

Vegetation dynamics in temperate lowland primeval forests

Ecological studies in Białowieża forest

by

J.B. FALIŃSKI

(with the assistance of Krystyna Falińska)

1986 **DR W. JUNK PUBLISHERS**
a member of the KLUWER ACADEMIC PUBLISHERS GROUP
DORDRECHT / BOSTON / LANCASTER



Contents

Preface	VII
Acknowledgements	VIII
Chapter I. AIM AND PREMISSES Janusz Bogdan Faliński	
I.1. Introduction, aim and subject	1
I.2. Theoretical basis	4
2.1. Ecosystem theory and Białowieża Forest studies	4
2.2. Vegetation dynamics as an ecological process	5
I.3. Study area. Methodical basis. Material	8
3.1. Object	8
3.2. Organisation and methods	11
3.3. Nomenclature, abbreviations	13
Chapter II. THE AREA – BASIC DATA ABOUT BIAŁOWIEŻA FOREST Janusz Bogdan Faliński	
II.1. General features	15
1.1. The vegetation	15
1.2. Topography	15
1.3. Physico-geographical situation	16
II.2. Biogeography	17
II.3. History	24
II.4. Climate	32
II.5. Geology	34
II.6. Terrain formation and relief	34
II.7. Hydrology	36

Chapter III. GEOBOTANY

Janusz Bogdan Faliński

III.1.	The flora	39
1.1.	Statistics and general characteristic of the flora	39
1.2.	Participation of trees, shrubs and undershrubs	42
1.3.	Geographical characteristic of the flora	46
1.4.	The flora of the Białowieża Forest against the background of that of the adjacent areas	48
III.2.	Forest building trees and tree stands	51
2.1.	Habit, age and dimensions of Białowieża Forest trees	51
2.2.	Review of tree species	52
2.2.1.	The spruce (<i>Picea abies</i>)	52
2.2.2.	Scotch pine (<i>Pinus sylvestris</i>)	58
2.2.3.	The fir (<i>Abies alba</i>) and the yew (<i>Taxus baccata</i>)	59
2.2.4.	Oaks (<i>Quercus petraea</i> and <i>Quercus robur</i>)	61
2.2.5.	The linden (<i>Tilia cordata</i>), maple (<i>Acer platanoides</i>) and hornbeam (<i>Carpinus betulus</i>)	62
2.2.6.	The elms (<i>Ulmus glabra</i> , <i>U. minor</i> , <i>U. laevis</i>)	64
2.2.7.	The ash (<i>Fraxinus excelsior</i>) and alder (<i>Alnus glutinosa</i>)	68
2.2.8.	The aspen (<i>Populus tremula</i>) and birches (<i>Betula pendula</i> , <i>B. pubescens</i> , <i>B. carpatica</i>)	68
2.2.9.	The willows (<i>Salix sp. div.</i>)	69
2.3.	Structure of the forest stands	70
2.4.	Age and origin of forest stands	71
2.5.	Stand growth increment	73
2.6.	Popular names of the forest types	73
III.3.	Forest vegetation	74
3.1.	Deciduous forests (class: <i>Querco-Fagetea</i>)	76
3.1.1.	General characteristics	76
3.1.2.	Mesophilous deciduous oak-linden-hornbeam forest (<i>Tilio-Carpinetum</i>)	76
3.1.3.	Streamside alder-ash forest (<i>Circaeo-Alnetum</i>) and riverside ash-elm forest (<i>Ficario-Ulmetum</i>)	82
3.1.4.	Thermophilous oak forest (<i>Potentillo albae-Quercetum</i>)	87
3.2.	Coniferous forests (class: <i>Vaccinio Piceetea</i>)	89
3.2.1.	General characteristics	89
3.2.2.	Meso-oligotrophic mixed forest (<i>Pino-Quercetum</i>)	89
3.2.3.	Spruce forest (<i>Querco-Piceetum</i> and <i>Sphagno-Piceetum</i>)	91
3.2.4.	Fresh pine forest (<i>Peucedano-Pinetum</i>) and other pine forests on mineral habitats	92
3.2.5.	Bog pine forest (<i>Vaccinio uliginosi-Pinetum</i>) and forest raised bog (<i>Sphagnetum medio-rubelli pinetosum</i>)	95
3.3.	Bog forest and bush (class: <i>Alnetea glutinosae</i>)	96
3.3.1.	General characteristics	96
3.3.2.	Black alder bog forest (<i>Carici elongatae-Alnetum</i>)	97
3.3.3.	Willow bog bush (<i>Salicetum pentandro-cinereae</i>)	99
3.3.4.	Low birch bush (<i>Salici-Betuletum humilis</i>)	100
3.3.5.	Bog oak forest (<i>Carici elongatae-Quercetum</i>)	101
3.4.	Flood-plain alluvial willow forests and bush (class: <i>Salicetea purpureae</i>)	103

III.4.	Natural and anthropogenic non-forest vegetation	104
4.1.	General remarks	104
4.2.	Water plant communities (<i>Lemnetea</i> , <i>Potametea</i>)	104
4.3.	Ephemeral silt communities (<i>Bidention</i> , <i>Chenopodion fluviatile</i> , <i>Nanocyperion</i>)	104
4.4.	Forest edge herbaceous communities (<i>Alliarion</i> , <i>Geranion sanguinei</i>)	105
4.5.	Reed swamp communities (<i>Phragmitetea</i>)	105
4.6.	Communities of meadows and pastures	106
4.7.	Clearing communities	107
4.8.	Plant communities of forest roads (<i>Plantaginetea</i>)	107
4.9.	Trampling-resistant communities from dirt roads, squares and yards in settlements (<i>Plantaginetea</i>)	108
4.10.	Ruderal communities along railway tracks (<i>Sisymbriion</i> , <i>Onopordion</i>)	108
4.11.	Ruderal communities in settlements (<i>Eu-Arction</i> , <i>Sisymbriion</i> , <i>Onopordion</i>)	109
4.12.	Weed communities in garden and field crops	109
4.13.	Pioneering vegetation in artificial pits	111

Chapter IV. MAJOR NATURAL FACTORS DIFFERENTIATING THE FOREST ENVIRONMENT AND LANDSCAPE

Janusz Bogdan Faliński

IV.1.	General introduction	113
IV.2.	Soils in relation to forest vegetation differentiation	114
2.1.	Soil-forming factors	114
2.2.	Soil water types and the water balance	114
2.3.	Morphological-genetic soil types	120
2.4.	Relation between soil type and the vegetation	122
IV.3.	Ground frost and snow cover as ecoclimatic factors	125
3.1.	Introduction. Material	125
3.2.	Spring and autumn ground frost	125
3.3.	The snow cover	127
3.4.	The nature of ground freezing	127
3.5.	Modifications of forest vegetation under the influence of some ecoclimatic factors	129
IV.4.	The transition zone (ecotone) and its synchorological and syndynamic aspects	131
4.1.	Introduction	131
4.2.	Methodical basis	132
4.3.	Frequency of contacts between forest communities	132
4.4.	Width of the transition zone and sharp outline of boundaries	133
4.5.	Nature of floristic-phytosociological changes in the transition zone	133
4.6.	Factors associated with spatial vegetation changes	142
4.7.	Seasonal vegetation dynamics in the transition zone	143
4.8.	Recapitulation	145
IV.5.	Uprooting of trees (tree saltation)	145
5.1.	Introduction	145
5.2.	Characteristic of the phenomenon	147
5.3.	Balance of wood volume from windfall and snag	150
5.4.	Problems of permanence of tree stands	150
5.5.	Windfall and deadfall as factors in the transformation of the forest biotope	151

5.6.	Uprooting of trees as a factor initiating succession towards bog ecosystems	153
5.7.	Uprooting of trees as a factor shaping the edges of raised bog	157
5.8.	Recapitulation	161
IV.6.	Impact of herbivorous animals on vegetation structure and dynamics	161
6.1.	Introduction	161
6.2.	Herbivorous mammal species and their influence on vegetation	162
6.2.1.	Historical data	162
6.2.2.	The European bison (<i>Bison bonasus</i>)	163
6.2.3.	Red deer (<i>Cervus elaphus</i>) and roedeer (<i>Capreolus capreolus</i>)	169
6.2.4.	The wild boar (<i>Sus scrofa</i>)	170
6.2.5.	Rodents (<i>Rodentia</i>)	183
6.3.	Discussion: Selected aspects of the impact of herbivores on the vegetation	188
6.3.1.	Seasonal variability of the activity of herbivores	188
6.3.2.	Influence of browsing on the habitus of woody species	188
6.3.3.	Influence of extent and way of woody food obtention on the structure and dynamics of the vegetation	189
6.3.4.	Food preferences of herbivorous animals and the stability of the species composition and structure of the phytocenosis	193
6.4.	Conclusions	195

Chapter V. FLUCTUATION, REGENERATION AND SUCCESSION IN FOREST COMMUNITIES UNDER NATURAL CONDITIONS

Janusz Bogdan Faliński

V.1.	General introduction	201
V.2.	Regression of thermophilous oak forest	201
2.1.	Introduction	201
2.2.	Methods	203
2.3.	Comparison of the stand structures	205
2.4.	Changes of the species composition and the distribution of plants	207
2.5.	Invasion of hornbeam and hornbeam forest species	210
2.6.	Age of the regression process	210
2.7.	Causes and course of regression	210
2.8.	Genesis of thermophilous oak forest and the nature of its contemporary transformations	213
V.3.	Field layer regeneration in pine forest (<i>Peucedano-Pinetum</i>) after ground fire	213
V.4.	Tree stand dynamics in <i>Pino-Quercetum</i> and <i>Tilio-Carpinetum</i> communities	217
4.1.	Methods	217
4.2.	Species composition of the tree stand in the <i>Pino-Quercetum</i> and the <i>Tilio-Carpinetum</i> and its changes in the period 1936–1969	220
4.3.	Influence of self-thinning processes and growing of trees on the specific composition and d.b.h. basal area in the stands	221
4.4.	Changes in the layered structure	221
4.5.	Natural regeneration	221
4.5.1.	Production of tree diaspores	221
4.5.2.	Extent of selfseeding	222
4.5.3.	Durability of the snow cover as a factor influencing the abundance of seedlings	224
4.5.4.	Relation between natural regeneration and the composition of the parent stand	224

4.5.5. Relation between natural regeneration and the situation of the parent trees. Influence of light conditions on the forest floor	224
4.6. Discussion	227
4.6.1. Influence of regeneration on the spatial structure of the stand	227
4.6.2. Tendency in the development of stands	228
V.5. Permanence of species composition and repeatability of seasonal rhythms in a many-years cycle as indicator of stability (homeostasis) of forest communities	228
5.1. Methods	228
5.2. The original situation	229
5.3. Changes in the number of species in the herb layer	229
5.4. Permanence of the species composition	230
5.5. Number of species reaching the reproduction phase in the communities considered	237
5.6. Frequency of generative reproduction and behaviour of species in time	238
5.7. Repeatability of seasonal rhythms	242
5.8. Recapitulation	243
V.6. Changes in the species composition and structure of the main forest and brush communities	244
6.1. Methodical remarks	244
6.2. <i>Circaeo-Alnetum</i>	244
6.3. <i>Carici elongatae-Alnetum</i>	224
6.4. <i>Salicetum pentandro-cinereae</i>	248
6.5. <i>Querco-Piceetum</i>	250
6.6. <i>Pino-Quercetum</i>	250
6.7. <i>Peucedano-Pinetum</i>	251
6.8. <i>Sphagnetum medio-rubelli</i> and <i>Vaccinio uliginosi-Pinetum</i>	254
V.7. State and dynamic tendencies of forest communities	256
7.1. Prevailing processes and state of forest communities	256
7.2. Spatial picture of dynamic tendencies in forest communities in a landscape dominated by forest of primary origin	260

Chapter VI. SEASONAL DYNAMICS OF FOREST COMMUNITIES

Krystyna Falińska

VI.1. Introduction	265
VI.2. Phenological characteristics of forest and brush communities	265
2.1. <i>Sphagnetum medio-rubelli pinetosum</i>	265
2.2. <i>Vaccinio uliginosi-Pinetum</i>	266
2.3. <i>Querco-Piceetum</i>	269
2.4. <i>Peucedano-Pinetum</i>	271
2.5. <i>Pino-Quercetum</i>	272
2.6. <i>Tilio-Carpinetum typicum</i>	274
2.7. <i>Tilio-Carpinetum stachyetosum</i>	277
2.8. <i>Circaeo-Alnetum</i>	278
2.9. <i>Carici elongatae-Alnetum</i>	283
2.10. <i>Salicetum pentandro-cinereae</i>	286
VI.3. Synphenological analysis	288
3.1. Seasonal rhythm of flowering and fruiting	288
3.1.1. Flowering rhythm	288

3.1.2. Fruiting rhythm	291
3.1.3. Phenological similarity between the forest communities – Interpretation of similarity dendrites	295
3.2. Analysis of synthetic phenological spectra	297
3.2.1. Basis for analysis	297
3.2.2. The vegetation period	297
3.2.3. Differences in the degree of intensity of herb layer communities development	298
3.2.4. Seasonal herb layer development – maxima and minima	298
3.3. Seasonal colour variation in forest communities	299
3.3.1. Colour aspects	299
3.3.2. Flower colour analysis	299
3.3.3. Seasonal rhythms of flowering of forest communities herb layer and colour aspects	299
3.3.4. Seasonal variability of herb layer colours	300
VI.4. Floristic-ecological analysis of seasonal dynamics of forest communities	301
4.1. Phenological plasticity of herb layer species and the ecological-phytosociological differentiation of forest communities	301
4.2. Correlation of seasonal rhythms of the herb layer with some selected ecological factors	302
4.3. Parallelism between phenological differentiation and floristic-ecological differentiation of forest communities	302
VI.5. Phytophenological seasons in the forest communities of the Białowieża Forest	304
5.1. Basis for distinguishing phenological seasons	304
5.2. Phytophenological seasons in forest and brush communities	304

Chapter VII. DYNAMICS AND STRUCTURE OF PLANT POPULATIONS IN FOREST ECOSYSTEMS

Krystyna Falińska

VII.1. The notion of cenopopulations and the basis for their distinction	307
VII.2. Phenological individuality of cenopopulations	309
VII.3. Reproductive strategy of perennial herbaceous plant populations in forest ecosystems	315
3.1. Reproductive effectiveness	315
3.2. Generative and vegetative reproduction of herbaceous plant populations	317
3.2.1. Generative reproduction	317
3.2.2. Vegetative reproduction	320
3.3. Types of reproductive strategy in perennial herbaceous plant populations	320
VII.4. Estimation of potential reproduction of forest phytocenoses	324
4.1. Total diaspore production	324
4.2. Variability in time and space of generative diaspore production	325
4.3. Phytosociological-ecological differentiation of the <i>Tilio-Carpinetum</i> and reproductive optimum of some species populations	325
VII.5. Plant populations in stabilised forest ecosystems	326
VII.6. Plant populations in the ecotones between forest ecosystems	332
6.1. Ecotone and plant populations	332
6.2. Plant populations in various types of ecotones	333
6.2.1. Ecotone between ecosystems with similar ecological-phytosociological conditions	334

6.2.2.	Ecotone between ecosystems with a high ecological-phytosociological diversity	334
6.2.3.	Ecotone between ecosystems: forest – meadow	335
6.3.	Modification of populations in ecotones	335
6.3.1.	Reproduction	336
6.3.2.	Size and habit of plants	336
6.4.	Types of contacts of the cenopopulations. The effect of contact	336
VII.7.	Population structure of forest communities	340
7.1.	Spatial organisation of the herb layer	340
7.2.	Population mechanisms responsible for the spatial structure of the herb layer	342
7.2.1.	Age structure	342
7.2.2.	Contiguity as effect of vegetative reproduction and development of polycorms	344
Chapter VIII. BEHAVIOUR OF NATURAL FOREST UNDER MAN'S ACTIVITY. SYNANTHROPISATION OF THE PLANT COVER		
Janusz Bogdan Faliński		
VIII.1.	Introduction. The notion of synanthropisation	347
VIII.2.	Factors of synanthropisation	348
2.1.	Early mediaeval burying grounds with tumuli as an example of the selective influence of man in the distant past on forest ecosystems	348
2.1.1.	Introduction	348
2.1.2.	Distribution and size of burying grounds with tumuli	349
2.1.3.	The occurrence of burying grounds with tumuli and the natural differentiation of the forest vegetation	350
2.1.4.	Differentiation of forest environment and ecological optimum for settlement	352
2.1.5.	The tree saltation hypothesis concerning the establishment of burying grounds with tumuli	355
2.1.6.	Recapitulation	356
2.2.	Gathering	356
2.3.	Trampling as the simplest and oldest anthropogenic factor influencing the vegetation	357
2.4.	Roads as migration routes of synanthropic plants and as habitats of secondary anthropogenic plant communities	363
2.5.	Primitive chemical wood industry as factor disturbing the forest stand structure	365
2.6.	Colonisation and agriculture as main causes of the shrinking of the surface area of forest	368
2.7.	Hunting and other forms of natural management	372
2.8.	Forest management	373
VIII.3.	History of anthropogenic changes in the plant cover of the Białowieża Primeval Forest	377
3.1.	Sources and reconstruction method	377
3.2.	Period 1: up to the 10th century	378
3.3.	Period 2: from the end of the 10th century to the mid 16th century	378
3.4.	Period 3: from the 16th century to 1888	378
3.5.	Period 4: from 1888 to 1915	379
3.6.	Period 5: from 1915 to 1930	380
3.7.	Period 6: from 1930 to 1960	380
3.8.	Period 7: from 1960 to the present	381
VIII.4.	Some selected phenomena	382
4.1.	Neophytism in the plant cover of the Białowieża Forest	382

4.1.1. Problem. Aim of study	382
4.1.2. Methods	383
4.1.3. Characteristics of neophytism in the Białowieża Forest	385
4.1.4. The role of neophytes in the herb layer of forest communities and their effects on the other components	388
4.1.4.1. Results of comparative studies	388
4.1.4.2. Results of experimental studies	390
4.1.5. Discussion and recapitulation	393
4.2. Permanence of forest relicts in the agricultural landscape	395
4.3. Fate of forest species after permanent total annihilation of forest biocenoses	396
4.4. Syngeneses of scrub communities (order <i>Prunetalia</i>) on forest edges and along lanes in fields	400
4.5. Most recent transformations of anthropogenic vegetation	402
VIII.5. Relations between anthropogenic vegetation and habitats of definite forest communities	408
VIII.6. Changes in the abiotic environment	413
VIII.7. Tentative balance and generalisation	414
7.1. Surface balance of deforestation consequences	414
7.2. Changes in the surface area of the main forest communities	414
7.3. Changes in the distribution of the flora and plant communities	416
7.4. Level of plant cover synanthropisation in the Białowieża Forest	416
7.4.1. Synanthropisation as a phenomenon in time. Steps of synanthropisation	416
7.4.2. Distribution and range of synanthropisation processes in the Białowieża Forest	417
7.5. Synanthropisation of the Białowieża Forest and other larger forest areas in north-eastern Poland	421
7.6. Factors limiting synanthropisation of the Białowieża Forest	421
 Chapter IX. SPONTANEOUS RETURN OF FOREST ONTO ONCE CLEARED AREAS – SECONDARY SUCCESSION Janusz Bogdan Faliński	
IX.1. Introduction	423
IX.2. Examples of spontaneous changes in vegetation on anthropogenic terrain forms and secondary habitats	424
2.1. Development of <i>Echio-Melilotetum</i> on the surface of a railway embankment after interruption of weed control	424
2.2. Formation and regression of <i>Leersio-Bidentetum</i> on silt from the bottom of a water reservoir	425
2.3. Vegetation on charcoal piles	430
IX.3. Secondary succession in a mesotrophic oak-linden-hornbeam forest habitat	433
3.1. Methods	433
3.2. Formal-statistical analysis and characteristic of the transformations	436
3.3. Floristic-structural analysis and characteristic of transformations	436
3.3.1. Participation of annual species	436
3.3.2. Participation of perennial species and the dominance structure	439
3.4. Appearance and participation of seedlings of woody species	441
3.5. Changes in the participation of native and foreign species during succession	442
3.6. Discussion and conclusions	443

XVIII

IX.4.	Secondary succession in an oligotrophic pine forest habitat and the role of woody species	444
4.1.	Introduction and methods	444
4.2.	Course of secondary succession	447
4.3.	Development of a <i>Juniperus communis</i> population	454
4.4.	Participation and role of other dioecious species in the course of secondary succession in <i>Peucedano-Pinetum</i> habitats	460
4.5.	Vegetation succession and development of juniper and aspen populations	463
IX.5.	Properties, role and origin of woody species participating in secondary succession in permanently deforested habitats	463
5.1.	Properties of pioneer species	463
5.2.	Changes of sex structure in populations of pioneer species. Tentative explanation of dioecism in the course of succession	465
5.3.	Review of pioneer species	468
5.4.	Effectiveness of seeding woody species on permanently deforested land	469
5.5.	Origin of pioneer woody species	476
IX.6.	Time indispensable for recreation of the main types of forest ecosystems by way of secondary succession	477

Chapter X. RECAPITULATION: FOUNDATIONS OF FUNCTIONING AND PERMANENCE OF LOWLAND PRIMEVAL FORESTS

Janusz Bogdan Faliński and Krystyna Falińska

X.1.	Character and causes of contemporary differentiation of vegetation in the Białowieża Forest	479
X.2.	Dynamic tendencies in natural vegetation released from anthropogenic pressure. Role of biotic-biocenotic factors in vegetation dynamics	482
X.3.	Essence of phenological vegetation differentiation and its connection with differentiation and stability of environmental conditions	486
X.4.	Effect of anthropogenic transformations of the plant cover and their importance for the permanence and functioning of forest ecosystems	487
X.5.	Ecological and technical-organisational bases to ensure the permanence of relict primeval lowland forests	489
Annex		495
Bibliography		501
Subject index		517
Systematic index		525