

Ecophysiological studies on the shrub *Vaccinium myrtillus* L. taken from a wide altitudinal range

F.I. Woodward

Department of Botany, University of Cambridge, Downing Street, Cambridge, CB2 3EA, UK

Summary. Observations have been made on the gas exchange and morphology of *Vaccinium myrtillus* taken from altitudes of 200 m, 610 m and 1,100 m along an altitudinal gradient in central Scotland. Under saturating irradiance, optimum temperatures and a range of vapour pressure deficits, photosynthetic rate and stomatal conductance increased with the altitude of origin of the populations. Correlated with these increases was an increase in the adaxial stomatal density with altitude. This response to altitude could be simulated in controlled conditions, by growing plants in a CO₂ concentration below ambient, similar to that expected at altitude.

Plant height decreased with altitude, a feature which was maintained in cultivation. Stem rigidity declined with altitude, in a manner which is predicted to limit the reproductive capacity of the population from 1,100 m in high wind speeds.

Total leaf nitrogen increased with altitude. The nitrogen economy of the shoot is discussed in terms of nitrogen availability for stems and leaves and its control over maximum rates of photosynthesis, competitive ability and reproductive capacity.

Key words: Gas exchange – Morphology – Altitude – CO₂ effects – *Vaccinium*

The classic studies by Turesson (1925, 1930) and Clausen et al. (1940) have demonstrated the powerful selective pressures of climate on genetic divergence within plant species. Their studies concentrated on genetic rather than plastic responses to the altitudinal variation of climate.

In contrast, work aimed at explaining the altitudinal distribution of plants has been generally concerned with investigations on interspecific differences in response to changes in climatic variables (e.g. Woodward and Pigott 1975). Of these variables, temperature and atmospheric pressure decrease with altitude, whilst wind speed increases. The irradiance on a clear day increases with altitude, although the long term mean irradiance may decrease, dependent on the frequency and depth of cloud cover (Barry 1981).

Woodward (1975, 1979, 1983) has shown that interspecific differences in leaf and plant form are crucial in determining the response of plants to temperature and wind and therefore can control plant distribution.

The search for physiological changes with altitude (for example Billings et al. 1961; Mooney et al. 1964, 1966; Gale 1972; Tranquillini 1979) has centred on photosynthetic responses to the reduced partial pressures of carbon dioxide with altitude. However no consensus has emerged which discriminates between species of diverse altitudinal range.

In a related area of study Körner et al. (1979) have shown that the stomatal conductance of *Vaccinium myrtillus* increases with altitude in the Austrian Alps. In addition the leaves are hypostomatous in the lowlands but amphistomatous on the mountains. Davies et al. (1978), working on prostrate and erect plants of the shrub *Cytisus scoparius* from exposed and sheltered sites, have shown population differences in stomatal behaviour which are correlated with growth form and habitat and may also reflect differences in response to the water vapour pressure deficit of the air. In general, the vapour pressure deficit decreases with altitude whilst wind speed increases (Barry 1981), suggesting that along an altitudinal gradient there may be selection for prostrate habit, in relation to high wind speeds, but alongside changes in stomatal behaviour which may lead to higher stomatal conductances.

It appears therefore that interrelated changes in plant gas exchange and plant form may occur with altitude, however the nature of this link is unclear. This paper reports on investigations which attempt to quantify these relationships and in particular sets out to investigate the following four responses of *Vaccinium myrtillus* to the changes in climate with altitude on a British mountain:—

1. The photosynthetic responses to the fall in partial pressure of carbon dioxide with altitude.
2. The response of stomatal conductance to variations in the water vapour pressure deficit between the air and leaf.
3. The changes in stomatal density with altitude.
4. The changes in plant form with altitude.

The overall objective of the study is therefore to investigate the relationships between ecophysiological responses of different populations and the typical climate of these populations.

Materials and methods

Field data

The field sites were on the mountain of Ben More in the Central region of Scotland, Great Britain. Further details of the mountain and its climate are described by Woodward

(1983). *Vaccinium myrtillus* L. occurs from the base of the mountain, at 200 m, to just below the summit at 1,150 m. Ben More has no significant tree cover because of clearance by man and populations of *Vaccinium* therefore occur in open, often sheep grazed habitats at all altitudes. This is in contrast to its regular, but not obligate occurrence as an understorey dominant under *Pinus sylvestris* L. in other areas of Scotland.

Five populations, up to 100 m apart, at each of the three altitudes of 200 m, 610 m and 1,100 m were selected for ecophysiological investigation. The sites all had the same north-westerly aspect, similar slopes and acid soil types. *Vaccinium* was the co-dominant species at each site. Species diversity decreased with altitude and only the montane moss, *Racomitrium lanuginosum* (Hedw.) Brid. occurred at all of the sites.

The requirement for complex and extensive measurements on plant gas exchange could not be realised in the field and so plants were transplanted from the field to a controlled environment facility at the University of Cambridge. The plants were collected from the field on July 4th, 1984. At each altitude two sections of turf of about 300 mm × 150 mm were removed from each of 5 discrete populations of *Vaccinium*. The turf was removed to the depth of the underlying rock fragments (120 mm at an altitude of 200 m, declining to 30 mm at 1,100 m). The turf was irrigated with distilled water, placed in polyethylene containers and transported to Cambridge, within two days of collection.

Controlled environment conditions

In Cambridge, the populations were placed in a growth chamber with a 14 h photoperiod at 18°C and a night temperature of 7°C, with a relative humidity of 75% throughout and a mean CO₂ mole fraction of 309 μmol mol⁻¹. This treatment corresponded with the mean temperature during the growing season at an altitude of about 600 m (Woodward 1983). The mean irradiance was 300 μmol m⁻² s⁻¹ and was provided by a Wotan HQI 1,000 W lamp, with a spectral distribution very similar to sunlight. The single treatment was used to provide a controlled environment for the measurements of gas exchange in a climate similar to that in the field. The measurements of gas exchange were taken soon after removal from the field, in order that the measurements should be close to those in situ.

The plants were watered regularly and experimental studies were instituted after 6 days in the controlled environment. This allowed sufficient time to detect damaged or dying plants and for equilibration of plant water potential. Water potential was measured with a J-14 hydraulic press (Hunt et al. 1984) and at the end of 6 days all measurements of leaf water potential fell in the range of -0.6 to -1 MPa, typical of that recorded in the field.

The experimental period lasted for a further 14 days and all measurements were carried out on plants with leaves which had developed in the field. Plants with leaves which had expanded in the controlled environment were not used.

Measurements of plant gas exchange

The areas of individual leaves of *Vaccinium* were small, in the range of 15–150 mm², so in order to maintain sensi-

tivity in the measurements of gas exchange, shoots of 6–8 fully expanded leaves were sealed in cuvettes. The leaves on the shoot were illuminated with similar irradiances at a mean of 500 μmol m⁻² s⁻¹, at which point the photosynthetic rate of all plants had been shown to be light saturated. The shoot cuvette was constructed of glass and a fan ventilated the cuvette, providing a mean boundary layer conductance of 0.4 mol m⁻² s⁻¹. The measurements of gas exchange were carried out in the controlled conditions described above. The cuvette temperature was not controlled and consequently leaf temperature varied between 19 and 25°C. Measurements showed that over this range of temperature and at a mean leaf water vapour pressure deficit of 10 mmol mol⁻¹, the photosynthetic rate was optimal and rather insensitive to temperature.

The supply air, with a CO₂ mole fraction of 390 μmol mol⁻¹, was passed to a mass flow controller (Vacuum General), which provided a constant flow of air to be humidified at 25°C. After humidification the air was bubbled through water at selected, controlled temperatures, in order to provide a range of dew-point temperatures. The variations in leaf temperature and the dew-point of the inlet air to the cuvette provided a range of water vapour pressure deficits between 5 and 20 mmol mol⁻¹. The accuracy of the required humidification was checked with a dew-point hygrometer similar in design to that described by Easty and Young (1976).

The effect of the reduced partial pressure of carbon dioxide, with altitude, on photosynthesis was simulated by subjecting shoots to a range of dilutions of carbon dioxide from the supply air concentration to 25 μmol mol⁻¹, using a critical-flow orifice diluter (The Analytical Development Company Ltd.) and at a constant vapour pressure deficit of 10 mmol mol⁻¹. The effects of the shoot on the carbon dioxide and water vapour concentrations of the gas stream through the cuvette were measured with a dual differential water vapour and carbon dioxide infra-red gas analyser (Binos 2, Leybold-Heraeus Ltd.). The units of measurement for the leaf conductance to water vapour and carbon dioxide are those defined by Cowan (1977).

Other plant measurements

Measurements of shoot height, leaf area, leaf thickness, stem diameter and specific leaf area were taken within 48 hours of collection on 10 shoots originating from the different populations at the three altitudes. Leaf thickness was measured under a microscope on fresh leaf sections. Stem diameter was taken as the mean of 10 measurements along the stem with a micrometer.

Measurements of stomatal density were taken on the 5 most recently expanded leaves from samples of each of the populations at the three altitudes, using ethyl acetate impressions of the adaxial and abaxial surfaces.

Total leaf nitrogen was determined on two batches of 40 leaves from each of the three altitudes, using the technique described in Harbinson and Woodward (1984).

The mechanical properties of the shoots were measured as elastic and plastic moduli in the manner described by Grace and Russell (1977). These measurements were used in combination with wind speed profiles, at wind speeds of 3, 5 and 12 m s⁻¹ above the shoots in the turbulent flow in a wind tunnel (Woodward 1983), to predict the bending stress exerted on shoots at a range of wind speeds.

The drag coefficients of leaves were determined by measuring the bend of the stem after the successive removal of pairs of leaves at similar insertions, until the shoots were denuded of leaves. The force required to bend the stem is known from the measurements described above and the force absorbed by the leaves is determined by difference. The drag coefficient was determined as described in Grace (1977) and Jones (1983).

The sensitivity of elastic and plastic stem displacement in relation to wind speed for plants bearing fruits could not be tested directly because all of the plants that were collected were vegetative. Fruits of *Vaccinium* (mean weight 0.36 g) were therefore collected later from an altitude of about 600 m and attached to stems with fine copper wire. Stem displacement was then observed in the wind tunnel, at wind speeds of 3, 5, and 12 m s⁻¹.

Simulating the effects of altitude on stomatal density

An experiment was designed to test the possibility that the observed changes in the stomatal density of the leaves of *Vaccinium* may respond to changes in the partial pressure of CO₂ that occur over an altitudinal range of about 1,000 m. Although the partial pressure of CO₂ declines with altitude, the mole fraction remains close to constant (Gale 1972). An ideal simulation of the effects of altitude mediated by CO₂ should therefore be carried out at reduced pressure. This has not yet proved possible in the controlled environment facility at Cambridge and so the altitudinal changes in CO₂ partial pressure, and therefore concentration, have been achieved by changes in the CO₂ mole fraction.

Plants of *Vaccinium* which were collected from 1,100 m in 1984 had been grown in the Botanic Gardens in Cambridge. In May 1985 these plants were removed to a controlled environment chamber operating in the same environmental conditions as described above. Eighteen plants, which were actively undergoing leaf expansion, were selected as experimental material for observing the response of stomatal density to the mole fraction of CO₂. Each plant was enclosed within a cylindrical cuvette of glass which was 20 mm in diameter and 35 mm in length. Carbon dioxide was supplied to each chamber from a gas cylinder, following humidification to an average dew-point temperature of 10° C. Three mole fractions of CO₂ were used; 250, 350 and 450 μmol mol⁻¹ (all ± 5%). Each gas cylinder delivered gas to six plants, at a rate which maintained the mole fraction within the nominal range.

An evaluation of the altitudinal simulation may be best realised in terms of CO₂ concentration, which takes into account the effects of altitudinal changes in both pressure and temperature. The CO₂ concentrations in the cuvettes were 470, 655 and 842 mg m⁻³, compared with CO₂ concentrations of 544, 574 and 600 mg m⁻³ at altitudes of 1,100, 610 and 200 m, predicted on the basis of the climatic conditions described by Woodward (1983) and the change in atmospheric pressure described by Jones (1983). The two lower concentrations of CO₂ in the experiment therefore bracketed the predicted range of concentrations in the field. The highest concentration was included to determine the breadth of the response of stomatal density and distribution to CO₂ concentration.

The plants were maintained in the experimental treat-

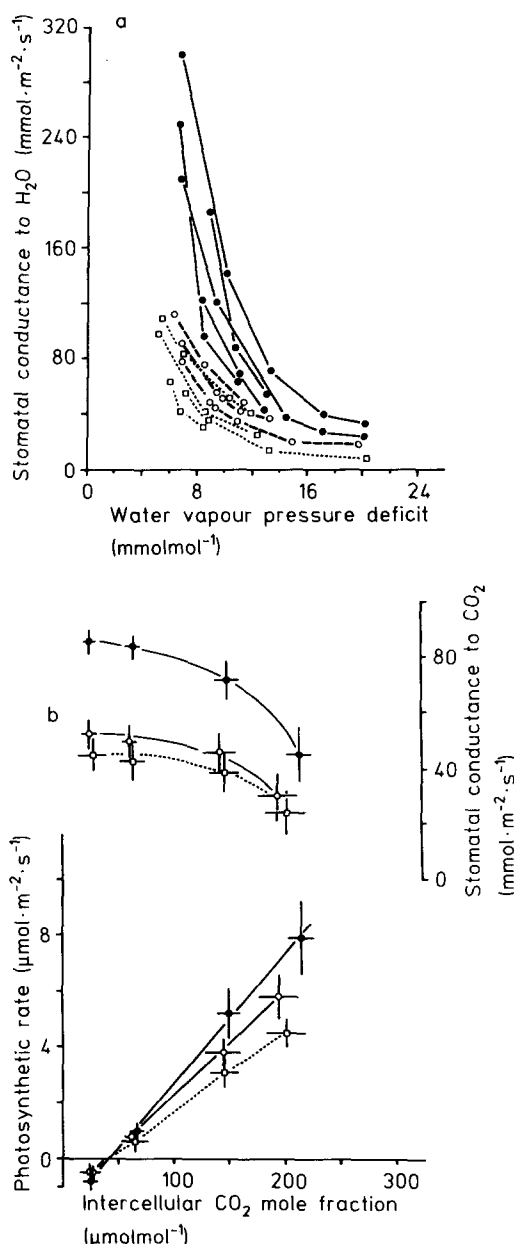


Fig. 1 a, b. Stomatal conductance of three populations of *V. myrtillus* in response to variations in ambient conditions. a Response to water vapour pressure deficit. b Response of stomatal conductance and photosynthetic rate to intercellular CO₂ mole fraction and showing standard errors for the mean values of 10 different shoots. □, population from 200 m; ○, population from 610 m; ●, population from 1,100 m

ments for about three weeks, after which the newly expanded leaves were analysed for stomatal distribution.

Results

The response of stomatal conductance to changes in humidity and the CO₂ mole fraction

The response of stomatal conductance to the vapour pressure deficit between the leaf and air is shown on Fig. 1a. All three populations of *Vaccinium* show the similar response of decreasing conductance with increasing vapour

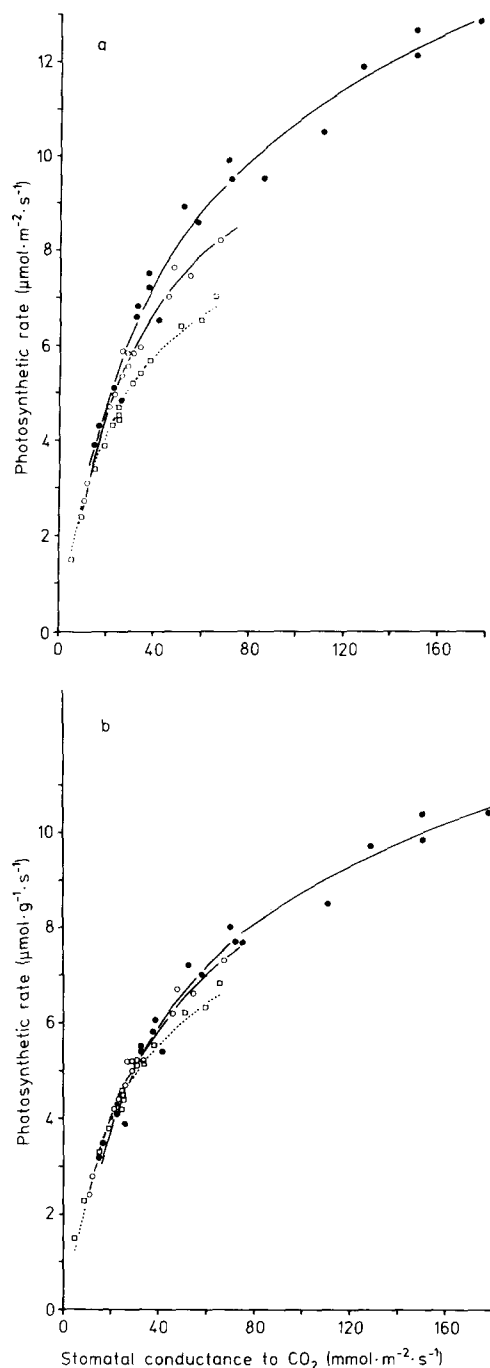


Fig. 2a, b. Photosynthetic rates of *V. myrtillos* at different stomatal conductances. **a** Leaf area basis. **b** Leaf nitrogen basis. Symbols as for Fig. 1, curves are power regressions, which gave significant fits to the data ($P < 0.05$)

pressure deficit. The populations also fall in a series of absolute conductance, increasing with the altitude of origin.

A similar series of responses to the intercellular CO_2 mole fraction may also be seen (Fig. 1b), with all populations of *Vaccinium* showing a decrease in conductance with increasing CO_2 , and the population from 1,100 m having the highest stomatal conductance. The altitudinal differences in the responses of the photosynthetic rates and stomatal conductances to the CO_2 mole fraction and to the water vapour pressure deficit remained unchanging

throughout the experimental period, implying that the laboratory measurements are fair representations of differences in the field. The differences in the photosynthetic rates have also been confirmed by limited field observations (Butler and Woodward unpublished work).

Photosynthetic responses

The responses of photosynthesis to changes in the intercellular mole fractions of CO_2 are shown on Fig. 1b. The slopes of the linear regressions between the photosynthetic rates and intercellular mole fraction of CO_2 were used to estimate the mesophyll conductance (Jones 1983). The mesophyll conductance increases significantly ($P < 0.05$) from $28.8 \text{ mmol m}^{-2} \text{ s}^{-1}$ for the population from 200 m, through $37.0 \text{ mmol m}^{-2} \text{ s}^{-1}$ for 610 m to $46.6 \text{ mmol m}^{-2} \text{ s}^{-1}$ for the population from 1,100 m.

The change in the partial pressure of CO_2 with altitude will also be accompanied by an equal, relative change in the partial pressure of oxygen. The reduction in the partial pressure of oxygen may also affect the altitudinal trend of the photosynthetic rate through reductions in the rate of photorespiration. Data of Slatyer (1970) for *Atriplex hastata* show that per unit decrease in the partial pressures of the gases, the ratio of the decrease in the photosynthetic rate due to the fall in CO_2 , to the increase in the rate due to oxygen is about 2,200 to 1. Ignoring the effects of oxygen over the altitudinal range of 200–1,100 m will lead to an underestimate of the photosynthetic rate by about 5%, which is well within the errors of measurement and may be discounted.

The influence of stomatal conductance on photosynthetic rate is shown on Fig. 2a, using measurements of the photosynthetic rates and stomatal conductances from the experiment on the response of stomatal conductance to humidity (Fig. 1a). Once the stomatal conductance exceeds the magnitude of the mesophyll conductance, the photosynthetic rate at a given conductance increases with the altitude of origin of the experimental material. The effect of the higher stomatal conductances of the population of *Vaccinium* from 1,100 m is a greater potential range of photosynthetic rate than for the populations from lower altitudes.

The altitudinal differences in photosynthetic rate on a leaf area basis are diminished when the rate is expressed on a leaf nitrogen basis (Fig. 2b). This reflects the slight increase in leaf nitrogen per unit of leaf area with increasing altitude (Table 1), although there is no obvious altitudinal trend in either specific leaf area or leaf thickness (Table 1).

The dark respiration rate, measured at a mean temperature of 21°C , increased from $0.55 \pm 0.05 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ (standard error of the mean for 9 plants) for the population from 200 m, through $0.59 \pm 0.11 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ at 610 m to $0.92 \pm 0.07 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ at 1,100 m.

Morphological and anatomical observations

The measurements of plant height and stem diameter (Table 1) show that plant stature declines with altitude, although stem diameter only declines above 610 m.

Adaxial stomatal density increases with altitude in the same manner as *Vaccinium myrtillos* in the Austrian Alps (Körner et al. 1979). In this case *Vaccinium* grew in the open, whereas the observations in the Alps were also confounded with shade, with populations of *Vaccinium* from

Table 1. Characteristics of shoots of *Vaccinium* at 3 altitudes

Measurement	Altitude		
	200 m	610 m	1,100 m
Plant height (mm)	48 ± 4	32 ± 3	11 ± 1
Stem diameter (mm)	0.83 ± 0.04	0.86 ± 0.04	0.71 ± 0.01
Mean stem weight (mg)	7.6 ± 1.5	6.0 ± 1.2	1.4 ± 0.4
Mean leaf area (cm ²)	0.29 ± 0.06	0.30 ± 0.06	0.19 ± 0.04
Mean leaf number per stem	5.3 ± 0.2	5.5 ± 1.0	4.9 ± 0.5
Leaf stomatal density:			
adaxial surface (mm ⁻²)	12 ± 5	17 ± 3	63 ± 4
abaxial surface (mm ⁻²)	287 ± 24	239 ± 10	229 ± 10
Specific leaf area (mm ² mg ⁻¹)	13.7 ± 0.9	17.5 ± 1.0	16.0 ± 0.8
Leaf thickness (mm)	0.20 ± 0.01	0.17 ± 0.01	0.21 ± 0.01
Total leaf nitrogen ^a (g _N m ⁻²)	1.02	1.12	1.23
Total leaf nitrogen per stem (mg)	0.157	0.185	0.115
Drag coefficients			
Youngest leaves	0.57 ± 0.04	0.57 ± 0.03	0.51 ± 0.03
Remaining leaves	0.48 ± 0.03	0.31 ± 0.03	0.19 ± 0.02

Standard errors shown

^a Mean of two measurements, each of approximately 40 leaves

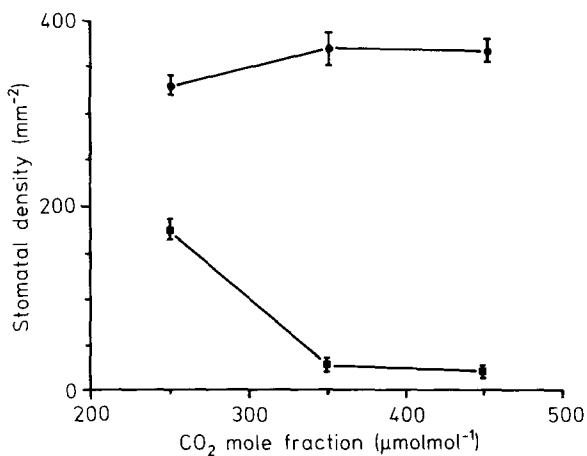


Fig. 3. Response of stomatal density to the ambient mole fraction of CO₂. ■, adaxial surface; ●, abaxial surface. Standard errors of the mean for 6 shoots

lower altitudes only found in forest shade. This may explain the hypostomatous nature of *Vaccinium* in lowland Austria but an absence of hypostomaty from open sites in lowland Scotland.

In controlled conditions the adaxial stomatal density was found to be sensitive to the mole fraction of CO₂ below 350 μmol mol⁻¹, with almost an order of magnitude increase in density at the lowest mole fraction of 250 μmol mol⁻¹ (Fig. 3). Leaf area, epidermal cell area and abaxial stomatal density were insensitive to changes in the mole fraction of CO₂.

Aerodynamic properties of Vaccinium

Leaves of *Vaccinium* from 1,100 m had the lowest drag coefficients (Table 1) and would therefore be subjected to the lowest transfer of momentum at a given wind speed. The

effect of the absorption of momentum on the elastic and plastic bending of stems was measured at wind speeds of 3, 5 and 12 m s⁻¹ and bending at higher wind speeds was predicted from these measurements.

The short, vegetative stems are expected to survive wind speeds up to 30 m s⁻¹. However there was very clear differentiation between populations when the stems bear fruits. When loaded with two fruits (Fig. 4), stems of *Vaccinium* from 1,100 m were readily bent with the flow of wind and predictions indicate that irreversible displacement of the stem to the horizontal should occur, perhaps with stem breakage, when the wind speed above the plants exceeds about 28 ms⁻¹. In contrast, it was predicted that plants from both 200 and 610 m should be barely affected by such wind speeds (Fig. 4).

Discussion

Tureson (1925, 1930) and Clausen et al. (1940) demonstrated that an obvious effect of the mountain environment was on plant form, which became more prostrate with altitude. This feature was retained during cultivation in lowland gardens, demonstrating genetic control. This is also true for plants of *Vaccinium* originating from 1,100 m. This prostrate, or low growing characteristic has been shown to be a competitive disadvantage in lowland sites where the vegetation is taller (Woodward and Pigott 1975) but reduces the sensitivity of plant growth to the high wind-speeds on mountain tops (Woodward 1983). These opposing selective forces correspond with altitudinal differentiation in *Vaccinium* with maximum stem extension in the lowlands and the converse at the mountain top.

Correlated with these genetically controlled changes in stature are increases in stomatal conductance, photosynthetic rate and total leaf nitrogen. The prostrate population from 1,100 m exhibits the highest stomatal conductance, a response which will be amplified by the decrease in vapour

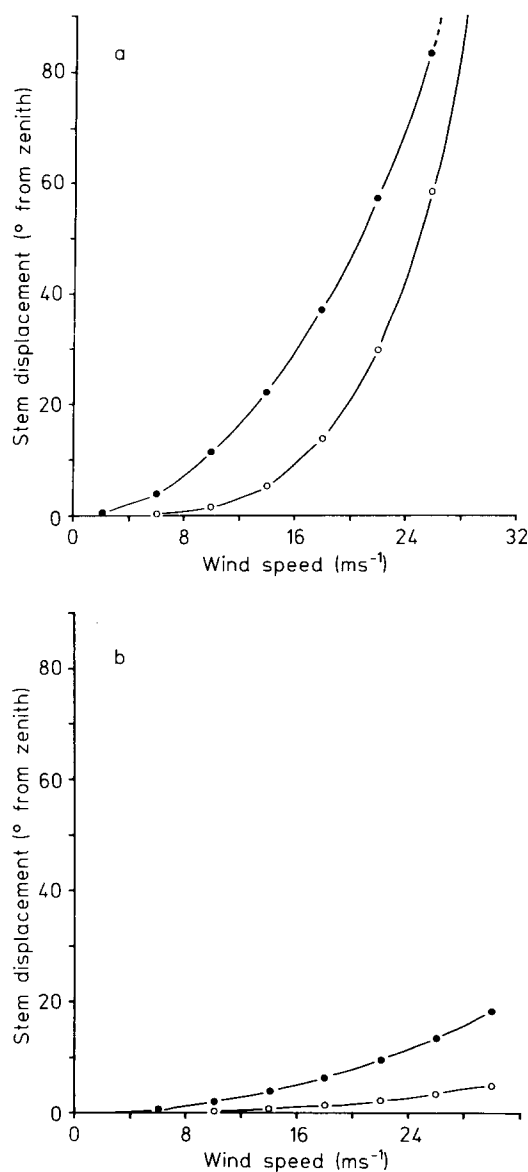


Fig. 4a, b. Predicted elastic and plastic displacement of stems of *V. myrtillus*, bearing two fruits, at different wind speeds. **a** Population from 1,100 m. **b** Population from 200 m. ●, elastic displacement; ○, plastic displacement

pressure (Fig. 1a) with altitude (Körner and Mayr 1980). In addition the small plants are close to the frequently wet substrate of the moss, *Racomitrium lanuginosum*, a feature which will also minimise the leaf vapour pressure deficits.

The short stems of the plants from 1,100 m are also the least rigid. Predictions from wind tunnel measurements show that these thin stems will survive wind buffeting in high wind speeds. However if the stems are reproductive and bear two fruits, then stem breakage may occur above wind speeds of about 28 m s^{-1} . Records from British Meteorological Stations in Scotland (Meteorological Office 1983) show that gusts of 40 m s^{-1} occur regularly through the summer above 800 m, suggesting that the control of stem rigidity at high altitudes will be at the expense of reproductive capacity. The likely selection pressure will be for one, or at the most two fruits per stem in exposed

sites, a prediction which is born out by observations in the field at high altitude, where stems rarely bear more than one fruit.

The growing season decreases markedly with altitude on British mountains (Woodward and Pigott 1975). In addition the CO_2 concentration declines monotonically with altitude (Gale 1972), a feature which will reduce the maximum photosynthetic rate. Populations of *Vaccinium* provide clear evidence of increasing stomatal conductance (Fig. 1) and photosynthetic rate (Fig. 2) with altitude, responses which are correlated with increases in the adaxial stomatal density (Table 1). This increase in density may be simulated by changes in the CO_2 mole fraction (Fig. 3), indicating a method by which the plant can detect altitude. The field response has been observed in high (about 1,000 m) altitudinal transplants for populations from both upland and lowland sites (Butler 1985), indicating that the response is not just a feature of populations of *Vaccinium* from high altitude.

The proportion of the total conductance due to the adaxial stomata has been predicted from established equations for diffusion theory (Jones 1983) and using microscopic measurements of fully open stomata. These measurements show that the adaxial stomata contribute little to the total stomatal conductance in populations from 200 m (3%) and 610 m (5%). However this proportion rises to 21% in the population from 1,100 m.

The increase in stomatal density with the decline in the CO_2 concentration with altitude (Fig. 3) plus the increase in stomatal conductance with decreasing CO_2 concentration (Fig. 1b), and in addition to the maximisation of stomatal conductance at low vapour pressure deficits (Fig. 1a), all act in combination to maximise the potential range of stomatal conductance at the highest altitude. The total effect on conductance may be realised in an increase in the photosynthetic rate in the shortened growing season at altitude; however the potential increase will also be limited by the mesophyll conductance (Fig. 2).

Measurements of the photosynthetic rate at a range of CO_2 mole fractions, from $390 \mu\text{mol mol}^{-1}$ to below the CO_2 compensation point (Fig. 1b), show that mesophyll conductance increases with altitude. Within the errors of measurement and replication, the mesophyll conductance is constant over the normal range of CO_2 mole fractions likely to be experienced in the field. This implies that the amount of the enzyme ribulose biphosphate carboxylase-oxygenase (Rubisco) is controlling the rate of photosynthesis, at a fixed CO_2 mole fraction, (Farquhar and Sharkey 1982) and that the mesophyll conductance is a measure of the amount of Rubisco in the leaf.

Rubisco is the major protein in the leaf, with a level which is closely correlated with total leaf nitrogen (Ryle and Hesketh 1969; von Caemmerer and Farquhar 1981). The observations of an increase in leaf nitrogen with altitude in *Vaccinium* may therefore explain the increase in mesophyll conductance with altitude.

The general trend of soil nitrogen with altitude is opposite from that observed for leaves (Wielgolaski et al. 1975) suggesting the occurrence of some mechanism for maximising leaf nitrogen, which should in turn lead to an increase in mesophyll conductance. In the case of *Vaccinium* this maximisation should be considered along with the nitrogen status of stems, which will also be sinks for nitrogen. Measurements of stem nitrogen were not made on the popula-

Table 2. Nitrogen economy of stems from three altitudes

Measurement	Altitude		
	200 m	610 m	1,100 m
Total leaf nitrogen per stem. (mg)	0.157	0.185	0.115
Total nitrogen in stem at 0.97% of dry weight (mg)	0.074	0.058	0.014
Proportion of total nitrogen in leaves. (%)	68	76	89
Proportion of total dry weight in leaves (%)	60	61	81

tions studied here, however measurements of stems from adjacent sites in Scotland showed that stem nitrogen, on a unit dry weight basis, was unchanging between altitudes of 200 m–1,000 m, with a mean content of 0.97%. This measurement has been used to predict the total nitrogen in stems of *Vaccinium* in the present study, alongside the measurements of leaf nitrogen (Table 2).

The nitrogen in leaves, as a proportion of the total in stem plus leaves, increases with altitude and provides evidence for the maximisation of leaf nitrogen with altitude. As stem nitrogen remains a constant fraction of dry weight with altitude, any reductions in stem weight with altitude may increase the supply of nitrogen to the leaves. The proportion of above ground dry weight in leaves also increases with altitude (Table 2), in similar ratio to the proportion of nitrogen in leaves, suggesting that reducing stem stature with altitude increases the available nitrogen supply to leaves.

In conclusion, for populations of *Vaccinium*, tall stems in the lowlands, where competition for irradiance is most intense, is at the expense of maximum photosynthetic rate but maximises radiant interception, with no limitations on the ability of the stem to bear a number of fruits. In the uplands, where the competition for irradiance is not high but where the growing season is short, a short, weak stem will effectively lead to greater rates of photosynthesis than in the lowlands, through the nitrogen economy of the leaves and the maximisation of stomatal conductance, but at the expense of reproductive capacity.

Acknowledgements. I am grateful to Dr. Ch. Körner for many discussions on the ecophysiology of mountain plants and to Dr. P.J. Grubb and Dr. B.G. Williams for valuable comments on the manuscript.

References

- Barry RG (1981) Mountain weather and climate. Methuen & Co.Ltd., London
- Billings WD, Clebsch EEC, Mooney HA (1961) Effect of low concentration of carbon-dioxide on photosynthesis rates of two races of *Oxyria*. *Science* 133:1834
- Butler P (1985) The ecology of dwarf shrub species from diverse altitudes and latitudes. PhD thesis. University of Cambridge, p 187
- Caemmerer S von, Farquhar GD (1981) Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* 153:376–387
- Clausen J, Keck DD, Hiesey WM (1940) Experimental studies on the nature of species. I. The effect of varied environments

- on western north American plants. Carnegie Institution of Washington Publication 520:1–452
- Cowan IR (1977) Stomatal behaviour and environment. *Adv Bot Res* 4:117–228
- Davies WJ, Gill K, Halliday G (1978) The influence of wind on the behaviour of stomata of photosynthetic stems of *Cytisus scoparius* (L.) Link. *Ann Bot* 42:1149–1154
- Easty AC, Young S (1976) A small scale dewpoint humidity measurer. *J Phys E* 9:106–110
- Farquhar GD, Sharkey TD (1982) Stomatal conductance and photosynthesis. *Ann Rev Plant Physiol* 33:317–345
- Gale J (1972) Availability of carbon dioxide for photosynthesis at high altitudes. *Ecology* 53:494–497
- Grace J (1977) Plant response to wind. Academic Press, London
- Grace J, Russell G (1977) The effect of wind on grasses. III. Influence of continuous drought or wind on anatomy and water relations in *Festuca arundinacea* Schreb. *J Exp Bot* 28:268–278
- Harbinson J, Woodward FI (1984) Field measurements of the gas exchange of woody plant species in simulated sunflecks. *Ann Bot* 53:841–851
- Hunt ER, Weber JA, Gates DM (1984) Differences between tree species in hydraulic press calibration of leaf water potential are correlated with specific leaf area. *Plant Cell Env* 7:597–600
- Jones HG (1983) Plants and microclimate. Cambridge University Press, Cambridge
- Körner Ch, Mayr R (1980) Stomatal behaviour in alpine plant communities between 600 and 2,600 metres above sea level. In: Grace J, Ford ED, Jarvis PG (eds) *Plants and their atmospheric environment*. Blackwell, Oxford, pp 205–218
- Körner Ch, Scheel JA, Bauer H (1979) Maximum leaf diffusive conductance in vascular plants. *Photosynthetica* 13:45–82
- Meteorological Office (1983) Monthly weather report, vol 100. Her Majesty's Stationery Office, London
- Mooney HA, Wright RD, Strain BR (1964) The gas exchange capacity of plants in relation to vegetation zonation in the White Mountains of California. *Amer Midl Nat* 72:281–297
- Mooney HA, Strain BR, West M (1966) Photosynthetic efficiency at reduced carbon dioxide tensions. *Ecology* 47:490–491
- Ryle GJA, Hesketh GD (1969) Carbon dioxide uptake in nitrogen deficient plants. *Crop Sci* 9:451–454
- Slatyer RO (1970) Comparative photosynthesis, growth and transpiration of two species of *Atriplex*. *Planta* 93:175–189
- Tranquillini W (1979) *Physiological ecology of the Alpine timberline*. Springer, New York
- Turesson G (1925) The plant species in relation to habitat and climate. *Hereditas* 6:147–236
- Turesson G (1930) The selective effect of climate upon the plant species. *Hereditas* 14:99–152
- Wielgolaski FE, Kjelvik S, Kallio P (1975) Mineral content of tundra and forest tundra plants in Fennoscandia. In: Wielgolaski FE (ed) *Fennoscandian Tundra Ecosystems. Part I. Plants and microorganisms*. Springer, Berlin, pp 316–332
- Woodward FI (1975) The climatic control of the altitudinal distributions of *Sedum rosea* (L.) Scop. and *S. telephium* L. II. The analysis of plant growth in controlled environments. *New Phytol* 74:335–348
- Woodward FI (1979) The differential temperature responses of the growth of certain plant species from different altitudes. I. Growth analysis of *Phleum alpinum* L., *P. bertolonii* D.C., *Sesleria albicans* Kit. and *Dactylis glomerata* L. *New Phytol* 82:385–395
- Woodward FI (1983) The significance of interspecific differences in specific leaf area to the growth of selected herbaceous species from different altitudes. *New Phytol* 95:313–323
- Woodward FI, Pigott CD (1975) The climatic control of the altitudinal distributions of *Sedum rosea* (L.) Scop. and *S. telephium* L. I. Field observations. *New Phytol* 74:323–334.

Received September 19, 1985