides of the gas exchange chamber which enclosed the upper part of the experimental plant. The spectral properties of these lamps have been described earlier (LUUKKANEN 1973). Additional light was obtained from ten 40 W fluorescent light tubes placed in the growth chamber. The irradiance at the bottom level of the gas exchange chamber was 50 W m^{-2} of photosynthetically active radiation (PhAR), corresponding to an illuminance of 14 700 lx.

During the CO_2 exchange measurements the upper part of the experimental plant was enclosed in the gas exchange chamber and the chamber bottom sealed by a removable, air-tight plate. Temperature control was achieved using a pump which circulated water through the water jacket of the gas exchange chamber and a thermostat. Air temperature within the assimilation chamber as well as water temperatures at different points in the cooling system were monitored using Cu-constantan thermocouples connected to a multipoint chart recorder. During CO_2 exchange measurements the air temperature within the assimilation chamber was maintained within $\pm 1°$ C of the desired temperature. The lower part of the experimental plant was subjected to the constant environmental conditions of the growth chamber.

During the CO_2 exchange measurement procedure, Γ was first measured at the lowest or the highest temperature (one control block and the following stressed block of the experimental material were measured using the same starting temperature; thereafter the starting temperature was changed). Values of Γ were obtained by recording the equilibrium concentration of CO_2 in the closed system, after decreasing the CO_2 concentration of the system to near the expected value (using a KOH solution bypass in the air stream). After changing the temperature of the assimilation chamber the equilibrium CO_2 concentration was again recorded until Γ values at 10, 16, 22 and 28° C were obtained. Following Γ values, net photosynthetic rates at the same

temperatures were measured, starting with the last temperature used in the determination of Γ. Photosynthetic rates were calculated using the time required to lower the CO_2 concentration from 350 to 250 ppm and the known volume of the system. When necessary, the CO_2 concentration was increased by injecting CO_2-enriched air into the system with a hypodermic syringe.

As soon as the photosynthetic measurements had been made, the gas exchange chamber was put in absolute darkness, and dark respiration rates, at the same temperatures as mentioned above, were measured after an adjustment period of 15 min (so as to eliminate the effect of photorespiration in these measurements). However, the dark respiration time was recorded over the range of 50 ppm only.

Photosynthetic and dark respiration rates per seedling were converted to rates per unit of needle dry weight (mg CO_2 g^{-1} h^{-1}) using oven-dry needle weights determined immediately after completing the CO_2 exchange measurements. Photorespiration rates (per unit of needle dry weight) were calculated using Γ and net photosynthetic rates at 300 ppm for each temperature respectively, according to the extrapolation method described by Forrester *et al.* (1966) and Luukkanen (1971).

The chlorophyll content of the needles was determined from five samples per plant, each consisting of 50 mg of fresh needles. The first and the last sample were used for needle dry weight determination, and the three remaining samples were analysed following the method used earlier by Luukkanen (1969) and Pelkonen and Luukkanen (1974), with minor modifications. Chlorophyll content was calculated separately for chlorophyll *a*, chlorophyll *b*, and total chlorophyll, using the Arnon—McKinney equations given by Šesták (1971).

23 Field measurements of photosynthesis (preliminary experiment)

The experimental plants included in the preliminary field experiment were obtained from the same source as the material later used in the laboratory experiments. They consisted of five replications, each incuding one cutting from each of the four clones. In the field, four cuttings (one replication) were simultaneously measured during one whole day, and thereafter the procedure was repeated with another replication the following day.

At the beginning of the measurement period (17 August to 2 September 1972) the potted cuttings were transferred to the experimental site, which has earlier been described by Hari and Luukkanen (1974). There all plants were exposed to full natural light during and between the CO_2 exchange measurements. Light conditions were monitored using a Kipp & Zonen CM-3 solarimeter, connected to a multipoint chart recorder. The temperatures within and outside the gas exchange chambers were recorded by Cu-constantan thermocouples and a multipoint chart recorder.

The cuttings were maintained throughout the entire field measurement period at a soil moisture above 75 % of field capacity. Matric soil water potentials were followed using tensiometers (described by Ahti 1971), which were mounted in pots treated in the same way as those containing the actual experimental plants. Tensiometer readings showed that minimum soil water potentials did not extend below — 0.5 bar and that they generally were about — 0.1 bar.

Net photosynthetic rates were measured in the field using an open IRGA system, which included the same URAS 1 analyser as later used in the laboratory measurements of the same spruce clones. The setup was largely the same as that earlier developed for open-system measurements under laboratory conditions (Luukkanen 1973). The assimilation chambers were, however, modified for field use as described by Hari and Luukkanen (1974). A sequential valve supplied by the URAS manufacturer timed the consecutive CO_2 measurements of four assimilation chambers and of the ambient air. This switch also regulated the pneumatic operation of the trap-type chambers through electrical signals to solenoid valves which controlled the flow of compressed air to the assimilation chamber mechanisms.

The differences between the CO_2 concentrations in the ambient air and the closed assimilation chambers were recorded by a Hartmann-Braun MINICOMP multi-

point chart recorder. Net photosynthetic rates (per unit of needle weight) were calculated from these differences, using the known air flow rate (60 l h^{-1}) and oven-dry needle weights of the experimental plants.

24 Measurements of water balance

241 Transpiration measurements

Immediately after each series of CO_2 exchange measurements of an individual experimental plant in the laboratory (*i.e.* in the evening of both measuring days in the case of stressed plants), the plant was taken out of the gas exchange chamber and an average-sized shoot (representing the previous season's growth) was cut off. Exactly one minute after excision the weight of this shoot was determined using a balance with 0.1 mg accuracy and the determination of the transpiration decline curve was started, largely following the methods of FUKUDA (1935) and HYGEN (1951), modified by KOZLOWSKI and his coworkers (cf. SIWECKI and KOZLOWSKI 1973).

During the determination of the transpiration decline curve the excised shoot was kept on a small stand which was illuminated by a 500 W light bulb (similar to those used as light sources in measurements of photosynthesis), giving an irradiance (at the shoot level) of 70 W m^{-2} of PhAR, which roughly corresponded to an illuminance of 18 700 lx. A Petri dish, 91 mm in diameter and filled with water, was also placed on this stand and weighed at the beginning and at the end of each transpiration decline curve determination (so as to monitor potential evaporation rate). The evaporation from the Petri dish during these determinations did not vary very much; on an average the evaporative demand of the laboratory air surrounding the shoot was 1.38 mg cm^{-2} min^{-1}, with a standard deviation of the mean 0.012 mg cm^{-2} min^{-1}. Air temperature next to the shoot was about 33° C, ranging from 31 to 34° C.

After the initial weight determination of the excised shoot, successive determinations were made 5, 10, 20, 30, 40, 50, 60, 70, 80, 90, and 100 min after shoot excision. Final transpiration decline curves were based on oven-dry weights of the excised shoots; shoot weights were thus expressed as per cent of the dry weight as a function of time from excision.

242 Water saturation deficit measurements

Simultaneously with the start of transpiration measurements, the determinations of shoot water saturation deficit were started. After the removal of the experimental plant from the assimilation chamber, a shoot, similar to that used in transpiration measurements, was excised and weighed immediately. The shoot was then placed in a sealed beaker which contained enough water to immerse the basal end of the shoot. After being kept in the controlled environment of a growth chamber for about 24 h, the beaker was opened and the shoot weight at saturation was determined. The oven-dry weight of the same shoot was also determined. These determinations allowed calculations of shoot water deficit (*i.e.* the difference between fully turgid weight and fresh weight) expressed as a percentage of fully turgid water content (*i.e.* the difference between fully turgid weight and dry weight), according to the metod of calculation strongly recommended by BARRS (1968). For comparison, the dry weight or fully turgid weight was also used as the basis for these calculations.

25 Calculation procedure

In unstressed control plants the differences among clones were analysed for each gas exchange characteristic and temperature separately, using t-tests and variance analyses.

In two of the five blocks of unwatered experimental plants the soil water content was still well above the wilting point (as assessed using the oat seedlings) when the CO_2 exchange measurements were initiated. In these blocks (having 177 to 264 % soil water content) the CO_2 exchange or water balance did not significantly differ from that in the continuously watered blocks (cf. Figs. 22–23, 25–36). Therefore these two unwatered blocks were combined with

the continuously watered material, giving a total of seven replications (with four plants in each) in the treatment group of unstressed control plants.

The first block of plants measured (consisting of the first replication of unstressed control plants) was separately compared with the rest of the control plants in order to check the effect of an improvement in the sealing mechanism of the gas exchange chamber made at this stage. This comparison indicated that values of Γ and photorespiration rates in the first block distinctly differed from those of the rest of the control plants. Therefore in calculations of the variation in Γ or photorespiration among the clones, the first replication was omitted and only six replications were included. Since the technical improvement of the gas exchange chamber did not affect other gas exchange characteristics, all seven replications were used in the remaining comparisons among clones.

The stressed unwatered group of plants consisted of three blocks, or a total of 12 plants. Of these, 11 received the rewatering treatment (in one case this treatment was missing). Thus 12 unwatered and 11 rewatered plants were included when studying the effect of water stress and rewatering on CO_2 exchange (cf. Figs. 22–23, 25–36).

In comparisons among the three treatment groups (unstressed control plants, stressed unwatered and stressed rewatered plants), the most extreme cases of stress were excluded, so as to homogenise the stressed treatment groups. In comparisons of CO_2 exchange among the treatments, the three plants having a soil water content 36 % or lower and showing no net photosynthesis prior to rewatering (Figs. 22 and 23) as well as the plant lacking rewatering were excluded. Consequently eight plants were used in the stressed treatment groups. When analysing shoot water content, saturation deficit or transpiration in more detail, the plant having the lowest (1 %) soil water content and two plants with missing water blance measurements were excluded and thus nine plants from the stressed treatment groups were used in comparisons among the treatments.

In studying the effect of water stress and rewatering on CO_2 exchange or water balance (including transpiration), the four clones were combined. Consequently, the differences among clones were not studied. Within the unstressed control group of plants, however, the variation in CO_2 exchange or water balance was also analysed among the clones.

3 RESULTS

31 Preliminary experiment: CO_2 exchange under field conditions

Under field conditions, the response of the net photosynthetic rate of well watered plants to light and temperature varied somewhat among the four clones, as can be seen in Figs. 1–6. However, no clonal differences were statistically confirmed, since the photosynthetic rates varied considerably also among individual plants within each clone.

Light saturation was generally reached at total short-wave irradiances of about 100 $W m^{-2}$, the maximum irradiance observed

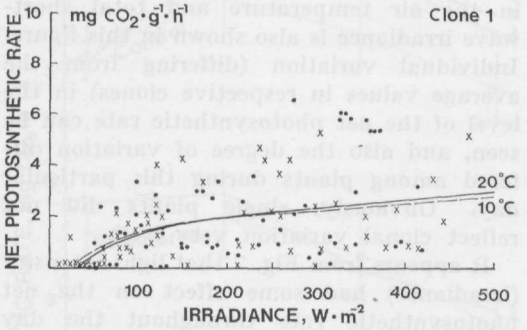

Fig. 1. Effect of irradiance on net photosynthetic rate under field conditions at 10° C (x) and 20° C (•) in clone 1.

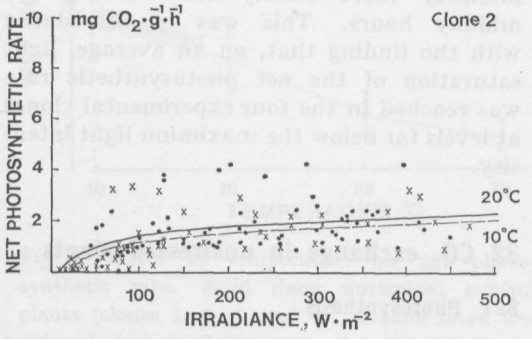

Fig. 2. Effect of irradiance on net photosynthetic rate under field conditions at 10° C (x) and 20° C (•) in clone 2.

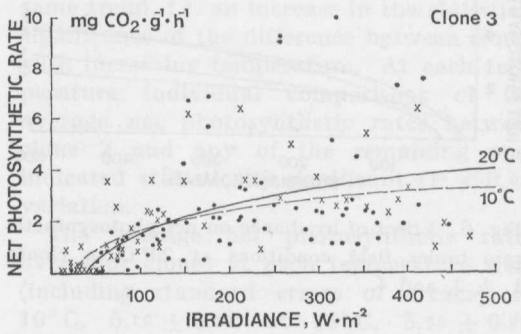

Fig. 3. Effect of irradiance on net photosynthetic rate under field conditions at 10° C (x) and 20° C (•) in clone 3.

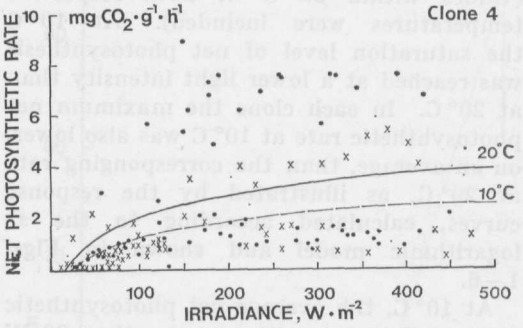

Fig. 4. Effect of irradiance on net photosynthetic rate under field conditions at 10° C (x) and 20° C (•) in clone 4.

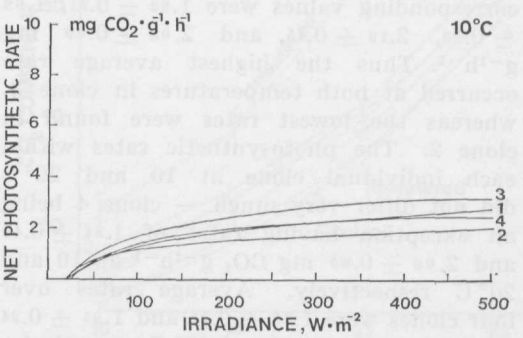

Fig. 5. Effect of irradiance on net photosynthetic rate under field conditions at 10° C in clones 1, 2, 3, and 4.

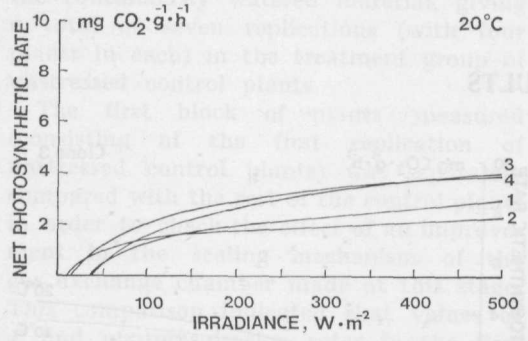

Fig. 6. Effect of irradiance on net photosynthetic rate under field conditions at 20° C in clones 1, 2, 3, and 4.

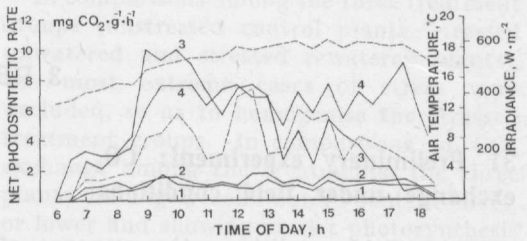

Fig. 7. The daily course of net photosynthetic rate in four plants, representing clones 1, 2, 3, and 4, in the field on 19 August 1972. The figure also shows the variation in air temperature (upper broken line) and irradiance (lower broken line).

being 520 W m^{-2}. The effect of temperature on net photosynthesis was studied by comparing the rates obtained at 10 and 20° C (values within 2.5° C of both respective temperatures were included). At 10° C the saturation level of net photosynthesis was reached at a lower light intensity than at 20° C. In each clone the maximum net photosynthetic rate at 10° C was also lower, on an average, than the corresponging rate at 20° C, as illustrated by the response curves, calculated according to the *x*-logarithmic model and shown in Figs. 1–6.

At 10° C, the average net photosynthetic rates at light intensities greater than 80 W m^{-2} were (including standard errors of the mean) 1.86 ± 0.40, 1.50 ± 0.41, 2.24 ± 0.45, and 1.54 ± 0.48 mg CO_2 $g^{-1}h^{-1}$ in clones 1, 2, 3, and 4 respectively. At 20° C, the corresponding values were 1.82 ± 0.51, 1.68 ± 0.29, 2.18 ± 0.45, and 2.08 ± 0.69 mg $g^{-1}h^{-1}$. Thus the highest average rate occurred at both temperatures in clone 3, whereas the lowest rates were found in clone 2. The photosynthetic rates within each individual clone at 10 and 20° C did not differ very much — clone 4 being an exception having rates of 1.54 ± 0.48 and 2.08 ± 0.69 mg CO_2 $g^{-1}h^{-1}$ at 10 and 20° C respectively. Average rates over four clones were 1.78 ± 0.21 and 1.94 ± 0.24 mg CO_2 $g^{-1}h^{-1}$ at 10 and 20° C respectively. As was the case with the differences mentioned above, this variation was not found to be statistically significant.

Fig. 7 shows the daily course of the net photosynthetic rates in four individual plants, each representing different clones, during a warm day with changing light conditions (19 August 1972). The variation in the air temperature and total short-wave irradiance is also shown in this figure. Individual variation (differing from the average values in respective clones) in the level of the net photosynthetic rate can be seen, and also the degree of variation differed among plants during this particular day. Obviously, single plants did not reflect clonal variation very well.

It appears from Fig. 7 that light intensity (irradiance) had some effect on the net photosynthetic rate throughout the day under the given experimental conditions. However, during the early morning and late afternoon hours net photosynthetic rates apparently followed the variation in light intensity more closely than during the midday hours. This was in accordance with the finding that, on an average, light saturation of the net photosynthetic rate was reached in the four experimental clones at levels far below the maximum light intensity.

32 CO_2 exchange in unstressed plants

321 Photosynthesis

Under laboratory conditions with constant light intensity, the net photosynthetic rate per unit of needle dry weight apparently varied among the four clones at each of the

four temperatures used (10, 16, 22, and 28° C). However, most of this variation was caused by the lowest photosynthetic rate in clone 2. No statistically significant variation was found among the remaining clones. The variation in clonal means of net photosynthetic rates with temperature as well as that in all unstressed (control) plants on an average is shown in Fig. 8, which also shows the average rates of stressed (unwatered and rewatered) plants.

The difference between clone 2 and the remaining three clones became successively more significant with increasing temperature (the variation among clonal means was significant at the $P < 0.001$ risk level, except at 10° C, where the risk level was $P < 0.01$). Comparisons between individual pairs of means, using t-tests, showed the same trend, *i.e.* an increase in the statistical significance of the difference between clones with increasing temperature. At each temperature individual comparisons of the average net photosynthetic rates between clone 2 and any of the remaining ones indicated statistically significant ($P < 0.05$) variation.

The average net photosynthetic rates over four clones at each temperature were (including standard errors of means), at 10° C, 5.16 ± 0.24; at 16° C, 5.66 ± 0.27; at 22° C, 5.34 ± 0.31; and at 28° C, 4.87 ± 0.29 mg CO_2 $g^{-1}h^{-1}$.

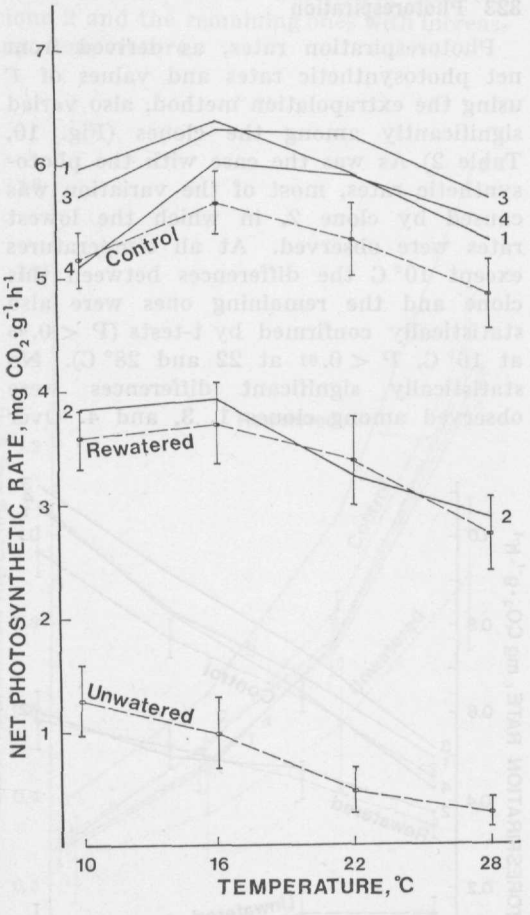

Fig. 8. Effect of temperature on net photosynthetic rate. Solid lines: unstressed control plants (clones 1, 2, 3, and 4). Broken lines: unstressed control plants, stressed rewatered plants, and stressed unwatered plants (rate means, with four clones combined; vertical bars indicate standard deviations of the means).

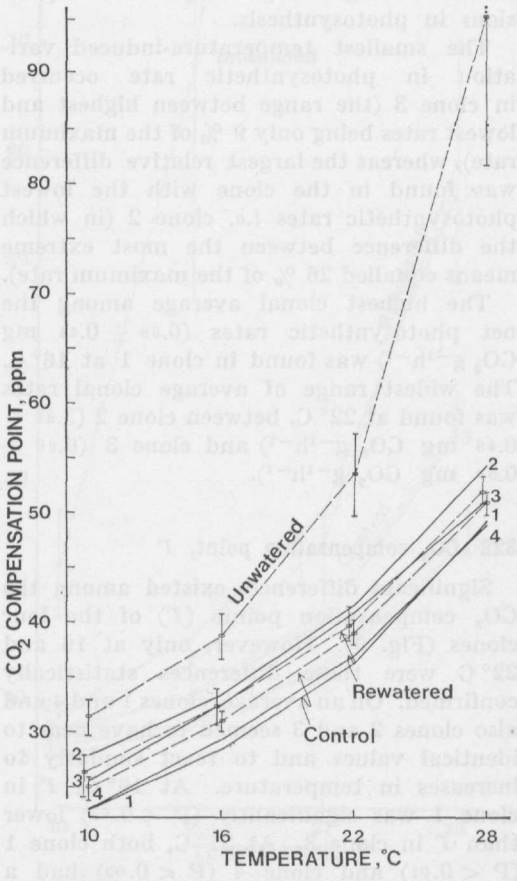

Fig. 9. Effect of temperature on CO_2 compensation point, Γ (cf. Fig. 8).

The temperature response of net photosynthesis showed a somewhat varying pattern in the four clones, although this feature was not analysed statistically. Maximum rates of photosynthesis were found at 16° C in all clones. However, interpolation of the response curves indicated that the real maximum rate was attained in clones 1 and 2 at temperatures somewhat lower than 16° C, *i.e.* at 14 or 15° C, whereas in clones 3 and 4 this maximum was at a temperature higher than 16° C *(i.e.* 17 or 18° C). The former clones also showed the lowest rates at 28° C, whereas in clone 3 the rates were equal at 10 and 28° C and in clone 4 the rate at 10° C was the lowest one. Thus, despite the difference in the general level of the photosynthetic rate, clones 1 and 2 showed similar trends in the temperature response, trends which also seemed to indicate a slight »high-temperature depression» in photosynthesis.

The smallest temperature-induced variation in photosynthetic rate occurred in clone 3 (the range between highest and lowest rates being only 9 % of the maximum rate), whereas the largest relative difference was found in the clone with the lowest photosynthetic rates *i.e.* clone 2 (in which the difference between the most extreme means equalled 26 % of the maximum rate).

The highest clonal average among the net photosynthetic rates (6.38 ± 0.44 mg CO_2 $g^{-1}h^{-1}$) was found in clone 1 at 16° C. The widest range of average clonal rates was found at 22° C, between clone 2 (3.27 ± 0.48 mg CO_2 $g^{-1}h^{-1}$) and clone 3 (6.26 ± 0.59 mg CO_2 $g^{-1}h^{-1}$).

322 CO_2 compensation point, Γ

Significant differences existed among the CO_2 compensation points (Γ) of the four clones (Fig. 9). However, only at 16 and 22° C were these differences statistically confirmed. On an average, clones 1 and 4 and also clones 2 and 3 seemed to have near to identical values and to react similarly to increases in temperature. At 16° C, Γ in clone 1 was significantly ($P < 0.05$) lower than Γ in clone 3. At 22° C, both clone 1 ($P < 0.01$) and clone 4 ($P < 0.05$) had a compensation point lower than that of clone 3. Throughout the temperature range, clone 2 had the highest Γ, but owing to the large scatter of individual observations in this clone, none of the comparisons between this and other clones indicated statistically significant differences.

The average values of Γ over four clones at each tempereature were, at 10° C, 24.8 ± 1.04; at 16° C, 30.9 ± 0.85; at 22° C, 38.9 ± 0.85; and at 28° C, 50.8 ± 1.00 ppm. Thus the temperature-induced increase in the CO_2 compensation point was distinct and, on an average, it showed a steeper trend at higher temperatures.

323 Photorespiration

Photorespiration rates, as derived from net photosynthetic rates and values of Γ using the extrapolation method, also varied significantly among the clones (Fig. 10, Table 2). As was the case with the photosynthetic rates, most of the variation was caused by clone 2, in which the lowest rates were observed. At all temperatures except 10° C the differences between this clone and the remaining ones were also statistically confirmed by t-tests ($P < 0.05$ at 16° C, $P < 0.01$ at 22 and 28° C). No statistically significant differences were observed among clones 1, 3, and 4. Over

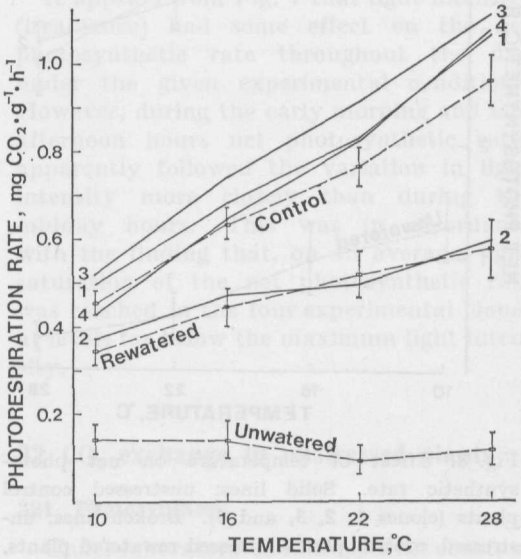

Fig. 10. Effect of temperature on photorespiration rate (cf. Fig. 8).

the temperature range used, however, the highest average photorespiration rates were measured in clone 3. This result was most apparent at 16 and 22° C.

The average photorespiration rates over four clones were, at 10° C, 0.45 ± 0.027; at 16° C, 0.64 ± 0.034; at 22° C, 0.77 ± 0.042; and at 28° C, 0.96 ± 0.056 mg CO_2 $g^{-1}h^{-1}$.

The increase in the photorespiration rate with temperature was more linear that that in Γ. In clone 2, however, the average elevation of Γ with temperature was smaller than in the remainig clones. This fact also contributed to the increasing significance level for the clonal differences between clone 2 and the remaining ones with increasing temperature.

324 Dark respiration

Dark respiration rates, as was the case with other CO_2 exchange parameters, also varied significantly among the clones (Fig. 11, Table 2). Most of the variation in these rates was caused by clone 3, which consistently, over the entire temperature range, exhibited the highest rates. No statistically significant differences were found among the remaining clones.

The dark respiration rates in clone 3 at 10° C differed more significantly ($P < 0.01$) from those of clones 1, 2, or 4 than at other temperatures. At 16° C, the difference between clones 3 and 1 as well as that between clones 3 and 4 were statistically confirmed ($P < 0.05$). At 22° C, the dark respiration rate in clone 3 also distinctly

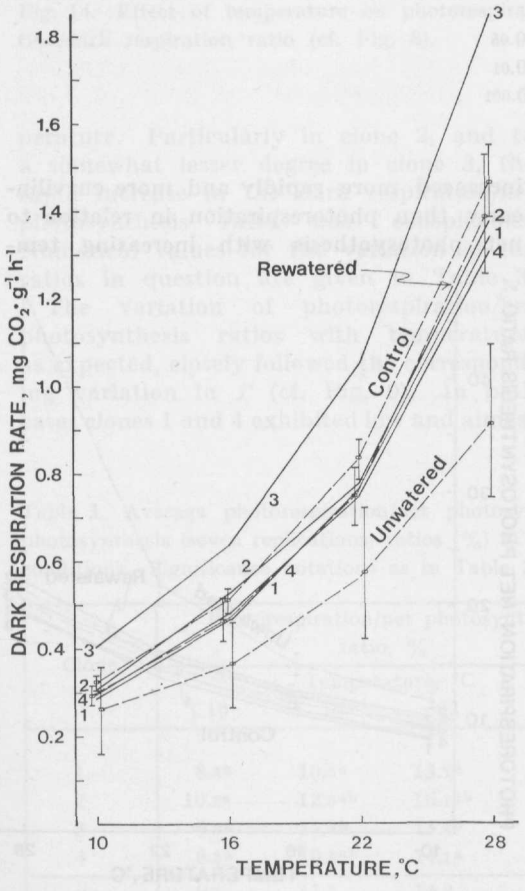

Fig. 11. Effect of temperature on dark respiration rate (cf. Fig. 8).

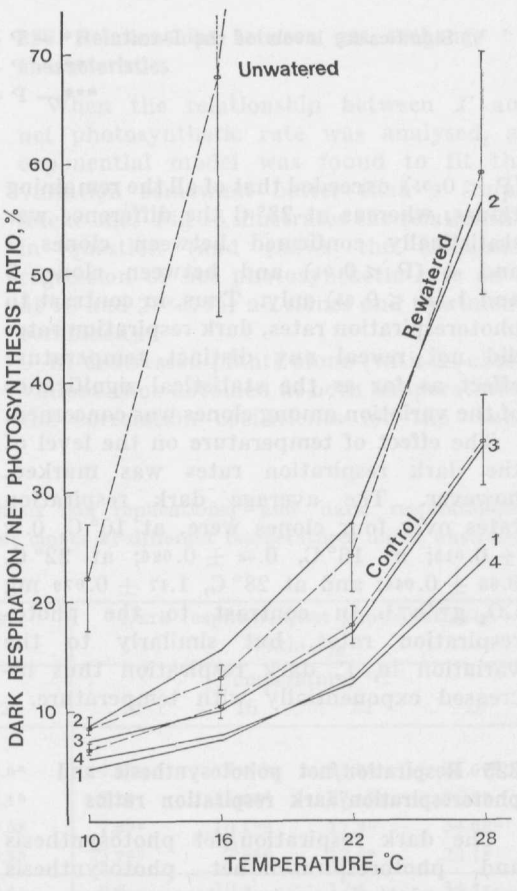

Fig. 12. Effect of temperature on dark respiration/net photosynthesis ratio (cf. Fig. 8).

Table 2. Average photorespiration and dark respiration rates (mg CO_2 $g^{-1}h^{-1}$) and the photorespiration/dark respiration ratios (%) in four clour clones at different temperatures under unstressed conditions (six replications in photorespiration rates and photorespiration/dark respiration ratios, seven replications in dark respiration rates). Statistically nonsignificant clonal differences at each temperature (as determined by t-tests between pairs of means) are indicated with the same letter index; if no identical indices are shown the difference between two clonal means is significant at the $P < 0.05$ or lower risk level[1]).

Clone	Photorespiration rate mg CO_2 $g^{-1}h^{-1}$ (dry wt.)				Dark respiration rate mg CO_2 $g^{-1}h^{-1}$ (dry wt.)				Photorespiration/dark respiration ratio, %			
	Temperature, °C				Temperature, °C				Temperature, °C			
	10	16	22	28	10	16	22	28	10	16	22	28
1	0.50^a	0.68^b	0.83^b	1.07^b	0.29^a	0.46^a	0.76^a	1.34^a	188^b	167^b	115^c	84^b
2	0.37^a	0.47^a	0.50^a	0.60^a	0.31^a	0.52^{ab}	0.77^a	1.38^{ab}	123^a	95^a	66^a	47^a
3	0.52^a	0.74^b	0.91^b	1.11^b	0.40^b	0.63^b	1.05^b	1.84^b	135^{ab}	121^{ab}	90^{ab}	64^{ab}
4	0.43^a	0.65^b	0.82^b	1.07^b	0.29^a	0.47^a	0.74^a	1.31^a	160^{ab}	150^b	122^{bc}	88^b
$\bar{x}$	0.45	0.64	0.77	0.96	0.32	0.52	0.83	1.47	151	133	98	71
$s_{\bar{x}}$	0.027	0.034	0.042	0.056	0.015	0.026	0.044	0.079	9.9	8.8	6.8	5.5
F	1.78	4.14*	10.51***	10.58***	5.00**	2.77*	3.25*	3.11*	2.55	4.82*	5.61**	4.20*

[1]) Significance levels of the F-test: * — $P < 0.05$
** — $P < 0.01$
*** — $P < 0.001$

($P < 0.05$) exceeded that of all the remaining clones, whereas at 28° C the difference was statistically confirmed between clones 3 and 4 ($P < 0.01$) and between clones 3 and 1 ($P < 0.05$) only. Thus, in contrast to photorespiration rates, dark respiration rates did not reveal any distinct temperature effect as far as the statistical significance of the variation among clones was concerned.

The effect of temperature on the level of the dark respiration rates was marked, however. The average dark respiration rates over four clones were, at 10° C, 0.32 ± 0.015; at 16° C, 0.52 ± 0.026; at 22° C, 0.83 ± 0.044; and at 28° C, 1.47 ± 0.079 mg CO_2 $g^{-1}h^{-1}$. In contrast to the photorespiration rates, but similarly to the variation in Γ, dark respiration thus increased exponentially with temperature.

325 Respiration/net pohotosynthesis and photorespiration/dark respiration ratios

The dark respiration/net photosynthesis and photorespiration/net photosynthesis ratios plotted against temperature are presented in Figs. 12 and 13. It can also be seen from these figures that dark respiration increased more rapidly and more curvilinearly than photorespiration in relation to net photosynthesis with increasing tem-

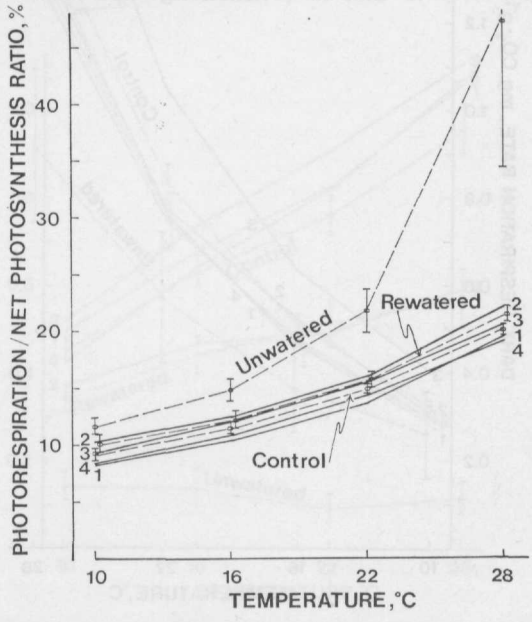

Fig. 13. Effect of temperature on photorespiration/net photosynthesis ratio (cf. Fig. 8).

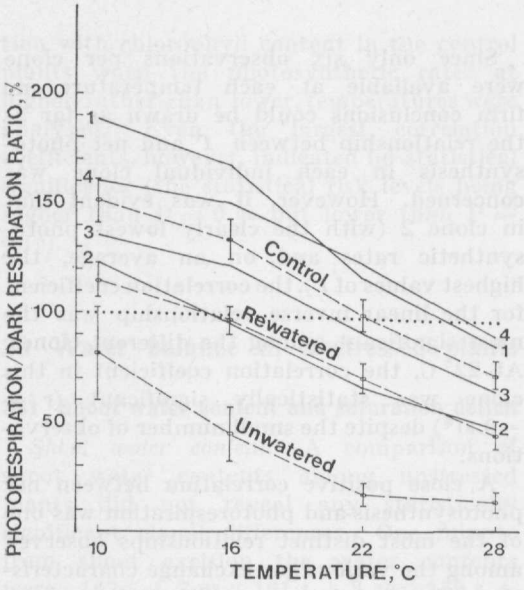

Fig. 14. Effect of temperature on photorespiration/dark respiration ratio (cf. Fig. 8).

perature. Particularly in clone 2, and to a somewhat lesser degree in clone 3, the rapid increase in the dark respiration/net photosynthesis ratio was conspicuous. Numerical values for the variation of the ratios in question are given in Table 3.

The variation of photorespiration/net photosynthesis ratios with temperature, as expected, closely followed the corresponding variation in Γ (cf. Fig. 9). In both cases clones 1 and 4 exhibited low and almost identical values, whereas clones 2 and 3 showed high but again very similar values.

As the temperature increased, dark respiration rates increased more than photorespiration rates. As a result, the photorespiration/dark respiration ratios decreased with increasing temperature. Fig. 14 and Table 2 summarise this variation.

As can be seen in Fig. 14, the decrease in the photorespiration/dark respiration ratios was almost linear in each clone. On an average, the photorespiration/dark respiration ratio was lowest in clone 2 and highest in clone 1 (at 10 and 16° C) or clone 4 (at 22 and 28° C).

Fig. 14 also indicates that dark respiration equalled photorespiration, on an average, at 14° C in clone 2, at 20° C in clone 3, and at 24 or 25° C in clones 1 and 4.

326 Relationships between gas exchange characteristics

When the relationship between Γ and net photosynthetic rate was analysed, an exponential model was found to fit this variation somewhat better than a simple linear one. Fig 15 illustrates the relationship in question (and shows the calculated regression of net photosynthetic rate on Γ at 10 and 28° C for all clones and treatments combined).

In unstressed plants alone (with 24 observations thus obtained at both temperatures), the correlation coefficients for the trans-

Table 3. Average photorespiration/net photosynthesis (six replications) and dark respiration/net photosynthesis (seven replications) ratios (%) in four clones at different temperatures under unstressed conditions. Significance notations as in Table 2.

Clone	Photorespiration/net photosynthesis ratio, %				Dark respiration/net photosynthesis ratio, %			
	Temperature, °C				Temperature, °C			
	10	16	22	28	10	16	22	28
1	8.3^{a}	10.5^{a}	13.7^{a}	19.6^{a}	4.8^{a}	7.4^{ab}	13.0^{a}	25.0^{ab}
2	10.3^{a}	12.5^{ab}	16.1^{ab}	22.1^{a}	8.7^{c}	15.6^{cd}	27.1^{b}	56.3^{c}
3	9.3^{a}	12.2^{b}	15.8^{b}	20.5^{a}	7.3^{bc}	10.1^{bd}	17.2^{b}	34.0^{bc}
4	8.3^{a}	10.8^{ab}	14.1^{a}	19.5^{a}	5.7^{ab}	7.8^{ac}	12.6^{a}	23.7^{a}
$\bar{x}$	9.1	11.5	14.9	20.4	6.6	10.2	17.5	34.7
$s_{\bar{x}}$	0.42	0.35	0.37	0.48	0.45	1.09	1.71	4.00
F	1.35	2.30	3.34*	1.68	5.62**	3.89*	6.08**	5.26**

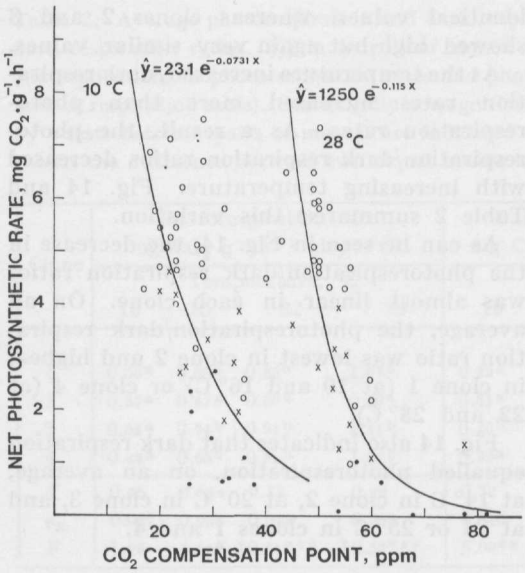

Fig. 15. Relationship between CO_2 compensation point (Γ) and net photosynthetic rate at 10° C and 28° C in unstressed control plants (o), stressed rewatered plants (x), and stressed unwatered plants (•), with four clones combined. Regression curves and equations include all clones and treatments and they are based on 43 plants at 10° C ($r = -0.59^{***}$) and 40 plants at 28° C ($r = -0.80^{***}$).

formed curvilinear models (not shown in Fig. 15) equalled -0.51^{*} and -0.62^{**}at 10 and 28° C respectively[1]). This indicated that there was a statistically significant inverse relationship between the two variables at both temperatures, with a somewhat higher significance level at the higher temperature. A non-transformed linear model yielded slightly lower but still significant correlation coefficients (-0.42^{*} and -0.61^{**} at 10 and 28° C respectively) between the two variables. A more linear relationship thus existed at 28° C than at 10° C; this is also shown by the nearly identical correlation coefficients in the two models at 28° C as compared with the quite different ones obtained at 10 °C.

[1]) Significance levels of r:
* — $P < 0.05$
** — $P < 0.01$
*** — $P < 0.001$

Since only six observations per clone were available at each temperature, no firm conclusions could be drawn as far as the relationship between Γ and net photosynthesis in each individual clone was concerned. However, it was evident that in clone 2 (with the clearly lowest photosynthetic rates and, on an average, the highest values of Γ), the correlation coefficient for the linear inverse relationship was the most significant among the different clones. At 22° C, the correlation coefficient in this clone was statistically significant ($r = -0.81^{*}$) despite the small number of observations.

A close positive correlation between net photosynthesis and photorespiration was one of the most distinct relationships observed among the various gas exchange characteristics. The correlation coefficient for a non-transformed linear model (all clones combined) varied from 0.74^{***} (at 10° C) to 0.95^{***} (at 28° C). Somewhat higher correlation coefficients (from 0.78^{***} at 10° C to 0.97^{***} at 28° C) were achieved when values of »total photosynthetic rate», *i.e.* net photosynthetic rates summed with the photorespiration rates, were used instead of net photosynthetic rates in the calculation. In contrast to this, no statistically significant correlation was found between the photosynthetic and dark respiration rates.

327 Chlorophyll content and its effect on gas exchange

The highest chlorophyll *a*, chlorophyll *b*, and total chlorophyll contents were found in clone 2, whereas the lowest values were observed in clone 4. The differences between these clones were also statistically significant ($P < 0.01$). Average contents over four clones, seven replications in each, were 4.31 ± 0.23, 5.30 ± 0.31, and 9.61 ± 0.53 mg g^{-1} (dry wt.) for chlorophyll *a*, chlorophyll *b*, and total chlorophyll content respectively. These mean values indicated an unexpected 1: 1.2 ratio between chlorophylls *a* and *b*.

Correlation analyses revealed that no clear relationships existed between chlorophyll content and gas exchange. On an average, the net photosynthetic rate showed a somewhat more distinct (inverse) correla-

tion with chlorophyll content in the control plants when the photosyhthetic rates at higher, rather than lower, temperatures were analysed. Even the largest correlation coefficients, however, indicated no statistical significance (the statistical risk levels being higher than $P = 0.05$ but lower than $P = 0.10$).

33 Water balance in unstressed plants

331 Shoot water content and saturation deficit

Shoot water content. A comparison of shoot water contents among unstressed plants did not reveal any statistically significant clonal differences. One minute from shoot excision the water contents were 167.5 ± 7.02, 161.7 ± 3.90, 169.3 ± 2.54, and 162.95 ± 4.39 % of dry weight in clones 1, 2, 3, and 4 respectively (165.4 ± 2.32 % being the average over four clones). Thus the highest water content was observed in clone 3, and the lowest one in clone 2.

Saturation deficit. No statistically significant clonal variation was found in the water saturation deficits of the unstressed plants. Average deficits, calculated on the basis of the amount of water at full turgor, were 16.5 ± 1.75, 16.1 ± 1.21, 17.6 ± 1.37, and 16.9 ± 1.73 % in clones, 1, 2, 3, and 4 respectively. The corresponding values calculated on a dry weight basis were 35.4 ± 5.76, 31.4 ± 2.62, 38.3 ± 4.63, and 34.2 ± 4.31 % respectively. Thus, on an average, the largest deficit was observed in clone 3, which also had the highest shoot water content, and the smallest one in clone 2, in which the lowest shoot water content was also observed.

A similar positive relationsip was also found in anlyses among individual observations of shoot water content and corresponding saturation deficits. When all the clones were combined, statistically significant correlation coefficients were found for this relationship. Interestingly, the most significant ($P < 0.01$) coefficient was found when the saturation deficit was calculated on the basis of shoot dry weight, and somewhat lower ($P < 0.05$) coefficients were observed when shoot fresh weight or shoot weight at full turgor were used in these calculations. The correlation coefficient did not reach a statistically significant level when the saturation deficit was calculated from water weight at full turgor.

As judged from analyses of variance, the greatest (although statistically nonsignificant) differences in saturation deficits among the clones were obtained using shoot dry weight as the basis. Somewhat greater differences were obtained using shoot fresh weight as a basis than using the amount of water at full turgor in these calculations, but the significance level did not in this case reach that found in the dry-weight-based calculations.

332 Transpiration

Fig. 16 shows the decrease in shoot water content in relation to the time after shoot excision in the individual plants from one block (No. 7) representing unstressed control plants. This graph thus shows an example of the transpiration decline curves obtained by these determinations. The average transpiration decline curves of different

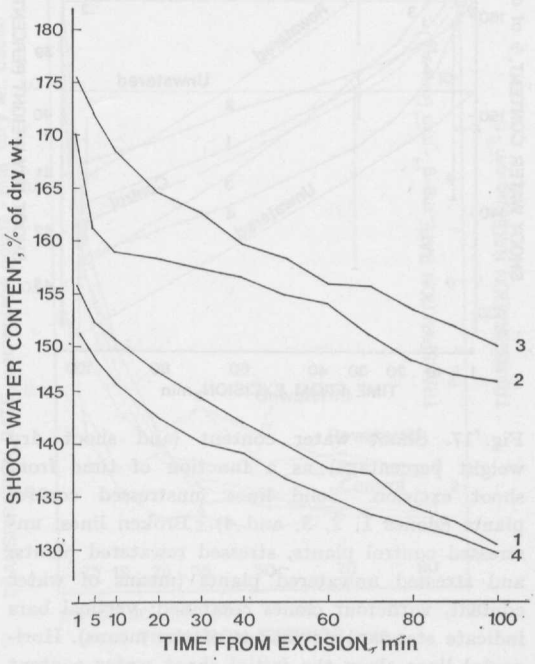

Fig. 16. Shoot water content as a function of time from shoot excision in four plants, representing clones 1, 2, 3, and 4.

clones (as well as those of each treatment, *i.e.* unstressed or control plants, unwatered plants, and rewatered plants) are shown in Fig. 17.

The curves shown in Fig. 17 are identical with those in Figs. 18 and 19, which, however, illustrate the relative changes from an equal starting point. Omitting the (statistically nonsignificant) differences in initial water content, Figs. 18 and 19 show the variation in curve shape, or transpiration rate, with time from excision. Fig. 18 shows the shoot water loss as a function of time from excision and calculated as percentage of shoot dry weight, whereas Fig. 19 demonstrates the same variation using water weight at full turgor as a basis.

Figs. 20 and 21 show the variation in actual transpiration rates with time from excision, expressed as percentage points of shoot dry weight or water weight at full turgor respectively. Percentage points, calculated from shoot dry weight, also equal the unit 10 mg H_2O g^{-1} min^{-1}, as indicated in Fig. 20. The third scale on the y axis of this figure shows the transpiration rate per unit of needle area. Needle area was calculated using the actual needle

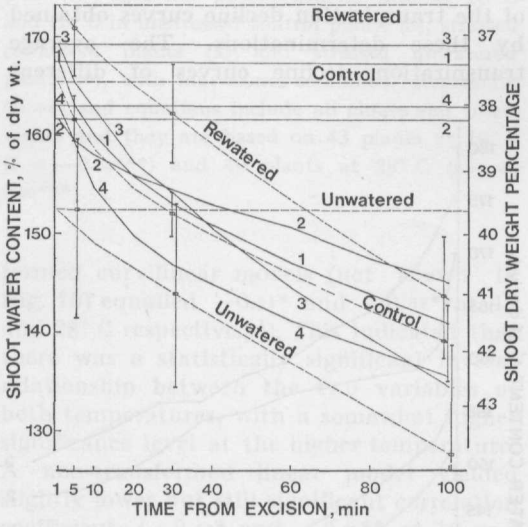

Fig. 17. Shoot water content (and shoot dry weight percentage) as a function of time from shoot excision. Solid lines: unstressed control plants (clones 1, 2, 3, and 4). Broken lines: unstressed control plants, stressed rewatered plants, and stressed unwatered plants (means of water content, with four clones combined; vertical bars indicate standard deviations of the means). Horizontal lines show the initial shoot water content for each clone and treatment respectively. Calculations are based on those times indicated on the x-axis.

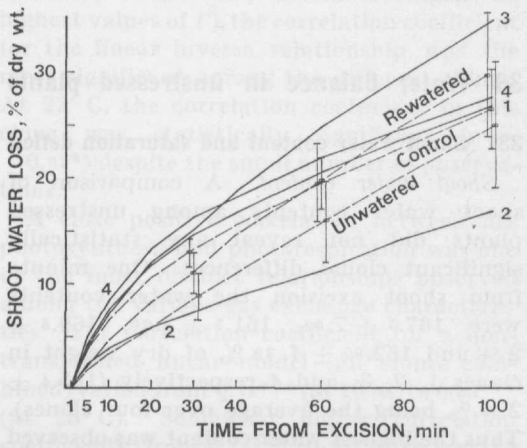

Fig. 18. Shoot water loss (as percentage of dry weight) as a function of time from shoot excision. Solid lines: unstressed control plants (clones 1, 2, 3, and 4). Broken lines: unstressed control plants, stressed rewatered plants, and stressed unwatered plants (means of water loss, with four clones combined; vertical bars indicate standard deviations of the means). Calculations are based on those times indicated on the x-axis.

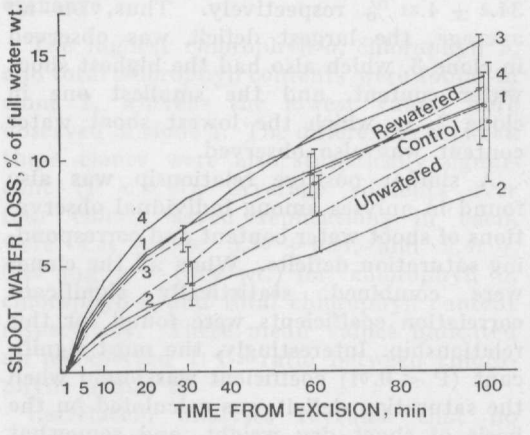

Fig. 19. Shoot water loss (as percentage of the amount of water at full turgidity) as a function of time from shoot excision (cf. Fig. 18).

weight/shoot weight ratios of the present material and an average needle area/needle dry weight ratio of 75 $cm^2\ g^{-1}$ reported in the literature for similar material (Šesták *et al.* 1971 b, p. 31; Beadle and Jarvis 1977, Lewandowska *et al.* 1977).

Transpiration losses were analysed in more detail using values obtained 5, 10, 20, 30, 40, 60, 80, and 100 min after shoot excision. Individual pairs of clonal means were also tested using t-tests. The two calculation methods, based on dry weight or water weight at full turgor, gave results with similar trends, although the weight of water at full turgor as a basis indicated statistically somewhat more significant differences among or between clones than did dry-weight-based calculations.

As can be seen in Figs. 18 and 19, the transpiration loss after excision was smaller in clone 2 than in the remaining clones. The difference between clones 2 and 4 was statistically significant ($P < 0.05$) in all cases except for the value 5 min from excision, based on dry weight. The clearest differences ($P < 0.001$) were found between these clones 20 to 60 min from excision. Statistically significant differences were also established between clones 2 and 1, 10 to 80 min from excision. The clearest differences ($P < 0.01$) were observed 20 to 60 min after shoot excision (full-turgor basis) also in this case. The greatest water losses were observed in clone 3 (40 to 100 min from excision when based on dry weight and 60 to 100 min from excision based on water weight at full turgor). Owing to the large error variation in this clone, the differences between clone 3 and the remaining ones were not confirmed statistically, however.

Figs. 17—21 illustrate some general differences in the transpiration pattern among the clones. For instance, a comparison of clonal curves to the average change in transpiration with time in unstressed plants indicated that curve shapes, or actual transpiration *rates*, were close to average in clones 1 and 4. The latter clone, however, had a lower initial water content and therefore also generally a lower water content throughout the observation period after shoot excision (cf. Fig. 17).

Clone 2, on the other hand, reached the final slow phase of transpiration earlier than the remaining clones, which resulted in a higher than average water content (and smaller than average water loss) at the end of the 100 min observation period. Nevertheless, the final transpiration rate in this clone remained very close to the average rate, as seen in Figs. 20 and 21. In contrast, clone 3, which showed the greatest water losses after shoot excision, clearly had the highest transpiration rates not only at the end of the observation period but already 30 min from excision. Extrapolation of the curves shown in Figs. 20 and 21 to zero time suggested transpiration rates in intact shoots equalling 0.4 percentage points min^{-1} in clone 2, *vs.* 0.6 to 0.7 percentage points min^{-1} (calculated from water weight at full turgor) in the remaining clones; these values correspond to 7 mg $H_2O\ g^{-1}\ min^{-1}$ in clone 2, *vs.* 11 to 13 mg $H_2O\ m^{-1}\ m^{-1}$ in the remaining ones. The final transpiration rate at the end of the 100 min observation period was about 0.11 percentage points min^{-1} (full-turgor

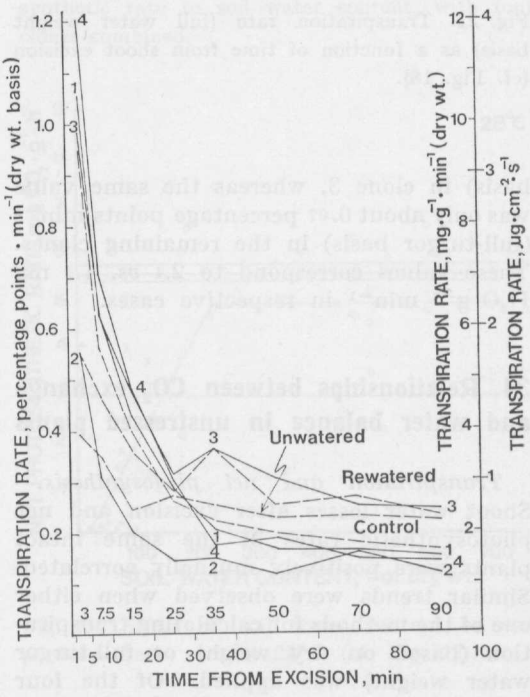

Fig. 20. Transpiration rate (dry weight and needle area basis) as a function of time from shoot excision (cf. Fig. 18).

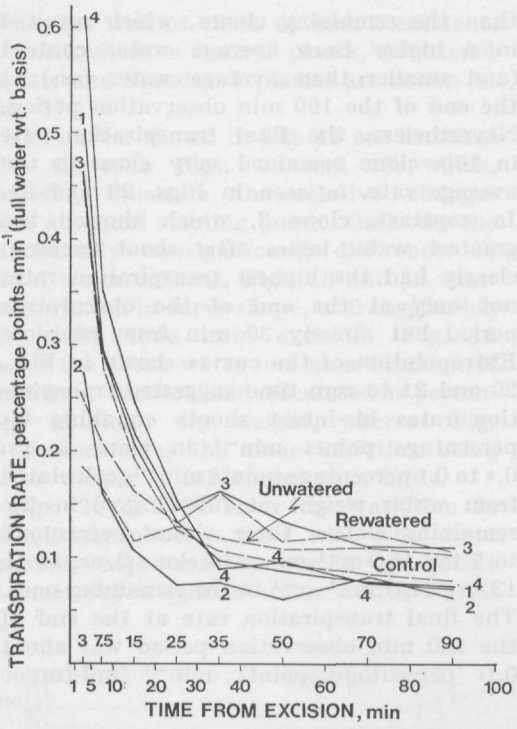

Fig. 21. Transpiration rate (full water weight basis) as a function of time from shoot excision (cf. Fig. 18).

basis) in clone 3, whereas the same value was only about 0.07 percentage points min^{-1} (full-turgor basis) in the remaining clones. These values correspond to 2.4 *vs.* 1.5 mg H_2O g^{-1} min^{-1} in respective cases.

34 Relationships between CO_2 exchange and water balance in unstressed plants

Transpiration and net photosynthesis. Shoot water losses after excision and net photosynthetic rates of the same intact plants were positively mutually correlated. Similar trends were observed when either one of the methods for calculating transpiration (based on dry weight or full-turgor water weight) was applied. Of the four different temperatures used in the photosynthesis measurements, the highest correlation coefficients were obtained at 22° C, followed by 28, 16 and 10° C. Of the different observation periods over which weight loss determinations were made, the values obtained 10 min from shoot excision were more closely correlated with photosynthetic rates than those obtained 5 or 30 min after excision. No statistically significant correlation coefficients were found for the relationship between net photosynthetic rate and water loss 60 or 100 min after excision. The highest observed correlation coefficient (with all clones combined), $r = 0.63^{***}$, was found in the relationship between the water loss 10 min from excision (full-turgor water basis) and the net photosynthetic rate at 22° C.

Individual clones showed some variation in the relationship in question, but the small number of observations, seven per clone, rendered the statistical confirmation of the clonal trends impossible.

Transpiration and CO_2 compensation point. Transpiration losses from excised shoots and Γ values appeared to be inversely mutually correlated when the whole material was combined. The transpiration loss 10 min after excision and Γ at 22° C showed the most significant correlation coefficient for this relationship ($r = -0.42^{*}$). Less distinct correlations were observed when transpiration losses after 5 min or periods longer than 10 min were analysed.

Transpiration and photorespiration. The relationships found between transpiration losses of excised shoots and photorespiration rates were similar to those found between transpiration losses and net photosynthetic rates. Statistically significant ($P < 0.05$) positive correlation coefficients were found for correlations between the 10 min transpiration loss and photorespiration rate at 22 or 28° C, as well as between the 30 or 5 min transpiration losses and photorespiration rates at 22 or 28° C.

Transpiration and dark respiration. In contrast to the relationship between transpiration loss of excised shoots and photorespiration, no statistically significant correlations were found between transpiration and dark respiration measurements. However, the results suggested somewhat closer (positive) correlations for this relationship in the cases when 100 or 60 min transpiration measurements were used instead of those made 30, 10, or 5 min from excision.

Saturation deficit and photosynthesis. No clear correlation was found between water saturation deficit and net photosynthetic rate in unstressed plants when all clones were combined, although, on an average, the relationship was slightly positive. One peculiar feature, however, was the contrasting trends in this relationship in different clones. For instance, the correlation in question was positive in clones 1 and 2, and despite the small amount of data (seven replications), statistically significant as far as clone 1 was concerned. The highest correlation coefficient, r = 0.92**, was found in the relationship between saturation deficit (with the amount of water at full turgor as a basis) and net photosynthetic rate at 22° C; all such correlations including net photosynthetic rates at other temperatures were also statistically significant ($P < 0.01$) in this clone. On the other hand, slight (nonsignificant) negative correlations seemed to exist between saturation deficits and net photosynthetic rates in clones 3 and 4.

Saturation deficit and other CO_2 exchange characteristic. An inverse relationship existed between water saturation deficit and Γ in some cases. For instance, statistically significant correlation coefficients ($P < 0.05$) were observed between the deficit (calculated as a percentage from water amount at full turgor) and Γ at 28° C (with all clones combined). On the other hand, a slight (nonsignificant) positive relationship seemed to exist between the deficit and photorespiration rates as well as between the deficit and dark respiration rates. The photorespiration rate at 22° C and dark respiration rate at 28° C were the rates most closely related to saturation deficit.

35 CO_2 exchange in stressed plants

351 Photosynthesis

The response of net photosynthetic rate to soil moisture was distinct, as can be seen in Figs. 22—24. With increasing soil water content, photosynthesis increased linearly and reached the average control level at a soil water content of about 200 % of dry weight. Individual observations (shown in Figs. 22 and 23 at 10 and 28° C respectively) indicated that net photosynthesis could no longer be detected when the soil water content was lower than about 40 %.

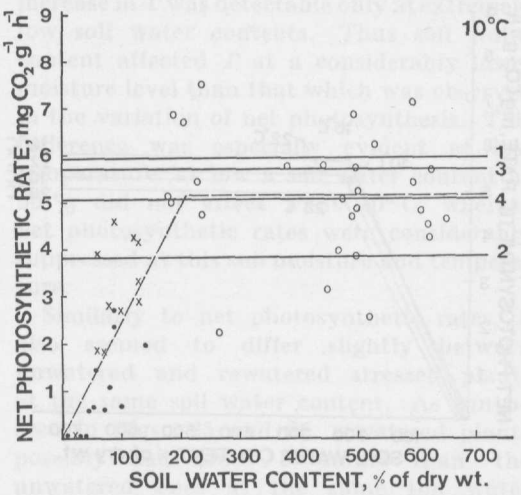

Fig. 22. Effect of soil water content on net photosynthetic rate at 10° C in unstressed control plants (o), stressed rewatered plants (x), and stressed unwatered plants (•), with four clones combined. Solid lines: rate means in unstressed control plants in clones 1, 2, 3, and 4 respectively. Broken line: average response of net photosynthetic rate to soil water content, with four clones combined.

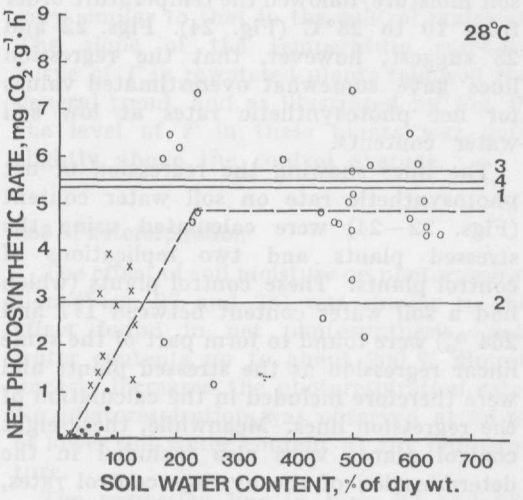

Fig. 23. Effect of soil water content on net photosynthetic rate at 28° C (cf. Fig. 22).

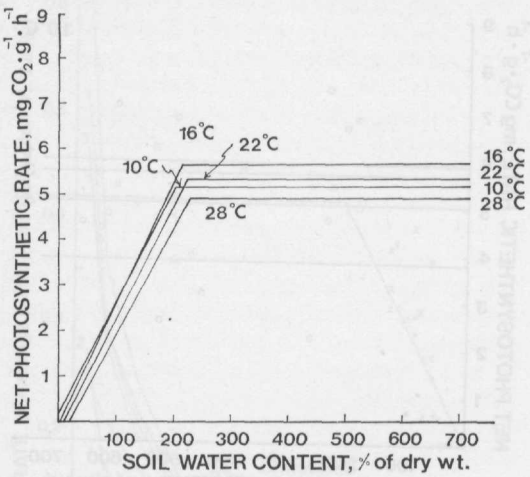

Fig. 24. Average response of net photosynthetic rate to soil water content, with four clones combined, at 10, 16, 22, and 28° C.

On the x axis, as well as on the control level of net photosynthesis when projected to the x axis, the intersection points of the different regression lines (showing the increase in photosynthetic rate with increasing soil moisture) followed the temperature order from 10 to 28° C (Fig. 24). Figs. 22 and 23 suggest, however, that the regression lines gave somewhat overestimated values for net photosynthetic rates at low soil water contents.

The lines showing the regression of net photosynthetic rate on soil water content (Figs. 22—24) were calculated using the stressed plants and two replications of control plants. These control plants (which had a soil water content between 177 and 264 %) were found to form part of the same linear regression as the stressed plants and were therefore included in the calculation of the regression lines. Meanwhile, these eight control plants were also included in the determination of the average control rates, indicated by horizontal lines in the figures.

Rewatered stressed plants generally seemed to have higher photosynthetic rates than unwatered plants at the same soil water content. This feature was most obvious at the highest temperature (28° C) where only one out of eight unwatered plants in the soil water content range 40 to 100 % reached the net photosynthetic rate of 1 mg CO_2 $g^{-1}h^{-1}$; among the six rewatered plants at this soil moisture the net photosynthetic rate varied between 1 and 4 mg CO_2 $g^{-1}h^{-1}$ (Fig. 23). One stressed rewatered plant, at 25 % soil water content, showed, however, no net photosynthesis at any temperature.

The temperature response of net photosynthesis in stressed plants also differed from that of the control plants, as shown in Fig. 8. Those stressed plants with a soil water content of 41 to 94 % (68 % on an average) under unwatered conditions are included in this figure (thus excluding those three plants in which no net photosynthetic rate was detected under unwatered conditions and one »missing plot» among the stressed plants). After rewatering, soil moisture in stressed plants included in Fig. 8 ranged from 69 to 127 % and averaged 103 % of dry weight (by comparison, soil moisture in control plants ranged from 177 to 649 % and was 438 % on an average).

Maximum photosynthetic rate in unwatered plants was observed at the lowest temperature (10° C), whereas rewatered plants resembled control plants in that the maximum rate was observed at 16° C. The interpolated highest net photosynthetic rate in rewatered plants was found between 16 and 10° C (at about 14° C).

The level of the net photosynthetic rate in stressed plants after rewatering remained, on an average, far below the level found in the control plants. As mentioned earlier, the four clones differed considerably as far as their levels of photosynthetic rate under well-watered conditions were concerned. Among the control plants those from clone 2 did not differ much from rewatered stressed plants in this respect. The decrease in the net photosynthetic rate in rewatered stressed plants, induced by high temperature, was also similar to that found in control plants representing clone 2 (Fig. 8).

Chlorophyll content was not affected by water stress. Average contents were almost identical in stressed and control plants as far as chlorophyll *a*, chlorophyll *b*, or total chlorophyll was concerned.

352 CO_2 compensation point, Γ

Soil water content had a clear effect also on the CO_2 compensation point, Γ (Figs. 25 and 26). The greatest deviations from the control level of Γ were found in plants growing at extremely low soil moisture. Particularly at low temperature a distinct increase in Γ was detectable only at extremely low soil water contents. Thus soil water content affected Γ at a considerably lower moisture level than that which was observed in the variation of net photosynthesis. This difference was especially evident at low temperature: as low a soil water content as 50 % did not affect Γ at 10° C, whereas net photosynthetic rates were considerably suppressed at this soil moisture and temperature.

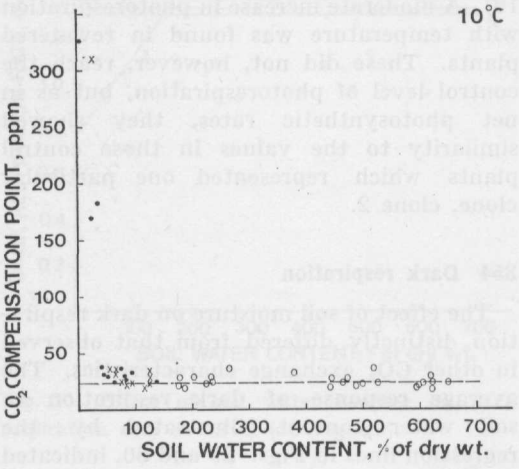

Fig. 25. Effect of soil water content on CO_2 compensation point (Γ) at 10° C in unstressed control plants (o), stressed rewatered plants (x), and stressed unwatered plants (•), with four clones combined. Broken line: mean of CO_2 compensation point in unstressed control plants, with four clones combined.

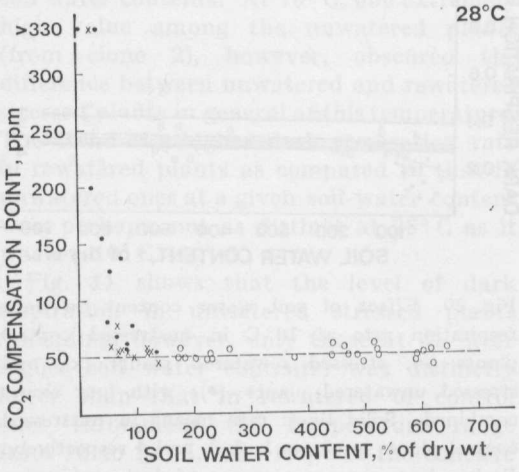

Fig. 26. Effect of soil water content on CO_2 compensation point (Γ) at 28° C (cf. Fig. 25).

Similarly to net photosynthetic rates, Γ also seemed to differ slightly between unwatered and rewatered stressed plants at the same soil water content. As can be seen in Figs. 25 and 26, rewatered plants possibly had lower Γ values than the unwatered ones at the same soil water content.

As with net photosynthetic rates, the variation in Γ with temperature was studied among the stressed plants at the level of 41 % or higher soil water contents only (Fig. 9). The difference between average Γ in unwatered and control plants was distinct (and statistically significant, $P < 0.01$) at 10° C and increased with increasing temperature. On the other hand, rewatered plants showed a variation in Γ which was very similar to that in the control material. The slope of the temperature response curve of Γ in rewatered plants followed the general trend, and as illustrated by Fig. 9, the level of Γ in these plants was only slightly above the control average.

353 Photorespiration

The effect of soil moisture on photorespiration (Figs. 27 and 28) was similar to the effect found in net photosynthesis. Soil water contents up to about 200 % almost linearly increased the photorespiration rate. No photorespiration was observed at 36 % or lower soil water content at any temperature.

The regression line in Figs. 27 and 28, showing the response of photorespiration to soil water content, reached the average control level of photorespiration at 190 % soil moisture at 10° C and at 225 % soil moisture at 28° C. Analogously with the regression of photosynthesis, the response line was also calculated using the control

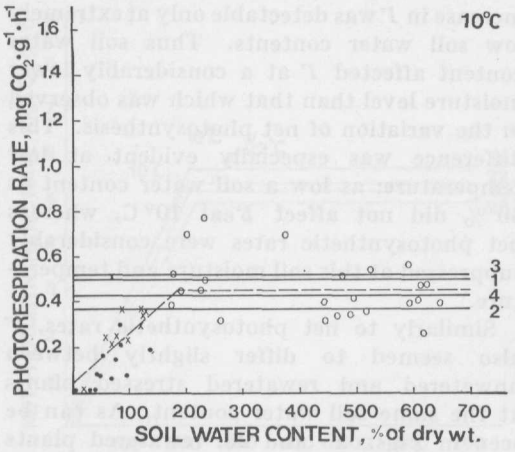

Fig. 27. Effect of soil water content on photorespiration rate at 10° C in unstressed control plants (o), stressed rewatered plants (x), and stressed unwaterd plants (•), with four clones combined. Solid lines: rate means in unstressed control plants in clones 1, 2, 3, and 4 respectively. Broken line: average response of photorespiration rate to soil water content, with four clones combined.

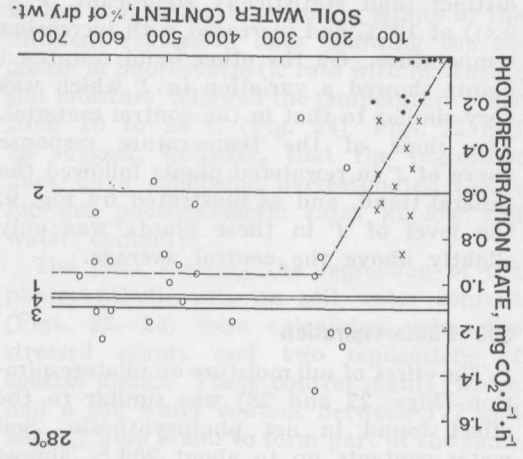

Fig. 28. Effect of soil water content on photorespiration rate at 28° C (cf. Fig. 27).

plants having a 177 to 264 % soil water content, in addition to stressed plants. The slopes of these regression lines were, however, distinctly different at the two temperatures, due to the higher photorespiration rates at high temperature. Similarly to the observations found in the variation in photosynthetic rates, the photorespiration results also suggested that rewatered plants possessed higher CO_2 exchange rates as compared to the unwatered ones at any given soil water content.

The temperature response of photorespiration in unwatered stressed plants was very weak and indicated a decrease rather than an increase with increasing temperature (Fig. 10). A moderate increase in photorespiration with temperature was found in rewatered plants. These did not, however, reach the control level of photorespiration, but as in net photosynthetic rates, they showed similarity to the values in those control plants which represented one particular clone, clone 2.

354 Dark respiration

The effect of soil moisture on dark respiration distinctly differed from that observed in other CO_2 exchange characteristics. The average response of dark respiration to soil water content, illustrated by the regression lines in Figs. 29 and 30, indicated a detectable rate even at 0 % soil water content. This rate was about 0.05 mg CO_2 $g^{-1}h^{-1}$ at 10° C and 0.5 mg CO_2 $g^{-1}h^{-1}$ at 28° C (the regression lines, based on plants

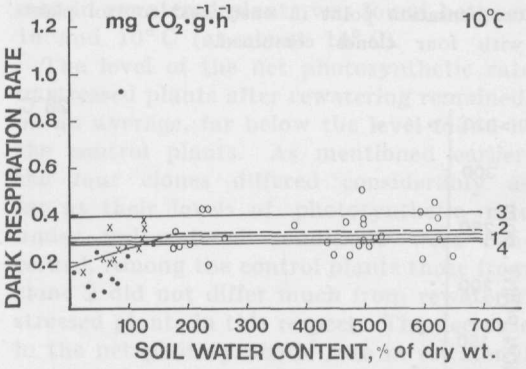

Fig. 29. Effect of soil water content on dark respiration rate at 10° C in unstressed control plants (o), stressed rewatered plants (x), and stressed unwatered plants (•), with four clones combined. Solid lines: rate means in unstressed control plants in clones 1, 2, 3, and 4 respectively. Broken line: average response of dark respiration rate to soil water content, with four clones combined.

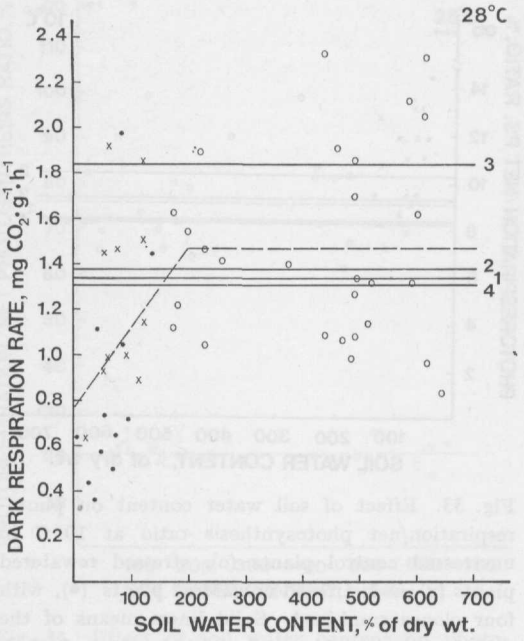

Fig. 30. Effect of soil water content on dark respiration rate at 28° C (cf. Fig. 29).

having soil water contents up to 264 %, clearly overestimated the respiration rate at very low soil water content). Figs. 29 and 30 also suggest that rewatered stressed plants possibly had higher dark respiration rates than the unwatered ones at equal soil water contents. At 10° C, one extremely high value among the unwatered plants (from clone 2), however, obscured the difference between unwatered and rewatered stressed plants in general at this temperature. The trend of a higher dark respiration rate in rewatered plants as compared to that in unwatered ones at a given soil water content was, perhaps, not as distinct at 28° C as it was at 10° C.

Fig. 11 shows that the level of dark respiration in unwatered stressed plants (including, however, only those at 41 % or higher soil water contents) was distinctly lower than that in rewatered or control ones throughout the temperature range from 10 to 28° C. The slope of the concave curve was also less steep in unwatered plants than in the other treatments. Rewatering caused the dark respiration rate to increase near to the control level (except that of clone 3 in which exceptionally high dark respiration rates were measured within the control material).

355 Respiration/net photosynthesis and photorespiration/dark respiration ratios

The dark respiration/net photosynthesis ratio was found to reflect changes in soil water content rather closely, as can be seen in Figs. 31 and 32. This was particularly clear at relatively high temperatures. At 28° C the dark respiration/net photosynthesis ratio sharply increased when the soil water content decreased to less than 100 %, and it often reached an infinite value at a soil water content of 60 % or less. This was associated with the fact that no net photosynthesis was detected at very low soil water content but dark respiration still reached a detectable level in this case. The increase in dark respiration/net photosynthesis ratio at low soil water content

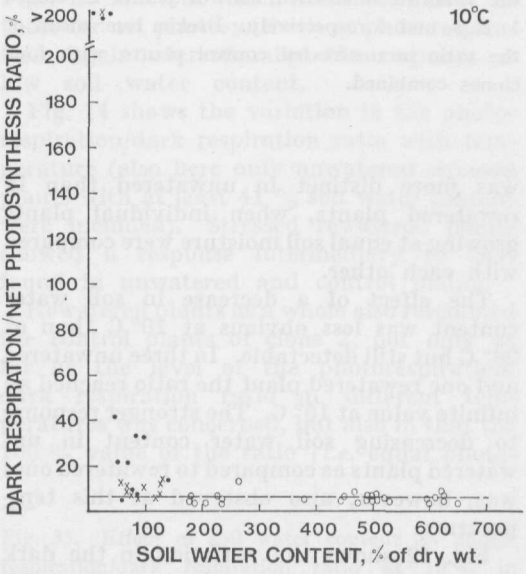

Fig. 31. Effect of soil water content on dark respiration/net photosynthesis ratio at 10° C in unstressed control plants (o), stressed rewatered plants (x), and stressed unwatered plants (•), with four clones combined. Broken line: mean of the ratio in unstressed control plants, with four clones combined.

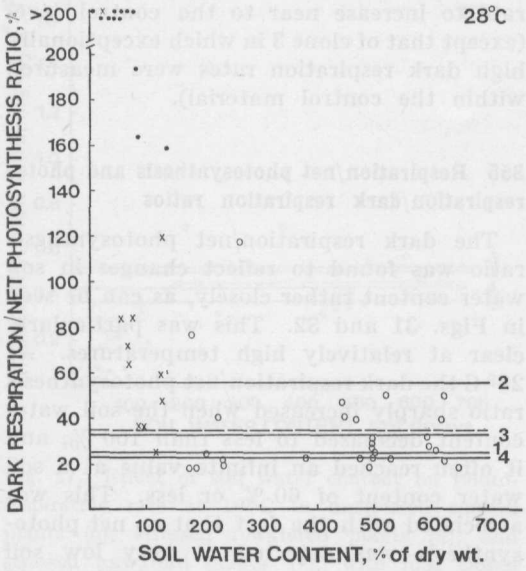

Fig. 32. Effect of soil water content on dark respiration/net photosynthesis ratio at 28° C in unstressed control plants (o), stressed rewatered plants (x), and stressed unwatered plants (•), with four clones combined. Solid lines: means of the ratio in unstressed control plants in clones 1, 2, 3, and 4 respectively. Broken line: mean of the ratio in unstressed control plants, with four clones combined.

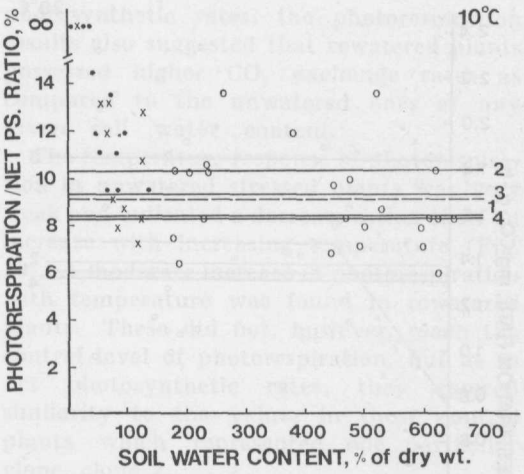

Fig. 33. Effect of soil water content on photorespiration/net photosynthesis ratio at 10° C in unstressed control plants (o), stressed rewatered plants (x), and stressed unwatered plants (•), with four clones combined. Soild lines: means of the ratio in unstressed control plants in clones 1, 2, 3, and 4 respectively. Broken line: mean of the ratio in unstressed control plants, with four clones combined.

was more distinct in unwatered than in rewatered plants, when individual plants growing at equal soil moisture were compared with each other.

The effect of a decrease in soil water content was less obvious at 10° C than at 28° C but still detectable. In three unwatered and one rewatered plant the ratio reached an infinite value at 10° C. The stronger response to decreasing soil water content in unwatered plants as compared to rewatered ones was, however, also observed at this temperature.

Fig. 12 shows the variation in the dark respiration/net photosynthesis ratio with temperature (also in this case omitting the stressed material growing at extremely low soil water content). The highest level and steepest upward trend of the curve was found in the unwatered plants. The ratio of rewatered stressed plants showed a somewhat steeper increase than that of the control material and remained at a higher level than the latter plants, especially at 28° C. The variation in the dark respiration/net photosynthesis ratio in rewatered stressed plants resembled to some extent that found in clone 2 among the control plants.

The variation in the photorespiration/net photosynthesis ratio (Figs. 13, 33, and 34) in stressed plants also closely followed that observed in Γ with varying soil water content or temperature.

Changes in soil moisture were generally also associated with variation in the photorespiration/dark respiration ratio. Figs. 35 and 36 suggest that this ratio increased with increasing soil water content and reached the average control level *(i.e.* 151 % at 10° C and 71 % at 28° C) at a soil water content of around 200 %. At 40 % or lower soil water contents the ratio equalled zero. The effect of soil water content thus also resembled the effect found in net photosynthesis or photorespiration. One fact adding to this resemblance was the result that rewatered stressed plants possibly had higher photorespiration/respiration

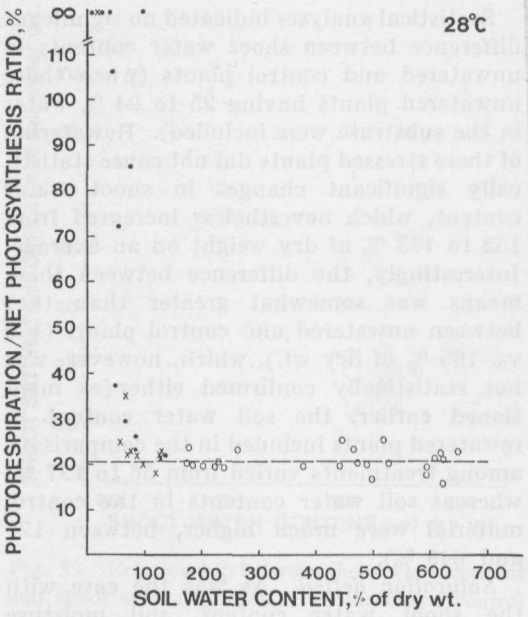

Fig. 34. Effect of soil water content on photorespiration/net photosynthesis ratio at 28° C in unstressed control plants (o), stressed rewatered plants (x), and stressed unwatered plants (•), with four clones combined. Broken line: mean of the ratio in unstressed control plants, with four clones combined.

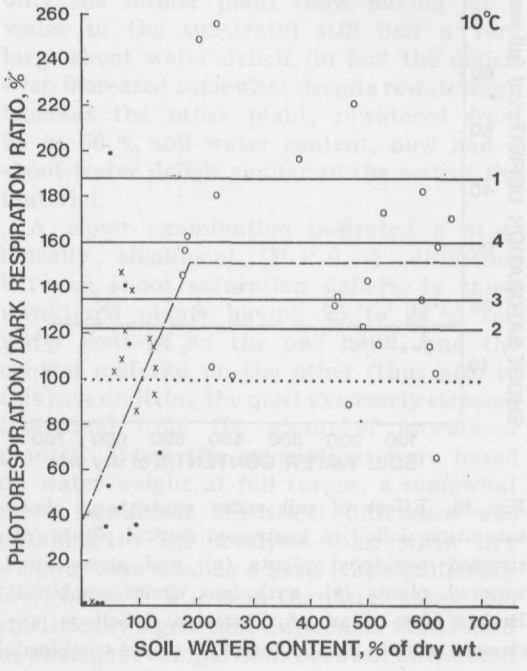

Fig. 35. Effect of soil water content on photorespiration/dark respiration ratio at 10° C in unstressed control plants (o), stressed rewatered plants (x), and stressed unwatered plants (•), with four clones combined. Solid lines: means of the ratio in unstressed control plants in clones 1, 2, 3, and 4 respectively. Broken line: average response of the ratio to soil water content, with four clones combined.

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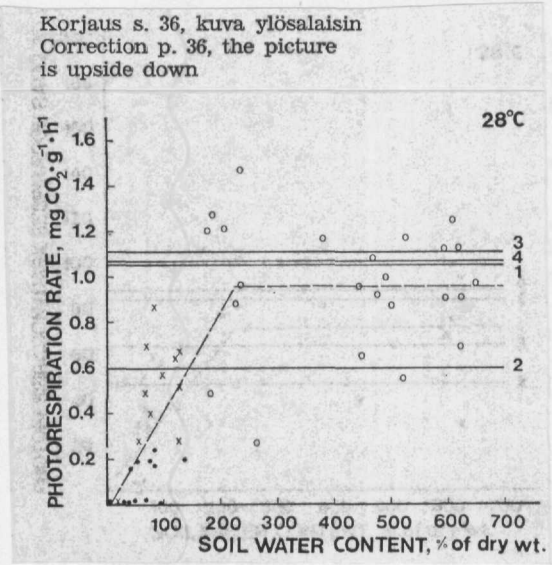

Fig. 36. Effect of soil water content on photorespiration/dark respiration ratio at 28° C (cf. Fig. 35).

ratios than unwatered plants at any given soil water content. The regeression lines in Figs. 35 and 36. which were calculated as those for net photosynthesis or photorespiration, again overestimated the response at low soil water content.

Fig. 14 shows the variation in the photorespiration/dark respiration ratio with temperature (also here only unwatered stressed plants with at least 41 % soil water content were included). Stressed rewatered plants showed a response intermediary to that found in unwatered and control plants.

Rewatered plants as a whole also resembled the control plants of clone 2, not only as far as the level of the photorespiration/dark respiration ratio at different temperatures was concerned, but also in that the 100 % value of the ratio *(i.e.* equal photo-

respiration and dark respiration rates) was interpolated in both cases to be around 14° C. In contrast, as seen in Fig. 14, in unwatered plants this ratio remained below 100 % even at the lowest temperature, 10° C, which indicated that in unwatered stressed plants, on an average, dark respiration always exceeded photorespiration.

36 Water balance in stressed plants

361 Shoot water content and saturation deficit

Shoot water content. In contrast to CO_2 exchange characteristics such as net photosynthetic rate, shoot water content (% of dry wt.) was not affected by a low soil water content, except for a few extreme cases (Fig. 37). In plants having 60 % or less water in the substrate, the shoot water content was slightly lower than that in the whole material on an average. A distinct decrease in shoot water content was found only in two unwatered plants and in one of these after rewatering; as can be seen in Fig. 37, in these cases the soil water content was 25 % or less.

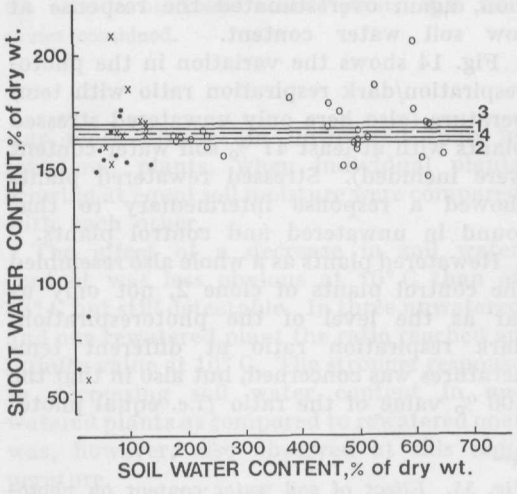

Fig. 37. Effect of soil water content on shoot water content in unstressed control plants (o), stressed rewatered plants (x), and stressed unwatered plants (•), with four clones combined. Solid lines: means of shoot water content in unstressed control plants in clones 1, 2, 3, and 4 respectively. Broken line: mean of shoot water content in unstressed control plants, with four clones combined.

Statistical analyses indicated no significant difference between shoot water contents in unwatered and control plants (when those unwatered plants having 25 to 94 % water in the substrate were included). Rewatering of these stressed plants did not cause statistically significant changes in shoot water content, which nevertheless increased from 152 to 173 % of dry weight on an average. Interestingly, the difference between these means was somewhat greater than that between unwatered and control plants (152 vs. 165 % of dry wt.), which, however, was not statistically confirmed either (as mentioned earlier, the soil water content in rewatered plants included in the comparisons among treatments varied from 56 to 127 %, whereas soil water contents in the control material were much higher, between 177 and 649 %).

Saturation deficit. As was the case with the shoot water content, soil moisture was found to have an effect on shoot saturation deficit only in two plants growing in extremely dry soil. Fig. 38, which includes the data on unwatered, rewatered, as well as control plants, indicates that only those

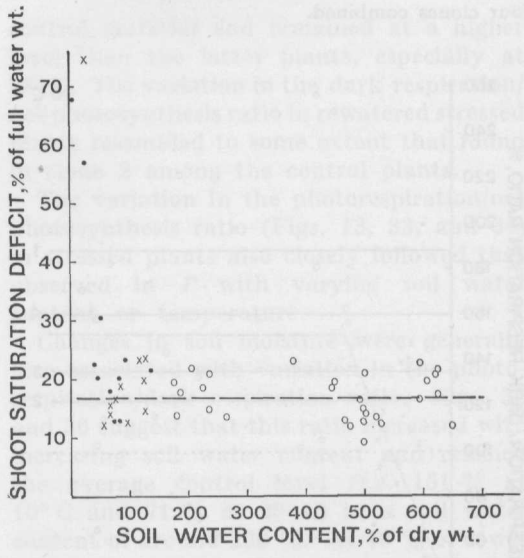

Fig. 38. Effect of soil water content on shoot saturation deficit in unstressed control plants (o), stressed rewatered plants (x), and stressed unwatered plants (•), with four clones combined. Broken line: mean of saturation deficit in unstressed control plants, with four clones combined.

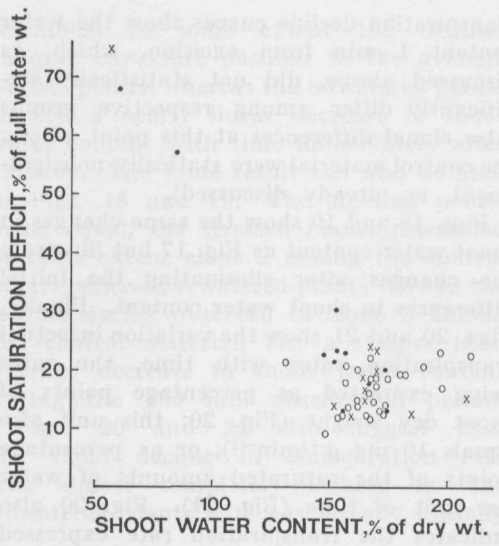

Fig. 39. Relationship between shoot water content and shoot saturation deficit in unstressed control plants (o), stressed rewatered plants (x), and stressed unwatered plants (•), with four clones combined.

two unwatered plants having 1 and 25 % soil water contents differed distinctly from the rest of the material. After rewatering, only the former plant (now having 25 % water in the substrate) still had a very large shoot water deficit (in fact the deficit even increased somewhat despite rewatering), whereas the other plant, rewatered from 25 to 56 % soil water content, now had a shoot water deficit similar to the rest of the material.

A closer examination indicated a statistically significant ($P < 0.01$) difference between shoot saturation deficits in those unwatered plants having 25 to 94 % soil water content on the one hand, and the control material on the other (thus also in this case omitting the most extremely stressed individual from the group of unwatered plants). When the calculations were based on water weight at full turgor, a somewhat more significant statistical difference was obtained in the analysis than when dry weights were used as a basis (the significance level being $P < 0.05$ in the latter case). No statistically significant differences were found in analogous comparisons between unwatered and rewatered or rewatered and control plants. On an average saturation deficits (based on full-turgor water content) equalled 24.5 ± 4.45 % in unwatered plants, 17.4 ± 1.42 % in rewatered plants, and 16.7 ± 0.73 % in control plants

Despite the limited size of the material, it was obvious that shoot water content and saturation deficit exhibited a mutual inverse relationship when all unwatered and rewatered plants were taken into consideration (Fig. 39). This result was in contrast to the distinct positive interrelationship found among control plants, but it was, at least in part, explained by the very limited ranges of both shoot water content and saturation deficit among the control plants — the few sharply differing observations representing the most stressed plants were enough to invert the earlier pattern.

362 Transpiration

In stressed plants rewatering caused a change in the transpiration decline curve towards the pattern generally observed in unstressed plants. This situation is illustrated in Fig. 40, which shows the individual results in one stressed plant (from clone 3) both prior to and after rewatering (cf. Fig. 16).

When all individual observations on decrease in shoot weight *(i.e.* increase in

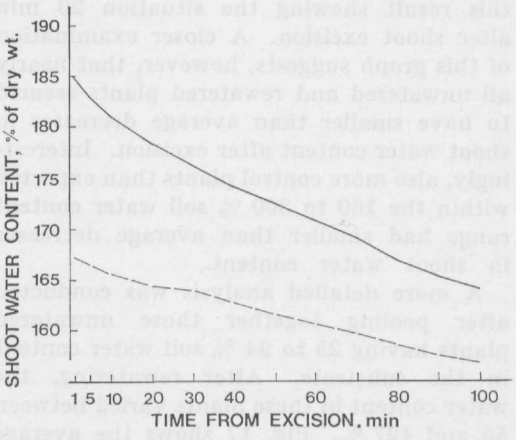

Fig. 40. Shoot water content as function of time from excision in a stressed plant, representing clone 1, prior to rewatering (broken line) and after rewatering (solid line).

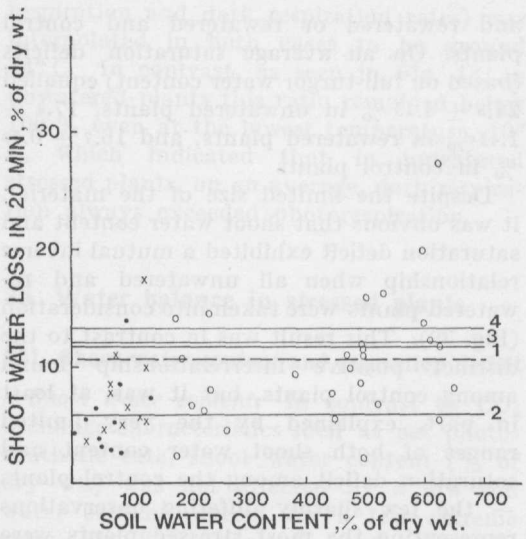

Fig. 41. Effect of soil water content on shoot water loss (as determined 20 min from excision) in unstressed control plants (o), stressed rewatered plants (x), and stressed unwatered plants (•). Solid lines: means of shoot water loss in unstressed control plants in clones 1, 2, 3, and 4 respectively. Broken line: means of shoot water loss in unstressed control plants, with four clones combined.

water saturation deficit) after shoot excision were plotted against soil water content, no straightforward pattern for the mutual relationship was found. Fig. 41 illustrates this result showing the situation 20 min alter shoot excision. A closer examination of this graph suggests, however, that nearly all unwatered and rewatered plants seemed to have smaller than average decreases in shoot water content after excision. Interestingly, also more control plants than expected within the 160 to 300 % soil water content range had smaller than average decreases in shoot water content.

A more detailed analysis was conducted after pooling together those unwatered plants having 25 to 94 % soil water content in the substrate. After rewatering, the water content in these plants varied between 56 and 127 %. Fig. 17 shows the average decreases in shoot water content as a function of time after shoot excision for unwaterd, rewatered, and control plants respectively. The starting points of the transpiration decline curves show the water content 1 min from excision, which, as discussed above, did not statistically significantly differ among respective groups (also clonal differences at this point among the control material were statically nonsignificant, as already discussed).

Figs. 18 and 19 show the same changes in shoot water content as Fig. 17 but illustrate the changes after eliminating the initial differences in shoot water content. Finally, Figs. 20 and 21 show the variation in actual transpiration rates with time, the rates being expressed as percentage points of shoot dry weight (Fig. 20; this unit also equals 10 mg $g^{-1}min^{-1}$); or as percentage points of the saturated amounts of water per unit of time (Fig. 21). Fig. 20 also indicates the transpiration rate expressed per unit of needle area (the area being calculated using data from the literature).

Throughout the 100 min observation period, shoots excised from unwatered plants maintained their lowest water content among the respective groups (Fig. 17). Statistical analyses indicated that the difference between average decreases in shoot water content in unwatered and control plants was most significant ($P < 0.001$) 20 min after shoot excision. Statistically significant ($P < 0.05$) differences were found among these groups when shorter (*e. g.* 10 or 5 min) as well as longer observation periods (up to 40 min from excision) were analysed. At 60 min from excision or after longer periods no such differences between unwatered and control plants were statistically confirmed.

Rewatered plants had a considerably higher water content throughout the observation period than any of the other treatment groups (cf. Fig. 17), but after adjusting the data to give equal initial water contents in respective groups (Figs. 18 and 19), the decrease in shoot water content was rather similar in rewatered and control plants. Rewatered plants did not statistically significantly differ from unwatered or control plants as far as decreases in shoot water content after excision were concerned.

The general appearance of the transpiration decline curves shown in Fig. 17 was somewhat different in the three treatment groups. The curve for rewatered plants

resembled to some extent the distinct concave curvature peculiar to the average control plants, whereas the unwatered plants showed a nearly linear decrease in shoot water content with time immediately after excision. The same result can also be seen in Figs. 18 and 19. The starting points being equal, the stressed plants resembled to some extent clone 2 among the control plants, whereas rewatered plants showed the feature earlier observed in clone 3 among the control material, *viz.* a steeper than average decrease in shoot water content during the 100 min observation period.

Figs. 20 and 21 also suggest that the rapid decline in transpiration rate was almost completely lacking in the unwatered plants and was already initially in the phase of linear decrease of water content and transpiration rate. Rewatered plants, on the other hand, had a somewhat more distinct decrease in transpiration rate immediately after shoot excision. This decrease remained, however, much smaller than that generally observed in the control plants.

At the end of the 100 min observation period the highest average transpiration rate among the treatment groups was found in rewatered plants. Also the rate in unwatered plants slightly exceeded that found in the average control plants. Both unwatered and rewatered plants thus resembled clone 3 among the control material as far as the final transpiration rate was concerned.

4 DISCUSSION

The net photosynthetic rates obtained under laboratory conditions in the present work corresponded well with earlier results. In a study including one Norway spruce population from southern and two from northern Finland (PELKONEN 1973, PELKONEN and LUUKKANEN 1974), maximum net photosynthetic rates were found at about 18° C and only a weak temperature response was observed within the applied temperature range (13 to 28° C). In the present study maximum rates for the four clones were found between 14 and 18° C. The earlier investigation indicated an average maximum rate of 5.1 mg CO_2 $g^{-1}h^{-1}$ (dry wt.), whereas in the present one it was, on an average, 5.7 mg CO_2 $g^{-1}h^{-1}$ at 16° C for the four clones.

Both of these results are within the range of net photosynthetic rates usually reported for conifers. However, much higher rates (up to 35 mg CO_2 $g^{-1}h^{-1}$) have been found in Scots pine when a specially designed assimilation chamber with diffuse light of very high intensity has been used (ZELAWSKI *et al.* 1973). Broadleaved species have considerably higher net photosynthetic rates, as indicated by a study on poplar clones under conditions comparable to those of the present work: average maximum rates in six clones were about 17 mg CO_2 g^{-1} h^{-1} at 30° C (LUUKKANEN 1971).

The present work indicated distinctly lower Γ values in Norway spruce than those reported earlier in Norway spruce seedlings. For instance, at 22° C, Γ was 39 ppm *vs.* 57 ppm found at 20° C by PELKONEN and LUUKKANEN (1974). The earlier study indicated, however, that northern spruce populations had a higher Γ and that the average Γ value in the southern Finnish population was 49 ppm. The present results correspond, however, quite well with the Γ values obtained in poplar clones (LUUKKANEN 1971), where the average value of Γ was 42 ppm (ranging from 39 to 50 ppm among six clones) at 20° C and 49 ppm (with a range of 45 to 57 ppm) at 25° C. The photorespiration rates (*e.g.* 0.77 mg CO_2 g^{-1} h^{-1} at 22° C) in the four clones of the present material were also lower than those found earlier. PELKONEN and LUUKKANEN (1974) obtained an average photorespiration rate of about 1 mg CO_2 g^{-1} h^{-1} (at 20° C), but, however, also a considerable amount of variation among the three sources. In this earlier study, family averages (among progenies from open pollination) varied from 0.89 mg CO_2 g^{-1} h^{-1} in a southern family to about 1.5 mg CO_2 g^{-1} h^{-1} in a northern one.

In the present study the increase in photorespiration rate (which changed almost linearly with temperature) was 113 % over the temperature range from 10 to 28° C, and this increase was smaller than generally observed in earlier investigations on conifers. For instance, BRIX (1967) reported that photorespiration rates in Douglas-fir doubled when the temperature increased from 20 to 28° C. However, this increase varied from 60 to 260 % in individual poplar clones when the temperature increased from 20 to 30° C, the average increase being 120 % (LUUKKANEN 1971).

Dark respiration rates in the four spruce clones were very similar to those measured earlier in Norway spruce seedling progenies. At 16° C the dark respiration rate was 0.52 and at 22° C, 0.83 mg CO_2 g^{-1} h^{-1} in the four clones, whereas the seedling progenies had an average dark respiration rate of 0.48 mg CO_2 g^{-1} h^{-1} at 20° C.

The dark respiration/net photosynthesis ratio values obtained in the present study were higher than those found earlier by PELKONEN and LUUKKANEN (1974) in Norway spruce seedlings. This ratio averaged 10.2 % at 16° C and 17.5 % at 22° C in the four clones, whereas the seedling progenies indicated a ratio value of 9 % at 20° C. In poplar clones studied by LUUKKANEN (1971) the ratio varied from 6 to 15 % at temperatures between 15 and 30° C (on an average in six clones) and amounted to 10.7 % at 20° C when calculated from clonal means of net photosynthesis and dark respiration.

As was the case with Γ values, also photorespiration/net photosynthesis ratios were much lower in the present sudy than those found earlier in spruce seedlings. At 16° C, an average ratio of 11.5 % was found, and at 22° C it was 14.9 %. In seedling progenies the average ratio was 23 % at 20° C. The lowest ratio (20 %) at this temperature was found in the spruce population from southern Finland. Within the whole seedling material, as well as in the four clones of the present study (under unstressed conditions), lower Γ values were thus always associated with lower photorespiration/photosynthesis ratios.

Photorespiration/net photosynthesis ratios comparable to those observed in the present work were found in the investigation on poplar clones mentioned above. At 15° C, this ratio varied form 8.9 to 11.5 % among six poplar clones (the overall mean being 9.7 % at this temperature). In all poplar clones the ratio increased with temperature so that the values of clonal average ratios varied between 17.2 and 20.3 % at 30° C (the mean over six clones being 18.5 %). In the poplar study, high »relative photorespiration» rates (photorespiration rates adjusted in relation to photosynthetic rates) were associated with high Γ value as well as with low net photosynthetic rates, when different clones were compared with each other. The mutual relationship between net photosynthesis and Γ followed an inverse curvilinear regression pattern, which fitted the variation in all clones.

An analogous result was also obtained in the present work. Clone 2 which possessed the highest photorespiration/net photosynthesis ratio and also the highest Γ throughout the entire temperature range from 10 to 28° C, also had the lowest net photosynthetic rates at all temperatures. In accordance with the poplar study, the regression pattern for the inverse relationship between net photosynthetic rate and Γ seemed to fit all clones and all treatments (cf. Fig. 15) equally well, although the material in both studies was too limited to allow this result to be statistically confirmed.

However, these observations were in accordance with those obtained by Chmora *et al.* (1976). In their studies on *Nicotiana*, plants with high or low photosynthetic rates all showed the same regression pattern in the inverse curvilinear relationship between Γ and net photosynthesis. Low photosynthetic rates were in this case obtained by introducing a nitrogen deficiency into the experimental material. The same authors suggested, after studying the effect of low O_2 concentration on Γ, that low Γ values were mainly caused by low photosynthetic rates rather than by increased photorespiration.

The low photorespiration rates found in the present work obviously contributed to the fact that the photorespiration/dark respiration ratios, on an average, remained much lower in the four clones than was earlier observed in the spruce seedling material. In the present study, at 16° C, a 133 % ratio and, at 22° C, a 98 % ratio was found in the four clones on an average. At temperatures higher than 22° C, the average photorespiration rate was lower than the dark respiration rate. In spruce seedlings (Pelkonen and Luukkanen 1974) the average ratio in the whole material was 272 % at 20° C; however, this value varied significantly among the three populations studied and the lowest ratio (234 %) was observed in the population from southern Finland. This ratio was, however, also much higher than that found in the present study.

The results of the earlier study on poplar clones (Luukkanen 1971, Luukkanen and Kozlowski 1972) indicated, that the photorespiration/dark respiration ratio may vary considerably among different genotypes under identical environmental conditions. The clonal means of this ratio varied from 47 to 270 % among six clones at 15° C, *i.e.* the lowest temperature used in this experiment. With increasing temperature the range of clonal means became smaller, but the average ratios still varied between 81 and 170 % at 30° C. Among various poplar clones, the photorespiration/dark respiration ratio increased, decreased, or remained almost constant, depending on the clone in question. It should be noted, however, that the poplar clones represented quite different genetic backgrounds, since they included a total of five different species. This variability of the material

was also reflected in the large variation in the optimum temperatures for net photosynthetic rates. Thus the clonal variation in the photorespiration/dark respiration ratio may be associated with different temperature responses of the different CO_2 exchange processes.

As emphasised earlier (LAÏSK 1977, p. 78), photorespiration rates and consequently also the ratios between photorespiration and dark respiration may vary because of stomatal movements, since the conventionally measured photorespiration rates do not take into account recycled photorespiratory CO_2 fluxes. Therefore, such variation as observed in the photorespiration/dark respiration ratio in the present study may also depend on differences in stomatal resistance among the clones, if such differences exist.

The analysis of water balance in the experimental plants yielded results which were correlated with the CO_2 exchange characteristics of the same plants. Transpiration measurements in excised shoots, as well as measurements of shoot water deficits, thus offered a method for explaining some of the mechanisms underlying the observed variation in CO_2 exchange among the experimental clones.

Under unstressed conditions, a higher rate of shoot transpiration (as indicated by a greater weight loss in excised shoots) was associated with a higher net photosynthetic rate. This was observed particularly clearly in clone 2, which had the lowest net photosynthetic rate and also the lowest shoot transpiration rate. All remaining clones had higher net photosynthetic rates and also high transpiration rates.

These results were interpreted as indicating a higher resistance to gas diffusion in clone 2 as compared to the remaining clones. Since both H_2O and CO_2 diffusion were impaired in this particular clone, an increase in the stomatal component of diffusion resistance in clone 2 seemed to be a conceivable explanation. This conclusion is in accordance with the results which indicate that differences in net photosynthetic rates among plant species at a favourable water balance are related to differences in stomatal rather than mesophyll resistance (HOLMGREN *et al.* 1965).

In addition to the lower than average level of transpiration in clone 2, the slope of the average transpiration decline curve (Fig. 17) of this clone supported the explanation that the stomata are the main factor regulating CO_2 exchange under unstressed conditions. After shoot excision, clone 2 reached the final slow phase of transpiration earlier than the remaining clones. This indicated a rapid closing of the stomata, possibly resulting from the fact that they were initially partially closed in this clone.

The final portions of the transpiration decline curves were interpreted as showing the phase of cuticular transpiration after complete or almost complete closure of the stomata (cf. SIWECKI and KOZLOWSKI 1973). Actual transpiration rates calculated from the transpiration decline curves and shown in Figs. 20 and 21 thus also estimate the transpiration rates of intact plants after full closure of the stomata under those atmospheric conditions which prevailed during the measurements (the possible effect of low light intensity on the stomata was eliminated by maintaining similar irradiance levels during CO_2 exchange and transpiration measurements). In an analogous way, extrapolation of the curves showing actual transpiration rates to the moment of shoot excision gave an estimate of the transpiration rate of the intact plant under these conditions. The rapid decline in transpiration during the first few minutes after excision, however, rendered this estimate somewhat difficult.

The positive correlation between transpiration (shoot weight loss) and net photosynthetic rate was clearest when shoot weight determinations made 10 min after excision were analysed. No statistically significant correlations were found when shoot weights after 60 min or longer periods were studied. This obviously indicated that once the cuticular phase of transpiration was reached, transpiration rates were nearly equal in the clones in question; also in clone 2 this final transpiration rate was close to the average for the whole material. On the other hand, weight losses only 5 min after shoot excision included a larger error component in the weight determination than the measurements made after longer periods of time. This could have explained the result

that the clearest correlations between transpiration and net photosynthetic rates were obtained with 10-min transpiration measurements.

The significant negative correlation between transpiration and Γ seems to be somewhat more difficult to understand if the stomatal component of the diffusion resistance is the main regulating factor, since the stomata cannot directly affect Γ. Thus it is likely that mechanisms other than stomatal ones were also involved in controlling the CO_2 exchange. Transpiration and CO_2 exchange measurements of stressed plants offered some further possibilities for discussing this problem, as presented later. The high significant positive correlations found between transpiration rates and photorespiration in unstressed plants do not directly explain the situation because of the *a priori* strong mutual intercorrelation between photosynthesis and photorespiration.

Water deficit had a marked decreasing effect on the level of the net photosynthetic rate. Under the experimental conditions which prevailed during the present study, a water content of 200 % (calculated from the dry weight of the peat substrate) seemed to be the limit for this effect, and apparent photosynthesis was not generally observed when the soil water content decreased to about 40 %. Temperature affected this variation in that the effect of water stress became apparent and also the zero level of net photosynthesis was reached at higher soil water contents at high temperatures.

The effect of water stress was much less apparent as far as the variation in Γ was concerned, particularly at low temperatures. Soil water contents as low as 50 % had only a slight effect on Γ at 10° C. A statistically significant difference was, however, found between Γ values in unwatered and control plants at all temperatures. This difference nevertheless remained relatively much smaller than that found in net photosynthetic rates. These results clearly supported the hypothesis that stomatal resistance is the main component regulating CO_2 exchange under conditions of moderate water stress and low temperature. On the other hand, during severe water stress, *i.e.* soil water contents of 50 % or less, Γ also sharply increased, which indicated a non-stomatal regulating effect on CO_2 exchange under these conditions. At higher temperatures this effect was noticeable at a higher soil water content.

Water stress caused a shift in the optimum temperature for net photosynthesis towards a lower temperature: in the stressed rewatered plants included in this analysis (Fig. 8), maximum net photosynthetic rates were attained at 14° C, whereas the optimum temperature in the whole control material was about 16° C (different clones showed, however, slight variation as far as the optimum temperature was concerned). Bearing in mind the results presented above, the main factor causing this change in optimum temperatures for net photosynthetic rate can be attributed to a stomatal mechanism.

Water stress decreased the dark respiration rates of the spruce clones at soil water contents which also affected the net photosynthetic rates in these plants, *i.e.* when the soil water content was lower than 200 %. With decreasing soil water content the dark respiration rate also decreased smoothly and indicated a detectable level even near to 0 % soil water content. At extreme stress, however, despite this observed metabolic activity, the experimental plants were showing symptoms of visible damage, *i.e.* shedding of older needles. Although determination of the wilting point in the normal sense was not possible in the conifer material, the oat seedlings planted in a few pots containing the experimental spruce plants, reached a permanent wilting stage at approximately 80 % soil water content.

No such increases in dark respiration rates were observed as reported by Brix (1968) in *Pinus taeda* during moderate stress. The results were, however, in accordance with those found by Zavitkovski and Ferrell (1970) in *Pseudotsuga* and which indicated similar decreases in net photosynthetic and respiration rates during water stress.

When the ratios between different CO_2 exchange characteristics were analysed during changing water stress, a few clear trends were found. The most distinct variation occurred in the dark respiration/net photosynthesis ratio, which increased sharply from the control level (7 to 35 %,

on an average, at temperatures from 10 to 28° C) to infinite values at temperatures above 16° C in the unwatered plants. This variation was caused by the decrease in net photosynthetic rates to or near to zero level in stressed unwaterd plants at high temperatures. A similar, although not as sharp increase was also found in the variation of the photorespiration/net photosynthesis ratio with temperature in unwatered plants.

For comparison, photorespiration/total photosynthesis ratios (total photosynthesis equalling the net photosynthetic rate added to the photorespiration rate) were also calculated. Since the trend of this ratio closely followed that observed in photorespiration/net photosynthesis ratios, these results were omitted from the results of the present study. As implied by the calculation method, a somewhat more distinct variation was, however, observed when net photosynthetic instead of total photosynthetic rates were used in these ratios, as far as responses to temperature or to water stress were concerned.

The photorespiration/dark respiration ratio was also affected by water stress, primarily because of the fact that photorespiration was more strongly suppressed by the treatment than was the case with dark respiration. The temperature at which the photorespiration/dark respiration ratio decreased below the 100 % level was distinctly lower in stressed plants as compared to the control material. This difference was also clear when stressed rewatered plants were compared to the control material (Fig. 14). The equilibrium temperature thus seems to possess a diagnostic value for studying the effect of water stress.

The inadequacies of the conventional methods for determining photorespiration rates (Laïsk 1977, p. 78) should be taken into account particularly when photorespiration in stressed plants is considered. Increasing stomatal closure will increase the difference between measured and actual photorespiration rates, and consequently the variation in the apparent photorespiration/dark respiration ratio among the clones may be, at least in part, caused by differences in water balance indirectly, without substantial changes in the photorespiration rate or the ratio on the mesophyll level.

The results of the present study indicated that the shoot water content remains on a fairly constant level under varying water stress conditions and that only a stress far stronger than that causing permanent wilting of oat plants also decreased the shoot water content of spruce under the experimental conditions of this study. In view of the stomatal regulation observed in the present study and discussed above, the stomata seem to be responsible for this mechanism which undoubtedly has an important adaptive significance. Although the differences in shoot water content among the clones in the control material were statistically nonsignificant, the slightly lower water content in clone 2 may have contributed to the rapid stomatal closure observed in control plants representing this clone. On the other hand this seems less likely in view of the saturation deficit analyses: the lowest water deficit was observed in this clone; however, this clonal variation was also statistically nonsignificant.

The different CO_2 exchange characteristics which were analysed all revealed a similarity between the reactions of clone 2 and the reactions of the average stressed rewatered plant material to moderate water deficit. The shoot transpiration results also indicated that the response of clone 2 was similar to that observed in stressed unwatered plants. This was particularly the case with rapid stomatal closure in clone 2 as well as in the unwatered plants.

Earlier studies (Jarvis and Jarvis 1963) have demonstrated that, among a number of tree species, the slowest stomatal closure during water stress occurs in *Picea abies*, whereas *Populus tremula* is most sensitive and *Pinus sylvestris* and *Betula pendula* are intermediary in this respect. The apparent insensitivity of the stomata to water stress in spruce also seems to underlie the relatively high transpiration rates found in this species. The present study did not, however, reveal such increases in transpiration rates during moderate stress as found by these earlier investigators. However, recent Finnish studies (Hallman 1976, Luukkanen *et al.* 1976 b) suggest that the stomatal responses and transpiration rates during water stress may differ also among spruce clones.

Rewatering, which in the present study consisted of a relatively small increase in the soil water content, clearly affected the CO_2 exchange of the stressed plants and generally changed the level of different CO_2 characteristics towards and often near to the control level. The results also indicated an adaptation to stress conditions in that a slightly higher activity was observed in rewatered plants as compared to those unwatered plants which had the same soil water content. This result resembled the situation found in *Pseudotsuga* seedlings by ZAVITKOVSKI and FERRELL (1970). According to their observations, net photosynthetic rates at low soil moisture content were higher during the second drying cycle as compared to the first one.

Furthermore, rewatering seemed to increase the shoot water content in the present study to higher levels than those observed in the control plants, although the soil water content in the case of rewatered plants remained very low as compared to that in the control material. This increase was, however, not statistically confirmed, possibly because of the limited number of stressed plants and the considerable individual variation found in this treatment group. In any case, this change in water balance also seemed to suggest the presence of an adaptive, water-conserving mechanism in spruce plants.

The increase in transpiration rate in the stressed plants after rewatering suggested that the changes in CO_2 exchange characteristics brought about by rewatering were associated with changes in stomatal regulation and especially with a lowered stomatal diffusion resistance to CO_2. On the other hand, rewatering also had a strong effect on Γ. While the values of Γ were significantly increased in unwatered plants, thus indicating a considerable non-stomatal component in the resistance to CO_2 diffusion, rewatering very distinctly decreased the value of Γ near to the level found in the control plants. Thus the adaptive mechanism induced by water stress and visible in the higher-than-expected CO_2 exchange activity after rewatering seemed to operate through adaptation of the stomatal as well as other resistance components.

A closer examination of the net photosynthetic rates among different clones and treatments (Fig. 8) revealed that differences in dark respiration or photorespiration rates did not satisfactorily explain the decreases in net photosynthetic rates caused, for instance, by the stress treatments, or found among the clones in unstressed plants. Dark respiration rates in clone 2 were very close to average values among the clones, although photosynthesis in this particular clone was distinctly at a lower level as compared to the remaining ones. In clone 3, which had the highest net photosynthetic rates at high temperatures, also the dark respiration rates were distinctly higher than those in the rest of the material, again, particularly at high temperatures. In unwatered stressed plants, both net photosynthesis and dark respiration were very low as compared to the corresponding values among rewatered or unstressed plants.

Rewatering increased the net photosynthetic rate of stressed plants only up to the level observed in the unstressed control plants of clone 2, *i. e.* not to the level found in unstressed plants on an average. However, dark respiration rates in the rewatered plants increased very close to the average level found in unstressed plants, which indicated that increased dark respiration may have to some extent contributed to the decrease in the net photosynthetic rate found in rewatered plants when compared to the unstressed control material.

The range of absolute values of dark respiration rate (which varied from 0.3 to 1.4 mg $CO_2\ g^{-1}\ h^{-1}$ between 10 and 28° C in unstressed or rewatered plants, and from 0.3 to 0.8 mg $CO_2\ g^{-1}\ h^{-1}$ between these temperatures in unwatered plants) did not exclude the effect of dark respiration on the general shape of the net photosynthetic response curves in relation to temperature (Fig. 8). Nevertheless, the effect of dark respiration on the *level* of net photosynthetic rates observed among clones or among stress treatments remained very small.

Photorespiration rates obtained in the present study by the usual extrapolation method were of the same magnitude as dark respiration rates (Figs. 10, 11, and 12). Thus their effect on the variation in net photosynthetic rates among clones or tretments also remained relatively low.

On the other hand, a strong mutual positive correlation existed between net photosynthesis and photorespiration. This result is in agreement with earlier studies and with the accepted biochemical relationship existing between these two processes (cf. LUUKKANEN and KOZLOWSKI 1972).

Photorespiration rates obtained by the usual extrapolation method generally tend to understimate the rates of the actual CO_2 output (which includes both mitochondrial and »peroxisomal» respiration) at the cellular level. Owing to increasing recycling of respiratory CO_2 from the intercellular space back to the liquid phase of the mesophyll, this error becomes successively greater with increasing stomatal resistance (LAÏSK 1977, p. 44).

Indirect evidence for this was also obtained in the present study when the photorespiration/dark respiration ratios (Fig. 14) were analysed. These results indicated that dark respiration rates measured in darkness exceeded the photorespiration rates, measured in light by extrapolation, in most stressed plants and in all plants at high temperatures. Even if dark respiration is suppressed in light, as often reported in the literature (cf. JACKSON and VOLK 1970; LAÏSK 1977, p. 166), it is unlikely, however, that this suppression would, on the cellular level, result in as low a CO_2 output as observed in the present study at the leaf level. The obvious understimation of photorespiration, particularly in the stressed material, should thus be taken into account when the variation in photorespiration or photorespiration/dark respiration ratios with temperature or the differences in these characteristics among clones or treatments are discussed and analysed further.

Keeping the foregoing consideration in mind, an attempt was made to quantify the effect of the calculation method on the results obtained, so as to facilitate comparisons between the leaf level results of the present study on the one hand, and the values pertaining to the cellular level and reported in the recent literature on the other.

Photorespiration rates were recalculated according to the models of CO_2 diffusion into the leaf during photosynthesis presented by GAASTRA (1959) and later summarised and developed further by JARVIS (1971) and LAÏSK (1977). The method applied to the recalculation procedure as well as the results obtained are presented in Figs. 42 and 43 and in Table 4.

The conceptual model assumes a relationship between the components of CO_2 diffusion resistance and the ambient concentration of CO_2, which can be presented as an equation in the following way (cf. JARVIS 1971, p. 605):

$$(1) \qquad \Sigma r' = r_{mx} + r'_s + r'_a = \frac{(C_a - \Gamma)}{q_v},$$

where $\Sigma r'$ indicates total resistance to CO_2 diffussion, r_{mx} mesophyll (liquid diffusion and carboxylation) resistance, r'_s stomatal resistance (including intercellular space resistance r'_j), r'_a boundary layer resistance, C_a ambient CO_2 concentration, and q_v CO_2 exchange.

If the rate q_v at a given value of C_a and the total gaseous resistance, $r'_g = r'_s + r'_a$,

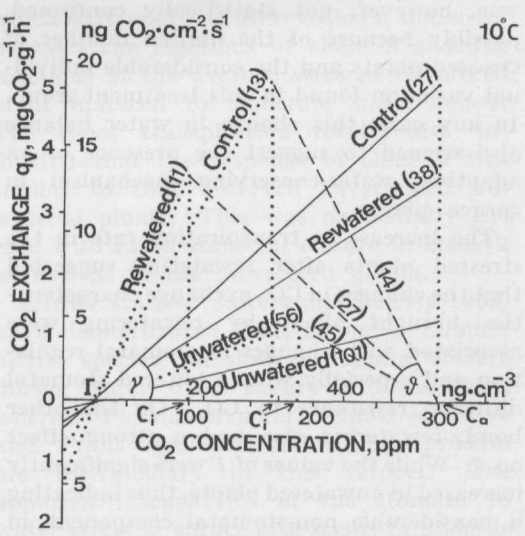

Fig. 42. Principles used in recalculation of photorespiration rate on the mesophyll level and estimation of different components of CO_2 diffusion resistance, with actual values of net photosynthetic rate and Γ at 10° C in each treatment group (unstressed control plants, stressed rewatered plants, and stressed unwatered plants respectively) as examples. Values given in parenthesis are estimates of $\Sigma r'$, r'_g, and r_{mx}, derived as explained in the text.

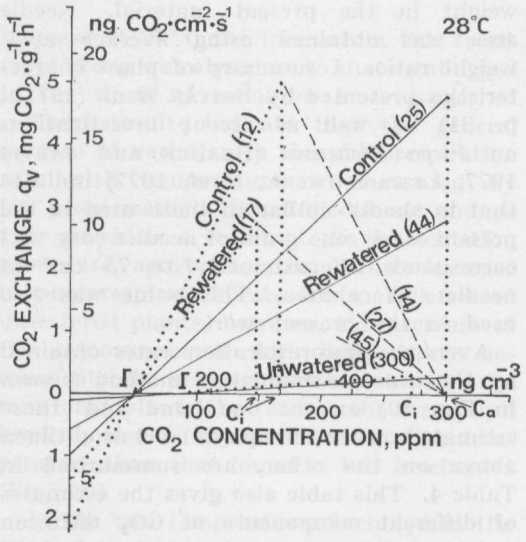

Fig. 43. As Fig. 42, 28° C.

are known, then the relationship between q_v and the CO_2 concentration in the intercellular space, C_i, can be determined using the following equation (Laïsk 1977, p. 43):

$$(2) \quad r'_g = \operatorname{ctg} \vartheta = \frac{C_c - C_i}{q_v},$$

where ϑ denotes the angle between the x axis and a line which, when drawn at the known value of C_a, passes through the point which denotes the values of q_v and C_i (Figs. 42 and 43).

When the relationship between q_v and C_i has been thus determined, r_{mx} can be calculated according to the following equation (cf. Jarvis 1971, p. 606):

$$(3) \quad r_{mx} = \operatorname{ctg} \gamma = \frac{C_i - \Gamma}{q_v},$$

where γ equals the angle between the x axis and the line which runs through Γ and shows the response of q_v to variations in C_i. The slope of this line ($\operatorname{ctg} \gamma$) thus indicates the total resistance to CO_2 diffusion in the liquid phase and in the carboxylation reactions within mesophyll cells. Extrapolation of the line to $C_i = C_a = 0$ yields an estimate of »true» photorespiration, *i.e.* an estimate which takes into account the recycling of respiratory CO_2 from the intercellular space back to the liquid phase and which can be compared to such values of photorespiration rates as those measured by Laïsk (1977).

If the solubility of CO_2 in the liquid phase is taken into account, a new curve can be constructed which shows the response of CO_2 exchange to the variation in CO_2 concentration in the liquid phase of the mesophyll, C_w. Such »PC_w curves» allowed Laisk and his coworkers (Laisk and Oja 1971, Laïsk 1977) to model CO_2 exchange kinetics in a precise way. These curves also enabled them to determine a CO_2 compensation point which was lower than the usual Γ and constant over a wide range of environmental variation, the »CO_2 photocompensation point», Γ^*.

As discussed by Jarvis (1971) and Laïsk (1977), several assumptions have to be made for calculations such as those outlined above. For instance, determination of the response of CO_2 exchange, q_v, to changes in C_a and C_i using only Γ and one measurement of q_v at 300 ppm (540 ng cm^{-3}) of CO_2, as done in the present study, may lead to overestimations of $\Sigma r'$ and r_{mx}, if the response actually is curvilinear, for instance in stressed plants. On the other hand, a distinct linear response of net photosynthesis has been frequently found in various species and under varying conditions within this range of CO_2 concentration. For instance, in a study with six poplar clones, the linearity was clear in all clones up to about 450 ppm of CO_2 (Luukkanen and Kozlowski 1972).

Using the results of the present study, the total gaseous diffusion resistance to CO_2 influx was estimated from average transpiration rates (Fig. 20) for each treatment group (unstressed control plants, stressed unwatered plants, and stressed rewatered plants respectively), using the general equation (cf. Laïsk 1977, p. 14):

$$(4) \quad r_g = \frac{A_i - A_a}{E_s},$$

where r_g denotes the total resistance to water vapour diffusion, A_i and A_a concentrations of water vapour in the intercellular

space (on the surface of mesophyll cells) and in the ambient atmosphere respectively, and E_s transpiration rate through the stomata. Owing to the convincing supporting evidence presented in the literature and discussed by LAÏSK (1977, p. 15), which demonstrates the effect of mesophyll resistance to water vapour and the effect of the water potential of the liquid phase as being very small, it was assumed that A_i equals the saturation concentration of water vapour at leaf temperature. Since the saturation pressure deficit of the ambient air during transpiration measurements varied neglibly, a constant value for A_a and thus consequently also for the difference ($A_i - A_a = 28\ \mu g\ cm^{-3}$) was used.

Transpiration rates, E_s, were obtained, separately in each treatment group, from Fig. 20 by subtracting the final transpiration rate (100 min from shoot excision, assumed to equal cuticular transpiration) from the extrapolated initial transpiration rates at the moment of shoot excision.

In order to convert the obtained estimate of r_g (which refers to H_2O diffusion resistance) to the corresponding value of gaseous resistance to CO_2, r'_g, the theoretical value of the ratio between the diffusion coefficients for CO_2 and H_2O at 25° C, given by LAÏSK (1977, p. 25) and equalling 1.6, was used.

Furthermore, it was assumed that a constant ratio existed between shoot dry weight and needle area of the shoot. Shoot weights obtained in transpiration measurements were converted to needle weights using the average value for needle dry weight which equalled 74 % of shoot dry weight in the present material. Needle area was obtained using average area/weight ratios. A summary of plant characteristics presented by ŠESTÁK *et al.* (1971b, p. 31) as well as recent investigations on *Picea sitchensis* (BEADLE and JARVIS 1977, LEWANDOWSKA, *et al.* 1977) indicate that in shoots similar to those used in the present study one gram of needles (dry wt.) corresponds approximately to 75 cm^2 of needle surface area. This value was also used in the present work.

Average photorespiration rates obtained by the usual extrapolation method (shown in Fig. 10) on the one hand and those estimated on the mesophyll level as outlined above on the other, are summarised in Table 4. This table also gives the estimates of different components of CO_2 diffusion resistance in each treatment group at 10 and 28° C.

Figs. 42 and 43 and Table 4 show that recalculated values of the CO_2 output in the mesophyll were generally higher than photorespiration rates at the leaf level. On an average, the recalculated rates were more than twice as high as those obtained by the ordinary method. An exception was found in stressed unwatered plants. In these plants only a small increase in the very low photorespiration rate was found after recalculation. Another exception from the general trend was the fact that stressed rewatered plants seemed to possess a CO_2 output rate on the cellular level which was more than three times that measured on the leaf level by the usual method. This result was, however, observed only at 10° C,

Table 4. Needle level (A) and mesophyll level (B) photorespiration rates and components of CO_2 diffusion resistance at 10 and 28° C in each treatment group of the experimental material, $\Sigma r'$ equalling total, r'_g gaseous, and r_{mx} mesophyll (liquid phase and carboxylation) resistance.

Treatment	Photorespiration rate mg $CO_2\ g^{-1}\ h^{-1}$				CO_2 diffusion resistance s cm^{-1}					
	10° C		28 ° C		10° C			28° C		
	A	B	A	B	$\Sigma r'$	r'_g	r_{mx}	$\Sigma r'$	r'_g	r_{mx}
Control	0.44	0.92	1.00	2.16	26.8	13.5	13.2	25.0	13.5	11.5
Rewatered	0.36	1.36	0.60	1.42	37.9	27.1	10.8	43.9	27.1	16.8
Unwatered	0.16	0.24	0.12	0.16	101	44.8	56.2	324	44.8	279

whereas at 28° C the increase in this treatment group was also close to that established in the whole material on an average.

These results indicate that the general pattern of variation in the photorespiration rate with temperature, as measured by the usual method (Fig. 10), did not change very much as a result of the recalculation procedure, apart from the distinct increase in photorespiration rate *levels*. In stressed unwatered plants, however, the decrease of the response curve with temperature became slightly steeper, whereas in stressed rewatered plants the rate at the mesophyll level showed a smaller increase with temperature than that found in leaf level rates (Fig. 10).

At the two temperatures included in the recalculation procedure, some trends in the relative values of photorespiration rates between different treatment groups were also observed. At 10° C, stressed rewatered plants clearly possessed the highest photorespiration rates at the mesophyll level, whereas the rate at the leaf level was highest in unstressed control plants at this temperature. At 28° C the photorespiration rate was distinctly the highest in unstressed control plants both at the mesophyll and at th e leaf level. The photorespiration rate in stressed unwatered plants seemed to be distinctly lower in relation to that in either of the two remaining treatment groups at 28° C as compared to the situation at 10° C, according to both calculation methods.

As was already obvious from the low net photosynthetic rates in stressed unwatered plants, the total resistance to CO_2 diffusion was distinctly the highest in this treatment group. Table 4 gives numerical estimates for this variation and shows that at 28° C, the total resistance in unwatered plants, was more than seven times greater than the value observed in rewatered plants, which in turn had an average resistance nearly twice as high as that found in unstressed plants at this temperature. At 10° C the difference between unwatered and rewatered plants and between rewatered and unstressed plants was considerably smaller.

In unstressed control plants the total resistance to CO_2 diffusion was nearly equally divided between a stomatal and a mesophyll component at both temperatures, whereas in stressed rewatered plants about two thirds of the total resistance was estimated to depend on the stomata and one third on the mesophyll at both temperatures. The decrease of r_{mx} to below the control level at 10° C and near to the control level at 28° C was thus one of the most distinct effects of rewatering in stressed plants, as also illustrated by Figs. 42 and 43. In stressed unwatered plants the main component in CO_2 diffusion resistance seemed to be the mesophyll one. With increasing temperature the significance of the mesophyll resistance also seemed to increase considerably in the stressed unwatered material.

The boundary layer resistance, r'_a, could not be separated from the total gaseous resistance under the conditions used in the CO_2 measurements. Instead, the stomatal resistance was assumed to equal the calculated total gaseous resistance ($r'_s = r'_g$). The boundary layer resistance to CO_2 diffusion during transpiration measurements was, however, estimated from evaporation rates (by placing a Petri dish, filled with water, close to the excised shoot), using Eq. (4) and the equation given by Jarvis (1971, p. 567):

$$(5)\quad r'_a = r_a \left(\frac{D}{D'}\right)^{\frac{2}{3}},$$

where the ratio between diffusion coefficients for H_2O and CO_2, $\frac{D}{D'}$, was assumed to equal 1.6 (Laïsk 1977, p. 25).

This calculation resulted in an esimation of r'_a of 1.7 s cm^{-1}. The air flow within the gas exchange chamber probably resulted in a lower actual value of r'_a within the chamber. These estimates are comparable with the range 0.5 to 2.0 s cm^{-1} for r'_a within leaf chambers, given by Jarvis (1971, p. 571).

It may thus be concluded that the actual values of stomatal resistance in the present material were somewhat lower than the estimates of r'_g presented in Table 4, but the difference was only about 1.5 s cm^{-1}.

Values of total mesophyll resistance (including liquid phase and carboxylation resistances) obtained in the present study are higher than usually reported in the literature (Ludlow and Jarvis 1971, Laïsk

1977, p. 32). In unstressed control plants the observed values at 10 and 28° C, 13 and 12 s cm^{-1} respectively, are not far from the values reported for conifers, however. LAISK's review also suggests that water deficit may cause increases in mesophyll resistance which are not not due to experimental errors (cf. also JARVIS 1971, p. 577). As emphasised by several authors (cf. JARVIS 1971, BJÖRKMAN 1973), all methods for determination of r_{mx} include sources of error, and consequently estimates such as those made in the present study should be discussed critically.

The present results concerning the variation in net photosynthetic rate and in the different processes controlling it are in agreement with our earlier studies, mainly conducted under field conditions and with *Betula* as the material. These earlier studies showed that during increasing water deficit, net photosynthetic rates became successively more sensitive to elevated temperatures. In some cases this effect was detectable for a time after the water supply to the plant had been restored, as shown in a *Betula* stand in the field (HARI and LUUKKANEN 1974) and in *Alnus incana* seedlings under laboratory conditions (HARI and LUUKKANEN 1973). Simultaneous measurements of net photosynthesis and transpiration in *Betula pubescens* (HARI *et al.* 1975 a) suggested that, at least to some extent, mechanisms other than stomatal ones are responsible for the decrease in the net photosynthetic rate during water deficit and also during several days after rewatering.

In these earlier investigations, relative indices for expressing the effect of environmental stress on net phtotosynthesis and transpiration were constructed. In the mathematically derived variable called physiological water stress, *w* (HARI and LUUKKANEN 1973, 1974), which has also been applied to models of seasonal variation in photosynthesis (PELKONEN *et al.* 1977), the exact physiological nature of this effect was not clarified. It is obvious, however, that a possible mesophyll regulation is included in this index.

Such a concept as the degree of transpirational control, *CT* (HARI *et al.* 1975 a, LUUKKANEN *et al.* 1975, SMOLANDER *et al.* 1975), obviously shows a strong relationship with stomatal resistance to H_2O or CO_2 diffusion, and it can also be used in quantifying the relative effect of water deficit on stomatal control, even under field conditions. Analogously, the degree of photosynthetic control, *CP*, used in connection with *CT*, is mutually correlated with total resistance to CO_2 diffusion during photosynthesis, $\Sigma r'$, and consequently *CP* can be used in quantifying the relative effect of water deficit on photosynthesis in the field as well as in the laboratory.

Our earlier investigations also demonstrated that an increase in Γ is associated with a decrease in net photosynthetic efficiency when different genotypes are investigated (LUUKKANEN 1971, LUUKKANEN and KOZLOWSKI 1972). Preliminary investigations also showed that this relationship seemed to exist during conditions of water deficit (LUUKKANEN 1976, LUUKKANEN *et al.* 1976 b).

The present study supports the earlier observations in two different ways. First, the decrease in the net photosynthetic rate observed, for instance, in field studies on *Betula* (HARI and LUUKKANEN 1974, HARI *et al.* 1975 a) can be explained by supposing that a prolonged water deficit affects the regulation of CO_2 diffusion on the mesophyll level, in addition to the obvious stomatal effects.

The varying results concerning aftereffects of water deficit on net photosynthesis could consequently be related to different rates of re-adjustment of the mesophyll portion of CO_2 diffusion control after rewatering: the present study indicates a very rapid recovery from water stress in spruce as compared to the prolonged effect earlier observed in *Betula*. However, the different experimental conditions in these studies may also have contributed to this variation.

The postulating of mesophyll resistance as a crucial factor in controlling net photosynthetic rate under stress conditions is in agreement with calculations of average values of mesophyll resistance in different treatment groups of the present study and with the results of other investigators on the effects of water deficit on photosynthesis (GAASTRA 1959, LAÏSK 1969, HANSEN 1971, REDSHAW and MEIDNER 1972).

Secondly, the present study offers further

evidence of the increase in the CO_2 compensation point during water deficit. This increase cannot be explained by stomatal movements, because of the *a priori* assumption of $C_i = C_a$ at Γ. Instead, this variation is to be attributed to changes in mesophyll resistance.

The present results also support earlier observations which demonstrated an increase in Γ accompanying the increase in mesophyll resistance during water stress (HEATH and MEIDNER 1961, MEIDNER 1967, REDSHAW and MEIDNER 1972). These earlier investigators concluded that such a variation was caused either by an enhanced respiration rate or an inhibition of the carboxylation reactions. Similar results have been reported in a number of species by TREGUNNA and coworkers (TREGANNA *et al.* 1975). Interestingly, recent studies on *Picea sitchensis* (BEADLE and JARVIS 1977) indicate that a change in the acitivity of Photosystem I, Photosystem II, or RuDP carboxylase is probably not the cause for increased mesophyll resistance during water stress. A different conclusion has recently been made by BOYER (1976) who reported an increase in Γ during water stress and suggested inhibition of the photosynthetic light reactions (particularly those of Photosystem II) as a main cause of this result.

A recent investigation (BUNCE and MILLER 1976, BUNCE 1977) has also shown that an increase in Γ (and mesophyll resistance) during water stress occurs in a number of tree species from a wide range of ecological conditions, but the variation in photorespiration shows different trends in different species.

Our conclusions or the earlier results referred to above are not in disagreement with attempts to explain the variation in net photosynthetic rate among different genotypes by postulating genetically controlled changes in the mesophyll part of CO_2 diffusion. The biochemical process which leads from the Calvin cycle through the glycolate pathway and culminates in the output of the main part of photorespiratory carbon dioxide, will remain one of the major objectives in further investigations on the complex processes involved in mesophyll resistance. Further studies will also clarify the exact physiological mechanisms of such genetically determined variation in net photosynthesis which depends on the carboxylation process and is associated with photorespiration.

5 SUMMARY

Carbon dioxide exchange was studied in two-year old transplanted cuttings of four *Picea abies* clones at different temperatures and at a varying soil water content. The aim of the study was to clarify the response of net photosynthetic rate per unit of foliage to different environmental conditions in different genotypes and to analyse further the factors responsible for the observed variation by studying separately the major CO_2 exchange processes. Attention was also paid to the relationships between CO_2 exchange characteristics and the water balance in the experimental plants.

A preliminary experiment was carried out under field conditions, using trap-type gas exchange chambers connected with a URAS 1 infrared gas analyser in an open measurement setup. The main part of the measurements was, however, carried out in the laboratory using the same analyser in a closed system which allowed rapid and precise temperature regulation of a water-jacketed gas exchange chamber.

Using techniques developed in our earlier investigations, the net photosynthetic rate, CO_2 compensation point (Γ), and dark respiration rate were determined at 10, 16, 22 and 28° C. In part of the experimental material, water stress was induced by maintaining the plants at low soil water content. With these stressed plants a complete series of CO_2 exchange measurements was carried out prior to and one day after rewatering of the plant with a small amount (100 ml) of water. This procedure permitted a closer examination of CO_2 exchange processes during and after water stress.

Values of the net photosynthetic rate and Γ were used in calculating the photorespiration rate using the extrapolation method. The water balance was studied by determining the transpiration decline curves from excised shoots immediatelly after the CO_2 exchange measurements. These curves enabled transpiration rates in intact plants to be estimated. In addition, the water content and water saturation deficit were also determined from excised shoots after each series of CO_2 measurements. Needle dry weight, needle chlorophyll content, and soil water content were additional variables used.

The results of field measurements suggested that genetically controlled differences may exist in net photosynthetic rates among the four clones. These differences were found to be distinct in subsequent laboratory measurements. Values of Γ, the photorespiration rate, and dark respiration rate also varied among the clones.

Optimum temperatures for the net photosynthetic rate varied among the clones. With increasing temperature, dark respiration increased more rapidly and more curvilinearly than did the photorespiration rate in relation to net photosynthesis. This variation caused distinct differences in the ratios between CO_2 exchange characteristics among the four clones.

An inverse curvilinear relationship existed between Γ and the net photosynthetic rate. This result was in agreement with our earlier observations on CO_2 exchange in *Populus* clones and suggested that Γ may possess a diagnostic value as an indicator reflecting the net photosynthetic efficiency within a species or within a group of closely related species. In unstressed control plants, transpiration rates correlated with net photosynthetic rates among the four clones. Such a result indicated that a stomatal mechanism was responsible for this variation under conditions of low water deficit.

Different CO_2 exchange characteristics were investigated further by analysing their variation with changing soil water content. It was found that net photosynthetic rates were more sensitive to a decrease in soil moisture than values of Γ, particularly at low temperature. Photorespiration rates followed the observed variation in net photosynthesis with varying soil water content and reached the zero level at low soil water content. In contrast to this result, dark respiration rates decreased with decreasing soil water content but remained

at a detectable level even during severe water stress.

Rewatering caused an increase in CO_2 exchange metabolism, which suggested a distinct adaptation to stress conditions: rewatered plants had slightly higher rates of net photosynthesis, photorespiration, and dark respiration than stressed unwatered plants at the same soil water content.

The ratios between different CO_2 exchange characteristics distinctly reflected the variation in soil water content. For instance, a sharp increase in the dark respiration/net photosynthesis ratio with increasing temperature was typical for stressed unwatered plants and also visible in these plants after rewatering.

Transpiration rates and shoot water content in stressed plants were lower than those in the control material. Rewatering caused, however, an increase in transpiration rate; the rate did not, however, reach the high level found in the control plants. These results thus suggested a stomatal regulation of gas exchange in stressed plants after rewatering despite the partial disappearance of the water deficit in this material.

These results were analysed further in order to clarify the rôle of different mechanisms controlling net photosynthetic rate and in order to compare the present results with those obtained earlier under field conditions. It was evident that the variation in dark respiration or photorespiration did not alone explain the distinct decrease in the net photosynthetic rate during water deficit. When analysing the correlation between photorespiration and net photosynthesis, the criticism made in recent literature about the usual method for determining photorespiration rate was taken into account as well as the present knowledge of the photorespiratory CO_2 output as an integral part of the carboxylation reactions. The »leaf level» photorespiration rates obtained in the present study were recalculated according to the method which estimates photorespiration on the mesophyll level, and the differences caused by the method were also discussed.

An increase in Γ is, according to the present results and in agreement with our earlier observations, a normal result of water stress, particularly at high temperature. Since a stomatal mechanism cannot completely explain this situation, it is to be assumed that an increase takes place in the mesophyll component of the resistance to CO_2 diffusion under these conditions.

For validification of this conclusion, stomatal and mesophyll resistances were calculated from average net photosynthetic rate, Γ, and transpiration rate in each treatment group (unstressed control plants, stressed unwatered plants, and stressed rewatered plants respectively). These calculations showed that values of mesophyll resistance in stressed plants after rewatering were near to or even lower than those found in unstressed control plants. Stomatal resistance decreased after rewatering but remained, however, distinctly higher than the corresponding values for the control plants. In stressed unwatered plants, the total resistance to CO_2 diffusion was, as expected, very high, but the major part of this resistance seemed to depend on the mesophyll component.

These results are in agreement with earlier field experiments which showed a sharp decline in net photosynthesis at high temperatures during conditions of water deficit. The present study supports the earlier conclusions according to which stomatal control determines the net photosynthetic rate during moderate water deficit, but a severe and prolonged stress leads to an increase in the relative significance of other regulating processes. The rapid disappearance of such mesophyll regulation after rewatering in *Picea abies*, as compared to earlier studies on *Alnus* and *Betula*, suggests that the after-effect is genetically determined. Such variation also offers a mechanism for explaining different patterns of adaptation to stress conditions among or within tree species.

Further investigations are needed to clarify the exact physiological and biochemical nature of the genetically determined control mechanism localised in the mesophyll. Among the processes which warrant further study, photorespiration is one of the most important.

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