GRADIENT ANALYSIS: THEORY, APPROACHES
AND APPLICATION

Nikolay Dyakov
Department of Dendrology, Faculty of Forestry,
University of Forestry – Sofia

Abstract: This paper presents a short review of gradient analysis basic theory, approaches
and application. Contradictory viewpoints of vegetation organization along the environmental
gradients are discussed. Different environmental gradients influencing plant species are con-
sidered. These are complex environmental gradients, resource gradients and direct gradients.
Two approaches of gradient analysis are reviewed: direct and indirect gradient analyses. The
most popular hypotheses in gradient analysis are also discussed. Contemporary state of gra-
dient analysis theory is presented and illustrated. Possible application of different views of
vegetation pattern is offered.

Key words: environmental gradients, ordination, continuum, vegetation

INTRODUCTION

Detailed analysis of the relationship between vegetation and environment
requires extensive knowledge of the ecological processes influencing plant
species (Austin, 2005). Plant species are distributed in variable habitats,
but within the limits of their area they are most abundant in places which
represent their ecological optimum. Because of this the composition of
plant communities is a function of changing habitat conditions along the
environmental gradients. The successive change of species abundance with
the changing environment takes place in the ecological space as well as in

Traditionally, in vegetation ecology there is a dichotomy between
experimental and observational studies. Investigations combining the two
approaches are very few. In gradient analysis predominate observational
studies falling in the context of vegetation-environment relationship. Gradient
analysis can bring answers to some essential questions like (Austin, 2005):
i) is vegetation pattern continuous or discontinuous and how this pattern
changes with changing environment?; ii) what theory and methods are most
appropriate in studying such a phenomenon?; iii) what is relative importance
of environmental gradients determining vegetation pattern? These and other
questions are to be answered in the following review.
VEGETATION PATTERN ALONG ENVIRONMENTAL GRADIENTS: CONTINUUM OR COMMUNITY

The concept of vegetation continuum and changing species composition along environmental gradients emerged as an antithesis of plant community paradigm. According to the latter, plant communities are natural groupings of coevolved species populations, forming discrete and discernible units (Austin, 1985).

One of the basic principles of the vegetation continuum concept, according to Whittaker (1975), is that: ‘Broadly overlapping species population and scattered species distribution along the environmental gradients is indication that most communities replace one another continuously and do not form clearly outlined boundaries.’ This principle is often associated with the individualistic paradigm of Gleason (1926), according to which: ‘Each species is distributed in its own manner, depending on species’ genetic makeup and physiological requirements and the way it responds to the environment, as well as on its interdependence with other species, therefore there is no two plants with completely overlapping distribution.’ Individualistic concept and the continuum paradigm of vegetation are not necessarily connected to each other. Vegetation composition can vary in continuous way, but the species may be distributed in no casual manner and have clear boundaries (Goodall, 1963).

Principle discussion concerning continuum concept is provoked by misinterpretation of some scientists, unfamiliar with it, that do not distinguish species location along environmental gradients and its positions along the field transect. Spatial relationship between plant communities, where the samples were taken, and its position along the environmental gradient are not necessary. Gradients are abstract dimensions of the environment, where, depending on the ordination method used, relative position of the habitat reflects the similarity of the ecological conditions or species composition between them (Austin, 1985).

The well-known debate from the 60s of XX century, concerning continuum theory and community theory, was focused on two basic issues: 1) whether field data (gathered by the continuum followers) are taken from climax or successional communities, and 2) whether the continuum is an artifact in consequence of the method used.

Continuum concept was supported by Wisconsin school studies and their approach called ‘continuum index’ (Bray, Curtis, 1957; Brown, Curtis, 1952; 1959; Curtis, McIntosh, 1951) and mostly by Whittaker (Whittaker, 1956; 1967; Whittaker, Niering, 1965) with his gradient analysis. Wisconsin’s school approach arranges the samples based only on their species composition. In gradient analysis directly measured environmental variables, such as elevation,
are used. Graphical results of these methods, without exception, show that plant species have broadly overlapping distribution. This was accepted as a proof in favor of continuum concept, which later brought consensus on this issue.

Analyzing his results on ecological niche partitioning along the environmental gradients, Whittaker (1978b) assumed, that when dominant species are less numerous and are nearly ecological equivalents to each other, they can be uniformly distributed along the environmental gradients (see also Gauch, Whittaker, 1972). The author gives an example with the conifer tree substitution along the elevation gradient on the north slopes of Santa Catalina and Pinaleno Mountains, Arizona. When there was deviation from this phenomenon the species were uniformly distributed along the second environmental gradient – the moisture gradient (Whittaker, 1978b; Whittaker, Niering, 1965).

TYPES OF ENVIRONMENTAL GRADIENTS

Austin, Smith (1989) discussed the current issues in continuum theory and offered a new model. The authors distinguish three types of gradients:

**Indirect gradients** – these are complex gradients (*sensu* Whittaker, 1978a) such as elevation gradient, for example. The influence of elevation is indirect, through variables like temperature and precipitation, which have direct effect on plant growth. These variables, depending on the site location, are in complex correlation with the elevation. Relationships between vegetation and these environmental gradients cannot be extrapolated beyond the studied territory;

**Resource gradients** – these are variable resources consumed by plants for their growth. For the autotrophy plants these resources are with limited number: light, water, CO$_2$, O$_2$, nutrients. Plant reaction to the resource gradients is relaxed. Plants react only to the toxic levels, exceeding normal concentrations in the environment;

**Direct gradients** – these are gradients having direct physiological effect on plant growth but are not consumed by plants, for example, air temperature and soil pH. Direct gradients regulate plant growth and support plant physiological integrity. Plant physiological response shows different adaptations in different temperature regimes and their fundamental niches are dispersed along the gradient (Fig. 1).

DIFFERENT APPROACHES IN GRADIENT ANALYSIS

The need for quantitative methods, studying vegetation continuum, accelerated development of ordination techniques (Curtis, McIntosh, 1951;
Whittaker, 1951). Goodall (1954) first introduce the term ‘ordination’, relevant to methods, which arrange samples or species in ‘multidimensional series’. However, problems with the interpretation of ordination results still provoke discussion today. There are issues with the compatibility of their mathematical basis with the vegetation ecological theory (Austin, 1980; Noy-Meir, Whittaker, 1978).

Ordination in vegetation ecology is the process of sample (or species) arrangement along one or more environmental gradients, or along abstract axes, which may represent important environmental gradients (Austin, 1976; Goodall, 1954; 1963). Ordination is a method for analysis, which seeks tendencies or patterns in the multivariate data matrix. The goal is raising a hypothesis as well as reducing the complex data to few dimensions (Austin, 1976; Dale, 1975; Noy-Meir, Whittaker, 1978).

Two different approaches are used. The first one is called direct gradient analysis (Whittaker, 1967; 1978a) or ecological ordination (Austin, 1968). In this technique vegetation data are investigated graphically or mathematically in the context of selected environmental gradients. Whittaker (1951; 1956; 1960; 1978b), Whittaker, Niering (1965) use direct gradient analysis for the first time analyzing vegetation pattern along elevation and moisture gradients. This method is a simple graphical technique for representation of species distribution along the environmental gradients, which a priori are considered as important for plants. The truth is that direct gradient analysis is left almost unchanged since its origin (Whittaker, 1951; 1956; 1960; Whittaker, Niering, 1965; Peet, 1978a; 1978b; Kessel, 1979; Gauch, 1982). In theory, any two or more environmental gradients can be used but in practice the moisture gradient measured in series of elevation belts is most frequently used. Position of a given sample along the moisture gradient is estimated depending on the site, from which it has been taken, for example, from deep moist ravines to xeric southwest facing slopes. Relative position of species and samples along the environmental gradient is estimated by calculation of weighted indexes. Estimated in this way, moisture index appears to be rather indirect (compositional) than direct (environmental) gradient (Whittaker, 1978b; Austin, 1980).

Peet (1978a; 1978b) tests the weighted averages of moisture gradient and independent measurements of sample topographic position (e.g. potential

Fig. 1. Distinction between the species physiological response to 1) resource gradients and 2) direct environmental gradients (acc. to Austin, Smith, 1989).
solar radiation). The author found very strong correlation between them. Moreover, he specifies the scheme and intensity of sampling procedure, so that, at least one sample falls within any one cell of the three-dimensional frame defined by the elevation, topography and stand age.

The other approach is *indirect gradient analysis* (Whittaker, 1967; 1978a) or vegetation ordination (Austin, 1968), in which mathematical methods are used for summarizing the emergent data structure of species and samples in a few abstract dimensions. In indirect gradient analysis there is not *a priori* assumptions about which are the most important environmental gradients influencing vegetation. Graphical result from the analysis shows which samples are located in extreme and intermediate parts of the environmental gradient. Next, appropriate statistical tests are used, which on the basis of statistically significant correlations, show the environmental variables having sense in the species and sample arrangement (Greig-Smith, 1983).

Vegetation ordination usually requires assessment of similarity or dissimilarity between the samples, according to the species composition (Green, 1980), or applying of some mathematical algorithm for data matrix analysis (Greig-Smith, 1983). Most of the multivariate ordination techniques are introduced in plant ecology from other disciplines, for example, Principal Component Analysis (PCA) (Goodall, 1954), canonical correlation (Austin, 1968), parametric mapping (Noy-Meir, 1974), and Reciprocal Averaging (RA) (Hill, 1973).

According to Austin (2005), ordination indicates the existence of some structure of vegetation along the environmental gradient, but cannot be used for proofing the continuum itself. However, indirect ordination can show the existence of discontinuity in the ordination space. Discontinuities most often are result from sharp difference in the site conditions. In mathematical models used in vegetation ordination there is beforehand assumptions about species response to environmental gradients. These assumptions can predetermine the ordination result.

**WORKING HYPOTHESES IN THE THEORY OF GRADIENT ANALYSIS**

Gauch, Whittaker (1972) hypothesized about species ‘behaviour’ along the environmental gradient. Their hypotheses are based on graphical results of the study without further statistical tests. The authors use their results to generate artificial data on which ground to compare different ordination methods. Their two basic hypotheses are that: 1) species distribution curves are similar to Gaussian curve, and 2) rarer species are distributed accidentally along the environmental gradients, while dominant species can have more uniformly distribution.
Hypotheses 3-5 (Gauch, Whittaker, 1972) concerned the statistical distribution of species importance values and other statistical parameters. Hypothesis 6 states that normal species distribution may be modified by competition. The basic assumption concerns the species abundance curve distribution along the environmental gradients, i.e. whether it has Gaussian or bimodal distribution. If response curves are not with Gaussian form, then most of their statements are inapplicable.

Species response curve along an environmental gradient in the presence of other species is equivalent to its realized ecological niche (Grubb, 1977; Whittaker et al., 1973). Some data of vegetation studies suggest that the realized species niche in one-dimensional space resembles Gaussian curve (Gauch, Whittaker, 1972; 1978b). However, in the published empirical studies predominate asymmetrical curves. For example, direct ordination results of Austin (1999) show that species response curves along environmental gradients can be variable, i.e. that symmetrical bell shaped curves are not dominant.

Bimodal curves seem to be more frequent than bell shaped ones, fact which appears to reflect the authors’ desire to publish deviation from given principle. The diversity of species response curves probably is an artifact coming from considering single environmental gradient and projecting it into the multidimensional ecological hyperspace. Averaging of data coming from different dimensions of this hyperspace may lead to doubtful bimodal curves. Available data cannot allow general conclusions to be made, regarding the species response curve form along the environmental gradients (Austin, 1985).

Like Gauch, Whittaker (1972), Austin, Smith (1989) also offer eight hypotheses incorporated in their continuum model. First one concerns the type of gradients already mentioned. Second states that species fundamental niches along resource-gradients take the form of series overlapping curves. Third, species fundamental niches along direct gradients take the form of series dispersed, weakly overlapping, independent curves. Fourth, species fundamental niches are shaped in such a way that in some parts of resource-gradient some species have relative advantage over other species. Fifth, species realized niche in multispecies groups can be defined through their fundamental niche, given the condition that species fundamental niches of all species are known in advance. Sixth, species richness (Fig. 2) along resource gradients as well as direct gradients will have two peaks located on intermediate position between the extreme gradient values. Seventh, dominance (maximal total biomass of single species) will have three maxima – under extreme gradient conditions, where only that species can survive, and under optimal gradient conditions, where the competition determines the species composition. Eighth, the total biomass of vegetation forms bell shaped curve along the environmental gradient.
Proposed hypotheses, as the authors (Austin, Smith, 1989) comment, concern the plant-environment relationship and they are static concepts. Herbivore pressure, diseases and disturbances are not taken in consideration as well as the role of reproduction, survival and senescence of the plants. The power of such processes may be influenced by environmental gradients also. It is known that the evolution of plant reaction toward the herbivore pressure is directly influenced by the nutrient availability. Grime (1973) and Chapin (1980) assume that the slow growth rate is an advantage in the poor habitats. However, slow growth rate decrease the plant capacity of recover after browsing and grazing. Because of this, plants with slow growth rate have ‘manufactured’ means of chemical defense from grazers, which assumes positive correlation between grazing gradient and nutrient availability.

According to Austin (1985) and other authors there were no formal attempts at that time for statistical or experimental tests of continuum concept (Austin, 1980; Gauch, 1982; Gauch, Whittaker, 1972; Goodall, 1954; Greig-Smith, 1983; Whittaker, 1978a). Approval of continuum concept is based on accumulating evidence in its advantage coming basically from the ordination studies (Curtis, 1959; Gauch, Whittaker, 1972; McIntosh, 1967; Whittaker, 1967; Peet, 1978a; 1978b; Austin et al., 1983). The unresolved difficulty with testing these models is due to environmental gradient nature, which is used in analysis of species response to its environment (Austin, 1985).

**HYPOTHESES TESTING IN GRADIENT ANALYSIS**

Relatively small number of studies tests directly the continuum concept or tries to delimit the community from continuum concept. For example, Minchin (1989) found that only 45% of the species have unimodal or symmetric curves along the environmental gradients studied. He analyzes 100 species from the mountain parts of Tasmania, using elevation and soil drainage gradients. The test for uniform distribution of species showed that species curves were clumped (all species), random distributed (major species) or variable, depending on the life form. The herbs had clumped distribution, while the other life forms had random distribution. Species richness of different life forms had unimodal distribution and their modes were centered in different parts of the environmental gradients.

Other studies also propose description models (Swan, 1970; Austin, Noy-Meir, 1971; Van der Maarel, 1976; Austin, 1976; Peet, 1978b) but
no one is mechanistic. Continuum concept and the graphic models used are truly phenomenological (Austin 1980; Gauch, Whittaker, 1972; Mueller-Dombois, Ellenberg, 1974). The alternative hypotheses, concerning vegetation pattern in the context of environmental gradients (Grime, 1973; Grubb, 1977; Tilman, 1982), gave rise to interesting ideas about species richness, depending on stress gradient and habitat productivity (Grime, 1973), species survival (Grubb, 1977), as well as competition, influencing species dominance (Tilman, 1982). Unfortunately, these hypotheses do not present clear statements about the species response curves or support in favor of any of the continuum/community concepts (Austin, 1985).

Salt (1983) discusses the current issues of experimental methods in community ecology and concludes that the most important steps, which should underlie in further investigations are: observation, modeling (theory), experiments, field tests, decision making.

According to Austin (1985), the hypotheses, concerning species response to environmental gradients, following that of Gauch, Whittaker (1972) and Austin, Smith (1989), have to be tested statistically with direct gradient analysis and the newer methods like General Linear Models (GLM). The descriptive techniques, especially ordination, may be useful to verify whether the main data variation corresponds to the preliminary chosen environmental gradients (Austin et al., 1984).

CURRENT STATE OF CONTINUUM THEORY AND ITS FUTURE APPLICATION

Contemporary state of vegetation continuum theory may be graphically represented (Fig. 3).

1) According to plant ‘community-organism’ concept, plant communities are composed of dominant species (e.g. trees) plus other species (shrubs, herbs), which by means of natural selection have adapted to live together in associations. Competition between dominant species leads to sharp boundaries between plant communities (Fig. 3a).

2) Vegetation continuum concept states that there is not sharp boundary neither between plant species nor between groups of plant species with similar distribution (Fig. 3b-f) (Austin, 2005).

Resource partitioning between species and the resultant competition assumes that species will be uniformly distributed along the environmental gradients (Pianka, 1981; ter Braak & Prentice, 1988) (Fig. 3b). If they belong to different vegetation strata or functional groups then species from each stratum will share the gradient independently from other strata (Fig. 3c). However, when there is more than two vegetation strata distinction between this model and the individualistic one becomes impossible (Austin, 1985).
Austin (1999) generalizes his results of some eucalypt species distributed along the mean annual temperature gradient. Species response curve form is dependent on the species' position along the gradient. He raises the hypothesis that species distributional limits toward the extreme parts of environmental gradient are determined by species physiology, while competition is responsible for the species response curve form in the intermediate parts of the gradient.

Vegetation science has no solid theoretical basis (Austin, 1985). In order to be accomplished such basis, synthesis of the ideas of ecological niche and continuum concept is needed, as well as deep understanding of the species ‘behaviour’ along the environmental gradients. Proposed models have to define the species fundamental niche and to show how species physiology influences the niche. An example for a null model is that fundamental niche remains unchanged in the presence of other species. If competition influence varies along the environmental gradients, then there will be needed detailed theories and models to be tested (Austin, 2005).

Discussing the two competitive concepts in vegetation ecology – continuum vs. community – Austin, Smith (1989) made the conclusion that: 1) continuum concept is applicable to the abstract environmental space and is not connected to some concrete geographical territory or indirect environmental gradient; 2) community concept can be adequate only for

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**Fig. 3.** Alternative models for vegetation pattern along environmental gradients (acc. to Austin, 2005)
a concrete landscape with its specific environmental conditions, because the community is a landscape attribute. Both concepts are compatible only if these conditions are met. For the environmental management, plant community concept is preferable only if there are clearly defined geographic boundaries, while when relationships vegetation/environment are studied, continuum concept has no alternative.

Gradient analysis is a powerful method for objective description and interpretation of vegetation-environment relationships. Therefore, its frequent employment in Bulgaria is strongly recommended.

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REFERENCES

ГРАДИЕНТНИЯТ АНАЛИЗ: ТЕОРИЯ, МЕТОДИ И ПРИЛОЖЕНЕ

Н. Дяков
Лесотехнически университет – София

(РЕЗЮМЕ)

Настоящата статия е кратък преглед на основната теория, подходите и приложението на градиентния анализ. Дискутирана са алтернативните гледни точки за организациите на растителността по направление на екологичните градиенти. Направен е анализ на екологичните градиенти, влияещи върху растителните съобщества. Това са комплексните (непреци) екологични градиенти, градиентите-резерви и преките екологични градиенти. Обсъдени са двете основни подхода за градиентен анализ: пряк и непряк градиентен анализ. Обсъдени са също така и най-популярните хипотези, на които се основава теорията на градиентния анализ. Направен е илюстративен преглед на съвременното й състояние. В заключение е представено възможното приложение на метода според различните схващания за организациите на растителността.

E-mail: ndiakov@yahoo.com