

The Relationship between Growth Rate and Emergence in Seedlings of *Picea Engelmannii* Parry

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ABSTRACT

Nursery-grown seedlings of Engelmann spruce were divided into two lots which differed only in fertilizer application, fertilized and unfertilized, when transplanted into a field trial. The seedlings fertilized in the field had faster growth rates and the focus of this study was to explore the relationship between growth rate and the degree of emergence defined as the difference in descriptions between parts and wholes. Seedling growth is the

result, and thus a measurement of, energy fixation and flow; emergence is one manifestation of the transformation of matter, the expression of information which accompanies energy flow. This study explores Taborsky's (1999) argument linking the flow of energy to the transformation of matter (expression of information); a more rapid flow of energy should give a greater transformation of matter and expression of information. The faster growing seedlings did show a higher degree of emergence thereby offering a verification of Taborsky's (1999) suggestions. This, in turn, provides grounds for suggesting that ontogeny results from the flow of energy and the subsequent transformation of matter, an interpretation that places ontogeny in the realm of events explained by natural laws, i.e., it is inevitable.

1 Introduction

Development is a constantly repeated, apparently inevitable event of the natural world that biologists explore and attempt to explain. Theoretical accounts of development often invoke concepts of information, which is continually expressed as development unfolds. In some attempts to explain ontogenetic change, this information expression is linked with entropy. In development, entropy is produced and exported from an organism (Brooks and Wiley 1988; Brooks 2001). This phenomenon is interpreted as a manifestation of entropy increase in complex open systems. Since the outcomes of development and evolution are never fully predictable, this entropic increase may also be interpreted as the generation of novelty.

Another theoretical approach has relied on the appearance of new information through the impact of the environment on ontogenetic change (Jablonka and Lamb 1995, Steele et al. 1998). There is, of course, transfer of information from DNA into the structures, and their functions, of an organism as described by much of modern molecular biology. But, the surfeit of details produced in such accounts, deals with small-scale mechanism - how the changing informational properties of an organism are correlated with variations in DNA, how information is elicited from DNA (how the expression of that information is controlled), or how that information is transferred from DNA out into the cytoplasm. While of interest, these details beg the question of why that transfer of information occurs; what global-scale forces and mechanisms would cause information in the DNA to be transcribed and translated in the first place? The concept of entropy production has been presented as part of the answer to this question: The expression of information is the result of (and results in) entropy production and exportation, which is inevitable under the second law of thermodynamics as expanded to incorporate open sys-

tems (Brooks 2001, Brooks and Wiley 1988, Prigogine 1980). Although these ideas offer an adequate, ultimate cause of development, they still leave the general mechanism through which this force acts unexplained - how is entropy production and exportation carried out?

Taborsky (1999) has offered a mechanism for the actions of a force such as the second law of thermodynamics and for the subsequent expression of novelty in biological systems. She has argued that energy never exists independent of matter. When energy flows from one part of a system to another it is through the agency of matter transformation. For instance, the energy in a cross-membrane hydrogen ion gradient flows and is then captured in the transformation of ADP + P into ATP. The energy in ATP is then captured in the transformation of a carbon compound from a three- to a four-carbon molecule. There are many other examples. This transformed matter is what Taborsky (1999) calls information.

Thus, using Taborsky's arguments, information transfer occurs concomitant with the flow of energy along energy gradients. This flow is inevitable in a live plant and information is carried along. The specifics of matter transformation will be a function of the organism within which it occurs, each transformation being an expression of the dissipation of entropy – the force that drives the expression of novelty. We feel it is possible to test Taborsky's (1999) proposed relationship between the flow of energy and the expression of information by using two groups of tree seedlings one of which has a higher growth rate, and thus an increased rate of energy flow, as the result of differential application of fertilizer.

In constructing these tests our first assumption is that more energy will be processed by “faster”, as opposed to “slower”, growing seedlings. As more energy is converted from sunlight into tissue, more matter will be transformed. In the design of this experiment the amount of incoming light energy was independent of fertilizer application; there were no differences in energy available to be incorporated into a plant body. But most of the light energy that strikes a plant is not utilized. What is important to the plant is the energy fixed through photosynthesis and that can be affected by many things, among them fertilizer application.

The next question is, how will transformed matter, the information, be expressed, and once expressed, how evaluated? One expression of information will be in the production of larger seedlings. However, seedling size alone is inadequate as a means of evaluating information expression since it would not capture the contribution of different plant parts to increasing size. In addition, knowing the size of a seedling does not permit addressing any estimate of integration, of the relationships among parts. Integration is the

primary means whereby biological entities are characterized; indeed, what makes organisms unique is how their parts are integrated into a functional whole. The evaluation of information expression should rest ultimately on the interaction of parts, how they are related to each other and how seedling growth rate affects those relationships. One way to evaluate the relationships among parts is to describe and analyze them as correlation matrices, as we demonstrate here.

In constructing our tests, the next assumption is that the greater expression of information, resulting from the transformation of a greater amount of matter, should result in seedlings within which correlation matrices show greater heterogeneity than those with a lesser amount of matter transformation. This assumption follows from a relationship between the elements of a correlation matrix, correlation coefficients, and relative growth rates; the correlation coefficients between two variables will estimate the growth of those two variables relative to each other. A high correlation coefficient indicates similar growth rates, lower correlation coefficients will result from less strongly coupled growth rates, or weaker relations between these variables. In seedlings with a higher rate of transformation of matter there will be a greater array of growth rates that give rise to individual variables with a greater variety of correlation coefficients and correlation matrices. The appearance of more growth rates with the transformation of more matter seems, to us, a deductive outcome of the variation inherent in living things, for, as more matter is transformed, one expression of biological information will be the appearance of more variable growth rates.

Correlation coefficients and correlation matrices are a statistical property of populations. Thus, to expand our argument, in 100 seedlings of lower energy transfer and matter transformation, there will be a certain number of growth rates realized, as revealed by a certain number of correlation matrices. In a collection of 100 seedlings of higher energy transfer and matter transformation, a greater number of different growth rates will be expressed, resulting in more numerous differences among correlation matrices seen within those 100 seedlings.

To expand this example, each set of 100 seedlings with certain growth rates can be viewed as having properties of a whole, two 50 seedling subsets, established by randomly dividing the 100 seedlings into two equal portions, of those 100 seedlings can be viewed as having properties of the parts. Thus, there would be a correlation matrix for the whole and two for the parts, one for each subset. In the faster growing seedlings, there would be a greater array of correlation matrices seen among the subsets than would be seen in the subsets of the slower growing set of seedlings. This increase in the number of different correlation matrices in the faster growing set will mean that there will be a greater differ-

ence between correlation matrices that describe part of the system; the subsets, and the one that describes the whole system. Or, there will be a greater difference between parts and wholes in systems that are processing more energy than in those that are processing less. We have used this distinction between parts and wholes to generate a descriptive attribute to compare different systems, i.e., emergence (Maze and Bohm, 1997; Maze 1998, 1999; Maze *et al.* 2000, 2001a, 2001b). Our concept of emergence is derived from Polanyi (1958) where lower hierarchical levels, the parts, have properties different from those of higher hierarchical levels, the whole. The properties of the higher level emerge from those of the lower, but they cannot be reduced to nor fully explained by the lower level properties. One analytical way to characterize Polanyi's formulation of emergence is that descriptions adequate for lower levels (the parts) are inadequate for the higher (the whole). The difference in descriptions between the parts and the wholes is what we call the degree of emergence.

One more point must be made clear. Emergence carries the inference of something new, often a new attribute. But the something new can also be the relationship among attributes, this is how we use it here.

It follows that systems processing more energy should show a greater degree of emergence - through differences in descriptions of parts and wholes - than those processing less energy, and ought to be those expressing more novelty. The purpose of this study is to test these assertions in seedlings of *Picea engelmannii* Parry, grown under conditions where sets of seedlings have been treated with different levels of fertilizer to produce different growth rates.

2 Materials and Methods

2.1 Study site, treatment and seedlings

This study was originally designated British Columbian Ministry of Forest SX86126K. For details of the study site, treatments given and the seedling sources see Maze and Vyse (1993); they are not required for the arguments we develop. As a result of the experimental design used in SX86126K, seedlings of 24 different origins, the combination of six different nursery treatments and four seedlots, were each given two different fertilizer treatments in the field. Thus we obtained 24 different contrasts of seedlings, fertilized and unfertilized, in the field; that is, 24 different instances where we could compare the degree of emergence in putatively identical groups of seedlings.

2.1.1 Variables

The variables analyzed were the height and diameter at planting, ht86 and dia86, and the increments of growth in height and diameter for 1987 – 1989, inc87 – inc89 and incdia87 – incdia89 respectively. These variables mark the growth response of seedlings subjected to different origins, seedlots, or treatments in the nursery and in the field.

2.1.2 Analyses

The first step was to establish that the fertilized seedlings had, in fact, undergone a greater amount of growth. The most direct way to do this was to calculate the relative growth rates (Evans 1972) for height and diameter for the different treatments in the field for each combination of seedlot and nursery treatment. We used a modified version of Evans (1972) formula since he used time as the denominator in his calculation of relative growth rate and all the seedlings here were analyzed over the same period of time, three years.

The analyses for the degree of emergence, the features used to compare the seedlings with different growth rates, were similar to those used in previous studies on emergence (Maze and Bohm, 1997; Maze 1998, 1999; Maze *et al.* 2000, 2001a, 2001b). The basic approach is to describe the degree of emergence for each group being compared. In this study the groups compared were the seedlings given different field treatments, fertilized and unfertilized, for each combination of seedlot and nursery treatment giving 24 comparisons. Those groups processing the most energy are those with the higher growth rates and are predicted to show the higher degree of emergence. The analytical steps are presented below so they can be reproduced.

1. Each system of interest, in this case each combination of seedlot, nursery and field treatment, are bootstrapped (Efron 1982) 50 times using the random sample generator in SYSTAT 4.1 (Wilkinson 1988).

2. Each bootstrapped sample is divided in half with each subgroup forming one of the parts and the entire bootstrapped sample the whole.

3. Each bootstrapped sample is analyzed with Pimentel's (1993) MPCA program. For each subgroup (part) and the entire sample (whole) the program calculates, among other statistics, an angle with a vector of isometry. This is the angle between the first PCA axis and a theoretical axis comprised of equal elements. For each combination of seedlot, nursery and field treatment 50 angles with a vector of isometry were generated for each subgroup (the parts) and for the entire sample (the whole).

4. The differences between the angles with a vector of isometry for the two subgroups and the entire sample, are then calculated and averaged. This we call AVGD (av-

erage degree of emergence) and it is a measure of the degree of emergence for that group analyzed.

5. The degree of emergence for the different field treatments for each combination of seedlot and nursery treatment were then compared using a Kruskal-Wallis non-parametric analysis of variance (see Maze and Bohm, 1997; Maze 1998, 1999; Maze *et al.* 2000, 2001a, 2001b).

If the predictions made in the Introduction are upheld, then the seedlings fertilized in the field should, for each combination of seedlot and nursery treatment, show a greater degree of emergence, that is, a higher AVGD value.

The raw data we used to assess ontogeny, increments of growth over time, are simple variables. They alone would be inadequate for a definitive test of a relationship between energy flow and matter transformation. The way those variables have been analyzed is what gives credence to our test because our focus is not on the variables used in our analyses, but our evaluation of the integration among those variables. Our comparison of the degree of emergence, expressed as AVGD, among spruce seedlings with different fertilizer regimes is derived from the integration among variables. Although our variables are simple, the way they have been analyzed allows us to assess the relationship between energy flow and matter transformation using concepts central to biology, integration and emergence.

3 Results

The relative growth rates for height and diameter for all possible combinations of nursery treatment, seedling and field treatment are presented in Table 1.

Table 1: Median values for combined relative growth rates (upper and lower hinges) for height and diameter for seedlings unfertilized (1) and fertilized (2) in the field.

Height		Diameter	
1	2	1	2
0.56	0.73	0.73	0.92
(0.43–0.69)	(0.57–0.88)	(0.56–0.92)	(0.74–1.09)

There are 48 combinations of relative growth rate between seedlings that did, or did not, receive fertilizer treatment in the field, 24 for height and 24 for diameter. Table 1 does not present all combinations but a comparison of combined groups. This was done for efficiency of presentation and comparison. Seedlings fertilized in the field have faster growth rates. The probability that the values for growth rates for fertilized and unfertil-

ized seedlings in the field is due to chance is $\lll 0.001$ as based on a Kruskal-Wallis non-parametric ANOVA.

Table 2 presents the results of comparing AVGD values for faster and slower growing seedlings, for those that process more and less, energy respectively.

Table 2: Median combined AVGD values (range between upper and lower hinge) for slower growing (1) and faster growing (2) seedlings.

1	2
5.63	10.45
(3.06–9.68)	(6.01–15.20)

There are 24 possible comparisons of all seedlot and nursery treatment combinations. As in Table 1 the AVGD values were combined and then compared with a Kruskal-Wallis non-parametric ANOVA. The faster growing seedlings had a higher AVGD value with a probability $\lll 0.001$.

4 Discussion

One of the first requirements of this study was the demonstration of treatment-dependent differences in growth rates. This does occur and it is hardly surprising.

Seedlings with the faster growth rate resulted in seedlings with a higher degree of emergence, as measured by AVGD. This relationship between growth rate and the degree of emergence, while significant, is not strong; the ζ^2 for a parametric ANOVA comparing AVGD for the faster and slower growing seedlings is 0.067. One reason for this may be the heterogeneity of the environment where the study was carried out. The micro-environmental differences individual seedlings would encounter could be considerable, from the small, but relevant, topographic variation to the differences in soil. A second reason for the weak relationship between growth rate and AVGD could be the within-seedlot variation in the seedlings planted. Conifers are notoriously variable, whether growth (Banerjee and Maze 1988; Maze and Vyse 1993; Maze *et al.* 1989), morphological (Chen *et al.* 1986; Lester 1968; Maze and Parker 1983), or molecular (El-Kassaby and Sziklai 1982; Yeh and El-Kassaby 1980) variables are analyzed. A way to partially circumvent environmental and organismal variation is to compare the degree of emergence within single conifers by analyzing needles on long (faster growing) and shorter (slower growing) branches. An even better approach would be to use plants that are less variable and grow them under more stringently controlled conditions.

The prediction derived from Taborsky's (1999) linking of energy flow and matter transformation (information flow) is corroborated though it should be subjected to further testing. An earlier study demonstrated a positive relationship between the degree of emergence seen in needles and the size of the tree, a rough estimator of growth rate, in ponderosa pine (Maze 1999). The degree of emergence as seen in increments of stem growth in faster growing seedlings of Douglas fir and increments of annual rings in faster growing mature trees of ponderosa pine both showed a higher degree of emergence than slower growing plants. The results from growth increments are presented only anecdotally as the plants with different growth rates were not the result of a manipulation designed to affect growth rate, but they are still of interest. One way to look at the energetics is from an accounting point of view. There is a "cost" for any change in relationships, or for a new structure. So, under higher growth rates it is easier to "pay the price" for having more diverse relationships.

The relationship between the flow of energy and the expression of information can be visualized as a flow and channel relationship. As energy flows it will do so along certain paths as determined by the plant itself, these are the material expression of Polanyi's (1976) boundary conditions. These boundary conditions, delimited by phylogenetic history and through the activities of development itself, will specify how matter is transformed into information.

The flow of energy, with its concomitant material expression, as directed by the constraints of the boundary conditions of a plant, is another way of saying that, given the flow of energy, a plant will develop. To put this in a slightly different context, energy flow can be viewed as the mechanism through which novelty and constraint, biological information, are expressed. The "force" driving biological forms to diverge is limited by nary and developmental history, as expressed through structural limitations and functionality specifying the form of living things.

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REFERENCES

- Banerjee, S. and J. Maze: 1988, Variation in growth within and among families of Douglas-fir through a single season. *Canadian Journal of Botany*. 66:2452-2458.
- Brooks, D.R.: 2001, Evolution in the information age: Rediscovering the nature of the organism. *Semiotics, Evolution, Energy, Development* 1(1), Retrieved June 2001 from <http://library.utoronto.ca/see/SEED/Vol-1/Brooks-Journal.html>.
- and E.O. Wiley. 1988. *Evolution as entropy*, 2nd ed. Chicago: University of Chicago Press.
- Chen, Z-Y., R.K. Scagel and J. Maze: 1986, A study of morphological variation in *Pseudotsuga menziesii* in southwestern British Columbia. *Canadian Journal of Botany*. 64:1654-1663.
- El-Kassaby, Y.A. and O. Sziklai: 1982, Genetic variation of allozyme and quantitative traits in a selection [*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco] population. *Forest Ecology and Management*. 4:115-126.
- Efron B.: 1982, The jackknife, the bootstrap and other resampling plans. *SIAM Monograph number 38*, Society for Industrial and Applied Mathematics, Philadelphia.
- Evans, G.C.: 1972, *The quantitative analysis of plant growth*. Berkeley:University of California Press.
- Jablonka, E. and Lamb, M.J.: 1995, *Epigenetic inheritance and evolution: The Lamarckian dimension*. Oxford: Oxford University Press.
- Lester, D.T.: 1968, Variation in core morphology of balsam fir (*Abies balsamea*). *Rhodora* 70:83-94.
- Maze, J.: 1998, Studies into abstract properties of individuals. II. Analysis for emergence in populations, species and a species-pair. *International Journal of Plant Science* 159:687-694.
- 1999, Studies into abstract properties of individuals. III. A study of factors affecting emergence. *International Journal of Plant Science* 160:809-817.
- , S. Banerjee and Y.A. El-Kassaby: 1989, Variation in growth rate within and among full-sib families of Douglas fir *Pseudotsuga menziesii* Mirb. Franco. *Canadian Journal of Botany*. 67:140-145.
- , S. Banerjee and K.R. Robson: 2001b, Studies into abstract properties of individuals. VI. The degree of emergence in individuals, populations, species and a three species lineage. *BioSystems* 61:41-54.
- and L.R. Bohm: 1997, Studies into abstract properties of individuals. I. Emergence in grass inflorescences. *International Journal of Plant Science*. 158:685-692.
- and W.H. Parker: 1983, A study of population differentiation and variation in *Abies procera*. *Canadian Journal of Botany* 61:1094-1104.
- , K.A. Robson and S. Banerjee: 2000, Studies into abstract properties of individuals. IV. Emergence in different aged needle primordia of Douglas fir. *BioSystems* 56:43-53.

- 2000, Studies into abstract properties of individuals. IV. Emergence in different aged needle primordia of Douglas fir. *BioSystems* 56:43-53.
- 2001a, Studies into abstract properties of individuals. VI. An empirical study of emergence in ontogeny and phylogeny in Achnatherum nelsonii and A. lettermanii. *Semiotics, Evolution, Energy, Development* 1(1), Retrieved June 2001 from <http://www.library.utoronto.ca/see/SEED/Vol-1/Maze-emergence.html>.
- and A. Vyse: 1993, An analysis of growth, growth increments, and the integration of growth in a fertilizer test of Picea engelmannii in south-central British Columbia. *Canadian Journal of Botany*. 71:1449-1457.
- Pimentel, R.A.: 1993, *BIOSTAT II: A multivariate statistical toolbox*. Sigma Soft, San Luis Obispo.
- Polanyi, M. 1958, *Personal knowledge*. Chicago:University of Chicago Press.
- 1976, Life's irreducible structure, in M. Grene, E. Mendelsohn eds., *Topics in the philosophy of biology*, *Boston studies in the philosophy of science*, pp. 128-142. Boston: D. Reidel Publishing.
- Prigogine, I.: 1980. *From being to becoming*. San Francisco: W. H. Freeman.
- Steele, E. J., R.A. Lindley and R.V. Blanden: 1998, *Lamarck's signature*. Reading, MS: Perseus Books.
- Taborsky, E.: 1999, Evolution of consciousness, *BioSystems*. 51:153-168.
- Wilkinson L.: 1988, *SYSTAT: The system for statistics*. SYSTAT Inc, Evanston.
- Yeh, F.C. and Y.A. El-Kassaby: 1980, Enzyme variation in natural populations of Sitka spruce (Picea sitchensis). I. Genetic variation patterns among trees from 10 IUFRO provenances, *Canadian Journal of Forest Research* 10:415-422.