Ecograms for phytosociological tables based on Ellenberg's Zeigerwerte

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ABSTRACT. – Description of the method to obtain ecograms, which can be calculated from normal phytosociological tables, plotting average values of Ellenberg's Zeigerwerte on 6 axes corresponding to diagonals of a hexagon. The ecogram is the ecological fingerprint of the association. With adequate software the ecogram can be obtained automatically. It makes possible the immediate comparison among different communities. Ecograms give the synecological characterization of associations and can be used for detecting ecological gradients and for the delimitation of higher syntaxa. A first example consisting of a selected group of 33 forest communities from Italy is discussed.

KEY WORDS – Ecograms, synecology, Ellenberg's Zeigerwerte.

INTRODUCTION

During the first phase of development of phytosociology (ca. 1920-1950) the study of vegetation was carried out at many levels, with particular emphasis on floristic composition and synecology; most studies included phytosociological tables as well as exhaustive investigations of soil conditions and ecophysiological responses of species or of the whole community, and this remained the rule at least until the fifties. Also in my first investigations on the vegetation of Venice and in the Alps (in the years 1953-66) the study of soil was an essential component. On the contrary, in the last decades phytosociological investigations remain more and more limited to the floristic composition and lack an instrumental analysis of ecological conditions.

This development is probably a consequence of the fact that during the same time soil science, ecophysiology etc. developed into distinct fields of study.

In addition, it seems – at least at an unconscious level – that every species has his peculiar ecology, so that, when this was studied, then results could be extended to any other example of vegetation where the same species or species combination occurs. Consequently, tedious ecological measures in the field appear unnecessary and can be bypassed; descriptions of plant associations became more and more summarized and now often consist only in the floristic table with laconic comments, papers become shorter but the total number of associations remains steadily increasing. It seems impossible to give a complete overview of the apparently endless diversity of species combinations occurring in nature.

A similar procedure is applied to classification and ordination of communities and higher syntaxa, and here results become really confusing. In this context it seems necessary to recall some basic concepts of vegetation science. Higher syntaxa (alliance, order, class) have the sense of ecological spaces which can be distinguished from one another only by instrumental methods; character species are the markers (indicators) of such ecological spaces. When vegetation is considered only at the level of floristical composition, then the possibility exists to describe an infinite number of different combinations among indicators, but this does not mean that every combination will give an unambiguous definition for a corresponding ecological space. Variations of the species composition can be caused by ecological factors, as well as by competition, other causes or chance, and consequently on the basis of the presence-absence of a species, ecological differences can be only supposed, but not verified. The true causal analysis proceeds from the ecological investigation to the presence of species, but not on the contrary. If only the presence of species is known, then species combination cannot be assumed as the proof of the existence of a certain ecological space: this would be a methodological upsetting. An ecological space identified only by a particular species combination remains at the most a hypothesis.

THE GENERAL PHILOSOPHY

The object of ecology is the study of relationships between living things and environment: as synecology is it understood to be within the context of a particular condition, when such relationships are in the frame of the community.

Communities can be recognized from their floristical composition, which deals with biodiversity; but species lists alone cannot describe completely the community and should be integrated with some form of quantitative evaluation of the role played by each species; this latter aspect deals with synecology. Consequently, we assume that vegetation consists of two complementary concepts: biodiversity and sinecology.

In fact, what is the real meaning of vegetation? Following the definition given by Westhoff (1951) the concept of vegetation is derived from vegetable mass, i.e. «mass of individuals of living or fossile plants, coherent with the spot where they thrive or have thriven, and in the arrangement taken by themselves»: it consists of plant individuals and of order (the arrangement). What is the essential element shared by both components? As to plant individuals it can be pointed out that they exist when growing in some vegetation and still continue to exist also when they are eradicated or cut and not composing vegetation any more. Order, on the contrary can be perceived only in vegetation and disappears when plants are cut or eradicated. Then, the only essential component of the community is order, whereas the presence of plant individuals is a necessary, but not sufficient condition.

Following the phytosociological paradigm, vegetation consists of an assemblage of associations. And, if the essential component of vegetation is order, then it is clear also that plant communities are based on order, i.e. they are immaterial. Associations are the conceptual tool to understand vegetation, they are not assemblages of plant material.

Where is the order underlying vegetation coming from? It should be assumed that a whole of different ecological factors exists, that can be indicated as «site ecology». This is a black box, because ecological factors are an elevate number and their interactions grow in geometrical ratio.

Site ecology is the source of order in vegetation. In fact, a condition of total indetermination can be imagined, where a seed bank gives every species the same chance to be present in the community: this is a condition of total symmetry. Ecological factors operate a selection among species and give more importance to species A, lesser importance to B, and eliminate C, i.e. they break the symmetry.

This process can be interpreted as a transfer of order from the site to vegetation. Site ecology determines the quantitative incidence of every species in the community, i.e. community composition and structure. With the inverse procedure, from community composition and structure it is possible to gain inferences on site ecology.

As a first conclusion, it can be pointed out that the study of plant communities is a method to obtain information on site ecology and that species composing the community can be considered as descriptors (markers) or indicators for site ecology.

Now, recall the first statement, that vegetation deals with biodiversity and with synecology:

– *biodiversity* can be investigated in many ways: at the species level (mainly to distinguish different associations), at the level of genera (for world-wide comparisons) and at a synthetic level as total of species present, chorotypes, life forms, polyploidy etc. All these features can be expressed as numerical values.

– *synecology* is mostly expressed with data on climate and soil, which are both very complex concepts, based on many variables, and can be expressed in numerical form only with some difficulty. E.g., in the mediterranean zone water factor is of primary importance, it is dependent on rainfall, but cannot be expressed only as total rainfall in the year because the crucial point is the alternance of humid and arid periods; in consequence, it is necessary to use some indexes, which are always questionable.

In this case it seems very useful to use bioindicators to quantify ecological factors. This is not as upsetting as in the preceeding case: there exists a large experimental evidence on ecological factors which are crucial for the presence of species. In consequence, every species has an indicator value (in german this is called «Zeigerwert»). Ellenberg (1974, further editions in 1989 and 1992) proposed a system of indicator values for all species of the flora of Germany; the ecology of every species is defined by 6 main factors:

- light
- warmth
- continentality of climate
- soil moisture
- soil pH
- soil nutrients

The six ecological factors are ordered following a logical principle: light for the ecosystem can be considered as an independent variable; warmth is partly dependent on light because of its thermal effect; the following factors are increasingly dependent upon the previous ones and upon external conditions.

Every factor can vary from 1 to 9 (humidity: 1-12) and the number of possible combinations goes into the hundreds of thousands; in fact, among the species of the flora of Italy there are very few examples of species with exactly the same values (and mostly in apomictic groups). Species are highly diversified as to indicator value.

On Ellenberg's Zeigerwerte

Indicator values were first introduced by Ellenberg for the flora of Germany, ca. 3.000 species. The list by Ellenberg was extended to Poland by Zarzycky (1984) and to Hungary by Borhidi (1993). We extended the system tentatively to the entire flora of Italy with ca. 3.000 species more, mainly with mediterranean distribution. The only relevant technical problem is the necessity to enlarge the scale for warmth: in Ellenberg (1974) the degree 9 indicates the most thermophilous species of Germany, but it is clear that in Italy much warmer conditions will occur, and consequently the scale will be enlarged to 12. This is not a difficulty, since the scale for humidity also goes to 12. Possibly in the future such Zeigerwerte may be used in the tropics and the scale for warmth will be further enlarged; for other factors this will probably not be necessary.

The extension to Central European floras as to Hungary and Poland does not bring completely new problems, because most species of these floras are also present in the flora of Germany; the ecology of species which have to be added can be obtained in most cases by comparison. For Italy the situation is different, because in this case a large stock of mediterranean species is included which are not present in Central Europe. Consequently we organized a data base with all species of the flora of Italy which are lacking in the list done by Ellenberg, and for every species results of ecological measurements as far as available are added. We hope to complete this data base in a relatively short time, the provisory values used here will be revised and then published in detail.

Some minor problems:

1 - In Ellenberg (1974) some species are labelled as resistent to salinity or obligate halophytes, with a reduced scale (1-2-3): these are only a few percent of

the total, so that this information may be used only by treatments dealing with coastal vegetation, but in other cases they can be neglected.

2 - For mediterranean species values of continentality are always very low and little distinctive: a better climatic evaluation would be based on mediterraneity, i.e. on the capacity to survive long periods of summer drought; otherwise such values are not significant for continental species. This last possibility was not experimented.

It is important to point out, that the Zeigerwerte do not correspond to the optimum of the species, but to their occurrence in competition with other species (Ellenberg, 1974). When a plant is cultivated under experimental conditions its optimum is in general described by the central value of a gaussian; in the natural community the optimum often shifts in the marginal area.

METHODS

Zeigerwerte are expressed with six numbers for every species. For the whole community average values are used (see Werner & Paulissen, 1992). In this case, the presence of a given species is interpreted as a message: for instance, the presence of *Oxalis acetosella* means 2 as value of light, the presence of *Vaccinium myrtillus* in the same relevé means 4 etc. This is repeated for the whole table and at the end the average values are calculated. In the normal procedure, for every species the indicator value is appended, then multiplied by the percent, then all indicator values of each of the six different factors are added together and divided by their number in order to obtain the average value in the table for each factor. For easier comparison we propose to calculate the *ecogram*, i.e. a graphic representation of average values.

The ecogram is obtained from the average values of the six factors calculated on a vegetation table. The table may be a normal phytosociological one, or also a table obtained with other methods, when giving the quantitative estimation of frequency for every species. As a standard procedure, synoptic tables with frequencies expressed in percent can be used. All species of the table can be considered, but species under 20 % in general bring differences only in the second decimal (and can be neglected). Every species enters with a different weight i.e. its percentual frequency.

The program «Ecogram Maker» was produced in order to obtain automatically the above described calculation. It works under Windows and can be applied to the analysis of a conventional synoptic table in text ASCII format. Tables have to be previously formatted following general rules concerning order and width of columns and coding of descriptors. After the analysis a report file is generated, in which for every column the description and average wheighted values of every ecological parameter are memorized; from these data it is possible to obtain the ecogram corresponding to any column which can be visualized and printed. It has to be pointed out that using as a source the text format it is also easily possible to analyze also tables which were previously memorized on commercial electronic sheet (QuattroPro, Lotus 1213, Excel etc.), which can be converted in ASCII format.

In many species it seems impossible to give a definite value for all of the six ecological factors: this is mainly because these are polymorphic species including infraspecific taxa with different ecological requirements or species having a wide adaptive capacity (in such cases Ellenberg uses notations as 0 or X). The informatisation can bring a solution: instead of one single value a field of variation can be described, with the probability values at the different degrees, e.g. a species with humidity value 4 to 6 and maximal frequency at 5. The treatment of such type of data by computer has no difficulties, at least in principle.

At the end of the elaboration, for each table six numbers are given, corresponding to the average values which are calculated for each ecological factor. They can also be expressed in graphic form as parameters along the diagonals of an hexagon and this graph is the ecogram (fig. 1).

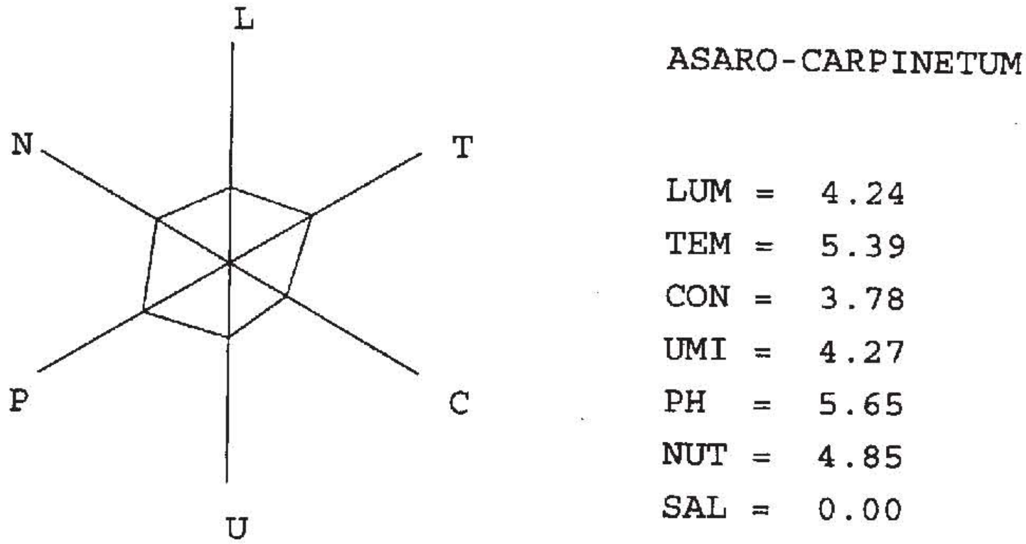

Fig. 1 - Example of an ecogram. *Asaro-Carpinetum*, mesophytic deciduous woodland in the Karst near Trieste; floristic data from Poldini (1989). L-light; T-temperature; C-continentality; U-humidity; P-soil reaction; N-nitrogen.

Results

In the first application ecograms were calculated for 33 different examples of woody vegetation from different parts of Italy (tab. 1). A rapid look at fig. 2 is sufficient to distinguish at least three major groups: the first one where ecograms are characterized by an acute point in correspondence of light (corresponding to *Vaccinio-Piceetea*), the second one with more or less a regular hexagon (corresponding to *Querco-Fagetea*) and the last one with more obliquous ecograms (*Quercetea ilicis*). Classes can be easily recognized, also lower units: in particular *Fagion* has a more symmetric hexagon, whereas *Carpinion* and *Quercion pubescentis* are increasingly obliquous. Only two ecograms deal with forests of scotch pine and this is not enough to have a clear idea of this vegetation; in any case, they differ substantially from other needle-leaved vegetation.

The acute point of *Vaccinio-Piceetea* is only partly dependent upon high values of light, but also upon the combination of very low values of warmth and nutrients: in fact, this class includes woody associations of cold climates occurring on nutrient poor soils. The symmetric ecogram of *Querco-Fagetea* reflects the fact that associations of this class in general occupy the middle of the variation field of major ecological factors in Europe. The obliquous ecogram in *Quercetea ilicis* depends upon high values in warmth combined with low values for humidity.

In fig. 2 the ecograms are roughly disposed along a climatic gradient from the deepest temperature in 1 (*Cetrario-Loiseleurietum* - Alps at 2500 m) to the hottest environment in 32 and 33 (*Oleo-Ceratonion*, Sicily, near to the coast). The modification in the aspect of ecograms shows clinal variation: they are referred to climax or climax-like vegetation; the only exceptions are 9 (*Erico-Pinetea*) and

TABLE 1

SOURCE OF TABLES

1 - Cetrario-Loiseleurietum	Alps	Giacomini & Pignatti (1955)
2 - Junipero-Arctostaphyletum	Switzerland	Braun-Blanquet, Pallman & Bach (1954)
3 - Empetro-Vaccinietum	Switzerland	Braun-Blanquet, Pallman & Bach (1954)
4 - Rhododendro-Pinetum mugo	Dolomites	Pignatti E. & S. ril. ined.
5 - Rhodothamno-Rhododendretum	Dolomites	Pignatti E. & S. ril. ined.
6 - Vaccinio-Rhododendretum laricetosum	E.Alps	Pignatti E. (1970)
7 - Larici-Pinetum cembrae	Alps	Filipello & al. (1980)
8 - Homogyni-Piceetum	Dolomites	Pignatti E. & S. ril. ined.
9 - Erico-Pinetum sylvestris	Dolomites	Pignatti E. & S. ril. ined.
10 - Astragalo-Pinetum sylvestris	Val Venosta	Braun-Blanquet (1961) tab. 49
11 - Oxalidi-Abietetum	prov. Bolzano	Rizzi Longo (1972)
12 - Oxalidi-Abietetum	Dolomites	Pignatti E. & S. ril. ined.
13 - Cardamini-Fagetum	prov. Bolzano	Rizzi Longo (1972)
14 - Carici-Fagetum	Dolomites	Pignatti E. & S. ril. ined.
15 - Asyneumati-Fagetum	Calabria	Gentile (1969) tab. 1
16 - Polysticho-Fagetum	Lazio	Pignatti ril. ined.
17 - Aquifolio-Fagetum	Calabria	Gentile (1969) tab. 3
18 - Ornithogalo-Carpinetum	Dolomites	Pignatti E. & S. ril. ined.
19 - Asaro-Carpinetum	Trieste	Poldini (1989) tab. 79
20 - Ilici-Quercetum	Sicily	Brullo (1983)
21 - Lauro-Carpinetum	Lazio	Lucchese & Pignatti (1991)
22 - Physospermo-Quercetum	N.Appennines	Oberdorfer & Hofmann (1967)
23 - Echinopo-Quercetum cerridis	Lazio	Lucchese & Pignatti (1991)
24 - Seslerio-Quercetum petraeae	Trieste	Poldini (1989) tab. 77
25 - Ostryo-Quercetum pubescentis	Trieste	Poldini (1989) tab. 76
26 - Orno-Ostryetum	Trentino	Braun-Blanquet (1961) tab. 53
27 - Scutellario-Ostryetum	Lazio	Pignatti ril. ined.
28 - Orno-Quercetum ilicis	Ancona	Biondi (1982) tab. 1
29 - Orno-Quercetum ilicis	Trieste	Poldini (1989) tab. 86
30 - Viburno-Quercetum ilicis	Liguria	Mariotti (1984) tab. 3
31 - Viburno-Quercetum ilicis	Lazio	Lucchese & Pignatti (1991) tab. 8
32 - Oleo-Lentiscetum	Sardinia	De Marco & Mossa (1980)
33 - Oleo-Euphorbietum dendroidis	Sicily	Brullo & Marcenò (1983)

10 (*Junipero-Pinetea*) which in Italy are only present as pioneer woods. Some clear trends can be recognized:

– Light has high values in the first group (1-6) adapted to the intense radiation of high mountains, then it is lower in the temperate broad leaved forest of beech (15-17) and oaks (18-22) and again becomes high in macchia vegetation (32-33).

– Average temperature regularly increases from 1 to 33, and this gives the progressive obliquous aspect to ecograms.

– Water availability is relatively low in the alpine and mediterranean vegetation and higher in the temperate broad leaved forest, in particular in beech woods; the same can be repeated for pH and nutrients, almost with a similar trend.

The ecogram is divided by the diagonal in two halves: light – temperature – continentality in the upper portion which is dependent upon climate, and humidity

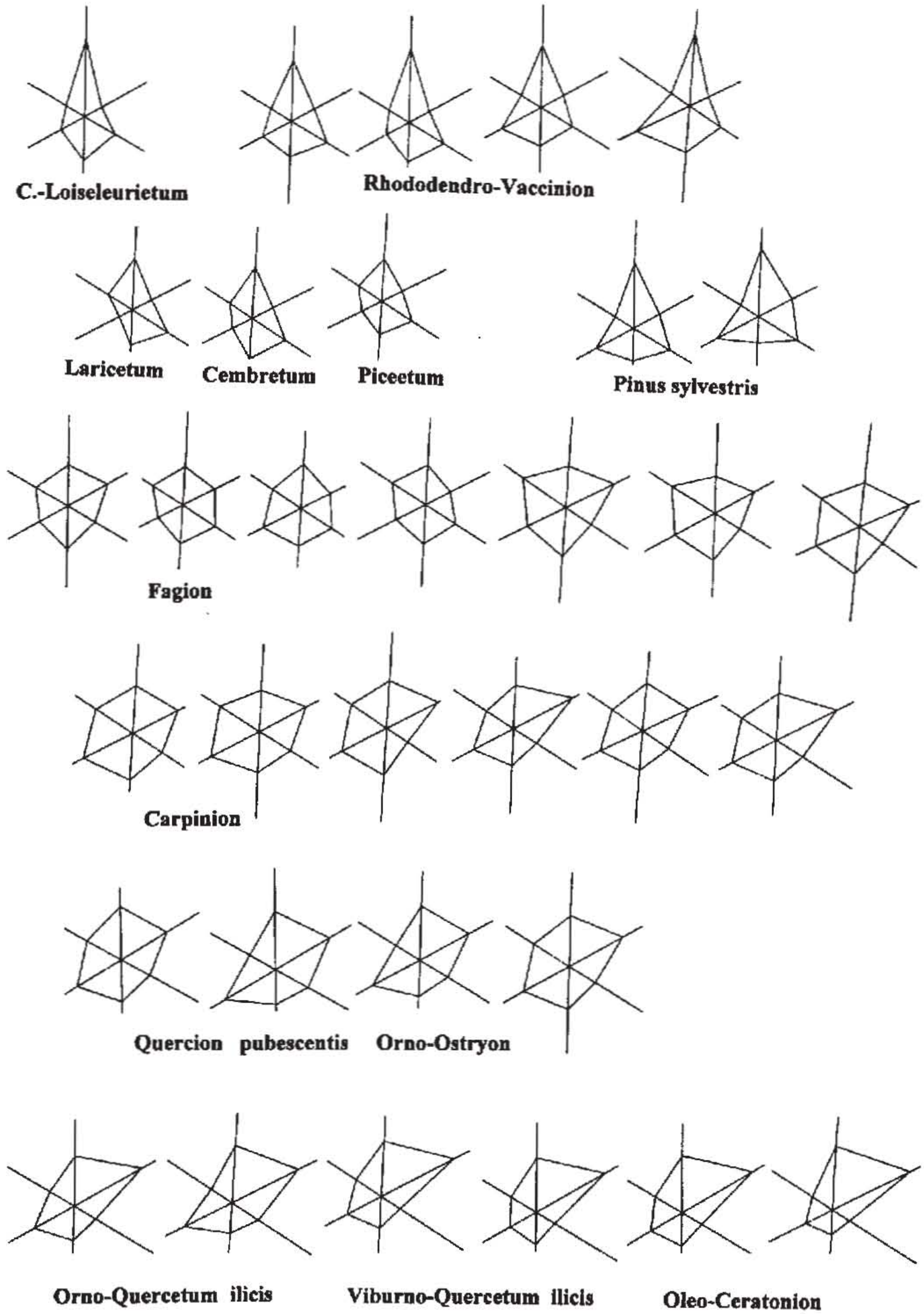

Fig. 2 - Ecograms of different types of woody vegetation of Italy from the alpine heath adapted to coldest conditions to thermophilous mediterranean maquis. Ecograms are ordered in the same sequence of Tab. 1.

– ph – nutrients which concern soil. This second portion is largerly developed from 15 to 24, corresponding to fertile brown soils and much smaller in 1-9 (podzol) and 28-33 (mostly on red soil). In the upper portion there are ecograms dominated by light (alpine vegetation) or by the combination light-warmth (mediterranean coasts) or by continentality (pine forests).

As a matter of fact, all these features can be detected also with the careful study of the table with average values of the six parameters. In the ecograms there is nothing more than in the numerical values, but they visualize these values and are a big help for making the comparison. The form of ecograms can be immediately perceived and evaluated: in this condition our brain works like a computer (con - putare means «evaluate together»).

Discussion

Ecograms can be used to investigate a quantity of problems dealing with comparison, classification and ordination of higher syntaxa which can be analyzed in detail. E.g., *Fagion* is characterized by the symmetric shape of the ecogram; but a particular regularity of the ecogram is evident only in associations of *Eu-Fagion,* whereas *Cephalanthero-Fagion* and *Fago-Abietion* can be recognized by small differences; in the form of ecogram *Luzulo-Fagion* is almost indistinguishable from that of *Eu-Fagion* but the shape is smaller, i.e. a colder environment with lower pH and poor in nutrients. The comparison among tables of the same association is easy, and average values can be treated by multivariate analysis.

It may be observed that this procedure presents the risk to be a tautology (the Zeigerwerte are deduced from relevés and then applied to other relevés). Indeed, the information on species ecology in origin is gained from experimental measures related to relevés and only in the following elaboration it is appended on their floristic composition: in consequence, this is a normal transfer of information and not a circle.

A second criticism may be that the ecology of a species does not remain unchanged all over the distribution range: *Quercus ilex*, e.g., in the mediterranean area is mostly growing on neutro-subacid soils, but approaching the northern boundary becomes more and more bound to limestone. These are relatively rare examples, which can be treated as polymorphic species.

Only a short comment on the particular regularity of the ecograms in *Fagion.* In the associations of this alliance the six ecological parameters have values which are remarkably near to 5, i.e. in the middle of the field of variation; this is particularly evident in the associations of *Eu-Fagion.* From this point of view, the beech forest appears as a «golden mean» of the european vegetation. This view may be supported by the fact that beech forests under their more favourable conditions are also a highpoint in primary production and produce the eutrophic Braunerde, a well balanced, highly productive soil. Biodiversity, on the contrary, reaches a maximum in *Carpinion,* at least as to the richness of the tree layer.

Indeed, the possibility exists that these values appear central only because they have been first given to the flora of Germany, where *Fagus* has its ecological optimum: in this case the centrality would be an artefact.

Conclusion

The floristical composition is what makes associations visible, but it can be considered as the consequence of ecological factors acting in the site where the association occurs. In consequence, species can be used as indicators of the ecology of the site. The indicator value of species was estimated as Zeigerwert by Ellenberg for the entire flora of Germany, and is now available for other regions of Europe.

The synecological characterization of an association is given by the average values of 6 factors: light, warmth, continentality of climate, soil moisture, soil pH and soil nutrients. They are expressed by numbers, which are difficult to compare and memorize. Here is proposed the use of ecograms, which are the graphical representation of the 6 factors; the ecogram is an ecological fingerprint of the community.

The possibility exists, that in syntaxonomy the floristical composition has been over-emphasized and groups based on differential species in many cases have to be regarded as more or less accidental assemblages.

Aknowledgements

We are indebted to Enzo Dominici (Rome) for computer assistance and fruitful collaboration, to Beagan Wilcox (Rome) and dr. Andrea Savoia (Rome) for a critical revision of the manuscript and to Giuseppe Pignatti (Trento) for multivariate analysis.

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