## Ecology of Central European Forests

Vegetation Ecology of Central Europe, Volume I

Revised and Extended Version of the 6th German Edition Translated by Laura Sutcliffe



## **Contents of Volume I**

| Pai | rt I  | The Natu  | ral Environment and Its History   |  |  |  |
|-----|---|---|---|--|--|--|
| 1   |   | Environmental and Historical Influences on the Vegetation of Central Europe |   |  |  |  |
|     | 1.1<br>1.2                                    | An Ov   | imate and Phytogeography of Central Europeerview of the Geology and Soils of Central Europe |  |  |  |
|     | 1.3   | Histori   | cal Influences on the Vegetation of Central Europe  |  |  |  |
| 2   | Life  | Life Forms and Growth Types of Central European                             |   |  |  |  |
|     | Pla   | nt Species  | S   |  |  |  |
|     | 2.1   |   | orms  |  |  |  |
|     | 2.2   | Endoge  | enous Rhythms   |  |  |  |
|     | 2.3   | Plant A   | Anatomy and Morphology  |  |  |  |
| Pa  | rt II   | The Role  | e of Man  |  |  |  |
| 3   | The Central European Vegetation as the Result |   |   |  |  |  |
|     |   |   | of Human Activity   |  |  |  |
|     | 3.1   | Phases  | of Forest Clearance   |  |  |  |
|     | 3.2   | The Ef  | fects on the Vegetation of Low-Intensity  |  |  |  |
|     |   | Grazin  | g and Woodland Use  |  |  |  |
|     |   | 3.2.1   | The Opening Up and Destruction of the Forest  |  |  |  |
|     |   | 3.2.2   | The Spread of Pasture Weeds   |  |  |  |
|     |   | 3.2.3   | Soil Degradation Through Low-Intensity Grazing  |  |  |  |
|     | 3.3   | From C  | Coppiced Woodlands to Modern Forestry   |  |  |  |
|     |   | 3.3.1   | Coppicing With and Without Standards  |  |  |  |
|     |   | 3.3.2   | High Forest Management  |  |  |  |
|     | 3.4   | The Do  | evelopment of Arable Cultivation and Arable Weeds   |  |  |  |
|     |   | 3.4.1   | Pre-industrial Agriculture  |  |  |  |
|     |   | 3.4.2   | The Effects of Technological Advances on Crop Fields  |  |  |  |
|     |   |   | and Low-Intensity Pastures  |  |  |  |

|     | 3.5   | The De   | evelopment of Meadows, Intensive Pastures               |
|-----|-------|----------|---|
|     |       | and Ot   | her Grassland   |
|     |       | 3.5.1    | Straw and Fodder Meadows                                |
|     |       | 3.5.2    | Continuous and Rotational Grazing                       |
|     |       | 3.5.3    | Agricultural Biocide Use, Energy Use and Crop Yield     |
|     | 3.6   | Change   | es in Landscape Hydrology                               |
|     |       | 3.6.1    | Modifications of River Valley Landscapes                |
|     |       | 3.6.2    | The North Sea Dykes and Their Consequences              |
|     |       | 3.6.3    | The Destruction of Mires, and Attempts                  |
|     |       |          | to Restore Them   |
|     |       | 3.6.4    | Increasing Exposure of the Vegetation to Drought        |
|     | 3.7   | Chemi    | cal Pollution of the Environment and Its Impact         |
|     |       |          | Vegetation  |
|     |       | 3.7.1    | Long- and Short-Range Effects of Chemical Pollutants    |
|     |       | 3.7.2    | Nutrient Enrichment of Soils and Water Bodies           |
|     |       | 3.7.3    | Acid Deposition   |
|     |       | 3.7.4    | Sulphur Dioxide and Ozone Emissions                     |
|     |       | 3.7.5    | Emissions of Heavy Metals and Other Substances          |
|     | 3.8   | Chang    | es in Game Densities and Their Effect on the Vegetation |
|     | 3.9   |          | uction of Non-native Plant Species                      |
|     | 3.10  |          | t Species Losses and Impoverishment                     |
|     |       |          | nt Communities  |
|     | 3.11  |          | fects of Recent Climate Change on the Vegetation        |
|     |       |          | · ·   |
| Par | t III | Genera   | d Ecology of Central European Forests                   |
| 4   | A hio | tic Cone | ditions, Flora, Ecosystem Functions                     |
| •   |       |          | Human Influence   |
|     | 4.1   |          | ora of Central European Forests                         |
|     | 4.2   |          | eographic Distribution of Forest Vegetation             |
|     |       | 4.2.1    | Zonal, Extrazonal and Azonal Forest Vegetation          |
|     |       | 4.2.2    | The Potential Natural Vegetation of Central Europe      |
|     |       | 4.2.3    | Altitudinal Belts of Forest Vegetation                  |
|     |       | 4.2.4    | Water and Temperature Limitations of Forest Growth      |
|     | 4.3   |          | onmental Conditions and Forest Habitat Classification   |
|     | 1.0   | 4.3.1    | The Climate of the Forest Interior                      |
|     |       | 4.3.2    | Soil Water Regime                                       |
|     |       | 4.3.3    | Soil Chemical Properties                                |
|     | 4.4   |          | arative Ecology of Central European Tree Species        |
|     | 7.7   | 4.4.1    | Important Characteristics of Crown Structure            |
|     |       | 4.4.2    | Traits Related to Productivity and Stress Tolerance     |
|     |       | 4.4.3    | Nitrogen Acquisition                                    |
|     |       | 4.4.4    | Stress Tolerance  |
|     |       | 4.4.5    | Litter Quality and Tree Species Effects on the Soil     |
|     |       | 4.4.5    | Competitive Abilities of the Tree Species               |
|     |       | 4.4.0    | Compounte Admines of the Tree species                   |

|     |      | 4.4.7    | The Effects of Elevation on Tree Growth            | 188        |
|-----|------|----------|--|------------|
|     |      | 4.4.8    | The Influence of Climate on Elevational            |            |
|     |      |          | Changes in Tree Species Composition                | 191        |
|     |      | 4.4.9    | Forest Cover in Central Europe and the Current     |            |
|     |      |          | Coverage of Major Tree Species                     | 194        |
|     | 4.5  | Forest   | Floor Plants and Shrubs of the Forest Interior:    |            |
|     |      | Ecolog   | gical Niches and Ecological Grouping               | 196        |
|     |      | 4.5.1    | Niches of Forest Shrubs                            | 196        |
|     |      | 4.5.2    | Ecology of Forest Floor Plants                     | 207        |
|     |      | 4.5.3    | The Ecological Grouping of Herbaceous              |            |
|     |      |          | Plants in Central European Broadleaved Forests     | 243        |
|     | 4.6  | Popula   | tion Ecology of Forest Floor Plants                | 245        |
|     |      | 4.6.1    | Phenology  | 245        |
|     |      | 4.6.2    | Life Cycles  | 249        |
|     | 4.7  | Produc   | ctivity and Cycling of Water and Nutrients         | 252        |
|     |      | 4.7.1    | The Biomass and Productivity of the Tree Layer     | 252        |
|     |      | 4.7.2    | The Biomass and Productivity of the Herb Layer     | 266        |
|     |      | 4.7.3    | Ecosystem Carbon Cycling                           | 270        |
|     |      | 4.7.4    | Water Cycling                                      | 272        |
|     |      | 4.7.5    | Nutrient Cycling                                   | 283        |
|     | 4.8  | Vegeta   | tion Dynamics                                      | 298        |
|     |      | 4.8.1    | Tree Layer Dynamics                                | 298        |
|     |      | 4.8.2    | Fluctuations and Succession in the Herb Layer      | 298        |
|     | 4.9  | Recent   | Human Influence                                    | 300        |
|     |      | 4.9.1    | Forest Damage in the Past and the Present          | 300        |
|     |      | 4.9.2    | Anthropogenic Changes in Forest Soil Conditions    | 301        |
|     |      | 4.9.3    | Recent Tree Damage and Its Potential Causes        | 310        |
|     |      | 4.9.4    | Anthropogenic Changes in the Herb Layer            |            |
|     |      |          | and in the Cryptogam and Fungal Flora of Forests   | 324        |
|     |      | 4.9.5    | Conservation and Restoration of Forests            | 337        |
| Par | t IV | Forest a | and Shrub Formations                               |            |
|     |      |          | lixed Beech Forests                                | 351        |
| 5   | 5.1  |          | lassification of Hardwood Broadleaved Forests      | 351        |
|     | 5.2  |          | lassification of Beech Forests in Central          | 331        |
|     | 3.2  |          | estern Europe                                      | 356        |
|     | 5.3  |          | Forests on Rendzina and Pararendzina               | 361        |
|     | 3.3  | 5.3.1    | Mesic Limestone Beech Forests                      | 301        |
|     |      | 5.5.1    |  | 261        |
|     |      | 522      | (Hordelymo-Fagetum)                                | 361<br>366 |
|     |      | 5.3.2    |  | 300        |
|     |      | 5.3.3    | Sedge Beech Forests on Dry Slopes                  | 368        |
|     |      | 521      | (Carici-Fagetum)                                   | 300        |
|     |      | 5.3.4    | Beech Forests Without a Herb Layer (Fagetum nudum) | 372        |
|     |      |          | (ragetum mudum)                                    | 3/2        |

|   |      | 5.3.5   | Yew-Beech and Seslerio-Fagetum Forests              |     |
|---|------|---------|---|-----|
|   |      |         | on Steep Slopes                                     | 375 |
|   |      | 5.3.6   | Montane Beech and Fir-Beech Forests                 | 379 |
|   |      | 5.3.7   | Subalpine Sycamore-Beech Forests (Aceri-Fagetum)    | 388 |
|   | 5.4  | Beech   | and Mixed Beech Forests on Moderately               |     |
|   |      | Fertile | Cambisols   | 391 |
|   |      | 5.4.1   | The Galio odorati-Fagetum and Related               |     |
|   |      |         | Communities   | 391 |
|   |      | 5.4.2   | Mixed Beech Forests on Moist Soil                   | 399 |
|   |      | 5.4.3   | Beech and Mixed Beech Forests Rich in Ferns         | 403 |
|   |      | 5.4.4   | Beech Forests Rich in Festuca altissima             | 408 |
|   | 5.5  | Beech   | and Oak-Beech Forests on Highly Acidic Soils        | 409 |
|   |      | 5.5.1   | Moder Beech Forests (Luzulo-Fagenion)               | 409 |
|   |      | 5.5.2   | Climatic and Edaphic Forms of Moder Beech           |     |
|   |      |         | Forests and Oak-Beech Forests                       | 416 |
|   |      | 5.5.3   | Acid Beech Forests on Limestone                     | 421 |
|   | 5.6  | A Con   | nparison of the Habitats of Beech Forest            |     |
|   |      | Comm    | unities   | 422 |
|   | 5.7  | Beech   | Forest Dynamics                                     | 424 |
|   |      | 5.7.1   | The Inter- and Post-Glacial Development             |     |
|   |      |         | of Beech Forests                                    | 424 |
|   |      | 5.7.2   | Patch Dynamics of Beech Forests                     | 429 |
| 6 | Mixe | d Broad | lleaved Forests Poor in Beech Outside               |     |
| Ü |      |         | ns or Mires   | 443 |
|   | 6.1  | -       | - and Ash-Rich Mixed Forests                        | 443 |
|   | •••  | 6.1.1   | Habitat Classification of Maple and Ash Forests     | 443 |
|   |      | 6.1.2   | The Fraxino-Aceretum                                | 446 |
|   |      | 6.1.3   | The Aceri-Fraxinetum                                | 450 |
|   |      | 6.1.4   | The Carici remotae-Fraxinetum                       | 452 |
|   | 6.2  | Mixed   | Lime Forests  | 454 |
|   |      | 6.2.1   | The Asperulo taurinae-Tilietum in the Alps          | 454 |
|   |      | 6.2.2   | Mixed Tilia cordata Forests Outside of the Alps     | 456 |
|   |      | 6.2.3   | Thermophilic Mixed Large-Leaved                     |     |
|   |      |         | Lime-Maple Forests (Aceri platanoidis-Tilietum      |     |
|   |      |         | platyphylli)  | 457 |
|   | 6.3  | An Ov   | verview of the Mixed Oak Forests of Central Europe  | 459 |
|   | 6.4  | Therm   | ophilic Mixed Oak Forests (QUERCETALIA PUBESCENTIS) | 461 |
|   |      | 6.4.1   | 'Relict' Submediterranean Downy Oak Forests         |     |
|   |      |         | and Continental Steppe Forests                      | 461 |
|   |      | 6.4.2   | The Quercetalia pubescentis Across                  |     |
|   |      |         | a West-East Climatic and Floristic Gradient         | 466 |
|   |      | 6.4.3   | The Subcontinental Potentillo-Quercetum             | 474 |
|   | 6.5  |         | Oak Forests on Acid Soils                           | 476 |
|   |      | 6.5.1   | The Betulo-Quercetum and Related                    |     |
|   |      | 0.5.1   | The Betale Quelectum and Itelated                   |     |

|   |      | 6.5.2  | Thermophilic Acid Oak Forests and Sweet Chestnut |     |
|---|------|--------|--|-----|
|   |      |        | Coppices in Southern Central Europe              | 490 |
|   | 6.6  | Oak-H  | ornbeam Forests (Carpinion Betuli)               | 494 |
|   |      | 6.6.1  | Thermophilic Subcontinental Oak-Hornbeam         |     |
|   |      |        | Forests (Galio-Carpinetum)                       | 494 |
|   |      | 6.6.2  | Moist Subatlantic Oak-Hornbeam Forests           |     |
|   |      |        | (Stellario-Carpinetum)                           | 497 |
|   |      | 6.6.3  | Beech-Rich Oak-Hornbeam Forests                  | 502 |
|   |      | 6.6.4  | Lime-Hornbeam Forests (Tilio-Carpinetum)         |     |
|   |      |        | Outside the Range of Beech                       | 508 |
|   |      | 6.6.5  | A Comparison of the Environmental                |     |
|   |      |        | Conditions in Oak-Hornbeam Forests               | 518 |
| 7 | Pure | and Mi | ixed Coniferous Forests                          | 521 |
|   | 7.1  |        | ole of Conifers in the Forests of Central Europe | 521 |
|   | 7.2  |        | stematic Classification of Conifer               |     |
|   |      |        | Communities                                      | 525 |
|   | 7.3  |        | Fir Forests                                      | 526 |
|   |      | 7.3.1  | The Unique Position of Fir Communities           |     |
|   |      |        | in Central European Forests                      | 526 |
|   |      | 7.3.2  | Fir Forest Communities of the Alps               |     |
|   |      |        | and Their Foothills                              | 529 |
|   |      | 7.3.3  | Fir Forests of Low Mountain Ranges               |     |
|   |      |        | and Lowlands                                     | 537 |
|   | 7.4  | Spruce | e Forests  | 541 |
|   |      | 7.4.1  | The Natural Range and Habitats of Spruce         |     |
|   |      |        | Forests in Central Europe                        | 541 |
|   |      | 7.4.2  | The Systematic Classification of Spruce-Rich     |     |
|   |      |        | Conifer Forests                                  | 545 |
|   |      | 7.4.3  | Montane and Subalpine Spruce Forests             | 549 |
|   |      | 7.4.4  | The Role of Spruce in Lowland Areas              | 556 |
|   |      | 7.4.5  | Environmental Conditions in Various Spruce       |     |
|   |      |        | Forest Communities                               | 558 |
|   | 7.5  | Subalp | pine Larch-Swiss Stone Pine Forests              |     |
|   |      | and La | arch Forests                                     | 560 |
|   |      | 7.5.1  | Environmental Conditions of Larch and Swiss      |     |
|   |      |        | Stone Pine Forests in the Central Alps           | 560 |
|   |      | 7.5.2  | Larch-Swiss Stone Pine Forests in the Alps       |     |
|   |      |        | and the Tatra                                    | 565 |
|   |      | 7.5.3  | Larch Forests of the Southern Alps and           |     |
|   |      |        | Non-Alpine Larch Stands                          | 570 |
|   | 7.6  | Mount  | tain Pine Stands Outside of Mires                | 571 |
|   |      | 7.6.1  | Erect Mountain Pine Communities                  | 571 |
|   |      | 7.6.2  | Dwarf Mountain Pine Scrub Under Different        |     |
|   |      |        | Environmental Conditions                         | 574 |

|   | 7.7 | Pine Forests Outside of Mires and Floodplains |   | 581        |
|---|-----|---|---|------------|
|   |     | 7.7.1   | Central European Scots Pine Forests:                                |            |
|   |     |   | Variation with Environmental Conditions                             | 581        |
|   |     | 7.7.2   | Scots Pine and Black Pine Communities                               |            |
|   |     |   | in the Alps   | 585        |
|   |     | 7.7.3   | A Comparison of Pine and Mixed Oak Forests                          |            |
|   |     |   | in the Pleistocene Lowlands   | 590        |
|   | 7.8 | Conife  | r Forest Dynamics   | 598        |
|   |     | 7.8.1   | Conifer Regeneration  | 598        |
|   |     | 7.8.2   | Stand Dynamics  | 600        |
| 0 | г   |   | •   | 607        |
| 8 |     |   | ations and Clearingstion Communities in Comparison to Semi-natural  | 007        |
|   | 8.1 |   | <u>-</u>  | 607        |
|   |     |   | Communities   | 607        |
|   |     | 8.1.1   | Types of Plantation Vegetation  Conifer Monocultures in Broadleaved | 007        |
|   |     | 8.1.2   |   | 622        |
|   |     | 0.1.2   | Forest Habitats   | 622<br>626 |
|   |     | 8.1.3   | The Vegetation of Clearings and Burnt Areas                         | 020        |
| 9 | Woo | dy Veget                                      | tation of Floodplains and Swamps                                    | 633        |
|   | 9.1 | Flora a                                       | and Origins   | 633        |
|   | 9.2 | Habita  | t Conditions and Classification                                     | 636        |
|   |     | 9.2.1   | Floodplain Morphology and Local Climate                             | 636        |
|   |     | 9.2.2   | Soil Chemistry and Nutrient Supply                                  | 640        |
|   |     | 9.2.3   | Discharge Regime, Flooding Frequency                                |            |
|   |     |   | and Soil Moisture   | 644        |
|   |     | 9.2.4   | Stagnant and Flowing Groundwater                                    | 648        |
|   | 9.3 | Vegeta  | ation   | 652        |
|   |     | 9.3.1   | Woody Vegetation of Floodplains and Riverbanks                      | 652        |
|   |     | 9.3.2   | Swamp and Mire Forests  | 688        |
|   | 9.4 | Adapta  | ations to the Environment   | 700        |
|   |     | 9.4. <u>î</u>                                 | Flood Tolerance of Floodplain Species                               | 700        |
|   |     | 9.4.2   | Summer Drought Stress in Floodplains                                | 705        |
|   |     | 9.4.3   | Willows as Characteristic Species of Floodplains                    |            |
|   |     |   | and Swamps  | 706        |
|   | 9.5 | Popula  | ation Biology and Community Ecology                                 | 708        |
|   |     | 9.5.1   | Phenology   | 708        |
|   |     | 9.5.2   | River Valleys as Migration Routes for                               |            |
|   |     |   | Mountain Species  | 709        |
|   |     | 9.5.3   | Regeneration and Population Dynamics                                |            |
|   |     |   | in Floodplain Forests   | 712        |
|   | 9.6 | Produc  | ctivity and Cycling of Water and Nutrients                          | 715        |
|   | ,,, | 9.6.1   | Forest Structure, Biomass and Productivity                          | 715        |
|   |     | 9.6.2   | Water and Nutrient Cycling  | 716        |
|   | 9.7 |   | ation Dynamics  | 718        |
|   | 2.1 | 0.7.1   | Dynamics of Floodplain Vegetation                                   | 718        |

Contents of Volume I xv

|       |        | 9.7.2 Succession Following Disturbance                   | 721 |
|-------|--------|--|-----|
|       | 9.8    | Human Influence  | 722 |
|       |        | 9.8.1 Exploitation, Drainage and Destruction             |     |
|       |        | of Floodplain Forests                                    | 722 |
|       |        | 9.8.2 Conservation and Restoration of Floodplain Forests | 726 |
| 10    | Epipl  | hyte Vegetation  | 729 |
|       | 10.1   | Tree Bark as an Epiphyte Substrate                       | 729 |
|       | 10.2   | Epiphytic Algal, Lichen and Bryophyte Communities        | 731 |
|       |        | 10.2.1 Alga-Rich Epiphyte Communities                    | 732 |
|       |        | 10.2.2 Lichen-Rich Epiphyte Communities                  | 733 |
|       |        | 10.2.3 Bryophyte-Rich Epiphyte Communities               | 734 |
|       | 10.3   | Adaptations to the Environment                           | 737 |
|       |        | 10.3.1 Important Ecological Properties of Epiphytic      |     |
|       |        | Cryptogams   | 737 |
|       |        | 10.3.2 Carbon Assimilation as a Function of Moisture,    |     |
|       |        | Light Intensity and Temperature                          | 738 |
|       |        | 10.3.3 Chemical and Physical Properties of the Substrate | 740 |
|       |        | 10.3.4 The Effects of Toxic Substances and the Role      |     |
|       |        | of Epiphytes as Indicators                               | 741 |
|       |        | 10.3.5 The Importance of Stand Structure and Stand Age   | 742 |
|       | 10.4   | Recent Changes in Epiphyte Communities                   | 743 |
| 11    | Fores  | st Edges, Scrub, Hedges and Their Herb Communities       | 747 |
|       | 11.1   | Flora and Development                                    | 747 |
|       | 11.2   | Environmental Conditions and Habitat Classification      | 750 |
|       | 11.3   | Vegetation   | 756 |
|       |        | 11.3.1 Forest Edges, Scrub and Hedges                    | 756 |
|       |        | 11.3.2 Herb Fringe Communities                           | 763 |
|       | 11.4   | Adaptations to the Environment, Population Biology       |     |
|       |        | and Vegetation Dynamics                                  | 768 |
|       | 11.5   | Human Influence  | 771 |
|       |        | 11.5.1 Decline and Destruction of Hedges                 | 771 |
|       |        | 11.5.2 The Importance of Hedges for Agriculture          |     |
|       |        | and Agricultural Landscapes                              | 773 |
| 12    | Synta  | axonomic Overview of the Vascular Plant                  |     |
|       |        | munities of Central Europe: Forest                       |     |
|       |        | Scrub Formations   | 775 |
| D - 4 | Pa     |  | 701 |
| Kei   | erence | <del>2</del> S   | 781 |
| Ind   | lex    |  | 891 |