

V. *On the Direction of the Radicle and Germen during the Vegetation of Seeds.* By Thomas Andrew Knight, Esq. F. R. S. In a Letter to the Right Hon. Sir Joseph Banks, K. B. P. R. S.

Read January 9, 1806.

MY DEAR SIR,

IT can scarcely have escaped the notice of the most inattentive observer of vegetation, that in whatever position a seed is placed to germinate, its radicle invariably makes an effort to descend towards the centre of the earth, whilst the elongated germen takes a precisely opposite direction; and it has been proved by DU HAMEL\* that if a seed, during its germination, be frequently inverted, the points both of the radicle and germen will return to the first direction. Some naturalists have supposed these opposite effects to be produced by gravitation; and it is not difficult to conceive that the same agent, by operating on bodies so differently organized as the radicle and germen of plants are, may occasion the one to descend and the other to ascend.

The hypothesis of these naturalists does not, however, appear to have been much strengthened by any facts they were able to adduce in support of it, nor much weakened by the arguments of their opponents; and therefore, as the phenomena

\* *Physique des Arbres.*

observable during the conversion of a seed into a plant are amongst the most interesting that occur in vegetation, I commenced the experiments, an account of which I have now the honour to request you to lay before the Royal Society.

I conceived that if gravitation were the cause of the descent of the radicle, and of the ascent of the germen, it must act either by its immediate influence on the vegetable fibres and vessels during their formation, or on the motion and consequent distribution of the true sap afforded by the cotyledons; and as gravitation could produce these effects only whilst the seed remained at rest, and in the same position relative to the attraction of the earth, I imagined that its operation would become suspended by constant and rapid change of the position of the germinating seed, and that it might be counteracted by the agency of centrifugal force.

Having a strong rill of water passing through my garden, I constructed a small wheel similar to those used for grinding corn, adapting another wheel of a different construction, and formed of very slender pieces of wood, to the same axis. Round the circumference of the latter, which was eleven inches in diameter, numerous seeds of the garden bean, which had been soaked in water to produce their greatest degree of expansion, were bound, at short distances from each other. The radicles of these seeds were made to point in every direction, some towards the centre of the wheel, and others in the opposite direction; others as tangents to its curve, some pointing backwards, and others forwards, relative to its motion; and others pointing in opposite directions in lines parallel with the axis of the wheels. The whole was inclosed in a box, and secured by a lock, and a wire grate was placed

to prevent the ingress of any body capable of impeding the motion of the wheels.

The water being then admitted, the wheels performed something more than 150 revolutions in a minute; and the position of the seeds relative to the earth was of course as often perfectly inverted, within the same period of time; by which I conceive that the influence of gravitation must have been wholly suspended.

In a few days the seeds began to germinate, and as the truth of some of the opinions I had communicated to you, and of many others which I had long entertained, depended on the result of the experiment, I watched its progress with some anxiety, though not with much apprehension; and I had soon the pleasure to see that the radicles, in whatever direction they were protruded from the position of the seed, turned their points outwards from the circumference of the wheel, and in their subsequent growth receded nearly at right angles from its axis. The germen, on the contrary, took the opposite direction, and in a few days their points all met in the centre of the wheel. Three of these plants were suffered to remain on the wheel, and were secured to its spokes to prevent their being shaken off by its motion. The stems of these plants soon extended beyond the centre of the wheel: but the same cause, which first occasioned them to approach its axis, still operating, their points returned and met again at its centre.

The motion of the wheel being in this experiment vertical, the radicle and germen of every seed occupied, during a minute portion of time in each revolution, precisely the same position they would have assumed had the seeds vegetated at

rest; and as gravitation and centrifugal force also acted in lines parallel with the vertical motion and surface of the wheel, I conceived that some slight objections might be urged against the conclusions I felt inclined to draw. I therefore added to the machinery I have described another wheel, which moved horizontally over the vertical wheels; and to this, by means of multiplying wheels of different powers, I was enabled to give many different degrees of velocity. Round the circumference of the horizontal wheel, whose diameter was also eleven inches, seeds of the bean were bound as in the experiment, which I have already described, and it was then made to perform 250 revolutions in a minute. By the rapid motion of the water-wheel much water was thrown upwards on the horizontal wheel, part of which supplied the seeds upon it with moisture, and the remainder was dispersed, in a light and constant shower, over the seeds in the vertical wheel, and on others placed to vegetate at rest in different parts of the box.

Every seed on the horizontal wheel, though moving with great rapidity, necessarily retained the same position relative to the attraction of the earth; and therefore the operation of gravitation could not be suspended, though it might be counteracted, in a very considerable degree, by centrifugal force: and the difference, I had anticipated, between the effects of rapid vertical and horizontal motion soon became sufficiently obvious. The radicles pointed downwards about ten degrees below, and the germens as many degrees above, the horizontal line of the wheel's motion; centrifugal force having made both to deviate 80 degrees from the perpendicular direction each would have taken, had it vegetated at rest. Gradually

diminishing the rapidity of the motion of the horizontal wheel, the radicles descended more perpendicularly, and the germens grew more upright; and when it did not perform more than 80 revolutions in a minute, the radicle pointed about 45 degrees below, and the germen as much above, the horizontal line, the one always receding from, and the other approaching to, the axis of the wheel.

I would not, however, be understood to assert that the velocity of 250, or of 80 horizontal revolutions in a minute will always give accurately the degrees of depression and elevation of the radicle and germen which I have mentioned; for the rapidity of the motion of my wheels was sometimes diminished by the collection of fibres of conferva against the wire grate; which obstructed in some degree the passage of the water: and the machinery, having been the workmanship of myself and my gardener, can not be supposed to have moved with all the regularity it might have done, had it been made by a professional mechanic. But I conceive myself to have fully proved that the radicles of germinating seeds are made to descend, and their germens to ascend, by some external cause, and not by any power inherent in vegetable life: and I see little reason to doubt that gravitation is the principal, if not the only agent employed, in this case, by nature. I shall therefore endeavour to point out the means by which I conceive the same agent may produce effects so diametrically opposite to each other.

The radicle of a germinating seed (as many naturalists have observed) is increased in length only by new parts successively added to its apex or point, and not at all by any

general extension of parts already formed: and the new matter which is thus successively added unquestionably descends in a fluid state from the cotyledons.\* On this fluid, and on the vegetable fibres and vessels whilst soft and flexible, and whilst the matter which composes them is changing from a fluid to a solid state, gravitation, I conceive, would operate sufficiently to give an inclination downwards to the point of the radicle; and as the radicle has been proved to be obedient to centrifugal force, it can scarcely be contended that its direction would remain uninfluenced by gravitation.

I have stated that the radicle is increased in length only by parts successively added to its point: the germen, on the contrary, elongates by a general extension of its parts previously organized; and its vessels and fibres appear to extend themselves in proportion to the quantity of nutriment they receive. If the motion and consequent distribution of the true sap be influenced by gravitation, it follows, that when the germen at its first emission, or subsequently, deviates from a perpendicular direction, the sap must accumulate on its under side: and I have found in a great variety of experiments on the seeds of the horse chesnut, the bean, and other plants, when vegetating at rest, that the vessels and fibres on the under side of the germen invariably elongate much more rapidly than those on its upper side; and thence it follows that the point of the germen must always turn upwards. And it has been proved that a similar increase of growth takes place on the external side of the germen when the sap

\* See Phil. Trans, of 1805.

is impelled there by centrifugal force, as it is attracted by gravitation to its under side, when the seed germinates at rest.

This increased elongation of the fibres and vessels of the under side is not confined to the germens, nor even to the annual shoots of trees, but occurs and produces the most extensive effects in the subsequent growth of their trunks and branches. The immediate effect of gravitation is certainly to occasion the further depression of every branch, which extends horizontally from the trunk of the tree; and, when a young tree inclines to either side, to increase that inclination: but it at the same time, attracts the sap to the under side, and thus occasions an increased longitudinal extension of the substance of the new wood on that side.\* The depression of the lateral branch is thus prevented; and it is even enabled to raise itself above its natural level, when the branches above it are removed; and the young tree, by the same means, becomes more upright, in direct opposition to the immediate action of gravitation: nature, as usual, executing the most important operations by the most simple means.

I could adduce many more facts in support of the preceding deductions, but those I have stated, I conceive to be sufficiently conclusive. It has however been objected by Du HAMEL, (and the greatest deference is always due to his opinions,) that gravitation could have little influence on the direction of the germen, were it in the first instance protruded, or were it subsequently inverted, and made to

\* This effect does not appear to be produced in what are called weeping trees; the cause of which I have endeavoured to point out in a former Memoir. Phil. Trans. 1804.

point perpendicularly downwards. To enable myself to answer this objection, I made many experiments on seeds of the horse chesnut, and of the bean, in the box I have already described; and as the seeds there were suspended out of the earth, I could regularly watch the progress of every effort made by the radicle and germen to change their positions. The extremity of the radicle of the bean, when made to point perpendicularly upwards, generally formed a considerable curvature within three or four hours, when the weather was warm. The germen was more sluggish; but it rarely or never failed to change its direction in the course of twenty-four hours; and all my efforts to make it grow downwards, by slightly changing its direction, were invariably abortive.

Another, and apparently a more weighty, objection to the preceding hypothesis, (if applied to the subsequent growth and forms of trees,) arises from the facts that few of their branches rise perpendicularly upwards, and that their roots always spread horizontally; but this objection I think may be readily answered.

The luxuriant shoots of trees, which abound in sap, in whatever direction they are first protruded, almost uniformly turn upwards, and endeavour to acquire a perpendicular direction; and to this their points will immediately return, if they are bent downwards during any period of their growth; their curvature upwards being occasioned by an increased extension of the fibres and vessels of their under sides, as in the elongated germens of seeds. The more feeble and slender shoots of the same trees will, on the contrary, grow in almost every direction, probably because their fibres, being more dry, and their vessels less amply supplied with sap, they are



less affected by gravitation. Their points, however, generally shew an inclination to turn upwards; but the operation of light, in this case, has been proved by BONNET\* to be very considerable.

The radicle tapers rapidly, as it descends into the earth, and its lower part is much compressed by the greater solidity of the mould into which it penetrates. The true sap also continues to descend from the cotyledons and leaves, and occasions a continued increase of the growth of the upper parts of the radicle, and this growth is subsequently augmented by the effects of motion, when the germen has risen above the ground. The true sap is therefore necessarily obstructed in its descent; numerous lateral roots are generated, into which a portion of the descending sap enters. The substance of these roots, like that of the slender horizontal branches, is much less succulent than that of the radicle first emitted, and they are in consequence less obedient to gravitation: and therefore meeting less resistance from the superficial soil, than from that beneath it, they extend horizontally in every direction, growing with most rapidity, and producing the greatest number of ramifications, wherever they find most warmth, and a soil best adapted to nourish the tree. As these horizontal, or lateral, roots surround the base of the tree on every side, the true sap descending down its bark, enters almost exclusively into them, and the first perpendicular root, having executed its office of securing moisture to the plant, whilst young, is thus deprived of proper nutriment, and, ceasing almost wholly to grow, becomes of no importance to the tree. The tap root of the oak, about which so

\* *Récherches sur l'Usage des Feuilles dans les Plantes.*

much has been written, will possibly be adduced as an exception; but having attentively examined at least 20,000 trees of this species, many of which had grown in some of the deepest and most favourable soils of England, and never having found a single tree possessing a tap root, I must be allowed to doubt that one ever existed.

As trees possess the power to turn the upper surfaces of their leaves, and the points of their shoots to the light, and their tendrils in any direction to attach themselves to contiguous objects, it may be suspected that their lateral roots are by some means directed to any soil in their vicinity which is best calculated to nourish the plant, to which they belong; and it is well known that much the greater part of the roots of an aquatic plant, which has grown in a dry soil, on the margin of a lake or river, have been found to point to the water; whilst those of another species of tree which thrives best in a dry soil, have been ascertained to take an opposite direction: but the result of some experiments I have made is not favourable to this hypothesis, and I am rather inclined to believe that the roots disperse themselves in every direction, and only become most numerous where they find most employment, and a soil best adapted to the species of plant. My experiments have not, however, been sufficiently varied, or numerous, to decide this question, which I propose to make the subject of future investigation.

I am, &c.

T. A. KNIGHT.