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Basics, Methods and Case Studies

George Nakhutsrishvili

The Vegetation of Georgia (South Caucasus)

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Preface

Georgia, an ancient Christian country, occupies the central and southwestern parts of the Caucasus – an isthmus between the Black and the Caspian Sea. In the west, it is contiguous to the Black Sea, in the east to the intermountain depression of the River Mtkvari (=Kura) in the Caspian Lowlands (the Transcaucasian Depression), the northern border follows the high mountain tops of the Greater Caucasus, the southern one crosses the Lesser Caucasus (in the eastern part) and separates the Lesser Caucasus from the adjacent mountain ranges of northeastern Asia Minor. Politically, Georgia borders on the Russian Federation (to the north), Azerbaijan (to the east), Turkey (to the southwest) and Armenia (to the southeast). The borders have changed several times during the history of Georgia, especially in the earlier stages of the formation of the Georgian nation.

Kavkasioni, i.e. the Greater Caucasus range, rises up to 5,068 m (Mt. Shkhara, highest mountain within Georgia) and 5,633 m a.s.l. (Mt. Elbrus, in the Russian Federation), i.e. over 1,000 m above the eternal snow-line. Mountain passes at an altitude of 2,200–3,000 m a.s.l. were used as trade-routes from the earliest times. In the mountains of Kavkasioni, permanent settlements are found up to an altitude of 2,500 m a.s.l. Though the Lesser Caucasus mountains reach an altitude of 3,304 m a.s.l., there are no glaciers and no eternal snow.

The natural conditions of the so-called intermontane lowlands of Georgia, consisting of the Colchic Lowlands (adjacent to the Black Sea, in West Georgia) and the foothills between Kavkasioni (in the north) and the Lesser Caucasus (in the southwest), including the Mtkvari Valley (resp. Kura valley, in East Georgia), are favourable for settlement and mixed farming.

In the east, the Colchic Lowlands are surrounded by the Imeretian Elevation which connects the Greater Caucasus with the Lesser Caucasus. The highest part of it, the Surami range, divides the country into two major natural geographical regions: Eastern and Western Georgia, the first having been called Iberia and the latter Colchis by ancient Greek and Roman writers.

Diversity of climate and relief of Georgia has been highly important for its economic development since the early stages of human activities. Numerous rivers (more than 25,000), which promoted intensive agriculture, eliminated the need for irrigation systems, having proved so essential in the economy of the Ancient Eastt (Egypt, Babylon). Besides, these rivers served as trade routes. Due to their rapid current, the rivers were used for transportation of timber (especially in Colchis).

Georgia is rich in various mineral resources. In the mountains of Georgia, copper was extracted, essential for non-ferrous metallurgy, which by that time reached a high level of development. Rich iron deposits prompted the progress of ferrous metallurgy. Magnetic sands along the Black Sea were of particular importance. Rivers, containing gold dust, were known during the Greek Epoch.

Vakhushti Bagrationi, the prominent Georgian historian and geographer of the eighteenth century, distinguished two botanical and agricultural zones within Georgia: the mountainous and the lowland one. Since the Neolithic Revolution, these two zones represented one closely integrated system. The lowlands were characterized by rich harvest of grain crops, vineyards and orchards. In the mountainous areas, the harvest of grain crops was much poorer, and vineyards and orchards were absent.

Georgia covers an area of 69.500 km^2. The population is 5.5 million (two third being Georgians). The Georgians call themselves 'kartveli' (sing.) and 'kartvelebi' (pl.), hence the name of the country in Georgian language is 'Sakartvelo'. The Georgian language belongs to the group of Kartvelian languages, included in the family of Iberian-Caucasian languages. It is suggested that the Georgian language is related to Anterior-Asian languages, the Basque language (the Basque country lies partly in Spain, in the northern part of the Iberain peninsula, close to the Pyrenees). Connections to the Indo-European languages, however, are uncertain. Written Georgian dates back to the third century B.C. (to the reign of king Parnavaz).

Christianity, adopted as the official religion in 337 A.D., promoted the unification of Georgia and the development of written Georgian language.

In ancient times, Georgian tribes were known as skilful farmers, cattle-breeders and metallurgists. Various archaeological discoveries, as well as ancient oriental and Georgian manuscripts testify to an early economical, social, and cultural development of the Georgian people. According to these data, the leading branches of economy of the country must have been: (1) agriculture (field crop cultivation, vine making, horticulture, vegetable growing, etc.); (2) cattle breeding; (3) domestic craft (weaving, woodwork, blacksmith work, textile production, pottery, ceramics, etc.). Georgians developed plough-land cultivation and various forms of irrigation (especially in the mountain areas) aiming to increase crop capacity of natural grasslands (2–3 harvests per season). Of the 16 species of wheat, 11 are represented in Georgia.

Ancient Georgian manuscripts and special medical books ('Karabadini') contain information on various herbs. The first serious scientific information concerning the vegetation of Georgia was given by Vakhushti Bagrationi (eighteenth century). According to several historical sources and notes of foreign travellers, the plants from different parts of Georgia and from other countries were cultivated in the park of Georgian kings in Legvta Khevi (now Botanical Garden of Tbilisi). In the eighteenth century, foreign scientists became interested in the extreme diversity of Georgian vegetation and flora. In 1852, on the basis of rich collections of Caucasian plants, the Caucasian Museum was founded. In the beginning of the twentieth century, all the branches of botanical science (anatomy, physiology, taxonomy, floristics, phytosociology, etc.) started to develop in Georgia. The

Institute of Botany, which belongs to the Academy of Sciences, was opened in 1933. The book *Vegetation of Georgia* by N. Ketskhoveli was published in 1935 and 1960. Long-standing expeditions to different parts of the Caucasus and of Georgia, as well as monographic studies of separate taxa served as a basis for the eight-volume *Flora of Georgia*. In 1971, the first volume of the totally revised second edition of *Flora of Georgia* appeared (16 volumes (1971-2011) have already been published so far). Key to Plants of Adjara by Dmitrieva (1959) and four volumes of the Flora of Abkhazia by Kolakovsky (1980-1986) are also worth mentioning here. Later, it was decided to publish *The Vegetation of Georgia* under the editorship of the present author (Nakhutsrishvili 1990–1991). A brief description of the vegetation cover of Georgia by R. Kvachakidze was published in 2009. The books *Forest Vegetation of Georgia* by A. Dolukhanov and *The History of Flora and Vegetation of Georgia* by I. Shatilova et al. were published in 2010 and 2011, respectively. Until its complete publication, the author of the present book decided to characterize briefly the main types of vegetation of Georgia and to publish it in English. This present publication bears a special purpose: During the 75-year period of isolation of the USSR and of Georgia in particular, it was not so easy for foreign scientists to get adequately acquainted with the interesting plant life of Georgia and to compare the Caucasian flora and plant communities with those of other countries. Today, Georgian botanists are collaborating with scientists from many other countries.

The Number of Plant Taxa

The flora of Georgia comprises about 4,150 species of vascular plants, of which 260 species are endemic, while the flora of the Caucasus comprises 6,350 species of vascular plants, of which 1,600 species are endemic.

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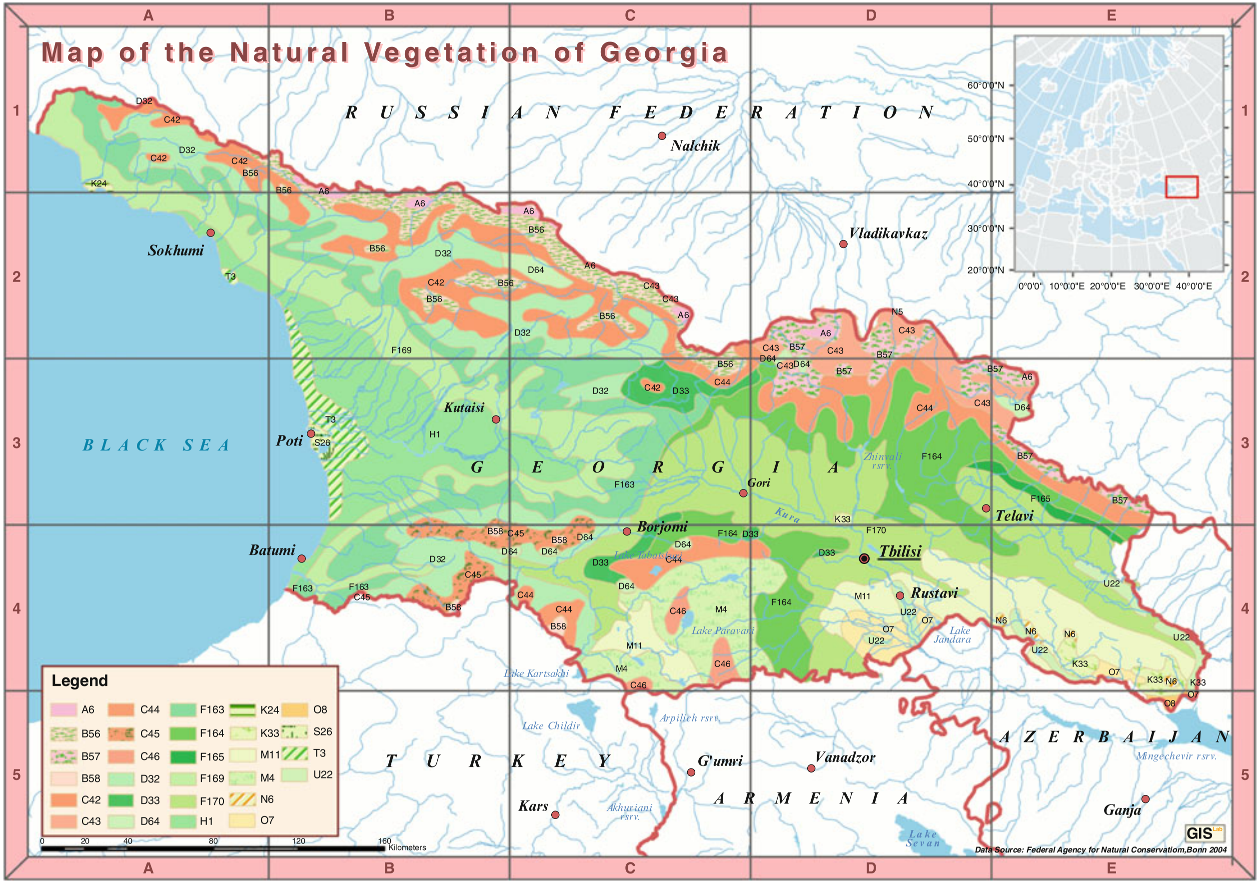
Map of the Natural Vegetation of Georgia
RUSSIAN FEDERATION
GEORGIA
TURKEY
ARMENIA
AZERBAIJAN
BLACK SEA
Sokhumi
Poti
Batumi
Kutaisi
Gori
Borjomi
Tbilisi
Rustavi
Telavi
Nalchik
Vladikavkaz
Kars
G'umri
Vanadzor
Ganja
Kura
Zhinvali rsrv.
Lake Tabatskuri
Lake Paravani
Lake Kartsakhi
Lake Childir
Arpilich rsrv.
Akhuriani rsrv.
Lake Jandara
Mingechevir rsrv.
Lake Sevan
Legend
A6
B56
B57
B58
C42
C43
C44
C45
C46
D32
D33
D64
F163
F164
F165
F169
F170
H1
K24
K33
M11
M4
N6
O7
O8
S26
T3
U22
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60°0'0"N
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20°0'0"E
30°0'0"E
40°0'0"E
GIS Lab
Data Source: Federal Agency for Natural Conservatiom,Bonn 2004

Expanded Legend

A6 Caucasian open vegetation of lichens and mosses (*Rhizoplaca chrysoleuca*, *Thamnolia vermicularis*, *Pohlia elongata*, *Dicranum elongatum*), with scattered vascular plants on rocky habitats (*Saxifraga ruprechtiana*, *Primula bayernii*) and on screes (*Cerastium kasbek*, *Delphinium caucasicum*, *Symphyoloma graveolens*, *Scrophularia minima*, *Lamium tomentosum*)

B56 West Caucasian alpine grasslands (*Geranium gymnocaulon*, *Nardus stricta*, *Festuca djimilensis*), calcareous rocks with *Geum speciosum*, *Carex pontica* and small herb communities (*Sibbaldia semiglabra*, *Ranunculus brachylobus*), alternating with shrub (*Rhododendron caucasicum*), rock and scree vegetation

B57 East Caucasian alpine grasslands (*Festuca varia* subsp. *woronowii*, *Nardus stricta*, *Carex tristis*, *Kobresia capilliformis*) with *Alchemilla elisabethae* and small herb communities (*Sibbaldia parviflora*, *Campanula biebersteiniana*), alternating with shrub, dwarf shrub (*Rhododendron caucasicum*, *Dryas caucasica*), rock and scree vegetation

B58 North Lesser Caucasian alpine grasslands (*Festuca varia* subsp. *woronowii*, *Nardus stricta*, *Carex tristis*, *Bellardiochloa polychroa*, *Scabiosa caucasica*) with *Agrostis lazica*, *Bromopsis variegata* and small herb communities (*Carum caucasicum*, *Campanula tridentata*) with *Gentiana pontica*, alternating with shrub (*Rhododendron caucasicum*), rock and scree vegetation

C42 Southwest Caucasian krummholz and open woodlands (*Betula litwinowii*, *Fagus orientalis*, *Acer trautvetteri*) with *Betula megrelica*, *Quercus pontica*, scrub (*Rhododendron caucasicum*) with Rhamnus imeretina (on carbonate rocks with *Coryllus colchica*), tall-forb communities (*Heracleum ponticum*) with Delphinium pyramidatum (on carbonate rocks with *Heracleum aconitifolium*, *Ligusticum arafoe*) and grasslands (*Calamagrostis arundinacea*, *Betonica macrantha*, on carbonate rocks with *Woronowia speciosa*, *Carex pontica*)

C43 Northeast Caucasian krummholz and open woodlands (*Betula litwinowii*, *Acer trautvetteri*, *partly Pinus kochiana*) with *Betula raddeana*, scrub (*Rhododendron caucasicum*, *Juniperus communis* subsp. *hemisphaerica*), tall-forb communities (*Heracleum sosnowskyi*, *Delphinium flexuosum*) and grasslands (*Festuca woronowii*, *Bromopsis variegata*), alternating with dry grasslands (*Festuca ovina*, *Carex humilis*)

C44 Southeast and Lesser Caucasian krummholz and open woodlands (*Betula litwinowii*, *Acer trautvetteri*, *Quercus macranthera*), scrub (*Rhododendron caucasicum*), tall-forb communities (*Heracleum sosnowskyi*, *Aconitum orientale*) and grasslands (*Festuca varia* subsp. *woronowii*, *Calamagrostis arundinacea*, *Geranium ibericum*)

C45 West Lesser Caucasian krummholz and open woodlands (*Betula litwinowii*, *Fagus orientalis*, *Acer trautvetteri*) with *Quercus pontica*, *Betula medwedewii*, scrub (*Rhododendron caucasicum*) with *Rhododendron ungernii*, tall-forb communities (*Ligusticum alatum*, *Milium schmidtianum*) with *Heracleum cyclocarpum*, *H. mantegazzianum* and grasslands (*Agrostis planifolia*, *Geranium platypetalum*) with *Euphorbia oblongifolia*, *Astragalus bachmarensis*)

C46 East Lesser Caucasian krummholz and open woodlands (*Quercus macranthera*, *Acer trautvetteri*, *Betula litwinowii*), scrub (*Juniperus communis* subsp. *hemisphaerica*, J. sabina), grasslands (*Festuca varia* subsp. *woronowii*, *Bromopsis variegata*, *Anemonastrum fasciculatum*) with *Trifolium bordzilowsky*, partly tall-forb communities (*Milium effusum*, *Gagea orientalis*) alternating with dry grasslands (*Festuca ovina*, *Carex humilis*) with true steppes (*Festuca valesiaca*, *Stipa tirsa*, *S. pulcherrima*), partly with thorn-cushion mountain vegetation (*Astragalus aureus*)

D32 West Caucasian fir, spruce-fir and beech-fir forests (*Abies nordmanniana*, *Picea orientalis*, *Fagus orientalis*) with evergreen understorey *Rhododendron ponticum*, *Prunus laurocerasus*, *Ilex colchica*), often alternating with Oriental beech forests (*Fagus orientalis*)

D33 Caucasian fir, spruce-fir and beech-fir forests (*Abies nordmanniana*, *Picea orientalis*, *Fagus orientalis*) without evergreen understorey, partly alternating with Oriental beech forests (*Fagus orientalis*)

D64 Caucasian pine forests (*Pinus kochiana*), partly alternating with birch forests (*Betula litwinowii*, *B. raddeana*) and spruce forests (*Picea orientalis*)

F163 East Euxinian-Caucasian Oriental beech forests (*Fagus orientalis*) partly with *Picea orientalis*, mostly with evergreen understorey (*Prunus laurocerasus*, *Rhododendron ponticum*, *Daphne pontica*) with *Hedera colchica*, *Ilex colchica*, *Ruscus colchicus*

F164 Caucasian Oriental beech forests (*Fagus orientalis*) with *Carpinus C. caucasica* partly with *Picea orientalis*, without evergreen understorey partly alternating with oak-hornbeam forests (*Carpinus betulus*, *Quercus iberica*)

F165 East Caucasian submontane to montane hornbeam-maple-Oriental beech forests (*Fagus sylvatica subsp. orientalis*, *Acer velutinum*, *Carpinus caucasica*) with *Hedera pastuchowii* in combination with hornbeam-chestnut-oak forests (*Quercus iberica*, *Castanea sativa*, *Carpinus caucasica*)

F169 East Euxinian oak and hornbeam-oak forests (*Quercus iberica*, *Carpinus orientalis*, *C. caucasica*), alternating with hornbeam-chestnut-Oriental beech forests (*Carpinus caucasica*, *Fagus orientalis*, *Castanea sativa*) with evergreen understorey

F170 Transcaucasian oak forests (*Quercus iberica*), hornbeam-oak forests (*Quercus iberica*, *Carpinus caucasica*) and Oriental hornbeam-oak forests (*Quercus iberica*, *Carpinus orientalis*), with *Sorbus torminalis*, partly in combination with shibliak communities (scrub)

H1 Colchic lowland to submontane mixed oak forests (*Quercus imeretina*, *Q. hartwissiana*, *Zelkova carpinifolia*, *Carpinus caucasica*, *Castanea sativa*, *Fagus orientalis*) with evergreen understorey species (*Rhododendron ponticum*, *Prunus laurocerasus*), alternating with oak and hornbeam-oak forests (*Quercus iberica*, *Carpinus betulus*) in the submontane belt

K24 West Caucasian *Pinus pityusa*-forests with *Carpinus orientalis*, *Cistus crecitus*, *Ruscus aculeatus*

K33 Transcaucasian colline-montane juniper open woodlands (*Juniperus polycarpos*, *J. foetidissima*), partly in combination with *Pistacia mutica* – open woodlands

M4 Transcaucasian altimontane herb-grass- and meadow steppes (*Stipa tirsa*, *S. pulcherrima*, *Festuca ovina*, *Carex humilis*, *Poa densa*, *Bromopsis variegata*, *Onobrychis altissima*, *O. transcaucasica*, *Aster ibericus*, *Scutellaria orientalis*)

M11 Pre- and Transcaucasian Stipa-steppes (*Stipa tirsa*, *S. pulcherrima*, *S. pontica*) with Onobrychis transcaucasica, Botriochloa ischaemum – steppes with *Onobrychis kachetica*, *Medicago coerulea*, *Polygala transcaucasica*, alternating with tomillares (*Thymus tiflisiensis*, *Scutellaria orientalis*) and thorn-cushion communities (*Astragalus denudatus*, *A. microcephalus*)

N6 East Transcaucasian thorn-cushion vegetation (*Astragalus caucasicus*, *A. microcephalus*, *Acantholimon lepturoides*. *A. fominii*) and tomillares (*Salvia garedji*, *Thymus tiflisiensis*)

O7 East Transcaucasian wormwood deserts (*Artemisia lerchiana*) with ephemeroids (*Poa bulbosa*, *Catabrosella humilis*)

08 East Transcaucasian *Salsola nodulosa* and *Salsola ericoides* – deserts with ephemeroids (*Poa bulbosa*, *Catabrosella humilis*), with *Artemisia lerchiana*

S26 Colchic herb-rich tall sedge fens with *Carex acuta*, *Cladium mariscus*, *Ludwigia palustris* in combination with Sphagnum-mires (*Sphagnum austinii*, *S. papillosum*) with *Rhododendron luteum*, *Osmunda regalis*, *Rhynchospora caucasica*

T3 Colchic alder carrs (*Alnus barbata*) in combination with alluvial forests (*Alnus barbata*, *Fraxinus excelsior*, *Pterocarya pterocarpa*), tall reed vegetation (*Phragmites australis*, *Typha latifolia*) and sedge swamps (*Carex* spp.)

U22 Transcaucasicum hardwood alluvial forests (*Quercus pedunculiflora*, *Ulmus minor*) in combination with poplar and willow alluvial forests (*Populus x canescens*, *P. nigra*, *Salix excelsa*) as well as *Tamarix ramosissima*-scrub

Source: The map is given according to Bohn et al. (2003), where the Caucasus part was prepared by D Bedoshvili, A Dolukhanov, M Ivanishvili, G Nakhutsrishvili, N Zazanashvili.

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Contents

Environmental Conditions

1

Georgia occupies an interesting geobotanical position as a part of Caucasia – the region which links Europe with Asia. The country is characterized by rather contrasting natural conditions which account for the extremely high degree of divergence of plant communities within this comparatively small area. The landscape of the country includes different types of desert and semi-desert vegetation mainly in the eastern parts of Georgia, luxuriant Colchic forests of moist, almost subtropical climate in the west, and high-mountain plant communities in the north and in the south (See "Map of the Natural Vegetation of Georgia" 2003).

The complex orographic structure of Georgia and its geographical position account for the geographical and ecological isolation of certain plant communities, which has resulted in a high ratio of local endemism (particularly endemics of the Greater Caucasus Range and of the Colchis) as well as a variety of species of different phytochorological groups, like Iberian and Anterior-Asian group, etc.

1.1 Orography

Geologically, the territory of Georgia belongs to the Alpine System of Eurasia. Its geological and geomorphological structure reveals a great genetic diversity, as a result of tectonic, volcanic, petrological, gravitational, erosional and other processes.

Structurally, the area can be divided into the following major landforms:

1. The range of the Greater Caucasus (Kavkasioni);
2. The Georgian Intermontane Area (between the Greater and the Lesser Caucasus);
3. The Mountain System of the Lesser Caucasus (Meskheti-Trialetian Range), including the South Georgian Volcanic Upland.

Georgia comprises the southern side of the middle part of the Kavkasioni as well as the north-western parts of the Transcaucasian Depression, the Lesser Caucasus, i.e. the South Caucasian Upland.

Altitudes in Georgia vary considerably from the sea level (at the Black Sea) to some of the highest peaks of the Greater Caucasus, reaching 4,695 m (mt. Ushba),

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DOI 10.1007/978-3-642-29915-5_1,

5,068 m (in the Shkhara massif), and 5,047 m a.s.l. (mt. Kazbegi, Kazbek). From the geological point of view, this area consists, mainly, of Meso- to Cenozoic deposits. Ancient Precambrian and Paleozoic formations are poorly represented and of secondary importance (Gerasimov 1966).

1.2 Climate

The climate is one of extremes. It is possible to distinguish several climatic zones from the humid, almost subtropical climate to the climate of permanent snows and glaciers. Such a considerable range of climatic conditions is caused both by the orographic structure and the presence of the Black Sea and the Caspian Sea. The Black Sea and high mountain ranges of the Greater Caucasus are the most important orographic factors determining the climate of Georgia by preventing the invasion of cold air masses from the north. The climate of the country has been formed by the air masses blowing from sea, as well as by the latitudinal position between southern Russia and the Inner-Anatolian mountains system.

The highest mean annual temperature amounts to 15 °C (Sukhumi in Abkhazeti, on the Black Sea coast). The warmest winter (5–7 °C, in January) is in Colchis (West Georgia, on the Black Sea coast).

Annual precipitations in Georgia range from over 4,500 to 400 mm or less. Increase of altitude e.g. in Svaneti (north-western Georgia) and Javakheti (south-western Georgia) is paralleled by reduction of precipitation, while in other districts (Kazbegi region, Kakheti, etc.) the amount of rainfall increases with elevation. The highest amounts of precipitation occur at the following altitudes: from 300–500 m to 3,500 m a.s.l. in Western Georgia, and from 1,200 to 3,500 m in the eastern part of the country.

The climatic conditions of several districts of Georgia are demonstrated diagrammatically (Fig. 1.1). Notwithstanding the short distance between these districts (60 km between Batumi and Bakhmaro, 380 km between Batumi and Shiraki, 155 km between Shiraki and Kazbegi), their climatic conditions are noticeably different.

1.3 Soils

There is a great diversity of soil types in Georgia. The following soil provinces can be distinguished:

1. The soil province of Western Georgia;
2. The soil province of Eastern Georgia;
3. The soil province of Southern Georgia.

The main types of soil are allocated in accordance with the altitudinal zones. In the Western Georgia soil province (between the Black Sea and Likhi mts.) it is possible to distinguish the bog and podzolic soil zone in the lowlands, the krasnozem and zheltozem zone in the hilly piedmonts, the zone of mountain-forest and the mountain-meadow soils.

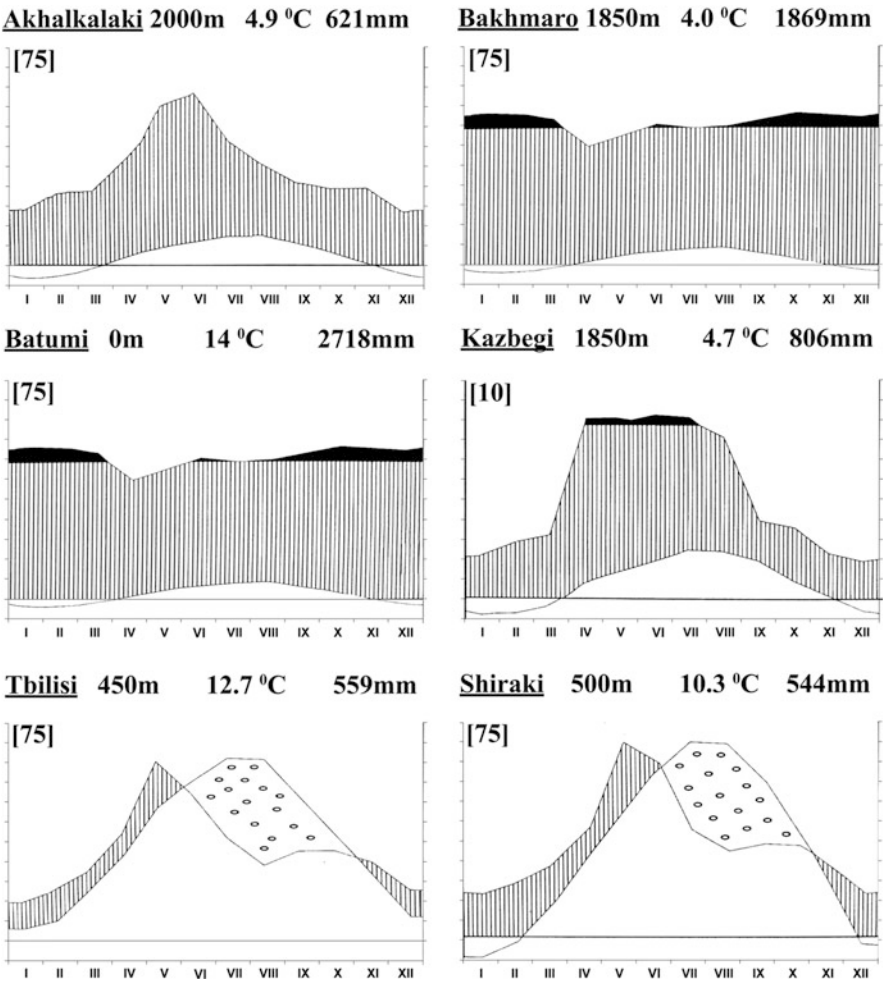

Fig. 1.1 Climadiagrams of several regions of Georgia

The soil province of Eastern Georgia comprises the plains, piedmonts and mountain massifs, situated eastwards from Likhi mountain range. Chestnut soils, chernozems, brown humic-sulphates, saline soils of steppes and semi-deserts, as well as intermediate forest-steppe and mountain-meadow soils occur in this province.

The Southern Georgia soil province includes Javakheti, Tsalka-Dmanisi and Erusheti uplands, the hollow of Akhaltsikhe, etc. A considerable part of this area is covered both with the mountain chernozems (which are formed at altitudes from 1,200 to 2,200 m) and meadow chernozem-like soils. In highlands they are replaced by mountain-meadow soils. Besides, the alluvial soils, redzinas, brown as well as the meadow-brown soils occur here, with the predominance of brown forest type of soil in the mountain forest belt (Urushadze 1987).

History of the Flora and the Vegetation

2

The history of the flora and, especially, the vegetation of Georgia is very complicated and, despite the intensive paleobotanical investigations of the recent past, still needs to be studied.

The earliest records of fossil flora stem from the Paleozoic. Species of *Lepidodendron* (large trees reaching a height of nearly 40 m), *Sigillaria* (high plants with erect stems and characteristic rhizophore system: stigmarias), *Asterocalamites* were determined from the Lower and Middle Carboniferous deposition of the Khrami crystalline massif (South Georgia). Cordaitales – a group with anatomical structures (tracheids, well-developed pith) very similar to that of conifers (Shatilova et al. 2011) – are known from the same period.

In the Early Jurassic, almost the entire territory of Georgia was covered by sea, except for Khrami, Loki and Dzirula ancient massifs.

The climate of this period was warm-temperate. Water temperature in the sea reached 23–24 °C, but in Late Toarcian it decreased considerably (7–15 °C). Calamitales are of special interest with the only species *Neocalamites hoerensis* present in the early Jurassic depositions. The above mentioned period was characterized by the wide-spread occurrence of equisetoids, which were restricted to marshes as it is nowadays (Svanidze 1972).

Pteridophytes were represented by 25 taxa. Microfossils found belong mainly to the genus *Cladophlebis* (Osmundaceae). At the same time *Ginkgo* was represented by two species: *G. mziae* (specific to Georgia) and *G. huttonii*. The species *Sphlenobaiera spectabilis* and *Phoenicopsis angustifolia* also belong to Ginkgoaceae. In the early Jurassic, a considerable group was formed by Bennettitales – the ancestors of the flowering plants (according to the viewpoint of several botanists). *Eucommiidites troedssonii* (gymnosperms pollen) and many other plants were present in the same period too.

In the Bajocian (Middle Jurassic) the entire territory of Georgia was under the sea; by the end of it, first the eastern part and afterwards (in Bithonian) the whole territory has emerged. The appearance of freshwater basins was characteristic to that period, as well as the process of peat accumulation (Kakhadze 1947). The Early Jurassic flora is much richer than that of the Early Jurassic. Today nearly 175 plant

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species are known from the Middle Jurassic. 55 of them are ferns (*Coniopteris,* Cyatheaceae*,* Osmundaceae*,* Gleicheniaceae) and representatives of *Paracycas* (Cycadaceae)*, Ptilophyllum* (Benettitaceae), etc. The climate of the Middle Jurassic was probably tropical; representatives of Cycadales and Ginkgoales dominated the woodlands (Svanidze 1972).

In the Late Jurassic the territory of Georgia was covered by sea, except the Svaneti Elevation, as well as the southern parts.

The occurrence of remnants of the new species *Angiopteris iberica (*Marattiaceae) in the Late Jurassic fossiliferous deposits is of great importance. It underlies the opinion that these archaic living ferns disappeared from the floras of the Northern Hemisphere after the Middle Jurassic.

According to Vakhrameev (cited by Shatilova et al. 2011), the Late Jurassic paleofloristic province of the Caucasus was a part of the Euro-Sinian region.

The flora of the above-mentioned province could be characterized by the presence of occasional equisetoids, a few ferns, Ginkgoales, the absence of *Czekanowskia* and the predominance of Cycadales*,* Bennettitales as well as *Pachypteris, Sagenopteris, Pagiophyllum.*

2.1 The Tertiary

In the **Paleocene** and **Eocene** a long island was formed on the territory of the Caucasus as a basis for further development of mountain range. In the Eocene, the dominant position was occupied by the Angiosperms, representatives of evergreen Fagaceae and *Myrica*.

At the same time the process of migration of the Boreal cold-resistant plants, which had begun previously in the Cretaceous, resumed at the end of the Eocene.

At the Eocene/Oligocene boundary, the folded structure of the Alpine system started to form in the Mediterranean orogenetic band. It comprised the (geosynclinal) regions of the Southern Slope of the Greater Caucasus range and Ajara-Trialeti, the main part of today's Georgia. Uplift caused a change in the climatic conditions; the latter determined the character of the vegetation: the number of conifers increased and warm-temperate plants became more numerous (Tumajanov 1955; Shatilova et al. 2011).

During the **Oligocene**, the Caucasus was a small island surrounded by a vast basin with scattered islands, where the tropical flora of the Poltava type (palms, laurels, etc.) was well developed. In West Georgia (near the town Chiatura), in the Oligocene deposits remnants of conifers (species of *Pinus*) were found, indicating the penetration of northern taxa into the Caucasus.

The Oligocene plant world was greatly influenced by the Arcto-Tertiary or Turgay flora, formed in the eastern and northern parts of modern Asia. Representatives of this flora, especially pines, penetrated into the Caucasus. Many botanists consider that migration of the Turgay elements became more intensive after the Turgay Strait had become dry by the end of the Oligocene.

According to Grossheim (1948), Turgay migrants began to change and gave rise to the ancient mesophytic forest flora, called Mediterranean-Turgay flora by this author.

During the **Miocene** the Caucasian island started to expand. Fossil assemblages from different parts of Georgia, especially from Western Georgia (Guria), confirm the subtropical nature of the Miocene flora with the predominance of evergreen woody plants, accompanied by the deciduous *Castanea sativa*, as well as by conifers of northern origin *(Pinus neptuni)*.

The following plants have been known since the Early Miocene deposites of Kartli (East Georgia): *Myrica neriifolia* (=*M. lignitum*), *Laurophyllum primigenium,* species of *Apocynophyllum*. Of the 46 taxa two are pteridophytes and five gymnosperms. The dominant position is occupied by Angiosperms, namely *Comptonia acutiloba, Myrica neriifolia* (=*M. lignitum*), etc. The greatest part of the Early Miocene flora, studied by macrofossils, is represented by Angiosperms. Among them the predominance of Myricaceae, Juglandaceae and Lauraceae should be noted, whose role has somewhat increased since the Paleogene. Evergreen Fagaceae, Lauraceae and other thermophilous plants, contributing to the formation of moist-subtropical forests in the Paleogene, adapted to the reduced humidity of the Early Miocene.

In the Middle Miocene plants of warm and dry climate participated in sclerophyllous formations. *Myrica* species covered river banks. Sclerophyllous plants were represented by the species of *Myrtus, Callistemophyllum, Acacia, Quercus (Q. drymeja)*. Several species of Lauraceae, *Sapindus, Smilax* and *Magnolia* formed moist-subtropical forests.

It is possible to suggest that an altitudinal differentiation of vegetation already existed in the Middle Miocene. Coastal and low mountainous areas were covered by subtropical forests with high numbers of Sterculiaceae, Araliaceae, Lauraceae, evergreen Fagaceae, arborescent ferns, *Hymenophyllum*, etc. The next altitudinal belt was occupied by mesophilous deciduous forests of *Platanus, Comptonia, Juglans, Pterocarya*, etc. Cold-resistant plants occurred even higher; mention should be made of species of *Betula, Fagus, Acer, Tilia, Ulmus,* accompanied by *Cathaya, Keteleeria,* etc. (Shatilova et al. 2011).

During the Sarmatian (Upper Miocene), the Caucasian island, known in the literature as Jephethis, was situated close to Iranian and Central Asian land. This encouraged the immigration of xerophilous elements into the Caucasus. It is suggested that the forestless formations of xerophytic plant communities were widely distributed during the Early Miocene. According to Grossheim (1946), *Pelargonium endlicherianum*, the fern *Ceterach*, etc., are relicts of the ancient xerophytic flora of this period.

The close position of Jephethis to the Iranian mainland, separated as a cape, caused a division of the mesophytic Mediterranean-Turgay flora into western and eastern parts. In the west, the Colchic flora began to form, while the Hyrcanian elements evolved in the eastern part. Both were of mesophytic nature. The analysis of the contemporary vegetation makes many botanists suggest the existence of a third xerophytic flora.

Based on the fossils, it is possible to build up a picture of the Sarmatian flora: evergreen *Magnolia dianae,* species of Lauraceae (*Cinnamomum, Laurophyllum primigenium, Laurophyllum pseudoprinceps,* etc.), as well as the representatives of the Mediteranean-Turgay and Turgay deciduous flora, such as *Salix, Pyrus, Carpinus, Juglans, Ulmus,* etc. Conifers (*Pinus saturi, Sequoia langsdorfii*) and xerophytic species of *Myrica* have been known from the same age.

Kolakovsky and Shakril (1976) pointed out that the richest Sarmatian floras occurred in Abkhazeti (Colchis). They were closely related to the southern subtropical and tropical floras (*Melastomites* sp., *Mastixia microphylla, Ventilago* etc.). The Sarmatian floras of Abkhazeti are very similar to Oligocene-Miocene European floras. These floras indicate the wide distribution of subtropical evergreen plants, mainly Lauraceae, such as *Ocotea, Persea, Aniba,* and many others, and the deciduous arborescent plants of warm climate which have survived until now only in Central and South America, partly in the Mediterranean area and in South-Eastern Asia. These forests show a great similarity to the vegetation, confined to mountainous Japan during the Miocene-Pliocene. It is suggested that this vegetation is similar to that now found in the mountain systems of South-Eastern Asia, Himalaya and China, where relic forests of *Ulmus, Fagus, Quercus, Abies* and *Cryptomeria* were well represented.

The Tertiary-relic species of Colchic type, such as species of *Buxus, Pterocarya*, etc. and the hemixerophytic Mediterranean plants *Arbutus, Celtis, Smilax, Thelycrania (Cornus), Quercus*, have been found in the Sarmatian deposites of Abkhazeti.

The territory of East Georgia, where steppes and semi-deserts are distributed now, is considered to have been covered with both sclerophyllous and moist-subtropical forests.

In South Georgia the shrubs of subtropical and temperate climate dominated by Lauraceae, were represented by narrow-leaved xerophytic elements.

In the Meotian, after the regression of the Mediterranean Sea, the strait separating the Jepethis from the southern mainland disappeared and the Caucasus became a peninsula. The formation of the main folded systems reached the final point, and the vegetational belts were formed. The Meotian macrofossils included *Cryptomeria japonica*, species of Lauraceae*, Salix coriacea, Myrica neriifolia* (=*M. lignitum*). Ferns, especially *Dicksonia*, were represented by a large number of species. Palynological data attest to the fact that the following genera of conifers were present: *Abies, Picea, Tsuga* (five species), *Cedrus,* as well as *Carya, "Castanopsis furcinervis"* (leaf remnants of *Quercus),* representatives of Hamamelidaceae or Altingiaceae *(Liquidambar*, etc.).

According to the composition of the fossiliferous deposits, in this period, coniferous and broad-leaved forests *(Taxodium, Cryptomeria, Magnolia,* species of Hamamelidaceae, etc.) with the species of *Quercus, Carya, Fagus, Castanea* and *Platanus* began to prevail.

Relatively dry habitats were occupied by the following hemixerophytes: *Quercus drymeja, Celtis punica, Pistacia miocenica, Sophora europaea, Pyracantha coccinea*. At the same time the following plants began to crop up (present-day

members of the Georgian flora): *Rhododendron caucasicum, Fagus orientalis, Zelkova crenata (=Z. carpinifolia)*. During the period of Pontian Sea expansion, the Caucasus and Transcaucasia became consolidated.

The fossil flora of Goderdzi pass (South-Western Georgia) was distinguished by the features characteristic of Sarmatian flora; in Pontic it had already been a relic flora.

Taking into account fossil deposits of this region, mesophytic flora obviously prevailed here. Representatives of Annonaceae, Hamamelidaceae and Lauraceae are known from this period which was characterized by a warm maritime climate. Ferns, distributed in Georgia during the Pontian, can now be found only in the tropics.

During the Pontian, gymnosperms were widespread. Nowadays, they occur in montane forests of tropical and subtropical countries. In the beginning of the Pliocene, *Pinus pithyusa* was widely distributed.

Investigations carried out by Kolakovsky (1964) in Kodori (Abkhazeti) point to the existence of lowland and low-mountain forests with *Myrica lignitum, Salix varians, Alnus subcordata*. Coastal lowlands were covered with forests of *Quercus kodorica* and *Carya denticulata*, while the riversides were occupied by species of *Liquidambar, Taxodium, Nyssa, Tectocarya, Ocotea,* evergreen Fagaceae like *Pasania, Castanopsis*, etc., which were characteristic of the subtropical forests of the Pontian. In the lower montane zone, considerable areas were populated by Laurisilva with tree ferns *(Cyathea, Alsophila, Dicksonia).*

In the lower montane zone sclerophyllous formations were distributed with the elements of maquis. Pines occupied rocky habitats.

Kolakovsky (1974) pointed out that an important change in the flora of the warm-temperate climate took place during the Pontian. The mid-mountain belt was populated by *Fagus, Castanea, Acer, Tilia* species. The presence of conifers – *Ginkgo, Keteleeria* – , ferns like *Polypodium*, etc., lianas like *Vitis betulifolia, Parthenocissus quinquefolia* becomes fairly possible.

Dark coniferous forests (with species of *Abies, Tsuga, Picea, Cedrus,* etc.) occupied relatively higher altitudes.

On the territory of West Georgia a great number of angiosperms has vanished since the Pontian.

In Cimmeridian (Middle Pliocene), the shrinking of the Tethys led to the exposure of new land, fit for colonization by xerophytic vegetation, such as semi-desert vegetation, shibliak, light forests, maquis, etc., so characteristic of the Mediterranean. Meanwhile, taxa of Araliaceae, as well as ferns were well represented. The dominant position was occupied by species of *Pteris* and *Polypodium*. According to Kolakovsky and Shakril (1978), forests of warm-temperate climate began to prevail in Cimmeridian; they were composed by the species of moist monsoon climate, now peculiar of the mountains of Eastern Asia and xerophytes, ecologically similar to the plants of xerophytic forests of the Mediterranean. Above the warm-temperate forest zone hardwood and coniferous forests grew.

During the Kuyalnitskian-Akchagylian (Upper Pliocene), a large part of East Georgia lay under the sea. The Greater and Lesser Caucasus were connected by a land bridge to the Near East (Asia Anterior–South-West Asia) in the south. The

most striking feature of the fossil floras of this period is the absence of Poltava floral elements and evergreen plants. The following plants are known from this period: species of *Populus, Ostrya, Fagus, Zelkova, Tilia, Pyrus, Ligustrum, Salix, Prunus, Acer, Quercus, Pterocarya*, together with representatives of *Carex* and *Phragmites*. All these plants are members of the present-day flora of Georgia, though they have changed their habitats. For example, remains of *Fagus orientalis* and *Ostrya carpinifolia* have been found in Akchagyl deposits of the Shiraki steppe. Due to increasing aridity, these trees are no longer there.

According to Grossheim (1948) the Akchagylian flora by its nature is closely connected with that of the Quaternary. To quote his words: "The period between Sarmatian and Akchagylian was the turning-point in the floristic history of the Caucasus; the tropical flora had been replaced by that of temperate climate" (Grossheim 1948: 171). Broad-leaved forests were replaced by conifers, namely species of *Picea, Abies,* and *Tsuga*. In general, during the late Pliocene, the role of polydominant forest vegetation was reduced and, instead, the formation of communities with one or two dominant species was stimulated. These changes in the vegetational cover were probably provoked by the intensification of cold at the end of the Miocene and in the Pliocene.

The existence of a dry and hot climate between the cold periods encouraged the enrichment of the Caucasian flora with xerophytes. In Akchagylian times, many recent Mediterranean plants penetrated into the present area from the west.

Therefore, in the **Pliocene**, the piedmonts and the lower montane zone were clothed by subtropical forest vegetation. Forests of warm-temperate climate were situated higher up. Many species known from this period are still members of the modern forest flora. In the beginning of the Pliocene, within the territory of West Georgia and adjacent areas (e.g., Turkey), a Colchic refuge was formed for many relics of mesophytic forest flora. This was a direct result of the warm and humid climate of this territory. The Colchic refuge was of great importance as one of the most stable "shelters" for relic species during the Late Pliocene and especially in the Pleistocene, including the Ice Ages. Many species, which continue to exist in the Colchis died out many millions of years ago on the territory of West Eurasia. Members of the Colchic flora are such relics and/or neoendemics as *Betula medwedewii, Quercus pontica, Rhamnus imeretina, Hedera colchica, Pterocarya pterocarpa, Laurocerasus officinalis, Arctostaphylos caucasica, Rhododendron ponticum, Rh. ungernii* and *Rh. smirnowii*. At present, their relatives with a similar autecology have mainly survived in the mountains exposed to the summer monsoon in eastern and south-eastern Asia, in the Appalachians of North America, etc.; for instance, the genus *Epigaea* is represented now by just three species, one of which is distributed in Japan, the second in North America and the last in Ajara (Georgia) and Lazistan (N. Turkey).